


The SAGE Handbook of
Evolutionary Psychology



Integration of Evolutionary Psychology with Other Disciplines

Edited by
Todd K. Shackelford



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PART I

Integration within Psychology



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Evolutionary Social Psychology

Michael Baker

A great deal of human emotion, cognition, and behavior serves social functions. People can interpret how a friend reacts to a comment about a current political topic by reading non-verbal cues such as facial expressions of emotion. When setting goals, people often consider the impressions that goal-related behaviors will make on other people as much as (if not more than) they consider how reaching these goals will impact their own well-being. Humans are intensely social animals with complex social structures that, similar to many other social animals, allow groups of individuals to accomplish feats that surpass the capabilities of solitary individuals. The production and programming of the ubiquitous smartphone would be an impossible feat for any single individual to accomplish, just as taking down a mammoth during a hunt would have been a herculean (if not impossible) task for our ancestors.

Aside from the importance of cooperative effort toward shared goals, humans, like other social animals, rely on social interaction to

accomplish the fundamental tasks of life: survival and reproduction. The myth of 'the solitary man' alone in the wild as the default state of humanity is based on a deeply mistaken understanding of human nature. This idea supposedly influenced Christopher McCandless' ill-fated solo expedition into the Alaskan wilderness, as documented in Jon Krakauer's 1996 nonfiction book titled *Into the wild* (Krakauer, 1996). This journey was reportedly motivated by McCandless' belief that in order to attain fulfillment and satisfaction, one must achieve true independence from other people and escape from being 'poisoned by civilization'. Similar views were held by Theodore Kaczynski, who initially sought to live autonomously in the wilderness of Montana and later carried out a series of bombings in rebellion against industrialized society, leading him to gain infamy as the notorious 'Unabomber'. On the contrary, psychological research points to the conclusion that individuals who form meaningful bonds with others and develop

a sense of connectedness to society are happier, healthier, and more satisfied with life than those who are socially isolated. In the words of Jonathan Haidt,

If you want to predict how happy someone is, or how long she will live (and if you are not allowed to ask about her genes or personality), you should find out about her social relationships. Having strong social relationships strengthens the immune system, extends life (more than does quitting smoking), speeds recovery from surgery, and reduces the risks of anxiety and depression disorders. (2006: 133)

Regular positive social contact is practically as important for humans as regularly consuming nutritious food. Being deprived of food results in starvation, which can cause serious physical harm and, ultimately, death. In comparison, being socially starved may not be fatal, but it is immensely unpleasant and ultimately harmful. Extreme cases of isolation, such as years-long bouts of solitary confinement, may even cause long-term damage to psychological functioning (Dingfelder, 2012). In addition to other advantages, an evolutionary perspective on social psychology can provide an understanding of why interpersonal connection is so critical.

There are several advantages of applying an evolutionary perspective to attempts to understand human social behavior. This perspective is able to provide a deeper, ultimate-level understanding of why humans engage in the various social activities that occupy so much of their lives. Most social psychologists focus on the pursuit of proximate understandings of social processes. In other words, they want to understand why certain factors in people's immediate social environment elicit predictable behavioral, cognitive, and emotional reactions. In contrast, evolutionary social psychologists seek a deeper understanding of why these reactions became part of the human behavioral repertoire in the first place: the 'why behind the why'. For example, a social psychologist studying the effects

of social rejection might observe that people are strongly motivated to avoid being rejected by friends, family, or (especially) romantic partners. A proximate explanation for this motivation might appeal to the feelings that rejection elicits. Obviously, rejection feels bad. People strongly dislike the feelings of sadness and loneliness that typically accompany a clear message of rejection from one of the aforementioned individuals. An evolutionary social psychological explanation will acknowledge the importance of this understanding of proximate processes while at the same time seeking an explanation of why rejection causes sadness, why loneliness feels bad, and why rejection by a romantic partner can be especially devastating.

FUNDAMENTAL SOCIAL MOTIVES

In order to better understand how the forces of evolution have shaped human social behavior, we can examine some key motives that drive this behavior. These motives, referred to as 'fundamental social motives' by evolutionary social psychologists who study them and use them as a framework to guide their research, have been defined as 'systems shaped by our evolutionary history to energize, organize and select behavior to manage recurrent social threats and opportunities to reproductive fitness' (Neel et al., 2016: 887–888). These motives reflect a number of different adaptive challenges that people must overcome in order to achieve reproductive fitness: Self-protection (motivation to protect oneself against other people who might harm them), Disease Avoidance (motivation to avoid coming into contact with people who might carry contagious diseases), Affiliation (motivation to seek social connections, be a part of a group, and avoid being excluded by others), Status Seeking (motivation to gain the respect of others and ascend social hierarchies), Mate Seeking (motivation to find romantic/sexual

partners), Mate Retention (motivation to preserve existing romantic/sexual relationships), and Kin Care (motivation to spend time with and take care of one's children and other family members).

Although the vast majority of psychologically healthy humans are thought to be driven by these motives, the degree to which any given individual's behavior will be driven by a particular motive varies as a function of life history factors such as age, sex, relationship status, parent status, and childhood environmental stability (Belsky, 1997). For example, as people reach sexual maturity during adolescence and young adulthood, it is expected that their mate-seeking motives will peak during this time and gradually increase with age along with diminishing fertility. Conversely, kin-care motives (particularly child care) are not expected to be particularly active during adolescence and young adulthood, but these motives should typically increase once an individual successfully procreates and shifts their focus toward the adaptive goal of ensuring their children's health and well-being. Even at a particular point in life, there are individual differences in the strength of these motives. If one were to select a random sample of two dozen 23-year-old women from the same population, it is likely that some will care a great deal more about status seeking than others. In order to effectively measure individual differences in the strengths of these motives, researchers have developed a 'Fundamental Social Motives Inventory' (Neel et al., 2016), which contains subscales for measuring each of the motives listed above and instructs users not to administer specific subscales to individuals to whom they do not apply (mate-retention motives are only measured in people who are involved in a relationship, and child-care motives are only measured among parents). The fundamental social motives approach has generated a great deal of novel research among experimental social psychologists, thus illustrating the benefits of employing

an evolutionary approach to understanding human social psychology.

SOCIAL PROBLEMS OF SURVIVAL

Disease Avoidance

There are many ways in which a person can come into contact with agents that might induce illness. Some of these involve non-social elements. For example, ingesting spoiled food or poisonous plants can be extremely detrimental to one's health. However, it is also the case that social contact with certain individuals who are themselves infected with pathogens or parasites might result in sickness. It is common for people to be concerned about the possibility that physical contact with these types of individuals could be potentially harmful. The contagious nature of many pathogens has led natural selection to shape the human behavioral immune system to be particularly vigilant when it comes to avoiding people who have poor hygiene, show outward signs of infection, or who engage in behaviors that increase the likelihood of infection (Tybur et al., 2009). Cross-cultural research studying disease concerns among American and Japanese participants has revealed that feces and other human bodily waste products are among the most frequently mentioned disgusting items (Rozin, 1996).

It is sometimes the case that the fundamental social motive of disease avoidance conflicts with other motives. For example, parents often have to come into contact with feces and other waste products produced by their children in the process of acting upon child-care motives. Interestingly, research suggests that disease-avoidance motives can be suppressed in these situations, better enabling parents to work toward the adaptive goal of caring for their children. For example, one study found that mothers rate their own infant's feces as being less disgusting

compared to feces of other infants, even when they were unaware of the source of the sample (Case et al., 2006). Likewise, intimate sexual contact, which is essential in order to satisfy reproductive motives, requires one to come into contact with bodily fluids of other people who might be host to any number of pathogens or parasites and might, therefore, elevate one's risk of infection. Some researchers have suggested that sexual disgust may be a specialized adaptation to this problem, motivating people to avoid potential sexual partners who they perceive as being especially likely to transmit diseases (Al-Shawaf et al., 2018; Fleischman, 2014; Phelan and Edlund, 2016; Tybur et al., 2013).

Self-protection, Aggression, and Violence

As with disease avoidance, there are numerous ways in which a person might sustain physical harm that do not involve social contact. For example, one could fall from an elevated surface, be attacked by a predatory animal, or be bitten by a venomous insect. However, other humans who were driven by hostile and aggressive motives were likely a serious recurring threat throughout evolutionary history (Chagnon, 1988; Tooby and Cosmides, 1988). Interpersonal aggression is typically regarded as one of the less desirable aspects of human nature, but it is important to acknowledge that it is, in fact, a fundamental component of humanity's evolved behavioral repertoire. Therefore, it is understandable that self-protective motives include a prominent social element. Although levels of violence have steadily decreased with the passage of time (Pinker, 2011), the threat of physical violence from other people remains an adaptive problem with which modern humans must cope.

A wealth of research has consistently found sex differences in aggressive motives and violent behavior such that men, especially younger men, tend to be more prone

to engaging in physical violence compared to members of other demographic groups (Byrnes et al., 1999; Wilson and Daly, 1985). This is not to say that women never engage in aggressive behavior. Indeed, aggressive acts are common among women. However, physical violence is less common among women than men. Aggressive acts carried out by women more commonly take the form of relational aggression such as denigrating the physical appearance of and spreading rumors about the behavior of rivals in an attempt to damage their reputation.

Proximate explanations for the aforementioned sex difference in violence and aggression tend to focus on gender roles and the impacts of different socialization practices for boys versus girls. Proponents of this perspective suggest that male aggression is considered more normal and expected and therefore more acceptable by many cultures, as illustrated by the dismissive aphorism 'boys will be boys'. Conversely, social-role theorists might argue that the same behaviors from a girl might be criticized as being less acceptable and that a girl engaging in aggressive or violent actions might be chastised for acting 'not very ladylike'. Although evolutionary psychologists acknowledge the important role played by socialization practices, particularly during childhood, there is evidence that boys and men are actually punished more harshly for engaging in aggressive acts (Kindlon and Thompson, 2000).

Another proximate explanation for sex differences in violent and aggressive behavior appeals to sex differences in testosterone, which is produced in much higher levels in post-pubescent males compared to females (Archer, 1991). Meta-analyses of correlational and experimental studies have shown a modest positive relationship between testosterone and aggression that is subject to individual and contextual factors (Carré and Archer, 2018). Although it is essential to acknowledge the impact of testosterone on aggression, this explanation does not account for the origin of sex differences in testosterone.

As mentioned at the outset of this chapter, evolutionary explanations for human social behavior, including sex differences in behavior, often appeal to ultimate-level explanations in addition to acknowledging the importance of proximate factors. Evolutionary theorists have suggested that basic differences in male and female reproductive biology may provide a deeper explanation for sex differences in relevant behavior and mental processes (Trivers, 1972). These sex differences in mating strategies, which will be discussed in detail in the subsequent section entitled ‘Sex and Mating’, are thought to have shaped behavioral patterns beyond those behaviors directly related to mating, including (but not limited to) aggression. Specifically, evolutionary biologists have found that selection favors riskier strategies in the sex with higher reproductive variance and fiercer competition between members of the sex with greater reproductive variance. Given that males tend to have greater reproductive variance, men, like males of many species, tend to act in a riskier and more aggressive manner.

SEX AND MATING

From an evolutionary perspective, basic differences in male and female reproductive biology are thought to have led to the evolution of different reproductive strategies in men and women. One factor of particular importance in the development of these strategies is the difference in reproductive variance between males and females. Due to the nature of female reproductive biology, women’s reproductive capacity is strictly limited by the number of times that she can successfully become pregnant, carry offspring to term, and successfully deliver babies between the age at which she reaches sexual maturity and the age of menopause. In comparison, the limiting factor of men’s reproductive capacity hinges upon their degree of sexual access to fertile women. This fundamental

biological reality results in men being able to generate a greater number of offspring than women. This biological sex difference is also thought to be responsible for the evolution of sex differences in choosiness when it comes to selecting sexual partners (women being more careful and selective than men when choosing sexual partners), which is discussed in more detail later in this chapter. These factors are thought to ultimately result in sex differences in reproductive variance. This difference is illustrated in dramatic fashion by examining the records of the most children produced by women and men in recorded history. Although detailed historical records are spotty, the most prolific mother reportedly gave birth to a total of 69 children by becoming pregnant a total of 27 times and delivering multiple sets of twins, triplets, and quadruplets (X. Y., 1783). Although biological paternity has historically been more difficult to establish (another biologically based sex difference thought to contribute to sex differences in reproductive psychology, which will later be discussed in more detail), there are dozens of men who have fathered over 100 children each, the most prolific of these perhaps being Genghis Khan, who is thought to have fathered at least 1,000 children and whose genetic analysis has suggested is an ancestor to approximately 0.5% of the world’s population (Bai et al., 2018). By definition, these cases of extraordinarily high levels of reproductive success do not represent typical reproductive outcomes. However, they serve as a powerful illustration of sex differences in reproductive variance.

Human mating has commonly followed a pattern referred to as ‘effective polygyny’, meaning that men have tended to have more female sexual partners, whereas women have tended to have fewer male sexual partners (for a discussion of evolutionary perspectives on homosexuality and bisexuality, see the relevant section under ‘Sex and Mating’ in this chapter). Effective polygyny results in some men getting more than their ‘fair share’ of sexual partners while other men have none

at all. Although a disparity in numbers of sexual partners certainly exists between different women, with some having many sexual partners while others have few or none at all, the aforementioned sex differences in reproductive biology makes this disparity less consequential for women in terms of reproductive success. Put more simply, a man who has sexual intercourse with 100 different women over a 10-year span could, in theory, father 100 or more children during that period. In comparison, even under ideal reproductive circumstances, it would be biologically impossible for a woman with an identical pattern of sexual behavior to give birth to the same number of children.

Mating is arguably the most important social behavior in which members of any sexually reproducing species engages. Likewise, mating-related motives are arguably the core motives from which all others are derived. Survival, which is promoted by the disease-avoidance and self-protective motives detailed in the previous section of this chapter, is primarily important because it is essential for an individual to survive to reproductive age in order to successfully reproduce and contribute to the survival (and possible reproductive success) of their offspring and other kin members. The genes of individuals who excel at survival but fail to reproduce are likely to be selected against by natural selection, unless they compensate for this lack of personal reproductive success by investing heavily in closely related kin members. Likewise, status seeking serves to promote mating-related goals. Men of higher status tend to be viewed as more desirable by women (Buss and Schmitt, 1993; Khallad, 2005) and therefore have better access to potential mates. Both men and women of higher status tend to have better access to resources, which helps them to ensure the survival of their offspring. Due to the key importance of reproductive outcomes, it should come as no surprise that there are thought to be multiple specific fundamental social motives associated directly with

reproduction: mate-seeking motives and two types of relationship-maintenance motives: general mate retention and breakup concerns.

Mate Seeking

Generally speaking, mate-seeking motives drive individuals to find new romantic/sexual partners. However, not all mate-seeking motives are created equal. These motives can drive individuals toward either short-term or long-term mating goals. Short-term mating is typically sufficient for production of offspring and is common in many species. Although long-term mating is relatively uncommon in the animal kingdom, there are multiple benefits associated with this strategy, particularly for humans, which can help to explain how this strategy evolved. Long-term mating promotes lower paternal uncertainty and greater levels of parental investment in offspring, which is beneficial for their survival and subsequent reproductive potential. The behaviors and preferences associated with these two strategies will be discussed in the following sections.

Short-term Mating

The likelihood that an individual will favor a short-term mating strategy depends upon a number of factors, the most important of which is likely to be whether that person is male or female. One well-known study by Clark and Hatfield (1989) provides a dramatic illustration of this. In this study, 48 men and 48 women on a college campus were approached by an attractive opposite-sex confederate who asked them if they would be willing to go to bed (i.e., have sex) with them that evening. None of the women who were approached agreed to this proposition, whereas 75% of the men agreed. Notably, an attempted replication by the same researchers four years later yielded nearly identical results, with none of the

women agreeing, but 69% of the men agreeing. Also of note is the different reactions that male and female participants had to this request. Men generally displayed positive reactions and some of those who declined even offered apologies or excuses. In stark contrast, the women who were approached generally displayed negative reactions, indicating that they had taken offense or were in disbelief at the fact that they had been propositioned in this manner.

The evolutionary explanation for the dramatic and consistent sex difference in receptivity to requests that are consistent with short-term mating goals hinges upon the differences in male and female reproductive biology discussed earlier in this chapter, as well as on sex differences in the minimum amount of biological investment required for men and women to reproduce. An act of casual sex might require a minimum of nine months of heavy biological investment in the form of internal gestation for a woman, whereas the same sexual act requires relatively little investment from a man.

Although it is true that some modern industrialized societies offer technological and legal methods that are relevant to this issue in the form of birth control, paternity testing, and legally required child-support payments from absentee fathers, it is important to note that these institutions are all evolutionarily novel. One key tenet of an evolutionary psychological perspective is that adaptation via natural selection takes a great deal of time, and evolved psychological mechanisms are therefore tailored to the environments in which thousands of generations of our ancestors evolved rather than to the modern world. Although modern humans are capable of reasoning that casual sex might be less biologically consequential if they can confirm that one or both partners are using birth control, the evolved fundamental social motives that drive much of human social behavior often influence downstream cognitive processes such as logical reasoning, leading people to conclude that even though a particular

behavior is logically acceptable, it feels wrong for reasons that they are often unable to verbalize or fully comprehend. This principle is perhaps best illustrated in Jonathan Haidt's (2001) research on incest-related disgust. Participants in this research were presented with a situation in which a brother and sister engage in a short-term sexual affair: a single act of intercourse in which both use birth control, agree never to tell anyone else, and enjoy the experience, therefore improving their relationship. Upon hearing this story, most people have the immediate reaction that the act was wrong. However, when prompted to explain why they feel this way, they have great difficulty doing so as the details of the story counter the typical logical objections: the fact that both siblings used birth control should prevent conception of a child who might be at elevated risk of developmental problems due to inbreeding; the fact that they agree never to tell anyone should prevent them from being socially ostracized or subject to legal punishment; and the fact that it improved their relationship suggests that the act did not damage their relationship with one another. Just as Haidt's participants felt like the incestuous act was simply wrong even though they could not voice logical objections, the women in Clark and Hatfield's study might have been offended by an offer of casual sex with a stranger even though pregnancy could have been easily prevented via birth control.

Aside from the general finding of a sex difference in overall level of desire for long- and short-term mating opportunities, there are a number of research findings that shed light on specific aspects of short-term mating strategies employed by men and women. For example, cross-cultural research has shown that men tend to desire a greater variety of sexual partners than do women (Schmitt, 2003). Across the world, it was found to be universally true that when people are asked to report how many sexual partners they would ideally like to have over a period of time in the future, men indicate a desire for a greater

number of partners compared to women. This is true even in cultures that have relatively high levels of gender equality such as Norway, where women reported desiring an average of about two partners over the next year, whereas men reported a desire for about seven. Furthermore, men of different ages and residing in different parts of the United States reported being inclined to consent to sexual intercourse after the passage of shorter intervals of time compared to women (Buss and Schmidt, 1993). While both men and women said that they would consent to sex with a potential mate after a period of five years, men's willingness to consent was significantly higher than women's at every interval of time that was shorter than this. Men are also more likely to lower their standards regarding who is considered to be an acceptable partner in short-term mating decisions (Buss and Schmidt, 1993) and to prioritize bodily attractiveness over facial attractiveness when considering casual sex partners. The latter of these two findings is understandable from an evolutionary perspective, given that waist-to-hip ratio may serve as a predictor of female fertility (Confer et al., 2010; Currie and Little, 2009). Furthermore, the so-called 'beer goggles' phenomenon, in which men are presumed to perceive women as more attractive the more intoxicated they become, may have little to do with intoxication. Rather, evidence suggests that this tendency may result from sensitivity to partner availability, with availability decreasing as the evening progresses and remaining potential sexual partners being consequently viewed as more desirable via a reduction of standards in order to increase opportunities for casual sex (Gladue and Delaney, 1990).

Both men and women employ strategies to avoid romantic entanglement when engaged in short-term mating behavior. However, men tend to use strategies that maintain their ability to pursue and engage in sexual relationships with additional partners, such as 'having sex with someone else' and 'maintaining multiple sex partners', whereas women are more

likely to use strategies that reduce emotional intimacy and prevent future contact, such as 'not holding hands' and 'giving the wrong phone number' (Surbey and Conohan, 2000). Likewise, both men and women are prone to sexual fantasizing, but men have been found to have sexual fantasies nearly twice as often as women do (Ellis and Symons, 1990; Wilson, 1987). This research also reveals qualitative differences in the sexual fantasies of men and women, with women more frequently fantasizing about intercourse with a current partner and men more often fantasizing about strangers or anonymous partners. However, there are substantial individual differences in fantasies, with many women fantasizing about sexual encounters with a stranger and many men fantasizing about a partner with whom they are involved in a committed long-term relationship.

A number of sexual behaviors are also indicative of sex differences in preference for short- versus long-term strategies. In most cultures, men tend to be much more likely than women to pursue extramarital affairs and to seek the services of prostitutes (Kinsey et al., 2003; Kinsey et al., 1998). More recently, studies of 'hook-up culture' and 'friends with benefits' relationships, in which individuals have sexual encounters with others with a mutual understanding that there will be no romantic commitment, have revealed that men are more likely to attempt to initiate these types of relationships (Garcia and Reiber, 2008). Men and women also have different ideas regarding the 'ideal outcome' of these types of relationships, with men being more likely to idealize more commitment-free sex and women being more likely to idealize the possibility of transitioning partners to a traditional romantic relationship. Finally, research on use of social media applications such as Snapchat, which allows users to make photos of themselves temporarily available to others, as well as online-dating apps such as Tinder, has revealed sex differences in the motivations of users such that men report a greater likelihood of

using these apps to seek casual sex partners than do women (Moran et al., 2018; Sumter et al., 2017). Although it is possible that the reported sex differences in these behaviors and mental processes are influenced by differences in gender roles, with casual sex being considered more acceptable for men than for women, the cross-cultural universality of these differences and the fact that they are found in completely private behaviors, such as sexual fantasies, that are reported under confidential or anonymous methods suggests that they may be the product of evolved differences in sexual strategies.

Long-term Mating

As seen in the previous section on short-term mating, women tend to be the choosier of the two sexes when it comes to mate selection, which is thought to largely result from the biologically rooted difference in minimum obligatory investment in offspring. Although this applies to some extent to long-term mating, long-term relationships, particularly those that involve children, require a great deal of investment from both parents. Therefore, from the perspective of parental-investment theory (Trivers, 1972), it is understandable that when it comes to choosing a mate with which one hopes to stay with for extended periods of time and share the responsibilities of parenting, men and women both tend to be more discriminating when it comes to partner selection.

Throughout human evolution, men and women have faced a number of adaptive problems relevant to long-term mating. Some of these problems have been of similar relevance to members of both sexes, whereas others have been more relevant to members of either one sex or the other. Both men and women have had to adapt solutions to finding a mate who is compatible in terms of personality and values. Regardless of sex, if one plans to spend an extended period of time cooperating with another person, it is

beneficial to ensure that they get along with that person. Indeed, research has shown that couples who are more similar to one another tend to bond more easily, communicate and cooperate more effectively, be happier with their relationship, and experience decreased risk of breakup, and this may even contribute to increased survival prospects for children (Buss, 2016; Castro et al., 2012). As a result, people display a preference for similarity when making mating decisions, relating to both dating (Wilson et al., 2006) and marriage (Buss, 1985). This preference for similarity is strongest when it comes to 'mate value' (e.g., people who are generally perceived as highly attractive tend to mate with others who are also highly attractive, whereas those who are of average attractiveness tend to mate with others who are average in attractiveness) (Edlund and Sagarin, 2014; Figueredo et al., 2015), as well as political and religious views and intelligence (Kardum et al., 2017).

Selecting a mate who is healthy is also a problem for which men and women have both had to evolve adaptive strategies. However, when it comes to standards used to judge physical attractiveness, the criteria used to establish male and female attractiveness sometimes vary. Men and women are similar in their preference for facial and bodily symmetry, as this is thought to be an honest signal of genetic quality or, more precisely, the strength of an individual's immune system (Gangestad and Thornhill, 1997). People who are more symmetrical have, in theory, been better able to combat forces that produce asymmetry, such as pathogens and parasites (Thornhill and Møller, 1997). More symmetrical individuals tend to be viewed as healthier and, therefore, as more attractive potential mates. Indeed, there is evidence that individuals with greater facial symmetry tend to be psychologically, emotionally, and physiologically healthier than those with less symmetrical faces (Shackelford and Larsen, 1997). Due to the fact that there exist genetic influences on immune-system functionality, these immunological benefits could then be

passed on to offspring, helping to ensure their own survival and proving beneficial to their potential reproductive success.

One health-related factor that is specific to women's preferences for long-term mates is a preference for facial masculinity (Johnston et al., 2001). Although high levels of testosterone, which tend to contribute to the development of more masculine features, tend to be detrimental to the human immune system, it has been theorized that healthier men are better able to offset this cost and, therefore, able to produce more testosterone, whereas the bodies of less healthy men must reduce testosterone production in order to ensure survival. The result of this trade-off is that men with the most effective immune systems tend to have higher levels of testosterone, which leads them to develop more masculine facial features. Consistent with this hypothesis, research shows that women with high levels of disgust sensitivity and those who reside in nations where there is an elevated risk of contracting a contagious disease tend to have stronger preferences for masculine features compared to other women (DeBruine et al., 2010; Pisanski and Feinberg, 2013).

Adaptive problems that have been more relevant to women than men include selecting mates who are willing and able to invest in potential offspring, able to physically protect her and her children, and able to demonstrate good parenting skills. In accordance, women's preferences for long-term mates reflect a desire for partners who possess qualities that are relevant to these problems. Large-scale international research shows that women tend to prefer men who are somewhat older than themselves – 3.5 years older, on average (Buss and Schmitt, 1993). The reason for this may be that age tends to correlate positively with other qualities that are relevant to the aforementioned adaptive challenges. Compared to younger men, those who are somewhat older tend to have higher levels of social status and better access to resources, which are both related to men's ability to provide for offspring (Jencks,

1979). Furthermore, somewhat older men also tend to have greater levels of physical strength (prior to a decrease in strength that typically occurs in the late 20s or early 30s), which is relevant to men's ability to protect a mate and her offspring.

Consistent with the aforementioned desire for a mate who has better access to resources, women in most cultures display greater levels of desire for a mate who is ambitious and industrious than do men. In other words, women do not simply desire men who have already acquired greater levels of wealth and power; they also desire men who possess personal attributes that are predictive of the attainment of these resources. Indeed, men who are more motivated and hard-working tend to achieve higher status and greater levels of income compared to their less-motivated peers (Kyl-Heku and Buss, 1996; Lund et al., 2007).

Ability to provide for offspring is, of course, different from willingness to do so. Many women might view a man who has vast resources but who is not dependable and is emotionally unstable, unwilling to make a commitment, and despises young children as less desirable compared to a man who has somewhat more modest resources but is highly dependable and emotionally stable, displays a clear desire for commitment, and interacts positively with young children.

Women in a majority of cultures consider dependability and emotional stability to be among the top three most desirable characteristics in a mate (Buss et al., 1990). Men too have been found to have a strong preference for mates who possess these qualities and possibly for similar reasons: women who are emotionally stable and dependable likely provide better care for children than women who have lower levels of these attributes. Furthermore, a preference for emotional stability should help individuals to be more successful in achieving long-term mating goals, at least to the extent that people are able to win the hearts of potential mates who possess high levels of this characteristic. Studies of

relationship success versus failure have found emotional instability to be a very consistent predictor of breakup and divorce (Kelly and Conley, 1987; Solomon and Jackson, 2014).

Unlike resources, willingness to commit cannot be directly observed and must therefore be inferred via cues such as acts of commitment. These cues can take the form of relationship exclusivity, verbal expressions of commitment, and stating a desire to have children with one's partner (Buss, 2018; Wade et al., 2009). One common behavior that has been speculated to serve the function of signaling intentions of commitment is the giving of costly gifts such as expensive dinners and diamond engagement rings (Camerer, 1988). Whereas the provision of these gifts may signal both resources and commitment, acceptance by the receiver may serve a similar function, signaling an intention to reciprocate by continuing to be a participant in the relationship. Conversely, when a suitor offers a costly gift that is subsequently rejected, they are likely to infer that the intended recipient has little interest in future relations.

Selecting a mate who is willing to invest in children is a challenge that is especially important for women to address when pursuing long-term mating goals. Although this is theoretically important for men as well, it seems to have little to no impact on men's mate preferences. Research findings indicate that men rate women who are standing alone as being equally attractive as women who are viewed interacting positively with a child (Brase, 2006; La Cerra, 1995). This may be due to the fact that women generally invest more heavily in offspring, due in part to their greater minimum obligatory investment in those offspring, as discussed earlier in this chapter. Men, on the other hand, have a relatively low biological obligation in offspring production, and they also have adaptations to the problem of paternal uncertainty – the lack of certainty that the child who their partner gives birth to is their biological offspring. The exclusivity that is a common element in long-term mating among humans can serve

to reduce (if not eliminate) this uncertainty. Furthermore, women's motivation to find a partner who is willing to invest in children is likely to have evolved as an adaptation to problems that arise due to men's aforementioned desire for sexual variety. This desire may lead a woman's partner to invest resources in the pursuit of alternative romantic or sexual partners, that would otherwise serve to benefit the children that he produced with her. Consistent with these adaptive challenges, women have been shown to find men more attractive as potential long-term partners when the men are viewed having a positive interaction with a young child compared to men who are alone, ignoring a crying child, depicted in the presence of a child but with no interaction taking place, or performing a helpful household task such as vacuuming a rug (La Cerra, 1995).

Mate Retention

One key challenge in long-term mating is ensuring that one's relationship persists over time by monitoring one's own behavior and mental processes, as well as the behavior of one's partner and potential rivals for their affection. Performing relationship-maintaining behaviors can serve to protect that relationship from internal threats (e.g., dissatisfaction) as well as external threats (e.g., mate poaching). Individuals who are highly motivated to maintain long-term relationships are more likely to engage in behaviors that signal their commitment to their partner, such as buying them gifts (Neel et al., 2016).

The emotion of jealousy plays an important role in mate retention. Although chronic romantic jealousy can be unhealthy, moderate amounts of this emotion reflect investment in a relationship. If a person were to have little to no emotional reaction upon seeing a potential rival flirting with their romantic partner at a party, this could be a sign that they are very secure in their relationship, but it could

also reflect a lack of commitment. One of the most robust findings in evolutionary social psychology is a sex difference in romantic jealousy (Sagarin et al., 2012). When forced to choose whether they would be more upset by acts of sexual or emotional infidelity, men tend to have stronger reactions to sexual infidelity and women tend to have stronger reactions to emotional infidelity. This difference occurs in scenarios involving both real and imagined infidelities. The theory of evolved sex differences in jealousy suggests that this difference emerged as an adaptation to selective pressures on women to ensure paternal investment and on men to deal with the problem of paternal uncertainty (Buss et al., 1992; Daly et al., 1982). Although the majority of this research has been conducted using samples of exclusively heterosexual individuals, a similar pattern has been found among bisexual individuals: bisexual men dating women were found to be more upset by the sexual aspects of infidelity compared to bisexual men dating men or bisexual women dating partners of either gender (Scherer et al., 2013). This lends further support to the notion that concerns about paternal uncertainty drive male sexual jealousy. Recent evidence has also suggested that a loss of perceived paternity opportunities, rather than a reduction in paternity certainty, may drive men's sexual jealousy (Edlund et al., 2019).

Consistent with this sex difference in relational concerns, men and women tend to differ in their use of mate-retention tactics (Buss and Shackelford, 1997). Men are more likely to employ tactics that minimize the sexual availability of a partner to potential rivals, such as concealing their mate or monopolizing their mate's time. Men are also more likely to use violence and threats of aggressive behavior toward rivals who express interest in their partner and toward partners who show interest in romantic alternatives (Wilson and Daly, 1996). Finally, men display desirable resources to their partners more than women do – buying gifts and jewelry and providing expensive meals.

Conversely, women are more likely to try to engage in mate-retention tactics such as attempting to make themselves look more physically attractive to their current partners and inducing jealousy by flirting with other men in front of their partner. The latter of these two tactics also serves to allow women to gauge their partner's level of commitment (Sheets et al., 1997).

Homosexuality and Bisexuality

The existence of individuals with sexual orientations that are not exclusively heterosexual has been a challenge for evolutionary psychologists to address. The finding that sexual orientation has a modest heritable component suggests that there is a biological basis to homosexuality and bisexuality as well as heterosexuality (Bailey et al., 1999; Ciani et al., 2018). Whereas the high frequency of individuals with heterosexual orientations is relatively straightforward to explain via evolutionary logic (experiencing sexual attraction toward individuals with whom one is reproductively compatible promotes successful reproduction and is therefore selected for), the persistence of genes that lead individuals to experience sexual attraction toward members of the same sex is a challenge. Between bisexuality and exclusive homosexuality, bisexuality is a lesser challenge for evolutionary theorists to tackle, as individuals who experience sexual attraction toward members of either sex can still achieve levels of reproductive success similar to heterosexual individuals by engaging in sexual relations with members of the opposite sex. In comparison, the evolution of genes that contribute to an exclusive same-sex attraction is more difficult to explain, as this type of attraction predictably leads to lower levels of reproductive success and therefore would, in theory, be selected against.

A number of explanations for how genes that predispose an individual toward a

same-sex orientation have been proffered by evolutionary theorists: the kin altruism theory, the alliance formation hypothesis, and the female fertility hypothesis. The first explanation that was put forth was the kin altruism theory, which suggests that these genes could have evolved if they led exclusively homosexual people to offset the costs of not having biological children of their own by investing heavily in the fitness of close genetic relatives (Wilson, 1975). Support for this theory has been mixed, with early studies finding no difference between the levels of kin investment between gay men and heterosexual men, but more recent research has found evidence that gay Samoan uncles invest more in nephew and nieces than heterosexual uncles within the same culture. In comparison, the alliance formation hypothesis suggests that same-sex relationships may serve the function of allowing participants in these relationships to form close bonds with members of the same sex who possess higher levels of social status, who can then serve as allies and ultimately elevate the individual's own status in social hierarchies (Muscarella, 2000). This theory suggests that this elevated status could ultimately lead the individual to have better access to opposite-sex mating partners, thus resulting in improved reproductive fitness. Given that the alliance formation hypothesis suggests that individuals engaging in same-sex sexual relationships will ultimately enhance their fitness by generating offspring of their own, this theory pertains more to bisexuality than exclusive homosexuality. However, it is possible that individuals who gain higher status would also be better able to accrue desirable resources, which could then be used to enhance the fitness of close genetic relatives, as suggested by the kin altruism theory. Both of these explanations have limited empirical support.

The most promising explanation yet offered for how genes contributing to a homosexual orientation among men could be selected for may be the female fertility hypothesis (Iemmola and Ciani, 2009). This

hypothesis suggests that these genes could evolve by leading female relatives who possess these genes to have greater levels of reproductive success compared to the female relatives of heterosexual men. The finding that the maternal female relatives of gay men have significantly more children than the maternal relatives of heterosexual men provides evidence in support of this hypothesis (Iemmola and Ciani, 2009; Rahman et al., 2008). In other words, the fitness costs associated with reduced levels of offspring production among men who inherit these genes may be offset by the enhanced reproductive success of their maternal female relatives. The nature of the mechanism driving this effect is still unclear but researchers have suggested that the genes in question may lead women who possess them to develop more highly feminine traits that lead them to be perceived as more attractive by men in many societies (Barthes et al., 2013). Although the female fertility hypothesis pertains exclusively to male homosexuality, similar evidence has been found for lesbian and bisexual women, as their genetic relatives have higher levels of reproductive success compared to relatives of exclusively heterosexual women (Ciani et al., 2018).

Finally, it is worth noting that there are important differences between the nature of male and female homosexuality as well as between the constructs of sexual orientation and gender identity. Whereas male homosexual tendencies typically develop early in life and persist throughout an individual's lifespan, female sexuality is generally more malleable and subject to environmental influences during development and change over time (Baumeister, 2000). Furthermore, gender identity (whether an individual identifies as male, female, or neither) is conceptually distinct from sexual orientation, as people's sexual desires and preferred sexual partners are not dictated by gender identity. In other words, regardless of an individual's gender identity, they may feel sexual desire exclusively toward men or women, or they

may have no exclusive preference or little to no sexual desire whatsoever (asexuality). Likewise, individuals of any gender identity may prefer to engage in sexual activities exclusively with men or women, with either men or women without preference, or they may prefer to forego sexual activity altogether.

PARENTING AND KINSHIP

Humans engage in more extensive parenting behavior than many other species. This is thought to be largely attributable to the prolonged period of time that it takes for young humans to reach maturity and become self-reliant. Evolutionary psychologists who renovated Abraham Maslow's well-known 'pyramid of needs' in 2010 placed parenting-related needs at the top of the hierarchy (Kenrick et al., 2010). This offers a stark contrast with Maslow's original formulation, which emphasized the ultimate goal of self-actualization. Indeed, once one becomes a parent, the survival and well-being of one's children becomes a central life goal, often superseding or taking a position of similar importance to one's own survival and well-being. From an evolutionary perspective, this makes sense, as offspring are the primary means by which an individual's genes survive. Therefore, ensuring the survival of one's offspring, although altruistic in one sense, can be considered to be a genetically selfish behavior, as a failure to ensure that one's offspring survive and have a chance to reproduce represents a failure to ensure the survival of one's own genes into future generations.

Although both mothers and fathers invest in children via parental care, mothers tend to invest more heavily than fathers (Bjorklund and Pellegrini, 2002; Geary, 2000). From an evolutionary perspective, this is thought to result largely from two factors: sex differences in minimum obligatory investment

in offspring and the issue of paternal uncertainty and sex differences in mating opportunity costs (Alcock and Rubenstein, 2019). As mentioned previously, whereas women are biologically required to invest high amounts of metabolic resources during pregnancy and have absolute certainty that the child to whom they gave birth is their biological offspring, men, in comparison, are biologically required to invest relatively little during pregnancy and lack certainty regarding their biological relation to infants once they are born. Likewise, because the reproductive success of men is largely limited by the number of women who they can successfully impregnate, dedicating resources to pregnant partners or their children exacts a higher 'opportunity cost' on men compared to women, as men who invest in this manner have fewer opportunities to increase their reproductive success by mating with various other women. In contrast, women do not experience this cost to the same extent, as mating with a variety of men will not increase their reproductive success similarly. Social norms and laws that have been established in different cultures sometimes aim to combat the tendency of men to invest less. For example, mothers may file a paternity lawsuit in an attempt to require a man who fathered her child but subsequently ended the relationship and provided no voluntary support to be legally compelled to pay child support. The ultimate-level explanation of differences in parenting tendencies provided by evolutionary social psychology provides an understanding of the biological factors that have shaped human psychology in a way that makes some societies deem these types of measures to be necessary.

Beyond the aforementioned sex differences, there are three primary factors that evolutionary theorists believe to have an impact on amount of parental care: perceived genetic relatedness of the child, ability of the child to gain fitness benefits from parental investment, and alternative uses of resources needed for investment (Alexander and Culligan, 1979). Biological parents have

been found to invest significantly more emotional and physical resources in their children compared to adoptive parents (Daly and Wilson, 1988). The finding that new mothers are about four times more likely to say that their children resemble their father than themselves is hypothesized to be an evolved strategy to combat the lesser levels of paternal investment that might result from paternal uncertainty (Daly and Wilson, 1982). While increased perceptions of genetic relatedness have been shown to be associated with greater parental investment, particularly by fathers (Apicella and Marlowe, 2007; Platek et al., 2002), a lack of genetic relatedness between parent and child can have dire consequences for the child as well (Daly and Wilson, 1980). Indeed, step parenthood has been identified as the leading risk factor for child abuse and child homicide (Daly and Wilson, 1988, 1996).

The two factors that have the most impact on the ability of a child to convert resources that are invested by parents into survival or reproductive success are the age and developmental condition/health of the child (Daly and Wilson, 1988, 1996). Children who are younger or have disabilities or congenital diseases have lower reproductive value than children who are comparatively older and healthier, as their odds of surviving to reproductive age and finding a mate are lower. Consistent with this, younger children and children with disabilities are at higher risk of abuse and neglect (Daly and Wilson, 1981).

As mentioned previously, trade-offs exist between investing time, energy, and other resources in offspring as opposed to other activities that might contribute to an individual's reproductive success, such as finding additional mates. Whereas men's ability to father children reduces gradually over the lifespan, women's ability to conceive drops more sharply as menopause approaches, and conception is no longer possible after this point. Therefore, women's opportunities for future reproduction correlate negatively with age to a greater extent compared to men. One

grim set of findings that has stemmed from this biological reality is that younger mothers are significantly more likely to commit infanticide compared to older mothers, who have fewer future reproductive opportunities (Daly and Wilson, 1988). This research has also revealed that, independent of age, women's marital status is a predictor of infanticide. In the case of infanticide, evolutionary logic suggests that younger mothers who are unmarried are most likely to commit infanticide, as the benefits that they would gain from investing resources in ensuring their own survival and attracting mates who would invest in future offspring are comparably greater than these benefits would be for older mothers.

Aside from the aforementioned extreme examples of child abuse, child homicide, and infanticide, it is common for less severe interpersonal conflict to occur between parents and children. Robert Trivers' Theory of Parent–Offspring Conflict provides a biologically based explanation for why parent–child relationships are often less than harmonious. Although each parent shares roughly 50% of their genes with a child, this also means that each child's genes differ from those of their parents by about the same amount. This leads to the conclusion that what is in the genetic best interest of parents and their children will inevitably differ and that children will often want more of the parents' resources for themselves than the parents are willing to provide.

STATUS

Like other social species, humans tend to form status and dominance hierarchies, in which group members differentially gain access to survival and reproduction-related resources according to their position in the hierarchy (Cummins, 1998). Those with higher status tend to have greater access to these resources compared to individuals with lower status. The fundamental social motive

of status striving appears to be universal (Anderson et al., 2015; Symons, 1979), and upon joining a new group, people tend to form clear hierarchies within a few minutes (Fiske and Ofshe, 1970).

Since fights incur costs for both victors and losers, settling disputes between individuals without resorting to a fight can be advantageous for all parties involved. Indeed, avoiding fights and the associated costs is a key function of both dominant and submissive behaviors. Beyond the benefit of avoiding costs associated with conflict, there are additional advantages associated with being dominant or submissive. The advantages associated with being dominant are somewhat more obvious, with dominant individuals gaining better access to resources and mates. In contrast, accepting a submissive status allows weaker individuals to maintain their group membership in spite of not being able to successfully compete with more dominant group members. Group membership in and of itself can be advantageous, as low-ranking group members will retain access to shared resources that they would not have if they were expelled from the group and forced to subsist as an extra-group loner. In other words, although submissive individuals may be at a disadvantage compared to higher-ranking individuals, they would still gain advantages from retaining group membership. Finally, it can be advantageous for dominant group members to tolerate individuals of lower status as these low-status individuals can contribute material and social resources to the group at little to no expense to dominant individuals. It is noteworthy that the aforementioned hierarchical principles have been found to apply to both humans and many species of non-human animals, suggesting a deep evolutionary history (Ellis, 1995).

As with evolutionary perspectives on many other domains of human social behavior, there is a sex difference in the strength of status-striving motives such that men tend to demonstrate a greater desire for achieving

social dominance compared to women (Maccoby, 1990; Pratto et al., 1994). Social constructionists might argue that this difference is largely attributable to socialization practices that emphasize the importance of dominance to men and boys to a greater extent than to women and girls. An evolutionary psychological perspective allows for the retention of this type of proximate influence but also acknowledges the ultimate biological origins of this difference. The tendency for males to compete more fiercely for status compared to females can be explained by sex differences in reproductive biology – namely, the fact that women can only become pregnant with one child at a time, whereas men can impregnate multiple females during the same period of time (i.e., sex differences in reproductive variability). This difference is thought to have led men to place a greater level of importance on gaining social dominance compared to women, as individuals with a greater level of status typically have access to more mates, more desirable mates, and more resources for offspring. This is not to say that social dominance confers no benefits to women. On the contrary, having access to more desirable mates and more resources for offspring can be just as advantageous for women as for men. However, due to the aforementioned sex difference in reproductive biology, gaining access to a greater number of mates at any given time is more biologically advantageous for men than for women, which is thought to provide an ultimate-level explanation for the evolution of greater levels of competitiveness among males of species that employ polygynous mating systems compared to females.

Aside from the aforementioned sex difference in social-dominance orientation, researchers have also identified differences in the behaviors that men and women perform as expressions of social dominance (Megargee, 1969). Dominant men have a greater tendency to use their status to get others to perform behaviors that benefit the dominant individual, such as improved personal gain or the

further elevation of their status. In contrast, dominant women are more likely to use their status to achieve group-oriented goals such as conflict resolution between third parties. Furthermore, additional research has demonstrated that men, but not women, engage in greater levels of resource-related risk-taking when they believe that their actions are being observed by people of similar status, but not of higher or lower status (Ermer et al., 2008). This effect is hypothesized to be attributable to the fact that outcomes are more uncertain among competitors of similar status compared to situations involving competitions between individuals of different status. Therefore, the potential status gains associated with risk-taking in the presence of an individual of similar status are greater than the potential gains associated with resource-related risks in the presence of individuals of higher or lower status.

Finally, some social psychologists have postulated the existence of a relationship between self-esteem and an individual's social status. Mark Leary and colleagues proposed the sociometer theory, which suggests that levels of self-esteem are correlated with an individual's degree of social acceptance, with higher levels of self-esteem accompanying greater levels of acceptance and loss of self-esteem accompanying exclusion and rejection (Leary et al., 1995, 1998). Although the original iteration of sociometer theory has its roots in evolutionary theory, it was not formulated with status tracking in mind. Regardless, a loss of respect or status can be viewed as a logical extension of a loss of esteem, and knowing where one stands with others is directly relevant to decisions regarding whether one should opt to challenge or submit in the event that social conflicts arise. A further expansion of sociometer theory by evolutionary psychologists has attempted to link the construct of self-esteem to perceived mate value (Kirkpatrick and Ellis, 2003). Research findings in relation to this proposed expansion have shown that factors such as sex and relationship status may moderate

the relationship between self-esteem and perceived mate value, as the relationship appears strongest among uncommitted men, who rate themselves as more desirable following acceptance by potential mates and as less desirable following rejection (Kavanagh et al., 2010; Penke et al., 2007; Schmitt and Jonason, 2019).

PREJUDICE AND DISCRIMINATION

Evolutionary perspectives on group-based prejudice (attitudes about others based on group membership) and discrimination (treatment of others based on group membership) regard these processes as a natural byproduct of group living. However, it is important to note that this assertion does not attempt to justify these processes or deem them as acceptable or inevitable. Rather, an evolutionary perspective seeks to explain how prejudice and discrimination came to exist as part of the human psychological repertoire. Just as people can be said to hold positive prejudice toward individuals who they view as desirable mates and discriminate in favor of these individuals when selecting a mate, as those who are perceived as having high mate value afford desirable reproductive opportunities, people tend to hold negative prejudice against others who they perceive as posing a threat.

Social psychologists have long noted that people are more likely to hold positive prejudice toward and discriminate in favor of those who they categorize as ingroup members ('us') and hold negative prejudices toward and discriminate against those who they categorize as outgroup members ('them'). This process of social categorization underlies group-related prejudice and discrimination. The specific ingroups and outgroups that people form are shaped by societal norms, which tend to change rapidly compared to an evolutionary timescale. For example, in the early 20th century, Irish

immigrants to the United States were widely considered to be categorically separate from the 'white' race. Individuals of Irish descent were consequently the subject of prejudiced attitudes and discriminatory treatment from those who categorized themselves as 'white', though this categorical separation gradually vanished from within US culture over the course of the 20th century (Jacobson, 1958). Although the construct of race often takes the form of a socioculturally defined categorical construct, modern biological research has concluded that biologically based differences between people are, in fact, continuous in nature, that adaptive traits do not define race in humans, and that describing racial differentiation in terms of separate branches on an evolutionary tree is socially irresponsible (Templeton, 2013).

Additionally, it is worth noting that people form numerous ingroups and outgroups at any given time, categorizing others by race, religion, gender, age, nationality, religion, and sexual orientation. The basic process of social categorization appears to be automatic and unlearned, suggesting that this process is a component of human nature. Research employing the 'minimal group paradigm' has revealed that people even have the tendency to categorize others according to completely arbitrary and superficial characteristics such as t-shirt color (Locksley et al., 1980). In spite of the fact that the specific categorizations upon which prejudiced attitudes and discriminatory behavior are often subjective, perceived threats from those who are categorized as outgroup members can be considered to be functionally relevant (e.g., threats of disease, violence, or non-cooperation) and can therefore be analyzed through the lens provided by evolutionary theory.

As the most common forms of prejudice and discrimination studied by social psychologists are sexism and racism, these have also received the lion's share of attention from psychologists who employ an evolutionary perspective. Some sexist attitudes can be viewed as a byproduct of conflicting

interests between men and women. As explained previously in this chapter, sex differences in reproductive biology have led to the evolution of different goals for men and women, with women having a vested interest in securing high-quality mates who are willing to commit and provide for offspring, whereas men have evolved a preference for sexual variety. These conflicting interests produce intersexual conflict that manifests as sexism. Haselton and Buss (2000) proposed that conflicting reproductive interests between men and women lead to implicit biases that may underlie sexist attitudes in their formulation of 'error management theory', which is the notion that people's cognitive mechanisms have been shaped by natural selection to lead them to avoid making the costliest errors when faced with ambiguous situations. Applying this notion to intersexual perception, this research found that among heterosexuals, men, on average, overestimate women's sexual intent (e.g., being more likely to perceive a smiling women's face as flirtatious), whereas women, on average, underestimate men's commitment intent (i.e., being skeptical of men's interest in forming a committed relationship following relevant courtship behaviors). The authors explain that men and women are attempting to minimize chances of making costly reproductively relevant errors (men missing out on desirable mating opportunities and women inferring a greater degree of intention of commitment from potential mates than actually exists). Conflict emerging from these perceptions may fuel sexist attitudes and, in turn, discriminatory treatment.

Although, as previously mentioned, racism and xenophobic attitudes are subject to shifting sociocultural forces, these attitudes remain common in many cultures around the world. This may, in part, be attributable to the relative infrequency with which most humans are thought to have encountered people from geographically distant locations for most of early human history (Stringer and McKie, 1997).

This historical circumstance, combined with the greater tendency of males to engage in greater levels of physically aggressive tactics, is thought to provide an ultimate explanation for greater levels of fear directed toward men from outgroups (Navarrete et al., 2010).

Disease-avoidance motives also appear to play a role in the development of prejudice. Historically, exposure to outgroup members may have carried health risks, as individuals from outside of one's regular group may have carried pathogens to which they themselves had developed resistance but to which one's own group had not yet been exposed. Consistent with this notion, evidence suggests that concerns about infectious disease predict both implicit and explicit racial prejudice in the United States (O'Shea et al., 2019). Active disease-avoidance motives have been shown to reduce perceptions of attractiveness (Phelan and Edlund, 2016), which may provide a proximate explanation for this positive relationship between disease concern and prejudice.

SITUATIONS

Historically, a great deal of social psychological research has focused on the impact of situations (i.e., factors that are external to the individual) on behavior and mental processes. One advantage of applying an evolutionary perspective to this type of research is that it can provide a framework with which researchers can identify functionally relevant elements that exist in different situations. Doing so can ultimately lead to a more in-depth understanding of which internal processes, such as emotions, motives, and goals, are relevant to a given situation. More specifically, the framework of fundamental social motives that was described early in this chapter can serve as a guide to understanding how various elements or 'cues' that are present in different situations can serve as indicators of threats or opportunities that are relevant to an individual's motives.

Expanding upon their prior work on the measurement of individual differences in fundamental social motives, Rebecca Neel and colleagues (2017) have provided a broad analysis of evolutionary perspectives on situations. Consistent with more general perspectives on social psychological processes, this analysis suggests that in order to gain a comprehensive understanding of the impact of situations on behavior, it is necessary to understand how individual differences in motivation interact with situational factors to influence behavior and cognition. Unlike more general perspectives, this evolutionary approach provides clear links between evolved motives and specific situational features. For example, the presence of a person who is coughing and sniffing is a situational cue that signals the potential presence of pathogens, which is relevant to an individual's fundamental disease-avoidance motives. This, in turn, might lead that individual to perform behaviors that reduce the risk of infection, such as avoiding close contact with the individual who appears to be ill and washing one's hands after touching any objects that this individual might have come into contact with. People with very strong disease-avoidance motivation would be expected to be more attentive to this type of situational cue compared to someone with weak disease-avoidance motivation and would, therefore, be expected to demonstrate more dramatic changes in behavior following exposure to motivationally relevant cues.

Evolutionary social psychologists have used the fundamental motives framework to understand how functionally relevant aspects of a situation impact goal-relevant behavior and cognition. This approach often involves the experimental manipulation of elements of situations to which participants are exposed and then measures the impact of these manipulations on subsequent actions and decisions. For example, participants would be randomly assigned to view attractive members of the opposite sex (e.g., Maner et al., 2003), instructed to watch a film clip in which the

actors are encountering a fundamental goal-relevant situation and imagine how they would feel and what they would do in that situation, or asked to imagine themselves in a hypothetical goal-relevant situation such as being alone in a house during an attempted break-in (e.g., Maner et al., 2005) or going out to dinner with a member of the same or opposite sex of varying degrees of attractiveness (e.g., Baker et al., 2019).

Other attempts to understand the functional relevance of situational factors have involved the development of measures that attempt to taxonomize situations according to the fundamental goal-relevant opportunities that they provide. For example, the Situation Affordances for Adaptive Problems measure (Brown et al., 2015) can be employed to have participants rate the importance of various fundamental social goals such as mate seeking, relationship maintenance, disease avoidance, kin care, status seeking, and affiliation in any given situation. The resulting measurement can shed light on the specific motives that drive behavior in different situations.

Evolutionary approaches to understanding the impact of situations on behavior often acknowledge the importance of individual differences in understanding why it is that not all people react in similar ways to a given situation. For example, for an individual who is involved in a committed romantic relationship, a situation in which they are interacting with attractive alternatives to their current partner might provide opportunities to seek new mates, preserve their current relationship by demonstrating their commitment to their current partner, or to affiliate others in a platonic manner. The manner in which any given individual behaves in situations such as the one described depends upon the interaction of personal and situational factors. Individuals who are highly committed may be more likely to signal their commitment by mentioning their current partner in an affectionate way and avoid behavior that could be perceived as flirtatious. Conversely, individuals

who are less committed may be more likely to test the waters for potential new romantic relationships via casual flirtation. Individual differences in life history strategy can also affect behavioral and cognitive responses to different situations. Life history theory suggests that the environment in which an individual develops shapes the strategies that they learn to use later in life (Stearns, 1992). The idea behind this theory is that ancestral childrearing environments were variable in quality, with some being more stable than others. Since individuals typically have limited resources, they must often make trade-offs between allocating resources toward immediate or future reproductive success. Different environmentally influenced decision rules are thought to have evolved, which result in patterns of behavior that are tailored to the environment in which an individual spent their formative years. Those who grow up in a harsh and inconsistent environment in which resources are erratically provided and/or the risk of experiencing personal injury is relatively high are thought to be more likely to develop a 'fast' life history strategy. This strategy is associated with greater risk-taking, more promiscuous sexual behavior, and earlier onset of mating-related behavior. In contrast, individuals who grow up in a more stable environment in which resources are reliably available are thought to be more likely to develop a 'slow' life history strategy, engaging in a more conservative pattern of sexual behavior by delaying reproductive efforts in order to focus on personal growth and development. The strategy that an individual develops ultimately shapes the style of attachment that they form when establishing social relationships (Chisolm, 1996).

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Evolutionary Cognitive Psychology

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Modern evolutionary (Buss, 1995a; Ghiselin, 1973) and cognitive (Bruner, 1956; Chomsky, 1975; Newell and Simon, 1972) psychological frameworks have distinct roots, yet both are interested in understanding why humans are the way they are. While human development could be viewed as a series of random co-occurrences, evolutionary frameworks have proposed that the evolutionary processes underlying the modern human brain were non-random (Duchaine et al., 2001). Specifically, the reason modern cognitions have their modern structures is due to how they simultaneously evolved. That is, to understand the driving forces behind human cognition, it is vital to consider the context in which an individual's processing is most efficient.

As such, it is necessary to consider the advantages these adaptations would have provided our Paleolithic ancestors as they interacted with each other within a hunting-gathering society (Cosmides and Tooby, 2013; Price and Brown, 1985). According

to the influential work by Darwin (1859; see also Dawkins, 1976) that has come to shape the framework for evolutionary theory, species (including humans) come to evolve as a result of *individuals* benefiting from genes that allow for successful reproduction. Reproductive success encompasses qualities that allow the individual to improve longevity enough to procreate as well as attract prospective mates. After all, less beneficial traits that dissuade mate attraction, even if they prolong the lifespan, will be transmitted at a lower rate.

Evolutionary psychology can be used as a framework in which to organize and understand a pattern of results from any domain (see Confer et al., 2010). It is used to answer the question of *why* current behaviors and physiology operate in their present state, by addressing adaptive functioning in terms of the specific internal and environmental input used to influence their development, activation, and expression (Cosmides and Tooby, 2013). By carefully analyzing the instances

in which modern cognitive processes operate in the most efficient manner (e.g., circumstances resulting in the greatest memory recall or attentional capture), circumstances that lead to efficient cognitive performance, as well as the instances in which errors occur (e.g., attending to task irrelevant information), it is possible to gain a deeper understanding for these adaptive functions from natural selection (Wang, 1996).

The modern human mind is a complex system that can be used to solve an abundant array of specific, specialized, and unique problems. However, the underlying components that interact to produce manifested behaviors are not totally distinct. Given the amazing capacity humans have to attend (Taatgen et al., 2007), select (Posner and Presti, 1987), retain (Craik and Lockhart, 1972), retrieve (Tulving and Thomson, 1973), and alter (Roediger et al., 2001) information from environments, it may be useful to consider how the cognitive ‘glue’ that links the functions of these processes was shaped by selection pressures. The present chapter aims to provide a synthesis of evolutionary research within the cognitive literature. That is, although the empirical research reviewed was largely conducted from a cognitive psychological framework, the outcomes can be reinterpreted to inform an evolutionary stance. This chapter will consider the current operations involved in modern information processing in an attempt to gain an understanding for the merits behind their evolutionary design. The selected topics explore more recent and expedient developments used in daily life, to understand how cognition continues to be influenced by processes evolved from our ancestral history.

THE COGNITION BEHIND INFORMATION PROCESSING

In order to begin to understand the influence of selection pressures on cognitive systems

(such as memory) and skills (such as learning), we must first understand how people can attend to information. Although attention can be both controlled (Carretié, 2014) and uncontrolled (Rueda et al., 2004), the way people are drawn to stimuli can provide useful insight for both cognitive (Schneider and Shiffrin, 1977) and evolutionary (Lu and Chang, 2012; Maner et al., 2008) psychological research. While inferences about attention are often attributed to affective systems (Öhman et al., 2001), others have found that implicit attenuation cannot always be attributed to such systems (Purkis and Lipp, 2007).

Clearly, great care is needed when theorizing how cognitive systems are interrelated, just as such caution is needed when considering how these systems may have been shaped by evolutionary processes. As such, the following section outlines research on how attention, memory, and emotion have been studied within an evolutionary psychological framework and how it has enhanced our understanding of human cognition.

Attention

In an ever-changing world full of an infinite number of stimuli, it is necessary to have a capacity to carefully choose where one allocates attention, whether it is within or outside intentional control (Roediger, 1990). Indeed, scholars have argued that both visual and auditory systems show an advantage when directed towards evolutionarily relevant problems (Jackson and Calvillo, 2013; Klein et al., 2002; Öhman et al., 2012; Wilck and Altarriba, 2018).

The ability to quickly and accurately detect threats in one’s surroundings is a vital skill for survival (Bell and Buchner, 2012; LeDoux, 2003). While it is possible for any object or stimuli to be used in a threatening manner, those that routinely elicit a fear response may have been evolutionarily selected. That is to say, the ability to automatically respond to

specific categories of objects promotes reproductive success.

Yorzinski et al. (2014) sought to understand what features are most salient in visual attention. Specifically, they were interested to know how animals known to be ancestral predators (snakes, lions) influenced eye movements. When shown an array of eight animal images and asked to locate the unique image, participants were quicker to respond when it was an ancestrally dangerous animal as compared to a non-dangerous animal (lizard, impala). However, the reverse was found when the to-be-detected image was a non-dangerous animal hidden among dangerous animals: the inability to disengage from the predators slowed detection of the benign animal image. The researchers concluded that natural predators automatically capture and maintain attention, resulting from an underlying design to detect potential danger, even when it is task irrelevant. It appears that human cognition developed with a propinquity for solving the adaptive problem of threat identification. Our ancestors who were able to notice and maintain spatial awareness of common predators in the environment would be able to successfully protect themselves and the longevity of their genes.

The notion that specific evolutionarily relevant threats ‘pop out’ in a visual scene more than harmless objects has also been observed when an individual does not expect to encounter said threat. Rather, potential danger that is detected, even when outside of the observer’s awareness, can still capture cognitive resources. For example, New and German (2015) surprised participants with fear-inducing images while they completed a computer task. When asked to identify the unsuspected image, accuracy was higher when it resembled a spider (an evolutionarily relevant threat, often harming with the use of venom) than a hypodermic needle (a modern medical tool that can be used as a weapon) or a housefly (a non-threat). Thus, the results suggest that attentional processing

has selected for identifying potential threats, even though detection of the image was not the intended focus of the participants.

However, the visual presentation of modern threats (e.g., guns; Carlson et al., 2009) has also been shown to automatically capture attention without the observer’s full awareness. Given the amount of time required for an adaptation to evolve (i.e., generations of gene procreation), it may seem surprising that modern objects can produce cognitions comparable to evolutionarily relevant objects. Evolutionary theory might suggest that today’s individuals have learned the association of a specific fearful context to certain modern inventions (see Confer et al., 2010; Cosmides and Tooby, 2000). The underlying mechanisms governing the learned adaptations can enable us to change our behavior when encountering specific forms of environmental and internalized information (i.e., a fear response to a snake or gun) that allows for these items to be selected for attentional salience. Indeed, there are numerous examples within the evolutionary literature that indicate novel contexts and stimuli can produce an instinctual response that surpasses that of natural and expected ones.

For example, a *supernormal stimulus*, or instances in which manufactured objects (e.g., cravings for junk food) can hold an instinctually preferential place over natural objects (Tinbergen and Perdeck, 1950; see also Barrett, 2010), indicates how the specific factors involved in adaptation and survival are not the only focus of attention. In a similar way, Pinker (1997) suggests that the underlying similarities between modern stimuli (e.g., guns) and evolutionarily relevant stimuli (e.g., snakes and spiders) can allow for mirrored cognitive processing. That is, modern stimuli can mimic the specific features of evolved threats to produce a similar cognitive response (see Shabbir et al., 2012, for evidence of pattern recognition). The evolved psychological attunement towards detecting objects historically associated with threats can be exploited to

encompass the specific details used in the design of modern objects.

Beyond the visual and gustatory senses, auditory stimuli also demonstrate attentional capture by specific noises. The use of language and vocalizations is an important tool that many humans use on a daily basis to attract the attention of others (a discussion of language and communication will be provided later in the chapter). Significantly, the qualities (e.g., tone, pitch, volume, prosody) that make up a vocalization can in themselves convey a message. To test the effectiveness of vocalizations with attention-grabbing intentions, Chang and Thompson (2011) performed a simple experiment in which they asked adults of parent and non-parent status to complete simple arithmetic problems while listening to various recordings. The recordings consisted of (a) whines, which tend to be interpreted as irritating to listeners and are used to encourage attention from others, (b) cries, which are the main means of infant communication, and (c) motherese, a soothing vocalization pattern used to gain a child's attention. All three sounds were better at distracting participants from successfully completing the simple cognitive task and produced more mathematical errors than did alternative sound clips (an unfamiliar language, woodshop noises, and silence). Interestingly, this pattern occurred regardless of participant gender and parental status, indicating that there is a natural inclination for all adults to prioritize attention towards these forms of vocalizations. The researchers suggested that acoustic information intended to convey information about environmental dangers or an immediate threat to personal safety are difficult to ignore and can interrupt cognitive processing (for similar results, see Chang and Thompson, 2010; Morsbach et al., 1986).

Why might irritating sounds and words intended for children be evolutionarily selected for in adult attention? Reproductive success involves not only the ability to propagate one's own genetic information but also

those genes continuing to be reproduced (Darwin, 1859). A natural inclination to attend to one's distressed offspring can aid in the child's ability to reach sexual maturation and reproduce. On the other hand, human children require years to reach physical maturity. Therefore, they can use these specific vocalizations as a tool to promote a reaction from capable individuals to solve problems, such as obtaining nutrition and protection (Cosmides and Tooby, 2000).

However, not all sounds in one's environment have a conversational intention. Yet, it is not uncommon for attention to be redirected towards a novel sound (Schröger, 1996). While this can effectively distract cognitive functioning, allocating attention towards a surprising sound can motivate an individual to modify his/her current behavior in an effort to prepare or protect him/herself from an unobserved threat. Overall, attention is allocated towards auditory information, whether it originates from another human or not, that may provide meaningful information about one's immediate environment. Importantly, these attention-grabbing sounds carry a specific message about the makeup of the immediate environment and changes that are occurring. By having evolved an attentional sensitivity towards particular sound cues, the individual is able to increase cognitive processing speed and accuracy for these possible warning signals (Parmentier, 2016). The ability to quickly and accurately detect and identify unforeseen environmental cues can permit the individual to make a behavioral modification that could allow for enhanced survival ability.

Attention, as discussed throughout this section, has been shown to be biased in favor of survival and evolutionarily relevant circumstances. However, attention is only one component of cognition. While there may appear to be an attentional advantage for survival, where exactly does such an advantage come from? Is it that attentional resources are implicitly directed towards threats? Or, perhaps people are quicker at purposefully

processing or recalling stimuli patterns that could pose harm. To better understand the nature of the evolutionary advantage within attention, the next sections will review recent research on memory and emotion processing.

Memory

Once information is acquired, whether through implicit or explicit processes, it can be stored in memory. In short, the widely cited memory model proposed by Baddeley and Hitch (1974) argues that information resides in multiple stores for both short- and long-lasting durations. An additional component known as working memory serves the purpose of engaging with a limited selection of the environmental input in active attention and coding it into a more permanent store. When a situation arises that will put the encoded information to use, it is necessary to transfer and retrieve relevant details from the memory stores (Ericsson and Kintsch, 1995). Indeed, a big part of cognitive research has focused on what type of information is most readily retrieved and remembered (Cowan and Davidson, 1984; Neisser, 1986).

Primarily, if cognitive processes associated with memory, such as attention, are the product of selection pressures that humans encountered during their evolutionary history, it stands to reason that fitness-relevant information (e.g., finding shelter, protection from predators, food sources, viable mates and kinship) may be processed more readily than other types of information. In essence, cognition is inherently influenced by external stimuli that shaped mental processes over evolutionary time, and, as such, contextual information must be considered when examining function. However, with speed of processing there can often be a trade-off with accuracy (Draheim et al., 2016; Mulligan and Hirshman, 1995; Reed, 1973), as a wealth of research has shown how memory systems can be biased on their own (Mather and Sutherland, 2011; Schacter, 1999), as well

as how interacting with other systems can result in errors (Verde and Rotello, 2004). The following section will explore the various modular systems under which memory processing evolved and the functions that have come to demonstrate a hyper-focus on survival-relevant information.

As previously discussed, evolutionary theory is based on the potential for an individual to propagate their genes. This ability is focused in terms of reproductive success, which encompasses the need for the individual to sustain themselves long enough to act on procreation opportunities. Remembering details relevant to survival success would aid in this endeavor. Over the past decade, the extent and limitations for processing information according to its survival relevance on memory have been examined (see Nairne and Pandeirada, 2016, for a recent review). In the traditional survival memory paradigm, participants are asked to imagine themselves stranded in a foreign grassland (similar to our ancestral environment), in need of resources, food, and protection (Nairne et al., 2007). Words are then rated for relevance to this scenario or an alternative situation (e.g., moving homes, general pleasantness). During a surprise recall or recognition memory test, superior performance is typically found for words that had been previously processed for their survival relevance, even when compared to other robust mnemonic devices (e.g., self-reference).

How might survival processing produce an attentional shift that leads to heightened memory? Although this survival-processing effect has been robustly found in the literature (see Kazanas and Altarriba, 2015), its proximate mechanisms have been questioned. For example, implied social isolation in the original grassland scenario may be leading to enhanced memory engagement, regardless of the level of survival threat present (Kostic et al., 2012). When one must rely solely on oneself to solve a task, the need to elaborate on all aspects of relevant information is apparent; there are no other people to assist

or use as resources. Leding and Toglia (2018) tested this notion by asking participants to imagine themselves in various survival situations (stranded in grasslands or going on a space mission) either alone or with a group of friends and to then rate words for relevance to the given scenario. When asked to recall the rated words (Experiment 1), a memory advantage for grassland survival processing was only present in the isolated condition. Furthermore, the perceived isolation of both the grassland scenario and the space mission scenario were rated highly, indicating that this factor alone is not fully responsible for memory attunement to survival-relevant information. Rather, the threat of social isolation may be enhancing elaborate processing and serving to strengthen memory for information pertaining to grassland survival. Memory appears to have selected for operating most efficiently when encoding circumstances that promote the need to think in a deep and elaborate fashion (Craik and Lockhart, 1972).

It appears that both attention and memory development resulted in an attunement towards contextual and environmental information that can indicate a potential threat to one's ability to survive. However, these enhancements do not appear to occur universally but rather are produced following the encoding of specific information (Hollingworth et al., 2001; Kuhlmann and Rummel, 2014). In other words, the details that are remembered for a given object or scene can vary based on the intentions one has while encountering it. As a result, a shift in attentional focus during encoding can alter what is later remembered.

A clear example of this memory context specificity can be found when examining the memory of individuals with varying attentional focuses. As one's situational circumstances change, their needs and motivational priorities may also fluctuate. For example, women who become pregnant display such cognitive changes. Pregnant women have a heightened investment to keep their

developing offspring safe. Therefore, a quick detection of potential threats would be advantageous as their physiological changes (e.g., increased body mass, frequent nausea) can decrease their physical ability to flee danger. However, non-pregnant women are not burdened with this additional care. To test for cognitive differences as a result of a shift in need, Anderson and Rutherford (2010) compared groups of pregnant and non-pregnant women's memory for faces. They asked the women to rate briefly displayed images of male and female faces for their appearance of health. The faces ranged in age from young adult to elderly and included a variety of ethnicities. Later, a surprise memory test was given in which participants were asked to indicate the faces that had previously been presented in the health-rating task. The results showed that pregnant women were more accurate at identifying the familiar faces than were the non-pregnant women, particularly for own-race male faces (but see Brett and Baxendale, 2001). The authors argue that this pattern of results may indicate an adaptive solution of trading the ability to physically protect oneself during pregnancy for a memory-retrieval enhancement that could allow ample time to find an alternative safety option (Burch and Gallup, 2004; Chang et al., 2005; Gazmararian et al., 2000). This indicates that human cognition has come to solve problems by reallocating cognitive resources towards tasks most relevant to one's current needs.

Threat towards one's safety is not confined to physical harm, as has been discussed thus far. As social individuals, humans routinely create social bonds for various reasons including the sharing of resources. However, it is also not uncommon for these bonds to be negatively affected by incompatible expectations within the relationship, and it is therefore beneficial to avoid such encounters. Specifically, there is an adaptive advantage to remembering information pertaining to the likelihood that a person will cooperate with or exploit others. According to the cheater-detection component of social contract theory

(Cosmides, 1989; Cosmides and Tooby, 1992, 2005), social cooperation among individuals can enhance fitness and lead to other benefits. However, reliance on others can also lead to manipulation and harm by those who cheat the agreed-upon expectations.

To minimize exploitation by cheaters, one would benefit from accurate cheater identification so as to avoid or act cautiously around them. Bell and Buchner (2009) tested the effect of trustworthy versus cheating behavior on memory for names of individuals. Participants gave a likeability rating for persons about whom they read a name and short description of their professional status and behavior. Following the last rating, a recognition test for the names of the people was administered, in which half of the names had been presented in the rating task and half of the names were novel. When a response indicating that the participant remembered the name being presented in the earlier task was given, they were asked to also indicate if the description associated with that name indicated trustworthiness, cheating, or neither.

Aligning with the predictions of a cheater-detection module, names that were recognized as originating from the likeability-rating task were best remembered when they were depicted as a cheater than as a trustworthy individual (see Buchner et al., 2009, for similar results using facial images). Information pertaining to a violation of social norms that could lead to harm appears to be beneficially retained in memory. While there is a conceivable advantage for remembering who is a trustworthy person, evolution selected for memory of cheaters so as to aid in solving problems of exploitation (Mealey et al., 1996; Vanneste et al., 2007; see Mehl and Buchner, 2008).

The examples provided demonstrate a clear memory attunement towards specific information pertaining to the individual's survival and safety. Aligning with an evolutionary framework (see Buss, 1995a; Cosmides and Tooby, 1997), these memory advantages are context and need dependent. However, as

with attentional focus, there also appears to be a modular structure in memory for information relevant to reproduction. That is, information most readily recalled about the opposite sex can be influenced by directing attention towards reproductive purposes.

Pandeirada et al. (2017) asked female participants to watch videos of male actors describing themselves. For some of the videos, viewers were instructed to decide how desirable each actor would be as a long-term co-worker, while for others, participants rated each actor's appeal for a long-term mating relationship. Later, participants were asked to remember the faces presented in the video. Participants displayed better memory for the faces presented in the context of a potential mate than in the context of a co-worker. The authors argued that memory for the facial details of potential mates, as opposed to co-workers, is an important component of mate selection as health and genetic-quality information can be observed and used to make reproductive decisions. These findings align with an adaptive-memory framework, as the ability to detect and identify potential mates can lead to successful outcomes in terms of reproduction.

Theories of human memory have been created and tested using experimental data that indicate when cognition functions most efficiently and when it fails. While much of the focus within the cognitive psychological literature has sought to address models for how memory is organized and operates (Squire et al., 1993), evolutionary psychology provides complementary theoretical frameworks for why it exists (Klein et al., 2002; Sherry and Schacter, 1987). Evolution has resulted in human memory that selectively recalls information that is particularly relevant to solving problems of resource depletion (Leding and Toggia, 2018) and appropriately preparing oneself for encounters with strangers (Anderson and Rutherford, 2010; Pandeirada et al., 2017).

Yet, memory accuracy is not solely determined by the degree of evolutionary relevancy

of the information being processed. As previously mentioned, attention plays a key role in determining what information becomes stored in memory. Furthermore, many scholars have also examined how attention is often linked with emotion to impact behavior, as well (Compton, 2003; Compton et al., 2003; Koole, 2009). The following section will examine how emotions can dictate the strength and direction of attentional capture and behavioral responses so as to achieve adaptive goals.

Emotion

What is the common factor between the attention-grabbing predator images, children's cries, and cheaters? According to the approach-avoidance framework, we are designed to identify adaptive solutions that maximize pleasurable situations while avoiding threatening ones that can cause a fear response (see Beall and Tracy, 2017). Thus, our emotions play an important role in the functioning of our cognitive systems (e.g., attention and memory) and resulting behaviors.

Evolutionary theories propose that specific types of threats that have been selected for should elicit an automatic fear response as a method to increase an individual's likelihood of survival (LeDoux, 1998; Öhman and Mineka, 2001). Accordingly, humans around the world are most likely to develop phobias in response to dangers our ancestors recurrently faced, including snakes, spiders, heights, and darkness (for a discussion of prepared fears, see Seligman, 1970, 1971). However, modern dangers, such as drunk drivers, are not fears that are readily developed even though they pose real threat to safety. Furthermore, these evolutionarily relevant fears are expressed in conjunction with childhood developmental stages (Scarr and Salapatek, 1970). For example, a fear of heights and strangers emerges in children of six months, corresponding with their ability

to crawl (Bertenthal et al., 1983). Those early months of fearlessness could be adaptive in that they promote environmental curiosity and exploration (Dahl et al., 2013). However, as a child is able to increase proximity from caregivers, they also increase the possibility of encountering cliffs and unfamiliar people who may pose a danger. The alignment of certain emotional developments with physical development seems to allow children to maximize their cognitive intake while selectively learning to keep themselves safe. The universal predictability of human fears demonstrates that this emotion is rooted in our design, rather than purely learned from cultural exposure.

Observing fear in others provides a clue as to the presence of danger. In particular, fearful facial expressions automatically capture attention by onlookers (Elam et al., 2010). However, a message of fear can be communicated without viewing an entire face. The presence of eyes alone has been shown to influence behavior in observers (Manesi et al., 2016). Fearful eyes, in which the eye-whites are enlarged and the pupils dilated, appear to have a powerful influence on attentional capture, as it appears to occur automatically and outside the observer's conscious perception. Carlson et al. (2016) conducted dot-probe experiments in which they asked participants to observe a screen and indicate the location (left or right) of a dot as quickly and accurately as possible. Prior to the dot's appearance, images of fearful eyes, scrambled eyes – same features, but presented in a non-meaningful arrangement (Experiment 1), or neutral-expression eyes (Experiment 2) were briefly presented followed by a visual mask that reduces the ease of conscious perception for the images. Participants were faster to identify the location of the dot when it appeared in the same spatial location as a fearful-eyes image than in either of the emotionless images, indicating that the masked fearful eyes facilitated attentional orientation towards its location. Furthermore, the researchers argued that fearful eyes not only

captured attention, but they also reduced attentional disengagement until a behavioral response was made.

The presence of information that could pertain to the location of a potential threat increased visual cognitive processing for its location, while decreasing the processing of alternative, less threatening locations. Even without the participant's conscious awareness of having perceived the fearful eyes, attention was captured nonetheless, implying that an automatic vigilance towards threat cues occurs regardless of awareness. Comparable results showing an automatic orientation towards potential threat has also been found for poisonous and predatory animals (e.g., spiders, lion, snakes; Blanchette, 2006; Öhman et al., 2001; Yorzinski et al., 2014), as well as for modern threatening inventions (guns; Carlson et al., 2009). An attuned perceptual system allows for the early detection of threat and the opportunity to flee or protect oneself (Coss and Goldthwaite, 1995). This automatic orientation towards information pertaining to certain dangers appears to have been selected for because it increases the likelihood of survival by allowing the individual the opportunity to engage with the stimuli in question until a threat-level assessment is made.

Similar to fear, disgust is another emotion thought to be universally displayed by humans (Curtis and Biran, 2001). The disease-avoidance hypothesis posits that disgust serves as a behavioral defense against biological disease (Oaten et al., 2009). When a rotted or infected stimulus is encountered, disgust promotes an increase in distance from it to avoid contamination. While this response has been found to be heightened in particularly vulnerable populations (Curtis et al., 2004), it can be overridden to successfully attend to more pressing adaptive problems (Case et al., 2006).

The ability to manipulate how strongly emotions are experienced, as in the case of disgust, can be beneficial. However, it can also be viewed as an adaptive error in emotion

processing. Underrating the affective component of an unpleasant situation that cannot be avoided can allow the individual to continue to engage in the necessary activity (e.g., removing soiled materials, bandaging an injury). Alternatively, overrating the degree of emotionality in a situation can also be adaptive. For example, the miscalibration often found in affective forecasting (e.g., we think we will be happier for longer than we are or that bad news will upset us more than it actually will) can be useful to the individual and align as an adaptive solution. For example, individuals tend to overemote imagined future events as compared to past events, even when they are hypothetical situations (Van Boven and Ashworth, 2007). This finding suggests that the act of anticipation enhances preparedness for encountering new, more intense experiences than what has already been experienced (Wilson and Gilbert, 2008). Therefore, if an individual anticipates a situation to be more unpleasant than it turns out to be, they may experience a feeling of relief. However, if the individual mentally prepares for a disastrous event and it does, in fact, occur as anticipated, he or she may be better equipped to handle it than other unsuspecting persons. At the same time, experiencing an event that is routine and appears emotionally 'ordinary' tends to elicit a weak emotional response and is noticeably distinct from extraordinary events that provoke elaborate effects (Frederick and Loewenstein, 1999; Wilson and Gilbert, 2008). The emotional intensity anticipated and experienced by an event can serve as a cue to prepare and maintain vigilance towards particular contexts.

There is no doubt that affective information provides a layer of contextual information about one's personal internal status, other's perceptive needs, and environmental circumstances. True emotions can lead to appropriate responses and understandings that can aid in protecting oneself and others from specific threats as well as promote the search for adaptive solutions. However, errors in emotional appraisal have also been shown

to serve as a protective mechanism in the face of unpleasant situations. Taken together, attention, memory, and emotion processing conjointly allow for an individual to acquire information. The behaviors and thought patterns that result from how this information is perceived and interpreted can be used to test theories surrounding the selection pressures leading to their modern operations.

HUMAN BEHAVIOR AND HIGHER-ORDER COGNITIVE FUNCTIONING

Human behavior can be influenced by a variety of factors, to complete both mundane and complex tasks. As a result, the choices and rationale one uses when completing tasks can differ based on the values and needs of an individual at a given time. For example, the goals of obtaining food or selecting a mate can vary over time and as resources and group dynamics change. However, as previously discussed, there is not always conscious access or awareness of the underlying mechanisms or rationale that produce cognitive behaviors. How human behaviors and experiences culminate must be considered within the circumstantial context as well as within the limits of human cognition.

Language

Verbal language is a tool that allows humans to communicate with one another using vocalization patterns often full of prosody and affect. From an adaptive standpoint, this complex cognitive ability allows for many communicative advantages. For example, language can be used to signal dangers and threats at a distance, to give directions and information without direct shadowing, and to form social bonds. The innate development of a first language in young children without formal training, the presence of complex yet universal grammar structures worldwide, and

specific brain areas devoted to language and speech processing all indicate that language is an instinctual cognitive skill built by natural selection over human evolutionary history (Pinker and Bloom, 1990). However, others have argued that the occurrence of language is a by-product of the human brain's relatively large size, without specification for communication advantages (Chomsky, 1991). Regardless of how and why we came to possess our current level of language skill, language can be used for a variety of purposes.

What conversational topics are processed the most efficiently by the modern human? Redhead and Dunbar (2013) sought to understand the cognitive underpinnings of language and how it allows information to be transmitted between minds. They hypothesized that language, like memory and attention, would be best attuned to information that promotes advantages for the individual in terms of personal safety or mate acquisition. Specifically, the researchers questioned if the ability to communicate was selected with the purpose of social gossiping (e.g., gathering information about the characteristics of others), mate advertising, social contract creation (e.g., forming bonds and exchanging resources), or exchanging factual information. Participants were asked to read short stories with content involving these four hypothesized purposes. When later asked to write down details from the stories, information involving social details (e.g., deception, relationship details) were better recalled than factual or ecological (e.g., how honey is made) information. This pattern occurred regardless of the story's contextual aim. Thus, language appears to have a particular sensitivity for conveying information about the social world. The researchers proposed that language initially evolved to enhance communication methods between groups of people. In other words, language appears to have evolved as a means of supporting human interactions. Once connections are made between people, language can be further used to support the completion

of specific goals (e.g., sharing one's interests with a romantic partner, explaining a recipe, bartering goods).

However, in today's society, it is common to encounter individuals who have differing native languages. The lack of a common language can, reasonably, create communication difficulties. Yet, humans are not limited to communicating via a primary language, as many have acquired the skills to use a second language, as well. What are the evolutionary benefits to second language learning? Children demonstrate a keen ability to learn multiple languages without formal training early in life (Hirschfeld, 2008). Moreover, a child's second language can quickly become indistinguishable from native speakers in the community, and infants are able to distinguish accents better than adults (Kinzler et al., 2007). However, adults who attempt to master a second language often require substantial effort and tend to show considerable variability relative to native speakers in terms of speaking fluency and accent (for a discussion, see Wilck and Altarriba, in press). While this difficulty of learning a second language as an adult may indicate that our ancestors lacked natural pressures to intermingle with diverse communities (Hagen, 2008), the ease for children to become multilingual may alternatively suggest selection for cooperation and social exchange between groups of different language speakers (Hirschfeld, 2008). From a cooperation perspective, language skills can encourage groups of people from diverse cultures to intermingle and rely on each other for benefits such as resource trading, idea exchanging, and alliance building.

With the numerous benefits that can accompany bilingualism and multilingualism, why do adults show difficulty in second language acquisition, as compared to young children? The differences in learning styles between children and adults may provide key insight into this answer. A more complete discussion of learning will be provided later. In brief, children are in a constant state of

learning and have an ever-growing store of knowledge. Adults, on the other hand, have accumulated a larger store of information that they can use to understand and navigate the environment. It has been suggested that children before the age of seven years are able to implicitly learn new languages that they are exposed to by unintentionally absorbing information necessary to hold a conversation (Ellis, 2005). When adults attempt to learn a new language, it is most often through cognitively demanding explicit instructional methods in which language rules are intentionally memorized (Ellis, 2016). The trend to change from an implicit learning style to an explicit learning style over the lifespan can provide insight into the finding of increased difficulty of second language learning with increased age (Bialystok, 1994; Paradis, 2004). However, controlled empirical examinations of children and adults have indicated that all ages are capable of using both implicit and explicit learning strategies to similar degrees when learning an artificial language (Lichtman, 2016). It appears that the differences in ease of second language learning between children and adults may not strictly result from cognitive maturation but may reflect contextual differences in the learning environments and the time needed to reach proficiency.

Problem Solving and Decision Making

The notion of human cognition evolving to solve adaptive problems has been a theme throughout this chapter. Problem solving is a complex task in which our ancestors must have done reasonably well, as it is a pinnacle ability for modern humans. However, the literature on complex mental processing suggests that humans often fail when it comes to logical thinking (Brown and Moore, 2000; Cosmides and Tooby, 1992, 2005). The kinds of problems solved most efficiently can be explained as having an evolutionary basis by

considering the specific contexts in which the necessary skills evolved.

In the classic Wason Selection Task, in which participants are asked to solve a logic problem by only turning over cards that will provide necessary information, participants will often perform extraneous flips that do not aide the task goal (Wason, 1966, 1968). However, when the task is reframed from abstract card flipping to solving a social dilemma, performance increases tremendously (Brown and Moore, 2000). While hypothetical and abstract problems often test the limits of our problem-solving abilities, grounding the information in a social context allows for logical thought to emerge.

Why is framing a problem in a social context beneficial for problem solving? Cosmides and Tooby (1992) have suggested that humans evolved to respond to problems that threatened their survival or reproduction. As social beings, many of these problems exist within the social domain and we have an inclination to make decisions based on their relative costs and benefits. Because the ability to successfully solve social problems increased procreation likelihood, human cognition has been shaped to be particularly apt at logical thinking in such circumstances.

Within a hunter-gatherer society, it is commonly understood that males and females have differing social and labor roles (Silverman and Eals, 1992). As a result, each sex faced unique problems and may have evolved diverging skills that would allow them to specialize in their modular tasks. Because women held the natural role of childbearing, they adapted to the role of childrearing to a greater extent than men. As a result of physical changes to the body during pregnancy, it is possible that this encouraged women to stay closer to the home and collect food sources through gathering. Women selectively developed exceptional recognition and recall of spatial configurations that supported successful location and foraging abilities for foods, such as berries, increased speed of memorizing scene details,

and abilities to learn object locations and identities with ease. On the other hand, men were known to take on the role of hunter and adapted skills such as tracking, orienting oneself, and mentally predicting the trajectory of objects and animals in order to be effective at pursuing prey. The specific skills for which individuals have developed a propinquity for are rooted in an adaptive context.

The decision-making processing involved during human interaction is another example of an evolutionary psychology theory integrated into cognitive research. Having the ability to interact with others allows for the creation of social bonds, group protection, and resource sharing. To obtain a benefit from a meaningful connection with others, whether for mating or kinship purposes, it is important for the bonds to be recognized (Buss and Duntley, 2008). For example, it is important to be able to distinguish kinship clusters for knowing who is likely to create alliances with whom during a hostile situation, identifying individuals who lack kin protectors, and recognizing those with protective kin. Naturally, human cognition appears to have selected for this ability and can readily identify connected individuals (Maloney and Dal Martello, 2006). For example, unrelated observers are able to correctly match newborn babies with their parents (Kaminski et al., 2010) and identify mother–daughter pairings from photographs (Arantes and Berg, 2012) with accuracy, even when they think they are guessing. This implicit ability to correctly assign kinship labels can be viewed as evidence that our ancestors were most successful at reproduction when they possessed this ability.

A fundamental ‘problem’ for an organism driven to pass on genetic information is to find a mate. As mating typically encompasses a selection process, we are faced with the decision of how we select a mate. When attempting to establish a meaningful reproductive relationship, one would want to display their most attractive qualities in order to demonstrate one’s good genes and effectiveness in contributing positive attributes to the

relationship. This includes demonstrating desirable mental traits, such as a good memory, when in the presence of potential mates. To test the evolutionary prediction that humans have a natural inclination to demonstrate desired traits, Baker et al. (2015) showed participants images of highly or averagely attractive opposite-sex faces while listening to a voice-recorded story. When asked to recall the details of the story, males who had viewed images of attractive women remembered more story details than males who had viewed images of women with an average appearance. However, women performed equally well regardless of the male images' appearance. In a second experiment, the researchers argued that this memory difference in males is a result of a selectively enhanced ability to retrieve the story details when exposed to attractive faces, rather than a decrement to learning the story details when viewing average faces. The increase in memory performance by males following exposure to images of physically desirable females supports the presence of adaptive differences in mating-related goals between the sexes. Females, but not males, tend to place a higher value on cognitive-skill display than on physical attraction, thus encouraging men to display the desired traits when encountering a potential mate to increase attractiveness (Beaulieu and Havens, 2015; Buss and Schmitt, 1993). How one chooses to portray oneself, both consciously and unconsciously, is in part dependent upon one's current goals and evolved reproductive motivations.

The presence of an attractive potential mate has also been shown to influence the behavioral choices one makes. For example, when assigned to a hypothetical dining partner of the opposite sex and asked to make a meal selection, the more attractive the dining partner was rated, the healthier was the food selection (Baker et al., 2019). The more an individual wishes to impress a potential mate, the more likely that individual is to portray a positive image such as signaling a healthy

lifestyle through lower-calorie food consumption (Otterbring, 2018).

Of course, when faced with a choice to be made or a problem to be solved, people attempt to make the best, most comprehensive, and thoughtful decisions possible. However, what exactly is meant by 'best' is not only rooted in the situational context but is also specific to the individual creating the solution. Adaptations are built by selection pressures. Indeed, these selection pressures can be derived from the environment (e.g., detection of berries and looming predators) but also from the benefits routinely gained by taking a certain course of action (e.g., kinship can lead to enhanced access to resources, such as through superior male spatial-navigation skills supporting nutrient attainment). Importantly, as research on decision making and problem solving implies, the selection pressures that result in cognitive adaptations can, in turn, accentuate and modify the skills needed to successfully complete these decisions.

Learning

Across a variety of abilities (e.g., attention, memory, emotion processing, language, decision making), there persists a selection for information that is relevant to ancestral survival or reproduction. While this can arguably benefit the individual's likelihood of survival through the process of evolution, it is not to imply that drawbacks do not exist.

Humans require a great deal of time to reach cognitive maturity. As a result, we are in a constant state of learning that extends throughout the lifespan, with a particular emphasis on knowledge absorption during the infant and childhood years (Bjorklund and Beers, 2016). From an evolutionary perspective, one can deduce that there are adaptive benefits to this slow maturation process. A brief observation of children will reveal the young thinkers' propensity to explore their environment through play. Children are also

keen at observing others and mimicking their tendencies as they learn to think for themselves (Simpson and Riggs, 2011; Tomasello and Carpenter, 2007). However, by lacking sufficient knowledge about how the world operates, children are also at risk of exerting energy on maladaptive or non-essential task methods (Keupp et al., 2013). Regardless, by imitating and emulating the acts of others, children are able to explore new skills, techniques, and ways of responding to situations that can lead to a more concrete understanding of the world (Wood et al., 2013).

While a cursory analysis may suggest a disadvantage for children with underdeveloped learning methods, an assessment of the differences between younger and older learners can provide insight into the benefits of slow cognitive maturation. Unsurprisingly, knowledge for factual and declarative information increases with age, experience, and exposure to ideas. However, when given the opportunity to think in creative and abstract fashions, younger children tend to demonstrate superior performance as compared to older children (Defeyter and German, 2003). In addition, young children, particularly infants, demonstrate superior performance in certain tasks, for example, comprehending differences between languages of differing accent and sound (Kuhl, 2004; Werker et al., 2012).

In a review of thinking patterns between younger and older learners, Gopnik et al. (2015) suggested two empirically supported possibilities to account for thinking-pattern differences. One possibility is that the increase in concrete knowledge results in a rigidness of thought patterns. New learners tend to display openness to exploring and generating new ideas. As we become more informed of the operations of our world and discover problem solutions that will effectively reach a goal, a reluctance to exert cognitive effort and resources encourages maintenance of known and tried ideas. Alternatively, Gopnik et al. (2015) suggest that cognitive flexibility may provide an explanation. Younger minds

and brains that are fiercely developing are also more flexible than their matured counterparts. This means that, compared to adults, children tend to show higher levels of divergent thinking and are particularly capable of making new connections between common stimuli, problems, and experiences. Parallel to their behavioral exploration, they are open to trying new ideas even though they may not be efficient. Over time, however, this flexibility and exploratory pattern decreases in favor of routine processing. While children intrinsically have cognitive limitations due to the design of human development, they can also demonstrate superior learning abilities in many domains.

The topic of learning provides an interesting example of how evolution can result in adaptive solutions to specific problems. Even though slow cognitive maturation may cause developing children to be dependent on others for an extended period of time, this adaptation allows learners to more openly explore their environment and test out a variety of ideas. As such, what may be viewed as a disadvantage can be analyzed from an evolutionary framework as an advantageous trait.

CONCLUSIONS AND RESEARCH CONSIDERATIONS

The domain of psychology is broadly concerned with understanding the functioning of the human mind and human behavior. Indeed, at its root, psychology is a science that is more than just biological reductionism (Yanchar and Hill, 2003). As such, the synthesis of evolutionary and cognitive psychology inherently captures the importance of psychology as a discipline. Cognitive psychology, for instance, is particularly concerned with addressing how cognition functions, including how cognitive skills may be acquired (Anderson, 1982). Yet, cognitive psychologists have realized the importance of the interaction between cognition

and the environment (Fiske and Taylor, 1991). In short, evolutionary psychologists seek to understand how psychological constructs can be viewed as adaptive. Indeed, evolutionary researchers have examined selection pressures on everything from sex differences (Buss, 1995b; Geary, 2010) to human culture (Kenrick et al., 2003), with a more recent emergence of literature understanding the adaptive components of cognition (Barkow et al., 1995; Haselton and Nettle, 2006; Reber, 1992; Sweller et al., 2011). However, with that in mind, a synthesis of the sciences requires more than borrowing theories or methods from one another. Rather, a mutually beneficial relationship can be created with a thoughtful integration of everything from hypothesis generation to experimentation using the tenets of both disciplines (see Figure 2.1). This chapter has aimed to provide a selected review of the literature on human cognition from an evolutionary psychology perspective to highlight the progress that cognitive psychologists have made in adapting evolutionary psychological frameworks. Cognitive evolutionary psychology can be used as an important framework for addressing *why* we gather and process information as we do (see Krill et al., 2007). By understanding the limitations and selected priorities of cognition, it is possible to secure a deeper understanding for how our information-processing systems operate. This information can be used to push our abilities towards greater achievement, both from an individual and societal standpoint.

Cognitive systems can be understood as having developed over generations in the same way that they have with respect to natural selection. These systems, such as attention, memory, and emotions, all converge on operating with particular care for connecting with individuals who can provide resources, social bonds, and/or romantic relationships. Furthermore, these processes can be used to direct behavioral responses and thought patterns. The ability to learn, communicate with language, and make decisions and problem

solve can all be broken down into their core operations and analyzed. Although the day-to-day encounters in modern society can be vastly distinct from those of our ancestors, the results of selection pressures exhibited by these cognitions remain parallel. This theoretical understanding allows us to make empirical predictions for cognitive tasks that align with an evolutionary framework.

Although there are clear benefits to exploring cognitive psychology with an evolutionary framework, there are also limitations that should be acknowledged when the approaches are not appropriately synthesized. The study of human cognition has been a rising field of importance since the mid 1950s, when it aimed to explain the underlying mechanisms that result in behavioral patterns using rigorous experimental methods (see Cosmides and Tooby, 2013). As such, a majority of the stimuli that have been developed for testing cognitive theories are simple, in an attempt to increase experimental manipulability (see Neisser, 2014). For example, basic shapes are often used in attentional search tasks and nonsense syllables in language-learning examinations. However, stimuli that are encountered in the real world tend to be highly complex and therefore the environmental stimuli to which evolution responds are often also complex.

In addition, a large majority of psychological experimental designs involve relatively short-term phenomena. Much of the research that is conducted within these domains occurs within laboratory settings and, as such, are subject to practical limitations such as monetary expense, participant availability, and ethical standards (see Shipman, 2014). That is to say, our understanding of how the human mind operates is largely based on the sorts of observations that can be collected within an hour (if not less). Yet, evolutionary theory is really about understanding how selection pressures over time have influenced development. To fully synthesize cognitive and evolutionary psychology, researchers are tasked with finding a way to test how adaptive

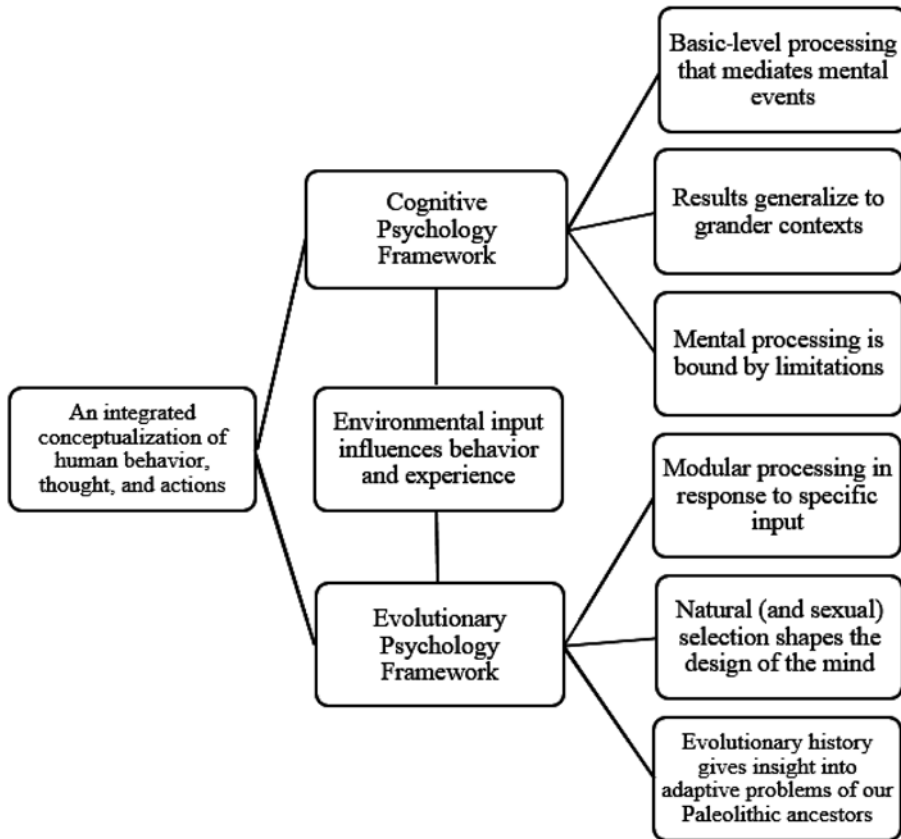


Figure 2.1 The basic tenets of both cognitive psychology and evolutionary psychology can be used to garner a deeper understanding of psychological functioning

long-term adjustments lead to differences in cognitions, while conducting relatively short-term projects.

Furthermore, it is common for cognitive theories to make predictions that explain the mechanisms behind a skill in a general-purpose fashion (see Iran-Nejad et al., 1990). That is, cognitive experimental data are often intended to be void of contextual information and seek to replicate across a variety of circumstances. Yet, as discussed throughout this chapter, evolutionary theory is grounded in understanding the context behind function and development (Kurzban, 2011; Tooby and Cosmides, 1992). Because of this, what is considered a useful adaptation can vary between contexts, domains, and goal

orientations. An evolutionary framework offers cognitive psychology the opportunity to integrate information-processing systems using an adaptive lens. This can occur by giving consideration to how they can be influenced by historical and social changes within a lifespan, as well as the evolutionary context. Studying cognitive psychology from an evolutionary framework can aid us in answering an array of functional-analysis questions that are otherwise often overlooked.

While it may seem that the fields of cognitive and evolutionary psychology hold opposing views in experimental design and purpose, this is not inherently the case. What types of studies, designs, or projects are needed to understand something from

both a cognitive and evolutionary psychology perspective? As the cognitive domain holds value in being able to address the basic, fundamental operations by accounting for the most amount of empirical data with the simplest explanation that holds across multiple circumstances, the question of generalizability must be considered. Alternatively, evolutionary theories propose modular explanations to specific problems as a result of natural selection. To satisfy both ideological concerns, it seems that projects with high ecological validity will yield the most satisfactory conclusions. For example, investigations on the effectiveness of second language learning by children versus adults in classrooms using specific skill techniques would provide a platform from which to investigate how various encoding methods influence cognitive acquisition as well test theories for why the groups might differ.

The literature reviewed indicates that our cognition operates in a way that aligns with the theories proposed to explain our highly social behaviors. Our base-level cognitive adaptations (e.g., attention, memory, and emotion) interconnect and allow for the scaffolding of our higher-level cognitive abilities (e.g., decision making and problem solving, language acquisition, and learning). By combining the perspectives of evolutionary and cognitive psychology, a deeper understanding of the design purpose and operation of the human mind is possible.

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Evolutionary Developmental Psychology

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Development (embryology) was initially important for understanding evolution for most early evolutionary theorists, including Charles Darwin (Darwin, 1860). However, the advent of genetics at the beginning of the 20th century, and the corresponding modern synthesis later on, displaced development from that central spot in biology (Gilbert, 2017). As a result, relations between development and evolution were seen as inconsequential for evolution (Dawkins, 1976). Conversely, evolutionary theory was important and inspiring for understanding development at the scientific beginnings of developmental psychology (child psychology) (Morss, 1990). Yet its influence on the discipline faded during the 20th century for different reasons (Charlesworth, 1992), with consideration of evolution being almost incidental in the second half of the century (with some notable exceptions, such as Bowlby's (1969) theory of attachment). For the last two decades, though, there has been a renewed interest in the relations between development and evolution, and its potential explanatory power in both biology

and developmental psychological science. Evolutionary developmental biology (evo-devo), in biology (Carroll, 2005; West-Eberhard, 2003), and evolutionary developmental psychology (EDP), in developmental psychology, have played leading roles in this reunion.

In this chapter, I provide a succinct overview of EDP by answering five main questions: 1) what is EDP and where does it come from?; 2) what is new in EDP in comparison with other evolutionary approaches to behavior?; 3) what are some core tenets and/or theoretical assumptions of EDP?; 4) how has EDP contributed to a better understanding of human development and evolution?; and 5) what are some of the significant challenges for EDP in the future?

WHAT IS EDP, AND WHERE DOES IT COME FROM?

EDP is a multidisciplinary perspective that focuses on the study of human development

from an evolutionary point of view. In a more formal and specific manner, EDP has been defined as ‘the application of the basic principles of Darwinian evolution, particularly natural selection, to explain contemporary human development’ (Bjorklund and Pellegrini, 2002: 4), entailing ‘the study of the genetic and ecological mechanisms that govern the development of social and cognitive competencies common to all human beings and the epigenetic (gene-environment interactions) processes that adapt these competencies to local conditions’ (Geary and Bjorklund, 2000: 57). In practice, this means that EDP is mostly interested in the evolutionary analyses of the human life span, with a particular emphasis on prenatal development, infancy, childhood, and adolescence, as well as the evolved parenting behaviors required to care for the developing child (Hernández Blasi et al., 2008). Therefore EDP aspires to be simultaneously: 1) a metatheory, or general psychobiological framework, for contemporary developmental psychology; 2) a source of new and challenging research questions and hypotheses; and 3) a cradle of insightful interpretations and organizing principles for extant and forthcoming knowledge on human development (Bjorklund and Ellis, 2014; Ellis and Bjorklund, 2012; Hernández Blasi and Bjorklund, 2003; Hernández Blasi et al., 2003).

More recently, EDP has become increasingly interested, following evo-devo rationale and guidelines (West-Eberhard, 2003), in the potential role of human development on human evolution (Bjorklund, 2006, 2018). In this sense, EDP can be also considered as an approach engaged with both an evolutionary analysis of human development and an epigenetic analysis of human evolution, conducive to understanding better both how human development has been shaped by evolution, and how human evolution might have been shaped by human development.

Science is a collective enterprise, and this is no less true for EDP. However, from

an epistemological point of view, EDP in its present form is chiefly the result of the efforts of David Bjorklund and his colleagues during the last two decades, with special importance of four seminal works: two papers published in 2000 in the influential academic journal *Child Development* (Geary and Bjorklund, 2000, and Bjorklund and Pellegrini, 2000, published in this order) and two books, *The Origins of Human Nature: Evolutionary Developmental Psychology* (Bjorklund and Pellegrini, 2002) and *Origins of the Social Mind: Evolutionary Psychology and Child Development* (Ellis and Bjorklund, 2005).

During the 1990s (and before), the terrain was extensively watered for the emergence of this approach. At least three different sources contributed significantly to shape EDP before it became EDP: 1) the arrival of evolutionary psychology as a new and challenging perspective of psychology (Barkow et al., 1992; Buss, 1989; Daly and Wilson, 1988); 2) the publication of several pioneering and influential books (e.g., Fishbein, 1976; Freedman, 1974; MacDonald, 1988) and papers (e.g., Belsky et al., 1991; Chisholm, 1993; Draper and Harpending, 1982; Geary, 1995) addressing important developmental issues from an unambiguous evolutionary perspective; and 3) the need for new metatheories and/or paradigms in developmental psychology after the waning of the cognitive revolution (see, e.g., Bjorklund’s (1997a) claims regarding cognitive development, after the decline of the dominance of Piagetian thinking in the field).

Obviously this short historical account of the origins of EDP does not pretend to be comprehensive, and certainly some important scholars, works, and issues contributing to EDP’s birth have been missed (see, e.g., Konner (2010: 37–38, 72–74) for a different, albeit complementary, account of EDP’s origins). However, I hope that overall this description provides a simple, but trustworthy, summary of the origins of current EDP.

WHAT IS NEW IN EDP IN COMPARISON TO OTHER EVOLUTIONARY APPROACHES TO PSYCHOLOGY AND BEHAVIOR?

One of the reasons that both evolutionary psychology and EDP have so powerfully caught the attention of researchers in psychology (or, at least, of a significant part of them) is the conviction that neither mainstream general psychology nor developmental psychology has taken seriously evolutionary theory for some time. This does not mean that evolutionary theory and approaches have been absent in psychological science all this time. On the contrary, many disciplines in psychology (e.g., animal psychology, comparative psychology) and those closely related to psychology (e.g., ethology, primatology) have been in touch with Darwinian theory since its inception and have often provided interesting and thought-provoking data. The ‘problem’, at least with developmental psychology, is that those disciplines have had a shallow influence on developmental psychology (Morss, 1990). This has been due, on the one hand, to the pervasive reluctance of mainstream developmental psychology to consider any perspective that, according to its view, could challenge its conviction on the central role of environment to improve children’s development and life (what has been called *meliorism*, see, e.g., Charlesworth, 1992). On the other hand, most of those disciplines have often not taken seriously development and, therefore, except for some cases (e.g., Bowlby’s (1969) attachment theory; Lorenz’s (1943) baby schema), evolution’s impact on thinking in developmental psychology has remained marginal (see, e.g., Hernández Blasi et al., 2003 and Hernández Blasi and Bjorklund, 2003 for more detailed analyses of the lack of influence of evolutionary theory on developmental psychology, as well as for a thorough description of the ups and downs of traditional evolutionary disciplines).

EDP is an evolutionary approach that specifically focuses on the development of human psychology and behavior, maintains a multidisciplinary perspective (e.g., primatologists’ works such as Call and Carpenter, 2003; and Maestriperi and Roney 2006; and comparative developmental psychological works such as Rosati et al., 2014, have been published in journals’ special issues on EDP), and subscribes, as we will see in more depth in the next section, to an epigenetic point of view about development and evolution. Moreover, EDP proposes the production of developmental research with humans of all ages, driven by evolutionarily informed hypotheses, whose results are analyzed and explained according to evolutionarily informed tenets. In this way, EDP is different from other evolutionary approaches, such as primatology and ethology, which do not necessarily focus on humans or on development. For the last decades yet, some primatology groups have been incorporating a comparative perspective, contrasting non-human primates’ with children’s performance on the same tasks types (see, e.g., Sánchez-Amaro et al., 2017, 2019, for some of the latest published works), and the results of this research are valuable for contemporary developmental psychologists.

EDP also is different from other evolutionary perspectives – such as evolutionary psychology that, although open to developmental issues and rejecting genetic determinism (Buss and Reeve, 2003), focuses its work on adults and often experiences a difficult time when dealing with the issue of plasticity, which is central to EDP’s view of development and evolution (see Hernández Blasi et al., 2008, for a more thorough contrast between evolutionary psychology and EDP). Problems dealing with plasticity have also challenged sociobiology and mainstream ethology, although in the latter case there have been some recent claims in favor of pushing ethology beyond its classical standpoints,

making it more compatible with the study of human development (Bateson, 2015).

WHAT ARE SOME OF EDP'S CORE TENETS/THEORETICAL ASSUMPTIONS?

EDP has typically sustained along its short history as a perspective a series of broad assumptions and/or epistemological tenets. Some of them are summarized in Table 3.1, and in the next sections I progressively unfold them and describe them succinctly.

Natural Selection Works at All Stages of Development, Not Just on Adulthood

One of the primary assumptions of EDP is that natural selection does not only operate on adulthood, but across all stages of development and, as in all species featured by a particularly long period of immaturity before reproduction, especially on the early stages of development. From an evolutionary point of view, development is a bridge that connects two shores: conception and reproduction (Bjorklund et al., 2015), whose crossing is mandatory in order to reproduce. In the case of humans, this bridge is exceptionally long, dangerous, and resource-demanding. First, it is long because the juvenile period in humans takes about 15 years, with females in

hunter-gatherer societies having their first births when they are about 18–20 years old, whereas, for example, the juvenile period in chimpanzees takes ‘only’ 8 years, with chimpanzee females reproducing approximately at 13–15 years old (Kaplan et al., 2000; Poirier and Smith, 1974). Second, it is dangerous because the probability of dying before reproducing has been high in our history as species. Namely, in hunter-gatherer societies, mortality rates in the first year of life have been estimated to be about 25%, with almost a 50% mortality rate before reaching adolescence (Volk and Atkinson, 2013). Third, it is resource-demanding because, in humans, given the degree of immaturity at birth and the long period of dependence on others, parental investment, and even in-group investment, is particularly large (Hrdy, 2009; Trivers, 1972). No wonder that the African proverb ‘It takes a village to raise a child’ has become a popular way to point out this circumstance.

The idea that natural selection acts at all stages of development is not new in evolutionary biology. In fact, British zoologist Peter Calow in the 1980s, and seemingly even Francis Balfour, one of the founders of evolutionary embryology a century before, suggested that natural selection could act upon any life cycle of multicellular organisms (Hall, 2012). We should notice, as EDP does, that in species with a long developmental period all evolutionarily-influenced characteristics in the phenotype of adults develop, and this requires a proper understanding of

Table 3.1 Some basic assumptions of evolutionary developmental psychology (adapted from Bjorklund and Pellegrini, 2002; Bjorklund et al., 2015; Hernández Blasi et al., 2008)

1. Natural selection works at all stages of development but especially during early development.
2. An extended childhood is needed in which to learn the complexities of human social communities.
3. Many aspects of childhood serve as preparations for adulthood and were selected over the course of evolution, termed *deferred adaptations*.
4. Some characteristics of infants and children were selected to serve an adaptive function at specific times in development and *not* as preparations for adulthood, termed *ontogenetic adaptations*.
5. Infants and children show a high degree of developmental plasticity and adaptive sensitivity to context.
6. All evolved characteristics develop via continuous and bidirectional gene-environment interactions that emerge dynamically over time.

function and performance, examining not only the functioning of these characteristics in adults, but also their correspondent ontogeny.

But what is entailed by assuming that natural selection works at all stages of development, particularly at early stages? And why, evolutionarily speaking, is human development so long? One of the obvious consequences of assuming the action of natural selection along development is that there must be adaptations along with it, that is, specific evolutionary solutions for the recurrent problems that infants and children have had to face in the environment of evolutionary adaptedness. And, although we do not know for certain, it makes sense to presume that two important problems for infants and children ancestrally were surviving and group living (the latter meaning the need to understand the complexities of social human groups' functioning in order to successfully join them). Therefore, one of the challenges of EDP is identifying the adaptations that natural selection might have shaped over evolutionary time to solve these two problems.

Regarding to the length of development, we do not have available a definitive answer. But it is not unwise to anticipate, on the one hand, that, from an evolutionary perspective, natural selection would have not shaped something as potentially costly as a developmental period not less than 15 years before reproduction (i.e., with a high possibility of dying before reproducing) unless there were also some equally significant benefits associated with extended development. In the end, as James Chisholm and his colleagues point out, development is itself an adaptation for reproduction, and 'adaptations for survival, growth and development evolved because they had the effect of enabling complex organisms to reproduce' (Chisholm et al., 2005: 95). On the other hand, comparative studies show, first, that species with a longer developmental period often have a larger brain (in comparison to body size) and more extended and complex social systems

(Joffe, 1997). Second, they suggest that the adaptive benefits of delayed maturation come in terms of more refined social, cognitive, and physical skills, conducive to better survival and reproduction in adulthood (Mayr, 1974). Therefore, it seems tenable to argue that, in humans, the benefits of an extended childhood might have to do with the need to learn the complexities of human social communities. This is precisely another of the core EDP assumptions (Bjorklund and Hernández Blasi, 2005; Bjorklund and Pellegrini, 2002; Geary and Bjorklund, 2000).

Developmental Adaptations were not All Selected as Preparation for Adulthood

Buss et al. (1998) some time ago made useful distinctions among adaptations, by-products, and noise, emphasizing the idea that only adaptations are the result of natural selection. They included an informative example about the umbilical cord, pointing out that the umbilical cord is an adaptation that solves the recurrent problem of nutrients supply and removal of wastes for the developing embryo or fetus during prenatal life. However, the belly button is not an adaptation, it has no function at all, but is a by-product, that is, a collateral effect of having an umbilical cord. Finally, the shape of the belly button is accidental or random, such that it qualifies as noise.

Following the same schema, EDP proposes two types of developmentally relevant adaptations – deferred adaptations and ontogenetic adaptations – and suggests also the existence of some other non-adaptive developmental outcomes akin in (non) function to those described by Buss et al. (1998): ontogenetic by-products, and ontogenetic-noise (Bjorklund and Pellegrini, 2000; Hernández Blasi and Bjorklund, 2003). An ontogenetic adaptation (Bjorklund, 1997b; Oppenheim, 1981) is a successful solution shaped by natural selection across evolutionary history to

solve a specific recurrent problem at only a certain moment in developmental time, after which it disappears. Hatching mechanisms in birds, the placenta and umbilical cord in mammals, as well as many human infant reflexes such as rooting, sucking, and the palmar-grasping reflex are examples of ontogenetic adaptations. In a way, an ontogenetic adaptation is a disposable adaptation that can be more often found when there is a dramatic environmental change, as happens, for example, with amphibian metamorphoses, where the change from an aquatic to a terrestrial environment makes necessary some temporary adaptations (gills) while living in the aquatic habitat (Hernández Blasi, 2018). Some drastic environmental changes are also involved in many bird and mammal species when switching from their prenatal to their post-natal environment. In humans, many post-natal adaptations are related to capturing adults' attention and/or guaranteeing adults' support at a time of particular dependence and vulnerability (e.g., attachment behaviors such as smiling, crying, and raising arms). Importantly, they often require a corresponding adaptation from the adult (e.g., adults' sensitivity to some body and facial cues, like those involved in the 'baby schema' described by Lorenz, 1943; or infant-directed speech, that type of speech displayed by an adult when addressing an infant, see, e.g., Fernald, 1992).

In contrast, a deferred adaptation (Hernández Blasi and Bjorklund, 2003) is a naturally selected solution to a recurrent problem faced by the developing organism along our species' evolutionary history at a certain moment in developmental time that simultaneously prepares it for adulthood. In a sense, this would be an ontogenetic adaptation that provides both some present and near-future adaptive benefits. A typical example of deferred adaptation is symbolic play, which helps preschoolers learn about their immediate environment, but also feeds them with critical knowledge about the world they will have to join as adults (Pellegrini

et al., 2007). Another good candidate for a deferred adaptation is Theory of Mind, an essential mechanism for human social relations. Someone with a Theory of Mind is able to proficiently 'read others' minds', that is, understand knowledge about people's mental states (e.g., their beliefs, feelings, motives), which allows them to predict their own and others' behavior. This mechanism begins to be available for children when they are about 4–5 years old (Perner et al., 1987), and it probably helps children to adapt to the increasingly out-of-family social world following weaning (that in traditional societies takes place about age 3 years), as well as to learn more about other's people minds and motives, something that will be valuable for their future social life as adults. Deferred adaptations are more apt to occur when the environmental features at the moment they arise in development are comparable to the environmental features in adulthood, keeping continuously active instead of disappearing (Hernández Blasi and Bjorklund, 2003).

Development and Evolution are Epigenetic Processes

'Plasticity, or environmental responsiveness, is a universal property of living things' (West-Eberhard, 2003: 34), and, accordingly, EDP assumes this must be taken into account to understanding the effects of evolution on human development (and to understanding the course of human evolution, as well). As Chisholm et al. (2005) describe, organisms organize themselves based on two sorts of information: 'old' information, provided by genetics, with DNA constituting an a priori knowledge of the environment of ancestors, and 'new' information, provided by the current environment. Obviously, as Chisolm et al. indicate, there might be also some 'new' genetic information from time to time in the form of mutations and/or recombinations that can, now and then, be useful. Development is the period of time when the

two types of information are going to meet, merge, and finally express in a specific phenotype.

It makes sense therefore that EDP assumes that all evolved characteristics become embodied in a certain space (i.e., ecological and sociocultural conditions) at a certain time (i.e., individual development), developing via continuous and bidirectional gene-environment interactions that emerge dynamically over time. This is what epigenetics is about. A simple example of this is language development. Language is an adaptive trait in humans that, depending on where someone is born, is expressed in one or another of the approximately 6,000 languages spoken across the world. Moreover, depending on the specific conditions of individual development, language may exhibit different paces and patterns (with some common disabilities, like stuttering, dysphagia, articulation disorders, and tongue curling being either favored or not removed by natural selection; see, e.g., MacWhinney, 2005).

From an EDP perspective then, it is assumed that there is no one-to-one correspondence between genotype and phenotype, and that adaptations can be expressed within an evolved norm of reaction (Del Giudice, 2015; Hill and Kaplan, 1999). Children cannot anticipate what type of environment they will be born into, so their adaptations are flexible enough to provide different options. This is reflected by the concept of conditional adaptations:

evolved mechanisms that detect and respond to specific features of childhood environments, features that have proven reliable over evolutionary time in predicting the nature of the social and physical world into which children will mature, and entrain developmental pathways that reliably matched those features during a species' natural selective history (Boyce, and Ellis, 2005: 290).

For example, Belsky et al. (1991) proposed that children make an (implicit) assessment of their environmental conditions during their first 5 to 7 years of life in a way that, if they suffered from harsh parenting,

conflictual family relationships, and/or insecure attachment, they would follow a so-called fast life history strategy. This strategy includes earlier pubertal timing and sexual debut, with less stable pair bonding, more children, and less parental investment. Conversely, if such an (implicit) assessment of the early rearing environmental conditions during those years depicted a more positive perspective about both their present and future conditions, children would follow a so-called slow life history strategy. This slower strategy involves a slower maturation, with a later arrival of puberty, fewer mates, more stable pair bonds, fewer offspring, and more parental investment per child. Almost 30 years later, the essence of these predictions have been empirically confirmed (see, e.g., Belsky, 2012; Belsky et al., 2012, but also Barbaro et al., 2017a, 2017b, challenging this perspective).

The phenomena of plasticity, flexibility, and epigenetics do not mean that 'everything is possible' in development and evolution (but see, e.g., Witherington, and Lickliter, 2016, for a more ambitious view of epigenetics). In fact, EDP assumes that development is constrained by genetic, environmental, and cultural factors. It explicitly adopts a 'soft' version of Developmental Systems Theory (DST), based on the theorizing of Gilbert Gottlieb and others (Gottlieb, 1991, 1992; Oyama, 2000). Accordingly, EDP considers that infants are not blank slates, and that both infants and children are biased or prepared by natural selection to selectively process evolutionarily relevant information in the realms of physics (things), psychology (people), and biology (life). However, prepared is not preformed (Bjorklund, 2003) and, in agreement with DST tenets, EDP postulates that every pattern of human behavior and cognition develops in a dialectic manner, as a consequence of a continuous and bidirectional gene-environment interaction over time (Bjorklund, 2016; Bjorklund, and Hernández Blasi, 2005; Bjorklund and Pellegrini, 2002). As Gottlieb and associates have shown

(see, e.g., Gottlieb, 1975, in ducks), what we call a species-typical pattern of development is the outcome of the interaction of a species-typical genome with a species-typical environment over time. In the case of human development, a species-typical environment may consist of, for example, a 9-month intrauterine gestation, lactation after birth, gravity effects over the body, light, air, regular human linguistic stimulation, and gentle touch or caress, among many others. Significant alterations in the species-typical genome or the species-typical environment yield species-atypical patterns of development in humans, as well as in other species.

HOW HAS EDP CONTRIBUTED TO A BETTER UNDERSTANDING OF HUMAN DEVELOPMENT AND EVOLUTION?

According to some scholars (e.g., Geary, 2006), since its inception EDP has been reshaping developmental psychology as an evolutionary informed and multidisciplinary domain. In the end, development is a biological concept (Bjorklund, 1997a) that requires examination from different approaches and levels of analysis, and developmental science is one of the life sciences. However, it is also true that developmental psychology, as a whole, has been slower than other psychological disciplines in (re)incorporating evolutionary theory. Apparently this has been due, in part, to the (false) belief that evolutionary thinking is anchored in genetic determinism and that it operates only at a species level (i.e., not at an individual level), making it untenable in practice to be applied successfully to sociodevelopmental relevant problems (Ellis and Bjorklund, 2012).

In the last decades, there has been almost no developmental psychology theme that has not been approached from an EDP perspective. Two edited books (Burgess and MacDonald, 2005; Ellis and Bjorklund, 2005) present collections of the classical

research areas, and two evolutionary oriented textbooks document the evolutionary basis of every topic (Bjorklund and Hernández Blasi, 2012; Smith et al., 2015). Both are testimony to the impact of EDP. For example, not pretending to be exhaustive in the listing (a full account of them can be found in the above-mentioned books), there has been evolutionary developmentally informed research on: 1) *physical development*: pubertal timing, incest avoidance mechanisms, brain organization, stress response; 2) *cognitive development*: infants' core knowledge (e.g., face processing, perceptive bias, understanding of causality), theory of mind, tool use, play (e.g., rough and tumble play, fantasy play), memory, inhibitory control, spatial cognition, adaptive role of cognitive immaturity, folk knowledge and academic learning, language (e.g., infant-directed speech), understanding of animal behavior, imitation and social learning; 3) *socioemotional development*: aggression, social dominance and peer relations, cooperative and helping behaviors, moral development, emotions, attachment, adolescents' romantic relations, sex differences; 4) *parenting and family behaviors*: parents–children relations, siblings relations, maternal investment, paternal investment, grandparents investment, effects of parental styles on reproductive strategies, differential susceptibility to rearing conditions, out-of-family socialization processes (e.g., role of peers; cooperative breeding); and 5) *applied issues*: pregnancy sickness, premature early stimulation, teenage pregnancy, effects of father absence, infanticide, child abuse, sibling rivalry, family violence, peer rejection, adolescent risky behaviors, school behaviors and disabilities.

There has also been important EDP theorizing efforts, applying, on the one hand, classical theories/models in evolutionary biology (e.g., inclusive fitness theory, Hamilton, 1964) to improve understanding of developmental issues, and, on the other, the generation of new theories (e.g., resource control theory, Hawley, 1999). In Table 3.2,

Table 3.2 Selection of theories valuable for and/or proposed from an evolutionary developmental psychology perspective

Inclusive fitness theory (Hamilton, 1964)
Attachment theory (Bowlby, 1969)
Life history theory (e.g., Gadgil and Bossert, 1970; Pianka, 1970)
Parental investment theory (Trivers, 1972)
Parent-offspring conflict theory (Trivers, 1974)
Psychosocial acceleration theory (Belsky et al., 1991)
Developmental systems theory (e.g., Gottlieb, 1992; Oyama, 2000)
Group socialization theory (Harris, 1995)
Resource control theory (Hawley, 1999)
Theory of developmental adaptive plasticity (West-Eberhard, 2003)
Biological sensitivity to context theory (Boyce and Ellis, 2005)
Adaptive calibration model (Del Giudice et al., 2011)

I present a selection of some of the more relevant theories. Conversely, in Table 3.3, I present a selection of topics approached in recent times from an EDP perspective. Some of them are ‘old’ topics (e.g., effects of early rearing stress), but research in the last few years has produced significant advances on these classic topics; other topics are new in the field (e.g., developmental psychopathology; mathematical modeling of early-life effects). Many accomplishments from the EDP perspective during recent years have come hand in hand with *life history theory* application (see, e.g., Bjorklund et al., 2015; Del Giudice et al., 2015).

Life history theory is a framework within evolutionary biology that emphasizes that living beings make decisions in the allocation

of their limited energy and time across the lifespan. These allocations can be assigned to competing sources of inclusive fitness (e.g., growth, body maintenance, reproduction), making a difference between (and within) species regarding their own individual life course. For example, resources allocated to early reproduction cannot be allocated simultaneously to body maintenance and longevity, although both types of investments are worthwhile for individuals’ inclusive fitness (i.e., current vs. later reproduction trade-off). In the same vein, resources allocated to raising a few offspring constitutes a different strategy than allocating the same amount of resources to raising, for example, 10 offspring, given that in the latter case, there will necessarily be less investment per offspring

Table 3.3 Some topics approached in recent times from an evolutionary developmental psychology perspective

Bullying (e.g., Hawley, 2015; Hawley and Williford, 2015; Volk et al., 2012, 2014)
Cognitive babyiness (Bjorklund et al., 2010; Hernández Blasi et al., 2017)
Cooperation (e.g., Tomasello, 2009)
Developmental adaptation to stress (e.g., Ellis and Del Giudice, 2019)
Developmental psychopathology (e.g., Del Giudice and Ellis, 2016)
Differential susceptibility to environment (e.g., Ellis et al., 2011a)
Effects of early rearing stress (e.g., Belsky et al., 2012; Simpson et al., 2012)
Mathematical modeling of early-life effects (e.g., Nettle et al., 2013, 2014)
Middle childhood (e.g., Del Giudice, 2014b)
Personality development (e.g., Del Giudice, 2019a)
Risky adolescent behavior (e.g., Ellis et al., 2012)
Sex differences in (cognitive) vulnerability (e.g., Geary, 2015, 2017, 2019)
Sex differences in attachment patterns (e.g., Del Giudice, 2009, 2019b)
Social learning (e.g., Nielsen, 2012, 2018; Tomasello, 2019)

(i.e., quality vs. quantity offspring trade-off). These resource allocation decisions reflect or express an organism's life history strategy. These strategies can be successful (or not) depending on a series of variables, such as, for example, ecological conditions (e.g., mortality-morbidity rates in the current environment or the potential availability of resources, such as food).

In humans, these trade-offs have been shaped by natural selection over evolutionary time, and have selected for a suite of traits involved in the human growth pattern, such as, for example: time of gestation, age of weaning, juvenile mortality profiles, age at maturation, adult body size, fertility rates, senescence, menopause, and life-span length (Hill and Kaplan, 1999). In addition, life history strategies are important for understanding human behavior in domains such as, for example: risk-taking, exploration, mating, aggression, self-regulation, and caregiving (Del Giudice et al., 2015).

Life history theory did not go unnoticed by the pioneers of EDP research (e.g., Belsky et al., 1991; Chisholm, 1993, 1996; MacDonald, 1997; Ellis, 2004), who had already incorporated this theory into their respective realms. However, it has not been until the last decade that life history theory has started to show its ability and potential to provide powerful insights into the interrelationships of evolution and development. One of the more significant topics for EDP has been the fleshing out of psychosocial acceleration theory (Belsky et al., 1991), which has shed light on the evolutionary basis of topics such as attachment types and sex differences, the effects of early stress on reproductive strategies, differential sensitivity to context, girls' pubertal timing, and adolescents' risk behaviors.

Effects of Early Rearing Stress

Belsky et al. (1991) proposed that a stressful environment during early childhood signaled the existence of stressful ecological

conditions, which in turn would favor a faster life history strategy, that is, a reproductive strategy tied to earlier physical maturation and sexual debut, and higher investment in mating than in parenting. Over the past decade, Ellis et al. (2009) have unpacked what a stressful environment might mean following life history theory and characterizing it on the basis of two dimensions: environmental harshness, defined as 'the rates at which external factors cause disabilities and death at each age in a population' (Ellis et al., 2009: 206), and environmental unpredictability, defined as 'the rates at which environmental harshness varies over time and space' (Ellis et al., 2009: 207). Then, predictions from psychosocial acceleration theory were tested in a series of longitudinal studies (Belsky et al., 2012; Simpson et al., 2012), with environmental harshness measured in terms of SES level and/or income-to-need ratio in the first 5 years of life and environmental unpredictability measured by means of a series of variables such as residential changes, parental transitions (e.g., divorce), and parental job changes in the first 5 years.

In sum, evidence has been favorable to Belsky et al.'s proposal, indicating, for example, that harsh and unpredictable environments in the first 5 years of life predict sexual behavior at age 15, although mediated by maternal depression and sensitivity (Belsky et al., 2012). Simpson et al. (2012) found that the best indicator of sexual and risky behavior (aggressive and delinquent behaviors) at age 23 was an unpredictable environment during early childhood (ages 0–5), regardless of environmental harshness in general or an unpredictable environment during later childhood (ages 6–16). In this vein, they suggested that the first 5 years of life might be a sensitive period for the assessment of environmental unpredictability. In addition, James et al. (2012) showed a strong relationship between stressful familial and ecological conditions and an earlier sexual debut and greater sexual risk taking in both boys and girls, with this

relationship partially mediated by pubertal maturation in girls.

Differential Sensitivity to Environment

Psychosocial acceleration theory was complemented later with a proposal about children's differential susceptibility to environmental influences. This proposal suggested that the effects of early environmental conditions on children's behavior were mediated by how sensitive (or not) a child was to environmental conditions (Belsky, 1997a, 1997b). Accordingly, more sensitive children would be more easily influenced by both negative and positive rearing environmental conditions, whereas less sensitive children would be less easily influenced by either of them. This would make sense from an evolutionary perspective given the uncertainty of rearing conditions both in ancient and contemporary times: a wider range of children's susceptibility to rearing conditions would thus enhance species reproductive fitness before, for example, the unknown variations in parental investment.

Later, biological sensitivity to context (BSC) theory (Boyce and Ellis, 2005) argued that what is behind evolved susceptibility differences are individual variations in activity of the stress response system. More specifically, BSC was defined in terms of neurobiological susceptibility, as measured by heightened autonomic or adrenocortical reactivity to environmental challenge (Ellis et al., 2011a). That is, subjects with a higher neurological susceptibility would be those more biologically sensitive to both the costly and the beneficial features of the environment. Some recent research seems to indicate that indeed this is the case (Ellis et al., 2011b; Gibbons et al., 2012).

The third link in this chain of evolutionary-developmental life history informed theories is the adaptive calibration model (ACM), an extension of BSC theory

(Del Giudice et al., 2011; Ellis et al., 2017), which focuses on individual differences in stress responsivity. Namely, it specifies four prototypical optimal stress patterns in response to different levels of contextual stress: 1) a sensitive pattern, in response to safe, low stress, environments; 2) a buffered pattern, in response to moderate stress; 3) a vigilant pattern, in response to dangerous unpredictable environments; and 4) an unemotional pattern, in response to severe traumatic stress. Preliminary data confirm, at least partially, these differential patterns of stress response (Del Giudice et al., 2012).

Adolescents' Risky Behaviors

One of the many positive consequences of the extensive theorizing and research around the seminal Belsky et al. (1991) work in the last few decades has been a better understanding of adolescents' behavior and development, as well as of some of the factors associated with adolescents' risky behaviors (e.g., aggression, drug use, promiscuity, reckless driving). Conventional studies in developmental psychology have identified, for example, how unfortunate outcomes can sometimes derive for girls from early pubertal timing, especially if unnoticed and/or without an additional parents' attention and support (Mendle et al., 2007). In addition, an evolutionary approach led us to understand better, as we have seen in previous sections, why some girls may experience an earlier pubertal timing than others. In a similar vein, an evolutionary approach to risky adolescent behavior can be illuminating and therefore contribute to a more optimal intervention and prevention than when the classical developmental psychopathology model is used alone. This model tends to consider the problems associated with adolescents' risky behaviors like maladaptive, caused primarily by personal vulnerabilities and/or detrimental environmental conditions during early rearing. However, an evolutionary approach focuses

more on the potential function of adolescence in human life span as well as on the potential adaptive benefits that risky behaviors can have for the adolescents who exhibit them. This is exactly what it is reflected in Ellis et al. (2012), who pointed out five critical evolutionary insights on risky adolescent behavior. On the basis of these insights, they suggest new directions in research and provide specific recommendations for social policy and practitioners.

Ellis et al. (2012: 601) indicate, on the one hand, that ‘from an evolutionary perspective, a major function of adolescence is to attain reproductive status – to develop the physical and social competencies needed to gain access to a new and highly contested biological resource: sex and, ultimately, reproduction’. Not surprisingly, this is the developmental stage, jointly with early adulthood, where both sexual promiscuity and sexual competition reach the highest level across life (Weisfeld and Coleman, 2005). In this context, risk taking should be seen as a signaling behavior serving to the adaptive function of establishing social status, prestige, and dominance among peers (distinction between function and form is essential for any evolutionary analysis of development, particularly if referred to potentially unpleasant or antisocial outcomes; see, e.g., Hawley, 2014). On the other hand, Ellis et al. (2012) unfold the evolutionary reasons to understand why risk taking behaviors during adolescence are more frequent in males than females (an explanation linked to Trivers’ theory of parental investment), in individuals who have experienced both harsh and unpredictable environmental conditions during early rearing (an explanation linked to a faster life history strategy profile; see, e.g., James et al., 2012; Simpson et al., 2012) and in environments quite different from those more typical in our ancient evolutionary past.

The latter would be the case of current adolescents who relate mostly with same-age peers, in comparison to adolescents in hunter-gatherer societies, who relate more often with

people of all ages, including younger children and older adolescents and/or adults, who apparently experience a significant reduction of same-age aggression and conflict (Gray, 2011; Hewlett and Lamb, 2005). Ellis et al. (2012) suggest that the daily involvement of adolescents in hunter-gatherer subsistence and nurturance tasks with adults and young children respectively would provide a natural scenario for peer status competition and assessment, where both parental skills and productive skills would become more visible to others, diminishing the need of risky behavior exhibition.

Sex Differences in Attachment

Another interesting outcome derived from Belsky et al.’s (1991) proposal in recent times has been the focus on sex differences in attachment. Attachment theory has been often used as an example of how fruitful the interplay between proximal and distal approaches can be for better understanding developmental issues (see, e.g., Simpson and Belsky, 2016, for a review). However, it has been recently pointed out that attachment theorizing has focused more on survival (i.e., keeping a caregiver within a close distance to secure protection from potential dangers) than on reproduction. Moreover, it has emphasized an intrapsychic cost-benefit analysis (e.g., the idea that children adopt an avoidant attachment pattern to prevent being rejected and stressed by uncommitted parents) than an evolutionary one and in practice has been sex-neutral (i.e., assuming that attachment process works similarly for the sexes across the lifespan) (Del Giudice, 2019b; Del Giudice and Belsky, 2010).

Once more, psychosocial acceleration theory provided insights into the effects of attachment styles on reproductive strategies. As Belsky et al. (1991) suggested, the type of attachment experienced during the first 5–7 years is a good indicator for children of the quality and predictability of the rearing

environment. Hence a secure attachment would be associated with a slow life history strategy, characterized by slower maturation, emphasis on long-term relationships, and more parental investment in fewer offspring. Conversely, an insecure attachment would produce a faster reproductive strategy, characterized by an earlier maturation, an emphasis on short-term bonds, and lower parental investment in more offspring.

Del Giudice (2009) proposed an evolutionary model that incorporated into Belsky et al.'s (1991) scheme sex differences in attachment. Del Giudice argued that sex differences in attachment have adaptive significance, arising during middle-childhood (6–11 years old), mainly because of endocrine functioning (adrenarche). In the case of young boys with an insecure attachment, they would become mostly insecure-avoidant during middle-childhood; but in the case of young girls, attachment would become mostly insecure-anxious if stress conditions at that time were moderate, or insecure-avoidant if stress conditions were high. According to Del Giudice, these patterns would extend to adulthood attachment patterns, with adult romantic relations being dominated by avoidance in males, and by anxiety/ambivalence in females.

Overall, empirical evidence on Del Giudice's proposal has been mixed. Although Del Giudice presented some empirical proofs in his seminal paper in its favor, a more thorough review of that evidence, as well as a complementary meta-analysis, revealed that only studies based on doll-play tasks, but not other types of studies (e.g., observational studies), produced results that were consistent with his predictions (Bakermans-Kranenburg and van IJzendoorn, 2009). New evidence shows that, in general: 1) no sex differences in attachment styles are found either in infancy or in early childhood; and 2) there are robust sex differences in attachment styles during middle-childhood, mirroring those found in adulthood, in North America, Europe, Israel, South Korea, and

China (with some puzzling results regarding Chinese adulthood pattern; Del Giudice, 2019b). It remains unclear yet if middle-childhood is the period of emergence (instead of a period of intensification) of these sex differences (Gloger-Tippelt and Kappler, 2016), as well as the specific role played by sex hormones, genetics, and children's experience with caregivers and social learning. This research is further testimony to how an EDP approach can both provide new insights into human development and promote creative and challenging research in the field.

Personality and Psychopathology Development

Other innovative evolutionary developmental proposals linked to life history theory address personality and psychopathology development. Both domains were referenced by Belsky et al. (1991). Indeed, these authors hypothesized, for example, that an opportunistic-exploitative personality, as well as externalizing behaviors such as aggression, impulsivity, and noncompliance before adulthood, on one side (more frequent in boys), and internalizing behaviors like sadness, depression and/or social withdrawal, on the other (more frequent in girls), would be a consequence of early stressful rearing conditions, preparing the child for a fast life history strategy. From their perspective, these should not necessarily be perceived as 'problem behaviors', in spite of their personally and socially dysfunctional outcomes, but rather as adaptive responses to certain ecological conditions that guide and favor the more suitable reproductive strategy. More recently it has been suggested, for example, that personality traits like agreeableness, conscientiousness, and honesty-humility are more consistent with a slow life history strategy, whereas other traits linked to extraversion and openness to experience (e.g., sensation seeking) are more related to a fast life history strategy (see, e.g., Del Giudice,

2019a; Del Giudice et al., 2015). Conversely, regarding psychopathology, it has been proposed, for example, that some mental disorders such as psychopathy and antisocial personality disorder (more typical in males) and borderline personality (more typical in females) would fit better with a fast life history strategy (Del Giudice, 2014a; Del Giudice and Ellis, 2016).

Bullying

Bullying is another topic that has been approached from an EDP perspective in recent years. Traditional views of peer aggression assumed that bullies are children and adolescents with limited or impaired social skills that, as a consequence, become systematically aggressive in their interactions. In other words, bullying has been considered the outcome of a maladaptive development and/or education (Smokowski and Kopasz, 2005). However, the incorporation of an evolutionarily informed perspective in the field of social peer relations provides complementary, and sometimes alternative, views. For example, Hawley and her colleagues indicate that peer interactions can be usefully analyzed from a social dominance and power perspective. According to her Resource Control Theory (see, e.g., Hawley, 1999, 2015), children's interactions at all ages should be examined in terms of individuals who use different (effective) strategies to get access to resources (e.g., toys, other's attention and support). Some children use only one strategy (prosocial controllers, coercive controllers); some use two strategies, using each contingently depending on the context (bistrategic controllers); and some, none (noncontrollers). From this perspective, it is not assumed either that all prosocial behaviors are altruistically motivated, or that all coercive behaviors are maladaptive (indeed, bistrategic controllers, who can be very aggressive with others, are among those with higher

reputations among their peers). Overall, these strategies are alternative forms to serve the same function (Hawley, 2014; see also Hawley, 2015, 2016, for a collection of misunderstandings on the nature of social peer interactions).

When it comes to understanding bullying prevention and intervention, this evolutionary account can make an important difference. For example, Volk et al. (2012) note that bullying behaviors have been found across all present and past human societies and cultures, as well as in many non-human species. They also consider that adolescent bullying, in spite of the serious damage caused to the victims, provides bullies with some real material and non-material benefits (e.g., reputation among peers; access to mates). Therefore, they argue that adolescent bullying is produced by psychological adaptation. Of course, they recognize that bullying is a complex and heterogeneous phenomena where no one-size-fits-all explanation and/or stereotyped intervention is tenable and/or advisable. For example, they argue that, although some bullies have some social processing information deficits, this is not the case for most.

More recently, following this evolutionary approach, Volk et al. (2014: 328) redefine bullying as 'aggressive goal-directed behavior that harms another individual within the context of a power imbalance'. They consider that this definition includes the three key issues that need to be taken into account to understand bullying: 1) it is a goal-directed behavior (aimed at some implicit/explicit benefits); 2) it arises in the context of an imbalance of power between the bully and the victim; and 3) it implicates a repeated infliction of harm to another, where harm = frequency x intensity. According to this framework, these and other authors (e.g., Hawley, 2015; Hawley and Williford, 2015) propose the application of a cost-benefit analysis approach bullying intervention. For example, they recommend interventions that increase the costs to bullies for behaving aggressively with others

(e.g., training parents to identify bullying behavior and to apply effective discipline strategies; training peers for assertive standup before potential bullies) and/or that provide bullies with alternative ways to get the benefits with lesser costs (e.g., promoting among male bullies the practice of sports in which competing aggressively but legally can show their skills and/or strength before others).

Cooperation and Social Learning

Evolutionary developmentally informed research emphasizing the potentially adaptive nature of some psychopathological and/or antisocial children and adolescents' behaviors does not mean that prosocial, cooperative, behaviors are not also part of human nature. In fact, the idea that humans, in general, and children, in particular, have been shaped by natural selection toward selfish behaviors and motivations is a common misconception about evolutionary theory (Hawley, 2016). On the contrary, evolutionarily informed research during the last decades, comparing human children and non-human primate development and often incorporating cross-cultural data, has shown that humans are not only a social species, but also a cooperative, prosocial one (Bjorklund et al., 2015). Children exhibit prosocial behaviors, such as helping, beginning early in development, not driven by parents' rewards, but instead mediated by empathy; these behaviors have also been found in elementary forms in chimpanzees, particularly the enculturated or human-reared ones (Tomasello, 2009, 2019). In addition, cooperation in humans is critical for survival, especially concerning aspects such as tasks distribution and coordination, and the transmission of culturally generated information between individuals and generations (Nielsen, 2012). In this vein, recent research indicates that children from different cultures are well equipped with developmental adaptations, such as over-imitation (copying

painstakingly the behaviors of a model, including the irrelevant aspects), in order to facilitate technological social learning (Nielsen, 2018).

In sum, during the last two decades, EDP has been contributing notably to a better understanding of human development and evolution in many domains (physical, cognitive, and socioemotional development, as well as contexts of development). This has been accomplished by different means: progressively extending its scope to new topics; refining its previous sights; applying classical theories from evolutionary biology to developmental topics (with a special emphasis in recent years on life history theory); and generating new mid-level theories and models.

WHAT ARE SOME OF EDP'S MORE SIGNIFICANT CHALLENGES FOR THE FUTURE?

EDP has two principal challenges to pursue in the near future: first, understanding better how natural selection has shaped human psychological development and, second, starting to understand how human development might have contributed, if at all, to human psychological evolution.

Regarding the first challenge, we still need, on the one hand, to disentangle what is adaptive (adaptations) from what it is not in human development (i.e., ontogenetic by-products and noise), particularly in the early stages of life, as well as to find out what types of adaptations they are (e.g., ontogenetic or deferred adaptations). Although we have made progress in this endeavor in the last few decades, we still need to analyze many current developmental issues. Only then will it be possible to elaborate a detailed catalogue of the number and type of developmental adaptations that have been shaped by natural selection. On the other hand, it is also necessary to describe how these developmental adaptations are phenotypically expressed

over the course of development, depending on their epigenetic conditions. In the end, and as far as we know, in biology there are always two inheritance systems to be considered, one depending on the DNA sequence, and another, the epigenetic inheritance system itself (Maynard Smith, 1989).

In parallel, in addition to individual development, it is also necessary to address the tasks described above (identifying and classifying adaptations) with reference to the contexts of human development. As noted elsewhere in this chapter, survival and social learning would not have been possible in infants and children without the efforts of parents and kin, as well as probably of peers and other in-group members. However, as Bjorklund and Pellegrini (2000: 1699) indicated in their seminal article, ‘there is no single evolutionary account for the role of parents and other cultural agents on the socialization of children’. This lack of evolutionary knowledge is even more considerable in the case of peers, given that to succeed in adulthood implicates going beyond the family realm and ‘navigating the peer group represents a significant adaptive problem’ (Machluf et al., 2014: 268; see, also, Dishion et al., 2012; Harris, 1995).

Regarding the second challenge, starting to understand better the potential role of development in the evolution of behavior, evo-devo biologists are showing us the way. They have come to know in the last decades that the role attributed to genes for most of the last century may not be entirely accurate: ‘genes are probably more often followers than leaders in evolutionary change’ (West-Eberhard, 2005: 6543), giving support to an epigenetic view of evolution. According to this view, genes do not make structures, but serve rather as a road map for development that produces the phenotype taking into account other non-genetic information as well, like, for example, ‘physical forces such as mechanic stimulation, temperature of the environment, and interaction with chemical products produced by other species’ (Hall, 2012: 184). Does this mean that both evolutionary biology and

EDP are coming back to the tenets of early evolutionary embryologists such as Balfour, Garstand, and de Beer (see Hall, 2000, for a review), or James Baldwin, in developmental psychology? It is hard to know, but, in any case, if epigenetic findings are questioning aspects of current evolutionary theory and change in modern biology (Gilbert, 2017), it makes sense that evolutionary approaches in psychology, like EDP, reconsider at least the potential role of children’s development in human evolution (Bjorklund, 2006, 2018).

CONCLUDING COMMENTS

In contemporary biology, few doubt the well-known Dobzhansky’s assertion that ‘Nothing in biology makes sense except in the light of evolution’. But does contemporary developmental psychology assume that, similarly, nothing in childhood/development makes sense either except in the light of evolution? We hope so, as well as that EDP efforts during the past 20 years have contributed in some way to support this claim, and continue doing so in the future. As I have shown in this chapter, EDP is a multidisciplinary perspective that strives to secure a better understanding of the evolutionary basis of human development and the developmental basis of evolution. It is also both a toolkit and a meeting point for evolutionary scholars interested in human development. It is, in the end, paraphrasing Cosmides and Tooby (1997) when referring to evolutionary psychology, a way of thinking about psychological development that can be applied to any topic within it.

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Evolutionary Neuropsychology

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Evolutionary neuropsychology is the study of the evolution of brain and behavior relationships. This chapter will trace the evolution of modern human brains and their functions from the first coalescence of cells through a timeline of modern human's common ancestors and their brains. This chapter will lean heavily on our previous work in this area (e.g., Coolidge, 2019, 2020; Coolidge and Wynn, 2001, 2005, 2018; Wynn and Coolidge, 2010). Evolutionary neuropsychology is a multidisciplinary science that uses findings from the fields of evolution, neuroscience, psychology, anthropology, and archaeology. A major assumption of evolutionary neuropsychology is that functionally specialized brain regions are adaptations naturally selected in response to challenges over the course of billions of years of evolution. These adaptations and their brain regions and circuitry may now serve new functions, and they are particularly involved in higher cognitive functions. As Charles Darwin noted:

Although an organ may have not been originally formed for some special purpose, if it now serves for this end, we are justified in saying that it is specially adapted for it [...] Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms. (1862: 348)

Thus, Darwin was the first to recognize that organs or structures may come to serve a different purpose over time. About 120 years after Darwin's claim, paleontologists Stephen Jay Gould and Elisabeth Vrba (1982) coined the term 'exaptation' to refer to features that have been co-opted from their initial adapted functions but now enhance individual survival or reproduction. They further proposed that the word 'adaptation' be restricted, as Darwin had originally proposed, to features created by natural selection for their current purpose. A classic example of an exaptation is feathers. Feathers were originally selected for the purposes of thermoregulation.

Millions of years of selection later, some creatures co-adopted feathers for flight and the faster mobility that they afforded. This exaptation gave these creatures a fitness advantage over those that were slower or flightless (e.g., Ardila, 2016). Employing evolutionary neuropsychology's foundational position, this chapter presents evidence that the original functions of neurons and neural circuits were later repurposed or reused to serve new and higher cognitive functions that uniquely characterize modern human brains.

A PROTOTYPIC BRAIN: A CELL'S NUCLEUS

Life's origins can be traced to almost the beginnings of earth itself. Earth began to accrete about 4.567 billion years ago, and living things began to appear about 3.9 billion years ago, about the time that earth was less volatile from volcanic action and meteoritic bombardments. And what is life? Perhaps a definition of life should be discussed before discussing its evolution. First, living things need to take in chemicals or materials to sustain their energy and to expel the waste products of those energy reactions. This process is called metabolism. It is also possible that living organisms may produce their own energy; but that would still require an external source of energy and a means to convert it. A common example of such a process is photosynthesis, whereby a cell changes sunlight into chemical forms that can then provide energy for a cell's actions. Second, living things need to either reproduce/replicate or, once created, be immortal or semi-immortal (this hypothesis is not so outrageous, as some kinds of bacteria and viruses seem fairly hearty in terms of longevity, measured perhaps in billions of years).

A cell wall was one of the first advances in the evolution of life. The earliest of these walled cells, called *prokaryotes*, had no

nucleus and a single strand of RNA (e.g., early bacteria), and they appeared about four billion years ago. Perhaps about three billion years ago, some of these prokaryotic cells surrounded their RNA with another membrane to form a nucleus; they are called *eukaryotes*. Thus, eukaryotes, with their nucleus directing their activities, may be considered the earliest prototype of a body (the cell) and a brain (the nucleus).

THE FIRST ANIMAL BRAIN

The first groups of multicellular eukaryotes – comb jellies and sponges – emerged about 700 to 600 million years ago, and they are considered the first members of the animal kingdom. While there is debate over which appeared first, comb jellies or sponges, it is clear that their cells had differentiated. In the case of comb jellies, although they lack a central brain and anything resembling neurons (specialized cells in a nervous system that communicate with other cells), they do have sensory cells and motor cells (cilia) and some rudimentary communication between these cells to guide movements. While juvenile sponges do float about, adult sponges are sessile, although they do exhibit cellular differentiation. Some sponge cells specialize in maintaining their position in their environment and others are involved in feeding and filtering. Sponges also lack neurons, a nervous system, and anything resembling a brain. However, both comb jellies and sponges have a large number of ancient genes that are strongly associated with the neurons and nervous systems of much more recent animals.

About 545 million years ago, simple flatworms appeared. They are considered *bilaterians* – that is, if split down the middle, both sides are nearly identical – and it is thought that bilaterality aided movement. From comparative studies of fossil and living flatworms, it is suspected that these first

forms of animal life had sensory cells, which themselves had already specialized for gustation and for vision (and perhaps the detection of movement and electrical fields of other life forms), motor cells guiding movements (towards appropriate stimuli and away from inappropriate stimuli), and the neurons that could interpret the sensory cell's information and subsequently appropriately coordinate the motor cells. As noted previously, it is this latter coordination between sensory and motor cells that formed the basis for the first animal brains. Notice, too, that at this time, rudimentary brains were already bilateral. It is not known why dual hemispheres were favored by natural selection, although it is speculated that it may have aided heat dissipation and that motor neurons controlling left and right sides of the body may have been more efficient and the consequences less disruptive if they were separated.

In order for a life form to sustain itself, it must be able to feed, excrete waste, and reproduce. All of those activities were enhanced by the ability to move. Organisms that developed cells designed for movement may have been at a distinct evolutionary feeding and reproductive advantage. Thus began the natural selection for sensory cells, motor cells, and the 'brain' (neurons and nervous system) that could appropriately coordinate the activities between sensory and motor cells. Thus, a simple observation: brains were originally selected to control movements.

FISHES, AMPHIBIANS, REPTILES, MAMMALS, AND PRIMATES

About 375 million years ago, a fish, *Tiktaalik*, began the transition from sea to terrestrial life. Its forward fins were supported by bones that heralded modern animals' shoulders, upper arms, elbows, and wrist joints. The first of the true amphibians appeared about 360 million years ago, and some, like *Acanthostega*, had gills and lungs. About 300

million years ago, the first strictly terrestrial animals appeared, reptiles, and evolved from the amphibians. About 250 million years ago, reptiles diverged into two major groups: the Diapsids, which includes dinosaurs, modern reptiles, and birds, and the Synapsida, which includes modern mammals. In the former group, brains remained small in proportion to their bodies, while in the latter group, the upper surface of the brain (cortex) began a significant expansion, such that in later mammals, it became known as the neocortex. This expanded neocortex meant that mammals became less reflexive and less instinctual than reptiles, and they became more behaviorally flexible. At this point, it may be important to note that the word *cerebrum* refers to the entire brain, that is, its upper surface (cortex), middle-brain structures, lower-brain structures, upper spinal cord, and the cerebellum. Frequently, people equate the cortex with the entire brain, but anatomically, the cortex consists of only the upper six layers of the brain and is about the thickness of an orange rind.

Primate Brains

About 65 million years ago, a branch of mammals began their own speciation: the primates. They were small, nocturnal, insect-, leaf-, and fruit-eating, tree-dwelling creatures, and probably more socially oriented than any ancestor. As fruit is more nutritional and was necessary to fuel their proportionately larger brains (compared to their bodies), these early small primates had to compete with birds, reptiles, and other animals for fruit. It is surmised that they did so by coordinating their foraging activities with vocal calls. Thus began the selection for social brains and the necessary apparatus, sensory and brain-wise, for the production and comprehension of sounds, that is, the foundations of language. Evolutionary neuropsychologist Francisco Aboitiz and his colleagues (Aboitiz, 2017; Aboitiz et al., 2010) have

discussed this specialized auditory/vocal neural circuitry – the phonological loop – and its importance in extending short-term verbal memory and increasing the capacity to not only hold and process sounds but also set the foundation for more complex utterances and communications. They also proposed that the phonological loop became a mechanism for transferring sounds to long-term memory, and they traced its origins to these early primates. It is the primate brain that has influenced modern human brains more than any other lineage.

About 40 million years ago, the primates diverged into two lineages: the simians (monkeys, apes, and us) and the prosimians (lemurs and lorises). About 20 to 15 million years ago, the taxonomic family Hominidae appears, which includes us and the great apes (also called hominids) – gorillas, orangutans, chimpanzees, and bonobos (pygmy chimps) – all extinct ancestors of *Homo sapiens* (the first term is the genus; the second is the species). As there is some confusion in the literature about the terms ‘hominid’ and ‘hominin’, hominids will be defined as the group consisting of all modern and extinct great apes, and hominins will be the more narrow term referring to all extinct and extant humans and all of our immediate and distant ancestors – after the chimpanzee line diverged from ours about 6 to 13 million years ago (that dating has also become a recent ‘bone’ of contention, and the divergence between chimps and ancestors of *Homo sapiens* may have occurred more than once).

Early Hominin Brains

The fossil record for early hominin evolution, beginning about six million years ago or earlier, is spotty, as hominins appear to have evolved primarily in moist, jungle-like conditions that are not conducive to producing fossils. One hominin who made a media splash in the 1990s was *Ardipithecus*

ramidus (*ardi* means ‘ground’ or ‘floor’, *pithecus* means ‘ape’, and *ramid* means ‘root’). At first, it was thought to be one of our more distant ancestors, but now it is thought to be an extinct cousin of modern *Homo sapiens*. It dates to about 4.4 million years ago, with a brain size of about 300 to 350 cc (the brain size of modern chimpanzees is about 390 cc, with a range from 275 to 500 cc). So the brain of *Ardipithecus ramidus* appears to be what would normally be expected of an early primate, that is, small brains relative to their body mass and a reliance on visual and auditory systems. The initial divergence from other African apes included a transition to partial terrestrial bipedalism (walking on two legs), yet the first hominins were essentially bipedal apes. Combined with evidence for an ape-like maturation rate, and lack of evidence for stone tools or other ‘new’ cultural behaviors, there is no reason to suppose that these early ancestors of *Homo sapiens* were cognitively much different from current African apes. However, there would be a more dramatic change in hominin evolution about one million years after the initial appearance of *Ardipithecus ramidus*. This is our earliest definitively known ancestor: *Australopithecus afarensis* (literally, ‘southern ape from the Afar triangle’, in Eastern Africa), better known as Lucy. It is currently thought that *Ardipithecus ramidus* might have been a ‘cousin’ of Lucy but likely not a direct ancestor.

Lucy's Brain

In 1974, paleoanthropologist Donald Johanson and his colleagues were digging in a remote section of Ethiopia, a part of the Afar Triangle. One day, he spied a fossil elbow joint, thigh bone, the back of a skull, some vertebrae, and a pelvis. He recognized that all of the bones were from a female individual and that they were much older than any previous hominid fossil. As the Beatles’ song

'Lucy in the Sky with Diamonds' was playing in the camp, Johanson nicknamed her 'Lucy' (Johanson et al., 1994). Many other skeletons around this age have been found subsequently, so the entire group is referred to as the australopithecines. They date from 3.9 to 2.9 million years ago. Their brain sizes range from about 375 to 550 cc (modern brains average about 1,350 cc). Lucy's skull is similar to that of a chimpanzee, except for having more human-like teeth. Lucy had an ape-like face with a low forehead and a bony brow ridge (called a *supraorbital torus*), which persisted in hominins, including Neandertals; however, it may have little or no explicit function and may have arisen through simple genetic drift (changes due to chance). Male australopithecines were larger than females, known as sexual dimorphism, and this implies that males may have fought each other for reproductive access to females. The skeletal evidence suggests that the australopithecines were bipedal (unlike modern chimps, who knuckle-walk, which is less metabolically efficient), but they probably slept in nests in trees at night for safety, as well as played in trees, and females nested their babies in them. Tooth analyses have revealed that the australopithecines ate soft foods like plants and fruit and some hard foods like USOs (underground storage organs, e.g., roots), and undoubtedly they supplemented their diets with scavenged meat – 'undoubtedly', because brains are expensive metabolic tissue, accounting for about 2% of a human body's mass but requiring about 20% to 25% of the total calories consumed. With a life in and among trees and nests, they probably did not use or manage fire.

About 3.4 million years ago, the first stone tools appeared (Lewis and Harmand, 2016). They were found in the Dikika area of Ethiopia. They were mostly sharp flakes used for scraping meat from (most likely) scavenged bones. The flakes were made (knapped) from larger stones (called cores). The cores could also be used as hammer

stones to crack open nuts and break open bones for the marrow. These flakes and cores are called Mode 1 stone tools.

The Brain of Homo habilis

About 2.5 million years ago, a hominin appeared in the anthropological record that was physically similar to the australopithecines. The first skeleton was discovered by paleoanthropologists Louis and Mary Leakey in the Olduvai Gorge, Tanzania (Leakey and Leakey, 1964). The site was unequivocally associated with Mode 1 stone tools and evidence of butchering, which meant that meat remained a part of this hominin's diet. Its braincase averaged 640 cc (ranging from 500 to 824 cc); thus, its brain was well over 50% larger than the average australopithecine. Because at that time, no stone tools had yet been found associated with the australopithecines, and because brain size had increased dramatically, Leakey and his colleagues decided to place this specimen in the genus *Homo* and gave it the species name *habilis* ('handy' in Latin). However, because its body and limbs were similar to the australopithecines, it was suspected of living and sleeping in trees. Again, because brain tissue is so metabolically expensive, *Homo habilis* must have increased the percentage of meat in its diet. And it is known that meat contains the critical amino acid phenylalanine, which converts to tyrosine and then into the important chemical neurotransmitter dopamine (e.g., DeLouize et al., 2016). There are arguments that *Homo habilis* should not have been assigned to the genus *Homo* but remained in the genus *Australopithecus*; however, given the near doubling (or, at the very least, a 50% increase) of its brain size and the consequence of a greater level of neurotransmitters like dopamine in the brains of *Homo habilis*, a jump to the genus *Homo* does not seem unwarranted. Importantly, the skeletons of *Homo habilis* have been found to date as recently as 1.6 million years ago

(making them unlikely to be the direct ancestor of *Homo erectus*, to be discussed next). There is some variation of morphology in the *Homo habilis* group, so they are often referred to as the habilines.

The Brain of *Homo erectus*

In 1984, a nearly complete skeleton was found near a region called Nariokotome, Lake Turkana, Kenya. It was identified as a boy who died when he was about eight to nine years old, and he lived about 1.6 million years ago. He was nicknamed Nariokotome (also Turkana Boy). He was not physically similar to the australopithecines or habilines, being much taller (about 5 ft 3 in.) and weighing about 110 lb. It was recently estimated that he would have attained an adult height of about 5 ft 11 in. and weighed about 180 pounds (Ruff and Burgess, 2015). Clearly, this type of hominin could not have lived in trees, and anthropologists classified him as *Homo erectus* ('upright man'). Because of variations in the species, the group is called *Homo erectus sensu lato* ('in a broad sense'). It has also been proposed that *Homo erectus* morphology may have been selected for long-distance running (Lieberman et al., 2006). Nariokotome's brain size was even larger than habilines', at about 880 cc, and he would have had an adult brain size of about 910 cc. The species' average brain size is about 930 cc (750 to 1,250 cc). As modern humans' average brain size is about 1,350 cc, *Homo erectus*' brain was about 70% to 90% the size of modern humans, but not the same shape, as will be shown later.

The stone tools associated with *Homo erectus* were remarkably different from the stone tools of the australopithecines and habilines. They were symmetrical, bifaced, and leaf-shaped (also called handaxes), and they were labeled Mode 2 stone tools. Their design apparently was so practical and useful that it persisted for well over the next one million years.

Terrestrial Life

Australopithecines and habilines lived most of their lives in trees, primarily for protection. However, there was probably a limit to the number of nests in a single tree because if there were too many nests, it might have the opposite effect and attract predators. Because of their size, *Homo erectus* had to have made the complete transition to ground life, and with that transition came a suite of new challenges, the first of which was predation. It is thought *Homo erectus* may have survived, in part, by strength in numbers. Anthropologist Robin Dunbar (1998) argues that groups of *Homo erectus* and later hominins may have approached 110 individuals, while, if extrapolating from modern chimpanzee troop size to the australopithecines and habilines, individual families might have numbered three to six members, and a community might have averaged about 40 to 50 members. Dunbar's (2013) social brain hypothesis proposes that larger brains were selected for in order to keep track of a larger number of individuals in a group – that is, who helps, who cheats, and who is lazy. As social hierarchies are ubiquitous to almost all extant non-human primates, a socially oriented brain would have been necessary for these larger groups of *Homo erectus* for efficient and successful formation of alliances, recognition of alpha members, and other social tasks.

The increase in brain size in *Homo erectus* again meant an even greater reliance on meat, and tooth analyses of *erectus* do reveal a greater reliance on meat, but also on plants and other foods. Another important technological development at this time, around 1.5 million years ago, was the use of fire. If, as some anthropologists think, *Homo erectus* was able to manage the effects of fire (or even able to create it intentionally), then there may have been a cascade of cultural advancements. First, fire could have been used as added protection against predators (people or animals). Many modern hunters and gatherers use fire

at night as protection when hunting. Second, the light from fire could extend *Homo erectus*' day, allowing activities such as stone knapping to continue after dark. Third, fire could increase the nutritional value of food, making hard, inedible foods edible and more digestible, reducing the amount of chewing required (and time spent chewing), killing bacteria in plants and animal foods, and making food taste better. Fourth, fire could have been used to harden the points of spears and change the nature of some types of stone to make it more knappable. Fifth, as psychologist Matt Rossano (2010) has proposed, sitting around a fire may help bond a group socially. And if *Homo erectus* had some type of protolanguage, stories and myths could have been told around the fire, which might have enhanced the bonding experience of the fire. Paleoanthropologist Jean Luis Arsuaga (2009) has proposed that story- and myth-telling might reflect some of the subtle cognitive differences that made *Homo sapiens* more successful than any of their extinct ancestors or cousins (e.g., Neandertals).

The Weed Species

As the number of individuals in a group increased, so too would the size of the territory necessary to sustain them. It is thought that the territory of *Homo erectus* may have expanded to 10 times that of the australopithecines and habilines, to perhaps over 100 square miles. Wells and Stock (2007) have hypothesized that *Homo erectus* represented the first of the hominins to achieve fully metabolically efficient bipedalism (including a body designed for long-distance running), which would have aided territorial expansion. Interestingly, it has also been suggested that the changes in the inner-ear bones of *Homo erectus* may have produced improved balance and coordination. Full, efficient bipedalism would have also allowed erectus to explore new territory, and the challenges associated with new territory may have

helped select for behavioral plasticity (i.e., an ability to solve novel problems, also known as fluid intelligence) that further challenged and enhanced the cognitive abilities of these larger-brained hominins. It is also known that from at least 1.8 million years ago (and probably earlier), *Homo erectus* began leaving Africa, as fossils of *Homo erectus sensu lato* have been found dating back that far in the Caucasus mountains (between Europe and Asia) and back to about 1.4 million years ago in Spain. Fossil remains of *Homo erectus* dating to at least 700,000 years ago have been found in Indonesia, and they persisted living in that region until about 70,000 years ago or even more recently. The discovery of *Homo floresiensis* – ‘hobbit-like’ individuals with very small brains (about 400 to 500 cc) – on the island of Flores, Indonesia, suggests that it was the australopithecines who may have left Africa first. It has also been suggested that they were a lineage of *Homo erectus*, already in Asia, and that they adapted to a restricted island environment by being smaller-bodied and smaller-brained. Cachel and Harris (1995) were the first to suggest that *Homo erectus* may be likened to a weed species: able to invade distant, disrupted environments (e.g., volcanic eruptions, floods, droughts, etc.) and thrive in them. Wells and Stock (2007) proposed that this behavior may have begun with the australopithecines but reached a demonstrable zenith with *Homo erectus*. As they further note, this capacity to adjust to fluctuating and unpredictable environments favors behavioral plasticity that ultimately maintains genetic variation.

The Brain of Homo heidelbergensis

In 1908, near Heidelberg, Germany, a fossil was found that seemed to be an intermediate between *Homo erectus* and modern human types. Because of its brain-size increase to

about 1,100 cc to 1,400 cc, the species name was recorded as *Homo heidelbergensis*. They were stockier and shorter than *Homo erectus*, suggesting that they had become cold-adapted, unlike the heat-adapted *Homo erectus*. *Homo heidelbergensis* either evolved in Africa and moved into Europe, or they evolved from *erectus* in Europe or Asia, became cold-adapted, and moved back to Africa. It is suspected that *Homo heidelbergensis* was the common ancestor of modern *Homo sapiens*, Neandertals, and other hominins. Again, it is important to note that its brain size overlaps with modern humans, but its brain was not the modern shape, as will be discussed shortly.

Neandertal Brains

The European version of *Homo heidelbergensis* may have given rise to the Neandertals (it may also be spelled *Neanderthal* – an original German spelling – but in German, either spelling is pronounced *Neander-tall*). The African version of *Homo heidelbergensis* may have given rise to our lineage, *Homo sapiens*. Although Neandertals and modern humans have a high degree of DNA similarity (about 99.5%), it is the very small differences in our DNA that may have led to Neandertal's extinction and our evolutionary survival. The two groups had separate evolutionary histories for about 500,000 years; Mendez et al. (2016) have dated the lineage split to about 588,000 years ago. DNA analyses also indicate that some limited gene flow occurred between Neandertals and some modern humans. Modern Eurasians have been found to have 0.5 to 4% of DNA from interbreeding with Neandertals about 80,000 to 50,000 years ago, although modern sub-Saharan Africans usually have little or no DNA from Neandertals (Green et al., 2010). Mendez and his colleagues (2016) also found specific protein-coding genetic differences between Neandertals and *Homo sapiens*, all of which resulted in threatening the viability

of male hybrids. Juric et al. (2016) have suggested another factor that ultimately increased the reproductive isolation between the two groups and may account for some of the deleterious genes that *Homo sapiens* inherited from Neandertals. They proposed that most of the alleles (alternative forms of a gene) were essentially neutral in Neandertals but were selected against in the larger-sized populations of *Homo sapiens*. Although the alleles individually probably had small effects, these alleles may have posed a greater threat to the early generations of *Homo sapiens*–Neandertal hybrids. Nevertheless, the last Neandertal died about 30,000 years ago.

The Neandertal skull was a combination of ancestral characteristics, cold adaptations, and derived features perhaps attributable to simple genetic drift (like their large, overhanging brow ridges). Their ancestral characteristics included a larger, longer, relatively flatter skull than *Homo sapiens*, with large faces, teeth, noses (for heat exchange during breathing), eye sockets, and expanded frontal sinuses (most of these features reflect cold-weather adaptations). The one feature that would seem to be a dramatic exception to this similarity to *Homo heidelbergensis* was brain size.

Neandertal brains were about 9% to 13% larger than those of modern *Homo sapiens*. Estimates of their cranial capacity range from about 1,250 to 1,740 cc, with mean cranial capacity varying from 1,430 to 1,550 cc (depending on the sample size and ratio of males to females in the sample). However, an important notion in brain evolution is that at some point, larger brains stopped being associated with greater intelligence, or more cognitive flexibility, or greater adaptability. Neandertal brains were also much larger than *Homo erectus* brains, but they were not simply scaled-up versions of *erectus* brains. Neandertal brains had a different shape than that of *erectus* or modern *Homo sapiens*.

There is another critical difference between these two human types that appeared after birth: a brain globularization phase unique

to *Homo sapiens*. It occurred during the first year of life (Gunz et al., 2012), and it resulted in a ‘rounder’ yet smaller brain in *Homo sapiens*, which appears to result primarily from an upper- and middle-brain (parietal lobe) expansion (e.g., Bruner, 2010; Bruner and Iriki, 2016). There is some evidence that Neandertals had slightly shorter life spans compared to *Homo sapiens* living at the same time, perhaps due to a more dangerous lifestyle, nutritional insufficiencies, disease, xenophobia, or even a penchant for cannibalism (e.g., Agustí and Rubio-Campillo, 2017).

BRAINS DO NOT FOSSILIZE, BUT SKULLS DO

Heretofore, we have mentioned only the internal volume of skulls as a proxy for brain size, since brains do not fossilize. At some recent point in the evolution of modern *Homo sapiens*, perhaps 100,000 to 30,000 years ago, brains became smaller (by about 10%) and they changed shape from earlier *Homo sapiens*’ brains. Currently, paleoneurologists (those who study the brains of ancient hominids) take internal measures of the inside of skulls (called *endocasts*) and use multivariate statistical methods (like principal components analysis) to determine not only the volume but more importantly the shape of ancient brains and how brain shape changed over time. This recent change in brain shape in *Homo sapiens* compared to Neandertals may weigh heavily on answering one of anthropology’s greatest mysteries: why did Neandertals become extinct after living successfully in Europe and Asia for well over 200,000 years?

Anatomically modern *Homo sapiens* left Africa for Europe at least 100,000 years ago (and not for the first time). They made it to the Levant (roughly the regions of Israel, Turkey, Jordan, Lebanon, Syria, and others) and then apparently retreated, presumably when they encountered Neandertals, who had

already been living in the Levant for tens of thousands of years. Sometime around 45,000 years ago, *Homo sapiens* swept through the Levant (successfully this time) and into Europe. It appears they were anatomically modern (skulls, brains, and bodies) and carried with them a complex culture known as the Aurignacian, which included sophisticated cave art, creative figurines, pervasive use of personal ornaments, and highly ritualized burials. Within about 10,000 years of their entry into Europe and Asia, Neandertals became extinct. There is little to no evidence of direct violence between the two human types. Currently, there are two general and opposite opinions about the Neandertal extinction. One is that the two human types were identical culturally and cognitively. This side endorses the idea that ‘there but for the grace of God, go us’. In other words, it was a simple twist of fate, and if history replayed itself, *Homo sapiens* would have become extinct instead of Neandertals (e.g., Finlayson, 2019; Villa and Roebroeks, 2014; Zilhão, 2013). This side also often vilifies, with accusations of racism and Victorian values, the opposing position that a small but significant difference in cognition, undoubtedly due to brain shape differences, allowed *Homo sapiens* to extract more resources from the same environments and not only survive but flourish (e.g., Coolidge and Wynn, 2016, 2018; Wynn and Coolidge, 2010; Wynn et al., 2016). We shall address the brain shape differences in much greater detail after the following discussion of hominin brains.

ADAPTATIONS AND EXAPTATIONS OF HOMININ BRAINS

As noted earlier, a prototype for brains began with the nucleus of the eukaryotes, and brains became the primary organ for interpreting sensations from a cell’s environment and conducting appropriate movements based upon those sensations. However, we

suspect no one would attribute *consciousness* to even multicellular eukaryotes. Bronfman et al. (2016: 9) proposed that minimal consciousness (basic consciousness or first-order consciousness) was ‘simple subjective experience ...experiencing of a feeling of comfort or fear, or colour [sic]’. Their transition marker was the ability of organisms to learn associatively (classical and operant conditioning) during the Cambrian explosion of life about 545 million years ago (Ginsburg and Jablonka, 2010, 2015). They noted that non-associative learning (habituation and sensitization) was limited to a small number of associations between stimuli and responses in the life of an organism. They proposed that associative learning, in contrast, was *unlimited* and, thus, they coined the term ‘unlimited associative learning’ (UAL), where the number of associations that can be learned and recalled within and between sense modalities exceeds the life span of an organism and also exceeds the number of individuals in a given population. Further, although the biological nature of an organism does constrain associative learning to some extent, ‘... the number of possible learned associations is vast, and learning-based plasticity is never fully exhausted...’ (Ginsburg and Jablonka, 2015: 59). Thus, UAL was Bronfman et al.’s (2016) transition marker to conscious brains. Interestingly, in this regard, consciousness may be considered an exaptation of the basic *learning* principles, which helped to form living things.

THE ADVENT OF MODERN NEUROSCIENCE AND CLINICAL NEUROPSYCHOLOGY

Russian neuropsychologist Alexander Luria (1902–1977) has been credited with founding clinical neuropsychology as a scientific discipline distinct from other medical and psychological endeavors. Neuropsychology is the study of brain and behavior

relationships. The adjective ‘clinical’ refers to the primary use of brain-damaged patients and animal models to understand the functions of different regions and networks of the brain. Luria began collaborating with Russian psychologist Lev Vygotsky and Russian psychologist Aleksei Leontiev. They formed a formidable intellectual troika that studied and performed experiments assessing preserved and lost behavioral functions in brain-damaged patients. Many of these patients were World War I Russian soldiers. Later, Luria not only assessed World War II brain-damaged soldiers but also began investigating methods for their rehabilitation. He remained a prolific writer and investigator throughout his life, but his tour de force book was *Higher Cortical Functions in Man*, first published in Russian in 1962 (in English in 1966). His lifetime contributions to the field were many. He helped establish and create an interest in child neuropsychology, where he noted that brain damage had differing effects and outcomes in children compared to adults. He studied identical and fraternal twins to assess contributions of genetics and culture to behavior (modern behavior genetics). He studied and delineated different types of aphasia (speech and language disorders). He conducted a varying battery of neuropsychological tests on his patients, that assessed an array of brain dysfunctions, although it is important to note that he stressed individual behavioral differences in brain-damaged patients such that a single, comprehensive battery of tests was difficult to attain. He was also particularly interested in frontal lobe-damaged patients and noted that the frontal lobes and prefrontal cortices are responsible for the most complex activities of all human behavior, that is, the ability to attend to present behaviors but also to imagine and integrate simulations of future behaviors. He viewed the frontal regions as a ‘superstructure’ above all other cerebral areas – that they had the critical responsibility of the general regulation of all behavior. Finally, Luria (1966: 79) astutely noted that ‘every higher

mental function ... is composed of many [neurological] links and depends for [sic] its performance on the combined working of many parts of the cerebral cortex, each of which has its own special role in the functional system as a whole'. In this regard, Luria presaged later works by Anderson (2010, 2016), who further noted that a single brain region may be involved in a multitude of functions, and any single cognitive human behavior has contributions from multiple brain regions and networks. Anderson (2010, 2016) also proposed that neural reuse (exaptations) may be considered a central organizing principle of the brain's evolution.

THE CEREBRAL HEMISPHERES

The clearest visual landmark in a human brain (cerebrum) is its two cerebral hemispheres. The left hemisphere is slightly larger than the right – in humans and other great apes – and in humans, the functions for each hemisphere are mostly different: the left hemisphere is genetically directed to process language; the right hemisphere performs complimentary functions for language and some specific nonverbal and visuospatial functions. The two hemispheres are *highly interactive* on nearly all cognitive and emotional functions. However, the two hemispheres also appear to have greater neuroplasticity (ability to handle different tasks other than their original functions) before puberty than after puberty. The two hemispheres are separated by the longitudinal fissure (a deep cleft between the ridges of the brain), which runs from the anterior (towards the front) part of the brain to the posterior (towards the back) part of the brain. The two hemispheres share and coordinate information by means of a commissure (communicative brain tissue): the corpus callosum. The corpus callosum lies beneath the dorsal (towards the top) surface of the cortex.

The Frontal Lobes' Adaptations

The frontal lobes are the largest regions of the brain. The inferior (situated below) convolutions of the frontal lobes are demarcated by the lateral fissure (also known as the Sylvian fissure, Sylvian sulcus, or lateral sulcus). The posterior portion of the frontal lobes is divided from the parietal lobes by the central sulcus (also called the central fissure, central sulcus of Rolando, or Rolandic fissure). The first adaptive functions of the frontal lobes in mammals and primates (and, even earlier, the first non-rudimentary brains in fish) was the planning and execution of motor movements for any muscle (e.g., fins, limbs, arms, hands, fingers, tongue, etc.). It does so in cooperation and coordination with many other areas of the cerebrum, as no brain region acts alone in any function. Obviously, these frontal lobe adaptations were important in early primate arboreal locomotion, and, as has been noted, primate brains have informed modern human brains more than any other earlier lineage.

Research has consistently demonstrated the importance of the anterior regions of the frontal lobes, the prefrontal cortex (PFC), especially for the control and direction of behavior. It is also further divided into the dorsolateral PFC (DLPFC), orbitofrontal cortex (OFC), and ventromedial and ventrolateral PFC (VMPFC, VLPFC). The PFC is critical to forming both short- and long-term goals and creating plans and strategies for attaining those goals. Neuroscientists Goldman-Rakic and Leung (2002) have wondered whether the PFC should be considered a 'center' of the brain because of its role in decision-making and selected attention in both humans and other animals. The DLPFC is associated with classic executive functions such as attention organization of tasks in space and time, selective inhibition, response preparation, speech sequencing and supramodal sequencing, goal attainment, planning, and flexibility. The VLPFC and VMPFC orbitofrontal are more closely connected to the brain's

limbic system and are associated with the processing of emotions and decision-making associated with social behaviors.

There is accumulating evidence that the OFC may be an important part of a large and complex neural network (with major input from the hippocampus and other parts of the limbic system) that forms a cognitive map that helps define the nature of a task or goal and form decisions on how to act to complete that task or achieve that goal. The OFC and this neural network may be particularly active when the decision to act depends on guesses or mental simulations of the possible outcomes of those actions. Thus, the OFC may be part of a system responsible for behavioral inhibition, calculating and signaling the consequences of errors, the attribution of errors to their appropriate causes, and inferring the value of alternative actions when those actions are mentally simulated (and not simply based on the prior outcomes). These associative cognitive maps, of course, would be critical in human evolution when alternative actions must be generated and a decision must be made with regard to one of them, especially when those ancestral human types encountered novel problems, where there was no prior, direct experience with them. It is again important to note that the OFC does not make these decisions in isolation but receives input from other regions, such as the parietal and temporal lobes, subcortical structures, and the cerebellum.

Superior to the corpus callosum and covering it is the cingulate cortex. Its function appears to be attention to and selection of appropriate stimuli in the external and internal environments and maintaining a consonance between short- and long-term goals. There is also evidence that the anterior portion of the cingulate cortex is part of a brain network involved with the emotions of anger and disgust, which would have been critical to the evolution of all early and later forms of animal life. The posterior portion of the cingulate gyrus is part of an important brain network (along with the hippocampus) that

is critical to forming representations of one's external environment for successful navigation. This region will be further discussed in the section on parietal lobes.

The Frontal Lobes' Exaptations

In the 1860s, French neurologist Paul Broca (see Coolidge, 2020) identified the left hemisphere as critical to language. His claim went against the prevailing thought of the time that there were no areas of the brain with specific functions (a consequence of Gall's discredited phrenology, also see Coolidge, 2020). Broca, based on many of his left hemisphere-damaged patients, proposed that the ability to speak was a left hemisphere function. An area of the left hemisphere, Broca's area (BA 44 or pars opercularis, and BA 45 or pars triangularis), is known to be critical to the production and sequencing of speech, and damage to this region results in Broca's aphasia, whereby patients retain the ability to understand spoken language but either cannot speak or speak haltingly. Broca's area has also been shown to be involved in word retrieval, word-sound assembly, and sequential word processing, and it serves as a supramodal (involved in all senses) hierarchical language processor. Thus, the major exaptation of the frontal lobes has been the reuse of motor neurons and motor circuitry for language. A major cognitive Rubicon in technology, as noted earlier, was the creation of the first stone tools (sharp flakes and cores) about 3.3 million years ago. A second major cognitive Rubicon was crossed with the development of the Mode 2 symmetrical handaxe about 1.8 million years ago. Although controversial, it appears that stone-tool knapping may have served as an intermediate exaptation between the original function of the frontal lobes in controlling motor movements and the most recent exaptation of the frontal lobes in language production and sequencing.

Parietal Lobes' Adaptations and Exaptations

The parietal lobes are situated posterior to the frontal lobes and central sulcus. This area is known as the somatosensory cortex, and it controls and integrates the tactile senses (touch), including the senses of pain, temperature, movement, pressure, texture, shape, vibration, etc. The somatosensory cortex has intimate connections to the thalamus, the latter of which is the gateway to and from the somatosensory regions. The parietal lobes are also critical in the manipulation of objects in visual space (visuospatial processing). Classic symptoms of damage to the parietal lobes are *apraxia*, an inability to execute intentional motor movements, and *agnosia*, an inability to recognize one's own body parts.

It is not surprising that sensory and motor cortices are adjacent in the brain, as early mammals and then primates originally occupied a nocturnal, arboreal niche. These brain regions were critical to living and moving successfully in trees. Even modern humans' parietal lobes have an inordinate representation for hands and feet, which would have been essential for early primates leaping among tree branches 65 million years ago. It is also not surprising to find that modern humans' brains have exapted these same regions and adjacent regions for a sense of self (e.g., who we are and where are we going [metaphorically]).

Two important regions in the inferior portion of the parietal lobes are the supramarginal gyrus and the angular gyrus. Both areas have been implicated in language processing, coupled with other neural networks. The supramarginal gyrus (in both hemispheres) has been shown to be critical to the temporary storage of sounds (phonological loop) and of the linkage of sounds to meaning. It has also been proposed that the supramarginal gyrus is 'the' site of inner speech. The supramarginal gyrus is actively recruited when human subjects are asked to concentrate on the sound

of words rather than the meaning of words. Neuroimaging studies have confirmed its role in the maintenance of a verbal trace but not, perhaps, in the encoding of meaning. It also appears to be critical to verbal working-memory tasks, for which continuous verbal information must be temporarily maintained and attended to despite interference. Again, one early adaptation of the inferior parietal regions was the storage of sounds, particularly in early primates, for their subsequent use to warn, assert dominance, and express emotional states to conspecifics and others. The later neural reuse of these same areas is thus not surprising.

The angular gyrus, sitting posterior to the supramarginal gyrus, has long been known to have a role in mathematical calculation, and damage to this area may result in various arithmetic deficits known as *acalculia* or *dyscalculia*. It is also suspected to be the brain area where written words are transformed into an internal dialogue. More recent work has shown that the angular gyrus is critical to word reading and comprehension, and also to semantic processing, making sense of external and internal events, the manipulation of mental representations, and even out-of-body experiences (particularly the right angular gyrus). Current research also supports the hypothesis that the angular gyrus may be a multimodal hub for processing multiple sources of sensory information and making sense of that information. For well over a decade, the angular gyrus has been suspected of being involved with metaphor production and comprehension; that role has been debated, but at the least, it is clearly activated when subjects are asked to compare concrete and abstract concepts (i.e., metaphor comprehension and production). Numerous studies have also confirmed its role in at least 15 different higher cognitive processes, including the verbal retrieval of numbers and their calculations, the verbal coding of numbers, the mediation of the spatial representation of numbers, the recollection of personal memories (i.e., autobiographical memory),

visuospatial navigation, theory of mind (i.e., the ability to assume and correctly understand the intentions and attitudes of other people), and others. Interestingly, it has also been implicated as part of the ‘default mode network’ of the brain that is activated when people are resting and involved in their own thoughts without external engagement but is deactivated when people are engaged in a goal-directed activity (e.g., Seghier, 2013).

Another area of the superior and medial regions of the parietal lobes is the precuneus. The original adaptation of the superior and lateral portions of the parietal lobes appears to be determining the location of objects in physical space and determining the relation of those objects to one’s body. Certainly, all intentionally moving animals relied on brain regions that allowed them to ‘understand’ their place in their environments, but this determination might have even been more critical for early primates who spent their lives living, moving, mating, playing, and sleeping in trees. One critical exaptation of the medial portion of the superior parietal lobes (the precuneus) is to produce and recall episodic memories and autobiographical memories and construct future memories (simulation). The latter may have played a major role in human evolution, as various problem-solving scenarios could be generated and internally debated, thus saving people from the dangers of trial and error (sometimes called *fatal* trial and error). Again, it is important to note that the precuneus and other brain regions rarely act alone. Many different functions may be attributed to single regions, and single regions are almost always part of multiple neural networks.

Laterally and just below the superior region of the parietal lobes is the intraparietal sulcus (IPS). It is a structure shared by humans and non-human primates, although the anterior region is more developed in humans. The IPS contains neurons that are dedicated to the recognition and appreciation of numbers (called *numerosity*). This also is a cognitive process shared by humans with

many other animals. There are at least two core processes in numerosity: subitization, the ability to differentiate between one, two, and three things, and small- and large-set differentiation. Coolidge and Overmann (2012) theorized that numerosity may have served as a rudimentary cognitive basis for abstraction, as the basic concepts of one, two, or three things can be applied to *any* objects in the world, like sticks, stones, bones, apples, and even mythical creatures like mermaids or even sounds. Further, since human infants (as young as eight months old) and monkeys demonstrate numerosity, it is functionally independent of language. It may have been useful evolutionarily to have a region of the brain (parietal lobes) that facilitates distinction between one, two, and three things, be they predators or fruits, and to pass that information on to other regions (frontal lobes) for a decision. In that same light, it may have been imminently useful to know that the 50 fruits in one tree is less than the 100 fruits in another tree, although knowing the exact number of fruits in each tree would not be necessary (e.g., Kutter et al., 2018).

Another area residing in the inferior portion of the parietal lobes, situated posterior and superior to the corpus callosum, is the retrosplenial cortex (RSC). Along with the hippocampus, thalamus, precuneus, and medial temporal lobes, the RSC appears to have played a major synergistic role in the evolution of hominin cognition, particularly in *Homo erectus*. Human and animal studies have shown that the RSC plays a central role in a network of brain regions for navigation, especially novel environments and spatial memories. This network has also been shown to have a role in episodic and autobiographical memories. However, its most critical function may reside in its ability to make transitions between an egocentric viewpoint (a view from one’s self), known to be a precuneal or posterior parietal cortex function, and an allocentric viewpoint, (viewpoint-independent or a view from another person or place’s perspective). According to Vann et al. (2009),

the place and grid cells of the hippocampus index locations contained within episodic or autobiographical memories, and then the RSC translates these indexes into egocentric information such that a location in a memory may be viewed from other points of view. It is suspected that the RSC may also act as a short-term storage buffer while information is being translated. Many human neurophysiological studies have confirmed that the RSC is significantly activated by many kinds of spatial navigational tasks including passive viewing of scenery, virtual-interactive spatial navigation, and active navigation of both new and highly familiar environments. The RSC is also highly active when topographical (map-like) information needs updating or for use of one's own motion to plan routes. Human and animal studies of brain damage in these regions also confirms the loss or major degradation of the aforementioned spatial abilities. As mentioned earlier, *Homo erectus* has been labeled a weed species, coming out of Africa many times over one million years or more, and is known to have expanded its territory far beyond that of the australopithecines and habilines. The ability of *Homo erectus* to be successful in these endeavors no doubt depended upon selection of a network of brain regions that could reciprocally translate these egocentric and allocentric viewpoints. Becker and Burgess (2001) have proposed that this translational RSC model may be related to imaginative or creative thinking for its basic ability to reconstruct scenes or imagine alternative scenes. Their model might help to account for the dramatic changes in technology from Mode 1 to Mode 2 stone tools. Thus, rather than the enhanced navigation abilities of *Homo erectus* and their bifacial handaxes being independently evolved behaviors, they may share a common exapted neurological substrate.

In summary, although specific brain regions and neuronal networks have been exapted for purposes other than their original function, they may often retain their original function. It appears likely that the parietal

lobes have undergone many exaptations such as taking on the functions of numerosity and higher number processing, a sense of self, autobiographical memory, prospective memory (relating to the future), mental time travel, and an awareness that the sense of time is relative (as one can recall past memories and manipulate them as well as fabricating future memories), which is called *autonoesis* (Tulving, 2002). However, it does appear that the parietal lobes did retain many of their original functions such as visuospatial relationships, directing limb and hand movements, finger recognition, etc.

Temporal Lobes' Adaptations and Exaptations

The temporal lobes occupy the position inferior to the frontal and parietal lobes. Anteriorly, they are separated by the lateral fissure from the frontal lobes. There is no clear demarcation from the parietal lobes as they lie adjacent and inferior to them, and they are adjacent and anterior to the occipital lobes, again with no clear demarcation. The temporal lobes surround the hippocampus and the amygdala, important limbic system structures, which will be discussed shortly. The neurons and neural circuitry of the temporal lobes are genetically predisposed to process sounds, their meaning, and language, and specific regions are referred to as auditory cortexes. The temporal lobes thus play the major role in thinking, inner speech, and, of course, memory.

The temporal lobes are also often referred to by its three gyri. The posterior portion of the superior temporal gyrus is called Wernicke's area (although there is no standard anatomical definition for it). In the later 1800s, German neuroanatomist Carl Wernicke (Coolidge, 2020) observed that not all aphasias result from damage to Broca's area, and he demonstrated that this superior temporal region was specifically responsible for the understanding of speech.

Another region within the posterior part of the superior temporal gyrus is the planum temporale. It is typically larger in the left hemisphere than in the right hemisphere, and this asymmetry has been claimed to be more predominant in chimpanzees. In humans, symmetry in the left and right hemispheres in this region has been found to be associated with learning and reading disabilities. The planum temporale has been shown to have a role in music, particularly the perception of pitch and harmony. The superior temporal gyrus also contains an area known as the transverse temporal gyrus, which is responsible for hearing and basic sound processing, and it receives input directly from the cochlea (inner ear). This area is also known as the primary auditory cortex.

The first terrestrial animals undoubtedly relied upon vision and audition as their primary senses, and this remained true for mammals and primates. Thus, one of the first adaptations of the temporal lobes of the brain was the maintenance of sounds and the application of meanings to them. This is not an exceptionally difficult cognitive process, as basic associative-learning principles (classical conditioning and operant conditioning) can establish reliable associations between sounds and basic meanings. As noted earlier, flatworms can be classically conditioned, and they have only rudimentary brains and nervous systems. Thus, another of the temporal lobes' first adaptations was auditory and visual memorization. Of course, as Anderson (2010, 2016) has noted, brain regions work in conjunction on nearly all behavioral functions, and so the temporal lobes work in unison with all adjacent lobes, particularly the hippocampus, which it surrounds. Interestingly, the associations of sounds and their meanings are not stored for long periods of time (no more than about two to three years) in either the temporal lobes or the hippocampus, but these two regions are necessary to create memories and then store them elsewhere in long-term memory.

The medial (middle) temporal gyrus, like the other two gyri of the temporal lobes, is involved with aspects of language processing and memory. It has also been implicated in judgments of the attractiveness of faces, which is not surprising given that it is adjacent and superior to the inferior temporal gyrus. It also appears to be part of a ventral temporal network involved in the recognition of objects and faces. In addition, it appears to be part of the brain's default mode network. The entorhinal cortex is in the medial temporal region, which appears to serve as an interface with the hippocampus; thus, its primary purposes may be the same as the hippocampus: spatial navigation and auditory-memory formation.

In the inferior temporal gyrus, one specific area – the fusiform gyrus – has neurons dedicated to the recognition of faces and objects, and this is found in humans, other great apes, and monkeys. In humans, the fusiform gyrus also selectively responds to word forms. Obviously, this function is an exaptation of an earlier adaptive function of the temporal lobes in primates. Interestingly, there is a large degree of lateralization of function between the left and right hemispheres for this region in humans. Written words activate the left fusiform gyrus, which is labeled the visual word form area (VWFA), and faces activate the right fusiform gyrus (fusiform face area or FFA). The VWFA is activated regardless of the writing system used, although it has been shown that nearly all writing systems employ only three basic forms. The inferior temporal gyri are also connected to the extrastriate cortex, a critical part of the primary visual cortex in the occipital lobes. The extrastriate cortex is also connected to the posterior portion of the parietal lobes. Damage to the left VWFA produces *alexia*, a complete inability to read words.

Occipital Lobes' Adaptations and Exaptations

The occipital lobes sit posteriorly to the parietal lobes and temporal lobes, and

their initial adaptation was primary visual recognition and processing. There are no clear demarcations of the occipital lobes from the parietal or temporal lobes, although a structure known as the lunate sulcus demarcates the occipital lobes from the parietal and temporal lobes in apes and monkeys. It does appear that the lunate sulcus has moved posteriorly in the evolution of the cortex of *Homo sapiens*, suggesting a diminished role of the primary visual cortex in modern humans compared to other primates. It has also been surmised that Neandertals had larger primary visual cortices than *Homo sapiens* living at the same time, which may suggest a more important role for the sense of vision in Neandertals, perhaps as a function of their cold-adaptiveness and more northerly occupation in Europe and Asia resulting in greater amounts of time spent in darkness (Pearce et al., 2013).

The occipital lobes' primary visual-processing area is at the extreme posterior end of the cortex, and its anterior regions, the extrastriate cortex, are involved in the perception of other people's body parts and their intended movements. These regions also process 'higher level' visual information like color, hue, object recognition, and movement. Information about the visual and spatial location of objects and their motion is transmitted from the occipital lobes to more posterior portions of the parietal lobes (called the dorsal stream or 'where' stream of information). Information about the nature of an object – its color, shape, or form (called the ventral stream or 'what' stream of information) – is transmitted to the temporal lobes. The ventral stream, along with temporal regions, is involved in word recognition and meaning, reading, attention, learning, and memory. Thus, the basic visual processing of objects was an adaptation of the occipital lobes, and its later exaptation was for higher cognitive processes like object recognition, word recognition, and reading. It is important to note that the latter cognitive processes, as has been stressed throughout this chapter, are

not solely a function of the occipital lobes and its associated extrastriate cortex. Again, as Anderson (2010, 2016) has noted, no higher cognitive process depends on a singular brain region. Word recognition and reading also depend heavily on the temporal and parietal lobes (and other cortical and subcortical regions). Thus, there has been a selection for the *concerted evolution* (evolving together) of these structures and their neural networks for reading. In evolutionary time, the *exapted* ability to read came about very quickly, within the last 5,000 years or more recently. However, this emergent property, the ability to read, depended on a long adaptational history of these various brain regions and their functions.

Insular Cortex's Adaptations and Exaptations

The insular cortex is a distinct oval-shaped group of gyri, deep within the lateral (Sylvian) fissure. It is overlaid by parts of the frontal and temporal lobes. It has reciprocal connections to the brainstem, thalamus, amygdala, basal ganglia, frontal, temporal, and parietal lobes, and all sensorimotor association areas. Its anterior portion, the anterior insular cortex (AIC), in conjunction with the anterior cingulate cortex (ACC) and the prefrontal cortices, plays an important role in emotional awareness and sensing physiological states of the body (e.g., temperature, pain, etc.). Thus, it is one of the initial adaptive functions in all early animal life, but again, particularly in mammals and primates. The AIC, ACC, and DLPFC have some large spindle-shaped cells called von Economo neurons (VENs), whose chief function appears to be transmitting information quickly across distant areas of the brain. As VENs are primarily found in larger-brained primates, like the great apes, it is suspected that they may have evolved relatively recently, perhaps within the last 20 million years. They are also found in larger-brained

and more intelligent mammals like whales. Thus, one of the later exaptations of these neurons is that they evolved independently (*convergent* or *parallel evolution*) in great apes and whales but serve similar purposes: rapid transmittal of information across brains as they expanded in size from the earliest primates to later hominids and hominins. VENs may have also played a role in the processing or maintenance of social behavior.

Hippocampus' Adaptations and Exaptations

The hippocampus is a bilateral horse-shoe-shaped structure whose first recognized purpose was the memorization of spatial locations in both humans and animals. As brains evolved to guide effective movements, remembering where to go and not to go (and their associated evolutionary fitness consequences) was an essential part of guiding movements. Thus, it is not surprising that a structure in the brain came under selective pressure (more specifically, the genes that developed that structure) to navigate and remember one's environment. That structure, whose primary adaptation was spatial navigation, was the hippocampus and its associated networks. Interestingly, one critical sense in the earliest evolution of navigation was olfaction, and intimate neuronal ties remain between the hippocampus and the human olfactory bulbs (to be discussed shortly). All mammals have a well-developed hippocampus compared to fish, reptiles, and birds. There are homologous structures in the latter animals, and those structures also appear to be involved in spatial cognition. Thus, one of the earliest adaptations of the hippocampus was visuospatial navigation. The German philosopher Immanuel Kant (Smith, 2011) had long ago proposed that the perception of space was a mental ability that existed independent of experience. In the 1960s and early 1970s, American-British

neuroscientist John O'Keefe (Burgess et al., 2002) substantiated Kant's hypothesis by finding that rats had *place cell* neurons that became active when rats were in a particular place in their environment. He also found that these place cells would rearrange themselves in new environments, thus creating new maps of those environments, and those maps remained stable over time. Norwegian neuroscientists May-Britt and Edvard Moser (Moser and Moser, 1998) found additional cell activity outside of the hippocampus in rats and mice, with connections to portions of the medial temporal lobes. They called them *grid cells* and found these cells were able to approximate distances, forming a neuronal basis for spatial navigation. For their combined work, O'Keefe and the Mosers were awarded the 2014 Nobel Prize in Physiology/Medicine.

Danjo et al. (2018) demonstrated the allocentric (from another's perspective) and conspecific (one's own species) recognition functions of hippocampal cells. Specifically, they found that a particular set of cells in the hippocampus had spatially receptive fields for the recognition of one's self and others, even when self or others are engaged in movements. This ability to be aware of an individual's position in space is critically important to all social animals, especially primates, in order to be able to learn by observation, engage appropriately and be successful in social interactions, and navigate while in groups. The hippocampus has maintained its original adaptive visuospatial, allocentric, and conspecific recognition purposes in humans, however, its exaptive value was not fully appreciated until the late 1960s. This recognition began with one of the most famous patients in neuroscience history, H. M., whose hippocampus was removed to ameliorate his severe epileptic seizures in 1953. During his recovery, it was discovered that he could no longer form declarative memories, although he maintained his ability to learn procedural memories. Even as late as the early 1970s, this differential role

of the hippocampus in declarative and procedural memories was not fully appreciated. However, it is now clear: the major exaptation in the evolution of the hippocampus in humans was its neural reuse for the formation of declarative/semantic memories, yet also its maintenance of the original functions for visuospatial navigation and olfaction recognition.

THE SMELL OF FEAR: THE AMYGDALA

The amygdalae are bilateral almond-shaped structures (amygdala is the singular form), on the anterior tips of the hippocampus. They play a well-researched role in emotional processing, particularly fear and rage responses. It has also been suggested that the amygdalae's chief function is to determine what an external stimulus is and what should be done about it. Although the amygdalae have often been touted as the neural home of emotions, an overwhelming majority of this research has been devoted to only two emotions: rage and fear. Amygdalae are also highly complex and interconnected with other regions of the brain, and so some suggest that they are not a single structural entity, nor should they be considered a single functional unit. Its basal nucleus receives input from all sensory systems. Its central and medial nuclei are involved with the output of innate emotions, and its cortical nuclei's input comes from the olfactory bulb and the olfactory cortex (also called piriform cortex). This olfactory input into the amygdalae's cortical nuclei gives a solid neuronal basis to the saying 'the smell of fear', as Mujica-Parodi et al. (2009) have empirically demonstrated that humans can detect airborne chemical substances from emotionally stressed novice skydivers, and functional magnetic resonance imaging revealed the activation of the amygdalae in the humans. The amygdalae

also have receptors for at least five different neurotransmitters, receptors for at least two different hormones, and peptide receptors for oxytocin, opioids, and others.

Because emotions play a key role in memory formation, amygdalae play an important role in learning and memory as well. The amygdalae and other limbic structures are phylogenetically much older than the surrounding cortex, and the amygdalae and other limbic structures are often more prominent features in the brains of reptiles; yet they are still important in mammals and primates. In the latter, amygdalectomies result in a 'taming effect', and electrical stimulation of the amygdala can instill rage reactions. Rage reactions have even been demonstrated in mice against much larger natural predators. Humans, whose amygdalae have been removed, become apathetic and show little spontaneity, little creativity, and do not show a variety of expressive emotions.

American neuroscientist Joseph LeDoux (2007) has noted that the amygdalae receive their sensory input from two different pathways: one fast ('the low road') and one slow ('the high road'). The fast pathway involves the recognition from the visual cortex of, perhaps, a fearful animal (a snake). This recognition is sent to the thalamus, and directly to the amygdalae, which may then elicit an immediate motor response – for example, 'jump'. In this circuit, autonomic responses also occur, like increased heart rate and blood pressure, without full conscious recognition that the object is a harmless corn snake. Meanwhile, the visual cortex has simultaneously sent that information about the snake to higher levels of cortical processing, providing much greater resolution about the snake ('Oh, it's not a poisonous coral snake, it's a harmless corn snake'). That information is still sent to the amygdalae for assessment, but it is a much slower process. Evolutionarily, it seems that this dual system of analysis allows both fast recognition and accurate recognition, albeit at different processing speeds.

The Cerebellum's Adaptations and Exaptations

The cerebellum (a diminutive in Latin meaning 'little brain' or 'lesser brain') has long been associated with the acquisition, maintenance, and the smooth timing and execution of motor movements. Even the ancient Greeks had some recognition of the role of the cerebellum in the physical movements of animals. Again, as late as the 1970s, only the fine and gross motor-movement functions of the cerebellum had been firmly established. In the 1970s, it was known that the cerebellum contained an inordinate number of neurons for its size compared to the rest of the brain, and it was also known that its dendritic branching was the most complex in the entire cerebrum. At the time, these facts led to the reasoning that fine motor movements and motor-movement sequencing must have required an inordinate amount of neural processing. In 1993, Japanese neuroscientist Masao Ito (1993) speculated that the cerebellum might control thoughts or ideas just like it controlled motor movements, and a host of neurophysiological studies over the past decade has substantiated his hypothesis. The cerebellum has now been implicated in a wide variety of cognitive functions including insight, intuition, creativity and innovation, novel problem-solving, language, affective word meanings, aspects of grammar, meta-linguistic skills (awareness of the subtleties of others' speech), verbal and visuospatial working memory, verbal fluency, reading, writing, and the rate, force, and rhythm of actions. In the great apes and monkeys, just as in humans, the anterior portion of the cerebellum controls motor movements, but it appears that the posterior and lateral portions of the cerebellum have been expanded in *Homo sapiens* and have been exapted for these aforementioned higher-order cognitive functions. Further, recent neuron analyses have revealed that of the approximate 86 billion neurons in the cerebrum (less than previously thought), about 69 billion neurons are

in the cerebellum. Thus, it may take a large number of neurons in the cerebellum to control motor movements, but the extraordinary number of neurons in the cerebellum may also have been required for these aforementioned higher cognitive functions.

It has also been suggested that the evolutionary expansion of the cerebellum in humans and its exaptation for higher cognitive functions did not occur in isolation (mosaic evolution: the independent evolution of brain regions) but occurred in tandem with the concerted evolution of the prefrontal cortices and motor systems. It appears that natural selection acted upon individual brain regions and on functional and interconnected brain networks. As the first technologies may have been stone-tool making about 3.3 million years ago, the brain areas required to make stone tools, such as the PFC, motor systems, and cerebellum, may have all been selected for in concert, and it may help to explain how subsequent higher-level cognitive functions like language may have been able to exapt systems already in place for other functions. Interestingly, recent research suggests that Neandertals may have had a smaller cerebellum than modern *Homo sapiens* (although the former had about 10% bigger brains than the latter).

SUMMARY

In this chapter, we have tried to summarize the major adaptations in the evolution of the modern human brain as well as its major exaptations. This was a Herculean task, as brain research is currently advancing at a more rapid pace than ever before because of technological progress in related disciplines like neurology, psychology, the cognitive sciences, genetics, and others. Our admittedly selective coverage included adaptations and exaptations of the frontal, parietal, temporal, and occipital lobes, and the insular cortex and

amygdala. In our opinion, the most dramatic exaptations occurred in the last two brain regions that we covered: the hippocampus and the cerebellum. As we have noted, the exaptation of the hippocampus for the formation and storage of declarative memories was only recognized in the last five decades or so. The exaptation of the cerebellum for higher cognitive processing was only recognized in the last three decades. It is a very exciting time in this new discipline of evolutionary neuropsychology, and we look forward to many more provocative discoveries.

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Comparative Evolutionary Psychology

Sarah F. Brosnan

Humans are an odd animal. On the one hand, we share numerous similarities with a wide variety of species, but on the other, while the old adage that every species is unique is true, our suite of characteristics makes us apparent outliers. These characteristics include traits that are distinctively human, such as language, as well as traits that are shared, but that we have to a greater degree, such as some cognitive abilities. Indeed, one focus of evolutionary psychology is to explain how we evolved this atypical suite of traits. Nonetheless, despite these differences, there are also fundamental similarities between us and other animals, and we can learn quite a lot about ourselves, including those traits that have been argued to be uniquely human, through studying other species. This is the focus of comparative psychology (Vonk et al., volume 1), which uses an explicitly comparative approach to explore how traits evolved across all species, including humans.

In the comparative approach, scientists study the evolution of behavior by exploring

how subjects of different species respond to similar circumstances. By comparing their responses, we can better understand what behaviors and capacities are shared, or not, and use this information to better understand how the trait in question evolved and the key ecological, social, or contextual factors that led to its emergence. In addition, we can compare across contexts, both within and among species, which allows for a better understanding of how selection pressures led to differences. While early work in comparative psychology focused on a relatively small number of model species, such as rats and pigeons, later work has broadened considerably in scope to look across the animal kingdom and consider how ecology influences subjects' behavior and cognition. This breadth of species and data has made the approach more amenable to asking fundamental questions about the evolution of human behavior.

Studying the evolution of human behavior is tricky as, unlike anatomical

features, behavior does not typically fossilize (although the results of behavior, such as footprints and nests, may: Martin, 2014), and no other human species survive. However, the comparative method provides an alternate approach. The key assumption is that by comparing human behavior to that of other species, we learn something about the behaviors that existed in our evolutionary history and, potentially, something about the conditions that selected for these behaviors. In short, behaviors that are shared between humans and other species may represent behaviors that were present in our common ancestors, whereas behaviors that are present, at least in some form, only in humans may represent more recent adaptations specific to humans. By comparing a sufficient number of species across a sufficient number of traits, we can begin to reconstruct something about the way in which our behaviors evolved.

There are two basic ways in which species share traits, homology and convergence. In homology, species share traits by common descent, meaning that they were present in the common ancestor from whom both species inherited them. A commonly cited example of this is that birds as disparate as robins, eagles, and hummingbirds share wings because they inherited them from a common ancestor. Homology is useful for determining when in evolutionary time a trait appeared. The second mechanism is convergence, in which species share traits due to similar ecological pressures. To continue the above example, insects and bats share winged flight with birds, despite having no common ancestor that did so. Presumably, both species gained selective advantages for adapting to take advantage of this open niche (the air). Correlations between the trait in question and other traits shared by these species can help us determine what characteristics in the environment may have selected for a given trait and, therefore, hint at its function. Although homology is perhaps more commonly meant when people talk about comparison,

convergence is particularly informative for understanding evolutionary pressures.

Another key issue is to not confuse mechanism and function. Niko Tinbergen was one of the founders of ethology, the study of how ecology and evolutionary history worked together to shape behavior. He proposed four questions that must be answered by anyone studying the evolution of behavior (Tinbergen, 1963). Formalized today as Tinbergen's four questions, these include understanding its development, how it manifests in the organism, its evolutionary trajectory, and the function for which it evolved. These can be further simplified into two key concepts: proximate and ultimate causation. Put simply, proximate mechanisms describe how a behavior comes to be in a given organism (how it develops, what are the hormonal, neural, etc., pathways through which it manifests), whereas the ultimate explanation describes its evolutionary function and how it evolved.

It is important to carefully distinguish between these for several reasons. First, failing to properly separate the mechanism and function means that you will not recognize the different levels of explanation, and risks the explanations competing with one another. Both functional and mechanistic explanations are equally correct, and neither has precedent because they are answering different questions. Second, it is important not to conflate the two; similar mechanisms may lead to different behavior, and behaviors that look the same may get there via different mechanisms. Just because two species share a trait does not mean that it necessarily involves the same underlying mechanism, nor do two species sharing the same mechanism necessarily display the same behavior. To give an example from my own work, both rhesus monkeys and humans are skilled at finding the best paying option in a coordination game called the Assurance game (Brosnan et al., 2012). However, they apparently do so in different ways (Parrish et al., 2014). Work exploring their responses to simulated partners found that rhesus developed a preference for the

(typically) higher paying option, whereas humans probability matched, playing the higher paying option with roughly the same probability as the simulation. Importantly, rhesus monkeys probability match in other contexts (Wilson et al., 1964), so in principle they could have used the same mechanism. A failure to test this outcome further could have led us to assume that there was more similarity between humans and rhesus than is actually evident.

This issue becomes particularly important when considering complex psychological phenomena, both because of an unfortunate use of the same words in different contexts and the tendency to ascribe intention to these behaviors based on the words used to describe them. The best example here is altruism, which has come to mean different things in different disciplines. Biologists use it to refer to a specific behavioral outcome, in which one individual provides a benefit to another at a cost to itself (Bshary and Bergmuller, 2008), and are agnostic as to the intent or goals of the actor who provided the benefit. Psychologists use it to refer to a selfless act providing a benefit to another at a cost to the self with the goal of helping the other (Batson, 1991). A biologist and a psychologist could easily misunderstand one another despite using their disciplinary terminology appropriately, and in particular, the psychologist may incorrectly assume that the biologists' use implies intent. In this paper, I follow the biologists' focus on costs and benefits, which are more straightforward to measure in non-human species and do not assume any intent unless specifically stated.

When studying complex human behaviors, we often are looking for the evolution of traits that are not in and of themselves shared with other species, such as language. How does one even study such questions? One useful approach is to break complex behaviors down into components. We can then trace the roots of our complex human behaviors by looking at how these components

manifest in other species, and the differences between other species and ourselves, to better understand under what circumstances and for what purpose our own, more complex behavior evolved. For instance, although language in the human sense is not seen in other species, there are precursors to language, such as vocabulary acquisition, syntax, and vocal and gestural communication, that appear in other species, and can be studied to learn something about how human language emerged (Hillix and Rumbaugh, 2004; Pollick and de Waal, 2007; Snowdon, 2000). Of course, such an endeavor is necessarily based on hypotheses and suppositions that might not always be correct, but by triangulating different species and approaches, we begin to understand how these traits may have evolved.

THE EVOLUTION OF MORAL BEHAVIOR

The study of the evolution of moral behavior through comparison with other species is not a new endeavor. Some of the first discussion of how moral behavior evolved, and in particular, whether it was shared with other species, emerged in the writings of Darwin, who famously speculated that 'any animal whatever, endowed with well-marked social instincts, the parental and filial affections being here included, would inevitably acquire a moral sense or conscience, as soon as its intellectual powers became as well developed, or nearly as well developed, as in man' (Darwin, 1981: 71–72). Indeed, in later writings, he went on to argue that even moral emotions in humans had their precursor in other animal species (Darwin, 1998). Writing a generation before Darwin, Adam Smith, the economist best remembered for *The Wealth of Nations*, wrote an insightful book on human behavior, *The Theory of Moral Sentiments* (1817), in which he asserts that humans share many passions in common with animals, both the negative 'brutish'

ones widely held to be animal-like and the more positive ones that we cherish:

Such is our aversion for all the appetites which take their origin from the body: all strong expressions of them are loathsome and disagreeable. According to some ancient philosophers, these are the passions which we share in common with the brutes, and which having no connexion with the characteristic qualities of human nature, are upon that account beneath its dignity. But there are many other passions which we share in common with the brutes, such as resentment, natural affection, even gratitude, which do not, upon that account, appear to be so brutal. (Smith, 1817: 30).

Subsequent to this, the study of complex behaviors, as well as emotions, in other species fell from favor. This was, no doubt, at least in part due to the emergence of behaviorism in the United States, which emphasized basic mechanisms, actively avoided more complex behaviors, and treated the mind as an unknowable black box. More recently, there has been a resurgence of interest (Bekoff, 2009; Brosnan, 2014; Flack and de Waal, 2000).

At its most basic, moral behavior¹ is simply behavior that promotes social regularity (Brosnan, 2011; Flack and de Waal, 2000). After all, while living in groups benefits individuals (on average), it also has costs, and animals do better if they can minimize the costs – for instance, through norms specifying patterns of response in a given context (these norms need not be conscious). However, it also includes behaviors that more closely resemble what we would consider moral. For this chapter, I will consider evidence suggesting that other species show aspects of moral behavior. First, animals show some of the behaviors that we might consider important for ‘being moral’, including prosocial behavior and responses to inequity or unfairness. Second, one cannot intentionally help another individual without some way of knowing what another is experiencing. While behavior can be functionally moral, with no intent on the part of the actor,

humans can be intentionally moral, in part due to our ability to empathize, another trait that has been argued to be present in several animal species. While I do not have space for comprehensive discussions of the work on these topics, here I summarize these topics to demonstrate how we can learn something about human behavior from studying other species.

Prosocial Behavior

Do individuals in other species ever make decisions that benefit conspecifics? Although it is challenging to know what other species’ intentions may be, we can explore the degree to which other species show behavior consistent with benefitting others. Indeed, fieldwork and observational studies offer evidence that animals routinely benefit conspecifics. For example, in the field, apes adopt orphaned infants and successfully raise them (Hobaiter et al., 2014; Thierry and Anderson, 1986; Wroblewski, 2008), even in cases in which the orphan is unrelated (Uehara and Nyundo, 1983). In captivity, there are numerous examples of apes behaving in ways that help others: they may assist each other in accessing food or water resources that are out of reach, rescue each other from moats, or even help members of other species (de Waal, 2006). De Waal tells the story of witnessing an adult female bonobo find a stunned, but otherwise uninjured, bird in her enclosure that she took to the top of a tree, oriented with wings outstretched, and released (de Waal, 2009).

However, relying on anecdotes is problematic for several reasons. First, it is impossible to do controlled studies to determine what the animal’s goal was in performing the behavior, much less whether the behavior was simply an accident – maybe the bonobo was just playing with the bird, and the fact that it was thereby released unharmed was a lucky mistake. Second, there is a reporting bias, whereby interesting behaviors are reported frequently, but negative or ‘boring’ behaviors

are rarely put in the literature; all of the situations of bonobos saving birds are reported, but the times in which apes find something in their enclosure that they do not rescue – or even harm – remain unmentioned. Third, without controlled studies, we cannot determine the contexts surrounding the behavior, nor determine what factors influence it. Lest this seem overly pessimistic, this is not to say that these behaviors *do not* exist, simply that, like any other behavior, they require sufficient evidence. Moreover, ironically, our human bias may lead us to miss interesting and important behaviors as well, either because we fail to recognize interesting behaviors that do not look like what we would do or because we fail to recognize that the conditions in a controlled study are not appropriate for the behavior to manifest (Brosnan, 2018; de Waal, 2016). Ideally, we combine observation and experimentation whenever possible (Janson and Brosnan, 2013).

The results of the first studies of prosocial behavior in experimental contexts showed no evidence of subjects providing benefits to their partners. In these initial studies, chimpanzees were given a choice between two options, one of which rewarded only them and one of which rewarded both them and their partner. The actor got the same reward no matter what they chose (controls were included to make sure that they were paying attention); thus, the key question was whether the actors were more likely to choose the prosocial option when a partner was present than when they were by themselves (next to an empty enclosure). The assumption was that if the apes were prosocial, they would choose the option that also rewarded their partner when they could. However, two sets of studies run in three different labs found no evidence that chimpanzees were prosocial: they chose between the options at the same rate regardless of whether their partner was present (Jensen et al., 2006; Silk et al., 2005).

One immediate criticism was that the visible food might have made it difficult for the chimpanzees to inhibit reaching for the

first available option (although note that in one of the two studies, at New Iberia, the rewards were hidden: Silk et al., 2005). Chimpanzees are notoriously bad at inhibiting in the presence of food (Boysen et al., 1996). However, a follow-up test that allowed them to first get their own food, then reward their partner if they wished to do so, also found no evidence of prosocial behavior (Vonk et al., 2008). Another study addressed this by having subjects choose from between two tokens, one that rewarded both chimpanzees and one that rewarded only the subject. As with the New Iberia study, food rewards were kept wrapped in paper, so that they were not visible until after the choice was made. This study found evidence of prosocial behavior (Horner et al., 2011), perhaps due to the different methodology, although this result was later challenged (Amici et al., 2014).

In the meantime, another set of experiments based on an instrumental helping paradigm was reaching a different conclusion. These explored how chimpanzees responded when given the chance to help their partners in non-food contexts; chimpanzees assisted both humans and other chimpanzees to acquire objects that they could not reach, and their behavior looked similar to that of young children (Warneken et al., 2007; Warneken and Tomasello, 2006). One obvious possibility for this discrepancy was that the apes were simply responding differently in the contexts with and without food. At the proximate level, as just discussed, chimpanzees do not inhibit well when food is present, although the fact that they were not always prosocial in the token prosocial choice tasks even when food rewards were hidden indicates that this is not the only explanation. At an ultimate level, there is more evidence of reciprocity of services, such as grooming or support, than of goods, such food (Borgeaud and Bshary, 2015; Duffy et al., 2007; Hemelrijk, 1994; Seyfarth and Cheney, 1984). Indeed, most foods that chimpanzees eat can easily be stolen, cannot be stored, and are only available at certain times, making them challenging for interchange (exchange of different resources), and food is a zero-sum

context, whereas services do not require storage, can be used at whatever time is convenient, cannot be stolen, and giving a favor to one individual does not preclude later helping another. Any of these possibilities could have explained the pattern of results.

Yet another explanation for this discrepancy is that the chimpanzees either did not understand the purpose of the tasks or are simply disinclined to help if there is not a reason to do so. Following up on Silk et al. (2005), Claidière et al. (2015) repeated the study with a twist: after having been a donor – and failing to make the prosocial choice – subjects were given the experience of being a recipient with a donor who was trained to always choose the prosocial option. Following this, donors were paired back with the original recipients, at which point they were more likely to make prosocial choices. Although it is difficult to exclude experience effects in this design, the authors argue that the donors' experience as a recipient could have led them to see the purpose of the task, which could have changed their behavior (Claidière et al., 2015). Another recent study gave chimpanzees the option to help a partner who had made the choice available at a personal cost. Chimpanzees chose the prosocial option when there was a cost to the original donor but failed to do so when the experimenter unlocked the experiment, requiring no cost to the donor (Schmelz et al., 2017). A logical interpretation is that the chimpanzees were repaying the cost the partner paid to make the choice available (Brosnan, 2018; Schmelz et al., 2017). These later two results highlight the challenge of understanding these tasks from the animals' perspectives. Despite the fact that researchers intentionally design intuitive, easy to understand tasks in order to maximize the subjects' chances of success, we are not chimpanzees and so may not understand how they see the task, or all the factors that they take into account when making a decision.

Chimpanzees are not the only species that make prosocial choices. Capuchin monkeys

(Barnes et al., 2008; Brosnan et al., 2010; de Waal et al., 2008; Lakshminarayanan and Santos, 2008), marmosets and tamarins (Burkart et al., 2007; Cronin et al., 2010; at least in some contexts: Cronin et al., 2009), and macaques (Massen et al., 2011; again, at least in some contexts: Sterck et al., 2015), as well as corvids (Horn et al., 2016; Schwing et al., 2016), wolves (Dale et al., 2019), domestic dogs (Dale et al., 2016; at least in some contexts: Dale et al., 2019), and rats (Hernandez-Lllement et al., 2015) all do so. In nearly every species tested, however, the results have been highly variable across studies, even within the same species (Cronin, 2012). This likely is because of the influence of factors such as context, relationships, and the subject's state. In addition, there is variability among species. One prominent hypothesis is the cooperative breeding hypothesis, which proposes that prosocial behavior evolved in the context of cooperative offspring care and should be more evident in humans, callitrichids, and other cooperatively breeding species (Hrdy, 2009; van Schaik and Burkart, 2010). Whether or not this hypothesis is ultimately supported, hypotheses like these that search for underlying evolutionary explanations for behaviors are extremely helpful in elucidating the function of behaviors.

Inequity and Fairness

Fairness is a cornerstone of human morality. It is also a social ideal, which makes it impossible to directly study in non-verbal species. However, we can explore aspects of the sense of fairness in other species by breaking it down into empirically testable components. The most obvious, of course, is how individuals respond when they get less than a social partner. Indeed, this is one of the first components of fairness that develops in humans. Across cultures, children from a young age are upset when they get less than others, and this response increases with age

(Blake et al., 2015). Of course, simply noticing when one is underbenefitted is not a sense of fairness as it is self-centered (more on responses to being overbenefitted later); however, it is a key step in the development of fairness, and one that is likely to evolve quickly because it obviously benefits the individual to rectify such a situation.

This was also the first aspect of fairness that was empirically studied in other species. My colleague Frans de Waal and I first tested for inequity in capuchin monkeys nearly two decades ago. We found that monkeys who had to complete a simple task (trading a token back to the experimenter for food) refused a food that they otherwise accepted when their partner got a more preferred reward for completing the same task, but accepted the less preferred reward as long as their partner also got it (Brosnan and de Waal, 2003). The latter is true even when subjects are (both) shown the better reward before receiving the less preferred one, indicating that it is not just the result of a contrast effect (i.e., subjects respond negatively when they expect one reward but receive a less preferred one: Tinklepaugh, 1928). Since that time, the same basic task has been used to test numerous species, including apes, several monkey species, dogs, wolves, corvids, and rats. In at least some contexts, some individuals of these species show the same response as these capuchins: they are more likely to refuse a food that is given as a reward for completing a task if their partner receives a better one than when their partner gets the same, less preferred, reward (reviewed in: Brosnan and de Waal, 2014; Talbot et al., 2016).

One of the intriguing things about this response is the variability seen both within and across species. For example, chimpanzees respond in some cases (Brosnan et al., 2005, 2010, 2015; Engelmann et al., 2017; Hopper et al., 2014) but not others (Bräuer et al., 2006, 2009), and even in those studies that find an effect, not every subject responds. Thus far, there is no factor researchers have found that consistently influences responses

across all studies, but some factors are emerging as important. Not surprisingly, dominant individuals respond more negatively to inequity than subordinates (Brosnan et al., 2010). Personality also influences responses, with subjects who are more social responding more negatively to inequity than others (Brosnan et al., 2015). There is no evidence as yet that relationship quality influences responses, although this is likely because most studies involve dyads that voluntarily separate as a pair from the rest of their group to complete tasks such as this; there is good evidence that these pairs have better relationship quality than those who choose not to separate together (Brosnan et al., 2015).

In addition, even the format of the test influences responses. For instance, chimpanzees who are positioned adjacent to one another for the study appear to respond more strongly to inequity than subjects who face each other across an open space (Bräuer et al., 2006; Brosnan et al., 2010). Work on capuchin monkeys shows that the rewards used influence responses as well; when comparing responses to low vs medium, low vs high, and medium vs high rewards, subjects only refused when they got the lowest value reward, regardless of what the partner received. The authors argue that this is because it is rather difficult to give up preferred foods, which is how a response to inequity is measured in these studies. That is, subjects are considered to be averse to inequity when they are sufficiently upset to actually give up food; it may be that they *notice* inequity in other contexts but do not respond by refusing the reward that they are offered (Talbot et al., 2018).

This highlights a challenge with experimental studies in non-human species: in order to run these studies, costs and benefits are operationalized with food rewards, despite the fact that there are many other commodities that subjects may negotiate for. Indeed, it is unlikely that inequity responses in the wild focus on food distribution but, instead, the distribution of grooming, support, etc.

Moreover, as mentioned earlier, on a practical level, we measure inequity responses by how often subjects refuse a reward, which is an expensive way to protest (and does not even change outcomes). In children, verbal protest appears in situations in which children still accept the inequity (LoBue et al., 2011), suggesting that it would be profitable to look for negative responses other than refusals. Although there is no such work in primates, work in dogs supports this. Dogs will accept less preferred rewards than their partners, but when they do so, they spend less time affiliating with both the partner dog and the experimenter (Brucks et al., 2016).

Aside from variability within species, there is also substantial variability across species. Some species, including chimpanzees, macaques, capuchin monkeys, and possibly bonobos, routinely respond negatively to inequity, whereas orangutans, squirrel monkeys, owl monkeys, and callitrichids do not. What leads to this variability? This is important to understand as the answer may suggest the contexts in which inequity responses evolved. It is clear, for instance, that this response is not a homology across the primates, or even the great apes. It also is not an artifact of brain size, as orangutans show no such response. It does not appear to be related to group size, as the gregarious squirrel monkeys do not respond to inequity. Based on current data, the best fit is that species that routinely cooperate with non-kin are also the ones that are the most likely to respond negatively to inequity in these laboratory tests (reviewed in Brosnan and de Waal, 2014). Indeed, if this is the case, it strongly implies that cooperation and inequity evolved hand-in-hand. One hypothesis from economics proposes that inequity is a mechanism by which individuals evaluate partners (Fehr and Schmidt, 1999). If one's partner in a cooperative endeavor consistently gets more, then it might be time to find a new partner. This hypothesis suggests that the inequity response is a partner choice mechanism at the individual level, and

moreover, that this pressure may have been a driving force in the evolution of cooperation.

The callitrichids offer a potential wrinkle in this hypothesis. These primates, marmosets and tamarins, are cooperative breeders that live in small family groups including a single breeding pair and adult offspring that remain at the nest to care for their younger brothers and sisters. Similarly, owl monkeys are pair bonded, with biparental care. Given the highly interdependent nature of their groups, one might expect these species to be particularly responsive to inequity, yet they failed to respond in nearly all cases (Freeman et al., 2013; McAuliffe et al., 2014; Neiworth et al., 2009; although see Mustoe et al., 2016 for the an exception). Why is this? One possibility, related to the cooperative breeding hypothesis mentioned above, is that their interdependency makes them unlikely to respond negatively to such a minor inequity. Indeed, this also makes sense with respect to the hypothesis that inequity responses are a mechanism for partner choice. Whereas a chimpanzee who is group hunting or a capuchin monkey who is looking for an alliance can easily go find a new partner within their group, callitrichids and owl monkeys do not have the option to easily find a new breeding partner. This lack of partner flexibility may make them tolerate a higher level of inequity because they do not have a partner choice option. If true, this suggests that they should be particularly sensitive to inequity during the pair bond formation, particularly if there are multiple available options.

While thus far I have discussed how subjects respond when disadvantaged, an important component of fairness is how subjects respond when they are advantaged. There is little evidence for this in species other than humans. Indeed, aside from possible anecdotes, I know of no empirical evidence in any monkey. There is, however, increasing evidence that chimpanzees notice when they receive more than another. The first evidence came from the inequity studies I mentioned earlier – in this case, however, subjects'

responses to high value foods were compared when their partners got the same high value food versus a less preferred food. Consistent with advantageous inequity, subjects were more likely to refuse their reward when the partner got less than them, as compared to situations in which both got the same (high value) food. The response was quite a bit less strong than their response to being disadvantaged, however, indicating that they either find this less aversive, or are less willing to give up a high value food (which is the case in capuchin monkeys: Talbot et al., 2018). Indeed, this pattern appears to be the norm in humans, too; in the aforementioned study on children's responses to inequity across seven societies, they were much more likely to respond to being disadvantaged than advantaged, and their refusals when they were advantaged commenced at a later age than their refusals when they were disadvantaged (Blake et al., 2015).

Another way to look at subjects' responses to being advantaged is to use the Ultimatum game paradigm. In a typical game, proposers are given a chance to divide a set amount of money between themselves and a partner. The partner then has the option to accept, in which case both subjects get the money as proposed, or reject. If the partner rejects, neither subject gets anything. It is not entirely agreed upon what is being tested, but two outcomes are clear: first, there is substantial variability across cultures in what is offered and accepted (Henrich, 2000). Second, in most cultures, proposers offer more than the minimum and partners reject offers that are too unfair by their cultures' standards (in modern western societies, most offer about half and offers of substantially less than that are frequently refused: Camerer, 2003). Although the focus has been on whether partners refuse, more recent evidence suggests that refusals may happen because they are the partner's only available response; when partners are given the chance to do something else, such as write the proposer a note, they do so and accept more unequal offers (Xiao and Houser, 2005, 2009).

A key question is whether this response is uniquely human, perhaps a result of cultural immersion in our economic systems, or whether there is a deeper biological underpinning, which would suggest evolutionary pressure to care about how others treat us even at a potential cost. If the latter were the case, then we would expect to see some aspects of this response in other species. Of course, it is not possible to replicate this game exactly with other species, because we cannot tell them how to divide amounts, so we use a so-called limited form game in which proposers choose between two restricted options. This is typically done by either having subjects choose between two trays with different food distributions or choose one of two token types, each of which represents a different distribution. Unlike with humans, there is no evidence that chimpanzees ever refuse (Jensen et al., 2007; Kaiser et al., 2012; Proctor et al., 2013), which has been hypothesized to mean that they are not treating the game in the same way that humans do (Jensen et al., 2013). However, there are several caveats to this interpretation. First, in most cases, subjects are splitting highly preferred rewards (e.g., banana slices), and we know that capuchins, at least, do not reject outcomes when they are highly valued (Talbot et al., 2018). Second, in these studies, the only way to refuse was to wait, typically for at least 30 seconds, which is difficult and leads to low refusal rates even in humans (Hachiga et al., 2008). Finally, although responders do not refuse, subjects change their preference between the options depending on the context.

In the Proctor et al. (2013) study, the authors compared proposers' choices when they simply chose a token and returned it to the experimenter (the tokens were worth either a 3/3 or a 5/1 split of banana slices, the latter favoring the proposer) to a situation in which the chosen token had to be passed to a partner, who could either return it to the experimenter (accepting the division) or hold on to it (rejecting the offer, in which case neither subject got anything). Proposers

overwhelmingly preferred the 5/1 split when the partner had no recourse but switched to a preference for the 3/3 split when the partner was involved. Thus, when their partner had the ability to influence outcomes, subjects chose *against* their absolute best interests. We repeated this with preschool children, who also never refused, and also switched preferences between the two conditions.

Perhaps tellingly, we saw some evidence of protest in both children and chimpanzee partners when they got the less good outcome. While there were not enough instances to analyze statistically, one possibility is that they were trying to change the proposers' behavior. Indeed, this highlights a key difference between the Proctor et al. study and typical human studies; rather than partners being anonymous strangers in a one-shot games, these pairs were interacting with a known member of their own social group in a repeated game (which was presumably also embedded in the repeated interactions that made up their daily life, for both the chimpanzees and the preschoolers). Indeed, when one has no recourse other than refusal, this may be a good response, but with known social partners, they benefit more by changing their partner's behavior so that they can engage in the long-term benefits that derive from cooperation (Milinski, 2013).

Fairness, then, may be uniquely human, but the basic responses underpinning it are not. Other species also care when they are disadvantaged, although this is apparently limited to species that routinely cooperate. This supports the existing hypothesis that negative reactions to inequity are a mechanism for identifying good partners and are related to partner choice. Indeed, Frans de Waal and I previously hypothesized that this reaction will be found in cooperative species throughout the animal kingdom, as it is a good way to identify beneficial cooperative relationships (Brosnan and de Waal, 2014). On the other hand, thus far, only chimpanzees have shown any evidence for a negative response to being overbenefitted. This response, too, benefits

individuals in the long run, as those who can recognize situations in which a cooperation partner is likely to get frustrated and act to avoid that frustration are more likely to be able to maintain these cooperative relationships. This requires an up-front cost (giving up a benefit) for a potential long-term gain from the continued relationship (Brosnan and de Waal, 2014). Thus, although this is beneficial, it is also cognitively more complex than responses to being disadvantaged, requiring a greater degree of inhibition (to avoid taking the good reward) and, potentially, planning and aspects of metacognition and theory of mind. Thus, it is likely to be limited to other long-lived, highly social, large-brained species, such as cetaceans, other apes, or elephants.

Empathy

One key mechanism argued to underpin moral behavior is empathy, or the ability to recognize states in others and identify with them (de Waal, 2009). It is typically assumed that being able to recognize when conspecifics are stressed or distressed would make it easier to provide appropriate intervention. Although some forms of empathy require high levels of cognition, such as theory of mind, at its most basic, empathy can be as simple as emotional contagion or basic perspective taking, abilities that are argued to be seen in other species as well (Preston and de Waal, 2002). Intriguingly, and presumably reflecting a bias in how humans perceive empathy, it is nearly always presented in a positive way (i.e., empathetic people understand others' needs and work to help them or alleviate distress); but empathy is neutral to valence, it can be both positive and negative. Empathy can help us understand how to help people, but also how to hurt them, and overly strong empathetic responses may blind us to more beneficial courses of action (Bloom, 2016). In addition, it can be difficult to discern whether a subject is empathetic from

their behavior alone. For example, in the section on prosocial behavior above, the studies described examine whether other species make decisions that help their partners, but are agnostic to whether empathy is the mechanism. It could be, but a subject could recognize that they may benefit by helping a partner without feeling any empathy for them.

Some of the best evidence of empathy is from studies of rodents. Bartal et al. (2011) gave rats a choice between releasing a group mate trapped in a restraint and ‘releasing’ desirable food, chocolate, ‘caught’ in an identical restraint. Rats quickly learned to free the trapped cage mate and, when given the choice between freeing the cage mate and the chocolate, typically freed the cage mate first and then shared the chocolate with them. This behavior appears to be underpinned by anxiety (but blocked by physiological stress: Bartal et al., 2016) and is at least in part mediated by familiarity, as subjects were more likely to release known individuals or those of the strain with which they were most familiar (even if it was different from their own strain: Bartal et al., 2014). Rats also respond negatively to others’ pain (Church, 1959), as do mice, who show a more negative response to their own pain if in the presence of a conspecific who is also in pain, as long as that mouse is a cage mate (Langford et al., 2006). Mice show inter-strain differences in responses, with some more gregarious strains consistently showing greater response to their partner’s distress, suggesting a genetic contribution (Chen et al., 2009) and a fairly widespread evolved tendency.

It is curious that we find such strong helping responses in rodents but not in primates. For instance, work on prosocial behavior suggests that primates often do not make any effort to bring food rewards to a conspecific. If rats are willing to free their social partners – and then share food with them – why are primates not even willing to expend the extra few seconds to choose an outcome that rewards their partner at no cost to themselves? One key difference between these two ‘helping’ conditions is that in the rodent

studies, the context is negative – rodents are freeing a partner from an unpleasant state (i.e., being trapped) or are reacting to their partner’s pain. The primate studies, on the other hand, occur in a more neutral context. These differ in both valence and intensity, and it may be that subjects are more likely to make empathetic responses in more intense negative contexts than in positive ones. This could be a difference in the willingness to help, or that the more stressful context and/or stronger responses of the partners are more likely to trigger empathy, even if only because the higher level of intensity is more likely to catch the subjects’ attention. Indeed, there is evidence from work published more than half a century ago that primates also find shocks to conspecifics to be aversive, sufficiently so that a few avoided eating for a substantial time period to avoid shocking a conspecific (Masserman et al., 1964; Wechkin et al., 1964). Although we no longer consider this methodology to be ethically appropriate, it is possible that primates’ outcomes would be more similar to the rodents’ in more similar contexts.

There are also other, more ecologically valid, contexts in which conspecifics have the potential to respond empathetically to another’s distress. One candidate behavior is consolation (Webb et al., 2017). Consolation occurs when an uninvolved individual makes affiliative contact with a recent victim of aggression, which may support the victim of aggression by providing stress relief and positive support (de Waal and van Roosmalen, 1979; Fraser et al., 2008; it also provides stress relief for the consoler, leading some to suggest that its primary function is not consolation: Koski and Sterck, 2007). It is more likely to occur after unresolved conflict and between individuals who affiliate frequently (a proxy for social closeness; Romero et al., 2010). In addition, oxytocin, a hormone associated with social interactions and bonding, including in empathy (Barazza et al., 2011; Barazza and Zak, 2009;), appears to play a role in consolation (Burkett et al., 2016).

Consolation is closely related to reconciliation, which is positive post-conflict interaction between two former aggressors that is hypothesized to repair the damaged relationship (de Waal, 1993). Interestingly, however, while reconciliation is common in both primates and other species (e.g., Cafazzo et al., 2018; Schino, 1998), consolation has thus far been seen only in apes (de Waal and Aureli, 1996) and elephants (Plotnik and de Waal, 2014). It is not clear why this is the case, but one hypothesis is that consolation requires additional cognitive capacities, such as theory of mind, in order to recognize the victim's state of mind and how affiliative contact could ameliorate their distress. If correct, this suggests a role for empathy.

CONCLUSIONS

Numerous species show evidence of some level of moral behavior. As discussed above, other primates sometimes behave prosocially and may respond negatively to inequity, occasionally even when that inequity benefits them. Whereas neither of these behaviors in and of themselves are moral, these are building blocks of the moral behavior that we see in humans. Finally, some other species have at least a degree of empathy, a behavior argued to be a mechanism for moral behavior. Although it is fairly context dependent, it appears that at least some forms are present at minimum across the vertebrates, suggesting that the roots of empathy are phylogenetically deep. Even when the specific behaviors themselves are not manifest in other species, understanding the roots of these behaviors helps us not only track how they evolved, but understand the environmental contexts that were important in shaping their evolution.

What is next? First, it would be useful to more thoroughly combine the comparative and developmental approaches, to get an understanding of both phylogeny and ontogeny. This has been done particularly

well in some topics, such as social learning and culture, and provides a broad base for understanding a behavior. Second, and related to this, a key issue in comparative research is that the procedures used with different species (or with different age groups) are typically quite different, making direct comparisons challenging. Apparatuses and procedures often must be adapted, and care should be taken to consider the ramifications and to 'back test' a new apparatus on a species with known behavior to ensure that the outcomes are the same. With humans, including children, there is the extra challenge that participants often receive substantial verbal scaffolding and cuing, as well as detailed verbal instructions, whereas nonhuman species do not. In addition, it is not always clear that we should be directly comparing adults of one species with children of another; ideally, we would compare juveniles with juveniles and adults with adults, as each species will gain specific knowledge and habits through development that may change behavior.

Third, it is important to try to develop paradigms that reflect natural situations in which aspects of moral behavior might manifest in the wild, in order to gain a better understanding of species' true abilities. Of course, more controlled tasks are still essential to tease apart mechanisms. In an ideal situation, work from the lab and the field are compared directly in order to understand both the mechanisms and where the behavior manifests (Janson and Brosnan, 2013). Fourth, and related to this, while much of the decision-making work I described involves pairs of individuals, to truly understand the evolution of moral behavior, which is inherently social, it will be necessary to expand to more complex social situations. This is challenging to design and interpret, but has been done to great effect with prosocial behavior (Burkart and van Schaik, 2013). Once we have a better idea of how subjects respond in more controlled dyadic situations, it may be easier to interpret the messiness of more natural interactions.

Moral behavior is not the only issue that can be addressed this way; there has been work on language, culture, cooperation, decision-making biases, metacognition, and numerosity, just to name a few topics. In each of these topics, understanding what other species do has helped us to better understand our own behavior. Although in none of these do other species show the same behavior as humans, understanding what they do nonetheless helps us understand how these behaviors evolved and what conditions selected for them. It will be fascinating to see what new we learn about ourselves through the mirror of other species.

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Note

- 1 I intentionally here refer to moral behavior, rather than morality, as moral behavior is simply the set of observable behaviors that describe a moral system, whereas morality implies the underlying intentions that drive it.

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Evolutionary Industrial and Organizational Psychology

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After the 2016 elections in the United States, with the accusations of election meddling on social media by foreign governments and others, Facebook began increasing the number of its ‘content moderators’ – people who view and regulate Facebook content (Newton, 2019).¹ During the course of a day, content moderators view anywhere from a few to many disturbing images and videos (e.g., animal cruelty, sexual violence, stabbings, maiming). For each image or video, content moderators make a judgment about whether to remove the post or allow it to remain on Facebook. Not surprisingly, many content moderators suffer a variety of ailments (sleeplessness, PTSD, anxiety, depression) that are probably caused by daily exposure to disturbing images (Newton, 2019). This job and its effects on the people who do it are creations of the modern world.

How might an industrial/organizational (I/O) psychologist – also a creation of the modern world – improve the working lives of content moderators? I/O psychology is an applied field that uses psychological theory,

research, and methods to help managers make more effective decisions about people, organizational design and change, and human resource systems. As a field of scientific inquiry, it focuses on people’s behavior in and the psychological dynamics of the workplace.² The ‘I’, often synonymous with personnel psychology, is associated with individual differences and their relevance (most often) to hiring, training, and job performance. An ‘I’ option for the content moderators would be to analyze the job and identify traits that predict who would perform the job well and be unlikely to suffer negative effects from viewing violent and hateful Facebook posts (perhaps a detail-oriented psychopath). The ‘O’ is associated with group and organizational characteristics, factors that influence them, and their effects on individuals. An ‘O’ option might involve giving job applicants a realistic job preview so that they would know what they are getting into before deciding to take the job, offering stress-reduction programs (mindfulness training, exercise facilities, access to therapists), or re-designing the

job or developing a job-rotation program to minimize exposure.

How would an evolutionary I/O psychologist look at this situation? She might start by asking, given what we know about human nature and the conditions under which people evolved, what would be the normal range of acceptable stimuli for most people? To what degree is the work environment of content moderators mismatched to our evolved psychology? What is the likelihood that people exposed to this environment would suffer? If so, how could this work environment be changed so that it is more compatible with human nature? An evolutionary I/O psychologist might conclude that the mismatch between the job and human nature is so severe that there is not much that can be done to improve the situation, other than to remove people from it. She might recommend that the company use computer algorithms to delete harmful images (McGilchrist, 2019).

The purpose of this chapter is to describe the burgeoning field of *evolutionary industrial/organizational psychology* (EIOP), largely within the broader context of traditional I/O psychology. EIOP has two components. The first is scholarship in domains of traditional I/O psychology (e.g., personnel selection, leadership, workplace sexual harassment) approached from the perspective of evolutionary psychology. The second examines work and organizational topics that have been ignored by most I/O psychologists but have evolutionary psychological roots and are commonplace in the world of work (family businesses, natural elements in the workplace, cooperation, and collective action). In both cases, what is critical for understanding EIOP is the intersection between *evolved psychological adaptations* and *features of the modern work environment*.

HUMAN NATURE AND THE MODERN WORKPLACE

Psychological adaptations are evolved (and hence heritable) cognitive and emotional

algorithms in the human mind that guide thought, emotions, and behavior when a person is confronted with specific environmental stimuli. Just as our physiology evolved in response to environmental pressures, so too did our mental processes. As humans evolved during the Pleistocene epoch, they encountered recurrent problems in the natural environment and from other people. Individuals who possessed traits that improved their chances of dealing successfully with these problems were more likely to survive and reproduce. Therefore, the genes contributing to those traits were more likely to spread throughout the population. For example, most people instinctively fear snakes and spiders because, over our evolutionary history, bites from venomous snakes and spiders could be debilitating or fatal. Therefore, people who had an instinctive fear of snakes and spiders were more likely to survive and reproduce than those who had no such fear. Most of our psychological (and physiological) adaptations evolved during the Pleistocene epoch (beginning about 1.2 million years ago and continuing to the Neolithic era, which began about 10,000 years ago). Evolutionary psychologists refer to this as the environment of evolutionary adaptedness (EEA). It was the time period when many species of hominoids came into existence and when ancient and modern *Homo sapiens* emerged (about 150,000 years ago) and became the dominant and (about 30,000 years ago) only hominoid species on the earth. Although we live in the modern world, much of our mental apparatus evolved in and was programmed for living in the Pleistocene. That is, our mental adaptations for perceiving, understanding, and reacting to the world and other people are pretty much the same as they were when we were living as hunter-gathers on the African savannas (Kanazawa, 2004; Tooby and Cosmides, 1990). Thus, many adaptations that influence our behavior at work today evolved during the Pleistocene era – long *before* the modern workplace.

However, the modern workplace and the context of work during the EEA are light-years apart.³ Many features of work in hunter-gatherer societies – the best analogues to how our ancestors lived during the EEA – differ from the features of the modern workplace. Among hunter-gatherers, work is integrated into community and family life, rather than being a separate sphere. People work with kin and close acquaintances. Work is governed by custom, tradition, and informal rules. Some hierarchy exists. People learn their work skills primarily by observation, imitation, and apprenticeship. Decision-making is less formal, without the benefit of mathematical decision aids, and influenced by cultural norms.

In the modern context of work, the features of work in ancestral environments are turned on their heads. Work is demarcated from non-work – in place, by activity, and by other people. Work is usually done somewhere other than the home or neighborhood (typically a place just for work), is often a specialized activity, and is done with people who are at best acquaintances – not close kin or companions. The modern workplace is governed (in principle) by rational-legal rules, with hierarchical authority structures. Hiring and promotions are (in principle) done on the basis of

achievement (credentials, experience, knowledge, and skills) rather than ascription. People acquire job knowledge and skills through general education and training that occur first outside of the job setting and then later on the job. Decision-making increasingly involves mechanical (analytical) decision aids (spreadsheets, algorithms). Organizational justice is codified in personnel policies, influenced by national legal systems, and is typically impersonal and transactional. Finally, there is often a clear distinction among workplace owners, managers, and workers (Diamond, 2013; Nicholson, 2012). Our current suite of psychological adaptations is predicated to life and work as it existed in the EEA, not as it is now (see Table 6.1). Therefore, our evolved psychology is mismatched to the modern work environment – a topic we discuss later in this chapter.

I/O PSYCHOLOGY – ITS BEGINNINGS AND CORE ASSUMPTIONS

Much of traditional I/O psychology evolved in response to social and economic conditions faced by employers and organizations –

Table 6.1 Work, organization, and management in early hunter-gatherer societies (Then) contrasted with contemporary models (Now)

<i>Then</i>	<i>Now</i>
Fuzzy boundary between work and non-work	Clearly demarcated work and leisure time
Close intertwining of consumption and production	Units of production and consumption mostly separated in time and space
Labor alongside and in cooperation with close or distant kinfolk	Collaborative endeavors often with non-kin and often with strangers (one-shot interactions)
Labor governed by informal agreements and norms of reciprocal exchange	Labor governed by formal contracts specifying rights, obligations, and rewards
Authority fluid and shared, based on availability, expertise, interest, or experience	Authority vested in positions, often hierarchical, based on formal criteria or selection processes
Skill developed by mimesis and mentorship	Skills developed primarily by formal education and training schemes
Rewards for labor that are intrinsic or collective (food-sharing)	Rewards that are extrinsic and individual, mediated by agents and contracts

Source: Nicholson (2012).

a characteristic of the field that continues to the present day.⁴ I/O psychology's beginnings are typically traced back to the late 19th and early 20th centuries, with the advent of the industrial revolution.⁵ This was a time when a confluence of social, economic, and scientific forces were ripe for the emergence of I/O psychology. Large masses of people left their homelands and traditional ways of making a living to work as laborers in factories and in other industries spawned by the industrial revolution. Factory owners and managers were faced with the novel problems of how to hire, train, and motivate large numbers of workers in the new industrial system. At the same time, scientific psychology emerged from laboratories in Europe and quickly spread to the United States and, along with the positivism of Auguste Comte, was part of the scientific and intellectual zeitgeist. Positivism was a philosophical program that argued that just as the natural sciences allowed for the greater understanding, manipulation, and prediction of natural elements and the natural world, the new social sciences could do the same with society and organizations. Many of the problems of society and the economy could be solved by programs that were informed by social science. I/O psychology emerged during this heady time. Psychologists (and others) believed that the principles, methods, and findings of scientific psychology could be applied to the new realities of industrialization to help make the acquisition and management of employees more effective and efficient. The founders of I/O psychology were among the most prominent psychologists of their day: Hugo Münsterberg at Harvard, James Cattell at Columbia, and Walter Dill Scott at Northwestern – all of whom had been elected President of the American Psychological Association.⁶ Other notables included Walter Van Dyke Bingham at the Carnegie Institute of Technology (now Carnegie Mellon University) and the industrial engineers Frank and Lillian Gilbreth and Frederick Taylor.

Much of the work of early I/O psychologists involved personnel selection – identifying traits that would be compatible with particular jobs and tasks.⁷ For example, Münsterberg (1913) developed a series of tests to help select motormen for a Boston electric-railway company. The goal was to reduce accidents by measuring the trait of accident proneness among applicants and selecting those who were the least accident prone. The apex of industrial psychology's early efforts in personnel selection was the development of the Army Alpha and Beta tests (verbal and non-verbal group-administered intelligence tests). These tests were used for selecting and placing recruits in the Army during World War I. James Cattell, Robert Yerkes, and Walter S. Bingham were their principal architects.⁸

The beginnings of organizational psychology are often associated with Elton Mayo and his research at the Hawthorne Works in Cicero, Illinois, in the 1920s and with Kurt Lewin's work in leadership and group dynamics after World War II. Mayo was critical of Taylorism, particularly because it paid little attention to human relationships and the larger social context of the workplace. Mayo, a professor at Harvard Business School, was interested in how social factors influenced productivity and morale. Lewin's famous dictum, 'there is nothing as practical as a good theory', conveyed his interest in using psychology to solve applied problems (Lewin, 1943, p.118). Although Lewin famously argued that behavior is a function of the person and the situation, his field theory emphasized forces in the immediate situation. Many of his experiments were motivated by real social problems and the belief that psychology could help. These included using group pressure to change eating habits, using groups to promote racial integration, and experimentally examining the effects of different leadership styles (Marrow, 1977). Another difference between the beginnings of personnel and organizational psychology was the humanitarian side of organizational psychology.

I/O Psychology and American Functionalism

Münsterberg and Cattell studied with Wilhelm Wundt in Germany. However, they rejected their mentor's structural psychology for American functionalism, advocated by William James at Harvard. This may have also attracted Münsterberg to James, ultimately leading to Münsterberg appointment as a professor of psychology at Harvard. Wundt and the structuralists believed that the project of psychology was to understand the general laws of behavior from the inside out, by identifying basic mental components through introspection and experiments (not unlike the goals of modern evolutionary psychology). Those in the American functionalist camp, led by James, were not interested in understanding the basic units of the mind and the laws governing them. Indeed, they believed such a project was impossible. Even if these basic units were discovered, they were not certain how they could be useful. Rather, they were interested in how individuals adapted to the environment and why some individuals adapted better (or worse) than others. The functionalist view was compatible with trends emerging in American psychology at the time – individual differences and behaviorism. Thus, the underlying premises of I/O psychology, over its 100-plus-year history, involve two seemingly contradictory beliefs about human nature: (1) stable individual differences and their importance for performing particular tasks and (2) the power of external forces for influencing the thoughts and behavior of individuals.

The pro-functionalist and anti-structuralist outlook of the early I/O psychologists offers a clue into the intellectual DNA of traditional I/O psychology, and it may also help in understanding why evolutionary psychology has been slow to make roads into I/O psychology. Although William James was one of the first American psychologists who considered himself a Darwinian, the tenets of

his functionalism were closer to those of the standard social science model than to those of modern evolutionary psychology, while Wundt's structuralism was similar in basic outlook to evolutionary psychology. Modern evolutionary psychology, like Wundt's structuralism, focuses on the underlying structures of the mind. The difference is that evolutionary psychologists are also interested in the evolutionary processes underlying how those structures of the mind came to be. Ironically, although I/O psychology emphasizes the importance of individual differences, it rarely acknowledges Darwin and evolution. The flip side is that although evolutionary psychology is solidly Darwinian, it has mostly eschewed individual differences, relegating them to random genetic noise (Buss, 2009; Tooby and Cosmides, 1990).

Despite these divides, there were areas of convergence – such as variation in traits – although they were largely implicit. However, as evolutionary psychology developed and gained broader acceptance in the late 20th and early 21st centuries, scholars with interests in both evolutionary psychology and I/O psychology began to find greater areas of convergence. They would come to view evolutionary psychology as a broad meta-framework for understanding the psychology of people in the workplace.

EIOP – TRADITIONAL DOMAINS OF I/O PSYCHOLOGY

Personnel Selection and Individual Differences

Variation in traits

Personnel selection, which is arguably the most prominent subfield in I/O psychology, has a strong evolutionary foundation – variation in individual traits.⁹ A fundamental premise of evolution by natural selection is that individuals vary in traits, and individuals with traits that are adaptive to their environment are

more likely to survive and reproduce. Variation in individual differences is also foundational to personnel selection.¹⁰ Traditional personnel selection assumes that (1) individuals vary in physical and psychological traits, which (2) by adulthood are relatively fixed through heredity, socialization, or a combination of both; (3) these traits exist in some quantity, can be measured, and individuals ranked accordingly; (4) possession of high levels of task-compatible traits enables an individual to perform more effectively than someone without or with a low level of the trait; (5) through valid testing procedures, organizations can select job applicants whose trait levels best match job requirements, thereby enhancing individual job performance and thus contributing to the overall effectiveness of the organization (Highhouse et al., 2015; Society for Industrial-Organizational Psychology (SIOP), 2018).

Criteria

Matching traits to environmental demands is fundamental to both evolution by natural selection and personnel selection. However, there are also fundamental differences, such as the criteria for a successful match between traits and environmental demands. With biological evolution, the criteria for success are straightforward: reproduction and surviving offspring. With I/O psychology, the criterion for success is some metric of performance – usually job performance at the individual level, but it can also be at the team or organizational level. Unlike biological criteria, performance criteria in I/O psychology and management are complex and ambiguous. Defining successful job performance is fraught with changing perceptions, judgment calls, and complexity (Colarelli, 2000). This is known as ‘the criterion problem’ – a problem that has plagued I/O psychology for years and is unlikely to be resolved (Austin and Villanova, 1992).

Selecting adaptive traits

Another difference is the optimal method for selecting adaptive traits. Biological and

social systems are so complex that it is difficult to know (in advance) the consequences of a trait. Thus, evolutionary theory assumes that adaptive traits are selected by *trial and error over deep time* – hundreds or thousands of years, depending on the organism and the trait. Moreover, these trials and errors *do not lead to optimal traits*. Rather, they result in traits that are ‘good enough’ – compromises that fit with other previously evolved traits (Partridge, 1982; Williams, 1966).¹¹ I/O psychology, on the other hand, assumes that *contemporaneous expert selection* leads to the identification and use of appropriate traits for achieving valued outcomes (such as individual and organizational performance). The typical approach is to identify a trait that is presumed to be useful in predicting a valued criterion, test employees or job applicants on this trait, and correlate their scores with the outcome of interest.¹² Now, this approach has proven useful in identifying traits, such as cognitive ability and conscientiousness, that predict job performance across jobs and across organizations (Barrick et al., 1993; Higgins et al., 2007; Schmidt and Hunter, 1998). However, there are a few caveats. Effect sizes are generally small (explaining about 3% to 10 % of the variance in job performance). This is not necessarily a problem if we view selection as compound interest.¹³ Over time, and by hiring large numbers of people, even small increments in validity pay off (Schmidt and Hunter, 1998). However, although aggregate IQ is associated with the productivity of organizations (Schmidt and Hunter, 1984) and national productivity (per capita gross domestic product; Jones, 2011a), it is not a guarantee against organizational failure. Investment banks and accounting firms typically recruit and hire only the brightest professionals; yet, the failures of companies like Lehman Brothers and Arthur Anderson (Collins, 2019; Lioudis, 2019) demonstrate that organizations full of bright, highly educated people can fail. Collapses of organizations teeming with talent could be due to the biological equivalent of genetic

drift – chance events that reduce the frequency of gene variants in a population (e.g., the giant meteor that wiped out the dinosaurs 65 million years ago). Organizational equivalents might be bad decisions by upper management, new government regulations, and unforeseen changes in the supply of critical resources.

Conflicts and incompatibilities

Conflicts and incompatibilities among traits and valued outcomes are other reasons why a trait that correlates positively with a valued outcome (e.g., IQ correlating positively with job performance) may not, from the perspective of the total system, be beneficial (Colarelli and Stumpf, 1990). A valued trait may be negatively related to valued outcomes other than the ones of interest. For example, cognitive ability is negatively related to job satisfaction (on less cognitively demanding jobs) and to organizational commitment (Ganzach, 1998; Steers, 1977), and it is positively related to turnover (Maltarich et al., 2010). Depending on the circumstances, conscientiousness is either negatively related to creativity (Egan, 2005; George and Zhou, 2001) or not related (Reiter-Palmon et al., 2009).

Modern versus Darwinian algorithms

A strongly held belief in traditional I/O psychology is that ordinary people cannot make predictive judgements that are as accurate as algorithmic decision systems using the results of scientifically designed tests – that is, psychometric (or mechanical) decision-making systems (Adams et al., 1994; Sawyer, 1966; SIOP, 2018). Psychometric selection involves selecting candidates who have high scores on tests that measure traits empirically linked to expected outcomes (in I/O psychology, this is usually job performance). Ideally, this takes decision-making out of the hands of people doing the hiring and those who would be working with the candidate (Colarelli, 2003), making the hiring process (ostensibly) more objective

and untainted by human judgment and biases. These methods have been in existence for about 100 years and became widely used in the past 50 or so years (Bock, 2015; Wigdor and Garner, 1982).

The use of mechanical decision systems for hiring can be reasonable and appropriate to modern situations where hundreds or thousands of candidates need to be assessed in short periods of time, as might be the case in the military, mass higher education, and large corporations.¹⁴ Although this is evolutionarily novel, with no analogue in our ancestral past, it is an example of cultural evolution, where an idea (in this case, psychometric selection) has caught on and continues to be used where it results in more benefits than costs. Colarelli (1996), for example, found that with larger organizations and job types where people are hired *en masse*, modern methods, such as multiple-choice personality and intelligence tests, are more common. However, in smaller organizations and in jobs where applicants are carefully vetted individually (e.g., managers and professionals), traditional face-to-face assessments (interviews) are still preferred (Colarelli, 1996). Thus, in most situations where people are making decisions about others with whom they are likely to interact for an extended period, psychometric methods are mismatched with the way people have made decisions about others for thousands of years – gathering information by face-to-face interaction and by reputation.

Humans evolved psychological mechanisms for judging other people: would a person be likely to cheat, cooperate, or deceive? Does he have useful skills, leadership potential, or potential as an ally or enemy? Therefore, many of our implicit judgments about people are likely to be reasonably accurate (Funder, 1995). This is why people still prefer what Colarelli (2003) has termed *traditional hiring methods* (methods that rely on face-to-face interaction or narrative) and why they are still widely used. These include the employment interview, job-sample tests,

and letters of recommendation. Indeed, the employment interview is still one of the most popular selection methods (Keenan, 1995; Shackleton and Newell, 1991).¹⁵

Leadership

Leadership is one of the most studied topics in I/O psychology and management (Hersey and Blanchard, 1982; Judge and Piccolo, 2004; Pearce and Conger, 2003). In general, traditional I/O psychology takes a pragmatic view of leadership – focusing on characteristics of leaders versus non-leaders, good versus bad leaders, leader relationships with subordinates, and leadership styles (Jokinen, 2005; Parris and Peachey, 2013; Yahaya and Ebrahim, 2016). For example, most I/O leadership textbooks discuss leader traits and behaviors, contingency theories of leadership, leader–member exchange, and transformational versus transactional leadership styles. The focus is on the mechanics of leadership – proximate questions. What qualities do leaders have or how must leaders behave to be successful? What are the differences in leadership styles and what difference do they make (Boehm and Staples, 2005; Weinberger, 2009; Zaccaro et al., 2013)? Evolutionary I/O psychology takes a step back and focuses on the functions and origins of leadership – ultimate questions. Why do social mammals have leaders? What is the function of leadership in social species? What are the adaptive benefits of followership? What motivates people to become leaders and to remain in leadership positions? What are the evolutionary advantages of being a leader? An evolutionary understanding of human leadership is unique in that it frames leadership in a broader context of adaptation and natural history.

Leadership among social animals

Before looking at the evolutionary psychology of leadership among humans, let's step back and take a short survey of leadership in

some other social mammals. Looking at leadership among non-human social animals provides a broader context for leadership by providing evidence for generalizable functions of leadership, psychological mechanisms for leadership (and followership), and how evolved leadership traits are both generalizable and dependent on a species' natural history (Smith et al., 2016). In evolutionary biology and evolutionary psychology, a clue that a trait or behavioral repertoire is an evolved adaption is that it is widespread and historical (Henrich and McElreath, 2003). That leadership is so widespread among different social species suggests that both leadership and followership are based on evolved psychological mechanisms (Price and Van Vugt, 2015; Smith et al., 2015): individuals who developed psychological adaptations to behave as leaders and as followers were more likely to survive and reproduce than those who were inclined to go it alone.

Social animals have leaders (King and Cowlshaw, 2009). Even social insects, whose behavior is mostly instinctual, have leaders. While leaders of social insects (the queens) do not engage in what we might typically characterize as leadership behaviors, they do direct and control critical activities – sex and reproduction – of the hive (Van Oystaeyen et al., 2014; Zweden, 2010). Social mammals, of course, operate in more behaviorally and ecologically complex environments than social insects and, therefore, their groups face more complex problems. This requires leaders with broad behavioral and mental repertoires.

For those unfamiliar with leadership among mammals other than humans, it is remarkable to observe it. Perhaps most famous are the scientific and popular accounts of chimpanzee leadership and politics. Notable are Jane Goodall's studies of chimpanzees of the Gombe in Tanzania (Van Lawick-Goodall, 1973) and Frans de Waal's description of chimpanzee politics among a troupe of chimpanzees in the Burgers' Zoo in Arnhem, the Netherlands (De Waal, 2000).

Less well known, but equally remarkable, are studies of leadership among, for example, elephants (McComb et al., 2001, 2011), feral horses (Berger, 1977), bottlenose dolphins (Lusseau and Conradt, 2009), various species of monkeys (Nishida, 2012; Perry et al., 2004), wolves (Peterson et al., 2002), spotted hyenas (Smith et al., 2015), and zebras (Estes, 1991; Smith et al., 2016).

It appears that leaders of social mammals perform common functions, which include group coordination, resource identification and allocation, enforcement of group norms, and conflict resolution (Smith et al., 2016). Experience, dominance (to varying degrees), social skills, and intelligence appear to be common traits among leaders of non-human social mammals (De Waal, 1996; Holekamp et al., 2007; Weissing, 2011). Leaders among social mammals behave in a dominant manner compared to others in the group, but the level of dominance and aggression varies by species and sex. For example, chimpanzee and spotted hyena leaders are domineering and aggressive, whereas among bonobos and elephants, leaders are more relaxed, social, and cooperative. The sex of leaders varies by species. Leaders are female among elephants, bonobos, and spotted hyenas, while leaders are male among chimpanzees, feral horses, baboons, and bottlenose dolphins (Feist and McCullough, 1975; Nishida, 2012; Stueckle and Zinner, 2008). Wolf packs are led by a dominant male–female (breeding) pair.

It appears that the sex of leaders is influenced by the ecology in which a species evolved and their mating systems (Low, 2000). For example, bonobos – close cousins of chimpanzees – evolved in the dense jungle of the Congo Basin in Central Africa. It provides bonobos with a rich environment for food and shelter. This – and the polyamorous sexual behavior of bonobos – probably contributed to the higher status of females and female leadership among bonobos. In contrast, chimpanzees evolved in sparser conditions, mostly in the forests bordering savannas, where control of territorial

resources is critical to survival. Hence, a more aggressive and combative style of leadership was adaptive.

Motivation to lead

What's in it for the leader? The benefit of leadership in animal societies seems to be clear: dominant members of a group tend to enjoy reproductive advantages. They produce more offspring, and their offspring are better provided and cared for, thus enhancing the chances of their surviving into adulthood (Alvard, 1993; Low, 2000).

What motivates humans to become leaders? Why do they stay in leadership positions? These ultimate questions are curious omissions from the traditional I/O psychology literature on leadership. From the EIOP perspective, there are three primary motivators for human male leaders: status, resources, and mating opportunities (Kniffin et al., 2014; Rueden et al., 2010; Van Vugt and Ahuja, 2011). Offspring are the currency of all sexually reproducing organisms. Thus, driving forces behind human and animal behavior are attracting and securing a mate, reproducing with the mate, and rearing offspring (Low, 2000). Among humans, women are the final arbiters in reproduction. They prefer men who have good genes, can provide resources for her and her children over the long term, and can protect the family. This translates into men who are socially dominant and have resources and status or the potential to acquire them (Buss et al., 2001). Hence, the appeal to men of leadership positions is that compared to non-leaders, leaders have greater access to fertile women.

Leaders accrue more resources than followers do.¹⁶ For example, in the United States, CEOs of *Fortune* 500 companies make, on average, 287 times more money per year than their employees. Larry Ellison, the Co-founder and Chairman of Oracle Corporation, received a compensation package of \$108.9 million in 2018, while the average annual salary of Oracle employees was \$90,000 (Sanders, 2018). The average

annual salary for a public school principal in the United States is about \$129,154, while the average teacher's salary is about \$45,082 (AFL-CIO, n.d.). Executive and managerial jobs are among the highest in occupational prestige (NORC Scores, 2012).

Physical features of leaders

Both natural and sexual selection also sculpted psychological adaptations for preferring certain characteristics in leaders: being a tall male with masculine facial features. Most political leaders in the world and the leaders of large organizations are men (Geiger and Kent, 2017; Mejia, 2018). Male leaders tend, on average, to be taller than followers (Lindqvist, 2012). In US presidential elections, the majority of winners are taller (Stulp et al., 2013; Young and French, 1996, 1998). In a study of US senate races, Todorov et al. (2005) found that politicians with masculine facial features (prominent square jaw, angular face, larger nose, smaller eyes, and low forehead) won 70% of the contests. They were also rated as more competent than their male competitors with 'baby-faced' features. Yet, the men with more baby-faced features tended to be more intelligent, more educated, and more likely to win military awards. Rule and Ambady (2008) found that naive perceptions of leadership ability based on CEOs' faces are significantly related to how much profit those CEOs' companies made. Wong et al. (2011) examined actual facial features of male CEOs, and they found that CEOs with more masculine features (wider faces relative to facial height) achieved superior financial performance, although this was moderated by the cognitive complexity of leadership teams – the lower the cognitive complexity of the leadership team, the stronger the relationship between masculine facial features and firm performance.

Formidability

An evolutionary psychological explanation for the preference of physically formidable male leaders with masculine facial features is

that these were the type of leaders that could have best led the small bands of humans when our distant ancestors existed as hunter-gathers. During the Pleistocene epoch, our human ancestors must have faced and dealt with more physical dangers – warring tribes, large predators, and physical confrontations among their own tribe – than we do now (Keeley, 1996; Pinker, 2012). In such circumstances, a physically formidable male leader would have increased the chances of a group's success and survival, increasing individuals' chances of survival and reproductive fitness. Hence, we probably inherited the psychological tendency to perceive the features 'tall' and 'masculine' to be associated with the 'big man' leader (Kniffin et al., 2019; Stulp et al., 2015). Being so perceived, it is easier for people with those features to rise to and assume leadership positions (Re et al., 2013).

Two questions follow from this: were leaders among our hunter-gatherer ancestors aggressive bullies, using their strength and physical stature to coordinate and command? And what about smaller men and women as leaders? When confronting some aggressive band members or warring tribes, physical formidability was surely an asset. Even in routine deliberations, a leader who *could* inflict harm would be more likely to be taken seriously. As the African proverb aptly suggests, 'speak softly – and carry a big stick – and you will go far'. However, this does not mean that shorter men cannot become, or achieve success as, leaders. Some notable examples include Napoleon Bonaparte (5'7"), Hồ Chí Minh (5'5"), Joseph Stalin (5'6"), Winston Churchill (5'6"), Deng Xiaoping (5'0"), Yasser Arafat (5'2"), Ariel Sharon (5'3"), Vladimir Putin (5'7"), Mark Zuckerberg (5'7"), and (at time of writing) the richest man in the world, Jeff Bezos (5'7").

Leadership mismatch in modern organizations

While height and masculine features are statistically associated with leadership, leadership behaviors win the day. In his seminal

work on leadership and hierarchy among hunter-gatherers and non-human primates, Boehm (1999) argues that – unlike the more rigid dominance hierarchies among our primate cousins – most human hunter-gatherer groups have modest to flat hierarchies. Effective and esteemed leadership in these groups requires strong social bonds, mutual trust, and rich communication. Moreover, it is through these features of human groups (as well as the use of weapons, which give the dominated a distinct advantage of non-human primates) that allow what Boehm (1999) calls a ‘reverse dominance hierarchy’ to emerge. In other words, the group keeps a leader in check if he becomes too aggressive or domineering. Price and Van Vugt (2015) and Henrich (2016) take this line of argument a step further by drawing the distinction between leader dominance and prestige. They argue that when both followers and leaders have strong negotiating positions (e.g., followers have exit options and leaders have skills that are valuable to the group), leaders and followers engage in a type of exchange. Followers give leaders status based on prestige, and the leader, in exchange, provides valuable services to the followers. When followers do not have strong negotiating positions (e.g., no exit options, poor access to information, weak communication networks, inability to think clearly, few or no weapons), leaders have the upper hand and gain status through dominance (i.e., the ability to harm followers).

According to Price and Van Vugt (2015), these strategies emerged from psychological adaptations that were sculpted over deep time as our ancestors endeavored to solve recurring problems associated with leadership and followership. Interestingly, these behavioral tendencies associated with leadership and followership have a good deal in common with non-evolutionary theories in traditional I/O leadership literature – for example, the social exchange (leader–member exchange) theory of leadership, transactional and

transformational leadership, and servant leadership (Price and Van Vugt, 2015).

There are several reasons for the over-representation of men in leadership positions. The mainstream I/O psychology, management, and gender studies literature suggest that it is due primarily to bias and discrimination – for example, socialization and educational practices that discourage women from leadership roles (Betz and O’Connell, 1989; Bogat and Redner, 1985; Broadbridge and Weyer, 2007; Veale and Gold, 1998). The lack of representation of women in positions of leadership is an unfortunate state of affairs in the 21st century, when physical prowess is, in most circumstances, irrelevant to leadership and influence and when social and cognitive skills are critical. Women do not differ from men in average cognitive ability, they are better communicators, more cooperative, and more concerned with the welfare of others than men are (Geary, 2010). One would think, therefore, that they would be naturals for leadership positions.

Although there are several evolutionary perspectives on sex differences in leadership attainment, we believe that the mismatch perspective holds promise. The mismatch hypothesis suggests that present-day humans are psychologically (and physically) mismatched to the modern environment (Li et al., 2018; Lieberman, 2013). Our psychological mechanisms for sensing and interpreting the world mostly evolved during the Pleistocene epoch, when our ancestors had lived in migrating hunter-gatherer bands while using primitive technologies to make a living. This was when our adaptations for leadership and followership evolved. Just as few people today die from snake and spider bites, most of us instinctively fear and recoil at the sight of them, even if they are just images on a movie screen – people are still likely to regard masculine men as leadership material, even though many women may be better qualified for the job.

Another mismatch involves our coalitional psychology. For most of human evolutionary

history, men operated in all-male coalitions focused on politics, big-game hunting, war, and economic activities. Women operated in all-female coalitions, focused on children and food production. Male–female coalitions occurred in the *family* sphere, involving sex, reproduction, rearing children, and family politics (Low, 2000). Therefore, male coalitional psychology does not involve women outside of the family sphere. Simply put, men evolved to compete with other men for status, resources, and sexual access to women, while women evolved to compete with other women to attract desirable men (Campbell, 2013; Low, 2000).

However, the modern world has turned this psychological calculus on its head. Women comprise at least 40% of the workforce in 80 countries. The median female workforce participation across the world is 45% (Fetterolf, 2017). Men and women must now compete with each other in economic organizations for salary, status, and job security. Yet, this type of competition is evolutionarily novel, and there are no evolved psychological mechanisms providing instinctual guidance. People often fall back on existing psychological mechanisms when navigating male–female coalitions in the workplace. This may be another reason why we still have few women in leadership positions. Many men and women feel awkward and are inept at working and competing with opposite-sex peers. Change is occurring.¹⁷ However, it will be slow because successful change requires policies and structures that counter our evolved coalitional psychology and perceptions of leadership.

Women and Work

Research in mainstream I/O psychology addresses differences between men and women, although it suggests that these differences are minimal, with a few exceptions (Hyde, 2005). In addition, these differences are mainly attributed to socialization and

cultural stereotypes (Browne, 2002). EIOP takes a broader perspective by considering both the accepted influence of socialization, culture, normative expectations, *and* evolutionary explanations of why sex differences exist.

Personality and behavior

In one way or another, personality plays a role in nearly every aspect of talent management (Bartram and Guest, 2013), and here, differences emerge between men and women – differences that cannot be fully explained by environmental factors, such as dominance and aggression, and where the effects are large, with a significant impact on employee outcomes, such as leadership emergence (Eagly and Karau, 1991; Krueger et al., 2008; Ritter and Yoder, 2004; Turkheimer, 2000).¹⁸ Women, on average, report higher levels of extraversion, agreeableness, and neuroticism compared to men (Weisberg et al., 2011). Even when men and women display comparable levels of traits, behavioral outcomes may vary (Gonzalez-Mule et al., 2013).¹⁹

In our ancestral environments, where many of our psychological responses and mechanisms were formed, women were segregated into caring roles, favoring selection for caretaking. Lower emotional stability may have been adaptive for women, enabling them to be more cautious in protecting themselves and their offspring. Alternatively, given that men and women typically display behaviors that would have helped them to attract mates and achieve reproductive success (Browne, 2002), it may have been adaptive for men to take more risks and be more dominant in social interactions.

Men and women also show temperamental differences that may be related to differences in leader emergence and selection (Browne, 1998). For men, intrasexual (male–male) competition is the prime avenue for reproductive success, but this is less so for women. Accordingly, we see generalized distinctions in temperament, preferences, and behavior

that contribute to differences in workplace status. Other researchers (e.g., Colarelli et al., 2006) have suggested that much deeper biological differences in the neuroendocrine systems of men and women may contribute to the sex differences that we often find in how women lead in work environments. Men have more testosterone and catecholamines than women; also, for men (but not in women), these hormones are boosted by competition and remain high after winning in a competition.

Many workplace roles require employees to monitor and modify their outward actions to fit in.²⁰ From an evolutionary perspective, men might have been under greater pressure to monitor and modify their outward behavioral display to build strategic ties to better compete with internal and external rivals, as compared to women, who were primarily caretakers and thus required fewer instrumental ties for survival (Eagly, 2013). This may result in the disparities often noted between men and women in terms of organizational achievement, as men engage in self-monitoring more often – a behavior that is linked to higher job performance and leadership emergence (Day et al., 2002).

Acknowledging our evolutionary past and plausible mechanisms that contribute to sex differences found today can help improve the methods of reducing sex bias. For example, identifying sex-based mismatches and how they hurt the bottom line may help to lower inequality in selection and promotion procedures. Further, training on how to deal with these differences and why they exist may inform leaders about embracing differences and utilizing them for competitive advantage, rather than attempting to downplay their existence.

Sexual harassment

Sexual harassment can take one of two forms: quid pro quo harassment and hostile-environment harassment, with women experiencing significantly more sexual harassment than men (Aggarwal and

Gupta, 2000). Quid pro quo harassment refers to the solicitation of sexual favors in exchange for rewards in the workplace, while hostile-environment harassment creates a workplace permeated by unwelcome sexual behaviors and innuendos. I/O psychologists have argued that sexual harassment stems from organizational characteristics, such as the organization's tolerance for sexual harassment and abusive, hyper-masculine cultures (Fitzgerald and Cortina, 2017; Willness et al., 2007). Power differences between men and women and traditional sex rules that spill over into the workplace are also thought to be causes (Lopez et al., 2009).

EIOP suggests that we should also consider how sex differences in sexual behavior and perceptions and reproductive goals influence the occurrence of sexual harassment (Browne, 1997). Recognition of evolved differences in sexual behavior allows for a better understanding of sexual harassment (Colarelli and Haaland, 2002). For example, the higher sexual drive of men compared with women suggests that when each is provided power in an organization, men are more likely to abuse that power – a common belief between feminist and evolutionary perspectives (Studd and Gattiker, 1991). It is further suggested that sexual harassment committed by men is, to some degree, a (misplaced) reproductive strategy (Muller and Wrangham, 2009). Thus, by acknowledging how evolved sex differences and strategies contribute to sexual harassment, the EIOP perspective suggests *stronger* policies and sanctions against sexual harassment compared to traditional I/O psychological perspectives.

Career issues

Although men and women are about equally represented at lower levels of organizations, fewer women are represented at higher levels (Powell and Graves, 2003). What roadblocks are women facing that keep them from

entering the pipeline to higher organizational levels at a comparable rate to men? Traditionally, I/O psychologists have approached this question by exploring structural and cultural inequalities, such as sex differences in performance standards and pay (Ginther and Hayes, 1999), differences in selection and promotion, stereotyping, and the effects of work–family conflict.²¹ For example, women who perform to a similar standard and have comparable experience to their male counterparts are frequently compensated less than their counterparts (Blau and Kahn, 2007). Further, women tend to receive fewer salary increases and fewer promotions (Chernesky, 2003) and experience work–family conflict more frequently than men (Martins et al., 2002).

In this chapter, we have argued that sex differences have – in part – an evolutionary basis; throughout most of our hominid ancestral past, where physiological and psychological mechanisms evolved, men and women performed different roles. For example, men seem to perceive risk-taking as an opportunity, yet women tend to view risk-taking as dangerous (Browne, 2002). This difference can be partially attributed to varied ancestral roles: men had to take risks to achieve their goals while women had to be more cautious for the welfare of their children (Duxbury and Higgins, 1991; Rhoads, 2004). Thus, women are more likely to choose jobs in helping sectors, such as education and health – a decision that is linked with fewer career ladders to corporate office jobs (Powell and Graves, 2003). Further, evolved preferences in men (e.g., competitiveness, risk-taking, dominance) are associated with leadership positions both in our ancestral past and in current C-suite boardrooms (Powell and Graves, 2003), though the actual job is not perceived as belonging to either male or female.

Evolutionary I/O psychologists acknowledge sex discrimination in the workplace, and they are interested in and committed to reducing it. The more we understand about sex differences – and evolutionary

psychology can help here – the better we are able to create non-discriminatory environments. Although several factors play a role in these differences, traditional I/O psychology seems to dismiss differences as unimportant and rejects evolved differences. Undoubtedly, cultural and societal factors impact women at work. Yet, I/O psychologists and the practitioners who apply I/O psychology to solve problems in the workplace may benefit from considering EIOP, which also incorporates evolved sex differences. We believe that EIOP provides a broader approach to addressing problems that women face in the modern workplace. By accepting the role of both culture *and* evolved sex differences, evolutionary psychology can help in strengthening policies to create safe, supportive, and equitable work environments for women.

Organization Design, Development, and Change²²

Most of traditional I/O psychology deals with individuals and the influence of organizations on individuals. Organization design, organizational development, and organization change – three closely related fields – focus on larger units of analysis: groups, teams, organizational departments, and entire organizations. Perhaps more than other subfields of I/O psychology, organization design, development, and change are also prominent subfields of management and organizational sociology.

Organizational design examines how relationships among people in an organization should be structured to achieve desired ends. It addresses how to modify an organization's structure and processes – typically, authority, control, and communication – to best adapt to internal and external conditions. These conditions would include state of the organization's environment (competition, turbulence, and uncertainty), technology (e.g., simple, complex, routine or non-routine),

and knowledge and skills of its workforce. Organization development involves the use of behavioral science knowledge to change and improve organizations to make them better places to work. Humanistic in outlook, it draws from a wide variety of behavioral science interventions and traditions – survey feedback, team building, process consultation, positive psychology – to (attempt to) improve the quality of work life, interpersonal relationships at work, adaptability, and productivity. The literature on organizational change falls into two camps: one – academic – seeks to understand the nature of organizational change (e.g., Weick and Quinn, 1999), and the other – applied – seeks to understand how to implement change in organizations (Gallos, 2006). The latter uses psychological theories, methods, and interventions to diagnose organizational shortcomings, formulate new goals, and implement programs that will help an organization change in the direction its leaders want it to go.

Traditional beliefs about how organizations work

Organization design, development, and change involve (implicit and explicit) theories and beliefs about how organizations work and how they can be manipulated to achieve desired ends. One reason for this is that traditional approaches to organization design, development, and change make a few basic assumptions about human nature. Traditional I/O psychology attributes much of human nature to internalized cultural factors and assumes that humans have relatively few specific needs or hardwired inclinations. Traditional approaches to design, development, and change also assume that deliberate interventions in social systems can produce desired, specific results. Improvements to organizations can be best attained by the controlled application of social technologies; social scientists and scientifically valid social technologies will produce results that are superior to practices employed by laypersons (Gallos, 2006). I/O psychologists refer to this

as the ‘scientist-practitioner’ model, which is a cornerstone of I/O psychology and is ‘the dominant model for training and practice in American applied psychology’ (Murphy and Saal, 1990: 49).

The traditional perspective views systems as collections of parts that relate to one another in a direct and consistent manner (Gharajedaghi and Ackoff, 1984). If the parts are assembled properly, a system should function effectively, with the parts working in a coordinated fashion to achieve the system’s goals. This suggests that the nature of the relationships among parts and outcomes is stable and that the strength of the relationships is consistent over time. The elements in a system relate to one another in reasonably specified ways. Therefore, given sufficient knowledge, one could predict the behavior of elements in a system, and one could use social technologies to achieve intended effects by adding or manipulating parts in a specified manner.

A *hierarchy of goals* is an important aspect of the traditional perspective’s approach to systems. For example, the purpose of organizations is to achieve overarching goals (e.g., profitability), and a hierarchy of subgoals is created for departments, groups, and individuals to facilitate overarching goals (e.g., Campbell et al., 1993). The traditional perspective also *minimizes conflicts and incompatibilities* among system components (Colarelli and Stumpf, 1990). Because of its concern with how specific interventions help in attaining goals, the traditional perspective places more emphasis on the degree to which an intervention influences intended goals and less on unintended consequences or incompatibilities with other goals.

The traditional perspective views scientifically verifiable knowledge as the primary and most appropriate orientation to reality (Toulmin, 1977). Action based on anything but scientifically valid knowledge is either based on ignorance or error, and it is unlikely to achieve intended effects. The traditional perspective, therefore, more often follows

a process of ‘forward engineering’, which emphasizes the use of scientific knowledge in solving practical problems. This is in contrast to ‘reverse engineering’, in which scientists examine successful practices that evolved more or less independently and then use scientific knowledge to understand why these practices work so well (e.g., Ericsson et al., 1993; Root-Bernstein and Root-Bernstein, 1997).

In general, the traditional perspective suggests that a scientific elite should play a central role in organizational design and change. Because laypersons’ beliefs, decisions, and actions are based on common sense and custom, they are likely to err in their methods and goals for organizing. The importance of experts and the fallibility of the layperson have been evident in applied psychology from its beginnings to the present (e.g., Hale, 1980; Henrich, 2016; Taylor, [1911] 1967). The application of science to human affairs is the primary means for organizations to progress and improve.

There are many examples from traditional design, development, and change literature that reflect these assumptions – for example, Blake et al.’s (1962) managerial grid, Nadler and Tushman’s (1980) congruence model, Galbraith’s (1974) star models of organization change, and Schein’s (1984) and Denison and Spreitzer’s (1991) models of organizational culture change. There are also more complex theoretical models of organizational change – continuous, episodic, punctuated equilibrium, and revolutionary – that, despite their complexity, suggest that organizational change can, ultimately, be understood and, to some degree, manipulated by knowledgeable managers and consultants (Weick and Quinn, 1999).

An EIOP perspective

Organizational change from the EIOP perspective involves two levels of analysis: (1) individual and (2) cultural and organizational. Evolutionary psychology focuses on evolved *biological* adaptations *within the individual*. Thus, the individual EIOP

approach to change attempts to modify organizations so that they are compatible with our evolved human nature (Fitzgerald and Danner, 2012). This might, for example, include providing more greenery in office buildings, structuring authority and control so that leaders achieve status through prestige rather than dominance, design office layouts to encourage face-to-face interaction, and provide opportunities and facilities for exercise. These are all good ideas *if* – and this is a big ‘if’ – you can get an organization to implement them.

The second level of analysis takes places through *cultural and social* evolution. The hallmark of evolution – and of organizational change – is the process of variation, selection, and retention. Through cultural selection mechanisms, organizations select some variations and typically retain those that are functional (Campbell, 1965, 1975). However, the usefulness of a social technology does not ensure that organizations will select it or use it. Circumstances must favor its inclusion into a pool of variations available to organizations, selection mechanisms must capitalize on it, and conditions must favor its retention.

The evolutionary perspective’s approach to change ranges from strict selectionist to selection-adaptation views. Hannan and Freeman (1989), representing the former, suggest that organizations are usually unable to change because of internal and external pressures that maintain structural inertia. Organizations that survive are those whose forms fit with their environmental niches. Should their niches change, those organizations will probably perish, and others (which happen to have more adaptive characteristics) will prosper. Nelson and Winter (1982: 135) also suggest that ‘highly flexible adaptation to change is not likely to characterize the behavior of individual firms’. Because routines become tacit knowledge, they are difficult to change. They are the ‘genes’ of organizational structures. However, routines are also the points where change efforts may have the most impact (Beer et al., 1990).

One evolutionary reality of organizational change is that when an organization attempts planned change, managed by the organization's leaders (and consultants), it will be difficult and most likely fail. There is ample evidence for this, ranging from reviews of the literature on planned-change interventions (Robertson et al., 1992) to the recurring failure rates of most organizations (Carroll and Hannan, 1995). For example, of the organizations included in the Fortune 500 in 1955, only 55 were on that list in 2018 (Perry, 2018).

Another evolutionary reality of organizational design, development, and change is that *evolution is smarter than we are*. Donald Campbell (1965, 1975) was one of the first scholars to point out that a good number of social practices and institutions that have withstood the test of time have figured out – through blind cultural evolution – how to be useful. Moreover, these prescriptions for living and organizing are probably more valid than most prescriptions from social scientists, simply because they have withstood the test of time. Henrich (2016) has expanded our understanding of cultural evolution, and he provides rich examples of wise cultural traditions that remain with social groups – traditions that help them survive, reproduce, and prosper: the complex preparation of manioc by indigenous people to avoid cyanide poisoning, taboos on ingesting teratogens during pregnancy and breastfeeding, the health benefits of eating ash, and divination as an effective decision-making tool. Yet, the people who follow these traditions have no idea why they work. Let us be clear, we are not saying that reason and the scientific method are not helpful to human progress – quite the opposite (e.g., Pinker, 2018). But one must understand that science is also an evolutionary process. Variation, selection, and retention of scientific ideas are guided more by reason and the scientific method than random chance; but chance and evolution play a role (e.g., Fleming's discovery of penicillin). The fact of the matter is that most scientific

theories are superseded or certainly modified over time as new evidence accumulates (Popper, [1934] 1959).

Implications

What, then, are the implications of the EIOP perspective on organizational design, development, and change? The first is humility. We must accept the reality that organizational change is complex, fraught with uncertainty and conflict, and involves goals that are at cross purposes (Colarelli, 1998). Thus, our prescriptions and promises should be measured. Second, don't underestimate the power of existing culture. Accept it and work with it. The 'shock therapy' strategy of economists and foreign policy specialists who assumed that they could, in a few years, make a democratic market economy out of the Soviet Union is a glaring example of the foolishness of such a hubristic, technocratic approach to large-scale change (Easterly, 2008; Walt, 2019). On the other hand, there are good examples of interventions that use local cultural traditions. Dr Dixon Chibanda, a psychiatrist in Zimbabwe, expanded mental health care by enlisting village grandmothers. In Zimbabwean village life, grandmothers are viewed as keepers of health; they are trusted and rarely leave their villages. By training grandmothers in the rudiments of cognitive behavioral theory and providing 'friendship benches' where people can sit and talk with these grandmothers, over 27,000 Zimbabweans suffering from depression and other mental illnesses were helped (Riley, 2019). Third, it is a good bet to run pilot studies and keep change efforts small, within reasonable bounds. Chances are, the intervention may not, initially, work. Pilot studies allow for adjustments and minimal damage when things go wrong. Starting small makes it easier to build on successes and make corrections when things go awry (see, e.g., Popper, [1934] 1959).

Finally, it makes more sense to approach design, development, and change in organizations as *applied evolution*. This involves

two avenues. First, when considering change interventions, try out different variations and see what works. Don't become fixated on one best way (Colarelli, 2003). Because organizations and changing organizations are complex, it is difficult to know in advance what will work. So, be tolerant and eclectic. Let the evolutionary process do its work. Frances H. Arnold won the Nobel Prize in chemistry in 2018 for using a similar approach to building enzymes. In the 1980s, Dr Arnold tried to create new enzymes from scratch by logic and reason. But because of the complexity of enzymes, she gave up on what she called this 'somewhat arrogant approach' (Garcia, 2018). She then tried to build new enzymes as nature would: by creating variations and then using ones that worked (Garcia, 2018).

The second approach is to design diversification into organizational processes. Processes such as diversification or under-engineering are likely to produce adaptive outcomes, although one cannot know in advance what the outcomes might be. For example, Markowitz (1952), who won a Nobel Prize for his work, argued that a diverse portfolio of stocks is more likely to generate favorable returns than any one stock. The same logic can apply to organizational interventions.

EIOP – TOPICS WITH EVOLUTIONARY ROOTS BUT RELATIVELY NEW TO I/O PSYCHOLOGY

Family-owned Businesses

Some of the largest and most prominent businesses in the world are family-owned businesses (FOBs) Nike, Oracle, Walmart, Ford, Samsung, Volkswagen (Stern, 2015). Depending on how you count, between 60% and 90% of all businesses in the United States are FOBs.²³ At the time of writing, approximately 62% of the workforce in the United States is employed in FOBs. The percentages are even higher in other parts of the

world. Consider Germany: 91% of all companies in Germany are family owned; 55% of all corporate wealth comes from and 57% of the workforce is employed by the largest 500 FOBs in Germany (Muller, 2017). Many modern German corporations (e.g., Aldi, Porsche, BMW, Bosch) are among the largest, most successful, and well respected organizations in the world (Campden, 2010). It is ironic that the person most responsible for pillaring family-owned enterprises was the German sociologist Max Weber. His theory of bureaucracy ridiculed the administrative structure of FOBs because advancement and authority were based more on family ties than expertise and qualifications. He held up the rational-legal bureaucracy as a paragon of efficiency and fairness.

From a business perspective, FOBs have advantages that publicly held firms do not. With a network of close (long-term) kin relationships, there is generally a higher degree of trust and lower levels of conflict than in non-FOBs, which in turn can lead to quicker and more flexible decision-making and a more pleasant, harmonious work atmosphere (Denison et al., 2004; Nicholson, 2015; Tagiuri and Davis, 1992; Vallejo, 2008). FOBs, when they are privately held, are not at the beck and call of shareholders (individuals with large stakes in the company, institutional investors, and hedge-fund managers) who are interested in short-term results and quick profits.²⁴ Freed from these pressures, FOBs can take a longer perspective in their planning and investments. They are also freer to make unpopular choices, to go against the grain, such as by choosing a wife or daughter to lead the firm. For example, the first female CEO in the United States, Anna Bissell (Bissell Corporation), and the first female CEO to lead a *Fortune* 500 company, Katherine Graham (Washington Post), led their organizations after their husbands died (Carpenter, 2007). Yet, with a few exceptions (e.g., Jones, 2011a; Jones and Stout, 2015; Spranger et al., 2012), there is little research on FOBs in the mainstream I/O psychology

and management literatures (e.g., Denison et al., 2004; Vallejo, 2008; Yang et al., 2008). Indeed, it is probably more common to find hostility from modern management scholars and I/O psychologists towards FOBs (Pearce, 2015; Swinth and Vinton, 1993). For evolutionary I/O psychologists, however, there is a natural affinity between evolutionary psychology and FOBs (Nicholson, 2015; Spranger et al., 2012; Yang et al., 2008).

Kin-based altruism and the family business

The family is the basic socio-biological unit of many species, including humans. Its primary function is the production and rearing of offspring; families are also a basic human unit for security, production, and belonging. Kin selection – that is, ‘kin altruism’ – is the psychological glue of family life, assuring that family members feel a close affinity towards one another and help and cooperate with one another. By kin altruism, we mean providing benefits to another without regard for the personal costs. Kin selection is a fundamental principle in evolutionary biology (Hamilton, 1964), supported by many studies of many species. Kin selection theory states that among social species, an individual will be altruistic to others in proportion to the degree of relatedness (Hamilton, 1964). The evolutionary logic for kin altruism is that by helping a relative, copies of an individual’s genes are likely to be spread into future generations, and the closer the relative, the more of her genes that will be sent into the future. Occurrences of kin selection are like the air we breathe – so much part of our daily life that we may not even notice – for example, parents’ financial, time, and emotional sacrifices for their children, bequeathments of estates from parents to children, and a mother’s love for her baby.²⁵

Goals of FOBs

The criticism that FOBs are poorly managed and rife with unfairness because of nepotism is a trope. In total, 64% of US gross domestic

product comes from FOBs, and 78% of new job creation comes from FOBs. In the S&P 500 companies, return on investment is greater in FOBs, with a 6.65 % greater return than non-family firms.²⁶ Besides being inaccurate, another pity of this trope is that it does not recognize the fundamental nature of FOBs. A FOB is a vehicle for kin selection writ large. Business and family goals are intertwined: to create and maintain wealth for the family. From an evolutionary perspective, the purposes of a FOB are clear: to provide family members with the resources – and the status to help maintain existing and acquire more resources – required to perpetuate the family’s genetic legacy over multiple generations. The ownership, management, and resources of the company are passed on to future generations of the family. For example, a son who grows up in a successful family business is not only likely to have a job waiting for him whenever he wants it but also a management-development plan, a path to the executive suite, and company ownership. A young man with this type of opportunity, resources, and status at his disposal is in a much better position to attract a wife (or several over his lifetime) and support, educate, and groom children than a young man with no such prospects.

The most important element of a FOB is the family. The fact that a family owns and controls the business means they are likely to manage it, staff top positions with family members, and pass on ownership and management to family members. These are all fundamental and distinctive characteristics of FOBs. These may also be the reasons why it is not a popular topic in the traditional I/O psychology and management literatures. By and large, these fields adhere to and work within the rational-legal bureaucratic model developed by Weber in Germany and by Taylor in the United States.²⁷ They posit that organizations are most efficient and effective when they are professionally managed: people should be hired and promoted based on achievements and job-related expertise;

authority should be knowledge-based; personnel decisions should be based strictly on achievement, not ascription. Indeed, most traditional I/O psychology textbooks are full of theories and techniques about job-performance criteria, measuring job performance, assessing individual abilities and skills, and predicting who will be most successful if hired or promoted based on such objective criteria. Hiring and promotions based on family membership, ascription, or other non-job-related criteria are an anathema in most, but not all, circles in mainstream I/O psychology (Jones, 2011b).

The effects of kinship ties in FOBs

Much of the traditional management research on FOBs simply looks at differences between FOBs and the non-family businesses (e.g., Miller et al., 2008; Rodríguez-Ariza et al., 2017) or at processes unique in FOBs, such as the succession of family members to executive positions (e.g., Brockhaus, 2004; Royer et al., 2008). However, in evolutionary-oriented work with FOBs, *kinship relationships* take center stage – their strength and number and how kin relatedness influences organizational dynamics. In one of the first studies using this approach, Yang et al. (2011) examined the effects of strength of kinship relationships on helping behavior and hiring practices among immigrant entrepreneurs. They found that, in line with evolutionary psychological theory, the strength of kinship ties was positively associated with help that immigrant entrepreneurs received. That is, the closer the kin relationship, the more help entrepreneurs received from a relative. Interestingly, Yang et al. (2011) found that immigrant entrepreneurs were *less likely* to want to hire kin and co-ethnics. Apparently, these entrepreneurs, many of whom had retail businesses, preferred to hire individuals who were ethnically similar to their market base. Yu et al. (2019) studied the effect of the strength of kin relationships in family firms on CEO succession and non-family executive pay. They found that when kinship ties in

family firms were weak, FOBs were more likely to appoint non-family CEOs and to pay executives less than in firms where kinship ties were stronger. Their argument is that socioemotional wealth is more important in family firms with strong kinship ties, and therefore personnel decisions in such firms are likely to be based on criteria that reflect a concern for the overall connection of employees to each other and the firm.

O'Brien et al. (2018) looked at the effects of kin relatedness from the other side of the coin, essentially arguing that closer kin relatedness would also foster a greater likelihood of overlooking misuse of company resources and a lower willingness to report misuse. Using a vignette study, they found this to be the case. In FOB situations where employees were closely related, misuse of resources and a lower likelihood of reporting misuse were more likely to occur than when kin relationships were distant.

Degree of relatedness in FOBs

Much of traditional research on FOBs is categorical in two respects. First, distinctions between family and non-family members in FOBs are categorical. Family members are in one group, with no distinctions typically made among them, and non-family members are in another. Yet, family members differ in their degree of relatedness. The kinship bond between a mother and daughter is stronger than the bond between two cousins. The second categorical distinction is between family and non-family businesses. FOBs are in one group and non-family businesses are in the other; yet they do not in fact differ categorically. Some FOBs are more ‘family’ than others. An important source of variation is the degree of relatedness among family members. FOBs with a higher proportion of family members *and* family members who are closely related have a higher degree of what Spranger et al. (2012) call *kin density*. Indeed, kin density within FOBs influences nepotism and justice perceptions. For example, when kin density is high,

family members perceive that higher levels of justice exist within the organization than when kin density is low. In high-kin-density organizations, non-family members have significantly higher nepotism perceptions than in low-kin-density organizations.

Close relationships at work

While much of the research, theory, and scholarly commentary related to FOBs has centered on nepotism (Astrachan, 2010; Pérez-González, 2006), there is also burgeoning research on close but non-kin relationships. Charitably, some refer to this as close relationships at work or workplace friendships (Dutton and Heaphy, 2003; Ferris et al., 2009); less charitably, some refer to these relationships at work as cronyism (Pearce, 2015; Pillemer and Rothbard, 2018). That there is such a wide spectrum of views on having kin or friends as colleagues and on the benefits – to employees and organizations – suggests that there is still little consensus on the nature of relationships among people in modern organizations.

Evolutionary Psychology and Workplace Design

Workplace design as a research topic has received little attention from traditional I/O psychology. The focus has been on *work* rather than *workplace* design, such as job design and ergonomics (e.g., man–machine interface). For instance, authors of popular introductory textbooks of I/O psychology have been silent on the workplace design (e.g., Riggio, 2012; Spector, 2011), and editors of major handbooks on I/O psychology have also overlooked the subject (Anderson et al., 2001; Dunnette and Hough, 1992; Schmitt and Highhouse, 2012). As Morgeson et al. (2012) admitted, it appears that the majority of the research on work design continues to use the job characteristic model developed by Hackman and Oldham (1975) over 40 years ago. In other words, very little

attention has been given to the processes involved in designing the workplace in its entirety. We attribute the current state of the I/O psychological research on workplace design to some underlying assumptions in I/O psychology. One is that traditional I/O psychologists have been reluctant to offer a coherent theory of human nature. All that is offered is that people are assumed to have a few built-in preferences, but, for the most part, people are assumed to be capable of adjusting to almost any environment.

Theoretical considerations

Modernist urban buildings attract attention as they are monumental and sensational; however, as Siegel (2014) commented, avant-gardist architects just want to build sculptural icons that attract attention to themselves, rather than building good and comfortable places for people to live and work. The unfortunate current state is probably due to the personal artistic vision or ambition exhibited by modernist architects who often ignore evolved psychological preferences and design principles (i.e., whole-to-part ratio, the unity in variations, and symmetry; Siegel, 2014). Given the increasing gap between man-made artificial environmental changes and the hardwired psychological adaptations shaped under ancient environmental pressures (Li et al., 2018), psychological mismatch explains why we often feel impressed but at the same time confused and perplexed when we are inside grandiose corporate buildings. This is why it is important to reflect upon the negative consequences of mismatch on the physical and psychological health and well-being in contemporary workplaces.

The idea of the restorative benefits of nature and natural representations on physical health and psychological well-being has been in the scientific literature since the early 1980s. With the notion of ‘biophilia’, Wilson (1984: 1) emphasized our ‘innate tendency to focus on life and lifelike processes’ and that *Homo sapiens* as a species

is designed to seek novelty and diversity in nature. Humphrey (1980: 63) also posited that it is nature's unique combination of pattern and diversity that appeals to us and that our aesthetic preferences emerged from 'the predisposition among animals and men to seek out experiences through which they may learn to classify the objects around them'. According to Humphrey (1980), this ability to classify enhanced the chance for survival of *Homo sapiens* by reducing the so-called 'thought load' on the brain to accelerate new learning and allow us to extrapolate what we have learned from one set of circumstances to another more efficiently.

Tooby and Cosmides (2001: 17) further proposed that we have evolved to experience some positive emotional reaction (e.g., aesthetical pleasure and beauty) towards objects that enhanced our fitness and some negative emotional reaction (e.g., ugliness or disgust) towards those objects that reduced our reproductive success; thus, we find something beautiful 'because it exhibits cues which, in the environment in which humans evolved, signaled that it would have been advantageous to pay sustained sensory attention to it, in the absence of instrumental reasons for doing so'. In fact, it has been reported that experiencing positive emotions such as awe, wonder, and beauty from nature or artworks has positive effects on physical health and even life expectancy, by lowering the levels of inflammatory cytokines (Stellar et al., 2015).

Orians and Heerwagen (1992) provided two major theoretical approaches to environmental aesthetics; in general, we tend to prefer (1) natural landscapes that look like the savanna environment in which our ancestors did most of their evolutionary flourishing (i.e., the savanna hypothesis; Orians, 1986) and (2) places where we are able to survey the landscape without any visual obstruction and hide from danger (i.e., the prospect and refuge hypothesis; Appleton, 1975).

Therefore, it is plausible that people are more likely to perceive any man-made

environment that replicates or imitates the features of the savanna-like natural environment as more visually pleasing. Hence, any man-made environment with the savanna-like elements such as a long-range view, refuge, greenery (trees), natural light, and sources of water will have positive effects on the physical health and the overall sense of well-being of the incumbents of the place.

Evolutionary psychology and workplace design: some empirical studies

The empirical evidence of the restorative benefits of nature and natural views are well documented. For instance, Ulrich (1984) found out that intensive-care patients were able to reduce their anxiety and the need for pain medications just by looking at natural objects such as trees and water. The notion of biophilia has also received some empirical support; people tend to prefer savanna-like environments over other types of landscapes such as forest or desert (Orians and Heerwagen, 1992).

Kaplan (1995) underscored the psychological mechanism of directed attention and its susceptibility to fatigue while emphasizing the importance of adding more greenery in the contemporary workplace. In a study of comparing the restoration in natural and urban field settings, Hartig et al. (2003) reported that after engaging in attentionally demanding tasks, (a) sitting in a room with tree views promoted a greater decline in blood pressure than sitting in a viewless room, and (b) walking in a nature reserve reduced blood pressure more than walking in urban surroundings, indicating greater stress reduction.

In terms of the relationships between natural elements and employee mental health and work attitudes, An et al. (2016) reported that (a) exposure to natural elements was negatively related to a depressed mood and positively related to workplace attitudes (i.e., job satisfaction and organizational commitment)

and (b) the relationship between role stressors and job satisfaction was lower for the participants with greater exposure to natural elements compared to those with less exposure to natural elements.

Based on their empirical studies on the effects of office-window views on psychological well-being, Van Esch et al. (2019) further claimed that it is not nature per se but certain view features, including the degree of coherence/legibility, complexity/mystery, prospect, and refuge, that actually better predict the psychological well-being. This finding has an important practical implication:

thoughtfully designed built environments could be as restorative as natural settings. (Van Esch et al., 2019: 63)

It has also been reported that exposures to the scenes of natural environments systematically lowered individual future-discount rates (i.e., future discounting), which is a built-in bias to discount distant greater future benefits for the sake of seeking instant and smaller short-term rewards. Van der Wal et al. (2013) found out that future discounting was reduced when participants were presented with visual cues of natural environments as opposed to those of man-made urban environments.

In addition to the positive effects of incorporating physical office-design features with more natural elements, it has been reported that the presence of a companion dog tends to have positive effects on people in work groups (Colarelli et al., 2017). Specifically, Colarelli et al. (2017: 77) found that ‘participants in the dog-present group displayed more verbal cohesion, physical intimacy, and cooperation’ and that ‘behavior in dog-present groups was rated more cooperative, comfortable, friendly, active, enthusiastic, and attentive’ compared to those in the dog-absent group. By acknowledging a unique symbiotic relationship between humans and dogs in the evolutionary history of the two species, Colarelli et al. (2017) attributed the

heightened pro-social behavioral patterns exhibited by the dog-present-group members to the positive emotional effects of the presence of a companion dog on their perceived intimacy and trust.

Practical implications

Given the empirical evidence of the effects of natural and man-made environments on the physical health and psychological well-being of the incumbents (Clements-Croome, 2018; Fitzgerald and Danner, 2012), it is safe to conclude that nature and natural artifacts have significant positive effects on physical and psychological well-being. For instance, in terms of applying the notion of biophilia into designing the built-in environment, Hase and Heerwagen (2000: 31) suggested that:

Designing architectural elements that repeat similar forms and shapes at different scales throughout the environment can help symbolize nature’s fractals or self-similarity at different scales [...] Natural habitats are visually stimulating and constantly changing through subtle motion. Workplace settings should include eye-pleasing and attention drawing items.

Oseland (2009: 252–253) also argued that:

Design should focus on meeting the individual needs of the occupants and functional needs of the organization rather than on saving space or creating aesthetically pleasing but dysfunctional buildings...The design of the office also needs to address the affinity with nature and be planned on a human scale with intuitive wayfinding.

Based on the findings of the empirical studies reviewed above, we thus offer a short list of practical advice to the key decision-makers and managers of organizations:

- 1 Make window views more attractive by allowing employees to enjoy natural views.
- 2 Incorporate nature and various natural representations or artifacts such as plants, photographs, paintings of nature or natural landscapes inside the built-in workplace.
- 3 Allow employees to have time for walks outside of their offices as regularly as possible.

- 4 Allow employees to bring their pets to the workplace and let them get some exercise during the day in order to be exposed to direct sunlight.
- 5 Exhibit some works of art (e.g., figurative and abstract paintings) to encourage employees to develop their skills for creative problem-solving and aesthetic sensitivity.

We would like to emphasize that there is a caveat, however. Evolutionary psychology does not offer the best definition of ‘good design’ or the timeless way of building. Instead, we suggest that industrial engineers and architects pay more attention to human nature and how our minds work. Here is a good example: the notion of open-space building has become quite popular, and it has been suggested that more open-space building will boost productivity and creativity (Waber et al., 2014). However, according to Waber et al. (2014), there has been no firm evidence to support the idea.

Digital-savvy millennials may want to work in the more open and permeable office environment, but that does not mean that our built-in preference for nooks and crannies, which offer a physical sense of closure, would be easily overridden (Tikhoniouk, 2015). Realistically speaking, we all know from our own experience that we need a private (cave) as well as a public open (café) space in the workplace. Hence, interior designs that incorporate some adjustable enclosures and fabric canopies or some dropped ceilings would be more desirable than purely open or conventional office arrangements.

Furthermore, as Humphrey (1980: 73) poignantly commented on the application of his concept of ‘natural aesthetics’ to cityscape, we do not want offices ‘tarted up to look like alpine meadows’ or the South African savanna. Instead, what evolutionary psychology suggests, we believe, is to envision the office space ‘in which the relations – temporary and spatial – between the artificial elements exhibit the felicitous rhymes of natural beauty’ (Humphrey, 1980: 73). In other words, the actual process of transforming the

conventional office space into a more environmentally and socially sustainable workplace should not be pursued in a mechanistic or superficial manner.

CONCLUSION

Evolutionary psychology can contribute to I/O psychology both theoretically and practically. Theoretically, it offers a meta-framework for understanding individuals and organizations. It provides additional insights into people’s motivation and behavior and why some behaviors are easy, and others difficult, to change. It helps us to understand why certain behaviors and perceptions in organizations tend to be common across time and cultures, such as perceptions of leadership qualities. Moreover, an evolutionary psychological perspective on I/O psychology helps us to navigate the intersection of the modern world and our ancient evolved psychological mechanisms – understanding the nature of evolutionary mismatch and its implications for organizations and organizational behavior. The larger evolutionary framework provides a useful way of looking at complex organizations and organizational change – that is, Darwin’s universal acid of evolutionary change via variation, selection, and retention (Campbell, 1960, 1965; Dennett, 1996).

Practically, interventions are much more likely to ‘work’ when they are based on a veridical view of human nature. If fundamental assumptions about human nature or human systems are inaccurate, then interventions based on those assumptions are likely to be ineffective (Colarelli and Arvey, 2015). While a number of traditional I/O psychology’s assumptions about human nature are accurate (e.g., people have some relatively fixed traits and there is variation among people’s traits), others are problematic (e.g., that kinship ties and nepotism make family businesses inherently

less effective than non-family businesses). Including an evolutionary psychological perspective may improve the practical utility of interventions. Bringing our evolved human nature into the mix will also help I/O psychologists understand why organizations use personnel practices that I/O psychologists seem to dislike and organizations seem to love, such as letters of recommendation and interviews (Adams et al., 1994; Colarelli et al., 2002).

Evolutionary psychology is becoming part of the mainstream in basic areas of psychology, although there are still roadblocks (Buss and von Hippel, 2018). The pace is slower in applied psychology. One reason is that *applied* evolutionary psychology is paradoxical: applied psychology is a social technology that seeks to reduce uncertainty and produce intended effects, but uncertainty is inherent in the evolutionary process. Causality in the evolutionary process – cultural or biological – is opaque. However, as we have argued above, using the evolutionary process to produce a variety of outcomes and then picking the best one is a good compromise. Moreover, an evolutionary understanding of people and complex systems suggests that by focusing on basic, evolved human processes – such as face-to-face communication – we can be effective in solving, through cooperation and collective action, what initially appear to be intractable social dilemmas (Lopez, 2019; Ostrom, 1998).

Another paradox is that interventions in I/O psychology seek to change people, yet a core premise of evolutionary psychology is that people come with more or less hard-wired adaptations that cannot be (easily) changed with psychological interventions. An evolutionary I/O psychologist, however, might suggest that if we know people's evolved preferences, we can understand the constraints we are up against and deal realistically with them to achieve desired outcomes. To paraphrase E. O. Wilson, biology keeps culture on a leash – so EIOP can help us understand how long and

flexible our different psychological leashes are. Still another paradox is that if people evolve and adapt to their environments, then why worry about improving environments? People (some of them) adapt. The problem is that human adaptations change slowly, over centuries. Our environments – and particularly technology – change faster than people do. In the modern world, most humans are mismatched to their environments. But in the meantime, EIOP knowledge can help to create environments that are more in line with human nature as it exists in the present.

We are optimistic about the future of EIOP. We believe that more traditional I/O psychology scholars and practitioners will adopt ideas from evolutionary psychology and that more I/O research and interventions will be informed by an evolutionary psychological perspective. Evolutionary psychology has crossed the Rubicon. It is part of mainstream psychological science, and because I/O psychology is inherently interdisciplinary, evolutionary psychology will become more commonplace in I/O psychology. Finally, there is less resistance to EIOP now. To paraphrase a somewhat cynical, but probably true, aphorism about progress in science, science proceeds by one funeral at a time (Azoulay et al., 2019). People who have been antagonistic towards, or ignorant of, evolutionary psychology are of an older generation, who are passing on. Graduate students and newer, younger psychologists are more exposed to and accepting of evolutionary psychology. This bodes well for a bright future for EIOP.

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Notes

- 1 Content moderators are typically not employed by Facebook but by other companies who are contractors to Facebook. At the time of writing, about 15,000 people work as Facebook content moderators (Newton, 2019).
- 2 I/O psychology can be defined as follows (Nguyen, n.d.): 'Industrial and Organizational (I/O) psychology is a subfield of psychology that studies people, their behavior (performance of tasks) in a working environment, and the settings in which people work and function, in order to gain a better understanding of behavior and how it can be influenced, changed, and enhanced to benefit the employees and the organizations.'

I/O psychology focuses on three aspects:

- 1 the person, the worker;
- 2 the work (tasks) that is (are) being performed; and
- 3 the context in which the work is performed.

The two fundamental goals of I/O psychology are (1) to understand the behavior...of people in a work setting; how people can become effective, satisfied, fulfilled, and rewarded; and how these outcomes can be maintained, and (2) to study how the organization can be sustained and developed and applying psychological principles, theory, research, and interventions in order to design and implement practical solutions to solve organizational challenges.'

- 3 The broad features of the human activity known as 'work' are essentially the same regardless of context. A dictionary definition of work is: "to perform or carry through a task requiring sustained effort or continuous repeated operations;... to exert oneself physically or mentally especially in sustained effort for a purpose or under compulsion or necessity" (Merriam-Webster, 2020).
- 4 In addition to research and applications that respond to social and economic shifts affecting the workplace, I/O psychologists have also focused on measurement and data analysis and the economic utility of psychological interventions in the workplace.
- 5 Specialized techniques for and theories about personnel selection and testing date back (at least) to the ancient Greeks. Plato, in *The Republic*, advocated that people could be divided into four types (iron, bronze, silver, and gold) and that the different types were typically suited to different positions in society: producers (farmers, artisans), auxiliaries (warriors), and guardians (rulers). Taking an essentialist view of human nature, Plato believed that a society works best with a rigid class structure where people are assigned

to positions that match their ability and temperament. Some of the earliest accounts of testing for work qualifications date back to the Qin or early Han dynasties, somewhere in the range of 200–100 B.C.E. (Bowman, 1989; Eberhard, 1977). The Han Dynasty used written assessments for selecting officials in 165 B.C.E. This imperial testing method persisted over a series of dynasties and evolved over time. Some scholars suggest that the Keju examination, used to select government officials without the influence of favoritism (Yuan and Cheng, 2009), is one of the most influential movements in testing and liken it to the Civil Service Examination of today. The use of this test for selection of government officials persisted and evolved over time and eventually made its way to Europe. In fact, a similar and revitalized test appeared in France in 1791 (Wainer, 1987) before being eliminated by Napoleon.

- 6 Over the course of the 20th century, the number of I/O psychology graduate programs expanded substantially. At the time of writing, there are 92 universities in the United States that offer a PhD in I/O psychology or related fields and 69 universities that offer just a MA degree in the field (Society of Industrial and Organizational Psychology, 2020). It is encouraging for ELOP that there are also a handful of universities where students have access to faculty in I/O psychology or related fields as well as faculty in evolutionary psychology (see HBES, 2020).
- 7 For readers interested in more historical detail, there are a number of comprehensive histories of traditional I/O psychology (Austin and Villanova, 1992; Katzell and Austin, 1992; Koppes, 2014; Vinchur and Koppes, 2011).
- 8 The gospel of worker efficiency got its start in the early 20th century as well, although the names most associated with this movement (Frederick Taylor and Frank and Lillian Gilbreth) were not psychologists but engineers. Taylor devised programs for breaking industrial jobs down to their most basic elements and rearranging them for economy of motion and efficiency – so that the workers wasted no effort in completing their tasks. Taylor added training, rewards, and management principles to his efficiency programs. His book *The Principles of Scientific Management* ([1911], 1967) is one of the most – if not the most – important books on management published in the 20th century. Taylor's focus was on managing the workforce to maximize productivity and profits. Münsterberg admired Taylor and saw a natural affinity between Taylor's ideas and industrial psychology. The Gilbreths were also interested in improving industrial efficiency and pioneered time and motion studies. However, unlike Taylor,

- they were also interested in designing work processes that would be comfortable – or, at least, not unpleasant and debilitating – to workers. The work of the Gilbreths was instrumental in the development of engineering (or human factors) psychology. In 19th-century Europe, theory relying on the distinction between man and machine proposed by Descartes gave way to a conceptualization of the ‘human motor’, viewing people as a different type of machine, but one that required attention to reducing fatigue (Rabinbach, 1990).
- 9 Yet this debt to evolutionary theory is rarely acknowledged. I/O psychology articles and texts on personnel selection rarely, if ever, mention the term ‘evolution’ or acknowledge the field’s debt to Darwin’s theory of evolution by natural selection.
 - 10 I/O psychologists have conducted important research on the nature and practical effects of individual differences (Arvey et al., 1989; Arvey et al., 1991; Judge and Hogan, 2015; Schmidt and Hunter, 1998).
 - 11 For example, the optic nerve in the human eye, because of its location in the retina, creates a blind spot, whereas the eye in the octopus evolved in such a way that there is no blind spot (Williams, 1966).
 - 12 In I/O psychology, the most common criterion is job performance; in educational psychology – another field that uses a traditional approach to assessing individuals to predict performance – it is grade point average.
 - 13 As financial planners recommend, making consistent, modest deposits into a savings or investment account will pay large dividends over the long haul, even if the return on investment is small. For example, investing \$1,000 a month at a 6% return over 20 years will result in \$467,912 (\$240,000 in contributions plus \$227,912 in growth); over 40 years, the net would be \$1,488,572. At a 10% return, the total accumulation over 40 years would be almost \$6 million. Applying this logic to personnel selection, tests with small increments in validity applied over many applicants over many years should also produce large returns.
 - 14 With the advent of ‘big data’ and artificial intelligence, algorithms are now widely used in many situations in addition to personnel selection, such as in criminal sentencing and assessing credit-worthiness. Eubanks (2018) and Noble (2018) argue that these algorithms often have diverse consequences for the poor and for minorities in the United States.
 - 15 It is not without irony that even graduate programs in I/O psychology continue to use letters of recommendation for selecting graduate students, and the interview is still *de rigueur* for selecting new faculty.
 - 16 Wealth is positively associated with the number of sexual partners among heterosexual men (Jackson et al., 2019).
 - 17 Women now comprise 11% of the *Fortune* 100 executives (up from 0% in 1980) and 24% of the US Congress (Warner Ellmann, & Boesch, 2018).
Mary Berra, the CEO of General Motors (GE), made \$22 million in 2018, while the average GE assembly-line worker makes \$45,000 annually. (Glassdoor, 2020; Klayman, 2018)
 - 18 We are aware that discussions of group differences can be contentious. Thus, it is important to bear in mind that the psychological differences between men and women are *group averages*. Individuals in each group vary, causing an overlap of the two groups for some individuals. Therefore, the findings are not representative of all persons in a group.
Yet, not all group differences are contentious, particularly when they are relevant to illness, health, and prevention. For example, African Americans are more likely to suffer from sickle cell anemia than Caucasians. Similarly, women athletes are more likely to suffer from ACL injuries than men. Cystic fibrosis and hemochromatosis are more common among Europeans. Tay–Sachs disease is more likely to occur among people with Ashkenazi ancestry.
 - 19 Counterproductive work behaviors are actions that harm or intend to harm the organization, employees, or other stakeholders of an organization (Miles et al., 2002).
 - 20 Generally, a greater ability to monitor and modify oneself would result in higher achievement, as a function of specific role requirements for varied jobs, such as service jobs or highly interpersonal jobs.
 - 21 Work/family conflict occurs when work tasks, roles, or responsibilities impede on family tasks, roles, or responsibilities (work–family conflict) or vice versa (family–work conflict). This type of conflict can be strain-based, time-based, or behavior-based. However, the literature is moving towards a more inclusive outlook of work–life balance (Greenhaus and Allen, 2011).
 - 22 Parts of this section were taken from Colarelli (1998).
 - 23 Although definitional specifics vary, a business is considered a FOB if members of a specific family own the business or if a majority or controlling interest of the shareholders are members of a specific family. Family ownership typically passes down through the generations over time, and family members are often (although not necessarily) members of the top management team and play an active role in the company’s strategy

and management. This contrasts with a non-family organization, in which ownership is dispersed among many shareholders and the mix of controlling ownership typically changes over time. Company board members and managers are selected based on external criteria, not necessarily on family or ownership ties.

- 24 Exceptions are FOBs that are publicly traded companies in which family members have a controlling interest (e.g., Ford).
- 25 Kin altruism, which involves providing benefits without the expectation of the favor being returned, is often compared to reciprocal altruism, which involves providing benefits with the expectation of return (i.e., tit for tat). Kin altruism typically (although not exclusively) occurs among family members, while reciprocal altruism typically (although not exclusively) occurs among people who are not related.

Parents, by our back-of-the-envelope calculation, will change about 7,000 diapers per child (from birth to age four). Middle-income parents in the United States will spend about \$230,000 to raise a child from birth to age 17. If you include four years of college, add another \$100,000 for a public university or \$250,000 for a private university.

- 26 Conway Center for Family Business (n.d.)
- 27 Even I/O psychologists who acknowledge the importance of an evolutionary perspective still adhere to the rational-legal model of organizations as the most appropriate way to design and administer organizational bureaucracies (e.g., Judge and Hogan, 2015).

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Evolutionary Clinical Psychology

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INTRODUCTION

The field of evolutionary clinical psychology (Kennair, 2017) has long been an intriguing and promising approach to mental disorder and abnormal psychology. This has been the case ever since the work of Freud on phylogenetic, albeit faulty, explanations of pathology. The Oedipus complex was framed in phylogenetic terms of the time, including Lamarckian thinking. However, for obvious reasons, fear of castration in young boys could not evolve. While evolutionary clinical psychology has evolved since these early origins, the promise of an evolutionary revolution within mainstream clinical psychology has yet to be fulfilled. As an applied field, evolutionary clinical psychology has yet to mature, with few notable treatment methods, such as compassion focused therapy (Gilbert, 2014). There are only a handful of conceptualizations that have influenced the field, such as the absence of theory of mind in autism, the role of subordination and defeat in depression, and the

general view that the mind and body contain adaptations that render humans vulnerable to developing disorders (Baron-Cohen, 1997; Sloman and Gilbert, 2000; Williams and Nesse, 1991). Finally, the large body of non-integrated theory to data ratio suggests the field needs further development to mature scientifically, too (see also Figueredo et al., 2005 for a comment on evolutionary personality psychology; Kennair, 2011).

Despite this critical initial assessment, there are several contemporary developments that promise to move the field along. Recent publication of two books (Del Giudice, 2018 and Nesse, 2018) that address the field from both a practitioner perspective and an academic, synthesizing perspective suggest that the field still can garner interest from readers. Further, we will address two contemporary developments, the analytical rumination hypothesis (Andrews and Thomson, 2009; Bartoskova et al., 2018) and the life history approach to mental disorders (Del Giudice, 2014, 2018), that both add a more empirical approach to

the field. These developments are therefore very promising, despite controversy.

This lack of scientific maturation and influence on applied clinical psychology is somewhat puzzling. Through the years there have been several evolutionary approaches to mainstream clinical psychology, the most noteworthy being Ainsworth and Bowlby's (1991) approach to attachment. Also, the general functional understanding of fear has been fundamental to the treatment of anxiety disorders, as we will see below. Clinical psychology has had just as much trouble to find an overarching metatheory as psychology in general. However, evolutionary psychology is historically better suited to address human universals (Tooby and Cosmides, 1990a) and thereafter sex differences (Buss and Schmitt, 1993) than individual differences (Buss, 1991), including mental disorder (Kennair, 2011). The evolutionary metatheory needs to be developed further to embrace individual differences, development, and behavioral genetics in order to fully be relevant for clinical psychology (Del Giudice, 2018; Kennair, 2011). Also, significant contributions to the field, such as Wakefield's (1992a) definition, demand a greater integration between abnormal and normal evolutionary psychology, in mapping both function and dysfunction.

The many differing, non-integrated evolutionary approaches to mental disorder throughout the decades have therefore suffered from a lack of a relevant and synthesizing evolutionary science (Del Giudice, 2018; Kennair, 2011). The current introduction to evolutionary clinical psychology will therefore attempt to highlight some of the fundamental issues and approaches, as well as illustrate the state of the field through two contemporary issues.

WHAT ARE MENTAL DISORDERS FROM AN EVOLUTIONARY PERSPECTIVE?

Mental disorders have, throughout history, been defined in the context of value-

judgments. An early example of the close relations between mentalistic concepts and value-judgments can be found in Plato's *Republic*, where mental health and ability to reason was linked with virtue (Stalley, 1981). The focus on value-judgments when considering mental disorders is reasonable since mental disorders are unwanted for the person with the disorder, people interacting with the person that has the disorder, or both. There are problems with defining mental disorders simply in terms of subjective evaluations, first and foremost because every mental trait could be a disorder. Further, in order to research mental disorders scientifically, some degree of objectivity is needed. Several attempts at defining factual criteria for mental disorders have been proposed that are not satisfying from an evolutionary perspective. Examples of such are (1) suffering, (2) statistical deviance, and (3) lesions (Troisi and McGuire, 2002).

Suffering as a criterion for mental disorder poses the same problems discussed with subjective value-judgment because suffering is a subjective state. The added credibility of using suffering, as opposed to a less defined subjective valuation, comes from the common-sense notion that mental disorder causes people to suffer. Albeit often correlated with disorders, not all people who might be characterized as having a mental disorder report to be suffering from it. Also, suffering could reflect normal responses to severe life experiences. It seems that suffering is too stringent to be a satisfying subjective criterion for a mental disorder and too subjective to be an objective criterion.

Defining mental disorder as deviance from some central tendency has been suggested as a possible path towards objectivity in diagnosis (Cohen, 1981). Statistical analysis alone will not satisfy as a basis for defining mental disorders. Traits that are valued as beneficial could be just as uncommon as traits that are valued as disadvantageous. It is also unclear why there should be any a priori link between statistical

normalcy and mental health – being different does not equate with being disordered. From an evolutionary perspective, variability is important because it is that which is selected from in evolution. This does not mean that designs that have been selected against are disordered. Selection often occurs in competition between fully functional designs where one design out-competes others in a given environment. Statistical anomalies may be caused by disorders or they may reflect extreme but normal functioning. Without further analysis it would be impossible to distinguish the two categories. Further, disorders may be the statistical normality in a given population, as when everyone is exposed to a highly potent toxin or pathogen.

In the search for objectivity in defining disorders, there is a long tradition of considering organic lesions as a criterion, at least in medicine (Troisi and McGuire, 2002). Exploring possible biological markers for mental disorders has been a significant endeavor for the scientific community, particularly since the invention of imaging techniques that can examine the living brain. Viewed through an evolutionary psychological lens, there are significant problems with relying on the identification of altered organic tissue as a criterion for defining disorders, in general, and mental disorders, in particular. The form and structure of the body is mostly selected through evolution for the effects it has on solving adaptive problems. It is the function of the organic tissue that is modeled or preserved over evolutionary time. Even vital functions can be sustained by a wide variety of normal variation of forms. Without an analysis of the functional consequences of a lesion, we would not be able to distinguish normal variation from lesion and disorder. Further, bodily tissue can evolve as by-products or be non-functional relics from phylogenetically distant adaptations. If this is the case, even total removal of the tissue may have no functional consequence (e.g. appendectomy).

The Harmful Dysfunction Analysis of Mental Disorder

As can be seen from the discussion above, there are numerous suggestions for both subjective and objective criteria for defining mental disorders. A satisfying definition from an evolutionary clinical psychological viewpoint needs to both delineate the facts of mental disorders and provide room for attributions of value. To solve the fact/value problem, Wakefield (1992b) suggested the *harmful dysfunction* model. For something to be a mental disorder, it needs to be judged as harmful, either by the person with the disorder or by the culture that the person is in, and it needs to be a dysfunction. Dysfunction in the context of mental disorders refers to the breakdown of the *natural function* of a psychological mechanism – that is, a breakdown which interrupts significantly or negates completely the intended effect of the mechanism and thus its purpose. It is the natural effects of those mechanisms that are assumed to be selected through evolution (Tooby and Cosmides, 1992). A psychological mechanism thus has an ultimate cause in the adaptive problem that it solves (Mayr, 1993). Evolutionary psychologists use knowledge about the adaptive problems humans faced over evolutionary time to hypothesize psychological mechanisms as adaptations. They also use knowledge about psychological mechanisms to theorize about adaptive problems humans could have faced (Lewis et al., 2017).

Since psychological mechanisms are shaped by evolution to solve specific adaptive problems, they take a modular form (Pinker, 1999). Here we refer to modularity as the functional separation in the organization of the information-processing machinery in the brain (Barrett and Kurzban, 2006). Modularity means that the mind has parts that could vary in their condition. If the mind is a highly organized collage of an undefined number of mental modules – that is, massive modularity – then the breakdown of one or

more of those could result in a dysfunction in the mind. If the effect of that dysfunction is judged as harmful, it would be a mental disorder. A clinical psychologist's ability to evaluate whether he is considering harmful effects of properly functioning psychological mechanisms or a mental disorder depends on factual knowledge about the psychological mechanism's purpose. Evolutionary psychology is the only scientific program that explicitly seeks such knowledge (Buss, 2015).

WHY ARE HUMANS VULNERABLE TO DEVELOPING MENTAL DISORDERS?

The evolutionary process works by constantly reducing maladaptive and pathological design. In fact, the evolutionary process is so effective at reducing maladaptive genetic variants, that a genetic variant that reduces fitness by just 1% can be removed from a population in just 10 generations (García-Dorado, 2012). Nevertheless, severe psychopathology, such as schizophrenia and the genetics associated with it, is still prevalent in the population. Why are mental disorders relatively common?

One potential reason for this conundrum is that 'disorders' in the Diagnostic and Statistical Manual (DSM) are not really disorders, but psychological adaptations, or 'defenses'. One example is the fear systems involved in anxiety, discussed below. Anxiety and depression might produce very uncomfortable mental states, but evolution does not select for happiness per se – it selects for design that, on average, enhances replication fidelity compared to available alternatives. Mental pain might be useful for avoiding social exclusion, developing friendships, finding mates, and so on, similar to how physical pain is useful for avoiding tissue damage. However, it is unlikely that every mental disorder can be viewed this way. Instead, a better research question to ask is why humans have evolved in such a way as to leave *some people*

vulnerable to developing mental disorders, rather than asking how any particular mental disorder might have some hidden adaptive benefit (Nesse, 2011). Another example from evolutionary medicine is that humans are susceptible to developing back problems because the design of the human spine is based on past designs from our sea-dwelling ancestors. The spine originally functioned as a 'coat hanger' for our internal organs. When humans evolved bipedality, evolution could not go back to the drawing board to design the organism from scratch. The design of the spine left humans vulnerable to back problems, but the back problem is of course not an adaptation in itself (Gilbert, 1998; Nesse and Williams, 1996).

Some mental disorders such as schizophrenia and bipolar disorder are very unlikely candidates for adaptations or evolved defenses, although evolutionary psychiatrists have hypothesized that they might be (Sherman, 2012; Stevens and Price, 2000a, 2000b). People that suffer from severe psychopathology have trouble functioning socially, retaining jobs and sexual partners, and have reduced fecundity (Keller and Miller, 2006; Power et al., 2013; Shaner et al., 2008), and inbreeding increases the likelihood of developing these disorders (Rudan et al., 2003). These are all tell-tale signs that these conditions are maladaptive. Psychological adaptations are typically activated in the specific circumstances where they are useful, such as fear in dangerous situations or sadness after loss. Further, psychosis and manic episodes are typically *not* responses to specific environmental conditions, another sign that they are maladaptive. Below, we will consider two selection forces from the field of evolutionary genetics that can explain why risk for severe psychopathology persists (Arslan and Penke, 2015).

Mutation-Selection Balance and Severe Psychopathology

Mutations are copying errors that occur during replication of DNA. The evolutionary

relevant ones are those that survive to the next generation. That is, mutations in sperm and egg cells. These mutations are passed on to every cell in the offspring's body. Examples of mutations are deletions, duplications, inversions, and translocation of base pairs (Arslan and Penke, 2015; Keller, 2008a). Only rarely will these random mutations increase fitness. Most of the time they will negatively affect fitness, ranging from very mild reductions in fitness-relevant traits (e.g. slight decrease in ability to regulate emotions) to extremely severe (e.g. death).

For a complex organ such as the human brain, the set of all mutations in an individual is likely to affect the development of the nervous system because the brain is highly polygenic (meaning that many genes affect the same trait). Indeed, about 50% of all 25,000 protein-producing genes that humans have will affect the development of the nervous system (Keller, 2008b; Keller and Miller, 2006). On average, people carry around 500 mutations, stemming from ancestors some generations back, as well as one or two that are unique to the individual (Eyre-Walker and Keightley, 1999; Fay et al., 2001). However, a key point is that people vary tremendously in how many mutations they have inherited, with the result that some people have a brain that is disrupted by relatively few mutations. People with many such mutations are at a much greater risk for developing aberrant behaviors and conditions that clinicians recognize as psychopathology. A finding in modern genetics that supports the role of mutation-selection balance is that the risk genes for psychopathology are many, with each individual variant having extremely low effect size. This suggests that rare and mildly debilitating maladaptive genetic variants contribute to the development of psychopathology, rather than just a few candidate genes (Chabris et al., 2015). Indeed, schizophrenia is extremely polygenic (Kavanagh et al., 2015) and evidence for the p-factor (Caspi et al., 2014), namely that the structure of psychopathology can be explained pretty well

with one factor, supports the role of mutation-selection balance in explaining why these risk genes persist. That is, if severe psychopathology was caused by differential mutation load among individuals, we would expect that symptoms of psychopathology clump up in these individuals, and that the genetic variants responsible are rare. The heritability suggested by twin studies would therefore be hard to account for in genome-wide association studies without extremely large sample sizes. This is exactly what modern psychiatric genetics suggests (Manolio et al., 2009).

Balancing Selection and Personality

People vary dramatically in their personality. Some are extremely risk-averse and easily experience negative emotions such as guilt, social anxiety, and sadness; others seek out risk and enjoy risk and often experience a plethora of positive emotions such as love, excitement, and happiness. These traits are captured by neuroticism and extroversion. Some people are politically liberal and interested in a vast array of ideas, art, and moral questions, while others are conservative and focus their intellectual resources on fewer topics (high or low openness to experience, respectively). Human societies contain many niches, where different traits are rewarded to different degrees. Humans seek out environments that rewards their suite of traits (called *active gene-environment correlation* in behavioral genetics, and *niche-specialization* in evolutionary psychology). This can maintain the genetic variation.

Both normal personality traits and personality pathology are heritable (around 40–60%), and the genetic variations underlying them are overlapping, but some of the genetic variance is also unique to personality disorders (Czajkowski et al., 2019; Kendler et al., 2008). In other words, personality pathology can be thought of as extreme normal personality, but not entirely: personality pathology

might also simply be maladaptive traits that are qualitatively different. Nevertheless, it is plausible that normal personality variations, but possibly also the ‘pathological’ variants, are maintained by selection due to the tendency for humans to select environments that match their traits. This will, in turn, increase their fitness, for example, due to an increased likelihood of developing friendships, finding mates, and increase social status. In evolutionary genetics this is called migration-selection balance or environmental heterogeneity (Arslan and Penke, 2015; Buss, 2009; Penke and Jokela, 2016; Penke et al., 2007). The key point is that the fitness of extreme personality traits might depend on time and place and, hence, selection favors the variation.

Another type of balancing selection that can also explain why risk genes for mental disorders persist is negative frequency-dependent selection. The key mechanism here is that the fitness of a trait can depend on its frequency in the population. If there are more females than males in a population, the male phenotype will become more desirable. Hence, the sexes are kept at an equilibrium. Mealey (1995) has argued that antisocial personality disorder is a ‘cheater strategy’ that can thrive when these strategies are rare and when most people that the psychopaths interact with tend to cooperate. In other words, if personality pathology is maintained by negative frequency-dependent selection (rather than mutation-selection balance) it means that antisocial traits are psychological adaptations – not the result of accumulated mutations. Antisocial traits can be very harmful for individuals and for society, but it would not be considered psychopathology from a harmful dysfunction point of view if it is maintained by frequency-dependent selection.

Mismatch and Common Mental Disorders

Adaptations are designed to work efficiently within specific contexts. In other words, the

past creates the present (Tooby and Cosmides, 1990b). That is to say, the logic of any adaptation has been generated by *past* selection pressures. Therefore, organisms are vulnerable to dramatic changes in their environment over a short period of time. Such dramatic changes have occurred for humans. The agricultural revolution started off a chain of cultural change that has occurred just over the last 10,000 years. Our diet changed (more calorie-rich and processed foods), we spend less time in the sun, and people are more sedentary (Eaton et al., 2002). These factors are well-known contributors to ‘diseases of civilization’ such as heart disease and diabetes (Hidaka, 2012). Can they also explain mental disorders, such as depression? Indeed, heart disease and depression are comorbid, and the amount of LDL cholesterol in monkeys has been found to correlate with depressive behaviors, defined as portrayal of slumped body posture and lack of responsiveness to environmental stimuli (Chilton et al., 2011). This is like the anhedonia (lack of motivation) and psychomotor retardation in human depression. However, it is still controversial whether mental disorders such as depression have increased in modern times, with some studies finding increases and others no differences over time.

EVOLUTIONARY APPROACHES TO SPECIFIC DISORDERS

There are several recent overviews of evolutionary approaches to specific disorders (Del Giudice, 2018; Kennair, 2012; Kennair et al., 2018). In general, though, almost none of these varied and largely theoretically non-integrated approaches to specific disorders are tested empirically, or replicated, especially not with clinical populations (Kennair, 2011). Further, after many years, very few are familiar within mainstream clinical psychology or have influenced the general understanding of disorders or how they are

treated (Kennair, 2011; Kennair et al., 2018; Nesse, 2005). We will therefore only briefly consider some of the different evolutionary approaches to specific mental disorders here; this may correctly be interpreted as criticism of the dearth of scientific progress and investigation of the differing, competing theories and lack of data.

Unipolar and Bipolar Depression

One of the first theories of the adaptive function of mechanisms underlying unipolar depression was Price's (1967) work on social rank theory. There is now an abundance of evolutionary psychological theories and perspectives addressing depression (Allen and Badcock, 2006; Del Giudice, 2018; Gilbert, 2006). Some analyses portray depression as an adaptation (e.g. Andrews and Thomson, 2009), while others label it a harmful dysfunction (e.g. Price et al., 2004). With the existence of such different conclusions about the natural function of mechanisms involved in depression, one might reasonably expect that the field would produce testable antagonistic hypotheses. However, the focus is often on different aspects of depression, which makes it challenging to evaluate the merits of one theory compared to the others. Theories might describe different aspects of a common, ultimate cause for the evolution of depression, they might describe independent causes leading to different types of depression, or they might simply be wrong.

Evolutionary theories on bipolar disorder are far fewer than for unipolar depression. Even so, the contrast between adaptation and harmful dysfunction are apparent in this area as well. Proponents of the latter view claim that symptoms of bipolar disorder are side-effects of extreme functioning of psychological mechanisms underlying traits such as artistic performance, leadership, or social skills (Akiskal and Akiskal, 2005). The genes that predispose individuals for manic and depressive episodes could prove beneficial

to fitness if they are expressed in less severe genomic contexts, such as in less severe bipolar disorder or in relatives of individuals with severe bipolar disorder. This is in contrast to theories that claim that the depressive and manic episodes themselves are adaptations to cold climate challenges (e.g. hibernation-like living and food shortages) (Sherman, 2001, 2012). Just like with the theories about unipolar depression, there is great need for empirical testing and theoretical integration.

Autism and Schizophrenia

Autism and schizophrenia have contrasted and unconnected etiologies and courses, but both have traditionally been viewed as harmful and dysfunctional and thus lack the theoretical controversies regarding adaptation that dominate evolutionary approaches to uni- and bipolar depression. However, evolutionary approaches to autism and schizophrenia need to describe the natural functions that break down in these conditions.

For autism, the most influential evolutionary psychological theory comes from Baron-Cohen's work on the theory of mind module (Baron-Cohen, 1997). Although the ability to mindread and its dysfunction in autism is of great clinical and theoretical importance, there is probably more to the evolutionary understanding of autism. Autism, even if caused by a harmful dysfunction, is characterized by extreme expressions of traits that vary normally in the population. Life history theory might be a theoretical framework that could link variations in those traits with risk for harmful dysfunction resulting in autism (Del Giudice, 2018; see below). Such an approach could make evolutionary psychological models more in line with the recognition of autism as a spectrum rather than a discrete disorder, reflecting the recent emphasis in diagnostic manuals (Wakefield, 2013).

Evolutionary approaches to schizophrenia vary from group selectionist to viral and

dietary explanations. Few, if any, argue convincingly that schizophrenia or its related manifestations reflect evolved adaptations designed for the ultimate purpose of propagating genes. Schizophrenia has been found to be heritable and evolutionary explanations will have to reconcile the fact that a genetically transmitted mechanism that reduces fitness is resistant to extinction through natural selection (Crespi et al., 2007). The schizophrenia paradox suggests a byproduct explanation, an influential version of it being that schizophrenia is a byproduct of unique human traits such as language (Crow, 1997). Or simply as maladaptive genetic variance maintained by mutation-selection balance (Keller, 2008a).

Other Disorders

Given evolutionary psychology's success in uncovering the functional, evolved human nature of sexuality, it is a paradox that so little is written about evolutionary explanations for its dysfunction. Insight from evolutionary psychology should be helpful in clinical sexology and understanding of sexual disorder.

Food and substance disorders are mostly explained by mismatch explanations. Important caveats exist for anorexia and bulimia nervosa. These disorders have been understood from a life history theory perspective to be a result of psychological mechanisms evolved for intrasexual competition working in the modern environment with its intense focus on (especially the female) the body as a criterion for acquiring mates (Del Giudice, 2018). Also, some debate has arisen about whether our evolutionary past was substance free or substance rich, culminating in theories about the possibility that recreational drug use might be the result of psychological mechanisms for parasite protection (Hagen et al., 2013). In conclusion, there has, alas, been very little influence on general, mainstream clinical psychology of any of the specific evolutionary approaches.

An Example of a Modular and Functional Approach: Anxiety Disorders

Anxiety disorders are probably the best understood category of mental disorders. These disorders are principally malfunctioning of normally adaptive fear and disgust mechanisms. For example, it is probably adaptive and socially intelligent to be aware of the negative consequences of negative evaluation of others, however social anxiety disorder will often cause self-imposed and totally unwarranted social ostracism. Functionally, species-specific defense responses (Bolles, 1970) and the adaptive nature of fear itself has been studied for years, and almost all anxiety researchers understand the function of fear, avoidance, and safety behaviors (Kennair, 2007; Marks and Nesse, 1994). This is probably the most functionally oriented area within mental health care, and almost all psychoeducative interventions will have at least a touch of evolutionary reasoning to normalize, de-catastrophize, and explain why we need to experience fear and how anxiety works. From a cognitive-behavioral therapy perspective, which is the most evidence-based treatment method for anxiety disorders (Kaczurkin and Foa, 2015), the approaches to anxiety disorders described below highlight the specific and modular approach that clinicians may adopt. Within the cognitive-behavioral umbrella, there are several different approaches, from exposure with response prevention (i.e. reducing avoidance and reducing safety/defense responses simultaneously) via cognitive therapy that changes specific beliefs about safety behaviors and catastrophes to metacognitive therapy (MCT) that addresses worry processing rather than thought content.

Anxiety disorders are modular and context specific, to a certain degree, given that it seems that there are specific mechanisms involved in, say, arachnophobia, social anxiety, and generalized anxiety disorder (GAD). While early anxiety treatment was based on

rather uniform behavioral models (Marks and Nesse, 1994) that were largely compatible with sociobiology as a behavioral rather than mentalistic science (Naour, 2009), modern models are based on cognitive and metacognitive theory (Kennair, 2007). That is, models that focus on the beliefs patients have, for example regarding normal increases in heart rate, or the importance of worry. Mirroring this transition of methods, we see an increased focus within evolutionary psychology research on specific stimulus processing modules for conditions such as fear of spiders (arachnophobia) (Gerdes et al., 2009; Hoehl and Pauen, 2017; Kennair and Lindner, 2017; LoBue, 2010; New and German, 2015; Rakison and Derringer, 2008).

Different anxiety disorders are treated with a host of specific interventions and manuals – ranging from classical behavior therapy that includes exposure and response prevention for simple phobias and agoraphobia to cognitive therapy for social phobia and panic disorder, and, more recently, MCT (Nordahl et al., 2018) for GAD. From a cognitive-behavioral approach, the specific disorders are defined largely by what the patient finds most threatening and what specific maladaptive safety behaviors the patient employs – that is, how the patient attempts to avoid the imagined catastrophe. For example, in simple phobias, avoidance is the major safety behavior, while the disorder is defined by heightened danger monitoring, fear, and disgust towards specific stimuli, and these are typically phenomena that were threatening in our evolutionary past, suggesting that the avoidance has some adaptationist underpinnings, although clinical phobias might not be adaptations in themselves (Kennair and Lindner, 2017). Social anxiety disorder motivates attempts to hide symptoms of anxiety, due to an exaggerated fear of social negative evaluation due to said symptoms (Kennair and Kleppestø, 2018); agoraphobia and panic are interwoven conditions where the former (a fear of not being able to get to safety) often is a response to

the latter (catastrophizing interpretation of harmless symptoms of anxiety leading to extreme anxiety attacks); while GAD is a worry disorder, where the worry is a form of safety behavior that the patient feels she/he has lost control over.

The behavioral, environmental approach to the etiology of anxiety, as defined by Mowrer's (1947) two factor theory (first classically conditioned aversive stimulus, thereafter operant conditioned avoidance), has lost support. Anxiety acquisition seems to follow a more innate, maturational pattern (Poulton and Menzies, 2002a, 2002b; Poulton et al., 1998, 1999, 2001). Rather than considering how anxiety is learned, the current question is how naturally occurring phobias are diminished and extinguished through the developmental process. Sandseter and Kennair (2011) suggest one of these evolved pathways is the child's proclivity to engage in risky play. Risky play is normal behavior, and despite the worry of parents, it is not particularly dangerous (Kennair et al., 2018). Children mature to adaptively fear dangerous behavior and ecological threats. But as the children develop and acquire skills that make it possible to cope with previously fear inducing threats, they start seeking the thrilling sensations that motivate risky play. This both provides further emotional and psychomotor training and development, effectively reducing anxiety.

A problem for many evolutionary approaches to specific disorders is a lack of state-of-the-art efficient psychotherapeutic approaches. Evolutionary psychology is largely a cognitive science. As such, the mental processes involved in disorders and the treatment of these should be at least of the same interest as physiological and genetic aspects, and especially mere behavioral descriptions. As in the discussion of depression below, it is not in line with evolutionary psychology metatheory to be panselectionist or panadaptationist; there is no reason for an evolutionary approach to necessarily discover that a specific

anxiety disorder actually increases fitness here and now or did so in the EEA. Rather, one may follow Wakefield's (1992a) harmful dysfunction approach and merely consider what specific mental mechanisms are malfunctioning. This is the most relevant approach within evolutionary psychopathology, despite the counterintuitive, original, and provocative findings of de Catanzaro (1995) on suicidal ideation suggesting that it may be adaptive to commit suicide when one's existence lowers one's inclusive fitness. These results need to be replicated and followed up in longitudinal, predictive studies – and this has yet to be done several years after the original research. Two obvious examples: social anxiety disorder does not *protect* against social ostracizing, rather social anxiety results in a self-imposed social withdrawal, with lowered levels of romantic activity and success and lower levels of status and educational or career accomplishments (Kennair and Kleppestø, 2018); panic disorder patients do not flee actual and present external dangers at high speed, quite the contrary, they misinterpret their anxiety symptoms and stay at home or lie down in fear of any physical exertion (Kennair, 2007).

Fear itself is the adaptation; fear protects us from clear and present danger. Several mental mechanisms involved in, for example, spider perception and detection are probably also adaptations (Gerdes et al., 2009; Hoehl and Pauen, 2017; Kennair and Lindner, 2017; LoBue, 2010; New and German, 2015; Rakison and Derringer, 2008). The ability to connect apprehension about future outcomes with negative emotion is maybe also an adaptation (Miloyan et al., 2016). Fear of venomous spiders and snakes is highly adaptive (Öhman and Mineka, 2003), as is the ability to learn that some spiders and snakes are harmless (Sandseter and Kennair, 2011). It should be obvious that there are poor grounds for hypothesizing an adaptive just-so story for unwarranted and debilitating arachnophobia.

TWO CONTEMPORARY ISSUES

For decades, there has been very little empirical research within evolutionary clinical psychology. Different theories were proposed, but little work went into testing these varied approaches. Further, to a large degree, there has been little overarching theory, and many that studied evolutionary psychopathology were not really a part of the general evolutionary psychology framework (Kennair, 2011). Recently, two empirically based contemporary issues have arisen: (1) the claim that rumination and depression is adaptive – rumination solves complex social problems (Andrews and Thomson, 2009; Watson and Andrews, 2002) – and (2) the life history approach to conceptualization of mental disorders (Del Giudice, 2014, 2018).

Is Depression Adaptive?

Several evolutionary approaches to depression have been offered throughout the last few decades (Gilbert, 1992; Kennair et al., 2017; McGuire and Troisi, 1998; Nesse, 2000; Sloman and Gilbert, 2000). Typically, these approaches have not considered depression to be an adaptation, rather, depression is the maladaptive result of processes in other evolved mental mechanisms. An important early example is the social competition model (Gilbert, 1992; Price et al., 1994). Ethological observations have suggested that animals (e.g. chickens) yield when they lose hierarchical positions. There is evidence that depression can be activated in humans when they feel trapped (Gilbert, 2000; Gilbert and Miles, 2000; Gilbert et al., 2009). A new development is the emergence of theories that consider the possible adaptive function of depression itself, such as Hagen's model of post-partum depression (Hagen, 1999, 2003; Hagen et al., 2004). The problem with this approach is that there might not be a specific condition that may be defined as post-partum depression; rather, it is merely

depression in that life situation. The condition does not differ in symptoms or likelihood from other times in the patients' lives. Another related approach is Watson and Andrews' (2002) social navigation model, which postulates that the adaptive value of depression is to solve social problems and force other people to help the depressed person. Typically, these adaptive approaches have not primarily been developed by clinicians.

An example of a disconnect between mainstream clinical science and academic evolutionary approaches may be seen in the discussion around the Adaptive Rumination Hypothesis (ARH) (Andrews and Thomson, 2009; Bartoskova et al., 2018). The main gist of this theory is that depressive rumination is an adaptive, dose dependent, evolved strategy to solve complex social problems. The organism will have trouble not ruminating and will reduce other hedonic activities to free up time for rumination. Rumination might feel both compelling and uncomfortable; however, the rumination is necessary to be able to solve the complex problem and will be adaptive for the organism in the long run. Conversely, interventions that merely treat the symptoms (i.e. reduce depressive symptoms or the rumination), without solving the complex social problem, will prove maladaptive in the long run. Interventions that intensify rumination would be favored from this perspective.

Simultaneously, within mainstream clinical psychology, the approach called MCT (Wells, 2009) has considered the effect of reducing rumination as an intervention against depression. Building on the same basic research of rumination as the maintaining factor of depression by Nolen-Hoeksema and colleagues (Nolen-Hoeksema, 2000, 2004; Nolen-Hoeksema and Morrow, 1993; Nolen-Hoeksema et al., 2008), both approaches agree that rumination is the major maintaining factor of depression. However, these two approaches differ in the conclusion of what consequences this has for understanding rumination and for interventions. ARH

and MCT actually draw diametrically opposing conclusions (Kennair et al., 2017). The same tenets that ARH claim for the adaptive nature of rumination are the very metacognitions that MCT seeks to challenge, including negative metacognitions about lack of control of rumination and positive metacognitions about the ability to solve problems. In this approach, the positive and negative metacognitions described above are challenged and weakened and rumination is discontinued (Wells, 2009). From a clinical, ethical perspective, it is worrisome that increased rumination is being recommended on the grounds of current knowledge. Mainstream clinical research trials suggest that discontinuing rumination and challenging and reducing belief in negative and positive metacognitions involved in depressive rumination is a very effective treatment of depression and maybe more efficient than other current evidence-based methods (Dammen et al., 2015, 2016; Hagen et al., 2017; Hjemdal et al., 2016, 2019). Note that in this method one does not attempt to solve any problem; rather, one teaches the patient that rumination does not solve any problem. Recently, a three-year follow-up of MCT for MDD was published, finding improved relapse protection, and increased quality of life and study or workforce participation (Solem et al., 2019). In other words, without working on problem solving, merely by discontinuing rumination, there seems to be improved and maintained function and less depression.

What is expected to happen to patients if they cannot solve their problems, and therapy gets in the way of normal and evolved processes, as suggested by the ARH? From Darwinian medicine, we know that treating the evolved defense mechanism may result in aggravating the actual disorder and causing more suffering (Nesse and Williams, 1996; Williams and Nesse, 1991). The critique that the results from MCT trials will not prove to be stable because hindering normal rumination processing will be akin to medically treating symptoms rather than the complex

social problem, is not supported. Follow-up data are very promising, and do not suggest that reduced rumination or lack of problem-solving causes increased future suffering (Hagen et al., 2017; Hjemdal et al., 2019; Solem et al., 2019).

Obviously, as we are involved in this debate, we therefore need to add this disclaimer that this is not a neutral account. Despite this, it is generally not considered ethical from a clinical perspective to prolong or intensify depression. Prolonged depression will predict chronification and risk of neurocognitive impairment. Suicide risk may also be increased. Rumination increasing interventions need to be considered with the utmost care. Clinicians are less willing to consider the adaptive aspects of rumination (Kennair et al., 2017; Nesse, 2018). It is worth noting that academic evolutionary researchers also doubt whether rumination solves social problems or aids problem solving in general (Nettle, 2004).

Evolutionary and adaptive approaches have a counterintuitive power that may contribute to original and testable hypotheses. At the same time, evolutionary psychologists are not panselectionists or panadaptationists, despite early claims of such from critics such as Gould and Lewontin (1979). Integration of academic evolutionary psychology and evolutionary clinical psychopathology is important for the field to thrive; however, it is a challenge for researchers to stay abreast with state-of-the-art developments in several fields and disciplines. Integration of clinical and academic evolutionary psychology is probably a fundamental issue for the development of both areas (Del Giudice, 2018; Kennair, 2011). This is illustrated by Wakefield's (1992a) definition of psychopathology: we need to both map the evolved modules of the normally functioning mind to be able to consider when there is dysfunction, and we need to consider what dysfunction may tell us about normal functions of the mind (Kennair, 2011).

Life History as an Integrative Approach

Life history theory is based on the idea that all organisms must invest the finite resources of time and energy into either reproduction or increased chance of survival (Stearns, 1992). Survival and reproduction have an antagonistic relationship because both require the use of precious energy. If an organism invests in one, potential investment in the other is lost. Hence, there is a fundamental tradeoff between *somatic effort* and *reproductive effort* that every organism must solve strategically – that is, with a life history strategy. Beyond the fundamental division between relative somatic and reproductive effort, there are also other important tradeoffs in life history strategies, the solutions to which will have variable fitness benefits in different species, sexes, and ecologies. Some examples of such tradeoffs are: when to begin investing in reproductive effort (current versus future reproduction)? How many offspring should one have and how much investment should be given to each (quality versus quantity of offspring)? How much investment should be given to promoting already acquired offspring and how much should be given to acquiring more offspring (parenting versus mating effort) (Del Giudice, 2018)? It is the clustering of different evolved solutions to these strategic problems that has been conceptualized as fast and slow life history strategies. Fast strategies involve transition to reproductive effort earlier in life with more investment in quantity of offspring and slow strategies involve transition to reproductive effort later with more investment in quality.

Del Giudice (2014) has championed a life history approach to mental disorder. In this approach, Del Giudice considers fast and slow strategies as the basis for differentiation. An extended version of the model is presented in Del Giudice (2018) and it merges the fast/slow continuum with the harmful dysfunction definition of mental

disorder. Fast and slow life histories are proposed to associate with different clusters of disruptions in the natural function of evolved psychological mechanisms, producing ‘fast-typical dysfunction’ and ‘slow-typical dysfunction’ that, when evaluated as harmful, result in fast spectrum (F-type) disorders and slow spectrum (S-type) disorders. In the extended version, a third category has been labeled defense activation (D-type) disorders. Albeit not being disorders as defined by the harmful dysfunction definition, the normal functioning of evolved psychological mechanisms could produce defenses that are experienced as harmful and possibly treatable (Cosmides and Tooby, 1999; Nesse and Williams, 1996; Wakefield, 1992a). Further, within the extended framework there are different profiles of fast and slow life history: antagonistic/exploitative and seductive/creative profiles on the fast side of the continuum versus prosocial/caregiving and skilled/provisioning on the slow side of the continuum. Combining the Fast/slow/defense (FSD) model with these personality profiles, Del Giudice (2018) provides a new foundation for evolutionary analysis of mental disorder through a life history perspective. Some examples are: understanding autistic-like traits as male typical variants of skilled/provisioning profiled slow-type disorder; understanding schizophrenia spectrum disorders as fast-type disorders associated with the seductive/creative profile, with some subtypes breaking the general pattern; understanding eating disorders as an expression of either a fast-type disorder with the seductive/creative profile or a slow-type disorder with the skilled/provisioning profile; and understanding GAD as a prototypical defense-type disorder.

Four casual pathways have been considered for the development of psychopathology on fast and slow spectrums (Del Giudice, 2014): (1) adaptive life history-related traits may be regarded as symptoms, (2) life history-related traits may be expressed at maladaptive levels, (3) adaptive strategies may yield individually

maladaptive outcomes, and (4) life history-related traits may increase vulnerability to dysfunction. Only pathway 4 (and possibly 2) would produce fast and slow disorders whereas pathways 1, 3 (and possibly 2) would produce defense activation disorders. For life history-related traits expressed at maladaptive levels to constitute a true disorder, the exaggerated expression must be a result of a dysfunction in the mechanism as opposed to the result of a normal response to a mismatch stimulus. D-type disorders are not expected to distribute along the same dichotomy as fast and slow spectrum disorders, however, there is a suggestion that one would see a higher prevalence in individuals with fast spectrum characteristics because these correlate with a higher incident of adverse life events.

The power of life history theory rests on its ability to integrate various psychological, physiological, and other traits according to how they function in supporting and/or regulating solutions to the dilemmas described by the theory. This has proved to be a challenging task at least when applied to humans and especially when used as an approach to the study of mental disorders. The basic distinction between fast and slow generally accounts for small variations in personality and behavior. The strongest and most stable link is between a fast life history strategy and impulsivity and risk-taking behaviors. The disentanglement of categorizing mental disorders according to the fast/slow profiles and explaining them through various causal pathways is an active area of theory development and research (Del Giudice, 2018). Some conceptual and empirical issues in life history theory remains before the clinical utility of the framework could be evaluated (Kennair, 2014). Key among them is how the model handles state versus trait distinctions and whether clinical populations can be differentiated in terms of the fast/slow continuum or any of the proposed profiles. Diagnostic manuals like the ICD-11 or DSM V are not developed within a life history framework and thus it is likely that every

diagnostic group would contain both individuals using fast strategies and individuals using slow strategies. Could patients with slow or fast profiles benefit from different treatment? Ultimately, the clinical utility of an integrative approach rests on the ability to transform the knowledge obtained from looking through its ‘glasses’ into actual treatment decisions. In the meantime, this approach has two important promises: theoretical integration of evolutionary clinical psychology and academic research and increased evolutionary clinical research. If this is achieved, the approach will have been a scientific success (Del Giudice, 2018; Kennair, 2011).

EVIDENCE-BASED EVOLUTIONARY CLINICAL PSYCHOLOGY

One limitation of evolutionary approaches to clinical psychology is the lack of practical or applied innovation. Nesse (2005) goes so far as suggesting that this is not even the main aim of evolutionary clinical approaches. A few clinical applications have been suggested (Gilbert, 2014; Ilardi, 2010). However, it is necessary to uphold the scientific rigor of mainstream evolutionary psychology when developing clinical interventions. Within scientific clinical psychology, a treatment method is considered evidence-based when it has been established through repeated randomized clinical trials. One tests against waiting lists to establish that the therapy is better than doing nothing, and one tests against established interventions to test for equal or superior effect. For depression, almost all interventions will show an effect if one does not control for waitlist, as depression usually will remit without intervention, although recurrent episodes are typical. Further, most manualized, established interventions for depression are not able to show evidence of superiority, partly due to underpowered clinical trials. Any new approach to the treatment of depression today needs to be able

to document rapid and good effect and preferably demonstrate improved relapse prevention (see Solem et al., 2019).

As far as we know, there has not been published treatment trials testing Ilardi’s treatment package, which combines different insights from an evolutionary perspective with techniques from cognitive behavior therapy. Gilbert and coworkers have, throughout the years, collected data on effect. Gilbert’s compassion focused therapy is, to date, the best documented intervention that is inspired by evolutionary theorizing (Gilbert, 2014). Nevertheless, even this method only has one randomized controlled trial with a clinical sample (Braehler et al., 2013; Leaviss and Uttley, 2015). For most suggested ‘evolutionary inspired’ interventions, the evidence base is poorly established. Further, there is an ethical side to interventions with suffering patients. It is not merely an academic exercise to suggest how depressed patients ought to be treated or taught to believe about their condition. A biophilic, metaphoric, and well-intended but not scientifically substantiated approach to mental health will cast evolutionary approaches more as alternative medicine rather than as a natural science-based intervention (see Nesse, 2018 for warnings against quick fix evolutionary approaches).

CONCLUSIONS

Evolutionary clinical psychology has yet to mature as a scientific, applied discipline. There are few applications or treatment methods that are explicitly inspired by evolutionary theory, and those few contributions lack the scientific foundation to be considered evidence-based for any specific disorders.

Wakefield’s (1992a) harmful dysfunction approach to the definition of mental disorder is an important contribution. However, practical application suffers from a lack of mapping of the normal functioning of mental

mechanisms, as well as good evolutionary psychopathology studies of malfunctioning mechanisms. Despite this, psychiatry and clinical psychology have no better approach for an overarching theory of pathology. Thus, these shortcomings highlight the need to improve evolutionary psychopathology research and integrate mainstream evolutionary psychology and clinical psychology (Kennair, 2011).

Recent topics within the field include the life history approach to conceptualization of mental disorders (Del Giudice, 2014; Del Giudice et al., 2015). It is too early to evaluate what concrete clinical contributions this approach may have, although the hope is that it generates more empirical research. Another contemporary issue, the adaptive approach to rumination (Andrews and Thomson, 2009; Bartoskova et al., 2018), is more controversial (Nesse, 2018) and, considering mainstream clinical research, is probably a pan-adaptationist dead end (Kennair et al., 2017).

In summary, after years of theorizing, the field of evolutionary clinical psychology is still poorly integrated, has not resulted in many applications, and is not very influential within mainstream clinical psychology practice. Hopefully, the recent developments may generate more data and help accommodate the evolutionary paradigm to the study of abnormal psychology.

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Evolutionary Cultural Psychology

Oliver Sng and Steven L. Neuberg

Lucia and Jeff are students at the same university. They have been in a relationship for three years. How likely do you think it is that they will break up after graduation? It turns out that people can have quite different answers to such a seemingly simple question (Ji et al., 2001). Students in the United States were more likely to say that the couple would stay together after graduation. Students in China, on the other hand, were more likely to think that the couple would break up after graduation. The argument proposed here was that the East and West have culturally different views about the nature of change (as influenced by different philosophical traditions), with the former thinking of change as more cyclical and the latter thinking of change as more linear. For readers who might belong to either of the two cultures, the typical response of individuals from the other culture may seem surprising. But such is the pervasiveness of cultural influences on the way we think about the world, whether we are conscious of them or not.

Indeed, this might be especially surprising for readers of this chapter. An underlying premise of evolutionary psychology is that selection pressures have shaped species-wide psychological adaptations. From this, one might expect evolutionary psychological work across societies to have focused more on testing hypotheses about cross-societal universals than on testing hypotheses about differences. And, indeed, it has (Gurven, 2018). For example, extensive cross-cultural work has been conducted testing evolutionary hypotheses on the nature of mate preferences (Li et al., 2011; Schmitt, 2005; Shackelford et al., 2005), kin detection (Sznycer et al., 2016a), cheater detection (Sugiyama et al., 2002), and the structure and function of emotions (Sznycer et al., 2016b). Yet, despite important cross-societal similarities, people in different societies also vary in psychologically meaningful ways.

Understanding similarities and differences in psychology requires an integrative consideration of evolutionary and cultural processes

and how these processes work together and also shape each other. Our aim in this chapter is modest – to provide a short discussion of three important questions that highlight roles that evolutionary and cultural processes play, together, in shaping human behavior: (1) what are the origins of psychological variation across societies? (2) How does culture spread and evolve? (3) How does culture shape biological evolution?

We begin with a definition of the core concept of culture. Then we review existing psychological differences, across societies, that have received substantial research attention, and we review prominent explanations for these differences. We do so to introduce the reader to the cultural psychological literature that has received less attention from evolutionary theorists. We then outline how evolutionary perspectives can speak to questions about psychological variability across societies, the origins of culture, the spread and evolution of culture, and how culture might shape genetic evolution. Finally, we outline several issues and questions that emerge from the current survey of the literature and highlight future directions.

CULTURAL VARIATION IN PSYCHOLOGICAL DIFFERENCES: THREE EXAMPLES

What is culture? Although a question of significant debate (Rohner, 1984), for the purpose of this chapter, we adopt this working definition: culture is a set of beliefs, practices, or behaviors shared by individuals who speak a certain language and reside in a specific location and time (Triandis, 1996). It is assumed that elements of culture are socially shared (Kitayama and Uskul, 2011) and that these elements are transmitted among individuals through various forms of social learning (Mesoudi, 2016). We begin by briefly introducing three prominent dimensions of culture empirically known to be associated

with meaningful psychological differences, which we use to articulate an evolutionary perspective on culture.

Individualism–collectivism

Fill in this blank: ‘I am ____’. What word or phrase came to mind?

If you responded with a trait like ‘intelligent’, that is a personal trait or quality. On the other hand, if you responded with a trait like ‘an evolutionary psychologist’, that is a statement of membership in a group or demographic category of individuals with some degree of shared experience. Members of largely individualistic cultures, such as the United States, are more likely to respond with a personal characteristic (Bochner, 1994; Bond and Cheung, 1983; Triandis et al., 1990); people in individualistic cultures have self-conceptions that view the self as independent from others, and they prioritize personal goals over the goals of the group (Oyserman et al., 2002; Triandis, 1996). In contrast, members of largely collectivistic cultures, such as Japan, are more likely to respond with a statement of social membership or relationship. Indeed, people in collectivistic cultures define the self in relation to one’s group and prioritize the goals of the group over their own goals. Subsequent work has further parsed individualism and collectivism into subtypes (e.g., Campos and Kim, 2017; Singelis et al., 1995).

Closely related is the concept of independent and interdependent self-construals (Markus and Kitayama, 2010), which are observed more in individualistic and collectivistic cultures, respectively. Independent self-construals are schemas of the self in which one’s behaviors are organized in reference to one’s own thoughts and actions. In contrast, interdependent self-construals organize behavior around one’s social relationships. Also, whereas people with independent selves tend to see less distinction between typical ingroup and outgroup members, people with interdependent selves

observe a larger ingroup–outgroup separation, which in turn motivates different behaviors toward ingroup and outgroup members. Recent work has further proposed that a seven-dimensional model more comprehensively captures cross-cultural differences in the self (Vignoles et al., 2016).

That cultures differ in individualism/collectivism and independent/interdependent self-construals has generated large bodies of work. Indeed, these particular differences have been influential in understanding and explaining a wide range of psychological differences across cultures. For instance, individuals from more collectivistic cultures, unlike those from more individualistic cultures, have less need to hold positive views of the self (Heine et al., 1999), show weaker endowment effects (Maddux et al., 2010), place less value on personal choice (Snibbe and Markus, 2005), perceive themselves as more flexible across situations (Suh, 2002), are less likely to seek social support from close others (Kim et al., 2008), and adopt a more ‘holistic’ style of cognition – paying greater attention to and reasoning about things in relation to their surroundings (Nisbett et al., 2001).

What leads to cultural differences in collectivism/interdependence and individualism/independence? One early explanation focused on historical philosophical influences (e.g., Confucian vs Greek) in the East and West (Nisbett et al., 2001). Other work has located the origins of these differences in the subsistence and resource-acquisition activities traditionally engaged in by different groups. For instance, to the extent that farming requires greater social cooperation than herding, groups that have traditionally engaged in farming are more likely to become interdependent in their psychologies than groups that have traditionally engaged in herding (Uskul et al., 2008). Moreover, because different types of farming require greater commitments to cooperation, one might make finer distinctions. For instance, because rice cultivation tends to require even

greater cooperation and coordination than does wheat cultivation, communities where rice farming is prominent are likely to generate especially interdependent psychologies (Talhelm et al., 2014). Note that cultural psychological differences created in such ways may not be limited to those individuals engaged in the particular form of subsistence activity. In other words, a person who has never engaged in rice cultivation but who lives in a rice farming community is nonetheless expected to be relatively interdependent in his or her psychology. This is presumably because beliefs and practices within the community spread through social learning across individuals (we elaborate more on cultural learning processes later in the chapter).

Yet, other work has examined the role of mobility in generating these cultural differences. There are at least two forms of mobility relevant here: residential mobility is the frequency with which individuals physically relocate in and out of a group (Oishi, 2010), whereas relational mobility is the ease with which individuals can choose and form new social relationships (Yuki and Schug, 2020). The two factors can be orthogonal, in that individuals could be living in environments that are high in one form of mobility but low in the other. High residential mobility tends to promote more independent self-construals (Oishi et al., 2007), as moving frequently disrupts one’s social groups and pushes individuals to rely more on their personal identity and less on their social identities. In high (low) *relational* mobility groups, more independent (interdependent) self-construals are also found (Thomson et al., 2018). In the context of low relational mobility conditions, interpersonal relationships are hard to change, and therefore interdependent selves function to maintain positive relationships with others.

Tightness–looseness

Another cultural psychological difference that has received increasing attention

is tightness–looseness (Pelto, 1968). Tight cultures are characterized by strong social norms, with behaviors that deviate from these norms being severely punished. On the opposite end, loose cultures are characterized by weak norms and greater tolerance of deviant behavior. Countries like the United States, Spain, and France are relatively culturally loose, whereas countries such as Pakistan, South Korea, and Egypt are relatively tight (Gelfand et al., 2011; Uz, 2015). Although earlier work noted the importance of this dimension (Pelto, 1968), more recent theorizing and large-scale cross-cultural studies have brought this cultural difference to the fore (Gelfand et al., 2011; Harrington and Gelfand, 2014; Triandis, 1996).

People living in tight countries report being more cautious, have greater impulse control, and have a greater need for structure in everyday life (Gelfand et al., 2011). Within the United States, people in tighter states are higher in conscientiousness and lower in openness (Harrington and Gelfand, 2014). Individuals in tight cultures are also more likely to endorse autonomous leaders (Aktas et al., 2016), less happy than those living in moderately loose cultures (Harrington et al., 2015; although see Chua et al., 2019), but also less likely to express negative emotions (Liu et al., 2018). At the societal level, tight cultures have stricter governmental laws and punishments and are also more religious (Chua et al., 2019; Gelfand et al., 2011).

Cultural differences in tightness–looseness have generally been attributed to historical differences in ecological threats such as natural disasters, disease, high population densities, resource scarcity, and territorial threats (e.g., Gelfand et al., 2011; Harrington and Gelfand, 2014; although see Chua et al., 2019, for some exceptions), presumably because such threats increase the need for stronger norms and norm enforcement to facilitate social coordination. That societal threats might create tighter cultures has also been supported by some evolutionary-simulation work (Roos et al., 2015).

Traditional/Secular-rational and Survival/Self-expression

Cultural differences in two value dimensions – traditional versus secular-rational and survival versus self-expression – have received significant research attention, particularly in the fields of political science and sociology. Derived from analyses of measures within the World Values Survey (Inglehart and Baker, 2000), these two dimensions capture about 70% of cross-national variation in values across 65 countries.

Compared to secular societies, traditional societies prioritize the importance of authority, family, religion, and more conventional values. Traditional societies are also more likely to have absolute standards for what is morally ‘good’. A typical statement that members of a more traditional society endorse is ‘It is more important for a child to learn obedience and religious faith than independence and determination’. Secular societies, on the other hand, exhibit the opposite pattern of traits.

The second survival/self-expression dimension also encompasses a range of traits. Survival-oriented cultures tend to prioritize basic needs for physical and economic security and hold strong materialist values. People in survival cultures are less tolerant of foreigners and other outgroups, seeing them as posing threats to security, and are less open to diversity, more generally. A statement endorsed in survival cultures is ‘When seeking a job, a good income and safe job are more important than feeling accomplished and working with people you like.’ On the other end of the spectrum is self-expression. When basic needs are fulfilled, diversity is not just tolerated; it can become valued as a form of novelty. Cultures high on self-expression are also more likely to value individual agency and autonomy.

Inglehart and Baker (2000) situated 65 countries along these two dimensions. For example, Pakistan was highly traditional and survival-oriented, whereas Sweden was

highly secular and self-expression-oriented. In the other two quadrants, Estonia was highly secular but survival-oriented, whereas the United States was highly self-expression-oriented but relatively traditional. Increases in secularism, not surprisingly, are related to increases in individualism (Grossmann and Varnum, 2015). Other work has also found that countries higher on self-expression are lower in corruption (O'Connor and Fischer, 2012) and show larger sex differences in personality (Schmitt et al., 2008).

Modernization theory has been proposed to explain cultural differences in traditional/secular and survival/self-expression values (Inglehart and Baker, 2000), with economic development posited to underlie variation in both dimensions. According to this view, increasing technology and mechanization resulting from industrialization reduces dependence on nature. This leads to a diminishing role for more traditional sources of control, such as religion, and enables the emergence of secularism. Separately, the rise of service and knowledge-oriented occupations in postindustrial societies leads people to become less dependent on nature and more dependent on what has been described as 'games between persons' (Inglehart and Baker, 2000: 22), thereby increasing the importance of self-expression. Presumably because of the relentless push toward an increased role of technology in economic life, most countries become more secular and self-expression-oriented over time (Inglehart and Baker, 2000).

EVOLUTIONARY PERSPECTIVES ON CULTURE

With the above cultural psychological differences as context, we now outline various ways in which evolutionary perspectives intersect with cultural psychology. Some hypotheses proposed at these intersections have been empirically tested; others have yet

to be tested. In doing so, we seek to address three questions: (1) what are the origins of cultural differences? (2) How does culture spread and evolve? (3) How does culture shape biological evolution?

The Origins of Cultural Differences

In the previous sections, we outlined a range of existing explanations for important cultural psychological differences. For instance, differences in collectivism–individualism might emerge as a result of differences in historical philosophies (Confucianism in the East, Greek in the West), which encouraged different beliefs and practices. This begs the question, however, of why *these* specific philosophical ideas emerged and persisted over time. One could imagine that other, potentially competing forms of philosophy existed. And, indeed, there were many other schools of philosophy in ancient Chinese history (Feng, 1983), such as the School of Names, a philosophy that focused on logic and definitions. So why did Confucianism persist rather than the School of Names? Explaining one cultural difference by invoking a second cultural difference simply pushes origin questions back further. Another explanation often invoked here is social learning: individuals learn collectivistic/Confucian practices and values from others. We discuss cultural learning in more detail in the next section. However, social learning assumes that others already have collectivistic values and practices, which begs the question of where others learned collectivism from.

Many explanations themselves require explanations, highlighting the distinction between proximate and ultimate levels of explanation (Scott-Phillips et al., 2011). In an evolutionary framework, ultimate explanations address fundamental 'why' questions, and they do so in terms of thinking about how a specific psychological trait enhanced ancestral survival and reproduction. In this section,

we explore how ultimate explanations might contribute to our understanding of the origin of cultural differences. Before doing so, however, we note two critical points. First, ultimate and proximate explanations need not contradict one another. They are simply explanations at different levels of analysis. For example, people could hold interdependent self-construals because they help maintain and enhance positive social relationships (proximate explanation). People could also hold interdependent self-construals because they enhanced ancestral survival and reproduction (ultimate explanation) *through* maintaining and enhancing positive social relationships. Second, ultimate explanations do not imply that individuals are consciously aware of the adaptive functions of their behaviors; individuals with interdependent self-construals are not necessarily thinking ‘I will be interdependent because it will help me survive and reproduce’. Indeed, theorizing about the evolutionary function of self-deception suggests that it can be useful to be unaware of the ultimate goals of one’s beliefs and behaviors (Von Hippel and Trivers, 2011).

One evolutionary perspective for thinking about the origins of psychological variation comes from the field of behavioral ecology, and it rests on the idea of *phenotypic plasticity* (Dingemanse et al., 2010; Piersma and Drent, 2003; West-Eberhard, 1989). Phenotypic plasticity is the ability for individuals with the same genes to adopt different traits and behaviors under varying environmental conditions.¹ To provide one example, killifish that develop in environments of high density (i.e., where there are many other killifish) tend to have fewer – but larger – offspring per brood (Leips et al., 2009). This is hypothesized to be an evolved reproductive strategy: because of the more intense social competition for resources under higher densities, female killifish in such ecologies concentrate their limited biological resources on fewer offspring, increasing average offspring size and thereby enhancing offspring

competitiveness. Such flexibility has evolved in killifish as a result of ancestral variation in encountered densities, which selected for a flexible reproductive strategy that adjusts to the density of an individual’s environment. Many forms of phenotypic plasticity have been uncovered across species, with plasticities and calibrated to many features of the environment (Davies et al., 2012).

With some exceptions, research on differences across societies and cultures has not drawn heavily upon the concept of phenotypic plasticity. However, recent theoretical and empirical work has outlined key dimensions of the ecology – population density, genetic relatedness, sex ratio, mortality risk, resources, and pathogen prevalence – for which human phenotypic plasticity might explain what is known about cultural psychological variation, enable the generation of new hypotheses, and inspire a reconsideration of the existing literature (Sng et al., 2018). The broad claim of this approach is this: *psychological variation across cultural groups might originate from variation generated by phenotypic plasticity, because different cultural groups reside in different ecological conditions.*²

Consider, for example, the question of where cultural differences in collectivism come from. At the core of collectivism/interdependent self-construals is the prioritization of group interests over self-interests. This is captured by a sample item from a popular measure of interdependence: ‘I will sacrifice my self-interest for the benefit of the group I am in’ (Singelis, 1994). At first glance, an interdependent self-construal seems to fly in the face of basic evolutionary principles. How could such a belief, and associated behaviors, have evolved? Simply, those with sacrificial interdependent selves would be out-reproduced by those with more independent selves, who themselves make no self-sacrifices but nonetheless benefit from the prosocial behaviors of interdependent individuals. This is the classic problem of the evolution of altruism, and, similarly,

the classic solution is useful here (Hamilton, 1964). From inclusive fitness theory, organisms have evolved traits that facilitate individual survival and reproduction but also the survival and reproduction of others that *share copies of one's genes*. Supporting this, a substantial body of work within behavioral ecology and evolutionary psychology finds that individuals, across species, are more likely to engage in prosocial behavior when in proximity of genetic relatives and toward genetic relatives (e.g., Griffin and West, 2003; Hesse et al., 2012; Lieberman et al., 2007; Russell and Hatchwell, 2001; Sznycer et al., 2016a; Wilkinson, 1985). The prototypical non-human illustration of this is alarm calling in Belding ground squirrels. Alarm calling draws the attention of predators and thereby puts the alarm callers' own lives at risk in order to alert other nearby squirrels of the predator. Interestingly, though, not all squirrels engage in alarm calling. In particular, female squirrels do so much more often than males, and certain female squirrels do so more than other females (Sherman, 1977). The critical factor is the presence of genetic relatives in the immediate surroundings and, consequently, the copies of the alarm caller's genes that might be subject to predation. The more relatives in the immediate vicinity, the more likely an individual is to alarm call. Put simply, if sacrificing oneself (100% of one's genes) could save three siblings (150% of one's genes), then behaviors (and an associated psychology) motivating context-dependent self-sacrifice could evolve. The inclusive fitness explanation elegantly accounts for both the individual variation and the sex difference in alarm calling, because ground squirrels are matrilineal: females tend to remain in the group they are born in and hence are more likely than males to be surrounded by genetic relatives.

One might thus hypothesize that human psychology should tend toward interdependence for individuals *living in groups with many family relatives* (or where cues suggest high degrees of genetic relatedness)

and toward independence for those living among non-relatives (or where cues suggest low degrees of genetic relatedness). That is, independent/interdependent self-construals may be a form of phenotypic plasticity sensitive to the prevalence of genetic relatives in one's group, shifting individual psychology and behavior toward a more interdependent self when surrounded by many relatives and toward a more independent self when surrounded by few relatives. In initial research supporting this, in countries where individuals live in groups with more kin, people report a more interdependent self, a greater willingness to go to war for one's group, and greater trust toward others in one's locale (Sng, 2016). Hence, an ultimate origins explanation for the question of why there are cultural differences in independent/interdependent self-construal is as such: individuals have evolved to flexibly switch between independent/interdependent self-construals (as a form of phenotypic plasticity), shifting toward interdependence in environments (social groups) where they are surrounded by many relatives and toward independence in environments with few relatives.

The prevalence of relatives is not the only relevant ecological dimension when thinking about interdependence/collectivism. Pathogen prevalence is another ecological dimension that has been recruited to think about cultural variation in collectivism (Fincher and Thornhill, 2012) and also a wide range of other cultural psychological differences (e.g., Conway et al., 2017; Gangestad et al., 2006; Murray et al., 2013; Schaller and Murray, 2008). The argument here focuses on the ingroup–outgroup distinction in collectivism–individualism. Specifically, individuals are hypothesized to have a plasticity that shifts them toward favoring ingroup associations and avoiding outgroup associations – that is, a more collectivistic psychology – under conditions of high pathogen prevalence. Supporting this, both across countries and within the United States, populations that live in ecologies with higher pathogen prevalence

tend to be more collectivistic (Fincher and Thornhill, 2012). There are at least two arguments for why collectivism might be more adaptive in ecologies with high pathogen stress. First, outgroup individuals may be carriers of novel pathogens that our immune systems, adapted to pathogens in our own local environments, may be unable to effectively cope with. Second, outgroup individuals may be unfamiliar with local customs and practices (e.g., food-preparation methods), which also often function to protect against local pathogens. Hence, outgroup individuals may pose threats to the maintenance of established social norms related to pathogen defense. Recent work has attempted to tease apart the two explanations, finding stronger support for the latter explanation (Tybur et al., 2016).

The parasite-stress explanation for the origins of cultural differences in collectivism, and other cultural psychological differences, has been influential, inspiring substantial bodies of literature (see Nettle, 2009, for a review). Some have argued, however, that the strong association between pathogen prevalence and collectivism at the country level may be an artifact of two distinct world regions – Western versus non-Western countries – being different in both collectivism and pathogen prevalence (Hruschka and Hackman, 2014). When analyses are conducted within each world region, pathogen prevalence within Western and within non-Western regions does not predict collectivism. In a similar vein, examinations of the influence of pathogen prevalence on correlates of interdependent self-construals within China do not find significant associations (Talhelm et al., 2014). Hence, the generalizability of the pathogen-prevalence explanation for collectivism might be limited. One difficult issue here is that the definition of collectivism/interdependence is broad, and there are also many ways in which the construct has been measured in the literature. It will likely be important for future work in this area to outline precise hypotheses about which aspect of an

ecology influences which aspect of collectivism/interdependence and why.

In summary, phenotypic plasticity provides an ultimate explanation for the origins of cultural psychological differences. As a species that has ancestrally encountered varying environmental conditions, evolution is likely to have selected for and shaped many different forms of phenotypic plasticity – flexibilities that shift human psychology and behavior in predictable ways, depending on one's ecology (Sng et al., 2018). Variations triggered at the individual level plant the seed for group- and society-level differences, which then may spread via social-transmission processes. We turn to this next.

The Spread and Evolution of Culture

Evolved phenotypic plasticity could, under some circumstances, be sufficient to generate stable differences in psychology across societies – differences that might appear as cultural differences. For instance, if individuals in a society lived under identical ecological conditions and those conditions elicited the same psychology and behavior (through phenotypic plasticity), this would emerge as a group-level (societal) difference in psychology. Note that this process so far does not necessarily involve social learning.

Of course, people do learn from one another, and this learning does shape psychology and behavior within groups and societies. In this section, we ask several questions related to the cultural development of within-group practices, beliefs, and norms: what do people learn? Under what circumstances is learning from others more adaptive than learning individually? When we seek to learn from others, which others do we choose? And what shapes cultural stability and change?

What do people learn?

Humans have evolved an incredible capacity to learn. However, learning is not

unconstrained. Human learning mechanisms ought to be adapted to learning content that has, across our evolutionary history, conferred greater reproductive success. Indeed, humans have evolved to learn certain content more readily than other content. For instance, we have evolved to readily learn to fear or avoid things that posed ancestral threats, such as snakes (Öhman and Mineka, 2003), spiders (Rakison and Derringer, 2008), and outgroup men (Navarrete et al., 2009). Children from both modern urban and hunter-gatherer populations quickly learn information about the dangerousness of animals and retain such information over time, relative to less fitness-relevant information such as animal names (Barrett and Broesch, 2012). Although people do transmit arbitrary information, and others can and do learn such information, we suspect that the most effective social transmission – in terms of what is communicated and what is attended to in learning – is the transmission of behaviors, practices, and norms relevant to the fundamental challenges humans have long faced (e.g., resource acquisition, disease avoidance, social affiliation and exchange, mating, kin care; Kenrick et al., 2010).

The content that one learns may also be influenced by current ecologies (see Mesoudi et al., 2016, for a review). Recall that high levels of relatedness in one's ecology might trigger a more interdependent psychology, to facilitate behaviors that enhance inclusive fitness. In such an ecology, those values and beliefs that match an interdependent psychology (e.g., Confucian collectivistic values) are likely to be more readily learned than other values, encouraging the spread of certain philosophies over others.

When do we learn socially?

Learning does not need to be social. Individuals can learn through individual trial and error. When, then, do we learn from others? Theoretical models and empirical work have provided certain insights (Boyd and Richerson, 1985; Caldwell and Millen,

2010; Kameda and Nakanishi, 2002). Generally, social learning is favored when individual learning is difficult and carries high energy and time costs. Ecological variability also plays a role, although not a straightforward one (Chudek et al., 2015). If there is little variation in the environment, evolution is more likely to select directly for genes that lead to adaptive behavior, as this would be a more efficient solution than selecting for costly social learning mechanisms. On the other hand, if environments vary too much, social learning is also not effective, as the adaptive problems that different individuals face, both across time and space, might be too different for solutions developed by one individual to remain useful to another. Hence, one might expect to see cultural learning occur most in moderately fluctuating ecologies.

Who do we learn from?

We discussed in the previous sections the biases people have in the content they learn, with people being better 'prepared' to learn evolutionarily relevant content. People also exhibit 'model biases', preferring to learn from certain types of individuals more than others. *Prestige bias* refers to preferences to learn from those that others pay attention to and learn from (Cheng et al., 2013; Chudek et al., 2012). For instance, one study found that when shown two adults, one to whom bystanders paid attention (prestigious model) and another to whom bystanders did not attend, children were more than twice as likely to copy the prestigious model's preferences than those of the control model (Chudek et al., 2012). *Success bias* refers to preferences to learn from those who experience positive outcomes. For instance, in a simulation of a stock market, individuals tended to copy the behaviors of others who they observed acquiring larger pay-offs than themselves (Berg et al., 2015). Finally, *frequency-dependence bias* refers to preferences for learning traits based on the prevalence of the trait in the population.

One form of frequency-dependence bias is sometimes referred to as the ‘conformist bias’, where individuals preferentially copy traits that a majority of others hold. The existence of such a bias has also been supported by empirical work and is especially observed when there are many different cultural alternatives that can be learned (Muthukrishna et al., 2016). Note that the conformity bias has a highly specific definition (e.g., individuals having a 90% chance of copying a trait that 60% of the population hold would count as an example of conformist bias) and may not be identical to social psychological treatments of conformity (Mesoudi, 2016).

There seem to be distinct differences in learning strategies between individuals. For instance, individuals can be clearly categorized as adopting a success bias or a conformity bias (Berg et al., 2015). These individual differences in learning strategies are relatively consistent even when measured a month later. Where do these individual differences come from? One possibility draws on phenotypic plasticity. Just as different traits vary in their adaptiveness depending on the environment, different learning strategies may also vary in their adaptiveness depending on ecological conditions. Hence, one might expect phenotypic plasticity that shifts individual learning strategies depending on environmental conditions. Indeed, a range of findings suggest that this is the case (Mesoudi et al., 2016). For example, zebra finches exposed to high levels of stress during early development prefer to learn to forage from non-related adult finches (rather than from their parents; Farine et al., 2015). This is arguably to facilitate avoiding the poor outcomes that their parents created (as developmental stress may indicate that one’s parents were relatively unsuccessful at foraging).

Cultural stability and change across generations

The social learning processes we have been discussing emphasize the importance of

replication – copying what others do. Such copying is assumed to have high fidelity. In other words, cultural practices, norms, and beliefs are transmitted accurately and maintain their original form across transmissions. However, work from a cultural attraction perspective has argued that the role of *reconstruction* is just as important as (if not even more important than) replication when thinking about culture (Claidière and Sperber, 2007; Sperber and Hirschfeld, 2004). Consider the following sentence: ‘In this chapter, we discuss theories connecting evolution and culture’. Now let’s say you had to communicate to another person the sentence you just read. You would likely recognize the error and rearrange the letters in your reproduction to read ‘evolution’. In this case, you did not just copy (replicate) the information. Instead, in the process of recreating the information, you modified (reconstructed) it. And this particular reconstruction is based both on a shared language and a conceptual understanding of what this chapter is about.

Reconstruction and replication can have strikingly different effects on the transmission of culture (Scott-Phillips, 2017). If one assumes primarily replicative processes in social learning, information is maintained with high fidelity across multiple generations. However, if one assumes reconstruction processes, only specific types of information, or ‘attractors’ (e.g., actual words, like evolution, as opposed to non-words), maintain their form across generations. Indeed, the very notion of ‘culture’ assumes some degree of stability in cultural traits for something to even be called culture. And cultural attraction theorists argue that attraction processes are critical for an understanding of culture (Sperber and Hirschfeld, 2004; also see Miton et al., 2015).

Cultural beliefs and practices, over time, can also undergo an evolutionary process of change similar to that of genetic evolution. For this to happen, certain conditions need to be met. First, there needs to be variation in cultural traits – and there

clearly is. Second, there needs to be mechanisms for transmitting this variation across generations – and there are, via replication and reconstruction processes. Third, some cultural variants must be more successfully transmitted than others. Consider, for example, recent work on the cultural evolution of ‘Big Gods’ (Norenzayan et al., 2016). The recent widespread emergence of very large cooperative societies represents a puzzle in human evolution, as it is difficult to account for using existing evolutionary ideas (such as inclusive fitness as discussed earlier). Co-occurring with this emergence was a similarly impressive spread of the Abrahamic religions, each of which included beliefs in a Big God – an omnipotent and omniscient being willing to punish immoral behavior. This spread of the Abrahamic religions stands in contrast to other religious frameworks in which associated deities were less powerful or less concerned with human actions. The argument here is that as human groups grow larger and more complex, and social coordination becomes more difficult, those groups holding beliefs that enhance within-group prosocial behavior and cohesion and reduce within-group competitive behavior – for example, Big God beliefs – would outcompete other groups that do not hold such beliefs, through intergroup conflict and demographic expansion. Over time, the former group and their associated Big God beliefs would be more likely to persist and spread.

Various lines of evidence support this argument. For example, increasing societal size and complexity predicts a greater prevalence of moralizing-god beliefs (Roes and Raymond, 2003), and stronger beliefs in moralizing gods predict increased sharing behavior with others who share the same religion, even when they are physically distant (i.e., not a member of one’s village) (Lang et al., 2019). Such behavior potentially functions to both attract new members to the religion and to enhance the competitiveness of one’s own religious group. Hence,

the cultural evolutionary account here also draws upon between-group-competition processes as a catalyst for the spread of Big God religions.

Returning to one of the key cultural psychological differences discussed earlier, cultural tightness–looseness has been hypothesized as an outcome of cultural evolutionary processes, specifically in response to ecological threats (Roos et al., 2015). This hypothesis was tested using a series of evolutionary game theoretic simulations. For example, individual agents in a public-goods game were programmed to each hold two behaviors – a contribution strategy and a punishment strategy – so agents could incur a cost every round to inflict costs on other agents. Punishment strategies included specifically punishing defectors (labelled as norm enforcers), ‘spiteful’ punishers that punished all the time, and non-punishers. Contribution strategies included the typical cooperators (labelled as norm followers) and defectors but also an opportunistic type that would cooperate or defect depending on what would lead to greater benefits, based on the punishment strategies of other agents. The simulations were run with varying conditions of ecological threat (simulated as an overall unavoidable cost inflicted on all agents in the simulation), and agents that received more benefits in a given round reproduced more in the next generation of the simulation.

Over multiple generations, under conditions of high ecological threats, both cooperators (norm followers) and agents that specifically punished defectors (norm enforcers) dominated the population. This did not occur under conditions of low ecological threat. These patterns corroborate the hypothesis that threatening conditions lead to the evolution of tight cultures, in which there is strong adherence to social norms and punishment of deviance. Interestingly, unlike the previous example of the cultural evolution of moralizing religions, the cultural evolution of tightness does not seem to require group competition processes.

Can Culture Shape Biological Evolution?

Cultural differences can originate from evolved phenotypic plasticity, and they can also spread as a result of cultural traits themselves evolving. Culture can also shape genetic evolution, termed gene-culture coevolution (see Laland et al., 2010; Moya and Henrich, 2016, for reviews). Consider the classic example of the distribution of the ability to digest lactose. In humans, the ability to digest lactose generally decreases significantly after infancy. However, the ability to continue to digest lactose in adulthood, and the associated alleles of lactase persistence, is prevalent in specific populations. A substantial body of work has accumulated that shows that this is a result of the spread of dairying practices (Gerbault et al., 2011; Holden and Mace, 2009). In societies that developed the cultural practice of dairying, individuals who were able to continue to digest lactose in adulthood would derive additional nutritional benefits compared to those not able to do so. Over time, then, societies with dairying practices would select for individuals with lactase persistence alleles. Culture then shapes genetic evolution.

With some exceptions (e.g., Chiao and Blizinsky, 2010; Mrazek et al., 2013), gene-culture coevolutionary ideas have not been widely used in the study of the kinds of cultural psychological differences we have been discussing. One example, however, is work on the coevolution of collectivism and alleles on the 5-HTTLPR region of the serotonin transporter gene (Chiao and Blizinsky, 2010). Individuals can carry two forms of the gene: the short (S) and long (L) allele. The S allele has been associated with greater anxiety, attention to negative information, negative emotion, and depression in reaction to life stressors. Interestingly, there are considerable differences across countries in the prevalence of the two alleles. For instance, about 80% of Japanese samples are S allele carriers, but S allele carriers only constitute 40%

of US samples. Chiao and Blizinsky (2010) propose that cultural differences in collectivism have shaped these population differences in alleles. Specifically, collectivism serves a ‘protective’ function, reducing exposure to environmental and life stressors (including pathogen stresses mentioned earlier; Fincher and Thornhill, 2012) and creating a ‘niche’ for S allele carriers. Another possibility is that the greater focus on negative information of S allele carriers facilitates maintenance of group harmony and interdependence in collectivistic cultures. Either way, tracking the gene-culture coevolution prediction, higher levels of collectivism uniquely predicted a greater prevalence of S allele carriers at the country level.

Note, though, that some have critiqued the above work, raising methodological issues with the cross-cultural comparisons used (Eisenberg and Hayes, 2011). One issue is the problem of non-independence of units of analysis: when the units of analysis (countries in this case) are related to each other (e.g., shared histories, languages), analyses without proper controls can lead to spurious effects. This issue is also relevant to cross-cultural analyses of pathogen prevalence and collectivism (Hruschka and Hackman, 2014). In related work, others have argued that the problem of non-independence is not an issue in practice (Mrazek et al., 2013; see Pollet et al., 2014, for a discussion). It is clear that gene-culture coevolution plays a role in the emergence of certain cultural traits, but more work will be needed to better understand how far coevolutionary processes go in shaping important cultural psychological differences.

EMERGING QUESTIONS AND FUTURE DIRECTIONS

We have outlined a diverse range of phenomena and perspectives at the intersection of evolutionary and cultural psychology. In this section, we discuss some broad issues and

questions that emerge from this accumulated body of work, and we highlight potential areas where future work might be particularly fruitful.

First, there is interest in many kinds of cultural differences. This is obvious from both the myriad of cultural differences that have been studied (e.g., interdependence, tightness, survival/self-expression values, learning biases, religion, cooperation, genes) and the equally diverse range of explanations that have been offered (e.g., historical philosophies, subsistence activities, mobility, ecological threats, modernization, intergroup competition, food practices). However, work on each cultural psychological difference is often focused on dominant explanations for that particular difference. Hence, the study of cultural variation is somewhat fragmented, with new differences and corresponding explanations continuing to emerge. This is not necessarily a bad thing. Indeed, it reflects the vibrancy of both theoretical and empirical work here. But one question is whether there are truly that many unique cultural psychological differences and unique explanations. More explicit cross-cutting work would illuminate this question. For instance, behavioral ecological perspectives have been used to answer questions about reproductive behaviors and food production/distribution (Nettle et al., 2013). Psychological self-construals, on the other hand, have historically been of little interest to behavioral ecologists. This represents an opportunity for future work. We have outlined some ways in which phenotypic plasticity might play a role in thinking about interdependent self-construals, but this is likely only scratching the surface. More generally, drawing upon ultimate evolutionary explanations, such as phenotypic plasticity, may help connect existing, diverse, proximate explanations for cultural differences (also see Sng et al., 2018).

One might also wonder whether a smaller, common set of cultural dimensions might underlie the many cultural psychological differences observed. We discussed several

dimensions earlier, such as collectivism, tightness, and secularism/self-expression. But these are obviously not exhaustive. Indeed, there are many other prominent cultural differences that we did not have the space to comprehensively cover here, including the broader set of both Hofstede's (2011) cultural dimensions and Triandis' (1996) cultural syndromes, Schwartz's (1994) values, and cultures of honor (Cohen et al., 1996). How might one examine this question? One approach is to factor analyze a range of measures capturing different aspects of our psychology. This was the approach adopted by Inglehart and Baker (2000), leading to the distillation of the two dimensions of traditional/secular and survival/self-expression values. However, such a data-driven method is limited by the measures that are used, and different dimensions might arise if other measures were to be included. And even if certain underlying common factors were uncovered through such a method, theory is still necessary for understanding and thinking about why *these* factors emerge and how they might relate to one another. Indeed, if there are a smaller number of cultural dimensions underlying existing variation, then our first point becomes even more important – existing explanations for one cultural difference will likely also be relevant to a second cultural difference, if the two kinds of cultural differences overlap.

Our final, and possibly most difficult, question is 'what *is* culture'? In the operational definition we began with, culture was defined as sets of beliefs, practices, or behaviors shared by individuals. But this seemingly straightforward definition belies deeper issues. For instance, what does it mean to say that culture is 'shared' by individuals? The phenotypic plasticity perspective outlined earlier proposes that cultural psychological differences could emerge as a result of individuals in different groups reacting to varying ecological conditions. But note that these group-level differences emerge as an aggregate of individual plasticity reactions and

do not necessarily require learning between individuals. Is that still ‘culture’? We admit that we have no clear answer.

This is not an inconsequential question, and it has implications for both empirical and theoretical work. Indeed, many important cultural psychological differences are measured using aggregates of individual-level measures (e.g., of interdependence, tightness, self-expression values). More broadly, how culture is defined, how it is measured, and what theories are relevant are questions that are inextricably linked. But the connections between each are more often implicitly assumed than explicitly outlined. The irony here is that some psychological differences observed across cultural groups may not be ‘cultural’ in either their origins or maintenance, depending on how culture is defined. That does not imply that such psychological diversity is not meaningful or important to study. But it may constrain the kinds of explanations that should be invoked. For instance, a cultural trait that is clearly socially transmitted or seemingly maladaptive in its ecology might require greater reliance on cultural evolutionary explanations. On the other hand, a cultural trait that seems independently held by individuals, or that seems to serve an adaptive function in the specific ecology, may find more productive explanations from a behavioral ecological/phenotypic plasticity perspective.

IN CLOSING

How universal or diverse is our psychology and why? We have summarized some key cultural psychological differences in the literature and a range of perspectives for thinking about the intersection of culture and evolution. Evolutionary and cultural psychological perspectives have much to offer one another. Each highlights theories and phenomena that the other has paid relatively little attention to. Both perspectives are also

united in trying to answer some of the deepest questions in the study of human behavior. We hope that the current chapter has provided a broad view of current topics at this intersection and the raw material for future work in this area.

Notes

- 1 We note that the historical focus of phenotypic plasticity has changed over time. Early work focused more often on (often irreversible) developmental plasticity and on variation in morphological traits as key outcomes of plasticity. More recent work has included reversible forms of plasticity and behavioral outcomes (for reviews, see Dingemanse et al., 2010; Piersma and Drent, 2003; Pigliucci, 2005). Here, we refer to phenotypic plasticity in its broadest sense.
- 2 This parallels the idea of evoked culture (Tooby and Cosmides, 1992), which has also inspired important hypotheses about cross-cultural variation (e.g., Gangestad et al., 2006; Schaller and Murray, 2008). Empirical work on phenotypic plasticity and evoked culture has traditionally focused on different areas, with the former’s attention focused on work with non-human animals.

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Evolutionary Educational Psychology

John Sweller

On the surface, Darwinian evolution and instructional design appear not to intersect and, indeed, the bulk of instructional design research and recommendations make no mention of evolutionary theory. The result of this omission has been chaos. Instructional recommendations advocate procedures that, from an evolutionary psychology perspective, are unlikely to be effective. Predictably, using randomised controlled trials, such procedures prove to be ineffective for apparently random reasons. Furthermore, because some of these procedures sound plausible and desirable, it can take decades before they are discontinued, but many of them reappear with different nomenclature. Equally, other procedures, that from an evolutionary perspective, provide prime candidates for study are either largely ignored or, in some cases, actively opposed.

In this chapter, cognitive load theory (Sweller et al., 2011) – an instructional design theory based on our knowledge of human cognition (which in turn is based on

biological evolution) – will be used to indicate the importance of evolutionary psychology to instructional design. I will begin by discussing David Geary's evolutionary categorisation of knowledge.

CATEGORIES OF KNOWLEDGE

Knowledge can be categorised in many ways. For example, we can and do categorise knowledge as concrete or abstract, declarative or procedural. Categorisation of knowledge may be useful for a variety of purposes, with instructional consequences constituting one of those purposes. In fact, instructional consequences for most knowledge-categorisation schemes are hard to find. If, for example, declarative knowledge requires the same instructional processes as procedural knowledge, then although the distinction may be important for some purposes such as philosophical treatises or psychological theories,

the categorisation system does not have instructional consequences.

In contrast, Geary's evolutionary educational psychology provides a knowledge-categorisation scheme that has unambiguous instructional consequences (Geary, 1995, 2002, 2005, 2007, 2008, 2012; Geary and Berch, 2016). Geary divides knowledge into evolutionarily (or biologically) primary or secondary categories. Primary knowledge refers to information we have specifically evolved to acquire over many generations, whereas secondary knowledge refers to information that we can acquire despite not having specifically evolved to do so. Culture and society rather than evolution provide the impetus for the acquisition of secondary knowledge.

Examples of evolutionarily primary knowledge are learning to listen to and speak our native language, as well as learning to generalise, learning to plan, and learning general problem-solving skills. Skills associated with primary knowledge are likely to have evolved during different evolutionary epochs, and so primary knowledge is modular with the characteristics of a primary skill, often bearing little resemblance to the characteristics of other primary skills. The manner in which primary skills are acquired and the cognitive architecture associated with each skill are likely to be specific to that particular skill.

Examples of evolutionarily secondary knowledge are learning to read and write, learning arithmetic and mathematics, learning how to compose an essay, and learning research techniques in a particular discipline. These are skills that are not universal, emerged relatively recently in human history, and do not typically emerge in the absence of formal education. Education and training systems were instituted to help people acquire secondary knowledge, and so almost everything taught in an educational context provides an example of evolutionarily secondary knowledge. The secondary system has a singular architecture (as discussed later) that is unlike the multiple architectures

associated with the primary system. As a consequence, the acquisition of all evolutionarily secondary knowledge tends to follow the same pattern.

A distinction between generic-cognitive and domain-specific knowledge and skills overlaps heavily with the distinction between evolutionarily primary and secondary knowledge and skills. Most evolutionarily primary knowledge results in generic-cognitive skills, whereas most evolutionarily secondary knowledge results in domain-specific skills (Tricot and Sweller, 2014). For example, a problem-solving strategy such as means-ends analysis (Newell and Simon, 1972), in which problem solvers attempt to find problem-solving operators that will reduce the distance between their current problem state and the goal state, can be applied to a large number of different problems. It is a generic-cognitive, evolutionarily primary skill. In contrast, learning how to multiply out a denominator when solving an algebra problem is a critical algebraic skill that is useless when solving non-algebraic problems. It is a domain-specific, evolutionarily secondary skill. Similarly, learning to listen to and speak a native language permits us to communicate with others on a wide range of topics critical to humans, while spatial-navigation skills allow us to traverse the many spatially distinct geographies in which humans live. Both skills are primary. In contrast, learning to deliver a particular speech or how to quickly traverse a particular route are domain-specific, secondary skills.

The relation between generic-cognitive and evolutionarily primary knowledge on the one hand and domain-specific and evolutionarily secondary knowledge on the other is strong. That relation is not surprising. Generic-cognitive skills are too important to be left to the vagaries of culture for their acquisition. They lie at the heart of what it is to be human. Without these skills, we would be a different species. If we have not learned to use means-ends analysis when solving problems such as finding our way from

Point A to Point B, we probably would have difficulty surviving. In contrast, most humans have been able to survive for most of human history without knowing how to multiply out a denominator in an algebraic equation or knowing how to write an essay on the historical causes and consequences of the First World War.

Domain-specific, evolutionarily secondary knowledge comprises almost everything taught in educational and training institutions. For good reasons, we devised educational institutions precisely in order to teach evolutionarily secondary skills. Without formal education, most of the domain-specific, evolutionarily secondary knowledge and skills will not be acquired. In contrast, primary skills will be acquired irrespective of attendance at educational institutions. Simple social interactions and modelling as well as exploration of the environment are sufficient for the acquisition of evolutionarily primary knowledge and skills.

There is a reason why educational institutions had to be established to teach domain-specific, secondary knowledge but did not have to be established to teach generic-cognitive, primary knowledge. Primary knowledge, because we have evolved to acquire it, tends to be acquired easily, automatically, and unconsciously, whereas secondary knowledge, which we have not specifically evolved to acquire, requires conscious effort and is often only acquired with difficulty. For these reasons, primary knowledge is not as relevant to education as secondary knowledge. It has some relevance, because, due to its relative ease of acquisition, it can be leveraged to assist in the more difficult acquisition of secondary knowledge (Paas and Sweller, 2012).

These differences in the roles of primary and secondary knowledge have instructional consequences, and a failure to acknowledge them has bedevilled modern education for many decades. For example, we can readily observe the ease with which complex information associated with learning to listen to

and speak a native language is acquired and processed without any formal tuition. It is much harder for many students to learn to read and write. It is all too easy to assume that the difference is due to inadequate instructional techniques. If, the argument goes, we only used the same natural procedures within classrooms as occur when learning outside the classroom, learning to read would be just as easy as learning to listen. We are not explicitly taught how to listen. We simply acquire the skill by immersion in a listening environment. If learning to listen and learning to read require similar cognitive processes, then immersion in a reading environment without explicit instruction in reading should be equally effective as learning to listen without instruction. The argument is faultless if the premise that learning to listen and learning to read require similar cognitive processes. Of course, the argument collapses if the processes are different, as suggested by the distinction between evolutionarily primary and secondary knowledge. Historically, we can see that mass reading skills developed only in societies that established schools to teach reading. Similarly, skills in mathematics and most other areas tend not to be acquired by simple immersion in the discipline (Geary, 1995). Such knowledge and skills need to be explicitly taught rather than acquired 'naturally' by immersion. Acquiring these skills and knowledge requires different procedures to those needed when acquiring evolutionarily primary skills.

HUMAN COGNITIVE ARCHITECTURE

There is a cognitive architecture associated with the acquisition, storage, and activation of evolutionarily secondary knowledge. That architecture can be used to design instruction to maximise learning and performance. Cognitive load theory was devised for that purpose. The relevant architecture indicates how humans process evolutionarily secondary

information and is closely analogous to the manner in which biological evolution, which is essentially an information-processing system, handles information. Both biological evolution and human cognition can be considered natural information-processing systems (Sweller and Sweller, 2006). Such systems can be described by five basic principles.

Randomness as Genesis Principle

Ultimately, the initial driver of all creativity, whether it is of the human mind or of evolution by natural selection, is random generation followed by tests of effectiveness (Simonton, 1999; Sweller, 2009). Without random generation, nothing new can be created. That basic principle is a well-known foundation of evolution by natural selection. All distinctions between all organisms can ultimately be sourced to random mutations of the genetic code. Without those random mutations, evolution by natural selection could not occur and there would not be any heritable differences between individuals or between species. Of course, although random mutation is necessary, it would be insufficient in isolation; it needs to be followed by natural selection that constitutes a test of effectiveness. Thus, evolution by natural selection is initiated by a random generation followed by the tests of effectiveness process and, in that sense, it follows a randomness as genesis principle.

Of course, the application of random generation followed by tests of effectiveness as a central component of biological evolution is well established and non-controversial. It does not have the same status when considering human cognition, but there seems to be no clear alternative to assuming it plays an analogous role in human thought and human problem-solving. Finding solutions to novel problems does not seem possible without the machinery of random generation with tests of effectiveness, just as biological evolution would not be possible without random

mutations. Both provide examples of natural information-processing systems.

Consider the problem-solving strategy of means–ends analysis. It can be used to solve a novel problem for which a person does not have a previously learned solution. The strategy requires us to consider our current problem state, consider the goal state, and find a problem-solving operator that can be used to reduce differences between the two states. Where does random generate and test fit into this process? When solving most problems, there are likely to be multiple possible moves that can move us towards the goal of the problem but no obvious way of instantly determining which of the alternatives will allow us to make progress or instead lead us to a dead-end. The only way in which we can determine the status of a move is to try that move and determine whether it has allowed progress or led to a dead-end. In other words, we must randomly choose a move and make that move either mentally or physically before determining its status. In that sense, random generate and test is unavoidable, and, indeed, as far as I am aware, all computational models of problem-solving include random generate and test as part of their structure (Sweller, 1988).

It may be argued that although means–ends analysis may require the randomness as genesis principle to function, other problem-solving strategies do not. In fact, it is difficult to find any problem-solving strategy that can be used to solve a novel problem, for which we have not already learned a solution, that does not require the randomness as genesis principle. Consider solving a problem by analogy to another problem (Gick and Holyoak, 1980, 1983). To solve a target problem by analogy to a source problem for which we already know the solution, we have to pick a source problem as the analogical problem. Now, because the target problem is novel for us, and with no known solution at this point, we cannot know whether a potential source problem provides a sufficiently close analogue to the target problem to be useful.

As far as possible, we will use knowledge such as similarities between the source and target problems, but those similarities may be misleading and result in a dead-end. Our only viable process is to choose a source problem as an analogy and see whether it assists in providing a solution to our target problem. If it does, we may have a problem solution; if it does not, we must try another solution. In other words, we must engage in the random generate and test process, which seems inevitable to all problem solving for which we do not have previously acquired solutions. The randomness as genesis principle is an integral part of a natural information-processing system, applying both to biological evolution and human cognition when dealing with evolutionarily secondary information.

Borrowing and Reorganising Principle

Although random generate and test is central to the initial construction of information, it is a slow, inefficient way of obtaining information. The alternative and major way in which natural information-processing systems obtain information is by borrowing it from others. Although all of the information held and used by either a genetic system or the human cognitive system must have initially been derived using random generate and test, neither a genetic system nor the human cognitive system can derive more than a tiny proportion of the information they need using this process. The alternative, far more efficient system is to obtain information that others have generated rather than generating it oneself.

Genetic systems borrow information from ancestors by reproduction. During asexual reproduction, the process results in copying that is exact, with the exception of mutations. In contrast, sexual reproduction, or any form of reproduction that involves more than one immediate ancestor, includes reorganisation as well as borrowing. By combining

information from two immediate ancestors, information transmission can never be exact, and, indeed, that is the function of sexual reproduction. Its purpose is to introduce additional variation above that of copying alone.

The human cognitive system also relies far more on information transmission using the borrowing and reorganising principle than information creation via the randomness as genesis principle. Information is obtained from others by imitating what they do (Bandura, 1986), listening to what they say, and reading what they write. Cognitive load theory (Sweller et al., 2011) is primarily concerned with the manner in which information can be effectively imparted during listening and reading. Humans are one of a small number of species that are capable of receiving from and providing information to other members of the species (Thornton and Raihani, 2008). It is a central human characteristic.

As is the case in sexual reproduction, reorganisation is integral to the process. Information from others is rarely stored in the form in which it is received. Rather, it is combined with previously stored information, resulting in reorganisation (Bartlett, 1932; Bransford and Johnson, 1972).

The randomness as genesis and borrowing and reorganising principles describe how natural information-processing systems acquire information from the external environment. The remaining three principles are concerned with how that information is processed within the information-processing system and how it results in actions that are congruent with the external environment.

The Narrow Limits of Change Principle

The amount of novel information that the randomness as genesis and borrowing and reorganising principles can obtain from the external environment is unlimited, with much of that information being of no use to the

information-processing system. Indeed, too much irrelevant information may disrupt rather than enhance the functioning of the system. It does not require many elements of information to overwhelm the system. Consider a system using generate and test via the randomness as genesis principle to assimilate new information. If there are three elements of information, there are $3! = 6$ possible permutations of those elements, assuming no information is available to indicate how the elements should be combined. If the number of elements is increased to 10, there are $10! = 3,628,800$ possible permutations. Although it may be easy for an information-processing system to conduct a generate and test process on six permutations to find one that is useful, conducting generate and test on 3,628,800 will be much more difficult. Machinery is required to limit the amount of novel information that the system must process. This function is addressed by the narrow limits of change principle.

The epigenetic system supplies the necessary machinery for evolution by natural selection. In general terms, the epigenetic system acts as a conduit between the external environment and the genetic system. With respect to novel information associated with mutations, it can limit and vary the number of mutations that can occur at given genomic locations, with some locations undergoing mutation rates thousands of times higher than other locations, depending on environmental need. For example, because prey are likely to adapt to the venom used by venom-producing predators, the mutation rates of the genes relevant to producing the venom may need to be rapid to ensure continuing effectiveness (Jablonka and Lamb, 2005). In this manner, the environment can become instrumental in genetic changes, including rates of mutation.

Another way in which the environment influences the genetic system can be seen by observing species that can exist in vastly different environments. Some plants can live in

water or on land (West-Eberhard, 2003). The land-based and water-based versions have exactly the same genomes, but if a mutation occurs, whether or not it is adaptive may depend on whether the plant happens to be in water or on land.

Notwithstanding the genetic system's requirement for mutations, a large number of mutations can compromise the integrity of a genome. Even at locations with high rates of mutation, genetic change must be slow. Small changes are made and tested for effectiveness using the generate and test mechanism. In addition, DNA repair is used to reverse the effect of mutations. Most mutations are not adaptive and must be discarded over time. Over many generations, only small adaptive changes are retained, resulting in new genetic combinations that are appropriate for the environment. In this way, the environment interacts with the genetic system to partially determine mutations, and it is this interaction that constitutes the epigenetic system under the narrow limits of change principle (a major function of the epigenetic system is to activate or silence genes, but this function will be discussed under the environmental organising and linking principle later in the chapter).

The slow rate of environmentally mediated change imposed by the epigenetic system has its analogue in the role of working memory in human cognition. Working memory is used to assimilate novel information generated either by the randomness as genesis or the borrowing and reorganising principle, using mechanisms that are similar to those used by the epigenetic system. Both the epigenetic system and the cognitive system determine which novel information is retained and used, and both severely limit the rate of change.

The rate of change due to the assimilation of novel information by the cognitive system is restricted by two well known characteristics of working memory: its limited duration and capacity. When it deals with novel, evolutionarily secondary, domain-specific

information – and only when it deals with such information – working memory is severely restricted in capacity (Cowan, 2001; Miller, 1956) and duration (Peterson and Peterson, 1959). With respect to capacity, Miller (1956) suggested that we could hold no more than about seven elements of information at any given time. Of course, for most cognitive purposes, we do not use working memory to simply hold information. We use it to process information, which involves manipulating it in some manner, and when processing information, the capacity of working memory is less, with Cowan (2001) suggesting a capacity of about four elements. Above this limit, working memory will not be able to process the information. With respect to duration, Peterson and Peterson (1959) indicated that after about 20 seconds, most of the novel information held in working memory is lost. It can be retained for indefinitely longer periods with rehearsal, but without rehearsal, the duration of working memory when dealing with novel information is very limited. In this manner, the capacity and duration limits of working memory provide clear examples of the narrow limits of change principle. Beyond these limits, the working memory system is likely to fail when dealing with novel information.

The narrow limits of change principle functions equally in cognition whether the novel information is obtained via the randomness as genesis principle during problem solving or via the borrowing and reorganising principle when obtaining information from others. It has less need to function when processing accurate information from others but treats all novel information from the external environment equally, irrespective of its origins.

As will be indicated in the following section, these limitations of working memory when dealing with evolutionarily secondary, domain-specific information have considerable instructional implications. The narrow limits of change principle is central to instructional design and cognitive load theory.

The Information Store Principle

To be subsequently beneficial, novel information that is processed must be stored for later use. The information store principle provides the necessary structures. Both evolution by natural selection and human cognition can only function in their complex environments with the assistance of their ability to permanently store enormous amounts of information. A genome provides that store in the case of evolution by natural selection, whereas long-term memory provides the analogous function for human cognition.

All genomes, even the smallest ones, store very large amounts of information. While there is no agreement on what constitutes an appropriate measure of genome size, whatever measures are used yield at least many thousands of information units (Portin, 2002; Stotz and Griffiths, 2004), with some genomes including billions of units. These large information stores are required to allow life to continue in its complex natural environment. As a consequence, genomes, with their large stores of information, are the central structures of the genetic system and evolution by natural selection.

Long-term memory provides an analogical structure for human cognition and plays a central role similar to the one played by genomes in evolutionary biology. Long-term memory is immeasurably large. Because we only are conscious of the contents of working memory, we only are aware of the relatively small amount of information that is transferred to working memory at any given time and so tend to subjectively underestimate the size of long-term memory. We never can be aware of more than a small proportion of the contents of long-term memory.

Evidence for the immense size of long-term memory as well as its role in the functioning of our cognitive system became apparent following the work of De Groot ([1946] 1965), initially carried out in the 1940s (an update can be found in De Groot and Gobet,

1996). He was concerned with the factors that determine skill in the game of chess. Chess masters and grand masters will always defeat amateur players, and De Groot wanted to explore the reasons why. There are at least two plausible hypotheses: chess masters may be able to consider a greater number of alternative moves at each choice-point (search in breadth), or they may be able to consider the consequences of a greater number of moves ahead (search in depth). De Groot considered both of these possibilities but found no evidence that chess masters engaged to a greater extent in either search in breadth or search in depth. He did, however, find one critical difference. He showed chess masters and amateur players a chessboard configuration, taken from a real game, for five seconds before removing the board and asking the masters and amateur players to replace the pieces in the positions they had just seen. There were large differences, with masters able to replace most of the pieces accurately, whereas amateur players could replace few of the pieces in their correct position. Chase and Simon (1973) replicated this result but, in addition, found very similar ability to remember chessboard positions between masters and amateur players using random board configuration, with both groups able to replace few of the pieces correctly. The only result that stood out was chess masters who could replace large numbers of pieces correctly but only when the configuration came from a real game. Similar results have been obtained in a variety of areas other than chess (Chiesi et al., 1979; Egan and Schwartz, 1979; Jeffries et al., 1981; Spilich et al., 1979; Sweller and Cooper, 1985). Experts in an area have a far better memory of the area than novices. Their skill derives from having stored enormous amounts of information in long-term memory.

It was indicated earlier that genomes have to incorporate a large amount of information to deal with the complex environment in which evolution by natural selection occurs. For exactly the same reason, the capacity of human long-term memory must be large

to deal with the complex environments in which humans must function. As is the case for genomes, there is no agreed-upon procedure for measuring the size of this information store. Nevertheless, it is clearly large if, for example, chess masters have memorised the tens of thousands of board configurations that they are able to recognise. Simon and Gilmarin (1973) estimated that chess grand masters recognise between 50,000 and 100,000 board configurations. At this time, the total capacity of long-term memory is unknown, but vast.

The findings from the game of chess and from other areas not only inform us of the scope of long-term memory but also of its role in human cognition. It is easy to assume that long-term memory has a minimal role in activities such as problem solving. Chess can easily be seen as a game of thought and problem solving. That characterisation is correct, but the contents of long-term memory are central to expert problem-solving and thought. For most people, it takes at least 10 years of deliberate practice to attain high levels of skill in any substantive domain, such as the game of chess or most of the subjects taught in most educational contexts (Ericsson and Charness, 1994; Ericsson et al., 1993). It is appropriate to ask, what is being learned during that long period? In the case of chess masters, the answer, as indicated earlier, appears to be tens of thousands of board positions from real games, along with the best moves for each position. A similar answer appropriate to the context appears to be required for all substantive areas of cognitive skill. The development of this expertise may be entirely dependent on the acquisition of knowledge held in long-term memory. Arguably, it may be the central component of human cognition.

The Environmental Organising and Linking Principle

The ultimate purpose of the information store in natural information-processing systems is

to enable the generation of action that is appropriate for the extant environment. The organising and linking principle provides that function. Signals from the external environment determine which information held in the information store is relevant to that environment, and that information then can be used to generate and govern activity appropriate to the environment. Both the epigenetic system and working memory are central to the environmental organising and linking principle, just as they are central to the narrow limits of change principle, but there is a critical difference. The characteristics of the epigenetic system and working memory when dealing with organised information held in the information store are very different to their characteristics when dealing with the vastly more extensive and largely unorganised information that needs to be processed when acquiring new information from the environment.

The epigenetic system uses environmental information to activate or silence particular genes. The consequence can be vast changes in phenotype, despite an identical genotype. We can see the effects of this process by considering different cells in a single individual. For example, for any given individual, the DNA in the nuclei of skin cells and liver cells are identical. Nevertheless, despite their identical genetic structure, a human skin cell has vastly different structures and functions than a human liver cell. The differences between the two types of cell cannot be due to genetic differences; they are caused by epigenetic differences. The epigenetic system, via the environmental organising and linking principle, uses environmental signals to marshal the huge amounts of information stored in the genome for appropriate purposes. Simultaneously, other information that is irrelevant to that particular environment is silenced. In this manner, a link between the environment and a genome is established to ensure that cell functioning is appropriate to its environment.

The analogy with the human cognitive system again is close, with working memory

playing a similar role to epigenetics. Using signals from the environment, working memory determines which information stored in long-term memory is required for that particular environment, resulting – as is the case for the role of the epigenetic system in evolutionary biology – in the environmental organising and linking principle.

Working memory characteristics when dealing with organised information from long-term memory are very different from working memory characteristics when dealing with environmental information through the narrow limits of change principle. Although working memory has very narrow limits of capacity and duration when dealing with environmental information, it has no known limits when dealing with information transferred from long-term memory to generate action appropriate to a particular environment. Vast amounts of such information can be processed by working memory for indefinite time periods. Indeed, the differing characteristics of working memory when it deals with organised information stored in long-term memory as opposed to environmental information during learning led Ericsson and Kintsch (1995) to propose a new structure: long-term working memory. The introduction of this structure was designed to account for the very different characteristics of working memory depending on the source of the information it is processing. Proposing two different structures with different characteristics or a single structure with different properties depending on the source of the information being processed leads to identical logical structures in both cases.

The environmental organising and linking principle provides the ultimate justification for natural information-processing systems, including the other four principles. The other four principles are needed to allow this principle to function. The randomness as genesis principle permits the initial generation of information that is needed by the system. The borrowing and organising principle allows that initial generation of information to be

used by any number of other units within the system. The narrow limits of change principle allows that initial information to be altered to better accord with the environment without destroying its utility. The information store principle allows unlimited amounts of that information to be stored for indefinite periods for later use. All of these principles allow the environmental organising and linking principle to have large amounts of readily available information to generate action appropriate to a particular environment. This system permits both evolution by natural selection and human cognition to automatically function as natural information-processing systems.

INSTRUCTIONAL IMPLICATIONS

This cognitive system, with its evolutionary foundations, has substantial instructional implications. It provides the origins for cognitive load theory (Sweller, 2011, 2012, 2015, 2016a, 2016b; Sweller et al., 2011) – an instructional theory based on the cognitive architecture outlined above. The theory assumes that in instructional settings, the bulk of the material dealt with consists of evolutionarily secondary, domain-specific information. Unlike evolutionarily primary information, which we have evolved to acquire automatically, the origins of evolutionarily secondary, domain-specific information lie in the random generate and test processes of problem solving. Information is randomly generated and tested for effectiveness, with effective information retained. Once useful information is generated and retained, it can be disseminated to others. Initially, novel information acquired either during problem solving or from other people must be processed by a working memory that is severely limited in capacity and duration. After information has been processed by working memory, it can be stored in a long-term memory that has no known capacity or duration limits. From long-term memory, the

information then can be transferred back to working memory, where it can be used to generate activity that is appropriate to the extant environment.

Although all of these processes, from the acquisition of novel information to the subsequent use of that information to generate action, are themselves evolutionarily primary, the information that this cognitive architecture processes is evolutionarily secondary. The evolutionarily primary processes that constitute the cognitive architecture are acquired automatically and do not require instruction. For example, we do not need to be taught to use the contents of long-term memory to govern our actions. In contrast, the evolutionarily secondary information that is stored in long-term memory and is the focus of this cognitive architecture is the subject of instructional design. Cognitive load theory has provided instructional design effects that can be used to indicate effective instructional procedures. Each effect is based on a series of randomised controlled trials. These effects have been summarised elsewhere (Sweller, 2010, 2011, 2012; Sweller et al., 2011) and will not be summarised in this chapter. Instead, more general instructional implications that flow from the evolution-based cognitive processes outlined in this chapter will be discussed.

Information Acquired in Educationally Based Contexts has a Different Evolutionary Signature from Information Acquired in Non-educationally Based Contexts

As indicated previously, one of the most important general implications of this instructional system is that the nature of the information that we acquire inside educational institutions is, from an evolutionary perspective, very different from the nature of the information we acquire in the natural contexts outside of educational institutions. The failure to realise this informational

dichotomy of evolutionarily primary, generic-cognitive knowledge on the one hand and evolutionarily secondary, domain-specific knowledge on the other has resulted in chaos for both educational psychology research and the entire field of education.

If there is no distinction between the type of information acquired in educational contexts and the information characteristically acquired outside of education contexts, then any differences in their ease of acquisition must be due to the differences in imparting school-based and non-school-based topics. In other words, we would need to assume that the reason we acquire information-dense skills such as recognising faces, solving novel problems, generalising what is learned, and planning courses of action automatically, easily, and without explicit instruction – in contrast to the difficulty many people often have in learning to read and write and learning simple mathematics and any of the other topics taught in educational institutions – is because of the way we teach in educational contexts. In this argument, if education-based instruction was conducted in a manner more similar to the way we learn outside of educational contexts, it too would be acquired naturally, automatically, and more easily.

It follows that school-based learning should be enhanced by, for example, emphasising child-centred, discovery-based, minimally guided learning procedures rather than teacher-led explicit instruction, because that lack of guidance is how we learn in the outside world. Alternatively, if the distinction between the education-based world and the non-education-based world is due to differences in the category of the information processed, as is assumed by the difference between evolutionarily primary and secondary knowledge, attempting to mimic the external world in class is likely to fail (Geary, 1995). Thus, we have two distinct hypotheses to explain the differences in acquiring information inside and outside of educational contexts. These hypotheses can be tested empirically.

Testing the Hypotheses

If the information acquired both inside and outside of an educational context are identical, then we should be able to enhance learning outside of an educational context by explicitly teaching the relevant concepts and procedures that usually are not taught, and we should be able to enhance education-based learning by using the procedures by which we learn outside of education. There is little evidence for either.

Evidence that the evolutionarily primary, generic-cognitive skills characteristically learned externally to an educational context are teachable requires studies testing for far transfer. If a generic-cognitive skill such as general problem-solving or self-regulation are being taught, the aim of the instruction is that the newly taught and learned skill will be used in a variety of areas unrelated to each other. There is little point teaching a generic-cognitive skill if it is only tested in the domain that was used for teaching the skill. Any improvement may be due to the acquisition of domain-specific knowledge, and if that is the sole area of improvement, this would vitiate the purpose of teaching a generic-cognitive skill in the first place. Despite over 100 years of attempts to establish evidence of far transfer after teaching generic-cognitive skills, there is no established body of evidence of far transfer following instruction (Sala and Gobet, 2017). A probable reason is that if we have evolved to acquire generic-cognitive skills because of their evolutionary importance, attempts to teach something that has already been learned are likely to be futile (Tricot and Sweller, 2014). Until evidence based on far transfer becomes available, there are no grounds for advocating the teaching of evolutionarily primary, generic-cognitive skills such as general problem-solving or self-regulation.

The lack of evidence for the efficacy of teaching evolutionarily primary, generic-cognitive skills is one side of the coin. On the other side of that coin is the strong evidence

that the evolutionarily secondary, domain-specific knowledge that is central to the educational enterprise, and so does need to be taught, should not be taught using the minimal guidance techniques that are used outside of educational and training contexts (Kirschner et al., 2006; Sweller et al., 2007). Again, the logic that explicit instruction should not be used in education is impeccable if we start with the premise that the information processed outside of an educational context is no different to the information processed within an educational context. Based on that premise, and given the ease with which we acquire complex knowledge and skills outside of education without explicit instruction, it makes sense to use the same procedures within an educational context. Of course, if the premise is wrong, if evolutionarily secondary, domain-specific knowledge is qualitatively different from evolutionarily primary, generic-cognitive knowledge, it makes no sense to use the knowledge-acquisition techniques that are appropriate outside of an education context when teaching evolutionarily secondary, domain-specific subject matter. Based on the cognitive architecture outlined previously, instruction should be direct and explicit rather than minimally guided.

Randomised controlled trials are the appropriate tool for testing the hypothesis that instruction should be explicit. The clearest evidence for the primacy of explicit instruction comes from the worked example effect – a cognitive load theory effect (Cooper and Sweller, 1987; Renkl, 2013, 2014; Sweller and Cooper, 1985). The basic experimental paradigm for testing the worked example effect requires one group of students to be presented a series of problems to be solved in a curriculum area such as mathematics. Another group is presented the same problems along with the steps required for their solution – a worked example. The worked example effect is demonstrated when the group presented with worked examples performs better on subsequent test problems than the group

presented problems to solve. That result is characteristically obtained.

Cognitive Load Theory

Cognitive load theory assumes that instruction is concerned with assisting learners to acquire evolutionarily secondary, domain-specific knowledge. To summarise, evolutionarily primary, generic-cognitive skills can be important in leveraging the acquisition of such knowledge (Paas and Sweller, 2012), but the knowledge acquired is evolutionarily secondary. There is a specific cognitive architecture that determines how humans acquire, process, store, and subsequently use evolutionarily secondary information, as outlined earlier. The manner in which humans process evolutionarily secondary, domain-specific information is analogous to the manner in which evolution by natural selection processes information. Human cognitive architecture can be used to indicate how we process both novel and familiar information, and that knowledge can be used to analyse the effectiveness, or otherwise, of instructional procedures.

That theoretical base has led to the generation of a large number of cognitive load effects (Sweller, 2010, 2011, 2012, Sweller et al., 2011). The worked example effect (discussed earlier), is one of those, and, like the worked example effect, all of the 15 or so effects are based on the results of randomised controlled trials that indicate superior learning by a procedure generated by cognitive load theory compared to a conventional, commonly used procedure. These effects and the instructional procedures that flow from them provide the primary justification of the theory.

CONCLUSION

The adoption of an evolutionary perspective applied to educational psychology has the

potential to transform those aspects of the discipline concerned with instructional design. One of the peculiarities of instructional design is that much of the work in the area seems to occur without a coherent, theoretical reference. Cognitive load theory, with its emphasis on evolutionary psychology and human cognitive architecture, can provide an appropriate context. When our knowledge of evolutionary psychology and human cognitive architecture are applied to instructional design, the resultant prescriptions can be very different to many currently used procedures. Because of those differences, data supporting the recommendations are required. Those data have been obtained by multiple, overlapping randomised controlled trials. The successful testing of hypotheses during this process provides a degree of validation for the theory that generated the hypotheses.

Based on the success of this enterprise, it is becoming increasingly clear that the knowledge and use of evolutionary psychology is becoming an essential prerequisite of research in instructional design. Without that evolutionary psychology base and its concomitant cognitive architecture, instructional design is blind.

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PART II

Integration with other Life, Social, and Behavioral Sciences



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Evolutionary Psychology and Biology

John Alcock

INTRODUCTION

Many people have said harsh things about the discipline of evolutionary psychology, starting in the mid 1970s (Allen et al., 1975) following publication of E. O. Wilson's *Sociobiology* (1975), the forerunner of evolutionary psychology. Subsequently, Stephen Jay Gould (1997), the chief disparager of evolutionary approaches to behavior, characterized evolutionary psychologists and other academics seeking to use evolutionary theory to explain human behavior as 'foolish, fatuous and pathetic proponents' of 'pop psychology'. Despite the effort of some to clear up the confusion and errors of Gould (e.g., Pinker, 1997), the philosopher Anthony Gottlieb (2012) completely ignored the evidence that rebuts Gould in writing an article entitled 'It [evolutionary psychology] ain't necessarily so'. Gottlieb even used Gould's 'just-so story' slur (the idea that evolutionary explanations are as simple-minded and far-fetched as Rudyard Kipling's *Just So Stories*,

about how certain animals gained some of their features – e.g., 'How the Leopard Got its Spots') to ridicule the practices of evolutionary psychology. The 'just-so story' criticism remains a popular way to depreciate evolutionary psychologists (Kurzban, 2010). In fact, evolutionary psychology has been attacked fiercely for this reason and other reasons spelled out by Jonason (2017).

The impact of Gould, an evolutionary biologist, is evident in an opinion piece written by the journalist Dan Slater (2013) for the *New York Times*. According to Slater (2013), evolutionary psychologists use evolutionary theory simply to back up their pre-existing conclusions about the putative behavioral differences between men and women. Slater referred approvingly to Gould's description (1997) of evolutionary psychologists as 'ultra-Darwinians' who somehow failed to understand the role of culture in shaping human behavior. More recently still, two women academics, Daphna Joel and Cordelia Fine (2018), published an opinion piece, also

in the *New York Times*, arguing that there are no differences between men and women in the operation of their brains – an argument that has been explicitly debunked by evolutionary psychologists. One would never know from the article that there were many relatively recent tests of evolutionary ideas about the adaptive differences between the sexes in psychology and behavior, as documented in the following sections.

THE SCIENTIFIC USE OF EVOLUTIONARY THEORY

In reality, scientists who view human behavior as the product of selection use Darwinian theory (Darwin, 1859, 1871; Hamilton, 1964) in the same way as biologists (i.e., sociobiologists, behavioral ecologists, and evolutionary biologists in general). These researchers use the theory as a guide to produce hypotheses on how particular traits or abilities might have helped individuals pass on their genes (Jonason, 2017). All biologists, but especially evolutionary ones, understand that selection is a process based on hereditary differences among individuals in their genetic ‘success’ – their contribution of their genes to the next generation. Traits, including proximate mechanisms, associated with genetic success will spread, while those hereditary alternatives that are linked to reduced genetic success will disappear over time. Three of the best extended presentations on the effects of selection are to be found in Williams (1966), Lieberman (2013), and Neuberg and Schaller (2015); since knowledge of evolutionary principles is weak in psychology (Burke, 2014), a reading of any or all of the three references should be recommended to students of psychology. Any of the above would disabuse readers of the widespread idea that species-benefit selection is the same as selection at the level of the individual or the gene. In his article, for example, Lebow (2013), a

political psychologist, asserts that natural selection involves both species-level selection (which, if Williams is to be believed, essentially does not occur) and individual-level selection, while incorrectly calling sociobiology an example of ‘updated social Darwinism’.

Therefore, when studying the ability of species to recognize others, learn about the relationships between those others, and anticipate what those others will do, researchers have established that these abilities are more often found in social species than in solitary ones. In other words, cognition has a strong social component in those species (including humans) that live in groups (Seyfarth and Cheney, 2015a). When applied to our species, the theory suggests that we, like all other organisms, should bear the imprint of natural, sexual, and kin selection – not group-benefit selection – in the form of social characteristics (developmental, physiological, and psychological) that help us pass on our genes.

For evolutionary psychologists, one such characteristic is the human brain, an exceedingly complex organ that presumably evolved by natural selection and therefore ought to advance the reproductive output of individuals (and thus their genetic success). One somewhat controversial view of the human brain argues that it is a collection of modules that promote specific adaptive behaviors, an argument that reflects the evolutionary psychologist’s belief in the effects of selection on the brain (Tooby and Cosmides, 1992; Pinker, 2002). But Gould, Gottlieb, and Slater, and many others, reject this possibility. They argue for another explanation for the brain and the behavior it controls. They point to the obvious fact that the members of different cultures differ in the behavioral traits they exhibit. The critics would ask, how can the behavior of a young Wall Street stockbroker and a Masaai warrior be explained in evolutionary terms given that their actions, appearance, traditions, technologies, and more are so very different?

For the critics of this sort, human behavior is to be explained largely in terms of what can be called the cultural conditioning hypothesis. People living in different cultures are exposed to different cultural conditions, which they learn, thereby shaping their behavior. According to this view, the brain has almost unlimited capacity to help its owner adopt the cultural rules and regulations that the person is exposed to, particularly as a youngster. Margaret Mead (1935: 280), the revered cultural anthropologist, encapsulated this approach when she claimed in her book *Sex and Temperament in Three Primitive Societies* that ‘We are forced to conclude that human nature is almost unbelievably malleable, responding accurately and contrastingly to contrasting cultural conditions’.

THE SOCIOCULTURAL VIEW: THE FOCUS ON PROXIMATE CAUSES

Everyone knows that we do indeed learn a great deal from our cultures – perhaps most obviously, the language that we speak and the clothes that we think appropriate – but in addition, the cultural conditioning hypothesis suggests that in Western societies, even our sexual preferences are determined by advertising and television. Given this reality, we do not (according to the critics) need evolutionary analyses. The sociocultural argument is surely influential (although it must be tested scientifically), but it isn’t really a true alternative to the evolutionary approach. Even if it is shown that learning is important in shaping our adaptive behavior, we can still ask what role selection played in the evolution of a brain that makes it possible for us to learn from cultural tradition how to behave adaptively (Tooby and Cosmides, 1992).

The critics, however, insist that sociocultural explanations of human behavior are real alternatives to evolutionary ones, demonstrating that either they do not know the difference between evolutionary (ultimate)

hypotheses and immediate physiological (proximate) explanations or else they are attempting to blur the distinction so as to confuse us in the service of winning an argument. Burke (2014) makes the point that an evolutionary perspective often is necessary to avoid misunderstanding the proximate basis of a behavior of interest to a psychologist. As evolutionary psychologists have noted repeatedly, the capacity to use sociocultural cues to alter brain functioning and thereby affect the development of our behavior depends on the operation of an evolved brain. It may very well be that sociocultural stimuli can alter the genes involved in the development of particular *adaptive* mechanisms and behaviors, evidence that (1) an interaction between genes and environment underlies all behavior and (2) the developmental outcomes of these interactions are limited, such that usually the outcome advances the ability of individuals to pass on their genes (Seyfarth and Cheney, 2015b). As we shall argue later, if an evolved brain capacity permits the adoption of any of several different developmental trajectories, the result can be adaptive behavioral differences even among members of the same culture. Behavioral flexibility is a common feature of human cultures, and, as it turns out, particular alternative behaviors occur in a great variety of other animal species as well (Dawkins, 1980; Gross, 1996), including insects (see Lee, 2005).

However, the critics tell us that the hypotheses presented by evolutionary psychologists and other evolutionists also have some evil side effects. In particular, these ideas are said to provide unwarranted justification for behaviors that most if not all of us would consider immoral and undesirable. So, for example, Gould stated that sociobiologists (again, they were really the first evolutionary psychologists) favored a supportive rationale for the political status quo in Western society and the corresponding depreciation of women, by proposing that males were evolutionarily predisposed to seek out political power. Many others have followed in Gould’s footsteps, as

illustrated by the journalist Sharon Begley's claim (2009) in *Newsweek* that attempts to study the evolutionary basis of rape gives rapists a 'get-out-of-jail free card'. In other words, if someone suggests that rape might have an adaptive basis of some sort, then this position could be used by lawyers to say that rape was natural, adaptive, and immutable, and therefore that evolution made the criminal do what he did, freeing him from personal responsibility.

Persons studying the evolutionary foundations of our behavior have, of course, been fully aware of the multitude of critiques of their field. They have responded quickly with rebuttals to the various criticisms including the justification complaint (e.g., Alcock, 1988). For example, they noted that persons who study how parasites and predators behave adaptively when living off their victims are not accused of justifying what tapeworms and hyenas do. Instead, everyone seems to understand that there is a difference between trying to explain why something occurs in tapeworms and other organisms (except human beings) as opposed to stating that the something is good, justifiable, and natural in the sense of morally desirable. Even so, the opponents of evolutionary psychology, from Gould in the mid 1970s to Begley in the 2000s, continue to conflate explanation and justification.

RESEARCH ON SEXUAL PREFERENCES BY EVOLUTIONARY PSYCHOLOGISTS

So, let's take a few examples of what evolutionary psychologists actually do to illustrate the explanatory, rather than the justificatory, nature of their research and their willingness to test their ideas, rather than simply settle for untested hypotheses. We start with the surely uncontroversial observation that older women are generally considered by men in our culture to be far less sexually attractive than women in their 20s. Brigitte Bardot in

her youth was unquestionably more beautiful and riveting to men than the Brigitte Bardot of today. I suspect that Donald Trump's first wife is now considered less good-looking in the eyes of almost all men in Western cultures than Donald Trump's current wife, a younger buxom model. Indeed, a male sexual preference for younger women appears to be universal among mature men, occurring across a wide range of cultures, as shown by the cross-cultural research of David Buss (1989). Buss (1989) queried more than 10,000 respondents from 37 cultures, including a number of non-Western cultures, and found a high degree of similarity in the answers received from the men as well as in the actual ages upon marriage of generally somewhat older men and younger women. Mature men everywhere prefer women with attributes that identify them as young individuals; women everywhere prefer men with attributes that identify them as relatively rich individuals with high social status. These differences between the sexes in their mate preferences have been documented for humans over and over (e.g., Kenrick and Keefe, 2011). The sociocultural hypothesis that men are conditioned by the traditions of their particular culture, which in turn are the products of human imagination, generates the expectation that in at least some cultures, men ought to be taught to prefer older women, with the result that they would learn to find older females more sexually appealing. This does not happen. Anywhere. Moreover, attempts to show that sociocultural explanations for the behavioral differences between men and women are correct have not succeeded inasmuch as these differences are actually larger in societies with more egalitarian gender roles than in cultures that offer less egalitarian gender roles, counter to sociocultural hypotheses and predictions (Schmitt et al., 2017).

So why not consider an evolutionary explanation for the male preference for younger women? If male sexual psychology is the product of sexual selection, Darwin's other

great theory, then our brains should help individual men seek out mates that are especially fertile, since a male enthusiasm for sexual activity results in genetic success only to the extent that a man succeeds in copulating with a fertile woman who then becomes pregnant. A few words on sexual selection theory. As Buss (2009a) points out, Darwin realized that selection could be divided into two components: selection arising from the struggle for existence (natural selection) and selection arising from the struggle for mates (sexual selection). Most modern biologists and psychologists interested in evolution know that both forms of selection are fundamentally similar in that they have the potential to cause changes in gene frequencies within a population. Thus, all forms of behavior are really reproductive in nature (or genetic in the sense of promoting genetic success) (Weeden et al., 2008), such as when better survivors reproduce more than poor survivors and when more sexually attractive males and females attract mates more readily than unattractive males and females. Still, the differences between the two categories of selection are worth emphasizing. By comparing natural with sexual selection, we are reminded that traits that promote the acquisition of mates can override traits that make it more likely that the individual will survive.

The classic example is the peacock's train, which is thought to make the male bird more vulnerable to predators (but see Thavarajah et al., 2016) yet at the same time makes the male more likely to reproduce, since peahens apparently prefer males with elaborate trains (Petrie et al., 1991). In other words, female mate choice can lead to sexual selection in favor of well-ornamented males even if natural selection would tend to act in favor of less ornamented, longer-lived males. By the same token, males may find certain females more attractive, leading to male mate choice for attractive characteristics in the opposite sex. Evolutionary psychologists could and did use this sexual selectionist hypothesis (a tentative explanation for the psychological preferences

of men) to produce testable predictions, one of which is that women in their 20s, who are generally preferred to older women, should be more fertile than older females (that is, have greater reproductive value). As predicted, to no one's special surprise, adult-female age is negatively linked to fertility in our species (Menken et al., 1986). In fact, women in their mid 30s are far less fertile than women aged 20–24, with fertility declining by 6% for 25–29-year-old women, another 14% for women aged between 30–34, and 31% for women aged 35–39 until, by age 50, women are essentially incapable of having children.

The point here is that evolutionary psychologists have engaged in science in the usual manner in attempting to *explain* why men everywhere tend to prefer younger women as potential sexual partners. These researchers employed evolutionary theory to generate a hypothesis; they used the hypothesis to produce a prediction, a result that had to be true if the explanation was correct; by checking whether the prediction was right, they tested the hypothesis in question. Because older women are in fact less fertile – indeed much less fertile (especially after the age of 50) – than younger ones, the scientists here correctly concluded that the evolutionary hypothesis had been supported. Note that these researchers were not trying to justify male sexual preferences, which can lead to cruel and unthinking sexism, but to explain why male mate choice is affected by the age of potential mates in evolutionary terms.

But come on: everybody knows that young women are more likely to become pregnant than older women, and so the prediction given above was not especially powerful. As a result of their awareness of this issue, evolutionary psychologists are no more satisfied with one or two tests of a hypothesis than are their critics or, for that matter, physicists. The more tests, the better. The more challenging the prediction, the more convincing the test. Here is an example of another test of the evolutionary hypothesis that male mating

preferences have been shaped by selection to increase the odds that a man will seek out fertile partners. If men have evolved to exhibit mate preferences that focus on fertile women, then adolescent males should show an interest in dating women who are *older* than they are, even though an adolescent's chances of securing partners in their 20s is close to nil. When this prediction was tested, adolescent males said that they would like to date women who were somewhat older than they were, rather than showing the supposed culturally induced preference for younger dates (Kendrick et al., 1996).

Yet another prediction taken from the evolutionary hypothesis that male mate choice will revolve about female fertility takes advantage of the commonly held view that neither men nor women can tell when a woman is in the ovulatory phase of her menstrual cycle. Despite this view, evolutionary psychologists predicted that men *should* have evolved the ability to detect subtle cues associated with ovulation when evaluating the sexual attractiveness of women (e.g., Thornhill and Gangestad, 2008). In what constitutes a test of this prediction, a team of researchers (Law-Smith et al., 2006) constructed two composite photographs of the same set of women, but one image was composed of these women when ovulating and the other was of the same women in the non-ovulatory portion of the menstrual cycle. The differences between the two composite images were very slight, and yet when men were asked which image they found more attractive, they selected the one composed of ovulating women significantly more often – as predicted from the evolutionary hypothesis under examination. In other words, men can tell unconsciously when a woman is ovulating, and their greater appreciation of the woman in this condition could motivate them to try to mate with her at a time when she was especially likely to become pregnant. I think it is fair to say that without Darwinian theory, this work would never have been done.

ANOTHER TEST OF THE HYPOTHESIS THAT MEN CAN DETECT WHEN WOMEN ARE FERTILE

And here is yet another example. You too can become an evolutionary psychologist for a moment by predicting the size of tips that lap dancers should receive in relation to their ovulatory cycle. Who should secure larger tips if female fertility is attractive to men: a woman on the pill, a woman off the pill and ovulating, or women off the pill who were in the non-ovulatory phase of their cycle?

The data collected by a team of evolutionary psychologists (Miller et al., 2007) at the University of New Mexico were clear and convincing. Ovulating lap dancers received significantly more money per five shifts from their male clients than non-ovulating dancers.

This research, admittedly somewhat risqué, was attacked by prudish critics, but the procedures followed were completely scientific. The hypothesis that the sexual attractiveness of a woman was influenced by her fertility was used to produce a prediction – namely, that fertile (ovulating) lap dancers and their behavior would be more attractive to male clients than non-fertile performers, resulting in larger tips given to those ovulating (Fink et al., 2012). The actual evidence showed that the prediction was correct. Conclusion: a possible explanation, an *evolutionary* hypothesis, was more likely to be true.

NATURAL SELECTION AND HUMAN BEHAVIOR

Although the gene-centered focus of evolutionary psychologists is most obvious when sexual selection theory has been used to develop hypotheses and predictions about mate choice and other sexual decisions of people, natural selection theory has also been used by researchers who have looked at the relationship between survival and certain

human traits. So, for example, why do women undergo menopause? An evolutionary explanation that has received considerable support is the grandmother hypothesis, in which women who end fertility early but remain vigorous can help their grandchildren survive by helping their daughters forage for hard-to-get food. In so doing, the post-menopausal women help their daughters reproduce, passing on shared genes to the next generation (Hawkes and Coxworth, 2013). Although menopause appears to occur in a few other species, our closest relatives, chimpanzees, remain fertile until they die, suggesting that the extension of life span and full activity exhibited by post-menopausal women is an adaptation that promotes the genetic success of women.

The proponents of the grandmother hypothesis point to the spread of savannah habitat in Africa and the corresponding spread of the difficulty to find and remove edible tubers as the ecological factor that favored grandmothers that helped their daughters secure food, which shortened the interval between births of their daughters. Male–male cooperation also probably evolved during the time that our ancestors faced drying conditions that eliminated the tropical rain forest in which our still-more distant ancestors evolved. As these recent ancestors moved out into the savannah habitat and began walking bipedally, they confronted lions and other large predators in African environments, animals that could only be dissuaded from feeding on carcasses attractive to hominins, and from attacking hominins themselves, through cooperative group action. Only if a group of ancestral humans cooperatively threw stones and other missiles at predators could they have chased these enemies away.

A prediction that follows from this survival-based hypothesis is that stone-throwing modern humans could repel human enemies on occasion, even if their opponents possessed the more modern weaponry. In his seminar, William von Hippel (2017) presented data from the Canary Islands and from

Australia, where stone-throwing aborigines successfully repulsed heavily armed and armored invaders with the deadly accuracy of their hurled stones. As von Hippel (2017) noted, modern *Homo sapiens* possess chest musculature quite unlike that of our closest living relative, the common chimpanzee – musculature that enables us to throw objects with much more force and accuracy than chimpanzees (see also Lombardo and Deaner, 2018).

Likewise, our wrist bones and associated ligaments differ greatly from those of knuckle-walking chimpanzees in ways that are related to our special capacity to throw items with power and accuracy (Rohde et al., 2010). In addition, although male common chimpanzees do cooperate by patrolling their territory in groups, the level of cooperation in this closely related species is much less than that exhibited by modern humans, who often cooperate with nonkin, a uniquely human behavior (Bingham, 2000). Our ancestors, unlike those of chimpanzees, faced predatory threats in open savannah habitats, where communal defense would have been beneficial to all cooperators. In addition, our ancestors apparently often clashed with other groups, so this defensive or aggressive cooperation would potentially have had payoffs for all the individuals involved, whether related or not (Bingham, 2000). It is the formation of coalitions, no matter the degree of relatedness, and the use of thrown weapons that permit injury or killing of fellow humans at a greater (safer) distance than if the defenders or aggressors were to engage the enemy in hand-to-hand aggression. The larger the group, the safer the simultaneous attack with thrown weapons. A striking feature of cooperative defense or offense is that individuals almost always favor their own group, and their cooperation does not extend to members of other groups (von Hippel, 2017). As such, our evolved tendency to prefer our own clan, team, group, tribe, and nation over others hinders the development of peaceful global security measures.

Bingham (2000) attributes the origin of cooperative coalitions among unrelated humans to the benefits accruing to individuals from the enforcement of cooperation on 'cheaters', who might otherwise permit other group members to take the risks associated with cooperation while they escape the cost of group action. The price of cooperative enforcement is greatly reduced to coalition members who can impose their will on others at a considerable distance. Predictions from this hypothesis include the expectation that humans would exhibit moral outrage at those who avoid their fair share of social enforcement costs (which they do) and the expectation that anyone who contemplated avoidance of his or her costly societal actions would feel guilt at their potential behavior (a common feeling in humans). The emotion of guilt 'encourages' individuals to behave in the interests of the coalition – and in their own genetic interests (Bingham, 1999).

KIN SELECTION AND HUMAN BEHAVIOR

In addition to natural and sexual selection, there is a third type of selection associated with biological explanations of behavior that can be and has been applied to humans. Kin selection causes changes in gene frequency due to treatment (positive or negative) of relatives (other than offspring) by individuals that affects the ability of these relatives to pass on the genes they share with those who help or hinder them. The 'discovery' of kin selection and its effects on genetic success, or inclusive fitness (the totality of genes transferred to the next generation through individual reproductive success and via effects on help or hindrance of the reproduction of relatives), was accomplished by the evolutionary biologist W. D. Hamilton (1964). As Mateo (2015) points out, Hamilton predicted that the ability to help relatives would favor kin recognition in social species,

a prediction derived from an understanding of evolutionary theory about a proximate ability that has proven to be true. In the human species, the cues associated with kin recognition include the odor and facial resemblance between two individuals and the period in which the individuals resided with one another and their biological mother – a variable that is very important to siblings (Lieberman et al., 2007).

So, let us see how kin selection theory has been used to cast light on the behavior of humans. First, the likelihood that two siblings will help each other is related to the number of years spent residing with each other and their mother, but not their father, who may or may not be related to them – a result that indicates that altruism usually occurs when two individuals are close relatives (Sznycer et al., 2016).

One prominent effect of kin selection is the avoidance of inbreeding, which would occur if close relatives (especially siblings) mated with one another. In fact, as Westermarck (1891) noted long ago, persons who live with one another during childhood tend not to find each other sexually attractive. In fact, inbreeding depression directly affects the inclusive fitness (genetic success) of siblings that marry, while indirectly reducing the fitness of those whose sibling marries a close relative by lowering the indirect gains that are possible when siblings help their brothers and sisters reproduce. Such outcomes account for the strong opposition to sibling marriages expressed by most people, an opposition that tracks the degree to which inbreeding would carry direct or indirect costs for the persons whose views on marriage between close relatives were solicited by researchers (Antfolk et al., 2018).

As also predicted, the longer children were reared together in the novel environment of the kibbutz, which involved their separation for most of the day from their parents, the more they found co-reared individuals of the opposite sex unattractive mates (Lieberman and Lobel, 2012). In other words,

co-residence is a cue for kin recognition that young persons use to avoid inbreeding.

Although sibling–sibling matings are unquestionably rare, they have occurred in some societies, usually when the advantages of keeping resources in a royal family are paramount (and when polygyny is practiced by the royal family as well) but also sometimes in other situations (Scheidel, 1996). Since the very few societies in which incestuous marriages occurred in ordinary families disappeared centuries ago, making a collection of data on inbreeding depression impossible, we have no way of knowing whether inbreeding contributed to the loss of sibling–sibling marriages in these societies. The abundance of current evidence on incest avoidance speaks to the robustness of the phenomenon.

Kin selection theory has been used to produce testable hypotheses on any number of other aspects of human behavior that could affect the genetic success of individuals, such as adoption, which at first glance appears costly and without fitness benefits for the adopter. However, in traditional societies, adoption of relatives appears to be the commonest form of this kind of cooperation between the adopters and those adopted (Silk, 1980). And adoption is far more likely to be practiced if the child being adopted is close kin, such as a nephew or niece, rather than a more distant relative, such as a cousin. Moreover, in five states in the United States, it was found that children who are related to their foster parents experience better outcomes than children who are placed with unrelated foster parents (Koh, 2010).

Additional aspects of human behavior that have been analyzed in terms of kin selection include helpful behavior provided to a mother by other women. For example, in the hunter-gatherer tribe the Hadza of Tanzania, women who are related to a mother with a youngster hold the child more than women who are unrelated to the mother and child (Crittenden and Marlow, 2008). In fact, the duration of holding is linked to the degree to which the helper is related to the mother and child. If

childcare of this sort promotes the greater reproductive success of the mother, as seems likely, then this study provides evidence of kin-selected cooperation in the Hadza.

Another possible effect of kin selection is on the occurrence of friendships, which have been shown to be ‘functional kin’ thanks to the genotypic similarity of friends (Christakis and Fowler, 2014). Note that thinking about how individuals might interact with genetically similar persons is at the root of all elements of kin-selected behavior.

HUMAN BEHAVIORAL UNIVERSALS

All this work, like much of evolutionary psychology, has succeeded in documenting a universal aspect of human behavior (exhibited by all members of our species or by all members of one sex), such as the human kin-selected tendency to help relatives as opposed to genetic strangers. The identification of universals is a major goal of the discipline, and there are many such universal behaviors according to Brown (1991). Some are products of kin selection, while others are linked to sexual selection, as in aspects of adult sexual preferences of humans (Buss, 1989; Geary, 1998). For example, the sexes differ in the nature of their sexual jealousy in ways that can be attributed to sexual selection, with men more concerned with the copulatory fidelity of a partner and women becoming more jealous if they learn of the emotional involvement of a partner with another woman. These differences have been linked to the fact that a woman’s sexual infidelity carries with it the risk that her social partner may care for the offspring sired by another male, whereas a woman’s maternal certainty is 100%. In contrast, a female’s jealousy is focused on the possible loss to another woman of the devotion of her mate, a worry that stems from the paired woman’s concern that her mate will provide resources to the new woman at the expense of her and her

offspring (Buss et al., 1992). This research was supported by various other studies, such as that of Weideman and Kendall (1999), in which Swedish students (a notably relaxed group with respect to sexual behavior) were also asked similar questions about copulatory versus emotional infidelity and who responded in a similar sex-specific manner.

A recent attempt to test whether the theoretical outlook of the researchers affected the outcome of the study showed that the sex differences between men and women in sexual jealousy were not influenced by whether the work was done by evolutionary psychologists or by other subgroups of psychologists, since the study was conducted by a wide variety of researchers (Edlund et al., 2018). Thus, although the work had previously been replicated with differing results and remains controversial with respect to the underlying causal theory, it appears that sexual jealousy is indeed fundamentally different for men and women, a fact that almost certainly is related to the degree to which a father can be sure of his paternity as opposed to the importance of a woman's ability to secure resources from a partner, which would have affected the survival of her offspring, especially in the past (but also in the present).

Another examination of the universal effects of uncertainty of paternity versus the certainty of maternity comes from the study of the importance of facial resemblance on a father's willingness to invest in his putative offspring (but not a mother's). In cross-cultural research on French and Senegalese families, the degree to which a young child resembled his father influenced the degree to which his father was emotionally involved or invested in his offspring. In France, if the male father thought his wife's infant looked like him, he reported feeling emotionally close to the child (Alvergne et al., 2010). The emotional involvement of the mother was unaffected by the child's appearance. In Senegal, a male's facial resemblance or similarity in odor to his wife's offspring determined how much he was willing to give resources to the

child and the extent to which the child thrived and enjoyed good health (Alvergne et al., 2009). Likewise, in a Chinese study, if the social father thought the child (whose average age was a little over four years) did not look like him, he was more likely to exhibit distress than the mother (Yu et al., 2016). In another study, the odor of an offspring affected the attachment of the putative father to the child in question (Dubas et al., 2009). Note that natural selection theory explains these psychological effects on fathers because the direct reproductive success of the male is affected by the degree to which he and the offspring of his wife share genes in common. Indeed, the sharing of genes has much to say about the cooperative behavior and psychology of in-laws, although they are not at all similar genetically to one another, but do share an interest in promoting the reproduction of their sons or daughters (Dyble et al., 2018).

In addition to the importance of the facial and odor resemblance between father and child, other universals apply to everything from the degree to which an individual can be shamed in relation to the cost to the person of an anti-social act (Sznycer et al., 2018) to the capacity of human beings to fantasize about killing another person (Buss, 2005). These universals indicate that selection has removed all but the one kind of behavior or psychological mechanism that results in maximum genetic success for individuals.

Several persons have argued that the focus on universals is problematic either because we cannot know much about the minds of our distant ancestors (Buller, 2009) or because much of human behavior varies from individual to individual, rather than being the same for everyone or for subsets of our species (Gurven, 2018). If the first objection were applied to humans, it should be close to impossible to analyze the adaptive value of the behavior of non-human animals whose ancestral species are either poorly known or not known at all, a proposition that is clearly not supported by the abundant behavioral

ecological literature on adaptive cognition in non-human species. In reality, Buller's (2009) article is designed to make studies of human behavior undesirable, as he signals in the title of his critique, which speaks of the fallacies of 'pop' evolutionary psychology. Since the authors that he focuses on – namely, Buss (1989, 2015), Pinker (2002), and Cosmides and Tooby (2013) – are among the most prominent and productive practitioners of evolutionary psychology, Buller seems to be warning all persons not to engage in evolutionary research, a warning that repeats a tactic of Gould, who claimed that there were shallow popularizers (i.e., evolutionary types) and serious researchers (i.e., Gouldian researchers). It may be significant that most of the critics of evolutionary psychology are journalists, philosophers, or neuroscientists who are decidedly not evolutionary biologists, with the exception of the ideologue Gould. His self-reported fondness for an environmental analysis of human behavior, which nonetheless did not match the Marxist enthusiasm of his colleague and co-author Richard Lewontin (Segerstråle, 2003), is linked to his view that an evolutionary analysis of human behavior leads us astray.

THE ADAPTIVE NATURE OF VARIATION IN HUMAN BEHAVIOR

As for the second objection that deals with the obvious observation that there is considerable behavioral variation among humans, the explanation at a proximate level is the primary goal of the discipline of psychology (Jonason, 2017) and cultural anthropology. However, evolutionary psychology has an interesting answer to the ultimate question, *why* do people vary so much behaviorally. One answer is that the differences in behavior are often adaptive solutions to problems arising from, for example, differences in the social environment of individuals or from some other evolutionary mechanisms such as

frequency-dependent selection, in which that rarer of two genotypes experiences a fitness advantage (Buss, 2009b). Since humans often confront social variation in their cultural environments, it often pays individuals to be capable of flexible responses, as is evident in the ability of humans to learn any of a vast range of languages if the learning takes place when the person is young.

To take another example, individual males and females can judge their sexual attractiveness relative to others in the population in which they reside. Persons who think (usually correctly) that they are especially good looking generally exhibit mate preferences for others of the opposite sex that are likewise unusually handsome or beautiful. Persons who believe that they are not particularly attractive are willing to accept someone who is in the same less attractive range that they are in (Buston and Emlen, 2003). This adaptive variation in mate choice saves an individual time that would otherwise be wasted in fruitless pursuits, and it occurs both in college students in the United States and in the largely Muslim population of Turkey (Göz et al., 2018). The cross-cultural flexibility involved suggests that the adaptive ability to choose mates depending on one's appearance is both universal and a cause for behavioral variation within populations.

The sex ratio of a population can also affect the frequency with which men and women attempt to lure a mate from an established couple (Buss, 2005). In cultures in which men outnumber women, men are far more likely than women to try to secure a sexual partner who is already married or in a committed relationship. In countries in which women are more common than men, women are the primary sex that attempts to engage in sexual activity with men who are already married. In both situations, the gender that is willing to have sex with an individual in a committed relationship is behaving adaptively: where men make up the surplus supply, they can sometimes have a married woman bear their child if they convince her

to have sex with him, a child that may be cared for by another (cuckolded) man who will unknowingly help the mate-poacher to pass on his genes; in countries where unmarried women outnumber unmarried men, a woman who mates with a married man may secure either useful resources from the man or persuade him to leave his partner and provide for her and her offspring, often to her fitness advantage.

The susceptibility of a person to losing a partner apparently depends on his resources or her physical attractiveness relative to that of the mate-poacher – another way in which individual variation affects the decisions and reproductive success of persons (Davies and Shackelford, 2017). Likewise, personality features of human beings vary considerably in ways that almost certainly promote adaptive responses to the social environment of the people in question (Belsky, 1999; Michalski and Shackelford, 2010). So, for example, very young children vary in their response to separation from their mother and the entrance of a stranger into a room where they have been left alone. Children who are secure about their relationship with a mother typically accept a brief separation without stress reactions, whereas children who are insecure often respond by weeping when their mother leaves and especially when a stranger enters the room (Ainsworth and Bell, 1970). To the extent that the various reactions reflect maternal variation in behavior, the infant's behavior can be viewed as adaptive in that the reaction of an insecure child represents an attempt to receive maternal protection when left alone in a dangerous world in which strangers, especially strange men, would have been threats to their well-being.

Jonason et al. (2016) specifically examined the conditional strategy hypothesis for a trio of traits that are often thought to be maladaptive (narcissism, Machiavellianism, and psychopathy) but may well be adaptive responses to difficult childhood conditions characterized by poverty and unpredictability.

Jonason's team found correlational support for the argument that resource shortages during childhood led individuals to exhibit these socially undesirable characteristics, which generally evoke attempts by others to eliminate the traits in question. The long-term persistence of socially undesirable behavior caused Jonason and his co-authors to speculate that, as required by a conditional strategy hypothesis in which certain conditions elicit certain personality traits associated with opportunism, selfishness, and exploitativeness, we may all possess the evolved potential to behave badly, but adaptively, if we are reared under conditions of deprivation when young.

The scientific nature of evolutionary psychology is now well known to most academics in psychology departments, although acceptance of the discipline may still be reluctant or partial by many psychologists. The use of well established evolutionary theories to produce testable hypotheses, often of a novel and unexpected nature, has resulted in a growing number of evolutionary psychologists who realize that they can test explanations for human behavior based on something other than sociocultural theory. The number of journal articles that included the term 'evolutionary psychology' or 'evolutionary psychological' in the title, abstract, or as a keyword has increased in five-year increments from 6 to 998 over a 20-year period beginning in 1985 (see Webster, 2007). The use of evolutionary psychology as a keyword for searches in the Web of Science reveals that in the period from 2006 to 2018, the phrase appeared 1,886 times. Today's critics do not seem to know of the success of the field as much as how the discipline is supposedly due for extinction (Simón, 2018). In reality, evolutionary psychology is flourishing – a form of standard science with a multitude of testable and tested hypotheses on many subjects. We are the better for it in terms of understanding the role of the various forms of selection in shaping our behavior.

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Implications of Genetic Research for Evolutionary Psychology

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During the past few decades, an incredible amount of research has been produced that has allowed for newer insights into the mechanisms that produce human phenotypes. The breadth and depth of such scholarly contributions is noteworthy. Neurobiological breakthroughs, for example, have allowed for a more detailed and nuanced understanding of how brain structure and functioning relate to certain traits and behaviors (DeYoung et al., 2010), sociological research has identified socialization processes that are linked to social behaviors (McMillan et al., 2018), genetic research has identified gene systems tied to a wide range of behavioral outcomes (Kim-Cohen et al., 2006), and psychological research has identified developmental trajectories that lead to a range of personality traits and cognitive abilities (Wrzus and Roberts, 2017). Despite the tremendous gains made in the knowledge of human phenotypes, much of the research produced in one discipline has had very little – if any – impact on other fields of

study. This is a particularly salient issue as the findings generated from a single field of study typically have applicability across multiple disciplines. Perhaps nowhere is this truer than when it comes to the results of genetic studies. Findings from these studies have made their way into a wide range of disciplines, including criminology (Wright and Boisvert, 2009), economics, (Beauchamp, et al. 2011), and political science (Alford et al., 2005), but they have been slow to be fully integrated into other fields of study. Evolutionary psychology is one area in particular that could benefit from a more complete integration of findings from genetic research.

While exceptions exist (Fitzgerald et al., 2010; Segal and MacDonald, 1998), evolutionary psychologists have been relatively reluctant to allow for findings from genetic studies to guide and inform their own theories and empirical research. Although there are many reasons for this, and certainly some of them stem from limited exposure to

the behavioral genetic literature, an equally important factor is that psychological scholarship has been grounded in what is known as the Standard Social Science Model (SSSM) (Tooby and Cosmides, 1992). According to the logic of the SSSM, human behavioral outcomes emerge independent of genetic influences, and, as a result, the focus of disciplines that adhere to the SSSM has been on how cultural and social factors account for human phenotypes. Evolutionary psychologists have followed this logic in their research designs and employed archeological records, naturalistic observations, and self-reports, among others, to examine the potential influences on phenotypes of interest. The common theme cutting across the theories, explanations, and methodologies in the majority of evolutionary psychological scholarship is that genetic influences are assumed to be orthogonal to the factors that are responsible for producing variation in human phenotypes (Tooby and Cosmides, 1990). From this point of view, many evolutionary psychologists, in their theory and research, do not directly study genetic variation as a source of variation in phenotypes, and, instead, phenotypic differences are typically analyzed in a way that attributes such variation to socialization, environmental, or cultural influences. While the SSSM is widely used and is responsible for producing a wealth of information – both within evolutionary psychology as well as in other disciplines – if the SSSM assumption of zero genetic influence is untenable, then the results generated from SSSM studies could be biased or completely incorrect (Harris, 1995, 1998; Segal et al., 1998; Zietsch et al., 2015).

Although scholars have drawn attention to the possibility that genetically informed research designs may have important implications for the refinement of theory and future empirical research in evolutionary psychology, the literature to date has tended to focus on environmental influences to explain differences in human behavior, in the absence

of considering genetic sources of differences. The key concern with this approach, however, is whether genetic influences are widespread and observable across phenotypes; if they are, then this should give reason to pause and reconsider whether the research that is based on the SSSM is inaccurate. Keep in mind that if genetic influences are important for a phenotype and the SSSM is employed, then it is possible that any findings generated would be misleading. And, what is just as important is that if an entire body of knowledge is based on the incorrect application of a methodology – in this case, methodologies grounded in the SSSM – then that entire knowledge base could be erroneous. At the same time, however, if genetic influences tend to be isolated to certain phenotypes or to certain areas of study, then perhaps the widespread use of the SSSM would not be cause for concern.

Whether the SSSM is useful in most mainstream evolutionary psychological research comes down to at least one fundamental question: to what extent do genetic influences matter for the phenotypes being studied by evolutionary psychologists? To answer this question, this chapter examines how information from the biological sciences will not only strengthen evolutionary psychological work but also complement and improve traditional theories of human behavior. Against this backdrop, the goal of the current chapter is twofold. First, we will provide background information about behavioral genetic research. This portion of the chapter will focus on explaining a selection of technical terms and concepts, introducing some of the widely used methodologies, and summarizing several key findings applicable to evolutionary psychologists. Second, based on our review of the genetic research, we will discuss some ways in which genetic findings could be used by evolutionary psychologists. In doing so, we will pay particular attention to studies that evolutionary psychologists have produced that have integrated genetic findings and research designs.

A BRIEF INTRODUCTION TO GENOTYPIC VARIANCE

A first step toward understanding the genetic basis to human phenotypes is to provide a concise introduction to deoxyribonucleic acid (DNA). DNA is the genetic code for life and is responsible for normal human development and functioning. It determines many observable human traits, such as eye and hair color, and influences the development of non-observable traits, such as personality traits and intelligence (Hoefnagels, 2018). DNA is passed from parent to child, with half of the DNA inherited maternally and the other half paternally. DNA is located in the cell nucleus, with its information stored as a code that consists of four nitrogenous bases: adenine (A), thymine (T), guanine (G), and cytosine (C). These bases bond with each other (A bonds with T (and vice versa) and G bonds with C (and vice versa)) to form what is recognized as the double-helix structure of DNA. In total, there are about three billion base pairs in humans. At certain segments along DNA, adjacent base pairs work in unison to perform particular tasks; the base pairs that work together are referred to as genes. Although DNA has the potential to carry information, the sequence of DNA determines the function of the gene, where some sequences instruct in the coding of amino acid sequences of proteins that form cell structures and others are involved in the regulation of certain cells or hormonal activities.

Most genes do not vary, meaning that every person has the same base pair sequence for those genes. For all healthy humans, for example, allelic invariance is present for the majority of genes that code for the production of two legs, one heart, and 10 toes. In contrast, for a relatively small percentage of all genes, there is at least some variation in the base pairs for a single gene. For instance, there is greater allelic variation present in genes associated with social behaviors. One

person could inherit a base pair sequence for a gene that is different from the base pair sequence of another person for that same gene. When a gene can vary, it is considered to be a polymorphic gene, and alternative copies (i.e., different base pair sequences) of that particular gene are referred to as alleles. For example, there could be a hypothetical gene, called hair-color gene, where there are different alleles, such as brown, blonde, and red. In this example, the alleles (brown, blonde, or red) for a genetic polymorphism (hair-color gene) determine the phenotype (hair color). A person's hair color thus depends on which alleles are inherited maternally and paternally.

There are several ways that genotypic variance can produce phenotypic variance, including polygenic effects, monogenic effects, and pleiotropic effects. First, when it comes to the connection between genes and phenotypes of interest to evolutionary psychologists, most genes do not determine the phenotype (as they did in the hypothetical hair-color example), but rather they work probabilistically, increasing or decreasing the likelihood of developing a particular phenotype or of scoring high or low on a phenotype. Depending on the particular trait or adaptation, there could be hundreds or thousands of genes involved in its architecture. While each allele would have relatively small effects on a phenotype, when examined cumulatively, the effect could be quite large. This is known as a polygenic effect, and thus polygenic phenotypes are affected by many genes, none of which is individually deterministic. For example, suppose there were three genes involved in the use of aggression: Gene A, Gene B, and Gene C. Also suppose that there are two alleles for each gene, which we will call the 'I' allele and the 'D' allele. The 'I' allele increases the use of aggression by one point and the 'D' allele decreases the use of aggression by one point. In this scenario, a person could receive an 'I' allele for both alleles (one maternal and one paternal) for all three genes and thus their aggression

score (based on these three genes) would be six (+6). Similarly, a person could receive a 'D' allele for both alleles for all three genes and thus their aggression score would be negative six (−6). Different combinations of the 'I' and 'D' alleles across these three genes would produce different values on aggression.

Note that while these three genes would have some influence over the propensity for aggression, none would determine the use (or non-use) of aggression in any particular situation; rather, all that these allelic combinations would produce are different propensities that may or may not surface in different situations. Individuals with a high genetic propensity for aggression are not destined to aggress; likewise, even those with the lowest risk for aggression may become violent if embedded in a certain environment. Therefore, behavioral responses result from a combination of genetic influences and environmental stimuli. For example, in a landmark study by Caspi et al. (2002), they investigated whether the effect of a genetic polymorphism – MAOA – was partially responsible for producing variation in antisocial phenotypes. The researchers reported that MAOA in and of itself had no influence on antisocial outcomes; however, MAOA was associated with antisocial phenotypes for males who had been maltreated in childhood, but not for males who were not maltreated. Taken together, these findings highlight the role that environments play when it comes to genetic effects.

The second way genes are connected to phenotypes is via what is known as a monogenic effect, where one gene is the cause of one particular phenotype. Sickle-cell disorder, as an example, is an inherited disorder that affects red blood cells. Individuals with sickle-cell disease were born with two sickle-cell genes, one from each parent, and thus the disorder is due to a monogenic effect. Lastly, pleiotropy captures the effects that a single gene has on various phenotypes. The allele that causes the disorder phenylketonuria, for

example, leads to an absence or deficiency of the enzyme (phenylalanine hydroxylase) responsible for processing the essential amino acid phenylalanine. These amino acids are important for proper growth and development, and, without treatment, affected individuals may experience neurological symptoms in addition to other psychiatric disturbances.

The genetic origins of complex human traits, such as personality and social behaviors, are largely polygenic, and, as a result, the influence of any particular gene on any particular trait tends to be very small and may be statistically undetectable. Even so, genetic polymorphisms are of particular interest to scientists because they have the potential to explain phenotypic variance. Genes that do not vary – that is, they are not polymorphic – could explain human universals, but they are typically assumed to be unable to explain phenotypic differences (though, theoretically, they could explain phenotypic differences via epigenetic effects, a topic that is beyond the scope of this chapter (but see Bateson, 2014)). As a result, most of the research that has attempted to examine genes associated with phenotypes has focused on examining whether different alleles of a polymorphism are correlated with phenotypic differences. For example, in an early candidate gene association study, researchers looked to see whether a specific genetic polymorphism – specifically, the D4 dopamine receptor gene (D4DR) – was associated with the human personality trait of novelty seeking (Ebstein et al., 1996). Individuals who score higher than average on the TPQ Novelty Seeking scale are characterized as impulsive, exploratory, excitable, quick-tempered, and extravagant, whereas those who score lower than average tend to be reflective, rigid, loyal, slow-tempered, and frugal. Researchers found that higher scores on the Novelty Seeking test were significantly associated with the long allele for the D4DR gene. Thus, they found evidence of an association between a specific allele and a behavioral outcome.

OVERVIEW OF BEHAVIORAL GENETICS

Behavioral genetic research is largely interested in determining the degree to which genetic variation accounts for phenotypic variation and the degree to which environmental variation accounts for phenotypic variation. For the most part, behavioral geneticists study the interplay of genetic and environmental influences on individual differences in phenotypes, whereas evolutionary psychologists tend to focus on the ultimate, universally adapted causes of behavior (Ferguson, 2010). While these directions may seem divergent, the two fields of study are more compatible than they initially appear. In the following paragraphs, we will present a brief overview of behavioral genetics, which should provide the necessary groundwork for understanding the key aims, methods, and findings of behavioral genetic research.

Behavioral genetic designs allow for the estimation of genetic and environmental contributors to phenotypic variance. To do so, most behavioral genetic studies have analyzed data from family members (e.g., parent–offspring, siblings, cousins, etc.). The key reason for analyzing family members is that by comparing the degree of genetic relatedness among family members and then contrasting that genetic resemblance with phenotypic resemblance, it is possible to estimate the effect of genetic and environmental influences on a phenotype. These types of genetically sensitive research designs stand in stark contrast to the SSSM, which typically only employs samples that consist of one person per family. The result is that the SSSM is unable to estimate genetic *and* environmental influences, and thus the parameter estimates generated from the SSSM could be confounded and systematically biased if genetic factors indeed underlie the observed association. This insight has led researchers working in biology, psychology, and

criminology, among others, to reconsider the established notion of how genetic and non-genetic factors work together to both guide and constrain human behavior.

In basic behavioral genetic studies (i.e., univariate studies), the proportion of phenotypic variance is divided into three components: a heritability component, a nonshared environmental component, and a shared environmental component. First, heritability captures the proportion of phenotypic variance that is accounted for by genetic variance (Plomin et al., 2013). Heritability estimates range between .00 and 1.00, with higher values indicating a greater genetic influence on phenotypic variance. Frequently, there are misunderstandings surrounding what heritability estimates can and cannot reveal. Two points are of particular importance in this regard. First, heritability estimates apply to the sample/population and they do not apply to an individual. For instance, a heritability of .50 means that 50% of the phenotypic variance in a sample is accounted for by genetic variance. At the same time, a heritability of .50 does not mean that 50% of the reason that a particular individual turned out the way they did was because of their specific genes. Although heritability estimates cannot answer specific questions about behavior at the individual level, recent work by Tal (2009) has revealed how heritability estimates can be applied to individuals, but *precise* heritability estimates generated from a sample do not apply to the individual. Second, heritability is not a fixed estimate that remains invariant across time and space. In fact, findings from a broad range of studies have shown repeatedly that heritability estimates can change across environments, across the life course, and across time (Briley and Tucker-Drob, 2013; Haworth et al., 2010). For example, researchers have found that the heritability of IQ increases from infancy through adulthood (Plomin, 1990).

There have been hundreds of thousands of subjects analyzed in behavioral genetic studies to estimate heritability on virtually every

measurable phenotypic characteristic, ranging from height and weight to aggression and health disorders. What is particularly fascinating is the degree to which heritability estimates converge across studies and across phenotypes. Perhaps the most compelling and exhaustive study on heritability estimates comes from the landmark research conducted by Polderman and her colleagues (2015). In their analyses, they reviewed every twin study published since 1958 and synthesized the results. Altogether, they found a heritability estimate of about .50 across virtually every phenotype. Their finding is truly remarkable, as it was generated from 14,558,903 twin pairs, 2,748 studies, and across myriad phenotypes.

If genetic influences account for about 50% of phenotypic variance, then the other 50% of phenotypic variance is accounted for by environmental influences (and error). Unlike most social science disciplines, such as sociology and criminology, behavioral geneticists delineate between two types of environments: shared environments and nonshared environments. The shared environment captures the effects of environments that make siblings more similar to each other (Buchanan et al., 2009; Plomin et al., 2013). Shared environments are often thought to be those environments found within the family, such as family-wide parenting influences, the socioeconomic status of the family, and exposure to family violence. If siblings experience these environments, and these environments are capable of exerting a noticeable influence on the siblings, then they should make the siblings more similar. For example, suppose divorce increases internalizing problem behaviors, such as being withdrawn or feeling lonely. If two siblings both experience divorce, then it should increase both of their chances for displaying internalizing problem behaviors, thereby making them more similar to each other. Nonshared environments, in contrast, are environments experienced by siblings that make them different from each other. Some common examples of nonshared

environments are unique peer groups, different prenatal environments, and idiosyncratic life experiences (Beaver, 2009). If these environments are important for human development, then differential exposure to such environments should produce phenotypic differences between siblings. To illustrate, suppose one sibling is embedded within an antisocial peer group and another sibling is embedded within a prosocial peer group. Since peer groups are central to development (Neyer and Lehnart, 2007), different peer groups should result in different phenotypic outcomes, such as the first sibling being more antisocial and delinquent than the second.

Specific estimates of shared and nonshared environments tend to vary across phenotypes and depend on sample characteristics (e.g., age range). Even so, when the estimates are collectively analyzed, two consistent patterns emerge. First, most studies have shown that shared environmental estimates range between .00 and .20. Shared environmental influences tend to be strongest early in life and then wane throughout the rest of the life course (Harris, 1995); by adulthood, most studies show that shared environmental effects are near zero (.00). Second, nonshared environmental influences account for most of the phenotypic variance not accounted for by genetic influences. As a result, nonshared environmental influences are typically viewed as falling around .40–.60. It is important to note, however, that the effects of error are captured within the nonshared environmental estimate and, consequently, the nonshared environmental estimate might be inflated (Plomin et al., 2013).

At this point, it is important to address a few of the main criticisms cited against behavioral genetic research. First, scholars are often concerned that because most environments are undeniably similar – for example, everybody brushes their teeth and goes to grade school – behavioral genetics underestimates the influence of shared environments. Although shared environments are generally similar, this is not always the case. Research

has shown, for instance, that parents often treat their children very differently at home (Caspi et al., 2004). Parents may be loving and kind to one child and disinterested and cold to the other. Thus, even the environments found within the same family may appear, at first glance, to be shared environments when they may actually be nonshared environments. Second, and relatedly, some behavioral geneticists have argued that virtually all environments – even if they are purportedly identical – will be interpreted and perceived differently by different people, and thus no environment can truly be considered a shared environment (Turkheimer and Waldron, 2000). Rather, every environment likely falls under the category of nonshared environment. Third, there has been some concerns raised that estimates from behavioral genetic studies are not valid or reliable. Recently, however, this concern has been addressed head-on via mathematical simulations and an exhaustive review of the literature, and the results revealed that estimates generated from twin-based behavioral genetic studies are actually quite accurate (Barnes et al., 2014b; Wright et al., 2015).

With that knowledge in mind, behavioral geneticists use three main types of methodologies that are able to account for heritability, shared environmental effects, and nonshared environmental effects. The first methodology – and the most widely employed design – is the twin-based research design. To understand the logic of the twin design, it is first important to recognize that there are two types of twins: monozygotic (MZ) twins and dizygotic (DZ) twins. MZ twins are, for the most part, genetic clones of each other, whereas DZ twins share, on average, 50% of their distinguishing DNA, meaning they are, genetically speaking, just as similar to each other as are regular siblings. At the same time, MZ twins (from the same twin pair) are assumed to have environments that are no more similar to each other than the environments experienced by DZ twins (from the same twin pair). This assumption – known as the equal

environments assumption – is key to the twin-based approach. If, for some reason, the environments of MZ twins are more similar than the environments of DZ twins, then heritability estimates should be upwardly biased. As long as the equal environments assumption is preserved, then the logic of the twin-based methodology is straightforward: the only reason that MZ twins should be more similar to each other than DZ twins is because MZ twins share twice as much genetic material as DZ twins. When the similarity between MZ twins is greater than DZ twins, genetic influences become stronger and thus heritability estimates are larger. Conversely, as the similarity between MZ twins becomes comparable to the similarity between DZ twins, heritability estimates decrease.

As with all research designs, there are limitations to the twin-based methodology. Perhaps the most salient concern with analyzing samples of twins is whether the equal environments assumption is tenable. Although studies have shown consistently that the equal environments assumption is typically not violated and that even when it is, the effects tend to be minimal (Barnes et al., 2014b; Felson, 2014), there are other methodologies available that can be used to estimate genetic and environmental influences. Of particular importance is that these alternative methodologies do not rely on samples of twins and thus the equal environments assumption is not a concern. One of these alternative methodologies is known as the adoption-based research design. This design analyzes samples of adoptees and then compares the adoptee to their biological parents and their adopted parents on a phenotype of interest. If the adoptee was adopted at birth and had no contact with their biological parents, then the only reason that they should be phenotypically similar to their biological parents is because of the genes they share with them. In contrast, if the adoptee was adopted by parents who were unrelated to them, then the only reason that they should resemble their adoptive parents on phenotypes is

because of the environment. The adoption-based research design has been widely used (e.g., Beaver, 2011; Mednick et al., 1984) and has generated results very similar to those produced by twin studies – that is, that genetic influences are significantly involved in the development of phenotypes (van den Oord et al., 1994).

The adoption-based methodology has been criticized on a number of grounds, including whether the findings generated from such studies would apply to non-adoptees (i.e., the results are not generalizable). There is yet another research design that can be employed, and which overcomes such a criticism: the family-based design. The family-based design is similar to the twin-based design, but instead of focusing only on twins, it analyzes samples that consist of different types of family members. Typically, this means a focus on full (regular) siblings, half siblings, step siblings, and, less frequently, cousins and other relatives. These biological relatives are then assessed to determine (1) how genetically similar they are to each other and (2) how phenotypically similar they are to each other. A genetic effect is detected when phenotypic similarity increases as a function of genetic similarity. Family-based studies have shown results similar to those generated from twin and adoption studies (Plomin et al., 2001). And what is particularly noteworthy to underscore is that family-based studies do not rely on the equal environments assumption being upheld and the results are likely generalizable to a larger swath of the population than are the results of adoption-based studies.

When all of the available behavioral genetic research findings are collated, it is clear that genetic influences account for around half of phenotypic variance and that the (nonshared) environment accounts for most of the remaining variance (Harris, 1995, 1998). These findings are robust, detected across heterogeneous studies, and apply to almost every phenotype ever examined (Polderman et al., 2015). To account for such a consistent pattern of findings, behavioral

geneticists recommend employing a genetically informed research design in research that seeks to explain variability in cognition, attitudes, emotions, or behaviors. This is true even if the focal point of the study is not on heritability but rather on the effects that certain environments might have on the development of a phenotype. After all, if genetic influences are affecting multiple phenotypes in a study (and at least some of these genetic influences are shared across phenotypes), then it is essential to account for such shared genetic influences. Failing to directly account for shared genetic influences in a study can lead to some serious consequences, a topic to which we now turn.

INTEGRATING GENETIC RESEARCH INTO EVOLUTIONARY PSYCHOLOGY

There has been a tremendous amount of genetic research produced demonstrating consistently that genetic variance is at least partially responsible for why humans vary in practically every behavior and personality trait (Polderman et al., 2015; Turkheimer, 2000). Even so, evolutionary psychology has yet to embrace and synthesize the results of genetic studies, despite the potential advancements that can be made by exploring the role of genes in phenotypes of interest to evolutionary psychologists. This is a particularly pressing issue as most research in evolutionary psychology has been estimated using assumptions of the SSSM. Yet, as was previously discussed, the SSSM is unable to account for genetic influences. As a result, findings generated from evolutionary psychological studies that use the SSSM are vulnerable to confounding that is due to unmeasured genetic influences (Barnes et al., 2014a). And, if the results generated from SSSM studies are misleading due to genetic confounds, then the conclusions drawn from those results could be incorrect. Although there are many areas where this is a notable

concern, researchers estimating parenting effects, in particular, have recently begun to recognize that their interpretations may be inaccurate inasmuch as genetics may be influencing both parental attachment and the development of certain phenotypes.

It seems commonsensical that parents play a pivotal role in shaping and molding their children into who they ultimately become. A number of scholars, led by Harris (1995, 1998; Pinker, 2002; Rowe, 1994), however, have challenged this conventional wisdom, based, in large part, on the findings generated from behavioral genetic studies. According to their line of argumentation, most research focusing on the effects of parenting has used the SSSM. At the same time, research has shown that parenting behaviors and the phenotypes that parenting behaviors are thought to cause are under significant genetic influence (Kendler and Baker, 2007; Spinath and O'Connor, 2003). Since parents and their biological offspring share 50% of their genetic material, research studies must account for this shared genetic material (i.e., genetic confounding). Studies that do not control for the shared genetic influences will likely detect an association between parenting behaviors and offspring phenotypes, not because the two are causally related, but because parenting and offspring phenotypes are confounded by unmeasured genetic material (Harris, 1998; Wright and Beaver, 2005). For example, a study might find that parents who are physically abusive (a genetically influenced trait) toward their children have offspring who, on average, are at risk of becoming aggressive and violent. If such a finding was detected using the SSSM, the interpretation of this finding is unclear. On the one hand, social scientists could argue that it is evidence that parenting has a causal effect on children. On the other hand, Harris and others (Pinker, 2002) could argue that the association is spurious and that the only reason parental abuse and offspring aggression are related is because the same genes that are causing the parent to be abusive were

passed along to their child, which caused them to be aggressive, too. To settle this dispute over the correct interpretation, studies would have to use a genetically informative design (e.g., a twin design) that would allow for the estimation of a parenting effect on offspring behavior independent of the effects of shared genetic influences.

A line of research has begun to follow the recommendation of Harris and others (Cohen, 1999) by using genetically informed research designs to examine (and reexamine) the influence that parents and other environments might have on child outcomes. In one of the first studies to do so, Wright and Beaver (2005) examined whether parenting was related to variation in self-control. According to at least one theory (Gottfredson and Hirschi, 1990), the key cause of variation in individual levels of self-control is parental socialization. Parents who rear their children effectively will, on average, have children with higher levels of self-control, whereas parents who rear their children ineffectively will, on average, have children with lower levels of self-control. Indeed, a line of empirical research has provided evidence purportedly supporting this explanation (Cullen et al., 2008), but many of these studies have used the SSSM. Wright and Beaver extended this research by examining the connection between parental socialization and self-control in a sample of children. They first estimated this association using the SSSM, and the results were in line with previous studies—that is, parental socialization had a significant influence on child levels of self-control. Next, they estimated the same models but controlled for genetic influences by restricting their sample to twins. The results of these models revealed that the previously detected parenting influence vanished from statistical significance. In other words, the parenting–self-control association was driven entirely by genetic confounding. Subsequent studies replicated these null results for self-control and other outcomes (Harden et al., 2007; Wright et al., 2008).

Another example of the limitations of the SSSM that has direct application to evolutionary psychology comes from research by Armour and Haynie (2007). They were interested in examining whether the timing of sexual debut was associated with an increased likelihood of engaging in delinquent behaviors. To address their main research question – that is, whether sexual initiation results in elevated risks of delinquency one year later – they employed the SSSM, even though the researchers analyzed data that included twins and siblings. The results revealed that adolescents who experienced sexual activity before their peers were at a higher risk of engaging in delinquent acts. This study seemed to fall in line with the belief that early sexual involvement has a criminogenic effect on adolescents. Of course, critics of the SSSM approach could have easily argued that the results were confounded due to unmeasured genetic influences. In fact, that is precisely what occurred when Harden and Mendle (2011) decided to replicate the original study to determine whether the results would be observed when using a genetically sensitive research design. Using the same data that had been employed in Armour and Haynie's (2007) study, Harden and Mendle (2011) found that after controlling for genetic influences, there was no longer a statistically significant association between sexual activity and delinquency in younger adolescents.

While the previously mentioned studies were not conducted by evolutionary psychologists, there is an emerging group of evolutionary psychologists who are beginning to employ genetically sensitive research designs in their own research. To demonstrate, scholars are reexamining the influence that familial environments have on particular life-history traits. The relationship between father absence and age at menarche, for example, has been documented consistently (Belsky et al., 1991; Ellis et al., 1999), but this association has been detected largely by research using the SSSM. This association has come under attack recently, as research has revealed

that both father absence and age at menarche may share genetic influences and thus may confound the previously estimated associations (Tither and Ellis, 2008). To examine this possibility, Barbaro and colleagues (2017) estimated the degree to which unmeasured genetic factors might account for the observed correlation between the two phenotypic traits of father absence and age at menarche. In contrast to findings generated from studies using the SSSM, they reported that about 90% of the association between the two variables was the result of overlapping genetic factors. These findings indicate that father absence may not be the mechanism responsible for individual variation in menarche timing.

The issue of modularity, as another example, has emerged as a topic of popular debate within the field, thereby providing researchers with a new theory of organismal structure and variation. The theory of modularity, wherein a system is characterized as modular if it can be divided into sets of strongly interacting parts that are relatively autonomous, suggests that genetic associations among traits can be explained by two different phenomena: pleiotropy and linkage disequilibrium. As previously discussed, pleiotropy is an important source of genetic association because it causes traits to be inherited together and, depending on the structure of pleiotropic effects of other contributing genetic markers, to vary together within human populations (Melo et al., 2016). Similarly, linkage disequilibrium refers to the nonrandom association of alleles at different genetic markers, and in the absence of selection, linkage disequilibrium is believed to be eliminated by recombination after several generations of random mating. For this reason, linkage disequilibrium is considered a transient source of genetic association. The picture that emerges from research that tests these perspectives is that most mutational effects are modular, with different sets of genes affecting different sets of functionally and developmentally related traits (Wang et al., 2010). In general, there are many other areas where genetics

research can make important contributions to evolutionary psychology.

Taken together, the findings of studies using genetically sensitive research designs to reexamine associations that were generated from the SSSM have, in certain cases, revealed different results. With the SSSM, environmental estimates have been found to be statistically significant and widespread, whereas genetically informative research designs – designs that produce more accurate parameter estimates – have shown that these environmental estimates are frequently inflated and biased. Of course, these findings have only been produced from a small handful of studies focusing on a small number of associations, and thus much more research needs to be conducted on this topic. That being said, studies that fail to control for genetic influences are at risk of producing findings that are biased, for drawing conclusions that are erroneous, and for testing theories in an incorrect way. It is important to note, however, that while the behavioral genetic framework has utility in studies that seek to explain individual differences, the framework is not always necessary in evolutionary psychology studies of the design features of adaptations that are universal to all humans, such as cheater-detection mechanisms.

CONCLUSION

Evolutionary psychology has made great strides in producing research findings that have contributed to the understanding of a broad swath of human phenotypes, ranging from emotions and behaviors to health and personality traits (Buss, 2009; Nesse, 1990). Research flowing from such studies have elucidated some of the mechanisms that might be at play when it comes to understanding some of the most complex human traits, such as grief, aggression, and sexual behaviors (Buss and Shackelford, 1997; Eagly and Wood, 1999; Nesse, 2005). While not a panacea to this problem, genetic

research holds promise in moving the field of evolutionary psychology forward and providing insights into human phenotypes. That being so, evolutionary psychologists have an opportunity to consider the importance of the findings elucidated by behavioral geneticists, as well as to reflect on the ways genetic findings could be incorporated into theories, explanations, and research questions. While certainly a challenge, there is no doubt that the ultimate payoff will be rewarding to the entire field of evolutionary psychology and will result in more complete, more accurate, and more scientifically grounded explanations of human phenotypes.

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Evolutionary Psychology and Anthropology

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INTRODUCTION

An interest in human evolution has a long history in anthropology, but it was not until the 1970s that an explicitly Darwinian view of human behavior galvanized scholars simultaneously in anthropology, biology, and psychology. The fields of evolutionary psychology and evolutionary anthropology share a theoretical foundation in natural and sexual selection, and both reject what Tooby and Cosmides (1992) have called the ‘standard social science model’ of human nature as a blank slate unconstrained by biology. Yet the early years were also fractured by disputes between the fields. Evolutionary psychologists faulted evolutionary anthropologists (especially human behavioral ecologists) for their assumption that behavior will be fitness-enhancing, arguing that adaptations to the ‘environment of evolutionary adaptedness’ (EEA) could be best understood by focusing on the evolved mental modules themselves (Symons,

1992). Evolutionary anthropologists, in turn, faulted evolutionary psychologists for giving insufficient attention to the trade-offs between different goals required to respond adaptively in different environments (Smith et al., 2001). These differences are waning as evolutionary psychologists expand their attention to environmental sources of variation and as evolutionary anthropologists consider the psychological mechanisms that mediate environmental influences on behavior.

Anthropology is defined by its temporal and cross-cultural breadth, both of which shed light on the contexts in which our psychological adaptations evolved. We begin by considering humans in a phylogenetic context, in order to understand the evolutionary antecedents of our cognitive abilities, prosociality, and psychological adaptations for social learning. We then consider what we can infer about ancestral humans from studies of modern hunter-gatherers and what we can infer about the selection pressures this

way of life imposed on human psychology and behavior. We conclude with a discussion of what anthropology can tell us about two sources of cultural variation identified in evolutionary psychology: ‘evoked culture’ (the responses of a shared human nature to different environments) and ‘transmitted culture’ (cumulative socially transmitted norms; Tooby and Cosmides, 1992). These sources overlap, but the distinction between them is relevant because research into them derives from different anthropological traditions. The anthropological field of human behavioral ecology (HBE) focuses primarily on variation arising from evoked culture, while the field of cultural evolution addresses the mechanics and dynamics of transmitted culture. Both have relevance for evolutionary psychology, as will be shown in the following sections.

EVOLUTIONARY ANTECEDENTS

A phylogenetic approach helps us to distinguish between aspects of human psychology that are ancestral (inherited from the last common ancestor of humans and other apes) and those that are derived (evolved after the separation of human ancestors from other apes). This can help us to understand the context in which important human traits evolved (Silk and House, 2016). For example, humans are exceptionally cooperative creatures. It is possible that human cooperation is built on the same evolutionary building blocks as cooperation in other animal societies – kin selection, contingent reciprocity, and mutualism – and that fundamental elements of the psychological processes that shape cooperation are shared with other closely related primates. On the other hand, humans may have derived capacities for collaboration and altruistic social preferences that are linked to the capacity for cumulative culture and group-level cooperation.

Primate Cognition

Primates have particularly large brains for their body size (van Schaik and Isler, 2012), with humans representing an outlier within the primate order. There is vigorous debate about the selective pressures that originally favored increases in brain size and cognitive abilities in primates and about the most informative measure of brain size (Deaner et al., 2007). Supporters of the ‘social brain hypothesis’ cite evidence that various measures of brain size (e.g., the size of the neocortex in relation to the rest of the brain) are correlated with proxies of social complexity, such as social-group size and number of grooming partners (Dunbar, 1998, 2003). However, others have argued that ecological pressures have favored increases in brain size (Reader and Laland, 2001, 2002). They cite evidence that measures of relative brain size are associated with several measures linked to foraging behavior, such as the amount of fruit in the diet, reliance on extractive foraging, tool use, and social learning (Reader and Laland, 2001, 2002). They point out that most, but not all, examples of tool use and behavioral innovation are linked to foraging.

The selective pressures that favored further increases in relative brain size in our own lineage are not well understood. However, it seems unlikely that environmental factors alone, such as increased seasonality in the environment, favored initial increases in hominin brain size, because other primates that lived in the same environments did not show the same changes in brain size (Elton et al., 2001). Instead, behavioral adaptations related to foraging, including increased reliance on animal prey and tool use, may have favored increases in cognitive ability.

Regardless of whether ecological or social pressures favored increases in primate brain size, it is clear that some monkeys and apes have well developed social cognition (reviewed in Seyfarth and Cheney, 2012). Studies of baboons, macaques, and vervets indicate that these monkeys recognize other

group members as individuals and know something about their own kinship and dominance relationships to other group members. They also know something about the kinds of relationships that exist among others, which is referred to as third-party knowledge. Third-party knowledge extends to kinship relationships and relationship quality. Very little of this kind of research has been done on great apes, but it may be reasonable to assume that their social cognition is at least on par with that of Old World monkeys.

Monkeys and apes seem to have some knowledge of others' mental states or have some theory of others' minds. A series of experiments that were designed to evaluate whether individuals were able to capitalize on discrepancies between their own knowledge and the knowledge of others in a competitive situation suggest that chimpanzees (Hare et al., 2000, 2001; Kaminski et al., 2008) and rhesus macaques (Flombaum and Santos, 2005; Santos et al., 2006) know something about others' knowledge and intentions. Chimpanzees may also know when others hold beliefs that they themselves know to be false (Krupenye et al., 2016).

Differences in the cognitive abilities of humans and other primates seem to be most pronounced in the social domain. Herrmann et al. (2007) compared the physical and social cognition of chimpanzees, orangutans, and human toddlers. There were no substantial differences between species in physical cognition, but the children were considerably more successful than the apes on tasks that required social learning, communication, and knowledge of others' minds.

Cooperation and Social Preferences

Primates cooperate in a number of behavioral contexts in the wild (e.g., social grooming, alloparental care, food sharing, coalitionary support, intergroup aggression), and the distribution of these forms of cooperation is

biased in favor of close kin and reciprocating partners (reviewed by Gilby, 2012; Langergraber, 2012). Cooperation is limited to members of the same social group, with the exception of bonobos. Females from different bonobo groups sometimes cooperate in coalitions against males (Sakamaki et al., 2018), and members of different groups sometimes share food (Fruth and Hohmann, 2018).

However, laboratory experiments point to important differences between chimpanzees and human children. These experiments suggest that chimpanzees are able to master tasks that require two individuals to work together to obtain a goal (Melis and Tomasello, 2013; Melis et al., 2006). However, in contrast to human children, chimpanzees do not prefer collaboration over working alone (Rekers et al., 2011) and collaboration does not prompt chimpanzees to share rewards equitably (Hamann et al., 2011). This suggests that chimpanzees may use other individuals as social tools to gain rewards but may not find collaboration intrinsically rewarding.

Tomasello et al. (2005) hypothesize that these differences between chimpanzees and children in aptitudes for collaboration reflect the fact that humans are uniquely motivated to share the attention, goals, and activities of others. They refer to this property as 'shared intentionality' and suggest that it plays an important role in social learning and teaching, both of which play an important role in cumulative cultural evolution.

A phylogenetic perspective is also useful in understanding the roots of human prosociality and the puzzle of altruism toward non-kin. The motivations that underlie altruism in primates are difficult to study in the field, so researchers began to explore the dimensions of altruistic social preferences in non-human primates using the same kinds of tools that behavioral economists have used to assess human social preferences (Jensen and Silk, 2013; Silk and House, 2016). In these kinds of experiments, animals are presented with a choice between options that have different

outcomes for themselves and others. For example, in a discrete version of the dictator game, subjects are presented with a choice between one option that provides a reward for themselves and an identical reward for their partner and another option that only provides a reward for themselves. These kinds of experimental procedures have been used to ask whether other apes have preferences for outcomes that benefit others, a sense of fairness, or punitive sentiments toward those that have harmed others. The results of these experiments with chimpanzees, bonobos, orangutans, and gorillas are largely negative (reviewed by Jensen and Silk, 2013; Silk and House, 2016), suggesting that they do not have generalized ‘other-regarding’ preferences.

Others have disputed this conclusion. For example, Warneken et al. (2007) created a situation in which the subject could remove a peg, which allowed another individual to open a locked door and gain access to food. These kinds of experiments generally produce positive results (reviewed in Jensen and Silk, 2013). However, Tennie et al. (2016) contend that these results may be related to flaws in experimental design. They designed an experiment in which identical actions by subjects produced different outcomes for others, and they found that chimpanzees were equally likely to perform actions that provided rewards to partners as actions that provided nothing to partners. Their results support the view that generalized ‘other-regarding’ preferences evolved after the divergence from the common ancestor of humans and chimpanzees/bonobos.

HUNTER-GATHERERS AND THE EEA

Evolutionary psychologists define the EEA as the selective context for human adaptations. While for many traits, that context antedates the origin of modern humans, extant hunter-gatherers are our best

ethnographic window into the EEA for human cognitive adaptations, and so ethnographic accounts of hunter-gatherer life are of special importance to evolutionary psychology.

Many problems resulting from the mismatch between forager lifeways and our current environment have been well characterized by evolutionary psychologists – for example, the impact of the media on attractiveness assessments (Kenrick and Guttieres, 1980) and the greater response of fear conditioning and phobias to ancient dangers, such as snakes (reviewed in Öhman, 2009). However, studies of modern foragers can shine a light on evolutionary novelties that warrant more attention than they have received, including the relative roles of mortality and reproduction as selection pressures. Buss’s excellent textbook *Evolutionary Psychology: The New Science of the Mind* (2019) has one chapter on challenges of survival and several chapters on challenges associated with sex and mating. This is both a fair representation of the field and a reasonable reflection of selection pressures in the modern industrial world. However, in foraging societies (and throughout much of human history), staying alive long enough to reproduce has been a major challenge, attained by only about half of individuals born: the life expectancy at birth among unacculturated hunter-gatherers varies from 21 to 37 years, with, on average, 57% surviving to age 15 (Gurven and Kaplan, 2007). Staying alive is a smaller but still significant challenge for forager adults, with implications for human perception, cognition, and emotion as well as social behavior and mate choice. Research on the behavioral immune system and other aspects of evolutionary medicine has begun to address this imbalance, but further collaboration between anthropologists and psychologists to explore the threats to survival in small-scale societies would further advance the field, as would research on the cognitive demands of hunting and gathering and other aspects of forager life.

Formal education is another evolutionary novelty, the implications of which are receiving new attention by evolutionary anthropologists who study how children learn in traditional foraging societies. Children in foraging societies are given considerable autonomy to explore and learn through experience, and 'teaching episodes are generally brief, subtle, indirect, and situated in a present activity (i.e., knowledge is not objectified or intended to be generalizable)' (Boyette and Hewlett, 2018: 771). Formal education, in contrast, relies on directed teaching of abstract, evolutionarily novel tasks (e.g., reading and arithmetic), and even minimal exposure appears to change how we think. Davis (2014) has studied the implications of education among Tsimane forager-horticulturalists and finds that they do not improve with age on a standard test of abstract reasoning (Raven's matrices) as would normally be expected, unless they have received a minimum of three years of formal education. In addition to its implications for human cognition, this is a useful caution for researchers applying and designing psychological instruments for use in cross-cultural studies, because hunter-gatherers will often personalize and attempt to contextualize hypothetical scenarios and abstract questions.

Many aspects of social organization in traditional hunter-gatherer societies also suggest factors of relevance to evolutionary psychology. Although hunter-gatherers are kin-based societies, a cross-cultural study of hunter-gatherer residence patterns found that they live with many individuals they are not genetically related to, which produces widespread networks of interaction across bands for both women and men (Hill et al., 2011). This supports the emphasis placed by both evolutionary psychologists and anthropologists upon the ubiquity of human cooperation beyond kin and the need for mechanisms in addition to inclusive fitness to explain it.

Reciprocal altruism is one such mechanism: generosity to non-kin can be favored, despite the immediate cost, if the favor will

be reciprocated at some future time when the help is needed. But reciprocation cannot be taken for granted, and some of the foundational studies within evolutionary psychology were experiments demonstrating that people have special cognitive adaptations for cheater detection (Tooby and Cosmides, 1992). This emphasis is supported by the importance of reciprocity in hunter-gatherer life. Sharing, and norms that facilitate it, is extensively documented for hunter-gatherers, where it helps buffer unpredictable variation in resources due to the vagaries of weather, animal movements, and luck. Gurven (2006) has shown that food sharing among Ache and Hiwi foragers is contingent on past behavior (people share more with those who have shared with them) and that Ache who shared more than average also received comparatively more food when they were injured or sick (Gurven et al., 2000). This supports reciprocal altruism as the mechanism underlying food sharing, but it remains a contentious issue within anthropology, and some anthropologists think meat sharing is better explained as a form of advertisement (costly signalling), with men showing their skill by deliberately targeting desirable resources that are hard to get (Hawkes and Bliege Bird, 2002; Smith et al., 2003; critiqued in Gurven and Hill, 2009). Because monopolizing resources is challenging in a hunting-and-gathering economy, and because a given item of food is likely to be more valuable to someone who has none than to someone who has a lot, some sharing also occurs through 'tolerated scrounging' (Blurton Jones, 1987). These explanations are not mutually exclusive, and support for the role of reciprocity is robust. In a meta-analysis that reviewed studies of sharing in both human foragers and other primates, Jaeggi and Gurven (2013) found that reciprocity explained food sharing even when controlling for the effects of kinship and tolerated scrounging, with all three processes being important predictors for both human and non-human primates.

They suggest that scorekeeping (required to know who to cooperate with) may take place through mechanisms that are not cognitively demanding – a topic deserving of further research within evolutionary psychology.

While research on hunter-gatherers can help illuminate the selection pressures and evolved psychological responses to a foraging way of life, it is worth remembering that all such groups today are in contact, directly or indirectly, with the world economy. It is also a biased sample, consisting chiefly of hunter-gatherers who live as small, egalitarian bands in marginal habitats. Historical and archaeological evidence suggests that hunter-gatherer fishermen who formerly inhabited resource-dense coastal and riverine areas lived in comparatively dense, sedentary communities, with a hierarchical social organization more similar to that of ethnographically described agricultural chiefdoms.

CULTURAL VARIATION

Henrich et al., (2010) documented that Western, educated, industrialized, rich, and democratic (WEIRD) societies are psychological outliers in many respects including visual perception, fairness and cooperation, and spatial frames of reference. Their first example was the large cross-cultural variation in the Mueller-Lyer optical illusion, which was most extreme in the US sample and absent among !Kung hunter-gatherers. This cross-cultural discovery was made in the 1950s by a fruitful collaboration between an anthropologist (Herskovitz) and two psychologists (Segall and Campbell), who asserted that their cross-cultural experimental study ‘by the very nature of the problem under investigation, had to be a joint anthropological-psychological undertaking’ (Segall et al., 1966: vi). They were inspired to do this by the work of anthropologist-psychologist W. H. R. Rivers, who

had discovered the anomaly a half-century earlier in his ethnographic work. Segall et al. (1966) suggested that the illusion arose from the perceptual bias of growing up in a carpentered world – an evolutionarily novel aspect of our modern environment that is so ubiquitous we take it for granted.

The psychology subject pool may, therefore, be an odd population from which to generate insights about human universals. In recognition of this, there have been a growing number of projects that incorporate the backgrounds and insights of both anthropology and psychology in studies of human cognition, morality, and social behavior in traditional anthropological populations. Some of these studies have supported the generality of results from WEIRD societies. For example, Shiwiari forager-horticulturalists respond the same way as Westerners to social-contract problems, supporting the argument for a universal cheater-detection module (Sugiyama et al., 2002). Males are more risk-seeking than females among Hadza foragers, as they are in WEIRD societies (Apicella et al., 2017). And men’s better performance on some spatial tasks is not limited to WEIRD societies but is found also in Hadza foragers (Cashdan et al., 2012) and Twa forager-agropastoralists (Vashro et al., 2016). But the magnitude of sex differences in spatial behavior and cognition varies across cultures, due to variation in habitat, subsistence, and mating patterns (Cashdan and Gaulin, 2016). Cross-cultural variation is typical in these studies, and some is counter-intuitive; for example, US participants offer more in an anonymous sharing game than people in small-scale societies who depend heavily on sharing in daily life, provoking new ideas about the cultural evolution of sharing norms in market-integrated societies (Henrich et al., 2010). Explaining cross-cultural variation requires theory from behavioral ecology (to understand the patterning in evolved culture) and from cultural evolution (to understand transmitted culture), the topics to which we now turn.

EVOKED CULTURE: ENVIRONMENTALLY CONTINGENT STRATEGIES

The concept of evoked culture (the responses of a shared human nature to different environments) is closely related to the biological concept of reaction norms (the pattern of expression of a genotype across a range of environments). Although individuals differ in both their baseline levels of a trait and in their degree of responsiveness to the environmental influence, the general shape of the response is an evolved feature, and so understanding it needs to be part of evolutionary psychology. Anthropologists, particularly those working in the tradition of human behavioral ecology and life history theory, have much to contribute to this. HBE uses theory from evolutionary ecology to model how trade-offs differ in different environments, leading to different optima.

These trade-offs are not unique to humans, and so HBE has drawn from ecological theory in efforts to understand them. Mating strategies are a case in point. Oklahoma soapberry bugs show a norm of reaction in response to sex ratio, with mate-guarding increasing as the ratio of males to females increases. A male may stay attached to his mate after insemination to guard her against other suitors, and where there are more males than females, this makes adaptive sense. But if male competitors are less numerous (lower sex ratio), males are more inclined to leave after inseminating the female and search for another mate (Carroll and Corneli, 1999). Oklahoma bugs, unlike those in Florida, evolved this responsiveness because sex ratio is variable in that environment. This classic study is unusual because Carroll and Corneli (1999) were able to show that the variation was due to the differential expression of a common genotype rather than to genetic differences between individuals, something rarely possible within evolutionary anthropology or psychology. Instead, human

behavioral ecologists implicitly assume this to be the case, in order to examine the costs and benefits that would make a particular facultative response adaptive.

Human sex ratios are also variable, and studies from evolutionary psychologists (Schmitt, 2005) and evolutionary anthropologists (Schacht and Borgerhoff Mulder, 2015) have converged on the conclusion that humans show a reaction norm similar to that of soapberry bugs: a scarcity of males is associated with short-term, low-investment matings. Human mating differs from that of soapberry bugs in that paternal investment is expected in middle-class WEIRD societies, and evolutionary psychologists have suggested that female preferences may drive this pattern: women have more bargaining power when men are abundant, and human males may need to invest in order to secure a mate. However, female choice and paternal investment are highly variable across societies, and some anthropologists have argued that the pattern depends more on male mating opportunities – as with the soapberry bugs – than on paternal investment. In a comparison of four hunter-gatherer societies, Blurton Jones et al. (2000) found that marital instability was associated more with a man's opportunities for new matings than with his effects on child survivorship. In a context where investing men are scarce, polyandrous mating may also benefit females by enabling them to secure additional resources.

This axis of variation is a cornerstone of 'sexual strategies theory' (Buss and Schmitt, 1993), with implications for sociosexual attitudes and behavior, sexual jealousy, mate preferences, and mate-attraction strategies. What HBE anthropologists contribute to this endeavor, in addition to a more explicit use of ecological theory, is the broader range of behavioral variation documented when one studies non-literate and small-scale populations. For example, evolutionary psychologists have shown that men are more likely than women to be jealous about sexual infidelity, which reduces their confidence in

paternity, while women are more likely than men to be jealous about emotional infidelity, which risks the loss of potential paternal investment (Buss et al., 1992). This pattern has been found to be robust but not invariant. In 9 of 11 chiefly non-industrial societies, men reported more jealousy than women about sexual as opposed to emotional infidelity, in response to a forced-choice question (Scelza et al., 2020). However, the considerable cross-cultural variation in paternal investment suggests that we should find a norm of reaction in the magnitude of sexual jealousy, an expectation supported by the finding that sexual infidelity was viewed more harshly by men in cultures where they invest more in children (Scelza et al., 2020).

Facultative variation in reproductive strategies is addressed more broadly within the framework of life history theory, which considers how trade-offs between growth and reproduction, and mating and parenting effort, are optimally allocated given environmental conditions. Building on early work by the anthropologists Draper and Harpending (1982), anthropologists and psychologists have provided evidence that growing up in father-absent homes (Draper and Harpending, 1982; Ellis et al., 2003) and harsh and unpredictable environments (Belsky et al., 2012; Belsky et al., 1991; Quinlan, 2003) is associated with earlier reproduction and other traits associated with a life history biased toward reproductive effort. Questions remain regarding the degree to which these associations reflect genetic confounds rather than environmentally contingent adaptations (Barbaro et al., 2017). Evidence in support of the latter comes from studies that compared biological sisters differing in the length of their exposure to low-investment fathering (DeLPriore et al., 2019; Ellis et al., 2012; see also Gaydosh et al., 2018, for a molecular genetic study). However, controlling for these effects is challenging.

A further complication is that the importance of paternal support and the reasons it might be absent differ across cultures.

Anderson (2015) found some support for the father-absence hypothesis among white but not black South Africans, perhaps because the extended family structure of black South Africans meant that other male relatives were often present even if the father was not. In Bangladesh, women who were father-absent due to divorce or desertion reproduced at earlier ages, consistent with findings from Western studies. However, women whose fathers were absent due to migrant labor showed the opposite pattern, with a later age at marriage and first birth. Those women benefit economically from the remittances their migrant fathers send home, which are invested in education, and so may benefit from a slower life history (Shenk et al., 2013). Despite these cautions, evolutionary anthropologists and evolutionary developmental psychologists share the perspective that fast life history traits, which are often viewed as undesirable (early sexual activity, small body size, short time-horizons, teenage pregnancy, unstable pair-bonds, etc.), are best understood as evolved adaptations to the constraints and opportunities of the local environment.

TRANSMITTED CULTURE AND CULTURAL EVOLUTION

Behavioral ecologists and evolutionary psychologists work from a similar set of evolutionary theories (for example, sexual selection, life history theory, and kin selection), but anthropologists interested in cultural transmission and cultural evolution argue that these theories are insufficient to understand the uniquely human breadth of behavioral adaptations (Boyd and Richerson, 1985; Henrich and McElreath, 2003; Richerson and Boyd, 2005). These theorists have developed additional theoretical models to understand how 'transmitted culture' evolves and how evolved psychological mechanisms make this possible and shape its spread.

Evolutionary psychologists have much to contribute to this field, because cultural transmission is both based in and biased by our evolved preferences and predispositions. In this section, we review some of the content and context biases that shape cultural transmission and the ways in which preferences are learned and taught, with the hope of furthering collaboration between these two disciplines. However, the readiness with which humans learn socially also leads to derived human characteristics not easily explained by the theoretical toolkit used in evolutionary psychology, and we review these briefly also, because they may lead to outcomes that run counter to expectations based solely on the process of genetic evolution. These include altruistic behaviors not easily explained by either kin selection or reciprocity, some of which may spread despite deleterious effects on individual fitness. They also include norms that lead to culturally distinct patterns of mating, cooperation, and competition. Because these also become the environment to which our evolved psychology must respond, we discuss briefly how cultural and genetic processes differ, and how they may interact.

Content, Context, and Teaching in Transmitted Culture

Transmitted culture is information acquired from others through social transmission, and one way in which it spreads is through selection for certain types of particularly ‘sticky’ content. This is the type of cultural transmission most familiar to evolutionary psychologists (e.g., Tooby and Cosmides, 1995). Cultural content that is more attention-grabbing, more memorable, or more likely to be passed on to others will survive and spread further and faster than content that does not possess these traits (Dawkins, 1976; Sperber, 1996). These preferences for certain types of content are known as content biases. Many of these content biases are believed to have

evolved because they increase attention to fitness-relevant information, such as what is potentially dangerous, or reputational information about those around you.

Because humans live in diverse physical and social environments, content biases function as domain-specific mechanisms for acquiring locally appropriate cultural information. This allows for heightened attention for learning such things as which animals in the local environment are dangerous (Barrett and Broesch, 2012) and socially strategic information (gossip) about others in one’s community (Mesoudi et al., 2006). Not all known content biases fit this description, and some content may gain attention or memorability as a byproduct of other cognitive systems (e.g., Boyer, 1994).

Though these biases allow for learning, they are still constrained and can become maladaptive when that content has lost its fitness relevance. Consequently, we remain more afraid of snakes and spiders than the much deadlier cars and swimming pools. Their rate of transmission can continue to increase even when the information conveyed is no longer of value, as is seen in the spread of disgusting or shocking urban legends (Stubbersfield et al., 2015). Similarly, content biases have been shown to play a role in the spread of viral media and fake news, where information about unlikely dangers or celebrity gossip spreads at a faster rate than other, potentially more reliable, information (Acerbi, 2019).

Content biases alone cannot account for the variety of ways humans select and transmit cultural information (Henrich et al., 2008). A different set of evolved cognitive biases – context biases – rely on our species-specific social learning abilities and play a far more important role in how humans transmit culture. Context biases are tendencies to preferentially learn in certain contexts and from certain people (Henrich and McElreath, 2003). This type of selective learning helps us filter our opportunities for social learning and increases the likelihood that we are

learning the highest quality information for a given environment.

To this end, we pay more attention to, and are more likely to learn from, certain types of people, such as successful or prestigious people (prestige bias; Chudek et al., 2012; Henrich and Gil-White, 2001). This increases the probability that we are learning the most successful content. We also learn preferentially from those who behave in a way that credibly supports our beliefs (credibility-enhancing displays; Henrich, 2009; Kraft-Todd et al., 2018). This is important particularly for costly or potentially costly behaviors, such as participating in religion, where the costs of time and tithes are only worthwhile if the beliefs and behaviors are shared and supported by the rest of the community (Willard and Cingl, 2017). We are also more likely to learn things that are endorsed by our community at a high frequency, and thus we adopt beliefs and behaviors that are widespread in the population (conformity biases; Henrich and Boyd, 1998; Nakahashi et al., 2012). The shared knowledge of the group is more than you can learn in a lifetime of trial and error on your own.

These and many other context-based learning biases have been supported by research in developmental psychology. For example, children preferentially learn from people of the same gender (Slaby and Frey, 1975) or with the same accent (Kinzler et al., 2011; Kinzler et al., 2009). When framed in cultural evolutionary theory, these learning biases are part of a set of evolved traits that help us ensure we are learning the norms of our community (Chudek and Henrich, 2011) and help us form recognizable and distinct cultural groups (Moya and Henrich, 2016).

Learning is only one piece of the transmission puzzle; humans also teach. Teaching serves as a way of narrowing the variety of inferences that a learner can make, thereby increasing the fidelity of transmission (Kline, 2015). Teaching, when looked at through an evolutionary lens, is a cooperative dilemma. Though there are clear benefits

to the learners, there are costs associated with teaching, such as reduced productivity (Hoppitt et al., 2008; Thornton and Raihani, 2008). These costs need to be countered for teaching to evolve. Looking at teaching in this way allows us to make predictions about where and when teaching should appear – for example, when it should take place within the family and be accounted for by inclusive fitness and when it should be done by experts and paid for with reciprocity or deference (e.g., Kline et al., 2013).

Teaching and learning biases help us to increase the probability that we are learning information with the highest fitness relevance for our environment. In doing this, they create distinct groups that share cultural knowledge. These mechanisms reduce the variance in the cultural phenotype of a social group by increasing the likelihood that everyone is learning similar information. These behaviors become ‘norms’, and they are enforced within societies through punishment of defectors (Chudek et al., 2013). This combination of norms and punishment allows groups to maintain adaptive knowledge and behaviors, particularly cooperative norms that allow people to live effectively as a group. Chudek and Henrich (2011) outlined how this type of ‘norm psychology’ could evolve through selective pressures for more coordinated and cooperative societies. The enforcement of different norms within different societies creates conditions where the variation in behaviors is mostly found between groups and not within them, and this is the origin of the cultural differences we see between different societies.

Cumulative Cultural Learning and Complex Culture

Learning biases and a norm psychology create the selective learning conditions necessary for cultural evolution. Error in transmission and innovation introduce variation into the selection process, and the impact

these variations have on fitness governs their future survival and transmission. Together, this leads to a process of cumulative cultural learning (Boyd et al., 2011). With each new generation, the innovations of the previous generation are accumulated, and the best tools and techniques are adopted and passed on. As these innovations accumulate, we end up with cultural content that is too complex for any single person to learn on their own in one lifetime (Tennie et al., 2009). Though simple technology like using a rock as a hammer can be recreated by any of us (Reindl et al., 2015), most of even the relatively simple cultural toolkits are beyond what we can create if left on our own.

These processes are largely comparable to those of biological evolution and are modeled in a similar way (Boyd and Richerson, 1985; Mesoudi et al., 2006). There are some notable differences. Unlike biological inheritance, cultural content is not always transmitted vertically from parent to offspring. It can also be transmitted horizontally from peers and obliquely from non-relatives in the previous generation. These modes of transmission, though different than what we see in biological evolution, can be modeled in a similar way to genetic inheritance (see Cavalli-Sforza and Feldman, 1981). Additionally, cultural content does not reduce to discrete replicators like genes and, through incorrect learning or memory lapses, is often not faithfully transmitted from one generation to the next (Sperber, 1996). These factors are also easily modeled within an evolutionary framework (Henrich et al., 2008). Discrete replicators are not a necessary assumption for selection (Henrich and Boyd, 2002), and the non-discrete traits used in models of cultural evolution are not much different from recent re-conceptions of genetic inheritance (Laland and Brown, 2011; Mesoudi et al., 2006; Portin, 2002). Though there must be fidelity in transmission for cultural evolution to take place, errors in the learning process introduce variation, which is an important part of innovation and

the evolutionary process (e.g., Eerkens and Lipo, 2005). Together, these processes mean that culture can adapt to new physical and social environments much faster than genes and can create large group differences within our single species. This has potential implications for how evolutionary psychologists understand ethnocentrism and group differences. For example, both evolutionary psychology and evolutionary anthropology have suggested that cultural markers, such as clothing and visual cues to occupation, are an important part of reinforcing ethnic-group distinctions, with implications for the stereotyping of such groups (Kurzban et al., 2001; Moya and Boyd, 2016).

One major difference between culturally evolved belief systems and biologically evolved psychological adaptations is that the former can spread because of benefits that happen at the level of social groups (Henrich, 2004; Richerson et al., 2016). In societies like our own, we interact with people who are not kin, not even fictive kin. Often, these are people we have no reputational information about and are unlikely to interact with again on a daily basis. Reciprocity and inclusive fitness cannot produce cooperation in these contexts, but culturally evolved belief systems, like religion, can. Growing evidence suggests that the belief in gods that will punish people who violate social norms was one of the cultural innovations that have enabled human groups to function as large-scale societies (Norenzayan et al., 2016). This helps to solve the large-scale cooperation problem, through the belief that breaking the rules will lead to punishment, even under conditions where social punishment is unlikely or impossible. If you steal something from a stranger, and no other person finds out, your god will know and punish you in either this life or the next. These beliefs have been shown to affect behavior enough to increase cooperation with anonymous strangers across a wide range of societies (Lang et al., 2019). The willingness to cooperate with anonymous strangers increases as the endorsement

of the moralizing and punishing tendencies of god(s) increases (Purzycki et al., 2016).

These beliefs can solve collective-action problems that can endanger the survival of the group. In Bali, for example, a complex system of water sharing among rice farmers is guided by religious beliefs and rituals (Lansing, 2012). This system effectively manages pests and maximizes the group yield by discouraging farmers close to the water sources from hoarding water to maximize their own crops, through a fear of the supernatural consequences of violating the religious rules.

Cultural evolution is a process that is not always tightly linked to biological fitness, and it can produce traits that are maladaptive to the individual. Some, though not all, of these maladaptive traits are maintained because they benefit the larger group, a factor not yet incorporated into mainstream evolutionary science. One possible example is the extreme ritual behavior found in some religions. In Mauritius, religious rituals require participants to put skewers through their skin, walk on the sharp edges of swords, and carry extremely heavy ritual objects to high temples in the heat of the summer sun (Xygalatas, 2012). Participation and viewing others participating in these rituals have been shown to increase cooperative behavior in the group, thus allowing for more successful groups (Xygalatas et al., 2013). These behaviors are maintained through a type of norm enforcement: although those that participate in these rituals do gain some individual benefits, such as prestige, participants are driven by the belief that they will receive a supernatural reward or punishment based on their actions, allowing for additional benefit to accumulate at the group level.

The enforcement of cultural norms can lead to costly individual behaviors across a number of domains, including war. Zefferman and Mathew (2015) give a clear example of this type of selection in Turkana warfare. Turkana pastoralists cooperate widely in warfare against neighboring groups, although the

costs of participation in injury and death – as much as 50% of adult-male mortality is due to war – are borne by individuals while the benefits accrue to the raiding group. In these conditions, strong normative rewards and punishment create strong support for war among group members. Groups that are more successful at raids, requiring a high level of within-group coordination and cooperation, end up with more wealth at the expense of competing groups. In both this and the ritual example above, the benefit of status given to the individuals who participate can offset much of the cost.

CONCLUSION

Evolutionary psychology is an inter-disciplinary field, and anthropology has contributed to it in various ways. To understand the evolution of human psychology, we need to know its phylogenetic antecedents – the features we share with other primates and how and why human psychology differs. Because human psychology evolved to be flexible in adaptive ways, we need to evaluate theories against the full range of human experience. In this effort, anthropology's ethnographic breadth and ecological perspective are essential. Evolutionary psychology must also consider the cumulative nature of complex cultural adaptations, which can lead individuals to make choices that cannot be understood with the theoretical tools of biological evolution alone.

At the same time, evolutionary anthropologists need input from psychology. Selection acts on the preferences and other psychological mechanisms that influence behavior, and so evolutionary anthropologists need to understand the psychological mechanisms that link selection pressures to behavioral outcomes. Cognitive neuroscience can help us understand the process of cultural evolution by studying the cognitive and neurobiological mechanisms that underlie social learning

strategies (Kendal et al., 2018). Furthering such cross-disciplinary integration will be essential for the future of the evolutionary human sciences.

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Evolutionary Psychology and Archaeology

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INTRODUCTION

Although speculation concerning the human mind and its origins within a modern evolutionary framework can be traced to the latter half of the 19th century, as is evidenced by Alfred Wallace's (1864) and Charles Darwin's (1888) writings, the development of scientific fields dedicated partly or entirely to broaching the evolutionary nature of the mind do not date until nearly a century later. Among the uniquely positioned scientific disciplines that emerged in order to shed light on the subject are: paleoneurology,¹ and the related field of evolutionary neuropsychology (see Coolidge and Wynn, Chapter 4), primatology,² evolutionary psychology, and archaeology (Wynn, 2017).³ These disciplines are all relevant to the evolutionary study of the mind as they function together to check and balance our interpretations of how the mind emerged, moving us ever closer to a more accurate understanding of the mind in the past. Archaeology, in particular, is indispensable in informing this

endeavor as it is the only discipline with direct access to traces of behavior from which one can infer cognitive processes in the past. And evolutionary psychology, for its part, provides a powerful framework for explaining how the psychological traits associated with these cognitive processes arose. Due to the complementary nature of the two disciplines, the interactive role of evolutionary psychology and archaeology is especially crucial for understanding the mind in the past and therefore will form the focus of this chapter.

The relationship between evolutionary psychology and archaeology has been an inextricable one. The collaboration between these two fields began in the 1990s and has proven to be a productive union for comprehending how certain properties of the human mind appeared, a process that began long ago in our lineage's past. In this chapter, the roots of the relationship between evolutionary psychology and archaeology will be recounted. This will be followed by a discussion of the main areas of inquiry on which both disciplines

have collaborated. Finally, the chapter will discuss a contending framework to evolutionary psychology known as material engagement theory (MET), which has recently gained traction in the archaeological study of the human mind. This contending framework will be critically examined, as it stands in opposition to the central nativist premise of evolutionary psychology and therefore questions evolutionary psychology's role in mind-related archaeological studies.

DARWIN, COGNITIVE EVOLUTION, AND ARCHAEOLOGY

When modern evolutionary psychological thinking arose in the late 1980s and 1990s (Barkow et al., 1995; Cosmides and Tooby, 1989; Tooby and Cosmides, 1989) out of earlier calls for the study of psychological states to be placed on a Darwinian foundation (Ghiselin, 1973), it became clear that evolutionary psychology, as a field of inquiry, would need to rely on archaeological research. The realization that evolutionary psychology would be dependent on archaeology, however, was not a new notion, as it was foreshadowed over a century earlier. Indeed, Charles Darwin (1872) and to a lesser extent Alfred Wallace (1864: clxvi-clxix) were among the first evolutionists to appreciate the importance of archaeological data for understanding the complexity of human evolution, particularly with respect to the development of mental faculties. Archaeological findings, such as those reported by John Lubbock (1865, 1870) and others, for example, had prominently figured into Darwin's (1872) research on the nature and evolution of the mind, known also as the study of *cognitive evolution*.

Archaeologists, for their part, have always been, if not completely accepting, at least sympathetic to evolutionism in general and its role in explaining cultural and cognitive developments evidenced in the archaeological record. By the mid-20th century, archaeologists would

begin to play a more active role not only by providing the data that were inherently relevant for the study of cognitive evolution, but by devising methods and theoretical frameworks for interpreting archaeological data in ways that could shed light on the mind in the past and how it evolved.

One of the most prolific of these archaeologists was the French archaeologist Andre Leroi-Gourhan. Leroi-Gourhan (1993) was the first to devise and advocate a method of analysis that he believed could glean important insight into the mind and its development. This method, which continues to be used by archaeologists, is known as *chaîne opératoire* (translated as 'operational sequence') and entails the study of the sequential organization of actions involved in toolmaking and other activities.

To go along with *chaîne opératoire*, Leroi-Gourhan (1993) developed a theoretical framework of his own that harbors certain notions that could be considered compatible with evolutionary psychology. A case in point is his assumption of the fundamental role of innate aptitudes in human behavior. Although Leroi-Gourhan believed that operational sequences, such as those involved in the manufacturing of a tool or the performance of a musical piece, are culturally learned behaviors and thus reliant on a particular environment for forming the memory traces needed for their expression, genetic aptitudes are at the core of these behaviors seamless execution. He believed that an individual is "gifted" with particular hardwired aptitudes and, furthermore, that a conducive learning environment is required to trigger these aptitudes. According to Leroi-Gourhan (1993: 224–225), it is because of the inextricable connection between genetic aptitudes and environment that humans invest so significantly in vocational guidance in their societies. Here, not only is it implied that Leroi-Gourhan believed that people are attuned to genetic aptitudes at an individual level, but that this allows people then to foster these aptitudes.

In line with his theoretical framework that emphasizes the joint role of innate aptitudes and the environment, Leroi-Gourhan (1993) also proposed that every operational sequence is undergirded by a syntax. This syntax, it was asserted, provides a certain amount of structure to the order of operations in the same way that the syntax of a language does for words in a sentence. Indeed, he believed that the syntax for both language and technical motor sequences were derived from the same pathway in the brain (p. 115). It was this latter suggestion that allowed him to claim that based on his analysis of ancient toolmaking operational sequences certain milestones concerning the development of language were reached in our evolutionary past (Leroi-Gourhan, 1993: 114–115). Although some of his theories and specific assertions have been questioned (Trigger, 1989: 395; Ucko and Rosenfeld, 1967), Leroi-Gourhan represents the first of a long line of cognitive evolutionary archaeologists who have taken seriously the notion of an innate relationship between toolmaking and language (Gibson et al., 1994; Hewes, 1973; Stout et al., 2008).

COGNITIVE EVOLUTION AS UNDERSTOOD BY DARWIN AND EVOLUTIONARY PSYCHOLOGISTS

Before the relationship between evolutionary psychology and archaeology is discussed, it is worth distinguishing the traditional Darwinian view of cognitive evolution, with which many archaeologists would tend to agree, from the neo-Darwinian view advocated by evolutionary psychologists. This clarification is important in order to see specifically how the interaction between archaeology and evolutionary psychology has played out.

Darwin and Cognitive Evolution

For Darwin (1888), the evolution of the human species could most aptly be described

as a synergism with roles played by the human body (or neurophysiology), the mind (or cognition), culture, and environment. There is little doubt that Darwin believed, like many evolutionary psychologists today, that among these changing variables, most central was the body, inclusive of the brain – the location of the human mind and the executive seat responsible for behavior and ultimately culture. However, what is also clear is that Darwin did not view the mind as coextensive with the brain (1888: 54–55). For this reason, it can be inferred that Darwin did not regard cognitive evolution as something that could be studied by examining changes in the brain alone, a point that will be revisited after discussing the relevance that the body, particularly the brain, held for Darwin's view on cognitive evolution.

Darwin (1888: 54) assumed that along with mental faculties, the properties of the brain also would have evolved through natural selection. Changes in brain size and brain-to-body size were the properties most often cited as signifying changes in mental or cognitive capabilities. Darwin would eventually be vindicated in making this assumption, but it would not be until the mid-20th century that his assertion would be placed on firmer ground. It was Santiago Ramón y Cajal's (1894) and Camillo Golgi's (1898) groundbreaking research on neurons and Donald Hebb's (1949) innovative studies on how the synapses of neurons are strengthened through persistent stimulation that provided the neurophysiological backing for natural selection's proposed role in cognitive evolution. These studies were among the first to embody cognition by suggesting that a cognitive task is accomplished through strengthening the synapses among neurons through continuous stimulation and through neural growth. In this way, a cognitive task involving learning to form associations between two concepts, such as 'color' and 'edibility' – a task which would have been essential for discerning what could be eaten in our progenitors'

environment in the distant past – effectively would have amounted to neural growth and pathway development among the respective assemblages of neurons embodying those concepts. Those individuals who were particularly suited to such a cognitive task as that described would have harbored the requisite associated neural cells and pathways, and they would have had a distinct advantage over others in terms of survival and passing down this cognitive trait by way of its heritable neurophysiological basis. It follows from this view on the correspondence between cognition and neurophysiology that one can infer from certain properties of the brain, such as more developed lobes, that certain cognitive tasks or capabilities were being enacted in order to aid humans' survival and reproductive success in the distant past.

As culture began to play a bigger role in how hominins adapt to the environment, the cognitive traits that intersect with culture along with their neurophysiological bases would have been naturally selected and passed down. Darwin (1888: 127) posited that human culture constitutes what can most accurately be described as an extrasomatic means of adapting to a particular environment, and includes such things as weapons, tools, and strategies. Humans do not only adapt to their particular environment directly through beneficial physiological traits, but they utilize their mental faculties to form culture outside of their bodies, which, in turn, facilitates adaptation. Mental faculties that contribute to conceiving of and promulgating culture vary from one individual to the next. Moreover, those mental faculties that have a role to play in the invention or proficient employment of culture in the form of tools or even art (Mendoza Straffon, 2016), for example, consequently contribute to the reproductive success of the individuals who host these mental faculties. In this way, mental faculties were seen by Darwin as traits that could be passed down to subsequent generations and could evolve. In short, Darwin was suggesting that natural selection acts on mental

faculties, albeit *insofar* as they produce or help to wield culture. Here, the key mechanism of cognitive evolution is natural selection, and it is only when the cognitive traits help produce or maintain the cultural means for increasing reproductive success that cognition evolves.

Darwin envisaged cognitive evolution to be an intricate process in which culture and cognition (accompanied by the associated neurophysiological substrate) interact. Like Wallace (1864), Darwin (1888) asserted that culture is a product generated and manipulated by way of humans' mental faculties or cognitive capabilities. For Darwin (1888: 129), culture was active in the sense that he believed culture acted on cognition to afford advantages to human fitness, thereby increasing the chances that one's descendants would inherit the cognitive traits associated with the production and utilization of the culture in question. Phrased differently, the relationship between culture and cognition was believed to be reflexive and perpetual. Cognition is responsible for producing and utilizing culture at the same time that culture ensures that the needed cognitive capabilities persist and proliferate. The outcome is that culture together with cognition form a shielding that effectively buffers one from having to directly adapt to the local environment. The result over the long term is that culture and cognition act together to obviate the need for human physical traits—with the exception of the brain—to change in lockstep with the environment, even as one's cognitive traits and associated culture continue to evolve.

Evolutionary Psychology and Cognitive Evolution

Evolutionary psychology takes a view that is compatible with Darwin's original premise, albeit with certain modifications. The view that culture and cognition are fundamentally dependent on natural selection for their perpetuation is maintained in

evolutionary psychology. However, evolutionary psychology introduces a unit of analysis that is not found in Darwin's account of cognitive evolution, namely the *psychological mechanism* (Buss, 1995: 5–6), or what I will refer to as a *psychological trait* to conform to the terminology I have been using above. A psychological trait can most adequately be described as an evolved functional unit that consists of an information processing system evolved to facilitate a response to a specific environmental input. The idea is that upon detecting a content-specific signal from the environment, the trait acts to regulate the appropriate physiological response. Understanding the mind in this way helps explain certain phobias, preferences, motivations, and personalities that people have today. An often-used example of a psychological trait is the fear of snakes, the function of which is to prevent being bitten by a snake through eliciting a flight response when a snake enters one's field of view (i.e., the stimulus). In contrast, Darwin understood mental faculties to be content-general, closer to what we refer to today as cognitive capacities and capabilities (e.g., general intelligence, memory, language, imagination, attention, conception, abstraction, reasoning, and self-consciousness) which, of course, he considered traits that could evolve through natural selection.

Most distinctive is Darwin's view of culture. For Darwin, the concept of culture is central to cognitive evolution since only culturally-relevant cognitive traits are passed down. In other words, although culture is inextricably connected to cognition by being acted upon jointly by natural selection, culture is its own entity separate from cognition. In evolutionary psychology, culture is seen simply as a byproduct of psychological traits, an epiphenomenon with little reflexivity in contributing to human fitness. This, of course, diminishes the role of culture in driving cognitive evolution, as well as avoids speaking of culture as extrasomatic and adaptive, a view

that runs counter to how Darwin envisaged culture.

With these modifications, evolutionary psychology has emerged as a subfield that explores how psychological traits in the human species can be interpreted as the result of adaptations to ancient environmental conditions, and it has contributed much to the study of cognitive evolution. In its traditional incarnation, known as the Santa Barbara School of evolutionary psychology, it was assumed that the Pleistocene was the time frame in which most human psychological traits evolved. It was further assumed that the Pleistocene was a time in which environmental change took place slowly and steadily in East Africa. In assuming this, evolutionary psychologists of the Santa Barbara School suggested that it was during this time that most if not all human psychological traits had the opportunity to evolve through natural selection. By the end of the Pleistocene, it was asserted that the environment began to change rapidly, so rapidly in fact that natural selection began to play less of a role in shaping psychological traits and, for all intents and purposes, cognitive evolution ceased (Bolhuis et al., 2011: 1). According to the traditional evolutionary psychological view, therefore, the modern human mind survives as a vestige from the Early to Upper Pleistocene. This is a mind fitted with innate modules that were programmed to thrive in East Africa, in what is generally taken at that time to be a savanna-like environment.

The roots of the modular model of the mind, in turn, can be traced to Fodor's (1983) two-tiered design, which envisioned human perception as a processing unit separated from a central general-purpose processor that primarily deals with conceptual information. The two-tiered design would have been advantageous from an adaptive standpoint as it could process information more efficiently than could an all-purpose processor. Eventually, more units, or modules, dealing with conceptual information were proposed, making for an even more efficient

system for processing information (Tooby and Cosmides, 1992); these modules today form the basis for the evolutionary psychological model of the mind. These domain-specific modules, it was suggested, would have evolved to solve specific types of problems upon which the perpetuation of our lineage depended. Accordingly, the psychological traits of humans today exist as naturally selected problem-solving traits from an ancestral past that have become hardwired in the human brain.

Beyond Natural Selection

Since the advent of the modern evolutionary synthesis (Huxley, 1942), mechanisms integral to biological evolution other than natural selection, such as mutation, also have been deemed feasible mechanisms for explaining how cognition evolves. Consideration of these other mechanisms, in turn, has percolated into both evolutionary psychology and archaeology. In the case of mutations, it has been suggested that anomalous alterations to the brain could instigate mental or cognitive changes responsible for a number of cultural developments that have been proposed by archaeologists, most notably language acquisition (e.g., Klein, 1992, 2008). Supposing this is the case, it could be said that considering the effect of brain mutations on cognitive development complicates Darwin's view of the process involved in cognitive evolution. However, it should be pointed out that despite the introduction of such mechanisms as mutation, ultimately natural selection still remains indispensable for understanding cognitive evolution.

INTERACTIONS BETWEEN EVOLUTIONARY PSYCHOLOGY AND ARCHAEOLOGY

Unlike evolutionary psychological research, which is mostly aimed at understanding

psychological predispositions and behaviors of people today, archaeological research on the mind and its development has tended to focus on understanding the rise of cognitive capabilities reflected by cultural developments and, to a lesser extent, on psychological traits. Those psychological traits that have been studied by archaeologists have tended to be treated as shared characteristics among conspecifics rather than as individualistic characteristics. Nevertheless, examining psychological traits on a species-scale is fundamental for understanding the macroevolutionary forces responsible for those psychological traits that are activated today in only some individuals. Archaeological studies investigating the rise of psychological traits in our species have generally focused on three areas. These are: specialized intelligence, emotions, and social interaction.

Specialized Intelligence

In evolutionary psychology, intelligence and creativity (or intellect-openness: Buss, 1995: 22) are seen to comprise one of five personality dimensions suggested to have been acted upon through natural selection (DeRaad and Hoskens, 1990). Cosmides and Tooby (1999) envision intelligence as being central to the study of evolutionary psychology and they define two kinds of intelligence, namely dedicated intelligence and improvisational intelligence, which roughly correspond to what have been referred to above as intelligence and creativity. More specifically, dedicated intelligence is defined as a computational system designed to solve a particular adaptive problem (Cosmides and Tooby, 1999: 11). Because humans have had to solve a number of particular adaptive problems in the distant past, humans have evolved a number of dedicated intelligences. Improvisational intelligence is defined as a computational system that also is designed to solve adaptive problems, but it does this through exploiting transient local conditions

which, in so doing, yields adaptive outcomes (Cosmides and Tooby, 1999: 20). Improvisational intelligence addresses the non-recurrent problems that humans sporadically have had to face. Improvisational intelligence has been also referred to as general or general-purpose intelligence, and it has attracted two schools of thought in evolutionary psychology. The first sees it as a byproduct of an architecture in which cognitive specializations are bundled together (Cosmides and Tooby, 1999). According to this view, improvisational intelligence is dependent on the dedicated intelligences for their inputs and respective processing capabilities. The effect is that the range of inputs and capacity to process these inputs are expanded. This is not, however, a general-purpose intelligence that is domain-general, dependent on content-independent procedures, but a quality that arises out of dedicated intelligences that evolved long ago. The other view sees general-purpose intelligence as simply another dedicated intelligence that evolved in order to adapt to the evolutionary novel or non-recurrent problems that arose in more recent times (Kananzawa, 2010). As such, it does not constitute a fully completed module, but one that nonetheless plays an important role in modern life. Whatever the view, intelligence is seen by evolutionary psychologists as an adaptation responsible for solving particular problems that individuals faced in the Pleistocene as well as more recently. Moreover, it is quite clear in evolutionary psychology that domain-specific processing capability is fundamentally responsible for the development of a number of specialized intelligences in humans.

Incorporating archaeological findings on specialized intelligence

The nature and evolution of human intelligence has been investigated extensively by way of archaeological research (Wynn, 1979, 1981, 1985, 1988, 1991). Some archaeological research on intelligence has been explicitly

framed in evolutionary psychological terms. Steven Mithen's *The Prehistory of the Mind* (1996) is one of the most notable archaeological works that has intersected with evolutionary psychology. Using an evolutionary psychological framework together with a well-versed understanding of the archaeological record, Mithen recounts how modern human intelligence came to be and with it the creativity we often attribute to our species.

Drawing on the works of Chomsky (1965, 1980) and Fodor (1983), and more crucially on the works of Gardner (1983, 1987) and Cosmides and Tooby (1987), Mithen presents an architectural plan of the mind in which intelligences are specialized modules that are responsible for processing concepts related to specific domains. Gardner's (1983) work in particular," plays an invaluable role as a platform that allows Mithen to examine intelligence in a way that dovetails with evolutionary psychology's mission. Gardner proposed that humans are equipped with eight intelligences that mediate one's interactions with the world. Moreover, Gardner proposed that each human has a distinct configuration of these intelligences, suggesting that each person will relate to the world in a different way. Unlike what motivates many evolutionary psychologists' research, however, Mithen's purpose is to address more generally how human intelligence and creativity emerged. This is to say, that rather than focus on the psychological pathologies related to having a relic mind – whether these are phobias or preferences (Buss, 1995: 6–7) – Mithen chooses to explore humans' general cognitive capacity for creating the distinctive cultural repertoire that humans developed.

A key departure from the traditional evolutionary psychological view is Mithen's incorporation of the ideas of Karmiloff-Smith (1992, 1994) and Carey and Spelke (1994), among others, who argue that domain-specific modules interconnect in ways that allow humans not only to amalgamate knowledge from different domains, but allow certain

modules to coopt knowledge that differs in some way from that for which the modules were originally designed. Both aspects of this brand of interconnected modularism, which Mithen calls 'cognitive fluidity', play a role in Mithen's explanation of major cultural developments such as the rise of art and religion.

Mithen sees Karmiloff-Smith's (1992, 1994) work as a significant contribution to the traditional evolutionary psychological model and incorporates her research in his own. Traditional evolutionary psychological doctrine (Buss, 1995: 13; Tooby and Cosmides, 1992) emphasizes that culture is a byproduct of evolved psychological traits which have formed domain-specific modules. Karmiloff-Smith, however, stresses the role of culture in creating the developmental conditions in which domain-specific modules coopt and begin to process information that they may not have been originally designed to process. In other words, Karmiloff-Smith sees culture as playing a feedback role in reprogramming modules to accommodate inputs for which they were not originally intended. Karmiloff-Smith sees this process as occurring ontogenetically. Expounding on Karmiloff-Smith's theory, Mithen (1996) presents an argument for this process occurring on a phylogenetic level.

Mithen's argument

Based on the evidence he sees in the archaeological record as well as in primate studies, Mithen (1996) proposes three main stages of cognitive development. The first stage is a domain-general mind which appears to have predated the divergence of anthropoids from the rest of the primates. The second stage is a mind comprised of independently operating domain-specific modules that supplement domain-general intelligence. And the third stage is a cognitive fluid mind in which all domain-specific modules, together with general intelligence, shunt information between each other without interruption.

Mithen argues that roughly 6 million years ago, well before the Pleistocene – the time

frame evolutionary psychologists generally attribute as the origin for most evolved psychological traits – our common ancestor with chimpanzees had a rudimentary operating domain-specific mind. This common ancestor had a partly developed natural history intelligence, a sufficiently developed social intelligence, but no marked technical or linguistic intelligence. Mithen hypothesizes that general intelligence continued to have a robust role by compensating for the specialized intelligences that were either partly developed or had yet to develop. Assuming that the cognitive capacities of chimpanzees remained relatively stable from the time humans and chimpanzees diverged, Mithen uses what is known of chimpanzee cognitive capacities to infer what the cognitive capacities would have been for our common ancestor.

By 2 million years ago, based on finds at Oldovai Gorge and other early hominin sites in East Africa, Mithen proposes that natural history intelligence and social intelligence continued to develop and that a technical intelligence formed. Based on archaeological evidence from archaic human sites, Mithen proposes that by 100,000 years ago, natural history intelligence, social intelligence, and technical intelligence were fully developed but remained in many cases isolated compartments responsible for processing different information. Relying on the research of Robin Dunbar (1993), which correlates brain size, social group size, and linguistic capability, Mithen further speculates that linguistic intelligence begins to emerge by this time and likely initiates the process of sharing information among the specific domains. Based on studies of archaeological sites between 60,000 and 30,000 years ago, Mithen (1994, 1996) suggests that humans developed the capacity to transmit domain-specific information among all of the modules, marking the beginning of what he calls 'cognitive fluidity' for our species. A number of findings, which include the earliest evidence of ritual, as well as the appearance of some of the

earliest bone artifacts (cf. Henshilwood et al., 2001) and images of animal-human hybrids in both parietal and portable forms, point to an amalgamation of domain-specific information. According to Mithen, fluidity among the modules would have been required for these cultural creations.

Through his research, Mithen (1996) has made a number of key contributions from an archaeological as well as an evolutionary psychological standpoint. First, Mithen suggested that an evolutionary psychological framework could be used to elicit cognitive evolutionary implications from archaeological remains. For archaeologists, this has further encouraged using what has been termed a 'conditional approach' in which archaeological remains are seen as markers of cognitive development (Abramiuk, 2012: 146–152). Second, whether or not one agrees with Mithen's interpretation of the three cognitive stages of the mind, Mithen observed correctly that the Pleistocene is too limited a time frame in which to study how our species' psychological traits evolved. Therefore, any insight based on archaeological remains concerning the hominin mind during the Pliocene also warrants attention from evolutionary psychology. Third, if one is to accept Mithen's hypothesis, then it is the informational exchange between the domain-specific modules as much as it is the information being recursively processed that led to the modern human mind. This means that domain-generalism as well as domain-specificity has a role to play in the development of the modern human mind and thus merits examination in evolutionary psychology.

Emotion

Emotion is another topic that features prominently in evolutionary psychological research (Buss, 1995: 14–18; Cosmides and Tooby, 2000; Ekman, 1999; Nesse, 1990; Tooby and Cosmides, 2008). Emotions, it is suggested, are means of adaptation. They facilitate the

decision-making process in situations in which complete information is unavailable for making optimal decisions (Oatley and Johnson-Laird, 1987). Fear, for example, is seen to incur a rapid behavioral response – fight or flight – which may constitute the difference between that individual's survival and his or her demise in the absence of complete information. Anger similarly has been proposed as having such a function. Although the number of emotional states varies among scholars, what is clear in biological understandings of emotion, of which evolutionary psychological thought is a part, is that there are a certain number of basal emotions that all humans share (Tarlow, 2000: 715–716). Of these, the most commonly reported emotions are sadness, happiness, fear, anger, and disgust (Mithen, 2006: 86). All of these, emotions generally initiate some physiological response that is proposed to have had a natural selective benefit to an individual in the past.

According to Mithen (2006: 86), basal emotions seem to be present in chimpanzees as well as in humans, and therefore can be assumed to have been present for the past 6 million years. The emotional states we are less certain were shared are shame, embarrassment, guilt, love, and contempt. These are emotions that have been argued to have played a role in developing social networks (Frank, 1988). They function to reassure a partner that one will not renege on one's commitments in the social relationship and will remain faithful and supportive. The proposed role of these socially-related emotions, taken together with the archaeological evidence of large social groups 1.5 million years ago (Hatala et al., 2016), suggests that if these latter emotions were not fully developed by this time, they were on their way to becoming fully developed. One's fitness within a large group size would have been determined in part by the perception of supportive personal bonds (Sarason and Sarason, 2009: 115–116), which would have been facilitated by the social emotions described above.

In general, emotion has not been researched by archaeologists as extensively as intelligence. This has to do with a number of reasons. The main reason is that there are few examples in the archaeological record that archaeologists can call indisputable indications of emotion. The first cultural remains that appear in the archaeological record are what archaeologists generally consider to be tools. As tools, it is difficult to say to what degree, if any, emotions figured into their manufacture and use. The Oldowan and Acheulean industries are examples of these early tools. The latter industry, which arose around 1.7 million years ago but reached its height in standardization by about 400,000 years ago, is markedly different from anything that came before it. Some Acheulean handaxes, for example, are simply too large or too perfectly designed to have been put to any practical use (Mithen, 2006: 191). Indeed, it may be that some of these so-called tools may not have even served as tools at all (see 'Social Interaction', below). If this is the case, then something else other than a calculated utility may be implied by their appearance. In either case, it is difficult to infer that particular emotions were involved in their manufacture or use.

Emotions connected to imagery

The first human-made images, comprised of patterned markings either incised in ochre or drawn using ochre 100,000–70,000 years ago at Blombos Cave in South Africa (Henshilwood et al., 2009, 2018), exemplify a similar quandary. Arguments could be made that the creation of these earliest images involved certain emotions or that the images served to arouse certain emotions in those who viewed the images. However, the earliest images can also be interpreted in a more straightforward manner, namely as serving a practical mnemonic or social function (Cain, 2006: 677–679). This is not to say that taking tallies or conveying social standing through mark-making entails no emotions, only that any emotional states

that might accompany the creation and use of marks for such purposes are not necessarily implied.

This state of affairs changes after 40,000 years ago. Around this time, the earliest *figurative* images begin to appear. Unlike the preceding patterned images, figurative images are difficult to understand without consideration of emotions. At Sulawesi Cave in south-east Asia, handprints and pig-deer imagery appear nearly 40,000 years ago (Aubert et al., 2014). The site of Lubang Jeriji Saléh, which dates slightly earlier, boasts the earliest figurative cave art depicting cow-like animals (Aubert et al., 2018). Cave sites in Europe, such as Lascaux, Altamira, and Chauvet-Pont d'Arc (dating to as early as 37,000 years ago) (Quiles et al., 2016), are replete with images that include geometric motifs such as dots, circles, and spirals, naturalistic forms such as handprints, as well as depictions of animals.

Probably, the most convincing explanation for at least some of this Upper Paleolithic art is that it constituted an individual's impression of his or her experiences while or immediately after being in a trance state (Lewis-Williams, 2004; Lewis-Williams and Dowson, 1988). Lewis-Williams has argued that the images that were painted during the Upper Paleolithic are in many ways the same as those that have been recorded being painted on boulders, in rock shelters, and in caves by shamans in the midst of an altered state of consciousness. Using what has been referred to as a general comparative approach in cognitive archaeology (Abramiuk, 2012: 112–121; Abramiuk, 2015), Lewis-Williams proposes that the individuals responsible for producing the Upper Paleolithic cave art would have served a similar social function as shamans and would have similarly engaged in trance-induced image-making.

His theory is further supported by the fact that the images that were painted in the Upper Paleolithic correspond to the kinds of well-documented images human subjects who are undergoing altered states of consciousness have reported seeing (Lewis-Williams and

Dowson, 1988). In the first stage of induction, the human subject sees geometric motifs such as lines, waves, squiggles, spirals, dots, and other designs that are now understood to be entoptic images (Lewis-Williams and Dowson, 1988: 202). As the trance deepens into the second stage, the subject begins to make sense of the geometric motifs by construing them as realistic forms, such as animals and other features that are recognizable and known to the subject. The third stage, which is often reached by moving through a perceived vortex, combines these more realistic images with the entoptic ones either by combining them or fusing them. Thus, the third stage is a kind of hybrid of the two earlier stages (e.g., an animal covered in dots or with squiggles for legs).

As a person advances through the three stages of altered consciousness, it is clear that emotions play an increasing role in the experience. Indeed, one of the motivations for Kalahari San for entering an altered state of consciousness is the sense of wellbeing or happiness that is generated from the experience (Parkington, 1989). The magnitude of the role that emotions play is likely connected to the stage the person is in. The feeling associated with envisioning entoptic images in the form of abstract geometric motifs might be more accurately described as sensation than emotion (Sayin, 2014). As the stages unfold, however, it is difficult to conceive how construing and hybridizing images is accomplished without accompanying emotions.

Whether one experiences emotion while in an altered state of consciousness also seems to be determined by the activity that is generating the conditions responsible for the induction of an altered state. Altered states of consciousness appear to interact with emotional states in varying ways and to varying degrees, depending on the activity in which the subject is involved. For example, meditators tend to report a sensation of unity (Dietrich, 2003: 243), while long-distance runners often report myriad emotional states

ranging from happiness to elation (Dietrich, 2003: 239). It is also worth noting that while meditators are intentionally able to block intense emotions through their activity, long distance runners are more apt to change their emotional states by disengaging.

Emotions connected to music

Music is also known to have the capacity to suspend or invoke emotions (Scherer and Zentner, 2001; Zentner et al., 2008). Like the earliest figurative art, the earliest evidence of music appears in the archaeological record around 40,000 years ago (d'Errico et al., 2003), and possibly earlier. The earliest of these finds amounts to what is arguably a Mousterian flute made from a cave bear femur found at Divje babe I cave in Slovenia (Turk et al., 2018; Turk et al., 2020). The next earliest finds, which are less contentious, date to 36,000 years ago and consist of several bird-bone pipe fragments discovered in a cave in Geissenklösterle, Germany (d'Errico et al., 2003). Dating not long after this is another larger assemblage of bone pipes that was uncovered in Isturitz, France (p. 39). All the pipes appear to have been fashioned in a way that would have allowed the performer to place the end of the pipe directly into the mouth, perhaps facilitated by the inclusion of a vibrating reed.

Although the pipes described above are the earliest direct archaeological evidence that points to musical acquisition, there is good reason to believe that the voice and other instruments, such as those dedicated to percussion (d'Errico et al., 2003: 46), were used much earlier. This was even speculated by Charles Darwin (1872: 317), who believed that the origin of music lay with the human penchant for song. The question of when this occurred is debatable but certainly inferable.

Sounds that were voiced, such as grunts, likely would have been utilized for communication purposes for most of the duration of the human lineage from its divergence from a common ancestor with the great apes. Indeed, the great apes still utilize

rudimentary vocalizations for communication, albeit to a limited degree, when compared to grooming (see 'Social Interaction', below). This all changed with the rise of archaic humans. It is at this time that we have anatomical evidence that supports the view that hominins had the capability to speak provided the neural wiring for language was present. The human-like hyoid bone (Arensburg et al., 1989; Lieberman, 1992), the dimensions of the hypoglossal canal (DeGusta et al., 1999), and the diameter of the thoracic vertebral canal (MacLarnon and Hewitt, 1999) all point to hominins that would have had voices not completely unlike those of humans today. Not only do we have evidence that articulated vocalization was possible, but it is likely that along with the emergence of voice, song would have arisen (Mithen, 2006).

Like images, music also arouses emotions in human subjects. Although there does not appear to be much cross-cultural consensus for listeners on the kind of emotion that is derived from a particular musical piece (Gregory and Varney, 1996), given particular musical structures, listeners and performers alike do experience emotion (Waterman, 1996). That emotions were undoubtedly involved with the emergence of music is quite clear, but the kinds of emotions that were being felt by archaic humans are difficult to surmise archaeologically.

What the archaeological record does tell us is that after 400,000 years ago and certainly by around 40,000 years ago, emotions were probably being artificially managed. Emotions were not only functioning as instinctive response mechanisms that contributed to the survival and reproductive success of hominins, as viewed in the traditional evolutionary psychological sense; they were purposefully being generated, altered, and perhaps blocked through cultural means. The capacity to evoke and control emotions from *without* may have been first achieved with the appearance of the earliest non-utilitarian artifacts (e.g., the Acheulean hand axe, provided it was meant to

signify), or the first figurative art images and musical pieces. Whatever the case, emotions were being reflexively attended to by using visual and auditory media for producing, altering, or suspending emotions.

Social Interaction

Another topic that has been explored extensively in evolutionary psychology is social interaction. Traditionally, evolutionary psychologists have focused on aspects of human social interaction such as sexual relations and competition (Buss, 1988, 1989), as well as friendships and coalitions (Shackelford and Buss, 1996). These interactions are generally seen to be the byproducts of the kinds of social groups that were formed in Pleistocene. In accordance to this view, the Pleistocene social group is seen as an environment like any other that humans would have had to navigate and to which they would have had to adapt (Tooby and Cosmides, 1992: 90–91). It is precisely within this social environment that people in the distant past would have needed to form strong bonds with a select few individuals.

Social group size

Archaeological and paleoanthropological research has produced invaluable information concerning the social environment, particularly with regards to social group size. According to Robin Dunbar (1993, 1998, 2003a), social group sizes begin to approximate those of modern humans rather late in human evolution, namely with later *Homo erectus*. This estimation was calculated based on extrapolating from what is known of the positive correlation between neocortical volume (an indicator of executive brain function) and social group size among primates. This positive correlation was also used to approximate social group sizes for several extinct species making up the hominoid taxon. Whereas, neocortical volumes could be precisely computed among extant species,

average neocortical volumes of species now extinct were estimated from total cranial volume. From these measurements, social group sizes of extinct as well as extant species could be inferred.

What Dunbar's (1993, 2003a) research has shown, using a series of graphs, is that our ancestors lived in group sizes of around 60 to 70 individuals from about 3.5 to 1.5 million years ago, at which time group size increased by about 20 individuals. This is followed by an exponential rise in social group size that begins around 1 million years ago. Dunbar argues that this latter increase eventually led to the need for language, which would have allowed for individuals to interact with fellow group members in parallel. Up to this time, the main means of social interaction was through grooming. The point in time at which some form of language is proposed to have arisen was extrapolated through determining when it was that 30% of the day was spent grooming, a kind of ceiling above which time spent grooming would have become unfeasible and language would have been needed. The tight correlation between grooming time and social group size suggests that the threshold of 30% would have been reached by about 500,000 years ago, corresponding to an age in which late *Homo erectus* and early archaic humans (i.e., *Homo heidelbergensis* and *Homo neanderthalensis* among others) would have inhabited the landscape. Group size around this time would have consisted of roughly 100 individuals. Language capability would have continued to develop and it is believed that it would have fueled the continuation of the exponential trend in group size, culminating in a group size that is commensurate with that for modern humans – roughly 150 individuals. This number corresponds to the total number of personal relations that are maintained by an average human individual (i.e., the number of individuals of whom we would feel comfortable asking favors).

Dunbar's (2003a) research directly supports the assumptions made by Tooby and Cosmides (1992: 90–91). This to say that the

social group likely did provide an environment within a broader natural environment for natural selection to play out. Referred to as the social brain hypothesis, Dunbar (2003a) asserts that the reason that social group size has increased together with neocortical size is that the cognitive demands required to live in larger social groups would have selected for larger neocortices. Remembering individuals, forming different types of relationships, and developing language would have been just a few of the many cognitive demands that would have been exacted of individuals throughout the Pliocene and Pleistocene.

Sexual relationships

Among the crucial kinds of relations that operated within the social group to keep it together is the sexual relationship. Through examination of skeletal remains, paleoanthropologists and archaeologists have inferred that *Homo erectus* underwent a process that resulted in decreased sexual dimorphism (Lieberman, 2007). This is seen not only in the reduction in large canines in males, but also in the body size of females which comes closer to that of males. Before the emergence of *Homo erectus*, sexual dimorphism is more pronounced. Based on studies of other primates (Clutton-Brock 1985), sexual dimorphism is usually found in groups that engage in polygynous behavior. The decrease in sexual dimorphism may mark the beginning of pair bonding, such as that found among certain lesser ape species, but it may also mean that female choice was playing a larger role in sexual unions. A female who is bigger affords more resistance to a demanding male. This argument seems to have gained traction in light of studies that have shown that it was the greater increase in female size relative to male size that led to the decreased sexual dimorphism (McHenry, 1996).

Accepting the reasoning that females as well as males are beginning to have a choice in their sexual unions indicates that sexual

selection was a mechanism that was playing a larger role in human evolution. Indeed, it has been postulated that Acheulean hand axes functioned as a means of sexual selection (Kohn and Mithen, 1999). Acheulean hand axes manufactured especially after 400,000 years ago are some of the most symmetrical in plan-view (Wynn, 2002; 2004: 34) and seem to offer no practical function other than as aesthetic markers. Whether these hand axes were made by males or females, it has been argued that they would have reflected the psychological traits that are crucial to the successful manufacture of an Acheulean hand axe, such as patience, perseverance, and precision spatial-rotational aptitude. These would have been highly desirable traits and therefore would have acted in a decisive way in attracting a mate, much like how the colorful tail of a peacock attracts a peahen as first explained by Darwin (1888: 432–434).

Manipulative Relationships and Metaconceptualization

Archaeological investigation can also provide considerable insight into when and how complex manipulative relationships developed. The ability to be manipulative and to be manipulated are characteristics that appear to have emerged long ago, before the divergence of hominins and apes. Indeed, we see the ability to manipulate in chimpanzees as well as in humans (Savage-Rumbaugh and McDonald, 1988).

The ability to manipulate is made possible through Theory of Mind (ToM), or what has been called second-order metaconceptualization. ToM is the ability to acknowledge as well as understand the mental states of others and to distinguish them from our own. Chimpanzees have ToM and they use it in order to anticipate the actions of other chimpanzees so that they may in some way benefit. What differs in humans is our ability to manipulate large groups of individuals more effectively. This is possible in large part because we are able to metaconceptualize to a greater degree. Using the frontal cortex volume as a surrogate for the level

of metaconceptualization achieved, Dunbar (2003a) suggests that third-order metaconceptualization arose sometime between 1.2 million and 500,000 years ago. The rise of third-order metaconceptualization would have implied that through abstraction one could, nest three concepts, which is essential for realizing things like, ‘*I know that he knows that my ornament means that I am the leader of the group*’. Archaeological evidence points to a much later date than Dunbar’s estimate, closer to 100,000 years ago and certainly by 70,000 years ago. The appearance of perforated shell ornaments 75,000 years ago at Blombos Cave (Henshilwood et al., 2009: 28) clearly suggests that third-order metaconceptualization had been attained. However, it may be that an earlier date, nearer to that of Dunbar’s proposed date for the rise of third-order metaconceptualization, is possible. For example, ochre has been found in archaeological contexts as early as the Middle Stone Age, roughly 285,000 years ago (Barham, 2002: 188–189). Although widely used for a number of pragmatic functions, ochre might have been used for body painting, possibly a symbolic act not entirely unlike dawning ornaments. Indeed, if Kohn and Mithen (1999) are correct in proposing that hand axes were means through which sexual selection was enacted, then third-order metaconceptualization might be pushed back another 115,000 years during the time at which symmetrical hand axes were becoming perfected. The significance attributed to hand axes, however, would have been denotative and would have afforded a rather straightforward meaning such as ‘technologically adept mate’, rather than representing a more complex meaning using an arbitrary signifier. Indeed, the same may be true of using ochre, which is perhaps why these earlier cases might be more accurately seen as lead-ups or ratchets that facilitated the development of third-order metaconceptualization. The importance of third-order metaconceptualization is that it would have been foundational for the laying down of social norms. Moreover, it would

have assisted individuals in rising to and maintaining leadership positions in society by communicating to others their status through symbolic media. Symbolic media in this sense would have acted as ‘social ratchets’ without which an individual would find it difficult to attain rank. It would take the development of fourth-order metaconceptualization, however, before facilitative social ideologies would be realized. An ideology could allow someone in a leadership position much greater control over a large group of people.

Evidence for fourth-order metaconceptualization arises with the earliest imagery of chimerical supernaturals around 30,000 years ago (Abramiuk, 2012: 242). Such images appear in both parietal and portable form. The bison-human hybrid painted image at Chauvet-Pont-d’Arc Cave in France and the carved lion-human figurine found in Hohlenstein-Stadel, Germany, are examples reflecting this cognitive development. It can be assumed that the individuals who manufactured and utilized these artifacts would *know* that another person in his group would *know* that a chimerical image *represents* a supernatural entity with human qualities to which one could *relate*. The ability to create these mental links would have been essential for wielding as well as being subjected to ideology. Such a cognitive prerequisite would have been essential for the rise of leaders who could convince large groups of people to coordinate and undertake large-scale projects on behalf of the leaders.

Recounting the advent of metaconceptualization through time not only helps explain what the cognitive prerequisites were for cultural developments such as the rise of social status and ideology, but it helps us understand individual differences insofar as social interactions are concerned. Differences in how individuals navigate the social environment and what they are able to accomplish in terms of social influence can be explained in part by differences in our capabilities to metaconceptualize. Dunbar

(2003a) has suggested that metaconceptualization is not a discrete capability that everyone in the population shares. Indeed, Dunbar proposed that fifth-order metaconceptualization is possible for some and that it is these individuals who have potential to become leaders. Whatever the case, the archaeological evidence points to these two higher orders of metaconceptualization capability arising quite late in time; hence, they must have been adaptations to more recent conditions.

CONTENTION WITH EVOLUTIONARY PSYCHOLOGY IN COGNITIVE ARCHAEOLOGY

Despite some of the productive inroads made by evolutionary psychological-minded archaeologists, these archaeologists have faced resistance in the past two decades of cognitive archaeological research. This resistance can be attributed to those archaeologists more inclined to take up a less nativist stance similar to that which ecological psychologists have taken. Referred to as the materiality approach (Abramiuk, 2012: 105–112; Abramiuk, 2015), it shares much with phenomenology in terms of how the mind is understood and how one is encouraged to study the mind. One of the more extreme views, known as material engagement theory (MET) (Renfrew, 2001; Malafouris, 2004), which also forms the basis for the research program known as radical enactive cognitive archaeology (Garofoli, 2017), exemplifies this alternative way of conducting mind-related archaeological research. Advocates of the harder-line materiality approach see neo-Darwinian frameworks as misguided (Knappett, 2016) and imply that as an explanatory framework, MET holds more promise than does evolutionary psychology for cognitive archaeologists (Garofoli, 2017).

MET owes much to the ontological stance upon which it is based. This ontological view

sees the mind as an embodied, extended, and enacted whole, which is to say that the mind is one with the material world, where 'material world' is taken to mean our bodies, surroundings, and actions in these surroundings. Implied in the embodied, extended, and enacted view is that the mind must be *explicitly* anchored in some bodily form within the material world. Heavily influenced by the philosophy of mind literature, an embodied (Merleau-Ponty, 1962), extended (Clark and Chalmers, 1998), and enacted (Varela et al., 1991) view has emerged as a stark reminder for archaeologists that a holistic examination of the material world is crucial for understanding how a *naturally* situated mind worked in the past (Barrett, 2013; Boivin, 2008; Knappett, 2005; Malafouris, 2013).

In evolutionary cognitive archaeology, MET has made a significant mark (Abramiuk, 2019: 368). Its roots in the archaeological literature can be traced in part to Merlin Donald's (1991) *Origins of the Modern Mind: Three Stages in the Evolution of Culture and Cognition*, which, although written from the perspective of a cognitive scientist, made extensive use of archaeological data to understand the relationship between culture and the mind and how they evolved together. According to Donald, the interaction between culture and cognition is largely evidenced from the end of the Pleistocene. It was from this time that culture began to take on the characteristic of a memory storage device, or what Donald refers to as external symbolic storage (pp. 305–306). The notion of external symbolic storage becomes particularly relevant in understanding the mind in the Holocene after the advent of writing roughly 5000 years ago (p. 285).

MET, however, goes further in suggesting that the role of material culture in cognitive development transcends that of external symbolic storage (Renfrew, 2001); therefore, material culture's role in cognitive evolution is not strictly limited to the late Pleistocene and Holocene. The application of MET in understanding the development of the mind

through Lower and Middle Paleolithic tool-making is a case in point. Whereas many evolutionary cognitive archaeologists are of the perspective that intermediate or final artifact form, such as an Acheulean hand axe, was dictated by an intentional state with morphology (Pelegrin, 1993; Schick and Toth, 1994) or function (Machin et al., 2007; Mitchell, 1996) in mind, advocates of MET see this interpretation as fallacious in two major respects. For them, it invokes the Cartesian fallacy, whereby intentional states are seen as *internal* and *mental* and artifacts are seen as *external* and *material*. It also makes the mistake of envisioning the knapper as the agent when, in fact, agency should be attributed to the whole system involved in the knapping process inclusive of the knapper and the rock being formed into an artifact. More specifically, MET advocates stipulate in Heideggerian fashion that the artifact is *brought forth* through the knapping action; it is not created through executing a mental image onto a rock (Malafouris, 2013: 172–173). In this way, MET advocates assert that intentionality or agency is bound up in the rock and in the knapper alike, and this is because the rock and every subsequently reduced version of it 'affords' being knapped. That an object or artifact can afford actions done unto it is a notion with phenomenological roots, but which also forms a central premise in ecological psychology (Gibson, 1979: 127). The term *affordance*, for its part, is a convenient way of describing how information from objects in the environment is picked up directly with minimal cognitive processing and how even certain meanings can sometimes be intuited.

Through its anti-dualist ontological commitment, MET not only challenges the evolutionary psychological view insofar as it explains toolmaking, but other watershed events such as the advent of art. A representational and, hence, dualistic explanation would have it that art represents or 'means' something internally to the individual creating or viewing the image, but where did

this ‘meaning’ come from in the beginning when things did not ‘mean’ anything? MET does not rely on positing internal representations and therefore is shielded from this dilemma. Instead, it advocates an enactive view of the mind in which meaning emerges in rudimentary stages beginning with the act of mark-making, culminating eventually in the creation of an image. As an example, Malafouris (2013: 204) proposes that mark-making, such as that found at Blombos Cave 100,000 years ago, formed the requisite cognitive scaffolding for the development of more intricate images (e.g., those at Lascaux and other Franco-Cantabrian caves) as well as the capacity for representational thought. As a result, mark-making would have gradually developed into image-making. The image, for its part, would have functioned as a device for the ‘liberation of sight’. The creation of the earliest images would have given our visual system, which was used to seeing things naturalistically, pause to interrogate itself and give rise to a perceptual awareness that it had never had. More generally, MET effectively asserts that it is our engagement with the world and incrementally adding more material culture to it that has enabled us to be self-conscious in experience as well as thought.

Reconciling the Issues Raised by MET

Although MET can be regarded as ontologically at odds with evolutionary psychology (Abramiuk, 2019), a minimal amount of overlap with evolutionary psychology can be observed in the empirical research on human perception. This overlap covers the research on what has been termed *direct perception* in the psychological literature (Norman, 1980).

Direct perception is generally considered the way that humans perceive in a natural environment in which they can move around freely and visually explore the

objects therein. Phenomena such as colors, basic shapes, and natural features seem to be directly perceived, and activities that require the subject to engage in a task, such as grouping, which involves color perception appear to be only slightly informed by culture based on linguistic studies (Abramiuk, 2012: 101–104). Subjects moving naturally through the environment and negotiating obstacles also extensively use direct perception and have been studied extensively by ecological psychologists (Burton, 1992, 1994; Mark et al. 1999; Snapp-Childs and Bingham, 2009). Artificial products, such as two-dimensional imagery (Deregowski, 1989), and more complex mind frames such as worldviews, on the other hand, are indirectly perceived and are largely culturally informed (Abramiuk 2012: 104–105).

In both evolutionary psychology and MET, the important role of direct perception in our interaction with the world is emphasized, but there are differences in how direct perception is explained. Whereas evolutionary psychologists see direct perception as having been hardwired into our species through natural selection, MET advocates see it as arising concurrently through our dynamic engagement with the things around us. In other words, for evolutionary psychologists, direct perception was built into our being as a means of adapting to an ancestral environment and, therefore, constitutes a vestige from the past. Advocates of MET, on the other hand, would argue along the same lines that ecological psychologists would—that it is the manner in which the body and environment articulate in a given situation and moment that gives rise to direct perception, the suggestion being that direct perception emerges through a concurrent process rather than a vestigial one.

Where the two schools also differ dramatically is with how each views indirect perception and cognition in general. This stems from different understandings of what constitutes culture. In evolutionary psychology, culture, which includes anything from worldviews

to languages, is the result of the different ways that innate, psychological traits are expressed when subjected to different environmental conditions (Buss, 1995: 12–14). These psychological traits, one should be reminded, are neurologically based and therefore hard-wired, but emerge as different forms depending on the environmental context. Being neurologically based, the psychological traits from which culture arises need to be converted into expressible form and therefore are sometimes envisaged as encoded rules or representations. In MET, culture, like cognition, is seen as embodied, extended, and enacted, which is to say that culture is the way that we engage with the world around us and the way that the world engages with us (i.e., a kind of ‘ecological’ system), rather than something that is composed through a process of conversions originating in the nervous system.

MET has challenged evolutionary psychology insofar as it suggests that the conversions, which are entailed in the way that cognitive evolution is conceived of in evolutionary psychology, may be superfluous. An example of this is whether we should be so quick to assert that mental images are required for the manufacture of certain tools. Still, MET has several pitfalls that only serve to highlight the strengths of evolutionary psychology as it relates to cognitive archaeology. The main pitfall is that although MET may contribute to our understanding of cognitive *functioning*, it tells us remarkably little about cognitive *evolution*. In other words, MET does not have an explanation for how cognition evolves or why it would evolve. Although MET does not explicitly disallow a role for natural selection in cognitive evolution, it effectively states as much through its anti-dualistic ontological commitment. It distances itself from alleged Cartesian fallacies, such as constructing artificial divisions, particularly those delineating mind, brain, body, and environment, and talking about what transpires *inside* or *outside* of those settings. As a result, MET becomes inherently incompatible with a Darwinian account of

cognitive evolution. Without natural selection or anything comparable to it, MET lacks a mechanism for ratcheting cognitive change phylogenetically. For this reason, MET can most accurately be described as a non-Darwinian approach to studying the mind in the past (Abramiuk, 2019: 371–373).

The empirical reality is that neurophysiological changes on a phylogenetic level have taken place throughout the course of our lineage that clearly have entailed natural selection (Evans et al., 2005; Weaver, 2005). Moreover, these changes have been shown to be related to enhanced cognitive efficiency and other cognitive developments. In the course of natural selection, phylogenetic cognitive development and associated neurophysiological changes would have necessitated a process of encoding and conversion (i.e., representation) *inside* the body which is fundamentally incompatible with MET’s ontological position. An example of one such cognitive development associated with a neurophysiological change is the proposed increase in metaconceptualization capability in our lineage over time. Metaconceptualization level is linearly related to frontal lobe size, (Dunbar, 2003b) which indicates that the two evolved together and were likely linked. Without a biological mechanism, such as natural selection, involving conversions for preserving and fostering this cognitive capability within the body, it is difficult to reconcile how such a relationship might arise.

Another weakness that MET faces is its overly ambitious agenda, which stems from what can most accurately be described as an ontological sense of security. MET’s ability to circumvent certain ontological fallacies in philosophy of mind is made possible through its adoption of an embodied, extended, and enacted view of the mind; however, empirical evidence throws some doubt on the infallibility of a blanket version of this view. While the ecological psychological research on *affordances* and the active role humans play in information pick-up

has proven compelling (e.g., Chemero et al., 2003; Cornus et al., 1999) and even useful in cognitive archaeology in inferring certain mind frames (Abramiuk, 2012: 105–112), to reduce all cognition to direct perception risks imagining that we are constantly locked in material engagements or bodily movements that are doing the ‘thinking’. According to this extreme view, our material engagements or actions within our local environment are, or should be, congruous with our proprioceptive experience. However, vibrotactile illusions and the more well-known Rubber Hand Illusion (RHI) seem to refute this fundamental aspect of the embodied, extended, and enacted view of the mind (de Vignemont, 2011).

In the RHI, a subject’s left hand is placed on a table behind a screen, and a rubber hand is placed in the subject’s view. Both are brushed with paintbrushes simultaneously. After a while, subjects begin to report feeling the brushing sensation at the location of the rubber hand. They also report that their left hand is closer to the rubber hand than it is, or feel as if their left hand is the rubber hand. Yet, when asked to use their right hand to point to the sensation, they point correctly to the location of their left hand behind the screen. Subjects are also able to correctly move their left hand in the direction of their right hand when asked to do so. In other words, their reaching movement or action is incongruous with, and therefore separate from, their proprioceptive experience. These experiments raise doubts about the embodied, extended, and enacted view of the mind and at the very least raise questions about considering it as a model for understanding how certain aspects of human consciousness – most notably, an accurate self-awareness – can arise.

Another limitation is MET’s preoccupation with ontology at the expense of epistemology. Its proponents see its monistic commitment as its strength; however, what it makes up for in ontological consistency, it loses in epistemological rigor. Part of the problem that the author sees with MET is the means by which data are synthesized by its advocates, namely through phenomenological descriptions that

do not allow for a critical examination of the variables being related. As a result, MET can fall prey to the impulse of attributing every cognitive process to engagement and interaction. MET advocates tell us, for example, that stone tools and intention can be ‘brought forth’ through the process of knapping (Malafouris, 2013: 172–173) and that images and associated perceptual awareness can be *brought forth* through mark-making (Malafouris, 2013: 203–205). Language acquisition also has been characterized as being *brought forth* through artifacts such as body ornaments, providing the social settings for the exchange of vocalizations (Garofoli, 2017: 17). The invariability of specific vocalizations in the presence of particular objects would have resulted in vocalizations being used to refer to those objects. Abstract concepts, on the other hand, would have found themselves tied to perceptual invariances detected in the course of persistently interacting with other people (Garofoli, 2017: 18). (The term *prestige*, for example, might become used in an abstract sense to refer to what individuals with more than one necklace have.) Such a broad-brush depiction of cognition as inseparable from action and interaction, however, has been significantly challenged on both empirical and logical grounds (Clark, 2009; Eliasmith, 2008). The problem is not that MET is incorrect in its depiction of the emergence of certain cultural expressions and thought as inculcated through action and interaction, but, rather, that it provides little prospect for resisting the claims it espouses from a methodological standpoint; therefore, as an analytical framework for testing suppositions, it is an insufficient replacement for evolutionary psychology.

CONCLUSION

In summary, evolutionary psychology plays a significant role in archaeology – and archaeology in evolutionary psychology. In this chapter, special attention was paid to the

study of cognitive evolution, which lies at the intersection of evolutionary psychology and archaeology. With regards to the study of cognitive evolution, cognitive archaeologists look at how the mind evolved within the human lineage, from a shared common ancestor with great apes to the present. Whereas cognitive archaeologists tend to be interested in the development of cognitive capabilities within the species, evolutionary psychologists tend to focus on the origins of psychological traits which clearly tend to be expressed differently from individual to individual. The particular areas that evolutionary psychology and archaeology have intersected include specialized intelligence, emotion, and social interaction. All three areas have proven fruitful research foci that address how humans evolved certain psychological traits.

Evolutionary psychology's role in archaeology has been challenged in recent years by a school of thought that emphasizes materiality over natural selection in explaining how cognitive change has taken place. This challenge, however, need not deter cognitive archaeologists from conducting evolutionary psychological research; rather, it should provide archaeologists of evolutionary psychological persuasion new topics to consider. One of these topics to be considered is the precise role that direct perception plays in cognitive development and whether there are aspects of our interpretation of the archaeological data that might be more parsimoniously explained through an enacted rather than a hardwired model of the mind. With this said, cognitive archaeological inquiry is unlikely to ever rid itself of its lynchpin, which is natural selection (Abramiuk, 2019), and this means that the role of evolutionary psychology in cognitive archaeology and the role that archaeology plays in evolutionary psychology are secure.

Despite the fact that certain assumptions made early in the development of evolutionary psychology have been found to be incorrect, natural selection, which forms the basis for evolutionary psychology, still most adequately explains how the human mind evolved. Since

the rise of evolutionary psychology in the 1990s, for example, researchers have learned that: 1) the Pleistocene environment was not as stable as was earlier surmised; 2) the rate of response to selection is faster than we previously thought among many animals, including humans; 3) culture can actually accelerate this rate in certain cases; and 4) the mind has evolved to include multiple domain-general as well as domain-specific mechanisms (Bolhuis et al., 2011). Although these findings contradict certain traditional evolutionary psychological precepts, the idea that our cognitive capabilities as well as psychological traits can largely be attributed to natural selection is one precept that is not easily rejected. What this suggests for evolutionary psychology is that like the evolution of psychological traits that it purports to study, evolutionary psychology itself has evolved over the years, and it will continue to do so.

Notes

- 1 Paleoneurology is the study of brain evolution through archaeological evidence in the form of fossil skull remains. Through measuring cranial capacity and endocasting, the paleoneurologist attempts to track brain enlargement as well as changes to brain anatomy throughout hominin evolution. In so doing, the paleoneurologist in certain cases can infer different cognitive stages with respect to cognitive capacity and function that are represented in our evolutionary line. As an example, the identification of petalial asymmetries in brain anatomy through endocasts has helped postulate functions and capabilities, such as symbolic and spatio-visual integration as well as the capacity for language (Holloway and de la Costelareymondie, 1982).
- 2 Primatology, the scientific study of primates, is a field that has a sufficiently broad scope for providing insight into the behavior and cognition of our shared common ancestors with other primates. That is, studying our closest relatives, such as orangutans, gorillas, and chimpanzees can allow us to approximate baselines for cognitive capabilities that subsequently changed over the course of human evolution. With this said, there is still uncertainty as to what our shared common ancestor was like (Wrangham and Pilbeam, 2002). This taken together with the complexities

that mosaic evolution poses (de Winter and Oxnard, 2001: 714) means that caution must be taken in projecting extant ape cognitive traits onto the extinct members of the human clade.

- 3 Although the evolution of the mind is not an explicit concern for *cognitive anthropology*, cognitive anthropology can offer some useful insights into the subject. Among its goals, cognitive anthropology examines how cognition unfolds among people of different cultures and whether there are any differences or congruencies (D'Andrade, 1995). Through this research, the universal aspects of cognitive capabilities can be gleaned as well as those cognitive aspects that are susceptible to change due to cultural differences. The universal aspects of cognition, for their part, can be used as baselines from which the researcher can extrapolate how and what people in the past—culturally differentiated or not—thought or experienced (Abramiuk, 2012: 47).

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Evolutionary Psychology and Sociology

Stephen K. Sanderson

INTRODUCTION

Sociology has lagged far behind its sister disciplines of psychology and anthropology in accepting and using evolutionary psychology. Although there are hundreds of psychologists and anthropologists who ground their research in this perspective, there are perhaps only a half dozen to a dozen sociologists who accept evolutionary psychology's basic principles and who use it in their research and theorizing. Nevertheless, many sociologists have turned to biology, in one form or another, as a guide to their research and have chided their colleagues for not taking biology into account. Let me call those sociologists who employ evolutionary psychology's principles of natural and sexual selection *Darwinian sociologists*. There is a second group that takes biology seriously, but it either makes no reference to evolutionary psychology or does so only marginally (or in some cases is opposed to it). I will call these sociologists *biosociologists*. The

biosociologists comprise an eclectic bunch. There is a third group whose representatives, despite exploring biological foundations, are explicit critics of evolutionary psychology and some other biological approaches. Let me call this group *evolutionary sociologists*. Evolutionary sociologists approach biology gingerly. I begin this chapter with a brief sketch and critical analysis of the main contributions of these groups, and then turn in greater detail to the principal areas that have been the focus of research and theorizing by all three groups, including family and marriage, human reproduction, status and social dominance, gender, crime and violence, and religion.

DARWINIAN SOCIOLOGY

The first sociologist to seek a return to the biological foundations of social behavior was Pierre van den Berghe. In 1975, van den

Berghe published *Man in society: A biosocial view*. In this work, he proposed that human behavior is grounded in a set of biological predispositions that he referred to by the German term *Anlagen*. These consisted of aggression, territoriality, hierarchy, male dominance, and incest avoidance. Humans are programmed for these behaviors, but only in a general sense. Humans are also biologically programmed for complex learning and thus the *Anlagen* interact with a range of socioecological conditions to produce the specific behaviors that humans display in specific environments.

Man in society appeared just a few months before E. O. Wilson published his groundbreaking *Sociobiology* in 1975, and thus van den Berghe could not make reference to it or take into consideration some of the specific principles Wilson pointed to, especially the concept of kin selection. In 1978, van den Berghe was able to make up for this by publishing a second edition of his book. Here he inquired into the basis of human sociality – what it is that ties societies together and keeps them together – and pointed to three fundamentals: kin selection, reciprocity, and organized coercion. Accepting the idea proposed by Richard Dawkins (1976) that the gene is the basic unit of selection, van den Berghe (1978: 60) proposed that kin ties will assume a fundamental importance because of the ‘successful reproduction of the genes carried by individuals who so behave’. Kin selection is the most ancient evolutionary basis of human sociality, but reciprocity is also ancient. It occurs among nonkin and involves the return of favors for mutual benefit. Coercion is the collective use of force and operates primarily in large-scale societies, especially those that have complex chiefdoms or states.

Later, van den Berghe embraced sociobiology more fully and wrote several additional books applying it, especially *Human family systems* (1979) and *The ethnic phenomenon* (1981).¹ In the former, he discussed the classical sociobiological problems of

parental investment, pair bonding and mating, sexual selection and sexual dimorphism, incest avoidance and exogamy, marriage systems (monogamy, polygyny, and polyandry), modes of marital residence, and systems of descent. In the latter book, he argued that ethnicity was a primordial human attachment ultimately rooted in kin selection. Ethnic groups are, he contended, very large extended kin groups.

Joseph Lopreato (1984, 1989) was another early proponent of a more biologically oriented sociology. Like van den Berghe, he emphasized human biological predispositions, listing four: (1) predispositions of self-enhancement (the search for individual advantage through the pursuit of status and wealth); (2) predispositions of sociality (which involve reciprocity, dominance, and deference but also the needs for conformity and social approval); (3) predispositions of variation (which include the need to avoid incest and to form family and ethnic groups); and (4) predispositions of selection (the denial of death and the need for ritual, and thus the biological foundations of religion). Lopreato situated these predispositions within the context of sociobiology’s *maximization principle*, a fundamental human motive, although largely unconscious, of maximizing the representation of one’s genes in present and future generations. Lopreato reformulated this as the *modified maximization principle*: people behave so as to maximize their inclusive fitness, but this can be modified or even neutralized by such things as the quest for creature comforts, by tendencies of self-denial or asceticism often stimulated by sacred beliefs and practices, and by motivations that once produced maximizing behaviors but that no longer do so in modern environments, such as sexual activity between individuals using some form of contraception.

Later, with his former student Timothy Crippen, Lopreato wrote an extremely important book, *Crisis in sociology: The need for Darwin* (Lopreato and Crippen, 1999). They

argued that sociology had entered a state of crisis, saying that this once promising science ‘is now awash in the flotsam of extreme cultural relativism and multiculturalism, postmodernism, political correctness, and, permeating these and other isms, an ideological agenda driven by provincial concerns of race, class, and the many grievances of a radical brand of feminism’ (Lopreato and Crippen, 1999: xii). They feared that the crisis had become so severe that sociology was at risk of being eliminated from academia altogether within the next few decades. What sociology needed, they argued, was a general unifying paradigm, and they believed that sociobiology was it. Indicating that their book was not merely programmatic or exhortatory, they devoted nearly half of it to Darwinian analyses of sex differences, marital and family relations, social stratification, and ethnic attachments.

Satoshi Kanazawa has embraced evolutionary psychology more than any other sociologist and, over a 30-year period, has published on a wide range of topics. These include the Trivers–Willard hypothesis (TWH), religion, happiness, intelligence, physical attractiveness, mate selection, parental investment, gender inequality, reproductive behavior, monogamy and polygyny, crime, and social capital. Rosemary Hopcroft is another leading sociological convert to evolutionary psychology. Most of her research has addressed the TWH, gender, fertility, and reproductive success.

Stephen Sanderson’s *The evolution of human sociality: A Darwinian conflict perspective* (Sanderson, 2001a) was a work of sociological and anthropological theory that proposed a need to embrace Darwinian theory (under the guise of sociobiology) as a means of rectifying many of the deficiencies of sociology’s and anthropology’s leading theoretical perspectives. Sanderson suggested a synthesis of Darwinism and some of the strengths of existing perspectives, a new perspective he called Darwinian Conflict Theory (DCT). After outlining a rudimentary version

of the new synthesis, Sanderson reviewed at length the research evidence supporting it in the areas of reproductive behavior, human sexuality, sex and gender, family and kinship, economic behavior, and politics and war. (A more elaborate version of DCT was published in 2015 and is outlined at the end of this chapter.) The leading ideas in *The evolution of human sociality* were extended and others were added in *Human nature and the evolution of society* (Sanderson, 2014). Most recently, Sanderson has turned his attention to religion by engaging the debate between cognitive and evolutionary psychologists concerning whether religion is an evolutionary adaptation or by-product of existing adaptations, taking the side of the adaptationists. An early effort (Sanderson, 2008) was followed by a lengthy article (Sanderson, 2018a) and a full-scale book, *Religious evolution and the Axial Age: From shamans to priests to prophets* (Sanderson, 2018b) – a work in which he traced the sociocultural evolution of religion with a special focus on the Axial Age, the period in the second half of the first millennium BCE when the major world religions were developing. Sanderson has also sought to revive interest in the early work of the Finnish sociologist Edward Westermarck (Sanderson, 2018c), whom he considers the first sociobiologist or evolutionary psychologist.

François Nielsen and Timothy Crippen are strong supporters of sociobiology (the term they prefer). Nielsen (1994) wrote an excellent article early on in which he laid out the key dimensions of sociobiology and showed how they have influenced some sociologists and can potentially influence others in the future. He discussed Darwinian psychology versus Darwinian anthropology, the levels of selection debate, inclusive fitness (identified as the cornerstone of human family relations), evolutionarily stable strategies, reciprocity, the TWH, male and female reproductive strategies, parental investment, sexual differentiation, the coevolution of genes and culture, and the compatibility between sociobiology

and sociological rational choice theory (the former providing the missing preferences for the latter). (Although Nielsen strongly supports sociobiology, his own research has been on the genetic basis of individual status achievement, discussed below.) Crippen (2018) provides a thoughtful and important discussion of the misunderstandings and distortions of evolutionary psychology even by other biologically oriented sociologists.

BIOSOCIOLOGY

Steven Goldberg is a sociologist who was one of the first to emphasize the role of human biology in a number of behaviors long thought to be environmental in origin. In strongly rejecting criticisms of biological explanations, he has declared that 'Sociology is rapidly becoming nothing more than a series of ideological claims that do not merely fail to address the relevant evidence but claim the opposite of what the evidence suggests' (Goldberg, 1991: 128). Although not a proponent of evolutionary psychology, he has nonetheless proposed biosocial explanations of such phenomena as male dominance, the causes of homosexuality and whether it should be regarded as normal or abnormal, the biological bases of black superiority in many sports, and the extent to which stereotypes may be true. Lee Ellis was another early proponent, claiming that in the near future sociology will dramatically decline and ultimately disappear from the academic world because most of its sociocultural explanations will be shown to be false, or at least very limited, only to be replaced by biological explanations (Ellis, 1977). He accepts much of sociobiology or evolutionary psychology but for the most part uses a different set of biosocial approaches to examine, most prominently, crime, social stratification, and gender. He has also studied the relationship between male dominance and reproductive success in a wide

range of animal species and in humans (Ellis, 1995) as well as sexual orientation (Ellis and Ames, 1987).

J. Richard Udry, once a traditional sociologist, has strongly embraced the role of biology. In his article 'Sociobiology and biology: What biology do sociologists need to know?' (Udry, 1995), he points out that traditional sociological explanation – the Durkheimian dictum that social facts can only be explained by other social facts – is not completely wrong but is seriously limited. Human biology also plays a major role, in fact, perhaps the predominant role. The biology that sociologists need to learn is sociobiology, behavior genetics, and behavioral endocrinology. Thinking of the three together, he formulates the following overarching principle: 'Evolution selects the genes that control the hormones that activate the genes that code for the neurotransmitters that control behavior' (Udry, 1995: 1268). Genes control both the uniformities and variations of behavior found in diverse societies throughout the world, as well as the individual differences in behavior found within a given society.

David Franks (2010) has formulated a biosocial approach that he calls neurosociology. Franks embraces the sociological approach known as symbolic interactionism. The key principle of this approach is that individuals create meanings in social interaction by, among other things, 'taking the role of the other'. Symbolic interactionism has a major concern with what its founder, George Herbert Mead, called the social self. Neurosociology seeks to locate the neurological structures of the brain that make symbolic interaction possible, but it is also concerned with the impact of social interaction on these neurological circuits. Marrying neuroscience to symbolic interactionism, however, is a challenging task because the former is highly deterministic and the latter one of sociology's most voluntaristic and indeterministic approaches. It is in fact a form of social constructionism, which stands at the opposite extreme from biological approaches.

EVOLUTIONARY SOCIOLOGY

Evolutionary sociology is primarily the creation of the sociologists Jonathan Turner and Alexandra Maryanski (Turner, 2015; Turner and Maryanski, 2015b). This term has been used by others to apply to biological approaches in general, but here I use it in the more restrictive sense in which Turner and Maryanski intend it. To understand evolutionary sociology in this sense, we need to begin with Turner and Maryanski's critique of evolutionary psychology. (A slightly broader version of evolutionary sociology is Turner and Machalek, 2018.)

Turner and Maryanski are not receptive to evolutionary psychology. Turner has long repeated the allegation made by Stephen Jay Gould many years ago that evolutionary psychology consists of nothing but 'just-so stories' – interesting but rather fanciful explanations of behavioral phenomena that lack any basis in empirical evidence. In response to Turner, it must be admitted that there are just-so stories in evolutionary psychology, sometimes rather embarrassing ones. However, most evolutionary psychology is based on hypotheses that have been tested, sometimes extensively so (hypotheses of mate selection and sexual behavior are particularly good examples of well-tested hypotheses). The problem is that, because of the long-standing opposition to evolutionary psychology and sociobiology by sociologists, very little research evidence supporting evolutionary psychology has been published in sociology's major general journals, such as *American sociological review*, *American journal of sociology*, and *Social forces*. Instead, the evidence is found in specialized journals highly receptive to articles in evolutionary psychology, such as *Evolution and human behavior*, *Human nature*, *Evolutionary psychology*, and *Behavioral and brain sciences*. Anyone who reads these journals regularly will see that many of evolutionary psychology's key explanations are

well supported by evidence. Evolutionary psychologists have also published important books summarizing much of the evidence (an enormous amount of evidence is summarized in Sanderson, 2014, 2015.)

Turner is also highly critical of evolutionary psychology's basic assumption of the modularity of the brain. He takes the standard sociological view that the brain is a general purpose organ. Evolutionary psychologists defend the modularity assumption on the grounds that a general purpose brain would be too clumsy to solve highly specific adaptive problems, such as that of evaluating the reproductive value of a potential mate. Specific adaptive problems require specific brain modules to solve them.

Turner and Maryanski also take evolutionary psychology to task for its failure to be able to explain complex sociocultural systems and their evolution over historical time. It is indeed true that evolutionary psychologists have failed to explain such phenomena, but explaining them has never been one of evolutionary psychology's goals. Turner and Maryanski stress the emergent character of sociocultural systems and sociocultural evolution, an eminently sensible point, but evolutionary psychologists do not deny emergence and do not claim that evolutionary psychological explanations apply to everything. Evolutionary psychology is not reductionist, despite what has often been claimed (Crippen, 2018).

Turner and Maryanski also reject the individual or gene selectionism of evolutionary psychology, at least as an exclusive focus. While there is an ongoing legitimate debate about the levels of selection – individual or gene selection versus group selection – the authors take the view that societies can be regarded as 'superorganisms' and that these entities have 'agency' somehow equivalent to individual agency. But, as Crippen has remarked, 'In what sense can it be said that a household, a village, a chiefdom, a state, a business enterprise, a marketplace, or any other manifestation of human groups have

“agency?” In what sense are they “actors” with “emergent” intentions?” (2018: 441).

In sum, although Turner and Maryanski edited a very important volume devoted to establishing a closer connection between evolutionary biology and the social sciences, *Handbook on evolution and society: Toward an evolutionary social science* (Turner et al., 2015), they turn out to be rather luke-warm about most biological approaches. Indeed, they actually warn social scientists against taking biology too seriously: ‘The enthusiasm with which many trumpet the coming of biology in the social sciences is, at the very least, overdrawn and, at most, harmful to the social sciences’ (Turner and Maryanski, 2015a: 92; cf. Crippen, 2018: 440).

Be all of this as it may, what then is the nature of Turner and Maryanski’s evolutionary sociology as an alternative evolutionary perspective? In an early paper, Maryanski (1998) coined the term evolutionary sociology and summarized the most important work that it included. This included the work of Pierre van den Berghe (1978, 1979), Joseph Lopreato (1984, 1989), Richard Machalek (1992), and Lee Freese (1997); the social evolutionary theories of Gerhard Lenski (1966, 2005) and Stephen Sanderson (1994, 1999); the biosocial approach of Richard Udry (1995, 2000); and the primate-oriented work of Maryanski and Turner (1992).

Later, this early version of evolutionary sociology was further developed and made more specific and focused (Turner and Maryanski, 2015b; Turner, 2018). Its core is the effort of the authors to use cross-species analysis to understand the evolution of human nature. As already seen, the authors reject the view of human nature proposed by sociobiology and evolutionary psychology and want a conception of human nature that makes sociology much more relevant. Their cross-species analysis focuses on the nonhuman primate background to human evolution. One of their major assumptions is that the last common ancestor (LCA) of humans and chimpanzees was a species with

low sociality. Monkeys are highly social and live in forests, but when the LCA ventured out of the forests into the African savanna, its low sociality became highly maladaptive. To survive, it needed to become more social for purposes of foraging and group defense. How was this achieved? ‘The key to hominin survival and ultimately to human organization’, they say, ‘was the dramatic expansion of the capacity for emitting more nuanced and complex emotions, thereby increasing sociality, attachment behaviors, commitments to conspecifics, and, most important, commitments to group formations’ (Turner, 2018: 99). They emphasize the sociological theories of Emile Durkheim (1915) and Erving Goffman (1959, 1982), especially Durkheim’s notion of ‘collective effervescence’ produced by religious ritual in primitive societies and Goffman’s notion of interaction rituals as the core of human social life. Concerning the latter, they say:

Emotion-arousing interaction rituals, with handshakes, pats on the back, active role-taking, and other emotional gestures, became hominins’ first language, and it is still the primal and primary language for humans when they engage in social relations. We watch emotions in face and body more than we listen to talk, unless inflections of talk reveal emotions. (Turner, 2018: 102).

They conclude that ‘we should reorient evolutionary sociology to studying emotions first and then to explaining what emotions made possible for hominins and then humans’ (Turner, 2018: 109). Thus it is that the central aspect of human nature is the vast array of emotional connections among humans. None of the features of human nature emphasized by sociobiology and evolutionary psychology – such as status-seeking, sexual attraction, kin selection, and ethnic affiliations – are mentioned at all. The authors play down the importance of kin selection in humans, claiming that the human nuclear family is built primarily by emotions of love and other positive sentiments rather than by kin selection. This is surprising in light of the fact that in an

earlier book (Maryanski and Turner, 1992), the authors gave great emphasis to the role of kinship in structuring social life in tribal societies (perhaps they have changed their minds).

THE CONTENT OF SOCIOLOGICAL WORK

We now turn to review research and theory in some of the content areas in which evolutionarily or biosocially oriented sociologists have engaged.

Incest Avoidance

The most fundamental fact about family relations in every society is that they should not be incestuous. The most popular theory of incest avoidance among evolutionary anthropologists and evolutionary psychologists today is sociologist Edward Westermarck's (1922) old theory, which turns out to be the theory for which there is now the most compelling evidence. Westermarck's argument was simple and straightforward: children of opposite sex reared in close contact with each other in early childhood will develop a sexual indifference or even a strong sexual aversion to each other. There is either no attraction, or the thought of sexual relations is repugnant. As a Darwinian, Westermarck reasoned that, because the offspring of incestuous unions tend to have above average levels of inbreeding depression – deformity and disease – such unions had to have been selected against in the evolutionary past. The brain had to have evolved a mechanism that would trigger disinterest or aversion, and thus sexual avoidance, under certain environmental conditions. The most common condition would be close contact early in life, because the parties in most instances would be sister and brother. But Westermarck said that the brain cannot distinguish actual siblings from stepsiblings or unrelated children.

All that matters is that the children, whatever their ancestry, be in close contact from a very early point.

Numerous anthropologists and evolutionary psychologists have carried out research to support Westermarck's theory (e.g., Fessler, 2007; Kushnick and Fessler, 2011; McCabe, 1983; Wolf, 1966, 1970, 1995; Wolf and Durham, 2004). Sociologists have paid little attention, but they have not been totally missing in action. The first to pay attention was Joseph Shepher (1969, 1983), who discovered an extraordinary set of mating patterns in Israeli kibbutzim. These settlements were devoted, among other things, to creating a communal economy and to eliminating the nuclear family, which was thought to be oppressive. Children were removed from their parents at birth and reared by teams of nurses in communal nurseries. Here they received their upbringing and education, and their parents had limited contact with them. Shepher examined the records of 2,769 marriages occurring in many different kibbutzim and found that only 14 took place between members of the same *kevtutza* (childhood group), a stunning 99.5% rate of outmarriage. These 14 exceptions turned out to be instructive in their own right. In seven of the marriages, the couple joined the same *kevtutza* between the ages of 4 and 8 years, and in five of the marriages, they joined between the ages of 10 and 15 years. In one case, the couple was together at birth but separated between the ages of 2 and 6 years, and in the one remaining marriage the couple was never in the same *kevtutza* (thus apparently misclassified).

To explain this striking pattern, Shepher went back to Westermarck's theory. Somehow *kevtutza* associates, most of whom were genetically unrelated and who (except brothers and sisters) were encouraged to marry (there was no incest taboo within a *kevtutza*), felt no attraction for each other. Or at least this is what they told Shepher when he asked them about their feelings. A common response was, 'We feel like brother and sister'. Thus did Westermarck's 'familiarity

breeds aversion' theory, dismissed by sociologists for decades, gain new life.

Jonathan Turner and Alexandra Maryanski are among the few sociologists who have studied incest and incest avoidance in a comprehensive way. In their book *Incest: Origins of the taboo* (2005), the authors accept the Westermarck hypothesis to explain incest avoidance between brothers and sisters. However, concerning father-daughter and mother-son incest avoidance, they depart from Westermarck. They contend that mother-son avoidance is hard-wired and has been so as far back as humans' ape ancestry. This is because the psychological effects of mother-son incest are much more devastating than incest within the other two family dyads. This is a biological explanation, but not of the Westermarckian type. What then of father-daughter avoidance? Here the authors contend that no Westermarck effect is at work and that there is frequent sexual arousal, especially on the fathers' part, and thus incest would often be likely to occur. If it did, the result would be an extreme disruption of family solidarity, and a culturally selected incest taboo had to be developed to prevent this from happening. (This type of argument has been the traditional sociological explanation of the incest taboo for many decades and is still held by the vast majority of sociologists.)

The authors reject a Westermarckian explanation for father-daughter incest avoidance for an additional reason. They claim that Westermarck's theory cannot apply to family members who are of different generations because they obviously could not have been childhood associates. However, Westermarck argued that there is a 'normal want of sexual intercourse between persons who have been living closely together from the childhood of one or both of them' (Westermarck, 1922: 194; emphasis added). Indeed, this must be the case if the Westermarck theory is true at all. In Darwinian terms, since all nuclear family dyads involve people who are related by 50 percent of their genes, there has to be equal selective pressure against incest in all

three dyads because the genetic consequences of inbreeding depression will be the same for each. It is implausible to argue, as Turner and Maryanski do, that the father-daughter aversion is not biologically predisposed just as the brother-sister aversion is; the father-daughter aversion, from a natural selectionist point of view, should also be explainable in Westermarckian terms.

Another way in which Turner and Maryanski's explanation falters concerns their claim that the growing intensity of emotional bonds between nuclear family members in hominin evolution would have led to greater sexual arousal. This is problematic in that the authors have conflated two completely different kinds of bonds: *familial bonds* and *sexual bonds*. One does not imply the other, in fact, evidence strongly suggests that they are inversely related. This evidence comes from Mark Erickson (1989, 2004), a psychiatrist who has treated hundreds of victims of incest. He found in his clinical practice that almost every incestuous relationship was associated with some sort of family dysfunction. This led him to the hypothesis, which is really just an extension of Westermarck, that familial bonding undermines or preempts sexual bonding. When the dyadic units within the nuclear family form strong familial bonds, somehow the individuals involved become unable to form, or at least highly unlikely to form, sexual bonds, i.e., to become sexually attracted to and interested in each other. Natural selection has produced this effect – whose precise mechanisms of action we do not yet understand – because inbreeding produces many harmful genetic consequences and this is fitness reducing.

Fertility

Sociologists have long had an abiding interest in fertility, and in recent years some of them have approached this subject in evolutionary psychological terms. One key issue is

the demographic transition, or the decline in the number of children being born in the early industrializing countries, starting around 1860–1870 and continuing until about 1930–1940. A common explanation of the transition is that fertility rates are mainly determined by the economic value of children's labor. With industrialization in the 19th and 20th centuries, the economic value of children's labor declined, and thus so did fertility rates. Another argument emphasizes female empowerment. As females have become increasingly empowered, they have chosen to have fewer children because having many children can be a burden to mothers.

Yet another way to explain fertility differences between agrarian and industrial societies comes from human behavioral ecology, evolutionary psychology's close cousin. As suggested by Bobbi Low (1993) and Paul Turke (1989), fertility behavior is a matter of adjusting numbers to socioecological conditions so that reproductive success is maximized. Sociologists Arlen Carey and Joseph Lopera (1995) employ this kind of argument, contending that the main determinant of the level of fertility is the level of infant or child mortality. Humans have evolved a 'two-surviving-children psychology', they contend, in which they gear their total fertility to the frequency with which offspring survive to adulthood. When infant and child mortality are high, fertility will be high in order to replace offspring expected to die before they reach reproductive age. But when infant and child mortality are low, fertility is adjusted downward. If two children born are both very likely to survive, why have more? Carey and Lopera (1995: 616) note that Darwin himself argued that,

despite the tendency of populations to outpace the growth of their resources, a countertendency toward population stability is a characteristic of all species. The theory of natural selection suggests that, given the real or potential Malthusian [resource] scarcity and the associated struggle for existence, the fertility of individuals displays a vigorous tendency to track mortality.

Carey and Lopera's argument that people in all societies aim for only two surviving offspring may be claiming too much, but their more general point that fertility should track mortality – higher rates of infant and child mortality tend to be accompanied by having more children (higher fertility), while lower rates of infant and child mortality tend to be accompanied by having fewer children (lower fertility) – can be accepted. In fact, demographers have long thought that fertility levels should be highly responsive to infant and child mortality, and a number of studies show this to be the case.

In an attempt to test the economic, female empowerment, and behavioral ecological theories directly against each other, Sanderson and Dubrow (2000) looked at fertility levels in 42 contemporary societies in 1960 and 63 societies in 1990. Results of their regression analysis consistently showed that infant mortality was the strongest determinant of fertility and the level of female empowerment the second strongest (although considerably weaker). When infant mortality was high, fertility was high, and when female empowerment was high, fertility was low. The economic value of children's labor was measured by using the percentage of the labor force working in agriculture along with the percentage of the population living in urban areas. Neither of these factors made any difference. A follow-up analysis of fertility rates in 145 societies in 2008 obtained essentially the same results (unpublished research by the author). Therefore, both the behavioral ecological theory and the female empowerment theory passed empirical scrutiny, but the economic value of children's labor theory did not.

It is often claimed that the decline in fertility with industrialization is maladaptive because people are no longer maximizing their reproductive success. However, the issue is not the total number of children produced, but the number of children who survive and have a chance themselves of being reproductively successful. Van den Berghe

and Whitmeyer (1990) have picked up on this theme by using the concepts of r and K selection. They suggest that three reproductive strategies can be found in modern industrial societies and that these vary by social class (and thus resource availability). The stable working class and the middle and upper-middle classes tend to follow an extreme K strategy. Here people limit themselves to two or three children in whom they invest heavily. There is a quality-quantity tradeoff in favor of quality. Parental investment involves high-intensity care and the investment of economic and educational resources in order to equip offspring for success in a highly competitive environment. A second strategy is employed by the upper classes, whose members can have both quantity and quality. This is a less extreme K strategy. Finally, the lower classes, especially stigmatized racial or ethnic minorities, adopt a more r strategy. Here fertility is higher and parental investment is lower. Quantity is preferred over quality as a strategy of reproductive success.

Another important issue in evolutionary analyses of reproduction is the relationship between social status and reproductive success, especially male reproductive success. Hundreds of studies have shown a close relationship between male dominance and reproductive success in a wide range of animal species. These studies assess reproductive success primarily in terms of the number of copulations, the number of copulations with estrous females, or the number of offspring sired. In an exhaustive review of these studies carried out by Lee Ellis (1995), 93% reported a positive relationship between male dominance and reproductive success for nonprimates and 83% a positive relationship for primates. In some cases, the relationship may be extreme. In walruses, for example, a single dominant male may sire up to 80% of the offspring.

Does this relationship hold for humans? Indeed, in nonindustrial societies it holds quite strongly (see Hopcroft, 2006: Table 1, for a review of 25 studies). It is often claimed

that it no longer holds for industrial societies, or even that the relationship has been reversed, but a number of studies suggest otherwise. Kanazawa (2003) used data from the General Social Survey ($n = 13,409$) in an attempt to replicate Daniel Pérusse's (1993) finding that high-status men did not have more biological offspring, but they did have more sex, leading Pérusse to conclude that in the ancestral environment, lacking modern contraception, high-status men would have had more offspring. Kanazawa found what Pérusse found, that high-status males had no more biological offspring but did have more sex. Rosemary Hopcroft (2006), also using data from the General Social Survey, found that high-status males, as measured by income level, actually did have more biological offspring. Fifty-year-old men at the highest income level had an average of 1.95 children, whereas men at the lowest income level had an average of 1.60. But for women the opposite was the case. Fifty-year-old women at the highest income level averaged 1.30 children, whereas women at the lowest level averaged about 2.50. Both sets of findings are, as Hopcroft concludes, consistent with the predictions of human behavioral ecology. In a more recent study, Hopcroft (2018) found that personal income and personal net worth are positive predictors of men's number of childbearing partners and fertility, whereas for women, personal income and personal net worth are negative predictors. These findings are thus consistent with Hopcroft's earlier study.

The Trivers-Willard Hypothesis

An important idea in evolutionary biology is the TWH, which addresses sex ratio at birth. The hypothesis holds that mothers in good health will produce more sons, whereas mothers in poor health will produce more daughters. There will also be a bias in parental investment after birth such that mothers in better condition will invest more in sons and mothers in poorer condition will invest more

in daughters. Trivers and Willard argued that, in the case of humans, good condition could be indicated by a high (or higher) position on a socioeconomic scale, whereas poor (or poorer) condition could be indicated by a low (or lower) position along such a scale. Mothers of higher status should thus produce more sons and favor them, whereas mothers of lower status should produce more daughters and favor them. This outcome is dependent on a correlation between reproductive success and social status in which the potential reproductive success of high-status sons exceeds that of their sisters, whereas the potential reproductive success of low-status daughters exceeds that of their brothers. (For a more detailed summary, see Salmon and Hehman, 2020).

Numerous studies designed to test the hypothesis have been conducted by evolutionary psychologists in a range of non-industrial societies and the hypothesis has been largely supported. But does it hold for modern industrial societies? Several studies have been conducted by sociologists but they come to different conclusions. One of the first studies designed to answer this question was conducted by sociologists Jeremy Freese and Brian Powell (1999). They studied several thousand 8th-graders and their parents and assessed parental investment in several ways: how much money parents had saved for college, whether they sent their children to private or public schools, the kinds and number of educational objects in the home, parents' involvement (or lack thereof) in parent-teacher groups, whether parents enrolled their children in cultural classes and provided them with other cultural activities, and whether parents knew their children's friends and the friends' parents. Results showed no support for TWH, with high-status and low-status parents investing about equally in sons and daughters.

In another investigation, sociologists Lee Ellis and Steven Bonin (2002) studied 11,000 college students in the United States and Canada. They determined the sex of each

student and the sex of their siblings. Using a variety of measures of the social status of the students' parents, they found no relationship between status and the sex ratio at birth.

By contrast, in a 2005 study Rosemary Hopcroft used data from a national survey of more than 22,000 Americans and measured parental investment in terms of the years of education attained by a child. Hopcroft contends that her results support TWH, but the differences in son versus daughter investment between high-status and low-status parents were very small. For example, sons of parents at the very highest level of socioeconomic status received 16.6 years of education, daughters 16.1 years. And sons of parents at the lowest socioeconomic level received 10.6 years of education whereas daughters received 11.0 years. In a later study, Hopcroft and Martin (2014), using similar but more recent data, obtained similar results. Yet once again the differences in parental investment in the education of sons and daughters were very small.

Because of the contradictory findings of these studies it is difficult to know what to conclude (several other studies, e.g., Keller et al., 2001, find no support for TWH in industrial societies). It may be that TWH does not apply to industrial societies for the simple reason that in such societies the reproductive potential of males differs little from that of females. This is because industrial societies have legally imposed monogamy, whereas most nonindustrial societies permit polygyny and high-status males tend to have several wives. Monogamy reduces male reproductive potential. In addition, the marital prospects of women in industrial societies, especially over the past century, have not differed significantly from the prospects of men.

Gender

Long before more than a tiny handful of sociologists had started paying attention to human biology, Steven Goldberg (1973)

wrote a book with the politically incorrect title *The Inevitability of Patriarchy*, which he revised in 1993 under the title, just as politically incorrect, *Why Men Rule*. Goldberg was primarily concerned with explaining why men in all societies monopolize political leadership and positions of high status. He concentrated on hormone differences between the sexes, pointing out that adult males have testosterone levels about 10 times as high as those of adult females. Testosterone is known to be closely linked to aggression and to dominance and competitive behaviors. Women are at a natural disadvantage in the competition for positions of leadership and status. Goldberg makes an important point, but his analysis is limited by an exclusive focus on a proximate cause. He fails to explain why it is that men have testosterone levels so much higher than women, i.e., why these levels have been selected for in biological evolution. The answer can be supplied by evolutionary psychology. Goldberg can be excused for this in 1973 inasmuch as evolutionary psychology did not yet exist, but not for it in 1993, when it had become established.

Lee Ellis and colleagues (2008) examined the results of some 18,000 studies of universal sex differences, which they referred to as average sex differences in cognition and behavior, or ASDCBs. These studies covered a large number and wide range of societies from all of the major regions of the world. Ellis and colleagues found 65 universal ASDCBs and organized them into seven categories: (1) Stratification and work (12 traits) – males work longer hours outside the home and are more likely to work in so-called male-typical occupations, such as supervisory, scientific, and engineering jobs; females are more likely to work in occupations that are more people-oriented and involve caregiving. (2) Drug consumption and illegal behavior (five traits) – males drink more alcohol and are engaged in more criminal behavior than females. (3) Social and play behavior (12 traits) – females are more cooperative and more likely

to help others, whereas males engage in more competitive behavior; males are also more likely to behave toward members of the opposite sex in openly sexual ways. (4) Personality and general behavior (seven traits) – males engage in more exploratory behavior, take greater physical risks, and are more likely to engage in aggressive behavior toward one another; females are generally friendlier and, in all countries, expressed more concern with being overweight. (5) Attitudes and preferences (12 traits) – males show more interest in science and technology and are more interested in participating in and watching sports; females have a stronger preference for marriage partners who are wealthier and taller than they are, whereas males prefer mates who are younger and shorter than they are; women show more interest in schooling, and men show more interest in sex. (6) Mental health (12 traits) – such behaviors as learning disabilities, hyperactivity, psychoticism, and autism are more common in males, whereas females display more anorexia, bulimia, and panic attacks. (7) Emotions and perceptions (five traits) – females are more likely to perceive hazards in their environments and greater feelings of stress, whereas males indicate more boredom.

Ellis (2018) explains these universal sex differences by means of a theory he calls the Evolutionary Neuroandrogenic Theory. This theory emphasizes that the proximate cause of the sex differences is the effect of sex hormones – androgens in the case of males and estrogens in the case of females. But why these differences in the sex hormones and their effects? Ellis joins proximate with ultimate causation in contending that natural selection has crafted these hormonal effects so that they promote the respective reproductive strategies of each sex. In this regard, he completes the proximate theory proposed by Goldberg.

To continue with the theme of hormonal differences, a major study of the influence of hormones on gender identity and gendered behavior was conducted by the sociologist

J. Richard Udry (2000). Udry relied on data from the Child Health and Development Study, a major research project in which blood samples were obtained from pregnant women between 1960 and 1969 and then frozen for 30 years. In 1990 and 1991, Udry and his research team interviewed many of the daughters born to these women between 1960 and 1963, who were by then in their late 20s. The respondents completed a variety of questionnaires designed to determine their degree of femininity or masculinity and their socialization experiences. Udry found that prenatal levels of sex hormone binding globulin (SHBG) had a strong effect on the daughters' levels of femininity or masculinity when they were adults. SHBG binds testosterone and transports it in the blood, and the higher the SHBG level the lower the level of testosterone. Women who had low prenatal SHBG levels (and thus high prenatal levels of testosterone) were significantly more masculine in their gender role orientations and behavior than women with high SHBG levels (and thus low prenatal levels of testosterone).

Because Udry was only studying prenatal hormone levels and masculine versus feminine orientations in females, and because there is much less variation in these orientations within the female sex than between females and males, his findings have major implications for male-female differences in gender orientations. Because males have much higher levels of prenatal androgens, it is unsurprising that their highly masculine behavior contrasts sharply with that of women's feminine behavior.

It is noteworthy that Udry found that socialization played a role in determining levels of masculinity and femininity, but in a very specific way inconsistent with traditional sociological explanations of gender. Socialization experiences interacted in an important way with prenatal hormone levels. Women who had low prenatal exposure to androgens were responsive to their parents' socialization efforts: feminizing socialization efforts made them even more feminine. But

women who had high prenatal androgen levels, and thus who tended to be more masculine right from when they were very young, were almost completely resistant to their parents' efforts to encourage feminine behavior. In fact, parents who worked hard to encourage femininity in less feminine daughters were not only unsuccessful, but their efforts tended to backfire: the daughters became even less feminine in adulthood.

Hopcroft (2002, 2009) has attempted to explain certain recurrent features of male-female interaction. She summarizes the results of experimental studies showing that, in mixed-sex groups, females report having lower task-related self-esteem compared to males. She also points out that throughout the world women tend to be deferential to men in many types of interactions. Hopcroft offers a sexual selection theory to explain these patterns, contending that they result from differential male and female reproductive strategies. Because men desire both youth and controllability in their mates, females evolved an unconscious psychological disposition toward deference because it advertised their desirability as mates. And males evolved a disposition toward greater self-esteem and authoritative decision-making because it advertised their competence as providers of resources and protection, traits highly desired by females. Interestingly, Hopcroft's research using data on 29 societies from the 1996 General Social Survey and the 1990 World Values Survey finds that women do not display lower self-esteem and deferential behavior once they have passed the age of menopause. This supports her argument because most postmenopausal women are no longer in the market for mates.

A subject of much discussion in recent years is whether cognitive skills are sexually differentiated. There is a great deal of evidence suggesting that they are. Women consistently score higher than men on tests of verbal ability, as well as on tests involving remembering the locations of objects, whereas men consistently score higher on

tests of spatial ability, route finding, maze running, and the mental rotation of objects. These differences have been found throughout the entire range of human societies and in many other mammalian species. Most of this research has been conducted by psychologists, including evolutionary psychologists, but the sociologist Irwin Silverman and his colleagues have also explored this research area. In their original research (Eals and Silverman, 1994; Silverman and Eals, 1992), the authors administered several tests to students from Toronto's York University. The first test was designed to measure spatial relations and mental rotation. Men scored much higher on both measures. A second test involved measures of object and memory location. As expected, women did better, although the difference was not large. A third test used a different measure of location memory. Once again, women scored higher, but in this case the difference was large, with women scoring 70% higher than men.

In another study, Silverman and colleagues again used a student sample from York University (Silverman et al., 2000). The most interesting part of this study was two 'wayfinding' tests. Students were led one at a time in a roundabout manner through woods and asked to do two things. First, they were stopped at certain prescribed locations and asked to place an arrow that pointed in the direction in which the walk started. Then they were asked to lead one of the experimenters back to the starting point via the most direct route. Results showed that males performed significantly better on both tasks than females.

To test for the extent to which these sex differences are widespread or, indeed, may be universal, Silverman and colleagues (2007) used data collected via the Internet by the British Broadcasting Corporation (BBC). Over 200 countries and 250,000 participants were represented in the study. The BBC researchers asked participants to respond to several tests, including tests that measured object location memory (OLM) and three-dimensional mental rotation (3DMR). The

authors used data from 40 of the countries and the seven different ethnic groups the BBC study included. In all 40 countries and seven ethnic groups, men scored higher than women on mental rotation. For 35 countries and all seven ethnic groups, women scored higher than men on location memory. The authors' conclusions?: 'This study unequivocally supported the universality of the male advantage in 3DMR across human societies. Though the same cannot be said for OLM, the data provided a strong suggestion of a universal difference' (Silverman et al., 2007: 267).

To explain these sex differences, Silverman and colleagues have proposed what they call the Hunter-Gatherer Theory. Their theory is based on the cognitive implications of the sexual division of labor in societies characteristic of the ancestral environment. Tracking animals and killing them requires different kinds of spatial skills than plant collecting. Tracking animals requires the kinds of skills at which men are consistently found to be superior: mental rotation of physical objects in three-dimensional space, maze learning, and map reading. By contrast, foraging for plants requires remembering the location of objects, a skill at which women are consistently found to be superior.

ADDITIONAL WORK

Space limitations prevent more than brief mention of additional biologically based research by sociologists. François Nielsen has done important research on individual achievement using behavior genetics. In an early article (Nielsen, 2006), he used data from over 1,000 US adolescents between the 7th and 12th grades. He found that genetic differences explained the majority of the variance in verbal IQ, grade point average, and college plans, whereas shared environment explained very little. Genetic differences explained 54% of the variance in verbal IQ, 67% of the variance in grade point

average, and 60% of the variance in college plans. By contrast, shared environmental differences explained only 14%, 0.2%, and 3%, respectively, of these outcomes. The rest of the variance was attributable to unshared environment. In a later study, Nielsen and Roos (2015) investigated educational attainment. Here the results were different, with genetic differences explaining only 23% of the variance in years of education and shared environmental differences explaining 41%. The authors conclude that these latter results, highly atypical for behavior genetic studies, indicate that the US still has a significant amount of inequality of educational opportunity across families.

Daniel Adkins and Stephen Vaisey (2009) have hypothesized that the strength of genetic influence on status attainment is moderated by two important environmental factors: the level of resource inequality and the level of social mobility. They argue that where inequality is low and mobility is high, the impact of genes will be substantially greater than where inequality is high and mobility low.

Adkins and colleagues (2018) have conducted research on social epigenetics. Epigenetics involves changes in gene function triggered by aspects of the social environment. Some environmental stressors, although not changing DNA nucleotide sequences, can alter gene expression by silencing some genes and activating others. For example, childhood abuse is known to produce epigenetic effects in the gene known as NR3C1, a gene that regulates stress hormone activity in the brain, increasing vulnerability to mental disorder later in life.

Kanazawa and Still (2000) have attempted to explain why men engage in much more criminal behavior than women in all societies. Their article is grounded in evolutionary principles and is closely related to the work of the evolutionary psychologists Martin Daly and Margo Wilson (1988, 1997) on homicide. Anthony Hoskin and Lee Ellis (2014; Ellis and Hoskin, 2015) use Evolutionary Neuroandrogenic Theory

(previously discussed as an explanation of gender differences) to explain criminality. The theory assumes that males evolved high levels of androgens relative to females in order to compete for resources. Males need resources to attract mates, and some males must resort to criminal behavior to acquire these resources. The authors test this theory by measuring the 2D:4D finger ratio of 445 individuals, 2D:4D being a measure of testosterone. Their results showed that 2D:4D ratios varied in the expected direction, i.e., higher levels of testosterone were associated with greater criminality. Interestingly, this was true for females as well as males; in fact, the relationship was even stronger for females: high-testosterone females were more crime-prone than females with lower testosterone levels. Along with Ellis, Anthony Walsh is one of the leading sociologists to take a biosocial approach to criminality. He has authored many publications on numerous dimensions of criminality (e.g., Walsh, 2002; Walsh and Jorgensen, 2018). Kevin Beaver has conducted extensive research on the genetics and genomics of antisocial behavior (e.g., Beaver et al., 2018). Jeff Davis and Kristen Damron (2018) have carried out important research on the evolutionary foundations of stress and stress hormones.

Anna Rotkirch (2018) has carried out research on what she calls evolutionary family sociology. She has written a particularly interesting article on what is called 'baby fever' (Rotkirch, 2008), a phenomenon in which many childless women develop a strong (often overpowering) desire to have a child around their mid 30s. Kanazawa and Still (1999) argue for a female choice theory of marriage practices. Their theory assumes that women determine the marriage practice and that they will choose polygyny when the resource inequalities among men are great and monogamy when these inequalities are relatively low (but see the strong critique by Sanderson, 2001b). Allan Mazur (2005, 2015) has carried out extensive research on the biosociology of dominance and

deference, particularly as it is expressed in face-to-face interaction, comparing humans to nonhuman primates.

Kanazawa (2015) and Turner and colleagues (Turner et al., 2018) have written on the evolutionary foundations of religion. Kanazawa's work is similar to Sanderson's discussed above in that he regards religion as a type of biological adaptation. He suggests that religion may have evolved to promote subjective well-being and a sense of meaning and purpose in life, secondary adaptations that have promoted the primary adaptations of survival and reproductive success. The work of Turner and colleagues is quite different. It takes as central Durkheim's classic view that what is most important about religion is its contribution to social solidarity. The authors attempt to show, through an analysis of hominin evolution, that religion evolved to bind highly individualistic hominins into cohesive social groups.

TOWARD THEORETICAL SYNTHESIS: DARWINIAN CONFLICT THEORY

Evolutionary psychologists have argued that their field, built as it is around one of the most successful scientific theories of all time, provides a unifying perspective for the social sciences. This is true to a large extent, but if they mean a complete theory then that cannot be the case. There is far too much variation in human behavior and human societies, both historically and cross-culturally, for that to be true. But it is a very good foundation on which to build. As noted above, Sanderson has attempted to synthesize evolutionary psychology with some existing sociological and anthropological theories to produce a more complete overall perspective, DCT. He identifies this as a research program (*sensu* Lakatos, 1970) rather than a theory *per se*. In its current and most fully developed form, it is contained in an article entitled 'Darwinian conflict theory:

A unified evolutionary research program' (Sanderson, 2015).

DCT attempts to link evolutionary psychology or, as Sanderson prefers to call it, sociobiology, with four existing theoretical programs: sociological rational choice theory, which assumes that social behavior is the result of individual actors who act purposefully to maximize benefits and minimize costs with respect to certain preferences or goals, but within a broad set of institutional and socioecological constraints; sociological conflict theory, especially in its Weberian version, which assumes that the essence of social life is the competition for scarce resources, especially economic and political resources; anthropological cultural materialism, as developed by Marvin Harris, which assumes that certain material conditions, especially modes of production and reproduction, are the predominant factors that shape the structure of society; and social evolutionism, which consists of a broad set of approaches that trace out and seek to explain long-term evolutionary trajectories of social change. DCT contains 51 axioms, 52 postulates, 18 theories, and 354 propositions. Space precludes more than a brief outline.

The axioms are considered self-evident truths that are assumed without proof for the sake of studying the consequences that follow from them. These are organized into seven categories:

- i General (4 axioms)
- ii Evolution of the Brain's Architecture (10 axioms)
- iii Adaptive Arrangements (5 axioms)
- iv Human Interests (4 axioms)
- v Socioecological Context (6 axioms)
- vi Self and Others (8 axioms)
- vii Culture Acquisition (13 axioms)

The postulates and theories are organized into 18 substantive (topical) sets. Sanderson defines a postulate as a fundamental principle that is less general and abstract than an axiom in that it is tied to a specific substantive content; a postulate expresses a known or assumed fact. A theory is a bundle of

interconnected propositions, and a proposition is a statement of relationship between variables. The topical sets of postulates, theories, and propositions are as follows:

- A Reproductive Strategies Theory (3 postulates and 13 propositions)
- B Parental Investment Theory (3 postulates and 16 propositions)
- C Economic Subsistence Theory (2 postulates and 12 propositions)
- D Economic Exchange Theory (5 postulates and 12 propositions)
- E Dietary Choice Theory (1 postulate and 19 propositions)
- F Incest Avoidance Theory (3 postulates and 7 propositions)
- G Mate Choice Theory (3 postulates and 19 propositions)
- H Sexual Choice Theory (1 postulate and 32 propositions)
- I Marital Choice Theory (2 postulates and 29 propositions)
- J Kin Selection Theory (2 postulates and 14 propositions)
- K Gender Differentiation Theory (3 postulates and 28 propositions)
- L Gender Inequality Theory (1 postulate and 12 propositions)
- M Status Competition Theory (5 postulates and 19 propositions)
- N Wealth Accumulation Theory (3 postulates and 14 propositions)
- O Geopolitical Theory (4 postulates and 39 propositions)
- P Human Aggression Theory (3 postulates and 26 propositions)
- Q Ethnic Attachment Theory (6 postulates and 14 propositions)
- R Religious Choice Theory (4 postulates and 27 propositions)

The Popperian philosophy of science specifies that the essence of science is the ability of theories and propositions to be subjected to falsification. If such statements cannot in principle be falsified, they do not count as scientific statements. In the case of DCT, 52 social outcomes are indicated that, if present to a significant degree, would lead to the falsification of DCT (or at least some

portions of it). For example, DCT forbids the existence of agrarian societies in which women plow and men engage in domestic work; the existence of polygynous societies in which most polygynists are low-status men; the existence of societies without sexual differentiation; the existence of societies in which women compete more vigorously than men for positions of high status; the existence of societies in which most homicides are committed by older women against other older women; and trajectories of social evolution in which large-scale and complex societies give way to smaller and simpler ones. These, along with the remainder of the 52, are only some potential falsifiers. There are many more.

CONCLUSIONS

Forty years ago, Lee Ellis (1977) proclaimed that by the year 2000 sociobiology would have absorbed much of sociology. Obviously, this has not happened, not even remotely. There has been real progress in that a greater number of sociologists are now taking human biology seriously (even though many of these still fail to embrace a fully Darwinian evolutionary perspective). Yet psychologists and anthropologists remain far ahead of sociologists, and for a number of reasons. They have always known much more human biology than sociologists have, with many sociologists' knowledge of human biology being embarrassingly thin. This has proved a serious handicap. Sociologists have also been handicapped by their almost exclusive focus on one type of society, modern industrial society, whereas by contrast, anthropologists' much greater knowledge of cross-cultural regularities and universals has sensitized them to the likelihood that such social and cultural patterns have deep biological roots. So sociologists have much ground to make up. Will they be able to do it? I see no reason for excessive optimism, but if they fail to do

so they will end up terribly marginalized as a discipline. A Darwinian perspective is the great unifying foundation that the social sciences need. Many psychologists and anthropologists learned this lesson several decades ago. Sociologists may eventually learn it. But will it be too late?

Note

- 1 I use the term sociobiology rather than evolutionary psychology when the scholars in question use that term. Otherwise I use the term evolutionary psychology. When van den Berghe wrote *Man in society*, the term evolutionary psychology had not yet been formulated. Actually, I prefer the term sociobiology because it is more suitable to the kind of work I do, but I also yield when necessary to prevailing usage.

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Evolutionary Psychology and Political Science: The Role of Human Psychology in Institutional Structures

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One of the theoretical and empirical problems confronting those concerned with the current decay, and increasing collapse, of the liberal international order revolves around the issue of why the liberal institutions we have counted on for stability and prosperity for the better part of the last century no longer appear sufficient to sustain world order. Part of the reason for this gap in understanding, and the subsequent inability to properly manage the current crises, results from an incorrect understanding of the nature of human psychological architecture on the part of most political scientists, scholars of international relations, and political policy makers. In particular, any investigation of similarities or differences between the ancestral conditions that shaped human responses to collective living and modern institutions designed to preserve the liberal order are completely neglected. Leaving aside the issue of whether or not the most recent instantiation of liberal institutions represent the best alignment with underlying human

psychology, it is clear that they may no longer offer the same benefits that might have existed in past collective life and thus may produce negative outcomes, including large amounts of inequality, exploitation, and poor health for the majority of people.

One of the fundamental limitations in most academic analyses of political science lies in the almost complete quarantine of individuals from any explanation of state-level outcomes. Indeed, the vast majority of models in political science have largely ignored or neglected the role of the individual in larger state action, assuming that state structures, institutions, and organizations drive important decisions and behavior independent of individual action. As a result, the importance of individuals and foundational aspects of human psychology have largely been either dismissed, ignored, or neglected in most dominant theoretical models in international relations, such as realism (Waltz, 2010), liberalism (Gourevitch, 1978; Keohane and Nye, 1977; Milner, 1997), or

even constructivism, which relies more heavily on sociological notions of intersubjectivity (Wendt, 1992). There are a few important exceptions, but these are rare (Jervis, 2017). Rather, it has been widely assumed that institutions can make appropriate corrections for individual human failings in rationality, balance out errors assumed to be random in nature, and provide appropriate incentives to encourage optimal behavior (King and Zeng, 2001). Therefore, potential ways in which systematic human traits or biases might combine across individuals to make things worse rather than better has received less attention. The way that tendencies can add up rather than cancel each other out is true, despite the fact that systematic biases have been demonstrated in studies conducted in social and cognitive psychology and organizational behavior (Kahneman, 2011). Potential misalignments between human psychology and state-level institutions have received very little attention in the mainstream political science literature.

Yet, if scholars are to provide any helpful redress to the increasingly existential challenges posed to the international system by strong forces such as populism, xenophobia, mass migration, climate change, and rising inequality, they will need to grapple with the powerful endogenous forces within the minds of the average person as well as the elites on whom the field has traditionally been focused. And to do so in an accurate way, the field needs to rely more heavily and explicitly on a much more robust, parsimonious, and useful theory of human psychology than the classical economic models, that largely depend on assumptions of rational choice in decision makers, that have largely dominated the field. There is little question that providing a more accurate model of human psychology might improve the theoretical accuracy and empirical validity of models in political science and international relations, which might also help to improve and stabilize the institutional structures that are developed by, and designed to serve, people. Models drawn

from evolutionary psychology offer a productive research agenda to accomplish this goal going forward.

The consequence of incorporating a more accurate model of human psychology and the behavior it motivates will help potentiate a more accurate view of both human nature and the institutions it builds that are meant to serve it. A productive research agenda based on a more accurate view of human psychology could examine the ways in which addressing or neglecting basic and longstanding human drives can enhance the success or precipitate the failure of political and social structures and institutions. Developing such models becomes an increasingly urgent concern in order to live successfully together in a world of accelerating resource depletion and environmental degradation. A model of human psychology based on powerful and parsimonious evolutionary theory can help establish a more accurate foundation for developing and sustaining successful institutional structures moving forward.

Hopefully incorporating more accurate models of human preferences and behaviors drawn from evolutionary psychology in a more explicit way can offer more effective intervention strategies for improving world order and stability. Without incorporating the innate forces of individual human psychology in an accurate way, all attempts to solve the world's problems through institutional procedures which are out of alignment with basic human nature are destined to fall short or fail entirely. This is because the people whose goals and desires are not adequately appreciated, understood, supported, or represented by existing organizations will eventually seek to destroy the structures and institutions that they think hurt them and do not serve their needs.

This chapter will discuss how models drawn from evolutionary psychology can help to both explain the forces of nationalism and tribalism currently engulfing the globe, as well as offer a productive research agenda going forward. There are at least

three important elements of the failure to more fully develop and incorporate accurate models of human psychology into our institutional models: its origins, its manifestations, and its consequences. Each will be addressed in turn in the following sections. This will be followed by an alternative set of conjectures drawn from evolutionary models around which a more successful set of political structures might be formulated. These are based on concerns that remain relevant to humans across time and place: resource allocation, control of sex and reproduction, in-group defense and out-group discrimination, and leadership. Each of these concerns have exerted a powerful influence on collective living and survival among humans over time and should be considered in the design of political institutions to maximize prospects for success in the future.

ORIGINS

The origin of the failure to incorporate accurate models of human psychology into our analysis of political structures lies in part, ironically enough, within the nature of human psychology itself, which prefers both certainty (Tversky and Kahneman, 1981) and simplicity (Pothos and Chater, 2002). Specifically, most people – even highly educated people – hold an incorrect view of biology, assuming it can only offer a static, essentialist view of behavior that remains impervious to change, while believing, often inaccurately, that environmental forces are much more variable and amenable to intervention. This view of human behavior is wildly inaccurate on both sides of the equation.

On the biological side, most of the public holds a view of biological processes and genetics that is heavily dependent on a notion of implacable heredity, with little to no understanding of the structure and function of genes or the core influence of environment

in gene by environment relationships (Caspi and Moffit, 2006; Hunter, 2005), much less the role of epigenetics in gene expression itself (Jaenisch and Bird, 2003). As a result, most people view genetic influences as unchanging, although current models and theories in epigenetics shows how responsive basic genetic, biological, and physiological features are to environmental input, from the food we eat to the environments we live in (Cole, 2009). This kind of adaptive system is of course necessitated by any proper evolutionary model that requires environmental input to trigger specific responses based on a variety of possible circumstances. Indeed, over time, associations between particular environmental cues and specific behavioral repertoires are generated through natural selection of basic psychological mechanisms that were associated with the greatest prospects for survival across billions of people over the course of millions of years. Although probabilistic in nature by necessity, even small differences in instinctual response, *contingent on specific environmental cues and triggers*, can provide enormous benefits in prospects for survival over time. It is only with such adaptability and flexibility that it would have been possible for humans to become the dominant species on the planet over time. Indeed, the assumed basis of human dominance now rests on the notion of humans as being uniquely generalist-specialists among animals, meaning we are both able to adapt to a wide variety of environments as well as deploy special adaptations to them, as can be seen from those who have more red blood cells at high altitudes to those who grow larger spleens for longer periods of underwater diving (Roberts and Stewart, 2018). This kind of ecological plasticity has been critical for human survival and would be impossible in the face of genetic inflexibility. In addition, critical aspects of brain development occur *in utero*, showing the deeply individual and idiosyncratic nature of biological formation and genetic expression. This highlights how even simple interventions, such as

greater attention to maternal nutrition, could affect broad aspects of public health and tendencies toward aggression across multiple generations, through shifts in various aspects of gene expression (Roseboom et al., 2006).

On the other side of the equation is the tendency to believe that environments, including political institutions and organizations, are much more amenable to change through external intervention than may be the case in reality. Anyone who has ever tried to intervene in a neighborhood mired in poverty, unemployment, and violence across generations knows how resistant to change entrenched environments can be. A long tradition of research in experimental psychology has demonstrated how powerful situations can be in driving and shaping all manner of behaviors, including processes of conformity, obedience, prejudice, and discrimination (Nisbett and Ross, 1980). For example, people will conform to agreements rendered by other people even when they objectively know that their answer is wrong (Asch, 1956). They will obey arbitrary authority (Milgram and Gudehus, 1978). They will adopt the norms associated with particular roles and scripts (Zimbardo, 2011). And, importantly for political purposes, they will privilege the in-group and discriminate against the out-group, even when such group definition is based on such transient and trivial characteristics as preferences for certain kinds of modern art (Tajfel, 1974). Moreover, individuals are often not aware of the powerful extent to which they and others are affected by these environments they consider so amenable to change. Experimental evidence abounds with examples of this. In early work, Nisbett and Wilson (1977) showed that people generated explanations for their behavior that clearly deviated from the real source of their preference, which often emerged from seemingly trivial environmental cues. In causal attributions about one's own and others' behavior, Ross (1977) showed that people tend to simultaneously overestimate the extent to which other people are affected by their personality and

underestimate the effect to which those others are driven by the environment, in a psychological error so basic it has come to be called the 'fundamental attribution error'. The notable exception is when people are trying to explain their own behavior, in which case they tend to experience themselves as being at the mercy of overwhelmingly powerful external forces over which they have, and can exert, little control.

Thus, just as individuals tend to believe that personality matters more than situations in explaining others' actions, they also tend to believe that biology is much more rigid than it is and that environments are much less influential than they actually are in driving human behavior. The bias of privileging environmental over biological aspects of human psychology in explaining behavioral outcomes establishes a deeply inaccurate view of the foundational bases for human behavior. The reality is that human biology and physiology are built to be supremely responsive to cues from the environmental right down to the genetic level on a moment-by-moment basis, and environments are often much more entrenched than they appear – at least partly because they often serve the interests of those seeking to exploit others, an issue we will return to in the next section. But this flawed view of human nature too often infuses scholarly understanding by privileging the power and influence of institutions over innate human psychology in seeking to understand and shape human behavior in collective political environments, including the propensity toward violence, conflict, and war.

MANIFESTATIONS

The manifestations of this failure to incorporate a realistic view of human psychology into our extant models of institutional functioning become apparent through the many ways in which institutional constraints are

currently failing to provide the stability and order they have provided in the past and which many assume they should be able to provide into the future. Specifically, when human psychology and institutions collide, it is typically not the institutions that win out in the end. When institutions meet important needs and provide certain support that large swaths of a population want and can benefit from, they can function well; but when resources are scarce, uncertainty reigns, inequality rules, violence erupts, or other challenges arise, people revert to their tribal affiliations for reliable cooperation and emotional support faster than many observers might have expected. Many even in the United States have been startled with the rapidity with which many long-standing democratic institutions have collapsed or atrophied since the election of President Trump; these effects are often laid solely at the feet of Trump alone, and yet he was brought to power by an election that reflected widespread dissatisfaction, for various reasons, with the existing political power structures.

These institutions, organizations, and structures had failed to take account of the large number of people feeling that the system was somehow unfair and rigged against them, either for economic (Inglehart and Norris, 2016) or social, sexual, and racial status (Mutz, 2018) reasons. When under threat, regardless of the source, people quickly and easily revert to their tribal communities, where trust is easily and clearly established through bonds of kin and marriage. Indeed, boundaries are most readily established by groups themselves along important coalitional lines that revolve around easily identifiable categories, such as race, sex, or age (Kurzban et al., 2001); these categories are often much more easily identifiable than abstract political ideologies like communism or fascism. The important insight that evolutionary models provide is not so much the obvious notion that people revert to foundational identities when they feel under threat

(although that is certainly true), but rather that the association that matters is fundamentally coalitional in nature.

Why would this matter so much? Human cooperation has allowed groups of individuals to achieve remarkable goals, but one of the first and most important drives and accomplishments relates to protection – from animals, the environment, and, most importantly, other people. To be effective in defense and protection, people had to band together throughout history, most often against non-kin; these coalitions prove essential for human survival, even today. Humans learned to cooperate in order to engage in combat against others more successfully (Wrangham, 1999). Moreover, to cooperate successfully, people need to know who is on their side and who constitutes an enemy, and they need to be able to figure that out in a rapid, effortless way, thus privileging obvious visual cues as indicators of coalitional status (Kurzban et al., 2001).

When laws exist and people trust the fairness and equality of the institutions that provide, regulate, and implement those laws, tribal associations become less critical for survival because processes of redress are clear, consensual, salient, and carry the teeth of enforcement by the monopoly of the mechanisms of coercive power (i.e. the army) that governments often claim. But when such processes are absent, or people do not trust these processes, then reversion to coalitional tribal associations can occur in rapid and powerful ways (Gambetta, 2000), exerting an impact on a variety of factors, from market development all the way down to basic exchange. Barter quickly replaces money under conditions of war and massive deprivation. For example, Cassar et al. (2013: 285) show that the presence of violence in the Tajikistan Civil War ‘undermines trust within localities, decreases the willingness to engage in impersonal exchange, and reinforces kinship-based norms of morality’. Here, the notion of kin becomes key, because in the absence of organizations or institutions that people trust

to protect them, kin-based networks become the best and, often, only reliable source of protection. However, these clan-based networks, agnatic in form, are also associated with high levels of both patriarchy and state instability, at least partly because of their powerful out-group discrimination practices (Hudson et al., 2015).

So here the conundrum of modern politics raises the ugly side of its head, and the mismatch between ancestral conditions and modern politics becomes both obvious and salient. In ancestral conditions, groups were small, and mechanisms such as cheater detection evolved to prevent exploitation and the imposition of fitness costs on a victim or the endowment of fitness gain on a more powerful individual. However, once the size of modern politics makes such tracking mentally impossible, the opportunities for exploitation by unscrupulous actors increase geometrically, and inequality can arise and increase rapidly as a result. This is not to imply that such exploitation is the only reason that inequality might emerge; certainly, it can result from individual differences in capability or effort as well. But leaders who fail to properly represent their constituencies have a greater opportunity for exploiting followers, when large size and multiple decisions make behavioral tracking more complicated. Such exploitation sets the stage for the emergence of the kind of violence that historically has served to overthrow leaders who privilege their own interests over that of the collective (Boehm and Boehm, 2009; Wrangham, 2019). Under such conditions of mismatch between the ancestral conditions under which the psychological mechanisms that govern approaches to collective living emerged and those that govern modern politics, negative outcomes including exploitation and inequality quickly come to prevail, just as ancient preferences for sugar, which helped humans survive in ancestral conditions, set them up for early morbidity and mortality as a result of diabetes and obesity in the modern environment of caloric abundance.

In this way, evolutionary models offer useful predictions regarding how and when powerful coalitional groups come to form, the function they serve, and how and when their constitution might shift (Barkow et al., 1995). Because the basic processes privileging in-group defense and out-group discrimination and destruction have remained the same across time and place, conscious awareness of the important role that equity, fairness, and representative leadership plays becomes critical in the design of institutions to instill trust in the populations they are designed to serve. Models drawn from evolutionary psychology can offer deep insight into the nature of populism, tribalism, nationalism, patriarchy, and other forces that are growing in strength around the globe, by highlighting the important nature, source, and function of in-group favoritism and out-group discrimination for human survival over time. For institutions to survive and thrive, they need to be aligned with the needs and desires of normal individuals to protect themselves from exploitation and harm by others; when political institutions fail to meet those goals, they will be brought down by those same individuals in processes similar to those we can witness around the world now. Seen in evolutionary terms, such a process of unseating those who have exploited their followers constitutes just another step in the mammalian drive toward egalitarianism (Boehm and Boehm, 2009) and self-domestication (Wrangham, 2019); when institutions, organizations, and other structures privilege exploitation by powerful leaders and processes that cause conflict and violence, the larger group will seek to unseat those actors who have created and benefitted from that system. From this perspective, it is not inequality itself that can inspire revolution, but the processes of violent conflict between groups that are instigated by inequality that would most likely spark systemic upheaval. Of course, economic and structural exploitation are not the only ones that can lead to such violence; climate change and other aspects of resource deprivation or

cultural upheaval, particularly around issues of sex and reproduction, can similarly generate the kind of violence that might encourage widespread attempts at systemic overthrow.

CONSEQUENCES

The consequence of incorporating a more realistic model of human psychology and the behavior it motivates, based on models drawn from evolutionary psychology, can result in a more accurate view of both human nature as well as processes of human change, including better prospects for peaceful transformation. Developing a research agenda based on a more empirically supported and theoretically rigorous model of human cognition will allow scholars, policy makers, and other actors and observers to both create new and change existing institutions and other state structures in ways that can more fully meet the basic psychological predilections of the vast majority of humans, not simply reflect the interests of those leaders who more often than not represent outliers in narcissism (Braun, 2017) and psychopathy (Landay et al., 2018), along with other deviant traits (Post, 2014).

A productive research agenda based on an accurate view of human psychology might examine the ways in which addressing or neglecting basic and long-standing human drives can lead to the success or failure for those political and social structures and institutions we need in order to live successfully together in peace and prosperity. There are at least two important areas in which theoretical revision might lead to more accurate and productive notions of human nature. The first has to do with improving definitions of rationality; the second, and related, demands a more accurate appreciation of the real factors that drive human divisions.

First, contrary to what economists argue (Friedman and Savage, 1948), most people value money less than they value their family

and their prospects for survival and reproduction; evolutionary models provide an alternative model of rationality built around this different notion of what is most important to people (Cosmides and Tooby, 1994). In a choice between their money and their life, money rarely wins and, in so doing, diminishes the prospect that such a propensity will be carried forward across generations, by definition. Ecological and evolutionary models of rationality demonstrate how economic notions of rationality fail to properly account for the ways in which most people's values do not privilege money over family and other meaningful coalitional associations. Even longevity data demonstrates that once past a subsistence level of income – around \$75,000 in the United States – more money does not make people happier; however, loneliness has a negative effect on health, an effect that now appears to be worse than the effects of smoking, although both appear to operate through cardiovascular impacts (Luo et al., 2012). In other words, the critical importance of healthy social relationships is baked into human biology in a way that money and finance is not; high levels of non-kin cooperation are not only what makes humans extraordinary but also literally prove essential for well-being and survival.

Second, evolutionary models help locate the enduring and universal factors that both drive and divide humans along coalitional lines. These have tended to revolve around three basic enterprises: resource allocation, control of sex and reproduction, and in-group defense and out-group discrimination (Hatemi and McDermott, 2012). The modern manifestations of these phenomena can change over time and place, but the underlying goal of trying to control and regulate the social world remains. For example, in the current environment, debates over welfare, transgender bathrooms, and immigration represent salient examples of modern instantiations of enduring concerns over resource allocation, sex and reproduction, and in-group favoritism, respectively. In England in

the 19th century, contemporary issues would have revolved around corn laws, prostitution, and slavery, but they would have tapped into the same underlying concerns. Moreover, when leaders are understood to privilege their own welfare over that of their populations, the population can organize and seek to overthrow the system, as the revolutions that raged across Europe in 1848 illustrate: leaders were not just voted out of office, they literally lost their heads to ‘Madame La Guillotine’.

What unites each of these topics are constructions of the relevant group identities: who is deserving of group support and who is not; who is responsible for having and taking care of children; and who needs to fight enemies and the environment. These constructions can be malleable at the margins, but under conditions of threat and uncertainty, they tend to revert to easily identifiable and loyal coalitions, including kin-based networks, where cheating can be easily detected and punished (Cosmides and Tooby, 2005).

Underlying each of these factors are assumed structures of dominance and privilege that both assert leadership but also demand a certain degree of followership. This highlights the various ways in which leadership can emerge and retain power through processes of prestige or coercion and dominance (Cheng et al., 2010). In this way, evolutionary models can provide predictions about what characteristics define each type of leadership and the environmental circumstances under which each is most likely to emerge and thrive. This is a topic that will be addressed in more depth below.

AN EVOLUTIONARY ALTERNATIVE

Thus, the origins, manifestations, and consequences of applying a more accurate evolutionary model of human psychology than the one provided by classical economic or rational choice theory to political structures,

institutions, and organizations clearly reflect the nature of those mechanisms. The challenge lies in the mismatch between the ancestral conditions under which the psychological mechanisms designed to organize collective social and political life evolved and the modern political circumstances that no longer reflect many of the same conditions. As a result, political institutions may not survive populist assaults for failing to meet their needs, and individuals may experience more severe stress and unhappiness as a result of the failure of these institutions to meet their basic needs.

This does not mean that progress cannot be made by leveraging insights garnered from a more realistic approach to human psychology, to create structures that are more closely in line with enduring human values, goals, and interests, even if the environment in which they operate differs substantially from the one in which these forces evolved. The following section briefly sketches out what an evolutionary approach informs us to be potentially the most important factors to consider in designing institutions that properly reflect the most universal and enduring of human interests and values.

BASIC ENTERPRISES

An evolutionary model of human psychology based on powerful and parsimonious theory and meticulous experimental and ethnographic empirical evidence can improve our understanding of the current tribal coalitional forces that threaten the current liberal international order and how they might best be mitigated, ameliorated, or overcome. Indeed, such an understanding may help create political structures that are more closely aligned with enduring human goals. By presenting such a model, it becomes possible to establish a more viable and successful model for institutional structures moving forward.

As noted above, the basic interests revolve around three fundamental areas of concern: resource allocation, sex and reproduction, and in-group favoritism and out-group discrimination. There is interesting and important experimental and empirical work supporting each claim. In the area of resource distribution, for example, Michael Bang Petersen and colleagues (2012) have demonstrated some remarkable findings. In one series of studies, they show that public attitudes toward welfare policy are shaped by anger and compassion and that these responses exist independent of political ideology (Petersen et al., 2012). For example, people show much more compassion toward those who they believe have fallen on bad luck, say as a result of illness that could befall anyone, than toward those who are judged to be lazy and show no inclination to look for work. They posit that such responses were shaped by the need to avoid exploitation by non-kin. Cooperation proves critical for human survival, but so too does the necessity of avoiding exploitation, especially under conditions of resource limitation.

Interestingly, Petersen and colleagues (2013) also demonstrate biological correlates of such drives. Specifically, they show that stronger men show preferences for economic redistribution that matches their particular situation: rich men oppose it more than poor men, while poor men support it more than weaker men. Moreover, transient states of deprivation also appear to affect these judgments. Hungry people are more likely to support welfare policies (Petersen et al., 2013), and this was measured through blood glucose levels (Aarøe and Petersen, 2013). Sznycer et al. (2017) united the motivational mechanisms involved in decision making around support for redistribution and showed how compassion predicts responses to others in need, self-interest guides responses toward the self, and envy drives reactions to outcompete others. These motivational systems predicted support for redistribution better than procedural or distributional fairness.

What is particularly compelling about all these studies is that they were able to show these effects across various cultures, including the United States, UK, Israel, and India, and across different political and economic structures and divergent social environments. This illustrates how underlying motivational mechanisms inform attitudes toward redistribution and shows how economic interests alone do not drive preferences. Rather, contextual factors matter in individual approaches to redistribution, and policy approaches that emphasize fairness alone are unlikely to be sufficient in developing strategies that will meet with widespread approval.

The second area of enduring concern relates to regulating sex and reproduction. Aspects of this question can take on many forms, from debates over transgender troops in the military (an issue that also overlaps with concerns around in-group defense) to divisions around abortion. David Buss and colleagues have explored issues such as jealousy (Buss and Haselton, 2005) and the misperception of sexual interest (Perilloux et al., 2012) from an evolutionary perspective. However, for current political purposes, the question is less about how evolution structures approaches to sex and reproduction but rather how groups promote different forms of regulation around sex and reproduction.

Every society needs to produce and cultivate children to survive and thrive; indeed, there are current large concerns about declines in birth rates in places like Japan, in particular, because of how it bodes for the smaller numbers of younger people available to support and care for large and ever growing numbers of older people (Semuels, 2017). Even the United States is reporting the lowest domestic birth rate in 2018 since 1937 (Tavernese, 2018). Various explanations for these phenomena range from economic recession to gender inequality and from technological interference with real-life sexual interactions to declines in male sperm quality over the last 30 years in Western industrialized countries. However, birth rates

would have been hugely contingent on variant environmental circumstances over time; floods, droughts, famines, and wars would have affected intermittent birth rates in various communities over millennia.

Of course, what is evolutionarily new about this circumstance revolves around the large number of people who are living well past their reproductive potential and well into old age. Most people throughout ancestral times did not live that long and did not use resources that needed to be devoted to cultivating the young. Now that so many people live well into their 90s, in advanced, industrial democracies, we need to find novel ways to support such individuals. Historically, families played such a role, but they typically did not need to do so for decades after their children left home. The drive to care for kin is both ancient and powerful, precisely because such associations provided the backbone of human survival in the ancestral past, and yet the drive has historically been directionally forward looking. Historically, people invested in caring for infants, not for adult offspring or octogenarian or nonagenarian relatives – experiences that have become increasingly common in the modern era. Indeed, 35% of American men aged 18–34 live at home with their parents (Fry, 2016). Certainly, declining birth rates may reflect delays in reproduction for a variety of reasons, including financial constraints as well as a preference for greater investment in fewer offspring, but the length of time involved in such investment is certainly historically novel.

The concern here is not that taking care of kids and elders is hard, although of course it is, but rather that people have different underlying values regarding such investment. One important manifestation of such differences in fundamental values involves notions of *how to regulate the sexual behavior of others*. Few people believe that others should have a right to regulate their sexual behavior, but the majority of people do seem to believe they have the right, even the obligation, to regulate and control other people's sexual

behavior. This is the crux of many policy debates around sex and reproduction: who gets to regulate and decide other people's sexual and reproductive behavior? Of course, in ancestral conditions, small communities would have made it hard for people to not know who the father of a baby was or to allow that father to abnegate responsibility for that child, except upon death, in which case more extended family would have assumed responsibility for helping to raise kin.

But in the modern world, none of that is necessarily true. And in many cases, the strongest sanctions against violating local cultural norms managed and performed by women, who both benefit from and are more seriously hurt by these customs than men. The evolutionarily relevant psychological mechanism that appears to drive much of this behavior lies in the intrinsic intra-sexual competition among women to gain access to male resources. Women who benefit from powerful and/or wealthy men and who are in sanctioned marriages (i.e. the current obsession with white college-educated suburban women in the US electorate) have a strong interest in keeping traditional gender norms and rules in place. This not only protects their position but also allows them to sanction other women and their husbands, who might be tempted to stray with such women. Women who have children without the presence of a partner benefit from systems of government that provide resources in the absence of men to help provide for their children. Such differences in privilege can be understood to emerge as a result of female intra-sexual competition.

One of the areas in which concern over regulation of sex and reproduction, high incentives for intra-sexual competition among and between women, and risk for conflict lies in the domain of polygyny. Empirically clear and strong associations have been found between levels of polygyny and 18 different negative consequences for women, children, and the stability of the nation state (McDermott, 2018a). Where polygyny rates

are high, there are not only negative domestic consequences, such as high rates of maternal mortality, reduced life expectancy, and lower levels of education for both boys and girls, but also significantly lower levels of political freedoms and civil liberties as well as higher weapons spending.

The final area of enduring concern related to in-group defense and out-group discrimination combines two distinct facets. Issues around securing the defense of the in-group can take various forms, with immigration policy presenting the most salient current demonstration of this concern. Genetic work, for example, shows an association between dispositional levels of social fear and opposition to immigration and support for segregation (Hatemi et al., 2013). But such issues relate not only to decisions around who legitimately belongs in the in-group but also to how best to protect and defend that group from outsiders who might wish to do that group harm. This means that this topic also engages issues of conflict and war.

Sell et al. (2009) examined the relationship between anger and support for aggression in a series of innovative experiments. Using welfare trade-off ratio logic, they examined the extent to which the ability to infer costs or withhold benefits could predict anger in conflicts of interest. They showed that physical strength could predict support for aggressive and interventionist foreign policy. In addition, they were able to show across multiple cultures and languages that individuals were remarkably accurate in judging physical strength and fighting ability from pictures of the face and body (Sell et al., 2008) and the sound of a voice (Sell et al., 2010). Additional genetic work provides support for a dispositional foundation for some attitudes toward aggressive foreign policy. Specifically, individuals with higher levels of physical aggression are not only more likely to show support for aggressive and interventionist foreign policy but also make more utilitarian choices in complex moral decision making (McDermott and Hatemi, 2017).

LEADERSHIP

Most people can share specific concerns regarding resource allocation, regulation of sex and reproduction, and in-group defense and out-group discrimination, even if they do not agree on how those challenges should be adjudicated. One of the challenges across time has been to overcome obstacles to collective action in order to engage in cooperative, coordinated action to overcome threats and risks posed by others and the environment. One of the mechanisms that has evolved to help solve that challenge is leadership. However, because leadership, or any form of enforced hierarchy, comes with inherent risks of exploitation, complex dynamics have evolved to not only regulate the relationship between leaders and followers but also reduce the opportunities for systematic exploitation of the powerless by those more powerful.

One of the ways that people have attempted over time to limit the potential for fitness costs at the hands of those who seek to exploit them has been the elimination of leaders who do not take care of their followers, who seek to take a disproportionate share of the resources, or who pursue their own interests over that of the group (Boehm and Boehm, 2009). Under such circumstances, the group will seek to literally decapitate those who fail to support increasingly egalitarian norms over time. Significantly, this process of increasing self-domestication, which can involve extremely high levels of short-term violence, is something we see not only in all primates but also in other mammals, such as foxes, minks, dogs, and horses (Cieri et al., 2014; Hare et al., 2012; Wilkins et al., 2014).

This perspective highlights an important distinction in the origins of human aggression between reactive and proactive aggression (Wrangham, 2018). Reactive aggression occurs within a group, without premeditation, and often in the heat of the moment;

most often, the acts occur as things we come to recognize as crimes of passion. Proactive aggression involves organized, premeditated acts of violence toward out-groups. This distinction becomes particularly important because the boundaries between in-groups and out-groups are malleable at times and susceptible to quick revision based on a variety of factors, including leader manipulation or group identification. From this perspective, rising inequality that offers a new definition of who constitutes the in-group and the out-group within existing institutional structures presents a threat to world stability because it allows psychological justification for violence against others who might have previously been understood to be off-limits members of the in-group.

As noted above, the basic psychology of in-group favoritism and out-group discrimination is long entrenched and robustly demonstrated in evolutionary models of human psychology (Barkow et al., 1995), as well as extant models of social psychology, such as Social Identity Theory (Tajfel, 1974). What changes, in part, over time is how the nature of the in-group and out-group are defined and where the boundary is drawn.

Leaders can manipulate the boundaries of identity through processes of emotional entrepreneurship, including the strategic deployment of fear and outrage (McDermott, 2018b). This can occur because followers receive an important benefit from the coordination that leaders provide in overcoming challenges to collective action; leaders can provide the signal mechanism around which actor expectations converge in a way that allows followers to engage in successful cooperation for in-group construction and out-group combat. This can have enormous benefits. Because the key determinants of victory before the developments of mechanized military might were size and surprise, a leader's ability to recruit a large group to support a military action would have conveyed an enormous advantage. Leaders who could successfully bluff an opponent

might offer a particular advantage because he might be able to get others to retreat without actually having to fight, simply by threatening an unacceptable level of damage; in this way, leaders skilled in the art of self-deception may be more successful in persuasion as well (Trivers, 2000). But this too can be manipulated by leaders for their own purposes. For example, because people are much more likely to support efforts to defend communities as opposed to offensive military campaigns, leaders have an incentive to misrepresent offensive campaigns as primarily defense in nature (i.e. pre-emptive strikes) to cheat the labor-recruitment challenge posed by offensive action (Lopez, 2017).

INTEGRATION

There is one aspect of this discussion worthy of consideration that has evaded discussion up until this point, and that is the role of political ideology. Here, the issue is not the political polarization that runs rampant between Democrats and Republicans in the current US environment. Rather, the reference here is to the historically enduring difference between those on the extreme left of the world political spectrum, as exemplified by communists, and those on the extreme right of that same continuum, represented by fascists. There is evidence that such a difference has existed across time and place (Hatemi et al., 2014).

This facet of human psychology is worth discussion and contemplation precisely because it operates as a top-down organizing mechanism to orchestrate perceptual, emotional, attitudinal, and behavioral responses to a wide variety of phenomena in the world (Hatemi and McDermott, 2016). In short, political ideology shapes and formulates the approach that individuals have to the issues discussed in this chapter, relating to resources, sex, and defense, in a coordinated

fashion. The benefits of this kind of coordination are vast: people can more successfully raise their children by sharing assumed central values with partners; those partners are then able to recruit support for child-rearing more easily if they are not in conflict with each other; and so on.

The challenge, of course, is that there is more than one type of organizing strategy and they are not always compatible. To oversimplify, one style privileges cooperation whereas the other emphasizes the importance of defense and protection. So, the obvious question from an evolutionary standpoint is why political ideology has not converged to universality in form and content, although it clearly has in its ability to structure coordinated responses to the challenges posed by living in social groups. And, again, the answer is clear: as with sex, for society to survive, it needs both types. It needs those who can cooperate and build cohesive in-group structures and institutions and those who will fight to defend those groups and structures from out-group threats posed by other groups and the environment. Each needs the other to survive, and if one form destroys the other, it destroys itself in the process, either by falling into massive internecine internal divisions, warfare, and civil strife and conflict or by being overcome and utterly destroyed by other groups who are more effective in their coordination.

This is not to imply that political ideology is meaningless. Indeed, just the opposite. As with many other kinds of organizing psychological processes and mechanisms, political ideology serves a vital purpose. Everyone has attitudes precisely because everyone has to live in complex social environments that require a great deal of coordination to negotiate successfully. Having an automatic and effortless system that helps to process environmental events and offer cohesive forms of meaning in a systematic, predictable, and comprehensive fashion offers huge advantages for coordination, cooperation, and survival.

CONCLUSION

A great deal of exciting work has begun at the intersection of evolutionary psychology and political science, although most of this has been done by psychologists who are interested in political topics than by political scientists who are interested in psychology. This limits the ability of political science to make use of new findings and perspectives that may prove useful and relevant to addressing current challenges in the discipline and in the political world at large.

The reasons for incorporating evolutionary psychology into political models are numerous and potentially transformative, not least because it would fit in with a renewed interest in the role of individual actors in political outcomes and with the role of behavioral models of decision making, which is beginning to achieve a resurgence in international relations, in particular.

An evolutionary perspective offers a particularly valuable lens through which to analyze events on the world stage, by focusing attention on those aspects of attitudes and values that have enduring and universal influence on human behavior, including processes related to resource allocation, the regulation of sex and reproduction, in-group defense and out-group discrimination, and the challenges involved in achieving effective leadership. Examining the sources of various attitudes and behaviors from this perspective can shed new light on events and outcomes. This perspective encourages analysts to ask new and different kinds of questions that are divorced from the typical preoccupation with purely economic factors, to interrogate the real source of human rationality in relative fitness advantages and costs. These questions allow scholars to search for novel forms of evidence. In this way, scholars can begin to seriously think through the potential misalignments between the ancestral conditions that gave rise to particular psychological mechanisms that evolved to allow humans

to live together successfully in groups and reap the vast benefits that derive from group cooperation and from modern political conditions and circumstances. These investigations can be undertaken with an eye to developing potential ways to overcome such mismatches and to develop institutions, structures, and political organizations that more accurately and effectively represent and maximize the enduring and universal goals, values, and interests that the vast majority of humans share. For example, devising policies simply to reduce inequality might prove insufficient; people want to help those who are worse off but penalize those who are better off. This insight could help generate a more acceptable tax and welfare structure. People often need hierarchy to engage in successful cooperation, but they are wary of exploitation; institutions that are designed to provide careful tracking of decisions and improve transparency about conflicts of interest could help reduce such concern without devolving into disorganized chaos. Political ideology may divide people on how best to address the pervasive concerns, but recognizing that these are the primary concerns and understanding the function they have served may help to design more effective compromises that respect the contribution and value of both cooperation and conflict.

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Evolutionary Psychology and Economics

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INTRODUCTION

How does evolution shape behavior? Economists believe that individuals have well defined preferences over actions and consumption that they can rank. For example, an individual who enjoys wine should be able to say if she likes red wine more than white wine and if she likes white wine more than beer. Such ranking or ordering of preferences follows certain intuitive properties that allow economists to represent preferences by means of a utility function.¹

A utility function stipulates a relationship between an action and a value. Indeed, if an individual prefers red wine to white wine, then presumably the value she derives from drinking a glass of red wine is higher than from drinking a glass of white wine. All other things constant, she will always choose red wine over white wine. Thus, from the point of view of economics, preferences determine behavior and behavior is aimed at choosing an action that achieves the highest

possible value. That is, the utility function is an objective function and individuals choose an action so as to maximize utility subject to constraints. However, are the concepts of preferences and utility consistent with evolutionary psychology? That is, is it reasonable to suppose that evolution endowed us with preferences and utilities?

Rather than preferences, which are intermediate to behavior, one can think of evolution as prescribing rules that program or 'hard-wire' us for behavior. Given that evolution is concerned with reproductive success, all we need is a set of rules that tell us what to do in each possible circumstance we face. For example, the rules would tell us that if we find high-caloric food, we should eat it right away. If we find a snake, we should avoid it. A problem with this view, however, is that the circumstances we face can change quickly. If one were being observed by a potential competitor, for example, the snake may be something to approach rather than to avoid, so as to signal bravery to a mate. If evolution

'hard-wired' us for behavior, we would need to have a rule for avoiding snakes, a rule for approaching snakes, and a rule for deactivating other rules. Prescribed rules for behaving in such a manner would require an adjustment process that is faster than we know it to be and for a milieu of an unimaginable number of situations (Robson, 2001a, b).

It makes more sense to see evolution as having equipped us with general goals or motivations that helped our ancestors achieve successful reproduction. These general goals or motivations should be coupled with mechanisms for adjusting behaviors (Samuelson and Swinkels, 2006). Adjustment mechanisms allow us to continuously learn and to respond to circumstances in the best way. For example, a goal such as status, along with the ability to learn which behavior is most likely to achieve this goal, will lead us to approach a snake in some circumstances, even if it is dangerous to do so. Under this framework, there is no need for rules that tell us what to do in each possible case; instead, all we need are general preferences and utilities coupled with learning algorithms.

At a more fundamental level, it seems reasonable to care about caloric foods and sex, but why do we need to care about status, beauty, or friends? That is, why should evolution prescribe a preference for anything other than successful descendants? Samuelson and Swinkels (2006) answer this important question. The authors posit that it is impossible for humans to have an accurate understanding of the causal and statistical structure of the world. For example, we don't know the exact probability of achieving a successful offspring from a sexual encounter, and humans cannot sample enough offspring to learn these probabilities. By attaching value or utility to beauty as represented by strength and symmetric features, for example, it is possible to 'learn' that age and health correlate with reproductive success. To compensate for the inability to perfectly know the world, evolution would equip us with a utility function

that would provide the goal for our behavior, along with a learning mechanism that would help us pursue that goal. As Samuelson and Swinkels (2006: 120) say: 'Defining utilities in terms of intermediate goods such as consumption gives us an objective that only approximates evolution's in return for giving us the means to effectively learn how to accomplish this objective'.

Despite being endowed with a learning mechanism, our understanding of the world is driven by our sensory perceptions. Because survival often depended on our understanding of the physical world, our brains adapted to make sense of things for which we have sensory perception. For example, we understand that when the Sun is out, temperatures tend to increase. We understand that because we feel warmer. We can therefore infer that sunlight brings warmer temperatures. A causal relationship can then be established between the intensity of sunrays and temperature. So, through sensory experience, we can make sense of our surroundings. Despite this having been an extremely useful tool, it has limitations in a modern world, as sensory perceptions are impossible to obtain in complex interactions.

UTILITY FUNCTIONS

As mentioned in the previous section, evolution seems to have endowed us with preferences for intermediate goods, such as consumption. Evolutionary psychologists presume human behaviors reflect the influence of physical and psychological predispositions that helped human ancestors survive and reproduce. In the evolutionary view, any animal's brain and body are composed of mechanisms designed to work together to facilitate success within the environments that were commonly encountered by that animal's ancestors. We can think of consumption as satisfying an evolutionary need. That is, the utility function of humans is

essentially the evolutionary fitness function – a fitness function is a particular kind of objective function that summarizes how close a given solution is to achieving set aims. This framework is dynamic and stipulates that preferences and the corresponding utility function guide us in taking actions that would have caused our predecessors to successfully survive and reproduce.

If we think about utility functions as an evolutionary fitness function, then there are some important implications to our understanding of economic behavior. For example, thinking of utility as a fitness function can give us a theoretical framework for making sense of differential behaviors across age groups and between men and women. In general, it is widely documented that older individuals and women are more likely to reject fair gambles² than younger individuals and men, respectively (see Albert and Duffy, 2012; Carstensen et al., 2006; Croson and Gneezy, 2009). However, despite the evidence, economists have not provided a satisfactory explanation for these observed differences (Capra and Rubin, 2011).

In contrast, Rubin and Paul (1979) provide an evolution-based framework for explaining different risk preferences between younger men and older men. The authors postulate a theory called life-history theory, which suggests that behaviors can be best understood in terms of effects of natural selection on the reproductive characteristics over the life cycle. In this context, young males need to acquire resources to obtain a mate so as to ensure they have offspring. Those who have no mates will not breed and will not leave any genes for the future. With this in mind, the general preference for taking a risky gamble over a safe one may be necessary. If the risky gamble pays off, it will enable the individual to breed. However, if the gamble results in losses (perhaps even resulting in death), then it will leave the young male's genes no worse off than if the risky gamble had been refused. That is, a young male who has no mate will always benefit from taking gambles. On the

other hand, an older male who has offspring does not have that pressure. Once a male gets older, it pays to become risk averse and avoid even fair gambles – particularly in a Malthusian world where survival is at risk.

As Rubin and Paul (1979) show, an advantage of seeing utility as an evolutionary fitness function is that it allows us to make the structure of the utility function more precise. In other words, it can give us a theoretical framework for making sense of why younger males are more risk prone than older ones. With respect to sex differences in risky behaviors, we can stipulate that males would be more risk seeking than females. Since successful males can have virtually unlimited numbers of offspring and successful females have much more limited fertility, under an evolutionary framework, males would be more willing to gamble than females.³

Evidence on sex differences in lottery-choice tasks is extensive. Byrnes et al.'s (1999) meta-analysis of 150 studies of male and female participants showed that male participants are more likely to take risks than female participants. The mean effect size for a given kind of risk taking was significantly greater than zero. However, the authors also found that sex differences varied according to context (e.g., driving vs smoking) and age; the gap peaked in adolescence and got smaller over time. In a survey of the experimental evidence, Filippin and Crosetto (2016) also find that the magnitude and significance of sex differences in risk taking is task specific.

An evolutionary psychological approach to sex differences in risk taking would predict context-dependent preferences. For example, recent experiments⁴ show that women – even highly successful Harvard MBA students – are less likely than men to enter profitable tournaments (Gneezy et al., 2003; Niederle and Vesterlund, 2007). This is the case in both intersexual and intrasexual competition; thus, females 'shy away' from competition. However, the source of these intriguing results may lie in evolutionary forces that have shaped sex differences in risk-taking

behaviors. As such, there should be a difference in intensity of competition with respect to the kind of reward and the kind of task participants compete over. For example, Cassar et al. (2016) study intersex and intrasex competition of mothers and fathers. The results of the experiment show that when incentives are switched from money to offspring benefits, mothers competed as intensely as fathers, erasing any sex difference in competition that were observed when the reward was monetary. From an evolutionary perspective, the results make sense. Indeed, looking at reproductive outcomes, we can see that both men and women have been subject to intense selection pressures (Knight, 2002). If competitive traits derive from selection pressures, then both men and women should each have evolved competitive traits. This may have been further facilitated by the successful spread of monogamous marriage norms.⁵

In economics, social preferences are represented by utility functions that include others' consumptions as arguments. Fehr and Schmidt (1999) introduced the idea of inequality aversion. An individual is said to be inequity averse if he dislikes the outcomes that are perceived as inequitable. The judgment that an outcome is unfair or inequitable, however, depends on comparing what one has to what others have. That is, relative payoffs matter. Clark and Oswald (1996), using a large sample of British individuals, show that comparison incomes have a significant impact on overall job satisfaction. Loewenstein et al. (1989) asked subjects to ordinally rank outcomes that differ in the distribution of payoffs between the subject and a comparison person. On the basis of these ordinal rankings, the authors estimated how relative material payoffs enter the person's utility function. The results show that subjects exhibit a strong and robust aversion against disadvantageous inequality.

Modern humans appear to care about both real income and relative income. Obviously, it matters how much my income can buy, but why should I care about how much your

income can buy? With respect to how individuals value others' consumption, evolutionary psychology can provide a useful framework. Status matters, because evolution has shaped traits that helped us survive and reproduce (Frank, 1985). Although absolute wealth helps the individual and his offspring survive, only relative wealth helps attract potential mates. In our evolutionary past, there is one resource that was in fixed supply and of enormous importance for male reproductive success: women. The ability to persuade one woman or more to produce children depended on a man's resources – material and otherwise – relative to those of the other men against whom he was competing. Similarly, the ability of a woman to persuade a man to produce children with her and help support them depended, in part, on her status vis-à-vis the other women on whose children that man might spend his limited resources. Thus, we would expect both relative status and real income to play important roles in the individual utility function produced by evolutionary selection.

Other authors such as Saad and Gill (2001) show that it is possible and fruitful to use evolutionary psychology as a framework to understand sex differences in bargaining. In the context of the ultimatum game (Güth et al., 1982), the authors found that men tend to offer better deals to women than to other men. In a bargaining field experiment in Peru, where confederate taxi riders followed a prescribed bargaining script, Castillo et al. (2013) found that women got lower ride fares than men for the exact same service. All taxi drivers were men.

ADAPTED MECHANISMS IN THE BRAIN

The idea that evolution endowed us with adaptive mechanisms is also consistent with the current understanding of neurobiology. The brain is a physiological system that

evolved from natural as well as sexual selection to solve problems that we faced in our evolutionary past. As with all existing organic systems, our brains and their resulting decision strategies adapt to the environment.⁶ It is generally thought that with the exception of the influence of learning to read and write, little evolution has happened since humans became civilized (about 10,000 years ago). Our current mental architecture is thought to have evolved from hunter-gatherer societies (Kline, 2000), and our minds are best adapted to such societies. As a consequence, the human brain is not a general-purpose computer able to perfectly compute optimal responses to problems, as researchers had previously thought. Instead, the brain contains specialized modules aimed at solving particular problems that are evolutionarily relevant (Barkow et al., 1992; Cosmides and Tooby, 1994). For example, there are modules associated with language (Pinker, 2003). There are also modules associated with sex and mating behavior (Buss and Greiling, 1999). There are even modules for the experience of anger, presumably developed in our evolutionary past to obtain advantages in bargaining (Sell et al., 2009). With respect to simpler social interactions, there is evidence that the evolved architecture of the human brain included specialization of reasoning for detecting cheaters. Leda Cosmides (1989) and Cosmides and John Tooby (1992) showed that participants who usually do very poorly in identifying logical rules, such as if P then Q, are remarkably accurate in identifying cheating in social exchanges, such as 'if you help me, I help you'. Clearly, there is an evolutionary advantage for identifying cheaters versus cooperators, which requires the ability to make logical inferences; however, that ability is constrained by the context in which it is called into action.

Through extensive work with human and non-human animals, researchers have been able to identify the reward system or group of structures in the brain that is responsible for

the processing of goals, motivation, value, and adaptation (Schultz, 2015). These structures are found along the dopaminergic or reward pathway that begins in the ventral tegmental area (VTA) and connects the basal ganglia to the prefrontal cortex. Reward cognition serves to increase the likelihood of survival and reproduction. Reward guides animals to learn, approach, and carry out actions that are correlated with positive emotions.

It is believed that rewarding stimuli can drive learning in both the form of classical conditioning (Pavlovian conditioning) and operant conditioning (instrumental conditioning). In classical conditioning, a stimulus causes approach and avoidance behaviors. In operant conditioning, a reward may act as a reinforcer, in that it increases or supports actions that lead to itself. The theory and data available today indicate that the phasic activity of midbrain dopamine neurons encodes a reward prediction error used to guide learning throughout the frontal cortex and the basal ganglia. Activity in these dopaminergic neurons is now believed to signal that a subject's estimate of the value of current and future events is in error and to indicate the magnitude of this error (Glimcher, 2011). This new theory of reward as being processed in the frontal cortex and basal ganglia is consistent with the idea that our brain has evolved to include an adjustment or learning mechanism that helps us learn.

LIMITS OF ADAPTATION: FOLK ECONOMICS AND THE CHOICE OF ECONOMIC INSTITUTION

We previously argued that evolution has endowed humans with general goals and motives, specific modules for behavior and a reward system that shapes learning and behavior. Given this knowledge, economists can produce models of behavior that can be grounded in evolutionary

psychology. Such models would include preferences that we developed in our evolutionary past and can capture with utility functions and learning algorithms that can allow us to model adaptation to the environment. Nevertheless, it is unlikely that the adaptive system that our brain is could have prepared us for today. As Pinker (2002) argues, our evolutionary past has not prepared us for our complex reality. It is highly unlikely that our brains have specific modules or tools to understand the complex modern economy. Instead, to navigate the modern economy, we probably utilize modules from our evolutionary past that helped us to conceive simpler social interactions. Thus, evolutionary forces that developed throughout most of our pre-modern human history have influenced and continue to influence our choice of political institutions.

Rubin (2003) advanced the idea of 'folk economics'. Folk economics refers to the notions that naïve or untrained individuals have about the economy. The idea is that during much of our evolutionary past, humans evolved in small groups of mobile hunter-gatherers. These groups not only were small, consisting of about 25 to 150 individuals, but they also had little social structure, had no food storage (were immediate consumers), and did not specialize, so division of labor was non-existent (Kelly, 1995). Anthropologists agree that there was very little room for investment in human capital; not even war resulted in specialization, as most attacks seem to have been unorganized raids on neighboring groups (Keeley, 1996). In addition, technological change and growth were also miniscule. In such an environment, the evolved economic module was essentially zero-sum. That is, if groups or parties engaged in interaction, there was always a winner and a loser.

In exchange, the sensory perception of having to pay somebody through currency or some other possessions, such as a cow or a chicken, is one of loss. A logical inference

of a mind that has developed to identify simple causal relationships of physical phenomena based on sensory perception is that this exchange is not advantageous. Understanding that a sensory loss may actually be an economic gain does not come naturally. Yet, we all know that it is clearly possible to attain. There are three ways in which our brains can be trained to identify benefits from complex interactions that may not render immediate sensory stimulus. These are training, experience, and observation.

The zero-sum mentality has shaped and still influences our understanding of social welfare and our choice of political institutions. For example, a naïve individual may not intuitively see mutual advantages derived from exchange specialization and incentives. A poor understanding of these may explain our natural tendency to be suspicious of policies that encourage the liberalization of trade, labor, and finance. As Pinker (2018: 333) says, 'Authoritarian populism can be seen as a pushback of elements of human nature—tribalism, authoritarianism, demonization, zero-sum thinking—against the Enlightenment institutions that were designed to circumvent them'.

Under folk economics, prices are thought to allocate wealth only and don't influence the allocation or production of goods and services. Individuals who are influenced by folk economics would support price controls of necessary consumption items, such as flour, salt, sugar, electricity, and water. The lower the price, the better off one is perceived to be. This way of thinking ignores the fact that very low prices artificially supported by controls also affect consumption and production. With price controls, consumption will surely end up exceeding production. An unbalanced market outcome will cause scarcity, which can then lead to conflict and other social maladies.

In folk economics, efficiency gains from economic activity are ignored, as the emphasis is on the distribution of wealth and income. There is evidence that, with notable

exceptions, wealth accumulation and income inequality are not seen positively. Yet, it is wealth accumulation that precedes economic growth, as capital can be made available for production and growth through credit markets. In the political economy literature, it is still debated whether the distribution is unequivocally positive (Aghion et al., 1999). Although high levels of income and wealth inequality coupled with lack of opportunities to develop human capital are detrimental to economic growth, redistribution in light of lower inequality and higher human development may also be detrimental.

The world of folk economics is a zero-sum world, where resources and the number of jobs are viewed as fixed. Because the number of jobs is seen as fixed, under folk economics, the act of buying from other nations, communities, or tribes is seen as a loss. The Survey of Americans and Economists on the Economy (SAEE), analyzed by Caplan (2001, 2002), shows that economists and more educated people tend to support free trade compared to the rest of the population. This sentiment is not new; Newcomb (1893) also indicated that the disagreement between economists and others is most profound with respect to trade. The argument against free trade is that it leads to job losses. In our evolutionary past, humans saw interactions with other tribes as zero-sum games, where the others' gains truly implied one's loss. However, in a modern economy, even if some people lose jobs, others gain jobs, and there are welfare benefits of free trade, such as lower prices of consumption goods.

Is it possible that folk economic beliefs are simply a representation of culture? This seems to be the approach that modern political economists are taking. Yet, this approach ignores evidence from biology and evolutionary psychology that there are innate tendencies driven by our genes that are basically the same across cultures. Today, mostly in developing countries – where training in economic reasoning even among elites may be limited by lack of opportunities, and

limited experience in exchange may be due to infrequent and underdeveloped markets, infrastructure limitations, or political repression – folk economics has a very strong influence on the policies that policymakers implement. From an economic point of view, this is problematic since it hinders economic development. From the social point of view, this can generate instability, as unsustainable economic policies are likely to emerge. In fact, Marxist ideology, which is still surprisingly prevalent around the world, is a representation of folk economics.

Nevertheless, if we analyze the choice of economic and political institutions from the perspective of evolutionary psychology, we cannot but conclude that political economists face a difficult challenge in trying to get people to understand the mutual advantages derived from exchange, specialization, and incentives.

Notes

- 1 The properties of preference relations include reflexivity, completeness, transitivity, monotonicity, and convexity.
- 2 A fair gamble is a gamble whose price is equal to its expected monetary value. A fair gamble has actuarially fair odds. Individuals who reject fair gambles are considered risk averse.
- 3 See also Netzer (2009) for an evolutionary perspective on risk and time preferences.
- 4 We emphasize experimental data here because in the real world, many behavioral differences between men and women may be influenced by variables that are difficult to control for. The laboratory environment provides researchers with the ability to control the environment and more effectively isolate the variables of interest.
- 5 Henrich et al. (2012) argue that normative monogamy increases child investment, reduces intra-household conflict, and economic productivity by shifting male efforts from seeking wives to paternal investment.
- 6 Modern theories of the evolution of the mind indicate that our brains evolved to solve problems that persisted in the environment of evolutionary adaptation (EEA). The EEA is the period when our ancestors were becoming humans. This period lasted for a very long time, possibly between 1.6 million to about 10,000 years before the present.

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Evolutionary Psychology and Business: Examining Life at Work through the Lens of Status

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The fields of business span diverse content areas including accounting, analytics, economics, entrepreneurship, finance, information technology, leadership, logistics, negotiation, sales, strategic management and marketing, and the more behavioral wings of the disciplines of those respective areas such as consumer behavior and behavioral accounting, as well as relatively new interdisciplinary fields such as neuroeconomics. In the behavioral (i.e., psychologically oriented) wings of these disciplines, the evolutionary perspective has been applied most extensively in the areas of organizational behavior (a subfield of management) and consumer behavior (a subfield of marketing). In the present chapter, we address how adaptationist thinking has been applied in organizational contexts.

Organizational psychology and organizational behavior, specializations within the fields of psychology and management respectively, have in recent decades been a source of novel research applying

evolutionary biological principles to understand how evolved psychological mechanisms shaped by early human conditions influence the behavior of modern humans interacting at work or in other professional settings. Yet, the application of evolutionary theory to work life is still in the early stages. This is despite many calls for expanding research that leverages this unique evolutionary conceptual framework (Benkler, 2011; Cosmides and Tooby, 2004; Kanazawa, 2006; Lawrence and Pirson, 2015; Nicholson, 2008, 2010; van Vugt and Ahuja, 2011). A larger proportion of the existing evolutionary-informed work in the organizational sciences focuses on leadership, while a smaller proportion focuses on varying related topics such as negotiation (Lee et al., 2017), ethics (Wasioleski and Hayibor, 2009), sexual harassment (Browne, 2006), emotion (Hill and Buss, 2006), and work performance (Pitesa and Thau, 2018). This list of biologically informed research topics and publications in the organizational literature is not exhaustive,

but provides examples of the arenas of work where the evolutionary perspective has inspired novel empirical research or conceptual development.

We approach our review of the organizational literature inspired by adaptationist thinking, and examine this literature through the lens of status seeking and status maintenance goals to gain greater insight into life at work. We examine how status-relevant resources influence leadership selection and negotiation processes, and how sex differences in these resources (as well as in how these resources are perceived) matter for the allocation of status at work. An evolutionary perspective presumes that people's criteria for elevating certain individuals to high status positions, including those we choose to be leaders or choose to defer to as experts or authorities, are rooted in our evolved psychology. We also examine how modern work environments present unique opportunities for people with diverse skills to attain status through niche construction. This evolutionary perspective on innovation has implications for the fields of entrepreneurship and creativity, as well as leadership. First, we will begin by outlining literature on the broad domain of status acquisition and maintenance and consider its intimate connection with leadership.

STATUS: THEN AND NOW

In front of the County library building in Hilo, Hawaii sits the Naha stone. Brought to the island of Hawaii from distant Kauai in a double canoe, it is purported to weigh thousands of pounds (about 1000 kilograms). The story of King Kamehameha, who is known for ending the deadly and lengthy intergroup conflicts among the previous Hawaiian island chiefs and eventually uniting the islands under his singular rule, includes an important connection with the Naha stone. It is reputed that a young Kamehameha lifted and

overturned the Naha stone – an achievement that confirmed among influential Hawaiians witnessing the event that he was destined to rule over the entire island chain. With roots in Polynesian societies organized by chiefdoms (Garfield et al., 2019), early Hawaiian culture emphasized physical formidability as an important necessary condition for assuming leadership. This is perhaps unsurprising given the recurring role warfare played in social life. Leaders were selected from males born into the ruling class, who often received special training in youth to prepare them to be the next generation of great warriors – a necessary but not sufficient condition for acquiring the highest levels of status and leadership in Kamehameha I's time. Some scholars argue that Hawaiian leaders such as Kamehameha were regarded more as gods than of similar status to the Polynesian regional chiefs of their recent ancestors (Kirch, 2010).

Humans have likely evolved specialized psychological mechanisms to deal with the recurring problems of intergroup conflict and warfare. Rulers such as King Kamehameha – who reportedly was nearly 7 feet tall and, as the Naha stone story attests, would have been physically formidable – needed more than brute force to triumph over other powerful competing male leaders and their armies. Status acquisition required political savvy and potent military strategies, and as such, King Kamehameha's story provides a window into the complexity of status acquisition and maintenance processes. An evolutionary perspective on status acquisition and maintenance acknowledges that people's judgments and behaviors in modern environments are still guided by the lingering influences of our ancestral environments.

Psychological mechanisms governing status acquisition and maintenance processes have been shaped by the forces of natural selection (e.g., acquiring status confers survival benefits, such as priority access to scarce resources) and sexual selection (e.g., maintaining high status confers reproductive

benefits, such as boosting desirability as a sexual partner and conferring greater ability to effectively compete for mates against members of one's own sex). Differential parental investment among humans leads to the prediction of sex-specific patterns of cognition and behavior in status acquisition and maintenance processes, as intrasexual competition differs in important ways for males and females (Trivers, 1972). Consider, for example, that while male intrasexual competition is based in part on physical prowess, physical formidability, and risk-taking, female intrasexual competition is more indirect and often aims to reduce exposure to risk, particularly to risks of physical violence (Campbell, 1999). Indeed, there is good reason to expect that male and female status hierarchies are structured and maintained according to somewhat different sets of rules (Hrdy, 1999, 2009). Yet, both men and women seek and value status, and though natural and sexual selection pressures on status acquisition and maintenance processes diverge for the sexes, the business organization often attempts to exert proximate pressures on these processes that at least aim to be more equivalent (i.e., blind to worker sex).

Status – the result of a malleable summary judgment by others that you are worthy of an elevated position in a group hierarchy – has the ability to afford both great pain and pleasure to the individual who possesses it (Anderson et al., 2015; Kifer et al., 2013; Pettit et al., 2010). As a central currency of social life, status is coveted, won, lost, and then sometimes recouped as fluid social hierarchies shift due to complex group dynamics. In the quest for status, everyone is essentially seeking the same outcome, but with an unequal distribution of resources that can be leveraged to meet the objective. In developed economies where organizations serve to apportion status among many people – working adults spend more of their waking hours operating within their organizations than anywhere else – status acquisition and status protection goals are subject to the structural

constraints and the collegial nature of the relationships operating within these organizations. As a result, people's status motives exert powerful influences over a great deal of their behavior in business environments. This chapter therefore focuses on how our evolved psychology leads to predictable patterns of cognition and behavior with regard to the allocation of status at work. Clearly there are motivations other than status acquisition and protection that have an evolutionary basis (Kenrick et al., 2009) and are relevant to business contexts. Yet status reflects a motive that is both under-researched and far-reaching in its implications for a wide variety of behaviors commonly observed in workplace settings. Status seeking implicates resources we commonly associate as important to our ancestral past (e.g., physical size and strength, indicators of dominance such as voice pitch and masculinized facial features), that are perhaps less relevant in current work environments. Our review reveals that these resources persist in their ability to be leveraged to acquire status despite modern deviations from typical ancestral conditions.

Status seeking is a human universal (Anderson et al., 2015); there are no known groups or cultures where people are unconcerned about their level of status within their key social groups. While status can be defined and pursued in diverse ways tied to cultural variation in status-related norms, and the particular resources that are most valued in a group or organization, there is also a remarkable consistency in the payoffs status affords individuals across cultures, such as the ability of high status males to attract high mate value women. In this chapter we focus much less on the benefits of status, which in evolutionary terms relates to either survival or reproductive advantages, and instead focus on the resources and paths that help people to attain status. As we will address briefly below, however, the payoffs of status-relevant resources are not identical for all people.

People pursuing status are constrained by their status-relevant resources. Some people

possess greater fluid intelligence, emotional intelligence, or physical resources that present as resilience to environmental threats such as parasites, environmental toxins, or the ability to navigate intragroup conflict and outgroup (competitive) threats. Some of the long-standing routes to acquire status (e.g., physical dominance among males) are becoming less relevant in some modern environments where the use of brute force to achieve status is subject to social controls (e.g., the threat of prison), or is simply less useful when fighting some unique modern battles (e.g., technology-based information warfare). Yet, vestiges of our distant evolutionary past, wherein physical dominance was vital to acquiring and maintaining status, still influence how we evaluate others in modern organizational settings. The likely adaptive value of physical dominance in times of conflict prompts responses to these dominance-linked physical resources in predictable ways, despite the mismatch (Li et al., 2018) between many current work environments and relatively stable features of the ancestral environments in which humans evolved.

First, we consider the role physical resources play in acquiring and maintaining status in professional settings, with a focus on observable characteristics linked to status achievement, including height, voice pitch, and facial features associated with social dominance and other traits relevant to perceived leadership potential. We will focus on research that examines organizationally relevant outcomes connected to these physical resources. In doing so, we will consider how these physical resources are distributed differently across individuals, and the implications of inequality in the distribution of those resources for work success and the attainment of positions of leadership within organizations. In organizations, and in other social hierarchies, the concepts of status and leadership have substantial overlap. High status individuals are more likely to be followed by others, and leaders have high status

in their respective groups or organizations. We will consider how status in the organization can be converted into investment in other important social domains. Lastly, we will examine how niche development may be a useful framework to apply to increase our understanding of how people acquire and maintain status in modern work environments, and how the meaning of work is changing in modern organizational life.

Where Does Status Come from?

From an evolutionary perspective, cognitive adaptations evolved because they enhanced survival and/or reproduction, given recurring features of the environment the organism operated within (Lewis et al., 2017). Status implies superior position in a group or society relative to others, which entails greater access to resources and benefits that are valued by those group members. Status also implies enhanced influence over other group members (Bastardo and van Vugt, 2019; Garfield et al., 2019; Sundie et al., 2012), in a manner akin to willing deference to a leader. Economic resources that aid in survival (e.g., protection from the elements, access to adequate nutrition) are more accessible as status increases, as are social (intangible) resources such as deference from other group members and perceived attractiveness for social and professional alliances (Winegard et al., 2018).

Humans can be thought of as pursuing a set of universal social goals (Kenrick et al., 2009). Status seeking is one of these goals. From an evolutionary perspective, status is better understood by considering, among other things, how it serves to enhance survival and/or reproduction. Status is a common currency that can be leveraged and traded for benefits in other fundamental social domains, in that achieving the other fundamental goals should be relatively easier for people who have already acquired high social status. While in younger adulthood status may be

utilized primarily for mate attraction, later in life status is more likely to be invested in offspring and other kin care, as many adults form committed partnerships that result in dependent offspring and extended kin groups requiring that care (Ko et al., 2020). In developed economies, people rely primarily on employers or their own businesses as their primary source of status and economic resources (through pay or profit from work) to enable this familial care. People across cultures, whether they are young or old, single or in committed relationships, report familial care as their most important concern (Ko et al., 2020). This implies that while corporate officers aim to maximize profit and/or shareholder value, employees are more likely to evaluate their role in the business through the lens of the familial care that is enabled by their achieved status and work compensation.

Having high status entails enduring high costs. High status people in ancestral environments faced increased chances of death or injury due to violent confrontations with others in warfare. A critical event in Kamehameha's ascent was his facilitating the murder of a primary competitor at a heiau (temple) built to honor the god of war (Kirch, 2010). Predation both from outgroup members and ingroup member coalitions are risks, as sometimes others have incentives to alter the high status person's superior position within their group. In modern environments, while direct physical aggression is perhaps less likely to occur, other non-physical forms of aggression such as professional undermining by ambitious subordinates may require constant monitoring (Mead and Maner, 2012). High status individuals are expected to take on greater responsibility for lower-status others and to utilize the greater resources at their disposal for the benefit of others within the group.

Therefore, people likely have psychological adaptations for status maintenance and protection that are behaviorally costly to implement. Attaining high positions of status

involves substantial investments of time, mental and physical energy, and effort that enable (when successful) a person to funnel substantial economic and social resources to his or her kin. However, at the same time, effort and energy directed toward acquiring and maintaining one's status at work may also strain close kin and mateships as other goals such as relationship maintenance (including mate guarding) and the provision of direct kin care are necessarily crowded out (i.e., there are work–life balance tradeoffs). Overinvestment in status acquisition and maintenance at work may also lead to burn-out, that if left unchecked, can ultimately undermine one's status in the organization (Maslach et al., 2001).

The 3 Cs of Status

In small-group living environments, such as those that humans evolved within for thousands of generations, group members knew each other well and had ample opportunity to form holistic impressions of their cohorts to aid in decisions about the allocation of status, based on a long history of interactions. In modern environments, where people routinely interact with strangers or distant acquaintances, status judgments (as well as those about who is a good candidate for a leadership role) must often be based on limited exposures, such as job interviews. In these organizational contexts, cues or heuristics associated with status may carry more weight (Bastardo and van Vugt, 2019).

Ancestral environments were also different in numerous other ways from our modern environments, making different resources (characteristics) more helpful in solving the recurring social problems our ancestors faced. In other words, the rules we rely on today to allocate status may no longer be the best fit to solve the challenges humans face in modern environments.

When deciding who will attain high status in a group, evolved psychological mechanisms likely reflect stable aspects of our ancestral environments rather than the unique challenges faced in today's world.

High status individuals are expected to differentially contribute to solving problems their groups face, in order for other group members to support their superior position in the status hierarchy (Winegard et al., 2018). Here, we refer to three key recurring types of problems as the three Cs: cooperation, coordination, and conflict management. Cooperation involves motivating individuals with different goals and objectives to meaningfully contribute to the organization's goals (Smith et al., 1995). Status is afforded to people who can build coalitions within their organizations and help people negotiate through differences in personal agendas to achieve important collective outcomes. Cooperation also involves incentivizing people to help other group members when they are in need, even if it imposes costs on relatively advantaged group members in the short run (De Cremer and van Knippenberg, 2002). In ancestral environments, examples of cooperation might have been collective child rearing, or sharing meat (a scarce resource) from a successful hunt. In the modern organizational environment, examples of cooperation might be motivating individual salespeople to support each other's efforts to win a team-based internal sales competition or to engage in extra-role behaviors that benefit the organization, even if they might not directly benefit the individual employee (Nielsen et al., 2012).

Coordination involves ensuring each group member in a collective activity is doing his or her part, and has the resources he or she needs to contribute to a collective outcome of interest that benefits all parties. In ancestral environments, examples of coordination might have been leading a group hunt for large prey, or mobilizing one's group to travel long distances to follow seasonally varying food sources. In the organizational environment, coordination might involve getting

team members with unique areas of expertise to work well together in a dynamic environment (Day et al., 2004). For example, the highest levels of success in operating room teams occur when leaders of these teams encourage members to speak up, adopt multiple roles to meet shifting team needs, and coach individual members to help them learn new skills (Edmondson, 2003).

Conflict management involves effectively resolving conflicts when they occur between group members (intragroup conflict), and across groups (intergroup conflict). In ancestral environments, examples of conflict management might have been leading one's group into a physical battle with an outgroup, or resolving disputes about free riding within the group. In modern professional contexts, conflict management might involve actively intervening to diffuse or preempt potential co-worker conflicts, or ensuring that all team members have an opportunity to convey their ideas and opinions involving critical team tasks (Behfar et al., 2008; Simons and Peterson, 2000).

People who differentially contribute to the achievement of cooperation, coordination, and conflict management within their groups or organizations are likely to be afforded status in the form of promotions, higher compensation, leadership positions, and increased supervisory responsibilities. How do employees decide to whom this status is afforded, and why? Rather than reflecting what may be most necessary for success in modern environments, again, reliance on some features of a person such as physical strength to assess ability to achieve the 3 Cs may be a vestige of early ancestral environments when that resource was perhaps more diagnostic.

Affording status to such individuals – those who would have excelled at achieving the three Cs when humans lived in small groups with kin and close others – also increases the risk of another 'C': coercion. People who attain high status also have the ability to use that status to coerce others to provide them with personal benefits, and

people expect that high status others may indeed attempt to do just that (Lukaszewski et al., 2016). Achievement of coordination, cooperation, and conflict management objectives will benefit all group members to some degree, while coercion benefits only the higher status person at the expense of lower-status group members. Hence, cues to trustworthiness (a sincere interest in achieving what is best for the other party in a social transaction) are also preferred in high status individuals such as organizational leaders. Below, we address physical features people rely on when permitting others to ascend to such high status positions.

CONVERTING OBSERVABLE RESOURCES INTO STATUS

Height and Physical Formidability (Strength)

Height, often thought to be a cue to status, is connected with a variety of status-linked affordances. Height provides a resource advantage to men (relative to women) in the workplace, since the average height for men is about 5 inches taller than the average height for women. This sex difference favoring men is documented in every human culture that has been studied (Gaulin and Boster, 1985), reflecting the selection pressure of greater competition among men for access to female mates, consistent with differential parental investment theory (Trivers, 1972). Ellis (1994) conducted a qualitative analysis of a range of studies linking height to social status, across cultures, in both industrial and preindustrial societies. This analysis was more heavily weighted toward samples of men, showing positive correlations between height and status, though a smaller subset of samples that also investigated women found similar positive associations between height and social status. Judge and Cable (2004) found benefits of height for both male and

female workers, with the strongest effects of height on others' esteem-related perceptions of the worker, compared to weaker effects on more objective outcomes related to leadership (e.g., organizational rank), or more objective performance measures (e.g., sales). In certain types of jobs – for instance, those that are client-facing – height was more strongly correlated with success (e.g., sales) than it was in other occupations (e.g., clerical). Though the average effect of height on achievement of status at work was larger for men than for women in the Judge and Cable meta-analysis, the difference was not statistically significant. It is notable that in 3 of the 4 new samples presented in Judge and Cable (2004), the association between height and workplace success was greater for men than for women. Taken together, this evidence suggests that when women are tall, they too may benefit in status from this physical resource. However, since at any above average height (e.g., 5'10) there will be far fewer women than men in the working population, this status-relevant resource is not evenly distributed across the sexes.

While the status value of height may be less critical to ascending the social hierarchy in some modern contexts – for instance, Jeff Bezos (currently one of the wealthiest Americans and founder of Amazon) and Mark Zuckerberg (Facebook's founder) are both 5'7" in stature, substantially below the 5'9" average height for American men – there is ample evidence consistent with the perceived connection between height and authority. For instance, a Canadian sample of approximately 4,000 workers showed a positive connection between sex and supervisory status or managerial status on the job, where men were able to convert their stature into authority within their organizations, in both 'blue collar' and 'white collar' jobs, even controlling for factors such as age, and family educational and professional attainment (Gawley et al., 2009). While both tall men and tall women were more likely to be judged as looking like a leader, this effect

was stronger for men than for women (Blaker et al., 2013).

In addition to the authority-linked benefits of stature, height also influences how men interact with other men (such as whether they engage in direct versus indirect aggression when resources are at stake; Knapen et al., 2018). This literature suggests that adaptations influenced by recurring features of ancestral environments, wherein dominance likely afforded survival and reproductive benefits, play an important role in status dynamics within the modern world of work. While height may not be differentially predictive of work performance for men versus women (Judge and Cable, 2004), there is also evidence that assessments of male workers' authority and dominance are more closely connected with their height than are similar assessments for women workers.

Height is to some extent correlated with physical formidability or strength, another feature that favors men in the pursuit of status. Lukaszewski and colleagues (2016) propose that, contrary to the dominance-prestige model of status (which distinguishes between status that is attained by force, or the threat of force, versus status that is willingly given by respectful followers; Blader and Yu, 2017; Maner, 2017) physical formidability afforded status in ancestral environments because physically strong men (but not women) were perceived as being better at achieving coordination, cooperation, and conflict management. While stronger men were also perceived as being more likely to use their physical dominance to attain personal gains at the expense of others within the organization (i.e., coercion), the threat of coercion did not explain the affordance of status to these physically formidable men in Lukaszewski and colleagues' studies (2016).

This association between physical formidability and the propensity to engage in exploitative behaviors is perhaps why other traits, such as trustworthiness, are also critical in leadership assessment by potential followers (addressed below). Indeed, using

aggressive tactics to pursue or maintain one's status leads to disrespect of the leader among group members, and therefore increases the aggressor's vulnerability to a takeover by coalitions of lower-status group members (Mead and Maner, 2012). This may be one reason why people who feel relatively low in power seek to affiliate with others (Case et al., 2015). Such affiliations may aid in coalition formation, and coercive leaders, seemingly understanding this, seek to discourage affiliation and instead stir up conflict among underlings (Case and Maner, 2014) to prevent opportunities for such coalitions to form. Leader aggression also encourages the exit of group members who feel they are being coerced into affording higher status to the aggressor (Lukaszewski et al., 2016).

Certain contexts may increase people's reliance on height or physical strength as status cues. There is ample evidence that people prefer dominant and strong leaders, such as when people are in a competitive 'wartime' mindset where real or imagined threats from an outgroup are imminent (Hehman et al., 2015; Spisak et al., 2012; van Vugt and Grabo, 2015). In these contexts, tall leaders may be particularly preferable. Alternatively, when in a cooperative 'peacetime' mindset, height may be seen as less central to status perceptions. This has implications for business environments: when competitive pressures on the firm increase, or when internal conflict within the firm is heightened, people may be more likely to fall back on cues to physical dominance such as height when deciding whom to select for entrance into the organization and whom to elevate to higher status positions within the firm.

Voice Pitch

The development and maintenance of voice pitch (i.e., whether the voice is 'high' versus 'low') depends on circulating androgen levels (e.g., testosterone) in the body. Despite testosterone's reproductively-relevant role in

producing secondary sexual characteristics, it also compromises immune function (Folstad and Karter, 1992; Thornhill and Møller, 1997). Therefore, a deep (i.e., 'low') voice may be a costly signal of genetic quality. Voice pitch may have been influenced by female choice as humans evolved, as there is evidence that women prefer masculine voices in short-term mates, and when ovulating. Feinberg and colleagues (2005) found that women's assessments of dominance varied with voice pitch, for male (and female) targets. However, men are also particularly attentive to the voice pitch of other men in competitive contexts, suggesting that voice pitch may have been influenced by intrasexual competition processes among men (Puts et al., 2006; Wolff and Puts, 2010). Puts and colleagues (2007) found effects of voice pitch on perceptions of physical dominance that were 15 times the size of other documented effects of voice pitch on attractiveness to women (Puts et al., 2006).

The pitch of a person's voice also prompts downstream conclusions about a person's leadership potential. Men and women are more likely to select a leader with a lower-pitched voice, whether that prospective leader is a male or female (Klofstad et al., 2012; Tigie et al., 2012). CEOs with deeper voices receive greater compensation than their higher pitched counterparts (Nair et al., 2016). When considering a person as a potential *wartime* leader, people expressed preferences for candidates with lower-pitched voices, and associated low pitch with physical formidability (Tigie, et al., 2012).

Baseline voice pitch is of course not equally distributed among men and women; voice pitch is higher among women (with men's half as high as that of women's pitch, on average). Voice pitch also varies within individuals in response to emotional states being experienced, and interactions with consequences for status such as competitive interactions with dominant individuals. Puts and colleagues (2006) examined ratings of male voices by male participants, finding

that manipulating the pitch of men's voices influenced both social dominance and physical dominance perceptions. Additionally, when speaking to a competitor in an experimental setting, men who felt relatively physically dominant lowered their voice pitch when addressing the competitor, while men who felt less physically dominant spoke in a higher pitch to their competitor. Hence, voice pitch may be helpful in acquiring and maintaining status positions in an organization, and also expressing deference and followership when appropriate.

Facial Features

A relatively large body of research, some informed by an evolutionary perspective, examines the influence of facial cues on interpersonal judgments about people's status-relevant traits and characteristics. In this research, participants are typically presented with disembodied faces (to achieve experimental control) and are asked to infer the appropriateness of those people pictured for various status-relevant outcomes, such as level of pay and leadership potential, as well as traits important for status acquisition and maintenance, such as dominance and trustworthiness. Some reliable patterns have emerged, and are summarized briefly below.

As the current chapter is focused on status in business contexts, we focus on research that demonstrates how facial features can provide people with status-relevant resources, and thereby advantages in status competition. We focus, for instance, on the status-relevant benefits of facial cues to dominance and who benefits from them (i.e., men versus women). We focus on research investigating four dimensions of facial judgment: masculinity/dominance, trustworthiness, attractiveness/health, and maturity/competence.

Masculinity/Dominance

Facial masculinity, reflected by features such as a pronounced jawline and brow (Pound

et al., 2009; van Vugt and Grabo, 2015), prompts conclusions about a person's dominance (Todorov et al., 2015). People preferred leaders with dominant faces when focused on winning intergroup competitions or conflicts, while feminized faces were preferred as leaders when people focused on the need to cooperate with other groups to achieve collective goals (Hehman et al., 2015; Spisak et al., 2012; van Vugt and Grabo, 2015). Manipulating the masculinity and dominance of photos of real political candidates provided evidence that even when people have more detailed information about the prospective leaders, such facial characteristics can shift evaluations of leadership fit (Grabo and van Vugt, 2018). CEOs with more dominant faces lead relatively more profitable companies than their less-powerful looking counterparts (Rule and Ambady, 2008), and Managing Partners of top American law firms who were rated as having more dominant and mature-looking faces tended to lead more profitable firms (Rule and Ambady, 2011). Men with masculine faces were successful in extracting greater benefits from other men in a competitive negotiation, but were less successful in reaching agreements when collaborative, integrative solutions were needed (Haselhuhn et al., 2014). The connection between facial masculinity and dominance appears to be stronger and more consistent for men than it is for women (Quist et al., 2011). Facial masculinity may predict testosterone-mediated behavior; after "winning" a laboratory competition, men with masculine faces had higher levels of circulating testosterone (Pound et al., 2009). This may explain why masculine faces are particularly preferred for wartime leaders, when aggression or the threat of aggression is leveraged to resolve intergroup conflict.

Trustworthiness

While there is inconsistent evidence about the accuracy of judgments of trustworthiness from facial stimuli, people do routinely

encode trustworthiness impressions from facial displays, and do so in a fairly automatic manner (Klapper et al., 2016). One downside of some masculine facial features is that they appear to be correlated with lower perceived trustworthiness; men with more masculine faces were more likely to exploit others for personal gain when given the opportunity to do so in a trust game (Stirrat and Perrett, 2010). This is consistent with the findings associated with physical formidability discussed above, which prompts concern over potential coercion that benefits high status people at the cost of those with lower status (Lukaszewski et al., 2016). Research participants afforded better pay to people who had faces that conveyed trustworthiness, and this was a more important factor in determining pay for a higher status upper management position, compared to a lower-level management role (Fruhen et al., 2015). Trustworthiness judgments in leadership assessment contexts may be intended primarily to detect whether high status individuals, who often are in a position to use coercion for personal gain if they choose to do so, are indeed prone to engage in exploitative behaviors within their groups or organizations.

Attractiveness/Health

Leadership researchers have argued that physical attractiveness, rather than benefiting people because of a domain-general halo effect, may be preferred because of the adaptive significance attractiveness conveys about leader health (Spisak et al., 2014; van Vugt and Grabo, 2015). Health, as indicated by facial appearance, was advantageous in status judgments (i.e., a preferred leader) across different kinds of social challenges – cooperation and competition, as well as exploration for and exploitation of resources (Spisak et al., 2014). In ancestral environments, where physical endurance and prowess were more essential for survival than they are in some modern environments, health may have been an important factor in status assessments. The preference for attractive leaders

may also be connected to disease avoidance mechanisms, as research has shown that when people are focused on the avoidance of contagious disease and contamination, they report heightened preferences for attractive others in high status roles (White et al., 2013). Further, US congressional candidates were more likely to win in districts with higher infant mortality and lower life expectancy (i.e., areas where disease threat is heightened) if those candidates were physically attractive, controlling for their incumbent status and political affiliation. In a time of heightened health threat, people who display cues to being immune-resilient may be more likely to be elevated to high status positions.

Maturity and competence

Some of the research reviewed above on facial cues to dominance combined facial ratings of dominance with facial ratings of maturity, which loaded on the same factor and were hence combined into a higher order concept: power (Rule and Ambady, 2008, 2011). Cues to maturity, though not old age, may elevate one's status (Henrich and Gil-White, 2001), particularly when group problems to be solved rely on crystalized intelligence and problem-specific expertise. However, when group challenges are novel, and therefore require new creative solutions, cues to fluid intelligence that peaks in early adulthood may be preferable (Beier et al., 2020; Kanfer and Ackerman, 2004). The same pattern may be expected for goals categorized broadly as raiding (where physical formidability is more important for status, favoring youth) versus trading (where intelligence and cooperativeness are important for status, favoring maturity).

Status-linked Possessions

There are early-stage perceptual biases toward the status symbols people choose to display. Maner and colleagues (2008) found

people were drawn to fixate on photos of dominant men (but not dominant women) in a visual array where dominance was conveyed by professional dress. Garcia and colleagues (2019) found that in the context of seeking new professional connections with competent others, people believed they would be perceived more positively when displaying status goods, and observers also preferred people with status goods as business partners compared to those displaying non-luxury products. In some professional and personal contexts, warmth may be a less important characteristic than competence, and status-linked possessions are indicators of lower warmth but higher competence (Cannon and Rucker, 2019).

In summary, there are numerous visible signals that predict successful status acquisition and maintenance. Most of these cues favor men. Women benefit professionally from height and certain facial cues as well (e.g., femininity in facial features enhances women's perceived ability to negotiate peacetime intergroup cooperation). However, effects of other dominance-linked characteristics are either smaller or nonexistent for women, or occur with such low frequency within the population of female workers (e.g., women who are taller than most men) that they are unlikely to contribute to solving the persistent problems of sex discrimination and pay inequity for women in the workplace. Many of women's physical features place them at a disadvantage when they are considered as leaders, particularly when in highly competitive contexts, including when inter-firm or intra-firm conflict or competition is heightened. In these contexts, reliance on features signaling physical dominance seem to carry even more weight in people's evaluations of who should lead.

Additionally, consider that a key, recurring group cooperation and coordination problem faced by humans was hunting. A largely male-centric activity, leadership dynamics in hunting groups would have largely excluded females, while also elevating individuals in

good health, who possessed adequate strength and endurance to participate in the hunt, and the influence necessary to lead the hunting team to a victory that would quite literally serve to sustain the entire group. The importance of hunting even in times of peace may be partly responsible for the emphasis placed on physical formidability and health among those afforded the highest levels of status (as superior hunters frequently are; Smith, 2004). A parallel activity central to group functioning in the lives of ancestral women was cooperative child-rearing (Hrdy, 2009). Women's approaches to resolving coordination, cooperation, and conflict challenges in caring for infants and young group members likely required different social influence processes than those utilized primarily by males in hunting groups, due to the more egalitarian nature of child-rearing cooperatives. Despite the crucial role of women's biological resources in reproduction and child-rearing, normal female biological processes (e.g., menstruation, breast feeding) remain largely taboo topics at work, and when made salient, constrain women's ability to acquire and maintain status in their organizations (Grandey et al., 2020).

There are correlations between at least some of the physical indicators of status, which may make such status signals mutually reinforcing in the minds of observers. Height is positively correlated with perceived physical strength (Lukaszewski et al., 2016), and sexually dimorphic acoustic features of men's voices predict their size, strength, and testosterone levels (Puts et al., 2012). Notably, a cross-cultural study provided data indicating that people in large urban developed societies make stronger associations between facial features (e.g., dominance) and behavioral characteristics (e.g., aggressiveness), suggesting that environments where people must interact with large numbers of strangers (as opposed to kin and other long-term interaction partners) may enhance the power of such physical resources in driving status assessments

(Scott et al., 2014). Next, we consider behavioral strategies that signal status to others in business-relevant contexts.

BEHAVIORAL STRATEGIES TO ATTAIN STATUS

Dominance, Prestige, and Charisma

Maner (2017) described dominance and prestige as two distinct *strategies* for achieving status. Henrich and Gil-White (2001) referred to dominance and prestige acquisition *processes*, emphasizing different paths by which people attain status, rather than a description of end states (i.e., a prestigious person versus a dominant person). Integrating the organizational literature to a larger degree, Blader and Yu (2017) reviewed various distinctions between status and respect, and discussed whether that particular delineation is useful for advancing research in this realm. Prestige was described as being freely granted to an individual by others in the organization or social group because of a person's superior resources or contributions to the group, whereas the dominance route to status was described as more akin to coercion.

Cooperation, coordination, and conflict management can be achieved in different ways, and the desire to achieve those outcomes that benefit all group members must be traded off against the potential for coercion by a strong leader. It should be easier for strong leaders to engage in coercive tactics when they are being protected by others above them in the hierarchy, when it is difficult to or takes an extended time for group members to exit, or when people's concern for safety in times of physical peril or violent intergroup conflict means that they are more willing to accept a selfish leader extracting benefits for himself or herself if the leader is able to successfully fend off the most pressing threat. Absent salient threats, strong leaders

are prone to resort to coercion to maintain power and control when they feel their social influence skills are lacking, or when freely given respect from group members (prestige) has hit a low point (Maner, 2017). The construct power shares many features with dominance and coercion and fewer features with prestige or respect (Blader and Yu, 2017). An exception is how Rule and Ambady's work (2008, 2011; described above) conceptualized power, which emphasized the role of maturity. Maturity was thought to be more strongly associated with prestige, as older individuals are better able to transmit important skills and information to others (Henrich and Gil-White, 2001).

A less frequently discussed route to attaining status in this literature is charisma (Bastardo and van Vugt, 2019; Grabo et al., 2017; Maner, 2017). Antonakis and colleagues (2016) defined a charismatic leader as a person who communicates values and a mission that are particularly attractive to a group of prospective followers. A person has charisma to the extent that he or she is able to identify with the audience (and vice versa), and appeal to the audience on an emotional level. As such, this route to status rests heavily on emotional engagement, which can be powerful in motivating people to support the charismatic person's agenda, and increase the willingness of lower-status people in the group to contribute to the work involved in executing this agenda. To the extent that charismatic individuals may be virtual strangers to an audience, they may be able to utilize emotional leverage to take advantage of audiences who possess little diagnostic information about the charismatic person's actual skills and abilities, or their history of coercion (Bastardo and van Vugt, 2019). The modern organizational environment may enable charisma to be a more viable route to status than it once was in smaller-scale societies where group members knew one another well, and could therefore better resist such identity-based emotional appeals from a person with deficits in other key status-relevant areas,

such as trustworthiness. For-profit organizations with pyramid-scheme structures, for instance, are often known for having charismatic leaders at their helms.

Leadership and Followership

A number of articles in recent years have emphasized followership psychology as an area that requires more study, and have argued for the benefit of an evolutionary psychological perspective in advancing understanding of followership (Bastardo and van Vugt, 2019; Garfield et al., 2019; van Vugt et al., 2008). Followership is akin to people accepting a relatively low-status position compared to others, and deferring to others' judgments and strategies for success at achieving group coordination, cooperation, and resolution of conflicts. A motivation for pursuing followership research is the frequency with which humans must engage in follower behaviors. Given the small number of high status roles, most people most of the time (particularly when the role is outside of their areas of expertise) must be willing to relinquish control to others who have superior resources. This has perhaps become even more common in developed, industrialized nations where specialization has increased. The number of expertise niches has grown considerably relative to ancestral environments due to societal complexity, which creates novel social problems to solve, but also the advent of technology (which requires narrow specialization and deep expertise to operate, and drive advances in it further forward). While the creation of new expertise niches provides an opportunity for more individuals to acquire status through cultivating valued, specialized skills, the inherent limitation on basic resources (time being a critical constraint) also makes the need to follow others more important in domains outside of one's own areas of expertise.

An evolutionary perspective presumes that people have acquired a set of psychological

mechanisms that have been shaped by natural selection to help people solve recurring social problems. Researchers applying an evolutionary biological lens to study followership have sought to reveal how such psychological mechanisms may function to aid people in decisions about when to be a follower (versus a leader) and who it is best to follow. Such decisions are contingent on shifting social variables, such as whether collective action is needed to achieve an organizational goal, who is willing to lead to achieve collective goals, and who (of those willing to lead) is able to attract followers presently (Bastardo and van Vugt, 2019).

Negotiation

The goal of a negotiation is for the two (or more) parties involved to reach an agreement. Yet, to achieve this end, some negotiators (particularly those who hold superior resources on important dimensions) attempt to wield any power they have coercively, to extract as much benefit as possible for themselves at the cost of the party or parties on the other side of the table. Negotiation experts (Fisher et al., 2011) attempt to teach people who must negotiate within or on behalf of their organizations to avoid such aggressive, coercive tactics as they are less likely to produce lasting agreements. People are also advised to avoid approaches to negotiating that, on the other side of the coin, involve simply trusting that other party will not exploit you. Negotiation is perhaps such a difficult skill to master, in part, because people routinely and automatically rely on assessments of trust when deferring willingly to others. In addition, many of the long-term costs of aggression and coercion in small, ancestral groups are less present in some modern business contexts where people commonly interact with near strangers to negotiate one-time deals.

An evolutionary perspective on negotiation would investigate how our evolved

psychological mechanisms may manifest in behavioral patterns that influence the negotiation process and its outcomes. A recent application of this perspective examined how mating motivation influences negotiations with people who would be considered mating competitors. In a study of working adults who engaged in negotiation professionally, men (but not women) with high levels of mating motivation reported engaging in more unethical behavior when negotiating (Lee et al., 2017). This may be because mating motivation encourages men to take greater risks and engage in other dominant, coercive behaviors against competitors in service of setting themselves apart from the competition. In experimental studies by that same research team (Lee and colleagues), men (but not women) who had high mating motivation, and were instructed to negotiate with a physically attractive person of the same sex, were more likely to engage in unethical behavior (i.e., outright deception about their party's position) in an attempt to reach an agreement. When the unethical behavior was less overt (i.e., dodging a question about their own position, rather than lying about it), women as well as men responded to mating competition by engaging in more unethical communication to attractive same-sex opposing parties in a negotiation. This research suggests that prominent mating motives may lead to less successful negotiation processes and outcomes, if people in that competitive environment are more willing to engage in unethical behavior as a means to win.

Women's Behavioral Strategies and the Meaning of Status among Women

We know much more about men's status acquisition and maintenance processes than we do about those same processes among women. With some notable exceptions of researchers who have investigated female

intrasexual cooperation and coordination processes (e.g., Campbell, 1999; Hrdy, 1999, 2009), human female status hierarchies and status competition have been relatively neglected in the evolutionary behavioral sciences. As a result, the emphasis on the unique aspects of male status dynamics has perhaps skewed our view of the more diverse forms status acquisition and maintenance processes can take. Ample evidence indicates that when women engage in dominant (agentic) behaviors, they have more difficulty securing promotions and leadership positions (Guadagno and Cialdini, 2007). This is perhaps because the female status hierarchies that women have evolved mechanisms to successfully navigate do not often fit the form of a rigidly hierarchical, vertical structure, and because men (who are still disproportionately in high organizational leadership positions) are inclined to miss, dismiss, or negatively evaluate these behavioral signals when they are sent by women, instead of by other men. There are ample opportunities for organizational researchers to push forward our knowledge about female status acquisition and maintenance processes, perhaps by studying female-dominated professions and organizations, and the emergence of status in female teams and groups.

Many researchers look to male-favored roles in warfare and hunting and female-favored roles in child-rearing in human history as being important for understanding the challenges women face in gaining status within their organizations. Vongas and Al Hajj (2015) review literature on the glass cliff phenomena in evolutionary perspective, suggesting that women's greater propensity to lead with empathy owing to different selection pressures women faced in ancestral environments contributes to their being differentially chosen as leaders to "weather the storm" rather than to "save the day". A similar argument is made by other researchers in predicting that women and those displaying cues to femininity are favored as

peacetime leaders, promoting cooperation, while men and those displaying cues to dominance and physical formidability are favored in wartime, or highly competitive contexts (Hegeman et al., 2015; Spisak et al., 2012; van Vugt and Grabo, 2015).

NICHES AND THE MEANING OF WORK

Humans can benefit from imitating skilled and successful others, and status serves as an important indicator of who to copy (Henrich and Gil-White, 2001; O'Brien and Bentley, 2018). Yet imitation alone cannot produce progress in the form of cultural innovations. Humans appear singular as a species in our ability to rapidly create a diverse set of new niches, defined as modifying one's physical and social environment through novel activities (Laland et al., 2000). As a population grows, more people can afford to specialize in some skills, and neglect investing in the acquisition of other skills, in order to direct more resources to status acquisition through deep expertise within a particular niche.

Some evolutionary researchers study niche construction as a factor that can influence natural selection (Laland et al., 2000; O'Brien and Bentley, 2018). Consider, for instance, that when West African farmers decided to clear more land for yam production, this generated substantial areas of pooling water that promoted mosquito reproduction, and the spread of malaria. This environment selected for genetic resistance to malaria, increasing the frequency of the sickle-cell allele in the local population. A similar argument has been advanced for populations that relied on dairy farming as a means of subsistence, which likely contributed the spread of genetic lactose tolerance in those populations. Many technological advances have increased the production of greenhouse gases, which are effecting rapid changes on many aspects of our physical environments

(i.e., climate change), with yet to be understood influences on the genomes of many of earth's species (Fitzpatrick and Edelsparre, 2018). Today, it is likely that the organization is a key player in niche construction (and destruction) processes. It serves as a primary vehicle through which humans, via collective actions, impose changes on their physical and social environments.

Niche creation today is in part responsive to the effects of prior niche creation, providing the opportunity to produce new countervailing forces that may mitigate negative effects of past niches. Genetic therapies for sickle cell disorder (i.e., CRISPR Tool treatments; Stein, 2019) are being tested to combat the deleterious effects of that inherited condition. Food scientists have created lactose-free dairy products, and food companies have successfully marketed them. Wind, solar, and other clean energy technologies are being designed and produced to replace those with more environmentally destructive emissions.

There are many reasons to suspect that niche creation is intimately connected with status acquisition and maintenance processes. An entrepreneur who can first convince investors of the potential in an idea, and subsequently successfully develop, refine, and sell that innovation, has unprecedented potential to elevate his or her status in modern environments, over a compressed timeframe. Mark Zuckerberg and Jeff Bezos are both examples of people who have radically changed their level of status via innovation. As technology advances and the human population that technology serves greatly increases in size, there is more rapid turnover in niches, and the life-cycle of some niches is necessarily quite short. People who are able to adapt to this rapidly changing work environment will be more successful in participating in niche construction processes. Organizational leaders are increasingly valuing creativity in their workers, reflecting a recognition that success in many business environments requires the ability to participate in the creation of

solutions to novel problems (World Economic Forum, 2018; Zhou and Hoefer, 2014).

In a fast-paced and competitive business environment, where people must quickly evaluate both new ideas for niches, and their creator's capacity for developing and propagating that niche (for instance, when venture capitalists must make decisions about where to invest resources), aggressive behaviors and strategies for short-term gain may be incentivized, and charisma given a premium in status acquisition. Exaggeration or puffery, and even outright lying about the popularity and feasibility of one's idea, product, or service are rampant in the entrepreneurial, or start-up, world (Pollack and Bosse, 2014). People with physical cues to status that were advantageous in ancestral environments may be more successful in acquiring resources in this context. To the extent that highly competitive business environments engage a wartime mindset among decision-makers, the importance of these status signals may be elevated, and the aggressive or coercive behaviors that can accompany them may be tolerated. The currently male-dominated nature of the venture capital profession is consistent with such expectations.

The meaning of work in an environment of rapid niche creation and destruction is changing for many in the workforce. For instance, workers are increasingly participating in the gig economy, and migrating to cities for employment opportunities. A status safety net is more reliable in a large city where job openings abound, compared to more rural environments where opportunities are limited and communities are therefore more susceptible to niche destruction events such as factory closings. Organizational researchers have yet to extend this evolutionary perspective on niches to study the design and meaning of work, or status acquisition and maintenance processes (Nicholson, 2010). Studying work through an evolutionary lens on niche creation and loss processes may help lead research in the business and organizational sciences in new, fruitful directions.

CLOSING REMARKS

Any attempts to understand organizational behavior and status acquisition and maintenance processes at work without the aid of an evolutionary perspective will be necessarily incomplete. Similarly, concerted efforts to combat biases in the workplace (that harm not only workers, but the overall success and profitability of their firms) without the benefit of an evolutionary functional lens on these biases will be less informed and effective than they could be. Businesses seeking to elevate diversity, for example, or address sexual harassment in light of the Me Too movement, can leverage the biological perspective alongside other theoretical perspectives on these issues to better design interventions to improve organizational cultures and climates. Continuing to elevate leaders based in part on physical features that would have helped them excel in hand-to-hand combat with neighboring tribes in ancestral environments, for instance, will result in affording high status to people who may be less effective as leaders in many modern (i.e., mismatched) work environments, compared to their competitors who possess fewer of these ancestrally-driven status cues. Similarly, ignoring or treating as taboo the normal biological experiences of female workers that result from differential parental investment and other reproductive dynamics that differ between the sexes (Grandey et al., 2020) can serve to reinforce problematic patterns of sex discrimination in organizations. Greater attention in future research to how status acquisition and maintenance processes at work may differ across individuals based on culture and individual difference variables, such as worker sex and age, can only serve to expand our understanding of organizational behavior and how to enhance the fairness and safety of organizations for workers. We feel an evolutionary perspective has much to offer in this pursuit.

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Evolutionary Psychology and Gender Studies

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INTRODUCTION

At first glance, using gender studies to inform an evolutionary perspective seems challenging, if not impossible. Gender studies relies on a social constructionist view to explain human behaviors such as identity formation, societal roles, and self-perception, while the overarching premise of evolutionary psychology is that people are a merger of their environments (including physical, social, and cultural contexts) with biology. Gender is about power dynamics and societal inequality, considerations rarely mentioned in evolutionary psychology. The fact that the fields rely on opposing structures (e.g., society versus interaction of biology with environment) as the root of human behavior is problematic when thinking about integrating gender studies with evolutionary psychology in any meaningful way.

Although divergent, both perspectives have interdisciplinary foundations, and researchers working within these disciplines seek to

better understand how people effectively live and function. This small but promising overlap may allow for gender studies to potentially inform evolutionary psychology, in at least a rudimentary manner, with the hope of arriving at a more accurate and complete view of human behavior.

Gender may be considered as having distinct facets, including identity and expression, and is at least partially removed from biological sex. By using this decomposition, it is possible to tease apart various social, cultural, and biological influences that have led to the construction of gender, sex, and gender/sex. This view is the cornerstone of the chapter, leading to concrete examples of how evolutionary psychology can profit from incorporating ideas from gender studies and vice versa. We note that our focus is on providing evolutionary psychologists ways to include gender theory in their work, given the intended audience of the volume.

Our goal is to show the main ways in which gender studies may be used to

propel evolutionary psychology into new areas of inquiry and highlight the benefits from expanding the discipline to be inclusive. Given both fields were founded on an interdisciplinary structure, using some of the approaches and perspectives from gender studies should be achievable for evolutionary psychologists. The key, then, is to demonstrate to those working in the areas that there are advantages to be gained.

FOUNDATIONS OF GENDER STUDIES

Defining Gender and Sex: Are They Constructed?

The meaning of ‘gender’ and ‘sex’, and the relationship between these two concepts, has significantly changed over the decades and remains challenging to clearly define. Indeed, scholars still write about the difficulty they face in accurately providing clear, non-overlapping distinctions between the two concepts (Fausto-Sterling, 2019).

It must be stated that some feminist scholars (including those working both within gender studies but also in other disciplines) hold that attempts to make any distinction between sex and gender work against feminist goals by replicating what they consider to be the androcentric dualities of mind/body, reason/emotion, and so on, in order to justify the oppression of women (Mikkola, 2019). Their reasoning is that when a dichotomy is created, one side is always valued at the expense of the other, and women are typically associated with the devalued characteristic. Women are largely seen to be more irrational and emotional than men and more identified with their bodies than their minds (see Fisher and Burch, 2019 for a review). Thus, they argue the exercise is repressive; it cannot be used as a theoretical tool for teasing apart concepts of womanhood, for example, from biological and reproductively associated characteristics (Fisher and Burch, 2019).

This caveat aside, gender as a construct is largely considered separate from sex by most researchers, although there is a growing movement to use the term ‘sex/gender’ (or ‘gender/sex’) to indicate the deep interlinkages between the two constructs. The concepts of gender, sex, and sex/gender are now explored, using a historical perspective to show how these ideas developed over time. Our aim is to help evolutionary psychologists more deeply understand some of the distinctions, such that they may use these terms with confidence in their work. It may also assist evolutionary psychologists in comprehending some of the criticisms their use of these terms may receive.

Historical overview

Until the 1960s, ‘gender’ was primarily used to refer to feminine and masculine words, such as ‘le’ or ‘la’ in French (Mikkola, 2019). Stoller (1968) began to refer to sex in biological terms and gender as the level of femininity or masculinity a person exhibited, to explain why some individuals were experiencing the sensation of being trapped in the wrong body. Starting in the 1970s, feminist scholars began to draw a distinction between sex and gender. Rubin (1975) posited that sex needed to be isolated as a single, nature-based category that was comprised of anatomy, phenotype, and physiology. She viewed sex as fixed from birth but proposed that it was not the primary factor in causing social inequality between men and women. Instead, gender was the culprit, with gender defined in terms of the socio-cultural meaning attached to the idea of man/male and woman/female and the ever-changing views of masculinity and femininity. She contended gender differences are the result of society dictating how men and women should behave. She further referred to gender as the ‘socially imposed division of the sexes’ (Rubin, 1975: 179). Sex may seem easy to determine based on the obvious anatomical differences between females and males. However, some bodies are not easily

distinguishable as female or male. Should sex be based solely on the presence of external genitalia, or should it be based on other phenomena such as the presence of hormone levels, chromosomes, or internal genitalia (Fausto-Sterling, 2019)?

There is still active debate about whether sex is a discrete and exclusively biological category. For example, Fausto-Sterling (2019) reviews how one group of scholars, including herself, argues that brains (and by association behavior) cannot be classified as female or male because they are housed in bodies with particular genitalia. Others, including those working within evolutionary psychology (e.g., Del Giudice et al., 2016), continue to argue the opposite.

Sex as a construct

Some gender theorists have proposed sex is a social construction. Their primary argument is that some secondary sexual characteristics, or bodies in general, may be modifiable by social practices. For example, Jaggar (1983) reasoned that women's lowered social status resulted in them having less food available, and that the lack of nutrition resulted in smaller stature. This example does not demonstrate an awareness about the transmission of genes and if it were true, then these undernourished women would presumably have decreased fecundity and experience lesser reproductive success. Further, Fausto-Sterling (1993) writes that if females and males engaged in the same level of exercise, sexual dimorphism would decrease. This sort of thinking poses a problem for evolutionary psychologists who are versed in anatomy and aware of the well established sexual dimorphism among the other great apes. Exercise is not the sole determinant of sexual dimorphism.

Another challenge to the definition of 'sex' is that intersexed individuals, or those who possess sexual characteristics that are not consistent with the prescribed categories of 'male' and 'female', have a combination of different characteristics or an absence

of particular sexual features (making up an estimated 1.7% of the world's population: Fausto-Sterling, 2000). Money and Ehrhardt (1972) analyzed intersexed individuals in terms of the assignment of sex at difference levels of anatomy, each of which may develop independently (e.g., chromosomes, differentiated gonads, hormones). Gender, then, was seen as an individual characteristic that is open to modification through child-rearing practices. This view led to the perspective that one could use socio-cultural perceptions about sex differences (e.g., gender) to inform how physical bodies should be, ultimately concluding with medical practitioners modifying bodies to better fit these standards via surgery.

Gender as a construct

Bem's (1981) gender schema theory accounts for how, at a cognitive level, individuals become gendered by society, and how sex-linked characteristics are maintained, signaled, and transmitted to others within a group. The underlying assumption is that gender is socially created and communicates one's identity to others. Bem argued that schemata concerning gender allowed this information to be readily assimilated by individuals. Further, individuals vary in the extent of sex-typing they undergo, such that individuals are influenced to align with sex-linked expectations by caregivers as children, media, school systems, and social structures.

For many years, gender was perceived to indicate one's level of masculinity and femininity, as culturally or socially constructed, while sex referred to their biological state (e.g., chromosomes, anatomy, gametes). Richardson (2015) outlines that leading up to the 1960s, gender referred to what may be loosely considered as femininity and masculinity, with direct links to behaviors that were considered socially appropriate for men and women. Later, scholars such as Butler (1990) called for a re-examination of labels and categories, suggesting that feminists

were mistaken in their attempts in making 'women' a discrete category from 'men', given how the effort reinforces the gender binary. Butler challenged the idea of biological, binary sex and proposed that gender and sex (and sexuality) are the result of norms surrounding individuals. These norms dictate all available options or possibilities in advance, meaning that individuals are provided with a small window of potential behaviors that are socially permitted and, hence, considered 'natural'. She argued that because binary sex appears natural, and is a 'fact' of science, it reveals how deeply these ideas have become entrenched.

Richardson (2015) reviews that gender has been ascribed personality traits and associated behaviors, such that men are typified as being aggressive and women as caring. Gender is also taken to indicate any social construction that distinguishes men from women (whether in a physical sense, such as their bodies, or in a socio-cultural manner), or where it results in hierarchical power differences with men having more privileges than women (Richardson, 2015).

Another issue concerns the shift within the past three decades for gender to be viewed as performative (Butler, 1988). Individuals act out a role in front of a social audience, such that the role in is keeping with historical social practices. This conformity, largely based on the internalization of scripts surrounding norms that are transmitted from generation to generation, helps individuals to avoid punishment for violating socio-cultural conventions. Butler's (1990) theory is that gender results from performing repetitive acts that are associated with being female or male, emphasizing what appears as the natural gender-binary. Humans are social beings, and as such they witness, model, reproduce, and internalize roles which eventually lead their actions to possess a theatrical, performative quality. Gender is therefore argued in this performative approach to be constantly created daily through social interactions with others.

Attempts to clarify terminology

A distinction between sex and gender may facilitate scholars arriving at an agreed set of definitions that may be used across disciplines. For example, Torgimson and Minson (2005) review how gender has become increasingly used in place of sex, and they report on the necessity of implementing standardized use of the terms. They present the possibility that some scholars are using gender instead of sex to be politically correct, while actually talking about sex, given that gender may be viewed as a less loaded term. It is possible that the same reasoning underlies decision-making by some evolutionary psychologists.

There is a potential solution to this problem. In a largely neglected paper, Gentile (1993) suggested the psychological community adopts standard terminology to reduce confusion. He proposed that the field use five terms: sex (biological function), biologically sex-linked (traits or conditions that are causally biologically related to being female or male), gender-linked (traits or conditions that are causally linked with maleness or femaleness but are culturally based as opposed to biologically based), sex- and gender-linked (traits or conditions that are causally related to both a biological component and a cultural component), and sex-correlated (traits or conditions that are related to being male or female without asserting a causal relation to either biology or culture).

We must also draw attention to the phrase 'sex/gender', which appears to be increasing in popularity. Initially, Rubin (1975: 159) introduced the phrase as 'sex/gender system' to describe 'a set of arrangements by which the biological raw material of human sex and procreation is shaped by human, social intervention'. Van Anders (2015: 1181, table 2) re-introduced gender/sex as 'whole people/identities and/or aspects of women, men and people that relate to identity and/or cannot really be sourced specifically to sex or gender'. We return to this topic in the next section when discussing binary categorization.

It exists separate from gender, which she defines as ‘aspects of masculinity, femininity, and gender-diversity that are situated as socialized, learned, and cultural (e.g., appearance, behavior, presentation, comportment). May refer to one’s internal sense of one’s self, culture, roles, other’s beliefs about one’s self, structures and systems, etc.’ (van Anders: 2015: 1181). Sex, meanwhile, is defined as ‘aspects of femaleness, maleness, and sex-related bodily features that are situated as biological, bodily, evolved, physical, and/or innate (e.g., vulvas, penises, breasts, body shape). May also refer to one’s internal sense of one’s self’ (van Anders: 2015: 1181).

Interestingly, gender as an idea is culturally grounded, as the languages of some countries do not contain words to differentiate sex and gender, for example. Thus, gender as a concept is not universal, and neither is the tearing apart of biology from an associated social construct. In many cultures, gender may be considered as having distinct facets, including identity, expression, and even biological sex (see Richardson, 2015, for a review). Additionally, cultures continue to shift these definitions, as language evolves. For example, while van Anders (2015) above clearly categorizes ‘trans’ with ‘transsexual’ under ‘sex’, the American Psychological Association (2020) defines transgender as ‘an umbrella term for persons whose gender identity, gender expression or behavior does not conform to that typically associated with the sex to which they were assigned at birth’. Not only does this definition place it squarely under gender, the definition itself labels any behavior that does not conform to a gender role as transgender. Therefore, transgender applies to any behavior, transient or stable, that ventures outside the society’s gender roles. As a consequence, what is considered transgender would shift with whatever assumptions a given culture makes about genders. In short, the definition of transgender, how it differs from transsexual, and whether it is categorized under sex or gender, is rapidly

fluctuating and has yet to become clearly delineated.

A final example of attempting to distinguish between sex and gender is provided by Alcoff (2006). She argued that feminism has faced an identity crisis, such that critiques about gender have fragmented the core concept of what it means to be a woman (versus a man), which served as the starting point for feminism itself. To resolve this problem, she developed a theory of gender as positionality, for which ‘gender is, among other things, a position one occupies and from which one can act politically’ (Alcoff, 2006: 148). Thus, the subjective experience of being a man or woman, and the identity of men or women, is created by one’s position in society. Further, men and women differ in objective terms based on reproductive roles. She writes, ‘Women and men are differentiated by virtue of their different relationship of possibility to biological reproduction....referring to conceiving, giving birth, and breast-feeding, involving one’s body’ (Alcoff, 2006: 172). As a result, individuals who would be typically seen as biologically female encounter a ‘different set of practices, expectations, and feelings in regard to reproduction’ than those typically viewed as male (Alcoff, 2006: 172). This difference in biology, associated with reproductive possibility, positions men and women differently in cultures and societies and, further, causes them to have separate lived experience. That is, one’s reproductive role shapes how one is positioned socially, leading certain gendered social identities to be developed. Last, given women are positioned uniquely in different contexts, there is no ‘gender essence all women share’ (Alcoff, 2006: 147–148); presumably, the same argument could be made for men. This view is raised here because it serves as an introduction to the idea that there is no general group of ‘women’ or ‘men’, and that attempts to speak about such categories in broad terms is misleading and inaccurate.

As a side note, while there is a much larger literature on women’s studies (perhaps

because much of gender studies has been tied to feminist scholarship), gender studies on men and masculinities has increased since the 1980s (Hearn and Collinson, 2018). Gender concerns all people equally and, as such, men and masculinities are equivalently considered with women and femininities, as well as anyone who defines themselves outside of so-called normative boundaries (e.g., LGBTIQ+: lesbian, gay, bisexual, trans*, intersex, queer, and other marginalized genders and sexualities). Hearn and Collinson (2018) discuss how gender studies has led to several approaches to understanding masculinities (in the plural), meaning there is now no universal, essential, singular category of 'masculinity,' just as there is no singular version of 'femininity'. In this vein, Hearn and Collinson argue that men are best conceptualized as a social category that is shaped by views of gender.

Why should evolutionary psychologists care?

It is important to use terminology in an accurate, agreed upon manner if scientists want to avoid confusion, be inclusive in their samples of participants (allowing for better generalization about humans), and create replicable studies with a clear understanding about who is included and excluded. Evolutionary psychologists, like other scientists, must use terms like sex, gender, and sex/gender in explicit ways if they want to meet these goals. The way that they use these terms does not have to be discipline-wide, but there must be some clarity about what they mean. For example, when describing 'women's mating strategies', which women are captured by the theory and findings? Are the only participants included in the sample those who self-report an agreement between their biological sex and gender identity as woman, and who have a consistent heterosexual orientation? If so, this sort of conceptualization needs to be explicit, given that it means other women

may be excluded, or that the researchers are building theories that may not be testable if their population is mismatched with assumptions. These are not political adjustments but methodological ones that improve the quality of research.

One concern to consider is that participants may not be linguistically aware of terms, nor understand what is being asked if they are given items that tear apart biological sex and gender identity. We have faced recent challenges in our research, where participants were asked about both, in addition to sexual orientation. In 2019, approximately one-fifth of college-aged participants (of a sample of 300) at a university in Eastern Canada indicated that they did not understand the questions. They recorded answers such as female or male, man or woman for biological sex, but then when asked about gender identity many participants left comments that they were confused about the item, reported sexual orientation, or in a small number of cases, used gender pronouns. Then, for the item about sexual orientation, there was again considerable confusion, with some writing in their romantic relationship status. Historically, when we have simply asked about sex and sexual orientation, there has been minimal (if any) confusion, especially when sexual orientation is accompanied by examples in common language (straight, gay, etc.).

The recognition or translation of academic concepts by the public has been a longstanding issue in sexuality research. In order to obtain accurate, insightful data, the participants must be familiar with the terms being used. This situation is made more difficult when these definitions are still being questioned, argued, or changed by the scholars creating the theories underpinning the research. It is critical for evolutionary scholars to understand that gender theorists are still questioning core concepts, such as how sex, gender, and sex/gender are distinct or not, and the consequences of creating or acknowledging distinctions.

Gender and Binary Categories

An assumption that has transcended decades of scholarship is that when talking about gender and sex, one was implying that there were only two types of humans: female and male, or man and woman. This gender-binary had a significant role in shaping psychology (Hyde et al., 2019) and, by extension, the field of evolutionary psychology.

From a gender theorist's perspective, the binary can only be left behind when one stops seeing gender and sex as essential categories that are self-explanatory and instead examines their socially constructed foundation (Balzer Carr et al., 2017). Therefore, one may question how these categories arise, who uses them, what purpose the categories serve, and so on. Put another way, academics categorize gender and sex based on their beliefs, even if such beliefs are grounded in what they consider objective science, or using empirical findings that are obtained with the scientific method.

An example is the distinction between sperm and ovum (egg) when discussing sexual reproduction. The majority of the literature positions the two gametes in binary opposition of being subject/object, active/passive, or aggressive/receptive (Martin, 1991). The very topic of sperm competition relegates the egg to a static fortress, with the sperm engaging in lethal competition with the winner successfully penetrating the outer sanctum of the ovum. Consequently, a sperm is inherently viewed as dominant and active, and the primary agent in the reproductive process. Further, sperm and ovum represent a binary view of the sexes, and are layered with views about the individuals who produce these gametes. Some textbooks, such as Cartwright (2000), explicitly state that these strategies of fertilizers (sperm) and energy provisioners (ovum) are played out by individuals, as they are the vessels for their gametes. It is important to mention here that these beliefs about gametes and the extension to individuals are both erroneous. Ova are not

passive; ova actively release chemicals (like bourgenol) to attract sperm (Stephenson, 2003). Women are not passive either, as we will review.

As mentioned, the growing use of the phrase 'sex/gender' indicates some scholars regard the ideas to be so inherently connected with each other (see, for a review, Fausto-Sterling, 2019). The overarching view is that there is no way to tease apart the roles that sex or gender have on the majority of behaviors, emotions, identity, or sexual orientation (Fausto-Sterling, 2019). In conclusion, gender theorists traditionally have argued against biological determinism and propose that gender differences are the consequence of cultural practices and societal expectation (Mikkola, 2019). However, there is ongoing debate as to the social practices that lead to gender, what social construction is, and what being (or doing) a gender means (Mikkola, 2019).

Sexualities within the Gender Perspective

It is challenging to discuss sexualities from a gender perspective because it is a rapidly changing area of theorizing. However, to start, MacKinnon (1987) presented the idea that gender is a theory of sexuality. Gender is caused by sexual objectification of women, such that they are viewed as sexual objects with the purpose of satisfying men's desire. Further, she proposed that masculinity is centered around sexual dominance, while femininity is about submissiveness, meaning that when talking about gender, one must address where that person is on the sexual dominance/submissiveness construct. Men, by virtue of their masculinity, occupy the dominant position, while women occupy the submissive position. She does not assume a stance of biological determinism (e.g., that men's inclination to sexually objectify women is innate, or that women are naturally submissive). Instead, she contends that

sexuality is socially constructed; society has conditioned men to believe women's subordination is sexy, while women have been conditioned to find that male view as erotic. Her theory rests on pornography as the vehicle for conditioning; pornography depicts women as being (and wanting to be) submissive, and if they do not submit willingly, force is acceptable. She concluded that men and women are socialized differently due to power inequalities, and these inequalities lead to specific gender-based traits, behaviors, and roles. Her view is an example of gender realism, in that women as a group are presumed to have defined membership due to a shared feature, experience, or commonality such that possession makes one a woman. Gender realism has been criticized by gender theorists for failing to consider how gender varies with experiences related to class, ethnicity, and so on (Spelman, 1988). This perspective has been specifically mentioned here, given that one area in which evolutionary psychologists face criticism is in how men are presented in the literature as sexually cavalier, easily arousable individuals who seek to mate with multiple women whenever the opportunity arises (Brunskell-Evans, 2017). Evolutionary psychology rarely tackles issues such as power inequalities when presenting findings about pornography consumption, for example, which means that those versed in gender studies may find evolutionary theorizing unsavory.

A different way to capture gender studies and sexuality is by exploring van Anders' (2015) sexual configurations theory. It is built on feminist and queer theories, with the understanding that sex and gender are intertwined and not easily separated. Moreover, it leaves theoretical room for individual differences, such that one can consider sexuality in dynamic, changeable terms that may include level of sexual attraction to others, physical aspects of attraction that are not based on gender (e.g., eye color, body shape), the preferred number of partners, the age and experience of others as compared to oneself,

whether attractiveness is related to dominance and power, one's preferred sexual role, and the types of sensations, fantasies, and experience one enjoys (van Anders, 2015). This theory is promising for its inclusivity, how it aligns with people's lived experiences, and for the new research directions it may provide (including ideas for evolutionary psychologists).

It is critical to remember, though, that disciplines related to sexuality studies are undergoing a re-examination. Hegarty and Rutherford (2019) highlight the way research carried out in the United States on a variety of populations (e.g., LGBTQI+) has dominated our psychological understanding, and call for more international research. Indeed, the majority of conversations on gender (including this one) assume the US view of gender – for example, adhering to a binary that other cultures may not emphasize.

A Brief Review of Queer Theory

Gender theory is distinct from queer theory. 'Queer' has many meanings in Western culture and academia. It may describe someone of a non-heterosexual orientation (including gay, lesbian, transgender, bisexual, pansexual, and asexual people) (Sullivan, 2003). Someone may self-identify as queer to signal their sexuality is fluid, or that they view their sexuality as divorced from gender norms (e.g., that they are celibate, practice bondage, or sadomasochism). In academia, queer theory typically refers to inquiry at the intersection of gender and sexuality with the goal of destabilizing binary constructs. That is, there is an attempt to remove the view that people are gay or straight, men or women (Balzer Carr et al., 2017).

Taking it one step further, Butler (1990: 25) proposed that scholars rely on 'a heterosexual matrix of intelligibility' which refers to how a constructed logic regarding sex, gender, and desire result in a coherent sexual identity with a corresponding gender identity.

In other words, it is how binary constructs appear to be normal and underlie the bridging of biological sex, gender, and sexuality. Queer scholars instead try to break these links by showing they do not apply to many individuals (Balzer Carr et al., 2017).

One feature of queer theory is the recognition of the diversity underlying gender and sexuality. Bem (1981, 1993) initially argued that gender must be entirely divorced from biological sex. Biological sex is about anatomy and reproduction, she claimed, while gender is intimately and inevitably part of social inequality and, hence, societies must banish the concept of gender in order to eradicate the power-based relationships that it causes. (Ironically, the study of divisions and ingroup/outgroup dynamics (tribalism) is prominent in evolutionary psychology and would help support Bem's point regarding power-based relationships). Later, Bem (1995) conceded that eradicating gender is likely impossible and it would be more useful to proliferate numerous gender categories. Thus, she joined queer theorists who embraced gender and sexual expressions as idiosyncratic, performative, hugely diverse, and far removed from biological essentialism.

There are many sources of potential dispute between queer theorists and evolutionary psychologists, with possibly the most significant being that queer theorists reject biological explanations. For example, when human gametes are described as active (sperm) or passive (ovum), or even the product of men's or women's biology, queer theorists argue that scholars are confounding biological sex with gender (Martin, 1991). Further, the idea of femininity and masculinity as the result of hormonal processes or genetic influences that are unevenly distributed according to sex is also rejected (Warner, 1993). Given the reliance of evolutionary psychology on biological explanations (including hormonal variation across and between the sexes, or the role of the genome in phenotypic outcomes), it

seems unlikely queer theory will be used by evolutionary psychologists. However, evolutionary psychology would benefit by being more inclusive in populations of study, and including more explicit theorizing about the role of environments (including social, cultural contexts) in their interactive models of behavior, for example.

Intersectionality as a View of Gender

A final topic is intersectionality, which is a theoretical approach to exploring social identity in relation to gender. It is a framework in which one's social identity is based on multiple factors, such as race, age, nationality, disability, religious affiliation, economic class, and gender, which lead to discrimination and prejudice (Crenshaw, 1989). Intersectional theory is based on the idea that people may be subjected to multiple sources of oppression.

In a rudimentary way, intersectionality refers to the need to analyze gender in the context of other social identities. For example, how gender is experienced similarly and differently between individuals depends on their ethnicity, socio-economic class, and sexual orientation, among other considerations. However, intersectionality has become a lightning rod for discussions about how social identities are comprised of more than these factors, and is part of critiques directed at identity as essential, universal, categorizable, and coherent (see Balzer Carr et al., 2017 for a review). The core concept is that one's overarching identity is founded on an unquantifiable number of other identities, which means that identity is not concrete. So, while everyone has gender, and it is part of their identity, the reason there is such divergent and idiosyncratic experiences with gender is because it intersects with race, class, and so on, but also with all of these other identities. The consequence of this view is that any attempt to make general statements of what it

means to be men or women is flawed. Going one step further, those who rely on intersectionality propose that if one attempts to use the notion of a generic or universal man or woman without context, they are being oppressive, because such views reinforce that the only version of men or women is White, middle-class, Western, heterosexual, and able-bodied, for example. Indeed, this issue causes those working within an intersectionality framework to discredit much of the evolutionary psychological literature, because at the very least, samples of participants are rarely described in sufficient detail, leading any findings to be potentially overgeneralized as representing all men and women.

In short, in addition to the arguments regarding the categorization of sex and gender, there remains the argument (and often omission) of types of sex and gender and the intersection of sex, gender, and other identities in human behavior. Researchers like Bem (1993) may point to political agendas for the miscategorization of sex and gender or even to eugenics as the source of prejudice that creates the necessity of studying intersectionality. However, even those specifically working close to sex and gender have sometimes failed to truly incorporate or study sex, gender, other categories, or the intersection of them.

Evolutionary-informed science has long suffered from the misinformation spread by eugenics and has tried repeatedly to combat this unscientific propaganda. Exclusion and ignorance of multiple sexes and genders has no place in evolutionary-informed fields. Sexes other than exclusively female or male have existed in the animal kingdom for millennia, and any evolutionary researcher should be familiar with them (detailed shortly). Current evolutionary psychological researchers have an uphill battle: the historical ramifications of eugenics, the fight against views of evolutionary psychology as biologically determinist, misrepresentations of evolutionary theory, and evolutionary psychology's tradition in adhering to a strict,

binary view of sex and gender have created lasting problems.

FOUNDATIONS OF EVOLUTIONARY PSYCHOLOGY

First, we must mention the multitude of fields that fall under evolutionary psychology, including biology, geology, anthropology, psychology, literature, and economics. In addition to evolutionary psychology, these fields have a history of predominately male researchers and authors. Each field has faced critiques and calls for more inclusivity among researchers and for more inclusive topics of research (Beery and Zucker, 2011; Bourguignon, 1983; Gannon et al., 1992). As we elucidate here, evolutionary psychology may be criticized, but its issues are not discipline-specific and they are not irreparable.

Sex and Gender Variation Throughout Species

Darwin first posited in 1859 in *On the origin of species by means of natural selection* that all living organisms are subject to the process of evolution and that these change in the population over time. The major power behind Darwin's theory was his substantial supportive data from species all over the world. However, he predicted, and feared, that readers of his work would not accept that the process of adaptation and evolution applied to humanity. 'Let us hope it is not true, but if it is, let us pray that it will not become generally known', is the widely reported, but poorly cited, statement of a woman in response shortly after the publication of *Origin* (Norris, 2019). Indeed, human exceptionalism has plagued the acceptance of evolutionary theory for over 150 years.

One would expect us, as evolutionary researchers, to argue that it is this human

exceptionalism that has kept sex and gender researchers from accepting evolution as a factor in human behavior. We must admit that this perspective is part of the problem, and we will elaborate later. However, we will also argue that human exceptionalism has prevented some evolutionary researchers from understanding the spectrum of sex and gender in the human species and, therefore, limited the utility of some tenets of sex and gender studies in evolutionary psychology.

For example, while evolutionary psychology is focused on the human species, there are myriad species with both genetically and environmentally dependent sexual variations that can provide insight to human sexual variation. Currently, the only known types of sex-differentiation involve the 'mating groups' of sex chromosomes of XY, ZW, and UV categories and haplodiploidy exhibited by insects (Beukeboom and Perrin, 2014). Although these clear delineations seem limited, these systems have variations within them. For example, the mushroom *Schizophyllum commune* has two mating type genes, with one having over 300 possibilities and the other 64, leading to a documented 23,328 distinct mating types (Casselton and Kües, 2007). Clam shrimp (*Eulimnadia texana*) have a male combination as well as two varieties of hermaphroditic 'females', which either self-fertilize or mate with males but cannot mate with each other (Chasnov, 2010). The protozoan *Tetrahymena thermophila* has seven distinct 'sexes' that can recombine and reproduce (Cervantes et al., 2013). It is important to reiterate that these are only a few examples.

Entire tomes can be written just on sexual variation (or variations on sex) seen in the animal literature. In terms of hormonal variation, in crustaceans, both an androgenic (male developmental path directing) hormone and a peptidic female sex hormone exist and they have no similarity with other hormones in other species (Katayama et al., 2013). Monotremes, which are also mammals, but which lay eggs, do not have the

SRY gene (the sex determining region of the Y chromosome in humans) but nevertheless differentiate into males and females (Wallis et al., 2007). Lek breeding Ruffs have three different forms of male, varying in reproductive physiology and appearance (Küpper et al., 2016).

Moreover, sex can be further divided into additional forms and can be dependent on context (for example, temperature). The relationship between reptile sex and temperature has been widely documented (Shine, 1999), as have been hermaphroditic fish species that change their sex based on mating competition and group composition (Munday et al., 2006). This overview is a small sample of variation on the planet. Entire books dedicated to variation in humans and other species (Bagemihl, 1999; Roughgarden, 2013; Schön et al., 2009) may begin to do the spectrum some justice, but suffice it to say it is far greater than two sexes or genders.

Although evolutionary psychologists may be quick to reply 'but we are not flatworms or crustaceans', this reply would be the same that scientists directed to Darwin, and those who may work more directly with evolutionary biology. While humans obviously do differ from other species, human exceptionalism can rear its head in a number of ways that limit our research and understanding.

Variation within the Human Species

Even within the human species, there are more sex chromosome matchings than simply the pairing of XX and XY. Variations such as X₁ (or XO), XXX, XXY, XYY, XXXY, XXXX, XXXXY, and so on, also exist, as do other hormonal variations including but not limited to adrenogenital syndrome, 5-alpha-reductase deficiency, and androgen insensitivity syndrome (Samango-Sprouse and Gropman, 2016; Kothari and Mehta, 2009). While researchers may argue that some of these variations lead to

infertility, and hence would be effectively ‘selected out’, that is not the case with all of these or with others that we have not listed here. This consideration also points to an important issue in the evolutionary sciences: if a clear survival/reproductive benefit (adaptation) cannot immediately be found, the category is often considered a research dead-end and ignored. This issue plagued Darwin when he first examined peacocks, and still plagues the discipline today. For example, decades of beliefs (including Darwin’s) regarding the appendix were shown to be incorrect (Smith et al., 2009).

Both evolutionary psychology and gender studies can agree that accurate definitions are key: ‘The literature is highly confusing—we need to clarify our terminology’ (Rolf Hoekstra, a geneticist interviewed in Whitfield, 2004: 718). Moreover, much research on evolution and human sexual behavior mitigates discussion of human flexibility in favor of generalities regarding the two predominant sexes. This pervading view of binary sex is particularly disappointing given the documented and lauded evolutionary benefits of behavioral and physiological flexibility in humans (Aureli and Whitten, 2003; Brown et al., 2011; Gowaty and Hubbell, 2005; McCabe et al., 2015; Nettle, 2009b). Humans are composed of layers; there exists behavioral variation on top of physiological variation on top of genetic variation. While researching the two predominant sexes may be convenient, it creates a body of literature that is far from complete and serves to misconstrue our understanding of people. The same can be said for making statements about the human species without investigating variation in gender, particularly cultural variations in gender, especially in light of evolutionary psychology’s adherence to interactionist views between the genes and environment. We note that there are exceptions; for example, there is birth order research on the *fa’afafine* of Samoa, who are biologically male but usually raised as females and identify as women and often

engage in heterosexual relationships with men (Vasey and VanderLaan, 2007).

Evolutionary Theory and Gender

As reviewed earlier in this chapter, theorists have long argued that gender is a social construction, and until recently evolutionary psychologists would have little to contribute on that matter. However, evolutionary psychology has expanded considerably, with an entire subfield dedicated to the evolution of culture and cultural practices (Henrich and McElreath, 2003). Culture is not antithetical to evolutionary theory; culture is created by humans who are the product of evolutionary processes and hence culture can be studied using the same principles (Nettle, 2009a).

What is exciting, then, is that gender studies would be a perfect field for evolutionary psychologists to further examine both the biological and cultural factors involved. Perhaps the lack of movement into this area is because of the relatively recent emergence of cultural evolution as a field, or because of evolutionary psychology’s restricted focus on the predominant sexes.

Evolutionary psychology’s view of women

Evolutionary psychology has been criticized as having a largely androcentric view (Fisher et al., 2013). Women have been viewed in various ways in the evolutionary psychological literature – originating with a passive, inactive role in human evolution – and particularly with respect to mating. This criticism has existed for almost as long as Darwin’s theory itself, in particular in response to *The descent of man, and selection in relation to sex* (1871). Darwin’s views of the human sexes were certainly influenced by his experience as a White man in Victorian England, and women rebutted his claims regarding their sex. For example, Eliza Burt Gamble responded with *The evolution of*

woman, an inquiry into the dogma of her inferiority to man in 1894.

To be fair, attempting to argue scientifically that women are inferior to men did not begin with Darwin (Vandermassen, 2005); however, the sticking point for feminists and other scholars is how these viewpoints have been carried forward in biology, psychology, and evolutionary psychology, such that the rebuttals did not end with Gamble (see Fedigan, 1986 for extensive critique). Fedigan (1986) cites several authors who have pointed out that Darwin projected his own beliefs of appropriate roles to the sexes, and that these views were based on Victorian society, not societies that fall outside of the prevailing group studies (i.e., Western, educated, industrial, rich, and democratic populations (WEIRD); Henrich et al., 2010). The lack of research on non-WEIRD societies in evolutionary psychology has been a critique of research as a whole as recently as 2020 (Burch, 2020).

It is important to point out that Darwin also made several exceptions for humans and often contradicted himself on the topics of sexual selection and sexual choice. Fedigan (1986: 27) reports, ‘the human species appears to be the only one for which Darwin argued that males presently exercise both the mechanisms of competition and choice’. Much evolutionary psychological research has reiterated the narratives of women being less aggressive or competitive with respect to mating (we refer to these as narratives as there is much data to the contrary) and has often neglected topics such as mothering, women’s social behavior, women’s reverse dominance hierarchies, as well as women’s formations of alliances, aggression, intra-sexual competition, and, generally, women’s role in evolution (Fisher et al., 2013). Fedigan (1986) lamented this relegation of women to the background and explored how this mindset continued for the next century despite mountains of evidence to the contrary. In a frustrating illustration of the persistence of this issue, almost 30 years later, Fisher et al.

(2013) again made the same arguments as Fedigan (1986) – that the evidence for the important role of women in evolution is overwhelming, that it has been ignored, and that androcentric views of human evolution are not supported by the literature.

To be clear, we are not saying that evolutionary-based research on women, flexible mating strategies, women’s mate choice, provisioning, and other important topics does not exist. As we have stated, it is just the opposite; anthropology, evolutionary biology, and evolutionary psychology contain volumes on these topics. The issue lies in the omission of this research in larger models of evolution. For example, let us examine the larger overview of human evolution provided in evolutionary psychology textbooks. Burch (2020) examined 22 introductory evolutionary psychology textbooks for their content on the role of women in evolution. The widely proclaimed ‘greater maternal investment’ was not reflected in textbook content. Many texts discussed reliance on men for child investment, and in particular, the emphasis women place on finding a partner who is willing to invest in them and their children. The majority did not discuss skills and strategies for women after they become mothers, only the choice of whether to keep a child. Overall, the material on maternal behaviors averaged just over three pages (textbooks, on average, were 413 pages in total).

Content on women’s relationships and the important role of cooperation in childrearing was also lacking. Less than 20% discussed alloparenting in any detail. Content on older women (not the young, fertile, attractive women often discussed in mating research) was scant or missing. In actual research, older women have been repeatedly shown to have a significant role in alloparenting, maternal assistance, provisioning, and sociopolitical counsel in non-WEIRD societies. Hawkes et al. (1989), for example, clearly demonstrated how Hadza grandmothers provide more to children than younger relatives who are girls, adolescents, or young adults,

while Sear and Mace (2008) documented that grandmothers in some cultures have a more positive effect on child survival than fathers.

Nineteen texts discussed physical attractiveness a factor in women's evolutionary success, while seven (often minimally) addressed women's intelligence or other traits. In addition to the age-bias, women are presented in narrow terms, which suggests that most academics hold a grim view of evolutionary psychology's account of women. The positive news is that the books misrepresented the field's actual views, which do consider older women and traits other than attractiveness as important.

We should mention that the sex of the textbook author had an effect on how women in the books were portrayed. Men who authored textbooks were more likely to echo Darwin's Victorian views that women were 'coy', 'inhibited', 'shy', 'modest', and 'sexually naïve' (a summary can be found in Burch, 2020). These authors also emphasized the role of men in sexual selection and provisioning. Texts with women authors provided more content on traits other than attractiveness (such as intelligence), women's strategies after mating, food provisioning, and the role of older women in families and society. In sum, men were far more likely to reiterate Darwin, while women voiced rebuttals similar to those of Gamble and Fedigan. This issue becomes magnified when one realizes the disproportionate number of textbooks (Burch, 2020) and journal articles within evolutionary psychology authored by men, especially with respect to the first author position (Meredith, 2013).

Evolutionary psychology's view of men

In terms of men's role in human evolution, Darwin (1871) believed them to be the competitors, the leaders, and the selectors (see Fedigan, 1986). That is, men were the active players in the evolutionary process. One of the most illustrative, and persistent, examples of this perspective is the model (or we

should say, the persistent narrative) of 'Man, the Hunter' (Washburn and Lancaster, 1968). Zihlman (1978: 5) summed it up this way:

The presently popular 'hunting hypothesis' of human evolution argues that hunting as a technique for getting large amounts of meat was the critical, defining innovation separating early humans from their ape ancestors. This view of 'man the hunter' has been used to explain many features of modern Western civilization, from the nuclear family and sexual division of labor to power and politics. But as more and more data have accumulated in recent years, and as approaches to them have changed, the notion that early man was primarily a hunter, and meat the main dietary item, has become more and more dubious. Consequently, interpretations of early human social life and the role of each sex in it must be reevaluated.

As Zihlman states, this model has been used to further Darwin's argument that human society and evolution rest on the backs of men. This narrative argues that hunting is the defining human adaptation, men are the primary evolutionary agents, and hunting is responsible for many of humanity's intellectual achievements, including language and complex cooperation (Washburn and Lancaster, 1968). As such, it implies the reliance of women on men and reiterates Darwin's arguments that women rode men's evolutionary coat tails throughout history. This view is contradicted by known practices in non-WEIRD cultures; not only is women's reliance on men neither universal nor absolute, but women also hunt and the division of labor is not nearly as 'divided' as theorized. To add academic insult to injury, knowledge of this inaccuracy is not new. As we have already seen with other examples, research directly contradicting this narrative was ignored before and after the development of 'Man, the Hunter'. Linton published *Woman the gatherer: Male bias in anthropology* in 1971 to directly rebut this narrative, and Zihlman responded with a series of articles on women in evolution, all stating that this hypothesis was not supported by data from non-WEIRD societies. However, this model

persists: evolutionary psychology textbooks still provide several more pages on the importance of hunting than gathering, even after pointing out the controversy and lack of supportive data (Burch, 2020).

Some may argue that introductory textbooks are a necessary but vague introduction to the discipline, and are at best incomplete, and at worst inaccurate depictions of the literature, and that researchers would find more accurate content if they only look more deeply. However, as Winegard and colleagues (2014: 475) state, detailed content, including corrections and clarifications in the scientific literature are read by few students and 'By contrast, textbooks are a crucial component of an undergraduate's education and are an important conduit of the ideas and data that comprise a paradigm of research'.

Parental Investment Theory

Parental investment theory provides a concrete example of a contribution that needs reconsideration. Dewsbury (2005) presented what he calls the 'Darwin–Bateman Paradigm', which was later combined with the Trivers–Willard hypothesis to form what is referred to as 'Parental Investment Theory' (terms also include 'Bateman Paradigm', 'Bateman's Principle(s)', 'Bateman's gradient', 'ardent male-coy female hypothesis'). This theory is a compilation of smaller-level theories and assumptions that provide a Darwinian overview of sex roles throughout human evolution. Dewsbury reviews newer models but returns to the reiteration of Darwin often, which is not surprising given the patterns we have already seen in the development and use of other evolutionary theories. In this case, Darwin's (1871) concepts, with contradictions and omissions, included the ardent male-coy female hypothesis, meaning that males are ardent, promiscuous, and fight intrasexually for access to female mates, whereas females are coy, rarely mate, and choose their mates carefully.

Bateman's famous experiment in *Drosophila* occurred in 1948 and was not without criticism of Darwin himself, arguing that the evidence for Darwin's hypothesis was circumstantial (Dewsbury, 2005: 832). Bateman found greater variation in male reproductive success, which he accepted as a sign of intramale selection. He concluded that female reproduction was limited by their number of eggs, whereas male fertility was unlikely to be limited by sperm production but rather by available females. This result appeared to confirm Darwin's idea that sexual selection acted more strongly on males than females, due to the biological costs of gametogenesis.

Bateman (1948: 367) did not study behavior per se but describes 'undiscriminating eagerness in males and discriminating passivity in females'. Consequently, females who mated but did not have progeny could have been miscounted. He was unable to provide accurate numbers of partners with which females mated or how often they mated with a given partner. In short, his definition of 'mate' was inaccurate, and misconceptions of his work have been carried forward in research on sexual selection. For example, Dewsbury (2005) could not locate any basis for statements made about Bateman's work in several studies on sexual selection throughout the 1970s and 1980s, including Trivers (1972). Indeed, Trivers' parental investment paper is extremely well cited (14,000 times as of January 2019). Further, it was the work of Trivers (1972) and Wilson (1975) that brought Bateman's work to the fore. Meanwhile, attempts to replicate Bateman's (1948) findings in other species have varied. In fact, replications of his work in *Drosophila* have failed to find similar results (Gowaty et al., 2003). However, the larger issue for contemporary researchers is how differences in reproductive success have been translated into behavioral differences. The evolution of anisogamy (i.e., sexual reproduction with unequal size of gametes (sperm and ova)), and the resulting male variance in reproduction

(Bateman, 1948) that leads to males pursuing a mating strategy of quantity and females of quality, is an area that is ripe for criticism. Gowaty has repeatedly made this point (e.g., Gowaty, 2003) as have others.

From the beginning, Dewsbury (2005: 831) makes it clear that these models were 'deeply embedded in the cultures in which these two Englishmen lived'. Once again, hypotheses were premised upon Western societies without supporting evidence from non-WEIRD cultures. Dewsbury (2005) writes at length about the persistence and exaggeration of Bateman's work and further reviews Darwin's (1871) opinions on the sexes, including that women are more tender and less selfish (but are more primitive) and men are more intelligent.

Parental investment theory (Trivers, 1972) posits that the sex with the most obligatory investment is the sex that then provides investment, while the other sex can (and often does) flee after mating. For humans, women at the minimum must carry the neonate and then breastfeed, meaning that their obligate investment exceeds that of men. Yet, humans are complex, and selection pressures have led to trends for both maternal and paternal investment. At the least, there are strong pressures for men to supplement a mother's ability to gather resources during the period she is breastfeeding, the most sensitive period of investment (Marlowe, 2000).

Parental investment theory (Bateman, 1948; Trivers, 1972) leads to the assumption that women are the more investing sex because of disproportionate costs related to their gametes, gestation, and postpartum childcare. It also results in conclusions that for humans and other animals, males profit more readily than females from repeated matings via increased reproductive success, that males are more eager and less discriminating in mating than females, and that male reproductive success is more variable than female reproductive success. As Kokko and Jennions (2008) report, this conjecture leads to committing the Concorde fallacy, particularly as

applied to females, which is when animals (including humans) defend an investment where the defense costs more than desertion or abandonment in favor of an alternative strategy. Humans, like other animals, must make decisions depending on future potential pay-offs, rather than past costs. Past reproductive decisions may affect future pay-offs, for example, a woman may have limited her ability to invest time and proper resources into her future children, but Kokko and Jennions show that, still, the argument remains weak and the theory centers on anisogamy, which must be applied with caution. The applicability of Trivers' and Bateman's work to the study of humans is problematic; the assumption of greater female investment in reproduction and greater male variation in reproductive success does not apply to all species, and, particularly, primates are an exception (Hrdy, 1986, 1999).

Past scholars who have pointed out these problems have remained relatively unheard, and those suggesting workaround solutions have been largely ignored. For example, Liesen (2013) proposes an easy solution: those interested in women's behavior should look at evolutionary biology and behavioral ecology, as evolutionary psychology relies on old models derived from those fields that do not incorporate recent findings on phenotypic and behavioral plasticity, the flexibility of mating behaviors in both men and women (Gowaty and Hubbell, 2005), and corrections to female passivity. Essentially, she argues, much of the current work by scholars using an evolutionary perspective to study human behavior is based on research that is either outdated, sensationalized and politicized, or (in the case of the naturalistic fallacy) misunderstood. She calls for evolutionists to examine the most recent, in depth, and nuanced research findings when building foundations for their arguments.

Interestingly, Gowaty (2013), in her argument that Bateman's findings were flawed, proposes that instead of examining sex differences, one should redirect the focus to

individual differences. This shift removes the possibility of politicizing sex differences. Heywood (2013) makes a similar case, contending that the use of genetic theory (and biological essentialism more broadly) leads to the belief that sex differences are hard-wired. Consequently, women are persistently seen as caretakers and mothers, given that theory surrounding reproductive success dictates their primary concern is to keep infants alive. Men, in contrast, are seen as needing to compete for mates and resources, which allows them to be more versatile and occupy more valuable roles.

In sum, this overview elucidates how an evolutionary perspective of the human sexes, and sexuality, is limited. It limits human behavior, which is widely varied and remarked upon for its flexibility, and it restricts the sexes into a binary, which defies research on human cultures. In summary, it omits and contradicts scores of studies from within its own discipline. The question that remains is how these views have persisted for so long. One could argue, as Burch (2020) did, that men as textbook authors are far more likely to further these narratives than women as authors, and the field has been dominated by men as researchers and authors since its inception, whereupon it emerged from fields dominated by men. Once women start to author more textbooks, and continue to research and question past assumptions, alongside work on non-WEIRD cultures, this androcentric narrative will fail to reproduce.

Sexualities within the Evolutionary Psychological Perspective

It is not surprising, given this historical restrictive view, that it has taken some time for evolutionary psychology to explore sexuality in any depth. As we have stated previously, the oversimplification of the human sexes (both in terms of sex and sexuality) is in stark contrast to zoology studies. The

animal kingdom has numerous examples of parthenogenesis (asexual reproduction), hermaphroditism (at least partial reproductive organs of both sexes), sexual plasticity (the ability to change from one sex to the other), promiscuity (multiple sex partners), and varieties of same-sex sexual encounters and relationships. This variation has been reviewed in large tomes such as *Evolution's rainbow* (Roughgarden, 2013), *Biological exuberance* (Bagemihl, 1999), and *Lost sex: The evolutionary biology of parthenogenesis* (Schön et al., 2009). Cultural anthropology has also historically provided a multitude of examples of sexual variation in the human species. Gray and Garcia (2013) reviewed variation in human mating systems, variation in marriage patterns, socio-sexuality, and sexual orientation. However, we posit that those following the traditional Bateman paradigm continue with restrictive views of what human sexuality entails, at times in the face of contrary evidence. With all of this variation, and the noted importance of variation and flexibility in the evolutionary process, the question yet again emerges as to why these restrictive beliefs have persisted in evolutionary psychology?

Take, for a specific example, the concept of the 'coy female'. Gray and Garcia (2013) comment specifically on women's variation, listing cultures where women take multiple lovers, have several potential fathers for their offspring, or are able to live more independently from men's control. Barrett and colleagues (2002: 94) made the point clearly that women may be choosy, but not chaste: 'It is important not to confuse this choosiness with coyness. Females may behave promiscuously and be adventurous in mating, but still be choosier than the males with whom they mate'.

The farther evolutionary psychologists move from the Darwin–Bateman paradigm, the better they will be able to study the variation in human sexuality. The future does look promising. Researchers have found ranges of promiscuity in women, preferences

for chastity in men, competition within both sexes, and even studied sexual positions (Gray and Garcia, 2013).

There are other promising places to begin. Evolutionary-based researchers are in a position to explore aspects of sexuality aside from attraction. Sexual configurations theory, reviewed previously, provides a framework for understanding gender/sex and sexual orientation. Evolutionary psychology tends to focus on a narrow range of behaviors in light of this theory, but that need not be the case. For example, evolutionary psychologists generally focus on partnered sexuality, but sexual configurations theory proposes that solitary sexuality is a valid area of exploration. Van Anders (2015) suggests that both forms incorporate eroticism (i.e., sexuality that is connected to pleasure, arousal, lust), and nurturance (i.e., intimacy, feelings of closeness). Evolutionary psychology could examine the possibility that some people are not sexually (or romantically) attracted to other individuals at all or are somehow drawn to them but not sexually attracted. It could readily become a field that includes exploration into the difference between feeling sexual attraction or lust toward someone but not romantic love, or vice versa (van Anders, 2015). Those who rely on interactionist models in their evolutionary research and who wish to incorporate gender studies could examine how one may engage in sexual experiences with someone they are partnered with but not attracted to due to societal/cultural expectations. Indeed, evolutionary psychology tends to take the view that mating is the desired outcome across all contexts and individuals, to the detriment of studying other forms and types of relationships. This narrow vision follows the research on men's mating strategies and perceptions where sexual interest is expected or perceived even where none exists (Abbey, 1987; Haselton, 2003; Haselton and Buss, 2000).

Additionally, just as with other species, there is variation in human sexual preferences and partners. There are promising

steps here, as evolutionary psychologists are examining sexual fluidity in women, as we detail shortly. In fact, Ganna and colleagues (2019) found that all tested genetic variants accounted for 8 to 25% of variation in same-sex sexual behavior and only partially overlapped between men and women. Moreover, the genetic effects that differentiate opposite-sex from same-sex sexual behavior are not the same as those that differ among non-heterosexuals in terms of number of partners and other sexual behaviors. Overall, the genetic variants do not allow for meaningful predictions of an individual's sexual behavior. The authors concluded that there is no single continuum from opposite-sex to same-sex sexual behavior. Moreover, this variation is a far cry from the 'ardent male-coy female' hypothesis, and this evolutionary emphasis on variation and behavioral flexibility in various contexts has allowed for enormous sexual variation in humans. As Gowaty (1997: 5) stated, one of the most recognized, if not the only, human universals is the vast 'diversity and variation among individuals'. It is this variation and flexibility that must be the basis for future evolutionary research in sexuality.

The lack of representation of different sexualities is not isolated to evolutionary psychology and systematically has been an issue in psychology and other fields as well. However, it is particularly problematic for a field that portends to study the entire species. The majority of articles published within evolutionary psychology exclude anyone who does not self-identify as heterosexual. We note that a significant turn has occurred though; using PsycINFO and searching for the terms 'evolutionary psychology' and 'heterosexual' revealed dozens of articles that explicitly include a comparison of heterosexual and 'homosexual' participants, according to titles. We have included the word 'homosexual' in quotations here because it is largely considered offensive; indeed, the GLAAD Media Reference Guide considers it one of the terms to be eschewed, in favor of saying gay or lesbian when referring to

those who are attracted to same-sex others. ‘Homosexual’ has a deep clinical history and has been used aggressively by anti-gay extremists to suggest gay/lesbian attraction is disordered, leading it to be avoided (GLAAD, 2020).

One possible reason for the dominance of heterosexual-based research in evolutionary psychology is that scholars may be focussed on reproductive success, defined as conception and subsequent birthing of children. Indeed, it seems to consider sexual orientation only in terms of who one is attracted to sexually, and does not deconstruct sexuality into identity, behaviors, and attraction, which may align or not (e.g., someone may be attracted to only men, seek experiences with only men, and self-identify as a highly selective woman, or they may be attracted to both women and men at times, but seek experiences only with women, and self-identify as a lesbian). This focus does not preclude other forms of relationships, nor does it necessitate that one enters into a stable long-term heterosexual relationship. Winegard and colleagues (2014) review that one of the criticisms of evolutionary psychology is this heterosexual focus and rebut by listing some of the work on non-heterosexual populations. We do acknowledge that there have been studies specifically including those who self-identify as gay/lesbian (Bobrow and Bailey, 2001; Mize and Shackelford, 2008) or sexually fluid (Diamond, 2007; Kuhle and Radtke, 2013), for example. These strides in understanding those who do not self-identify as heterosexual are important, but they remain considerably outnumbered by the work on heterosexuals. Further, sexual orientation is typically assumed by evolutionary psychologists as stable, and fails to incorporate those who might fall along non-extreme areas of the Kinsey scale, and does not consider sexuality as a dynamic or changing across one’s past, present, or idealistic future, such as captured by the Klein grid. As a field that recognizes serial monogamy and flexibility in sexual strategies, this limited view is disappointing.

Put another way, sexual orientation clearly stems from genetic variants but is also subject to experiential and environmental influences (Ganna et al., 2019), just as is the case for all behaviors. Evolutionary psychology takes exactly this approach to behavior, and therefore would be the perfect field to create a comprehensive study of sexuality. At the present, this state of affairs represents an untaken opportunity, and we hope that it is capitalized upon shortly.

Again, like other areas concerning gender, sex, gender/sex, and sexuality, we see small steps by those working in evolutionary psychology toward a more inclusive or accurate framework. Recently, Arístegui and colleagues (2019) examined transgender individuals and how they view romantic rivals. The premise for their work was that gender and sex represent “independent modules” and that ‘transgender individuals respond to romantic rivals in line with their gender identity and not with their biological sex’ (Arístegui et al., 2019: 1). They tested this hypothesis using the framework of jealousy in response to a physically dominant or physically attractive rival. Interestingly, they found support for their hypothesis: male-to-female individuals experienced more jealousy than female-to-male individuals in response to the attractive rival, and vice versa for the dominant rival. This line of research is exciting, as it represents some of the first to directly tackle gender and sex using evolutionary psychology and includes a highly marginalized population.

Evolutionary psychology is also uniquely suited to study gender identity. First, humans have several cultures that have historically (or in the case of the *fa’afafine*, currently) contained more than two genders. Second, research on neuroanatomy and physiology have shown clear relationships between hormones and gender identity (Swaab, 2004) and neurological differences in those who display ‘gender incongruence’ (Kreukels and Guillamon, 2016; Svedholm-Häkkinen et al., 2018). Third, emerging research on gender

identity has shown neurological processes that more accurately align with ‘gender identity’ than ‘biological sex’ in transgender individuals (Bakker, 2018; Burke et al., 2017). These findings harken back to the original issues with sexual categorization: gender identity, given this research, may not be socially constructed, but a different neurological/biological path. This interaction of biology and environment leading to gender identity is well-suited to an evolutionary approach, congruent with the potential to explore sexualities, attraction, and sexual orientation, among other topics. The only obstacle is the prevailing use of a narrow view by those relying on old theories about evolutionary principles, such as binary sex, or the Bateman paradigm.

CONCLUSION

Very few scholars, if any, have written about the possibilities of using gender studies to inform evolutionary psychology. Our goal in writing this chapter was to address this significant omission in the literature. Here we have presented various issues within gender studies, both historically and currently, in the hopes of providing a solid review so that evolutionary psychologists can become more informed.

Gender studies and evolutionary psychology rely on different epistemologies. What constitutes a sound argument in one field may not meet the standards of another; what is seen as satisfactory evidence may also largely differ by field. Both also have different language, tone, jargon, and even (especially) discrepant definitions for the same words, which all impact on comprehension when using gender studies to inform evolutionary psychology. The readings themselves create an obstacle, as evolutionary psychology largely rests on empirical studies with a ‘lab report’ feel and without acknowledgment of personal biases, while gender studies

often favors personal narratives with creative interpretations of experience (see, for example, differences in the social sciences versus humanities: Herrmann and Stewart, 1994). Scholars who attempt to bridge two such discrepant fields may feel marginalized and not be fully accepted by either field because they have tried to ‘walk toward the other side’ and in that process, lost credibility in their own field (Balzer Carr et al., 2017). If there is going to be a successful movement of any kind between gender studies and evolutionary perspectives of human behavior, it will take negotiation and re-examining priorities.

There remain many roadblocks to overcome. Not only does the field of evolutionary psychology need to create clear definitions about sex, gender, and sex/gender, and re-examine the reliance on sex as binary, it also must rethink sexual orientation. The benefits of this undertaking are, at the least, increased accuracy in research and stronger representation of humans (along with better generalizations about human behavior, cognitions, emotions, motivations, and so on).

There are battles ahead for those interested in bridging the gap between evolutionary psychology and gender studies. It will be challenging to work with gender theorists, given that many view evolutionary psychology with disdain. For example, Bem (1993) wrote about how evolutionary psychology is misleading scientists about the role of gender on behavior. She used Donald Symons’ (1979) work on evolution and human sexuality as the basis of her argument, suggesting that evolutionary psychologists start with the assumption that the sexes are different and then attempt to create a story regarding the origins of those differences to explain, normalize, and subsequently justify them. She concluded by proposing that socio-cultural explanations for any documented sex differences are more accurate and dismissed evolutionary-based reasoning. As we have reviewed, gender studies scholars rely on models that reduce or omit the role of evolutionary processes.

We have argued that while using gender studies to inform evolutionary psychology is difficult, it is possible and needed. We have reviewed that the foundation of gender studies is social constructionism which is used to build theory about identity formation, societal roles, and self-perception. Gender studies scholars discuss issues rarely studied within evolutionary psychology, including societal inequality and sex-based power dynamics. We also presented recent thinking about the gender/sex binary, as well the shift to consider how social identity is seen from an intersectionality stance. For evolutionary psychology, we started with a review about bias, in an effort to show the logic that has led to important issues that interact with the field's view of gender, sex, and sexualities. We discussed how evolutionary psychology typically examines men, women, and sexual orientation, with the hopes of highlighting, in concrete terms, the gaps in understanding or how it overlooks issues that have been raised in gender studies.

Advantages in Using Gender Studies to Inform Evolutionary Psychology

At the start of this chapter, we noted that we would focus on reviewing gender studies for the purposes of informing evolutionary psychologists. The chasm between the scholarship of those working in gender studies versus evolutionary psychology remains wide, yet evolutionary psychologists would reap many benefits from considering some of the tenets of gender studies that we have reviewed. One substantial benefit is simply that by exhibiting greater care in incorporating a wider variety of individuals, studies will become more inclusive to participants who might otherwise feel marginalized. Studies will also have increased generalizability and be more accurate. Further, by taking care to define terms with rigor, and describing participants in more detail, it may

become easier to replicate findings due to the increased precision.

It is possible to take some of the work from gender studies (or social constructionism, more broadly) and start to use key ideas for the formation of evolutionary-based hypothesis formation and empirical testing. For example, one promising line of inquiry that may serve as a point for scaffolding is the work of Nancy Chodorow (1995). She proposed that social learning theory was overly simplistic when attempting to explain gender differences and instead suggested that feminine and masculine personalities develop in infancy due to parental influence. She argues mothers (or other women) tend to be the primary caretakers of children, and mother-daughter relations differ from mother-son relations due to mothers more readily identifying with daughters, leading to different psychological development. As a result, sons are encouraged to be more independent and individuate themselves from the mother more quickly, leading them to develop a strong concept of self. Daughters are discouraged from doing so, leading to more emotional dependency on others later in life. This perspective could be included in models created by evolutionary psychologists when attempting to understand sex and parenting (and especially parent-offspring conflict perhaps) or tested by way of examining allocation of tangible and nontangible resources to daughters versus sons.

While Chodorow (1995) takes the stance that these differences should be changed, and that it plays a crucial role in why women may be overly attentive to others while men may be emotionally insensitive, we do not necessarily agree with her solution that mothers and fathers should be equally involved in parenting. Hrdy's (2009) work on mothering (and cooperative breeding) demonstrates that although others are often involved in children's lives, mothers are more highly invested in their children than fathers, as are maternal grandmothers and siblings (Sear and Mace, 2008).

This evidence does not mean fathers are uninvolved, but their involvement tends to be different, as well as less, than mothers (although even defining investment can be problematic and it shows ecological variability; Sear, 2015). Therefore, proposing that both parents need to be equally involved seems unrealistic and unattainable. Further research on how mothers and fathers treat their children needs to be conducted, especially in relation to the sex/gender of the child, before recommendations about parenting can be provided.

Another example of a possible springboard concerns the work of Spelman (1988), who argued that women do not experience womanhood in the same way due to the fact that gender is constructed within the lens of race, class, ethnicity, and nationality. Given that femininity is based on conditioning, and societies differ from each other, femininity must vary by society (and perhaps the same arguments could be made for masculinity, and other expressions of gender). This view may be valuable to evolutionary psychologists who examine individual differences as it represents another tool for understanding the unique factors that lead to ontogeny. Some steps have already been made: there are those who study the influence of issues such as gender inequality and life history (e.g., Zhu and Chang, 2019) and promiscuity and economics (e.g., Price et al., 2014).

For each of these examples, gender is viewed as a social construct that could fall under the umbrella of evolutionary theory. These avenues are simply possibilities, to show some of the avenues for future explorations. The work on biological bases and factors pertaining to sex, gender, sex/gender, and sexualities is growing and evolutionary biologists, psychologists, and endocrinologists soon will have a great deal to say about these topics. Evolutionary psychology is in a prime place to meaningfully contribute to this corpus of work.

In closing, evolutionary psychology is well positioned to meaningfully add to discussions

about the nature of gender, sex, gender/sex, and sexualities. Evolutionary psychology is noteworthy for being interdisciplinary, for having a strong overarching theory of evolution, for ignoring the false divide between the social and natural sciences, and for having incredible explanatory power. It is time to take these strengths and collectively use them to explore untapped issues, such as reviewed in this chapter.

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PART III

Integration with the Humanities



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Evolutionary Psychology and Ethics

Christine Clavien and Florian Cova

1. HISTORICAL BACKGROUND

There is an intrinsic relationship between evolutionary psychology and ethics because evolutionary psychology aims at explaining the psychological mechanisms underlying human social cognition and behavior, and ethics refers to one form of social cognition and behavior. But that relationship is not easy to spell out, and for historical reasons, it has become a sensitive topic.

The first major attempts to ground social and moral norms on evolutionary principles have led to Social Darwinism and eugenics. Social Darwinism is the view that natural selection, by selecting the fittest individuals, is a beneficial purification process. Thus, social inequalities should be protected or increased in order to help humanity to evolve to a higher level of development (Haeckel, 1876; Spencer, 1864). The closely related eugenics view (Galton, 1869; Davenport, 1910), according to which social policies should actively

contribute to the selection of desirable characteristics, was largely advocated in academic and political circles from the late 19th century to the Second World War. Eugenics theory served as a justification for all sorts of discriminatory and racist laws and exactions, including sterilization of “unfit” individuals (Bashford and Levine, 2010). Ultimately, both schools of thought were integrated in the Nazi ideology as a foundation for a reign of terror.

By the end of the Second World War, it became clear that the theoretical principles underlying Social Darwinism and eugenics could not be drawn from scientific evolutionary theory and genetics. They merely served dubious political aims. But the harm has been done, and the frightful consequences of these ideologies have generated a widespread suspicion against any attempt to reflect on the relationship between evolutionary theory and ethics. The subject remained temporarily taboo, before emerging again, notably (but not only), under

the pen of Edward O. Wilson and Leda Cosmides. For the sake of illustration, we will describe these two attempts at investigating how evolutionary knowledge impacts the field of moral philosophy.

1.1. Edward O. Wilson

In the 1970s, Wilson made an important biological contribution with his work on the evolution of social behavior. In line with Hamilton's mathematical models of evolution (1964), he approached social behavior through the lens of heritable traits (i.e. phenotypically expressed genes) propagating within a population (for historical details, see Segerstrale, 2015). Wilson (1975: 3) considered individuals mainly as 'temporary carriers' of genes. His detailed observations of the animal world (in particular, eusocial insects) provided numerous examples of the general evolutionary principles regulating social behavior, such as kin selection, reciprocity, and sexual competition.

But Wilson did not merely propose an analysis of non-human animal behavior. In one chapter of his famous book *Sociobiology* (Wilson, 1975) and in other writings (Wilson, 1980, 1978), he extended his evolutionary analysis to human morality. According to him, a scientific approach to human social behavior provides a better knowledge of human moral practices than philosophy-based approaches, and informs us about what type of moral system is more adaptive. In his words, 'the full exploration of the neural machinery of ethical judgement is desirable and already in progress' and 'the study of moral development is only a more complicated and less tractable version of the genetic variance problem' (Wilson, 1975: 562). What Wilson extracts from available scientific knowledge is a 'theory of innate moral pluralism'. Humans have an innate tendency to abide by different 'sets of moral standards' depending on their inclusion in different sex and age categories and depending on the

socio-environmental conditions they encounter (e.g., early phases of colony growth, periods of demographic equilibrium, or episodes of overpopulation). Thus, for instance, it is

of selective advantage for young children to be self-centered and relatively disinclined to perform altruistic acts (...). Similarly, adolescents should be more tightly bound by age-peer bonds within their own sex and hence unusually sensitive to peer approval. The reason is that at this time greater advantage accrues to the formation of alliances and rise in status than later, when sexual and parental mortality become the paramount determinants of fitness. (Wilson, 1975: 563)

In summary, Wilson (1975: 564) argues that science provides some guidance for moral theory: since universal moral standards would not be adapted to the individuals that are supposed to follow them, 'to impose a uniform code is therefore to create complex, intractable moral dilemmas'. Interestingly however, he does not explain whether and why dilemmas generated by the application of uniform but non-adapted norms are worse than dilemmas generated by the simultaneous application of different sets of moral standards.

Further, Wilson (1978: 38) asserts that the unique criterion for defining morality's function is its impact on adaptive behavior: 'Human beings are guided by an instinct based on genes' and

inevitably values will be constrained in accordance with their effects on the human gene pool. The brain is a product of evolution. Human behavior – like the deepest capacities for emotional response which drive and guide it – is the circuitous technique by which human genetic material has been and will be kept intact. Morality has no other demonstrable ultimate function. (Wilson, 1978: 167)

But is morality's function a criterion for grounding moral norms? On this point, Wilson is unclear. He recognizes that 'innate ethical feelings do not automatically constitute good impulses' (Wilson, 1980: 68). Nevertheless, 'long-term defections from the innate censors and

motivators of the brain can only produce an ultimate dissatisfaction of the spirit and eventually social instability and massive losses in genetic fitness' (Wilson, 1980:69). This is presumably why Wilson (1980: 69) asserts that 'incest is evil (this word can be used without embarrassment) by almost any conceivable standard, since it leads to a demonstrable high level of developmental abnormality due to the increased incidence of homozygosity of lethal and subvital genes'.

Wilson's views on human social behavior and, more generally, sociobiology as a discipline, have elicited heated controversies. On one side, some scholars argue that sociobiology has transformed traditional natural history into a more rigorous science and calls for a major redirection in the foundation and methods of academic disciplines such as sociology, anthropology, psychology, and even moral philosophy (Ruse, 1998): evolutionary models become necessary tools for studying human thinking, behavior, and culture. On the other side, many scholars fear the possible return of suspicious socio-political theories under the cover of a scientific discourse. Sahlins (1976: xii), for instance, argues that 'sociobiology has an intrinsic ideological dimension, in fact, a profound historical relation to Western competitive capitalism' (Sahlins, 1976: xii). 'It is a new variety of sociological utilitarianism, but now transposed to a biological calculus of the utilities realized in social relations' (Sahlins, 1976: x). Another worry is that sociobiology becomes a new vector of Social Darwinism, racism, sexism, eugenics (Schreier et al., 1975), or even genocide (Chorover, 1979). However, it is worth noting that no leading sociobiologist has endorsed any of these views. Wilson, for instance, spoke in favor of human rights, including the recognition of homosexuality and sexual liberation. The general feeling left from this controversy is that sociobiology does not lead to clearly founded normative principles.

1.2. *Leda Cosmides*

Following the rise of the controversial field of sociobiology, new interconnected subdisciplines were created, such as evolutionary anthropology (Gibson and Lawson, 2015), evolutionary ethics (Nitecki and Nitecki, 1993), and evolutionary psychology. Let us focus on the work of Leda Cosmides, one of the earliest and most prominent scholars in the field of evolutionary psychology. Beginning with her doctoral dissertation (1985), she has laid down the first steps of a hypothesis she later expanded and defended in collaboration with John Tooby and a number of colleagues. Inspired by the pioneering work of sociobiologists (notably Trivers, 1974), Cosmides and colleagues' (2019) view is that the human mind includes a multitude of evolved cognitive processes (now more commonly called 'modules') specialized for reasoning about social exchange. These modules are at the core of human moral reasoning. Each works as a 'special-purpose innate algorithm' (Cosmides, 1989). Some modules help their bearers to compute the value of resources, situations, and available choice options. Others are specialized in producing expectations of other individuals' behavior, such as the expectation that they reciprocate within a social exchange context or that they provide help to family members. Complementary modules help detect 'cheaters', that is, individuals who deviate from social expectations. When activated in combination with motivational modules (e.g., attraction towards valued resources, anger against cheaters), this complex web of cognitive mechanisms helped our ancestors solve specific challenges commonly encountered in their social environment: their contribution to adaptive fitness-enhancing behavioral choices (i.e. those that, in the end, lead to the production of an optimal number of healthy offspring) is the reason why they have been selected.

To sum up, according to Cosmides, our cognitive and affective mind is a patchwork

of task-specific and context-sensitive modules that evolved to solve specific social decision problems regularly encountered by our ancestors who lived in small hunter-gatherer societies. Interestingly, these modules may not be adaptive in contemporary social contexts composed of settled and densely populated communities. This evolutionarily inspired view of the human mind is antithetic with the more traditional 'blank slate' view that our reasoning and moral abilities are governed by a general-purpose, context-free faculty.

Further, Cosmides (1989: 232) examines whether people have a 'mental deontic logic', that is, 'mental rules of inference governing moral obligation and entitlement'. To some extent, and in limited social circumstances, this seems to be the case: 'for contexts involving social exchange, we do have mental rules of inference governing moral obligation and entitlement. These could be thought of as embodying a (highly circumscribed) deontic logic'. However, with the example of the cheater detection modules, she also stresses that 'the "look for cheaters" procedure will operate only when a rule has the cost-benefit structure of a social contract. This implies that a rule that lacks this cost-benefit structure, but that otherwise implies permission or obligation, will not elicit the effect' (Cosmides, 1989: 232). Thus we have a domain-specific deontic logic, but no single general faculty of moral cognition.

Evolutionary psychology has been greeted with skepticism by a number of scholars, due to its close relationship with sociobiology (Buller, 2006). It is worth noting, however, that terms like 'sociobiology' are not particularly controversial among biologists working on non-human social behavior. As explained by Alexander (1987: 6), 'No one is very upset if someone is wrong about the developmental basis of behavior in a frog, a bird, or an insect. To be similarly wrong about humans, however, can have decidedly pernicious effects'. Indeed, when a theory applies to humans, as is the case with evolutionary psychology,

there is no room for error. Incorrect hypotheses may produce dreadful social consequences, as illustrated by Social Darwinism and eugenics. Conversely, to properly assess the relevance (or weakness) of a given evolutionary hypothesis, it is important to understand the rules of hypothesis testing as well as the main principles underlying evolutionary theory and genetic expression. Since many scholars interested in human social behavior lack such training, misunderstandings are expected to occur repetitively.

2. CONTEMPORARY APPLICATIONS IN FOUR DOMAINS OF ETHICS

We have seen that Wilson, Cosmides, and others have defended a number of views regarding the interplay between evolutionary science and ethics. The normative scope of their assertions, however, is unclear. In order to take a stance on that matter, it is worth spelling out in a systematic way how knowledge and arguments from evolutionary psychology can be recruited in the different domains of ethics: descriptive ethics, meta-ethics, normative ethics, and practical ethics.

Descriptive ethics will be discussed in section 3. This domain of research focuses on explaining how humans think about ethical matters (including the exploration of universally shared norms and cultural differences and the investigation of brain mechanisms involved in moral evaluations), on the relationship between ethical thinking and behavior (action motivation), and on explaining how moral competencies have emerged. This is the domain of ethics for which the relevance of evolutionary psychology is least controversial. But as we will explain in section 5, from this descriptive research field, one cannot draw moral norms without further arguments.

Meta-ethics, a specific research field in moral philosophy, is not concerned with normative questions such as 'is lying wrong?' or

‘is it right to help someone commit suicide?’, but rather with abstract questions such as ‘what does it mean to say that something is right or wrong?’ (a semantic question), ‘are things really right or wrong or is it all in our head?’ (an ontological question), or ‘how can we know what is right or wrong?’ (an epistemological question). While results from evolutionary psychology have been mobilized for all three kinds of meta-ethical questions, we will focus in section 4 on the ontological and epistemological ones.

Normative and applied ethics are concerned with determining right or wrong – what we should or should not do. Normative ethics investigates what principles, general rules, or procedures help us evaluate what is right or wrong, whereas applied ethics is more concerned with finding practical ethical solutions to specific issues (such as the permissibility of euthanasia, animal experimentation, or the rights of illegal immigrants). In these fields of moral philosophy as well, results and theories from evolutionary psychology have been mobilized. This will be the topic of section 5.

3. DESCRIPTIVE ETHICS

There are two complementary and interwoven lines of research in evolutionary psychology. The first is to identify the information-processing and action-motivation systems (also called ‘mechanisms’, ‘processes’, ‘modules’, or ‘structures’) commonly found in humans. Observational studies in sociology and anthropology, complemented with experimental studies in psychology, behavioral economics, and neurosciences, contribute to this objective. Here are some paradigmatic examples related to human moral competences.

Proponents of the ‘Moral foundations theory’ (Graham et al., 2011) have done systematic work to identify cross-cultural sets of moral concerns upon which humans

construct their moral systems. These sets of moral concerns reveal the activity of distinct psychological mechanisms that produce in humans urges to regulate behaviors related to specific domains of activity. Researchers have found that humans are universally concerned by topics related to (1) harming and caring for other beings, (2) fair and reciprocal interactions, (3) loyalty towards ingroup members, (4), respect towards authority, and (5) standards for cleanliness, purity, or sanctity. In practice, some of these sets of concerns (in particular harm, fairness, and authority) seem to matter more, and they are interrelated. Moreover, there are important cultural differences in how these sets of concerns are expressed in practice: they are felt more strongly in some cultures compared to others, and depending on cultural contexts, the same set of concerns may generate very different regulating norms.

In complement to these moral foundations, researchers have pointed out many other mechanisms that impact on moral thought and behavior. For instance, studies show that humans are influenced by their audience and more willing to enforce moral norms when they are observed (Barclay, 2011; Kurzban et al., 2007). This suggests the presence of a mechanism dedicated to attenuating or enhancing social responses (e.g., moral reactions, computing own interest) depending on the presence or absence of observers. In line with these results, many studies have provided corroborative detail to Cosmides’ (1989: 232) theory of human deontic logic (see section 1.2).

The second main line of research in evolutionary psychology is to formulate and test hypotheses related to how the identified mechanisms have been shaped in the course of human evolution (Sperber and Hirschfeld, 2004): under what environmental pressures, and in interaction with what other mechanism, have these mechanisms evolved? To answer these questions, researchers ground their hypotheses on the results and knowledge acquired in evolutionary biology and

mathematical modeling. This field of research has identified different sets of principles underlying stable social equilibria which are indicators of selection pressures that shaped the human moral mind. In what follows, we present and discuss the main principles.

3.1. Lessons from Evolutionary Models

One general principle is that most traits (including psychological mechanisms) that can be observed today have been selected because they had positive effects on the fitness of their bearers – that is, because they helped our ancestors survive and reproduce. These mechanisms are described as ‘adaptive’. Fewer mechanisms have evolved by other means: by chance (i.e. they played no particular role but still made it to be transmitted, thanks to genetic drift) or in a parasitic way (i.e. they may have hitchhiked on other adaptive traits). But we cannot expect those mechanisms to have major negative fitness effects, as they would have been counter-selected in the course of evolution. Interestingly, some originally adapted mechanisms may have lost their beneficial function in the last 10,000 years since human social organization changed. Thus, some of our brain mechanisms have lost their adaptive character and may be counter-selected presently.

It seems that morally relevant traits are mostly linked to the regulation of complex social interactions (Alexander, 1987: 142). Evolutionary scholars have identified a series of principles regulating social interactions. Following is a non-exhaustive description of the prominent ones:

Principle 1: helping one's own children is adaptive. Within the human species, it is adaptive to invest a fair amount of energy in favor of one's own children (Clutton-Brock, 1991). Thus, one can expect the evolution of mental mechanisms devoted to promoting parental care. These mechanisms include love, compassion, a sense of connectedness with one's children, and low expectations for reciprocal help.

Principle 2: helping individuals who share one's helping trait promotes the transmission of that trait. Beyond the parent-child relationship, evolutionary models inspired by Hamilton's inclusive fitness theory (Gardner et al., 2011; Hamilton, 1964: 19; Lehmann and Keller, 2006) predict that a costly helping behavioral trait can be transmitted and stabilized within a population if recipients of assistance are likely to possess the same helping trait. This can occur if individuals are more likely to help their genetic relatives (aunts, cousins), or if they are able to identify (and favor) individuals sharing the helping behavioral trait (McNamara et al., 2009). The later case refers to the so-called ‘green beard’ effect (Dawkins, 1976). At the psychological level, this can be characterized by an increased sympathy and commitment towards specific types of individuals (Clavien and Chapuisat, 2016).

Principle 3: helping one's sexual partner is adaptive. Human offspring need significant parental investment and care to survive. To optimize reproduction and parental care, it is advantageous for sexual partners to help each other (Clutton-Brock, 1991). We can thus expect the evolution of psychological mechanisms supporting mutual aid and altruistic actions within couples: love feelings, attachment, etc.

Principle 4: reciprocal helping is adaptive. More generally, long-term reciprocal exchange relationships are beneficial among humans (Binmore, 2005). It is thus adaptive to strengthen these sorts of interactions with positive psychological feedbacks such as feelings of complicity or friendship whenever reciprocity is fulfilled (Trivers, 1971). It is also adaptive to react to unfair behavior, first by detecting exploiters, second by punishing or rejecting them (Krasnow et al., 2015), or, when possible, by changing partners (Baumard et al., 2013). Thus, mechanisms that help avoiding exploitation are likely to be selected.

Principle 5: interdependence between social actors increases the value of helping. Even more generally, social environments characterized by groups or networks of individuals that are mutually dependent on each other (because they divide tasks that cannot be accomplished by a single individual, because they have formed cooperative alliances, etc.) increase the objective value of own network members. Regardless of the existence (or not) of a direct reciprocal relationship, it is therefore adaptive to help members of one's own network or group and one can expect the evolution of psychological mechanisms along these lines, including mechanisms that motivate feelings of belonging to the same group (Tooby and

Cosmides, 1996). These mechanisms are particularly effective in crisis situations, when internal cohesion is crucial to survival (e.g., in the event of intergroup conflict or survival in hostile environments). In the case of intergroup conflict, and following the same principle, it is adaptive to show strong loyalty to one's group and take risks in order to inflict harm on outgroup individuals (Gardner and West, 2004).

Principle 6: costly reputation building can be adaptive. This principle indicates that individuals' behavior can be observed and commented upon within a social network. It may therefore be advantageous to invest in building a reputation (Alexander, 1987; Roberts, 1998). For example, individuals known as good cooperators are more likely to be offered opportunities to enter into mutually beneficial cooperative relationships (Nowak and Sigmund, 2005), and individuals known to reject unfair offers are less likely to be victims of attempts at exploitation (Jensen, 2010; Yamagishi et al., 2009). Another example is warriors' risk-taking behavior in favor of the group, which seems to increase men's sexual attractiveness (McDonald et al., 2012).

At this point, a few clarifications are needed. First, the above principles may overlap. For example, Principle 1 can be considered a subcategory of Principle 2. Similarly, Principle 6 is often linked to Principle 5 (Rusch, 2014). Second, saying that a behavioral trait is adaptive does not imply that all actions induced by that trait are individually beneficial; for a trait to be selected, it only needs to have been adaptive, on average for its bearers, in the ancestral past (Nettle, 2006). Third, even if the notion of adaptability involves a fitness calculation, it does not imply that human beings (or any other organism) consciously and purposefully deliberate over how to optimize their fitness when making their decisions; sometimes they are only able to express the behavioral trait when they overlook their personal benefits (Frank, 1988).

Another more general lesson from evolutionary models is that social equilibria may include different strategies represented with some proportions within a population (Maynard Smith, 1982). Thus, one can expect the evolution of a variety of personality traits which will be inherited by some, but not all,

individuals and will be expressed (or not) in given social situations. This is an indication that similar moral behaviors may be produced by different interactions of personality traits \times social situation. This analysis speaks against the idea that exemplar morality is the expression of one unique virtuous personality type (Walker et al., 2010).

3.2. *The Structure of the Moral Mind*

The variety of the above list of principles makes it clear that selection pressures differ across domains of social interactions and, consequently, that evolved psychological mechanisms track subtle features of social situations and prompt context-dependent responses (Cosmides et al., 2019). From this, evolutionary psychology takes the idea that human brains are patchworks of heritable mechanisms. In a similar fashion to genes, which have their own evolutionary story, brain structures are patched together in human cognitive architecture and each mechanism has evolved because it helped our ancestors solve certain survival and reproductive challenges they were regularly confronted with.

Thus, one key message drawn from research in evolutionary psychology is that there is no general-purpose brain mechanism such as a moral sense. Human thoughts and behavior result from the activity of a complex web of task-specific, but interacting mechanisms, some of which are shared by nearly all humans (e.g., mechanisms underlying basic social competences), and others are inherited by some but not all humans (e.g., variants of character traits). Moreover, among these mechanisms, some contribute to the *content* of moral thoughts, while others only regulate the *structure* of moral thoughts. To illustrate, let us present a (non exhaustive) series of examples.

Many mechanisms play a role in shaping moral norms (in combination with

socio-cultural constraints). For instance, since harming and caring behavior is crucial to individual survival, humans are sensitive to interactions involving harm and care. They are therefore particularly motivated to regulate this domain of interaction (Haidt and Joseph, 2008). Moreover, the content and reach of these regulating norms tend to follow some patterns: typically, caring for family members (following Principles 1–3) is considered more important than caring for other individuals (Krupp et al., 2008).

Another example is the importance of maintaining stable cooperation within groups (Principle 4), which has presumably imposed a strong selection pressure in favor of the evolution of regulating mechanisms such as cheater detection processes (Cosmides and Tooby, 2015) and an aversion to unequal shares or rewards, observed among humans and other primate species (Proctor et al., 2013).

Further, paleontological data indicate that our ancestors lived in contexts of social interdependence (Webb, 2018), which (following Principle 5) makes it adaptive (1) to value ingroup members more than outgroup individuals, (2) to value own group's benefits, and (3) to disvalue competitor groups' benefits. This is an evolutionary explanation for commonly observed pleasure responses to rival groups' failures, or pride (and praise) for killing enemies (Chagnon, 1988; Cikara et al., 2011). Such building blocks of human social behavior impact the content of moral evaluations: indeed, loyalty towards the group and responsibilities towards members of one's own social circle are commonly considered more binding than responsibilities towards distant individuals (Haidt and Graham, 2007). Interestingly, this position is also mainstream among professional ethicists (Chatterjee, 2003), although it is not easy to justify.

Even task-specific mechanisms that have nothing to do with prosocial behavior can influence the content of moral norms. For instance, since the probability of genetic

disease is higher among offspring produced by incest, there is a strong selection pressure against incestuous sexual activity. Studies indicate that the mechanisms that fulfil this function in humans are (1) a lack of attraction towards one's children and towards individuals with whom one has grown up, and (2) a tendency to feel an emotional rejection (disgust) against others' incestuous behavior (Borg et al., 2008; Lieberman et al., 2003). These mechanisms explain why incest is condemned across societies, except in cases of strong conflicting interests (e.g. marriage alliances between ruling families, necessity to avoid fragmentation of land property).

Finally, some task-specific mechanisms may be strictly devoted to regulating the *structure* of moral thoughts and motivation. One somewhat speculative example proposed by Clavien and FitzGerald (2017) is the feeling of rightness system (FORs), a mechanism that produces a vivid experience of having the right answer, which feels so compelling that it tends to shut down or bias further reflection. The evolutionary explanation for this mechanism is as follows. In the course of their evolution, humans evolved abstract thinking and reasoning which allowed them to communicate better and develop complex strategies and technologies (Barrett et al., 2010). However, in many circumstances, careful deliberation has its drawbacks; for instance, when quick decisions based on incomplete knowledge need to be made, it is often more adaptive to rely on simple mechanisms that have evolved precisely for dealing efficiently within specific types of situations (Gigerenzer et al., 1999). Thus, presumably, the emergence of human reasoning capacities has created a selection pressure for the co-evolution of one or several mechanisms that help to prevent excessive interference by rational deliberation. According to Clavien and FitzGerald, the FORs may play precisely this role: it is triggered when an individual experiences conflicting evaluations and prioritizes the responses that come quickly and fluently to mind, which, in practice, are those

produced by adapted task-specific mechanisms. The FORs thereby facilitates optimal decision-making. More empirical data are needed to confirm this theory, but if it exists, the FORs would be at the core of the production of moral intuitions without inducing any particular content. It would highlight why intuitions are so subjectively compelling and resistant to reasons intended to discount them. It would explain why humans think that there are moral truths while debunking the justification of this belief. As we shall see in the next section, this is a meta-ethical claim.

4. IMPLICATIONS FOR META-ETHICS

In this section, we will survey how various authors have addressed meta-ethical questions such as: are there really moral facts?; are there such things as right and wrong?; if there are indeed moral facts, can we actually know them?; do we have a special sense for that? As we will see, while drawing on evolutionary psychology's results and theories, different scholars have come to different conclusions and some arguments are more conclusive than others.

4.1. Evolutionary Vindications of Moral Realism

One position defended in meta-ethical debates is moral realism, the claim that morality is not just 'in our head'. This means two things. First, that when we say that something is morally wrong, we are not just expressing our disapproval, we are also attributing a certain objective property to this thing. The second is that there are objective facts that make these attributions true or false, independent of our beliefs about them. Thus, to argue for moral realism, one has to show that at least some moral beliefs can be justified on the basis of objective,

mind-independent facts, and some realists have thought that evolution could provide such a justification. For example, Campbell (1996) argues that morality (and belief in morality) has evolved because it was advantageous for us to be moral and to have moral beliefs, and this is a simple objective fact. Since, as a matter of fact, evolved moral beliefs are advantageous for humans, we are justified in holding them. In that sense, morality is objective and grounded in evolution. However, the fact that objective facts about evolution provide us with reasons to act morally does not show that moral judgments themselves refer to objective facts.

Sterelny and Fraser (2017) provide a more recent attempt to vindicate moral realism by appealing to evolutionary psychology. Their argument is that morality evolved to foster cooperation. According to them, this means that 'moral truths are truths grounded in facts about cooperation' (Sterelny and Fraser, 2017: 997). Or, to put it otherwise, a moral belief is true when the action it recommends (or prohibits) is actually beneficial (or detrimental) to cooperation. But, whether a certain course of actions fosters or hinders cooperation is an objective fact. Thus, at least some moral beliefs and moral norms (i.e. those that foster cooperation) are grounded in objective facts.

However, their argument relies on a problematic premise: that the truth of a moral belief depends on the facts it has evolved to track, and thus that the truth of a moral belief depends on facts about cooperation. Indeed, this would mean either (1) that saying that 'X is good' is the same as saying that 'X is beneficial to cooperation', or (2) that moral properties such as 'morally good' could be reduced to properties about what fosters cooperation. But these are two controversial theses, and grounding them on the fact that cooperation did evolve (and the stance that morality is about cooperation) is a weak justification at best.

To illustrate the problem with this kind of justification, let us consider similarly

structured arguments. For example, we might think that our aesthetic appreciation of persons of the other sex have evolved to 'track' facts about their being optimal mates in the context of reproduction. But it would be strange to conclude that saying a person is 'beautiful' means that mating with them will be the optimal strategy to transmit my genes. It would also be strange to conclude that the truth about a person's beauty depends on objective facts about whether this person has the potential for being an optimal mate. In this case, every time I claim that a person is beautiful, someone could object: 'Wait! We can't be sure that this person is beautiful until medical tests prove that this person is actually an optimal mate and a good reproductive partner'. However, this seems preposterous. Similarly, we can think that disgust evolved to track potential poisons and contaminants. Following the same argument, we should conclude that judgments such as 'X is disgusting' can be objectively true and will be so every time I judge disgusting something that is a poison or a contaminant. But imagine that I am presented with a slice of human meat that has been cooked so that there is no danger of being poisoned or contaminated. In this case, I might want to express: 'this is disgusting!'. However, according to this theory, we should consider that my expression of disgust is objectively wrong, as it would be objectively wrong to say that feces-shaped chocolates that are neither poison nor contaminant are disgusting.

Thus, critical analysis shows that attempts at vindicating moral realism based on evolutionary psychology rest on problematic premises that pose an equivalence between moral facts (e.g., 'X is wrong') and descriptive, natural facts (e.g., 'X promotes survival', or 'X promotes cooperation'). Not that reducing moral facts to natural facts is obviously absurd: this is a reasonable position in the meta-ethical debate, known as moral *reductive naturalism*. But whether moral reductive naturalism is true is a more fundamental meta-ethical debate that cannot

be settled by considerations about our evolutionary history.

4.2. 'Global' Debunking and Evolutionary Vindications of Moral Skepticism

Even though some authors have tried to use evolutionary theory for grounding moral realism (with the mixed results discussed above), evolutionary psychology is more often associated with skepticism about morality: that is, with the claim that we cannot trust most of our moral beliefs.

In meta-ethics, such arguments are known as 'debunking' arguments. They aim at rejecting one or a set of beliefs as unjustified by showing that the source of these beliefs is unreliable. To illustrate, let us consider a thought experiment: imagine that I have the belief that Napoleon lost Waterloo. However, one day, I discover that I hold this belief only because I was administered a special pill: all those who ingest this pill immediately form the judgment that Napoleon lost Waterloo. Learning that would lead me to question my belief that Napoleon lost Waterloo and to put it aside (at least temporarily) as unjustified (Joyce, 2007).

This example shows that, when we discover that we owe a belief to a process that does not 'track truth' in a reliable way, it becomes reasonable to treat this belief as unjustified (Jaquet, 2019). A process is 'truth-tracking' when the belief it produces would have been different if the truth had been different. For example, your belief that you are currently reading a book is the product of your visual (and maybe tactile) perception, and perception is a 'truth-tracking' process: if you were not currently reading a book but watching Netflix, your perception would have led you to form the belief that you were currently watching Netflix and not reading a book. On the contrary, in the pill case, the pill has led me to form the belief that Napoleon lost Waterloo whether he did or not. Of course, showing that my belief is the product of such

an unreliable process does not prove that my belief is false (Napoleon *did* lose Waterloo), but it gives us reason to treat it as dubious and lacking justification.

Now, let us apply that principle to ethics and evolutionary moral psychology. Suppose that evolutionary moral psychology provides a compelling Darwinian explanation of the origin of our moral beliefs. For example, there is a compelling evolutionary explanation for why we think that parents ought to take care of their children rather than abandon them (recall Principle 1, section 3.1). Similar explanations may be provided for most of our commonly occurring moral beliefs. But are the evolved psychological mechanisms underlying those beliefs reliable and ‘truth-tracking’?

Probably not, according to Sharon Street, who argued that moral realists face what she calls a ‘Darwinian dilemma’ (Street, 2006). Indeed, according to the majority of moral realists, at least some of our moral beliefs are true, in the sense that they reflect mind-independent objective moral truths. However, if evolutionary moral psychology is right in claiming that our moral beliefs are also the product of evolution, this raises a question: how are we to explain that natural selection, an amoral process, led to the formation of moral beliefs referring to mind-independent moral truths? How can we explain the surprising correlation between moral beliefs produced by evolutionary pressures and objective moral facts?

Thus, it seems that moral realists have to choose between two options: denying the existence of a connection between evolutionary pressures and objective moral truths (and thus accepting that this correlation is only a formidable coincidence), or admitting the existence of a connection between evolutionary pressures and objective moral truths (and thus accepting the task of explaining the nature of this connection). The first option (denying) is unattractive because evolution is a process that primarily tracks fitness-enhancing behavior and beliefs and there

is no reason to think that natural selection would lead to ‘true’ moral beliefs: rather, it will lead to moral beliefs that will ultimately increase our overall fitness (e.g., the belief that we ought to take care of our children and cooperate with each other). In the absence of a robust connection between evolutionary pressures and objective moral truths, the odds that evolution accidentally led us to form precisely the right moral beliefs is infinitesimal, and counting on such a coincidence amounts to believing in miracles.

But what about the second option: accepting the existence of a connection between evolutionary pressures and objective moral truths? Moral realists who choose this option face a difficult task: explaining the nature of this connection. Typically, this would involve explaining why forming true moral beliefs would contribute to one’s fitness, and why forming false moral beliefs would lower one’s fitness. However, it is not easy to come up with such an explanation. Of course, natural selection will sometimes favor true beliefs over false beliefs: a creature who believes that there are no predators while it is surrounded by them will be less likely to spread its genes than one who accurately detects predators and obstacles. But it is not clear that having false moral beliefs comes with the same kind of cost. After all, it is easy to imagine that false moral beliefs might turn out to be more advantageous to one’s reproductive success (for example, it might be morally wrong to eat meat or to have sex with non-consenting partners, but this does not prevent these strategies from being fitness-enhancing). Moreover, the idea that natural selection led us to form certain moral beliefs because they were true seems much less plausible than the claim that it led us to form these same moral beliefs because they contributed to our fitness.

Thus, according to Street (2006), moral realists have to face the following dilemma: either they accept that the odds that our moral judgments correspond to objective moral truths are infinitesimally small, or they

endorse a scientifically implausible account of how evolution led to the formation of our current moral beliefs. To quote Street herself:

At the end of the day, then, the dilemma at hand is not distinctly Darwinian, but much larger. Ultimately, the fact that there are any good scientific explanations of our evaluative judgements is a problem for the realist about value. It is a problem because realism must either view the causes described by these explanations as distorting, choosing the path that leads to normative skepticism or the claim of an incredible coincidence, or else it must enter into the game of scientific explanation, claiming that the truths it posits actually play a role in the explanation in question. The problem with this latter option, in turn, is that they don't. The best causal accounts of our evaluative judgements, whether Darwinian or otherwise, make no reference to the realist's independent evaluative truths. (Street, 2006: 155)

Overall, this dilemma suggests that, to the extent that our current moral beliefs are the product of our evolutionary history, we have no good reasons to consider them trustworthy. Indeed, it is hard to imagine how evolution could track moral truth in a reliable way.

Of course, moral realists have tried to escape the dilemma. A first line of answer is to point out that our general cognitive abilities allow us to track truths they were not selected to track. For example, FitzPatrick (2015) argues that, through development in cultural contexts, we were able to use our general cognitive abilities to track complex metaphysical truths (such as the fact that water is necessarily H₂O) that evolution never intended us to track in the first place. By analogy, why not think that we are able to use these general cognitive abilities to track objective moral truths and favor them over the unreliable moral evaluations that were selected for their usefulness?

One line of answer to this strategy is that general cognitive abilities (such as logic and reasoning) are incapable of tracking truths about the external world by themselves: a reasoning only tracks truth to the extent that its premises are already truth-tracking. In the case of metaphysics and science, such

premises are provided by our senses that can be considered as reasonably truth-tracking. But senses cannot give us access to moral truths. Thus, moral reasoning has to start from moral principles that are self-evident, that is from moral principles we are naturally drawn to and are the product of evolution. Reasoning can contribute to improve moral judgment, but it cannot track truth if the premises it starts from are already unreliable.

A second line of answer, the third-factor account, claims that evolution tracks moral truths even though we did not evolve in order to track them. The idea is that a third factor bridges the gap between evolution and objective moral truth because (1) it is adaptive, and (2) it correlates with objective moral truths. For example, one might argue that because cooperation is morally good, it is not surprising that evolution leads us to form true moral beliefs: indeed, cooperation is also evolutionarily advantageous. In the same way, Enoch (2013) claims that evolution tracks survival and reproductive success and that, since survival and reproductive success are also good in themselves, this means that evolution tracks what is good.

Street (2008) has criticized such third-factor accounts. According to her, they beg the question by taking at face value the kind of moral judgments that are under discussion: for example, taking as a starting point that cooperation is good seems to presuppose that we can trust those of our moral beliefs that are the product of evolution, which is precisely what is in question here. But, at the same time, it seems that Street's argument presupposes certain assumptions about morality (for example that morality is not about increasing one's reproductive success). Thus, before claiming that Street's Darwinian dilemma is successful, we first need to establish what assumptions moral realists are authorized to make (Vavova, 2015).

4.3. Evolutionary Vindications of Moral Anti-Realism

Even if Street's Darwinian dilemma (2006) turned out to be inescapable, it would not

prove that there are no objective moral truths (i.e. moral anti-realism): rather, it would only show that we cannot trust our moral beliefs and that we don't know what is morally right or wrong (and whether some things can really be said to be morally right or wrong) (i.e. moral skepticism). Indeed, Street's dilemma leaves open the possibility that there are objective moral truths we have no access to. But can we use evolutionary psychology to directly argue against the claim that there are objective moral truths?

One option is to use the classical argument from lack of explanatory power. This argument draws on the famous Ockham's razor: we should not accept new entities if we do not need them. When applied to moral truths, this line of reasoning is as follows: the existence of objective moral truths does not allow us to explain anything that we cannot already explain (without such a metaphysically heavy premise). Therefore, we are not warranted in accepting the existence of objective moral truths (Harman, 1977, 1985). This is where evolutionary psychology may come into play. It provides an explanation for all the ethically relevant phenomena: why people produce moral judgments, why they agree on a certain set of core moral beliefs (e.g., that incest is wrong, that parents should take care of their children, that it is morally reprehensible to harm people who helped you), why they tend to follow such judgments, etc. (see section 3). All these evolutionary explanations can be provided without having to appeal to objective moral truths. It is therefore more reasonable to give up the belief in their existence (Joyce, 2007). Of course, this argument does not prove the inexistence of objective moral truths (rather, it leads to a form of skepticism). Nevertheless, it shows that we have no reasons to believe in the existence of independent objective, moral truths. Together with the idea that moral truths are 'queer' entities (i.e. they are supposed to describe properties of objects but give us normative reasons to act at the same time),

this gives us reasons to prefer an ontology that does not include them.

To this, one may object that humans are naturally drawn to moral realism: it happens to be the default view. Thus, in order to convincingly apply Ockham's razor, at minimum, we need to explain why most of us are mistaken. Here again, evolutionary arguments have been proposed. Some authors (Greene, 2003; Joyce, 2007; Kitcher, 2011) argue that evolution led us to project our moral preferences and reactions onto objects and actions themselves, so that we attribute our moral disapproval of certain actions and traits not to ourselves but to the presence of some objective moral qualities within these objects.

There is an 'adaptationist' (Joyce, 2007) and a 'byproduct' (Greene, 2003) version of this claim, depending on whether the authors think of this 'projection' as the expression of a psychological mechanism that has been selected because of the benefits it brought, or as a side effect of something else. According to the adaptationist view, attributing moral disapproval to objective properties of objects leads us to be more committed to following moral norms and to resist the temptation to compromise with these norms (Joyce, 2007). In accordance with this claim, recent studies have stressed that belief in moral realism motivates people to be more likely to cooperate (Young and Durwin, 2013).

Note, however, that such a line of argument relies on the hypothesis that most of us are naturally drawn towards moral realism. But investigations in 'folk' or 'common-sense' meta-ethics have yielded conflicting results: it is not clear that most of us consider moral truths to be objective, mind-independent moral entities (Pölzler and Wright, 2019).

Other authors highlight alternative mechanisms that may indirectly lead us to be optimistic about the universal validity of our own evaluations. Recall the feeling of rightness system (FORs) mentioned in section 3.2. According to Clavien and FitzGerald (2017), when we frequently experience the FOR in

contexts of moral debates, as a side effect, we simply become more likely to believe that there are universal moral truths. Another psychological explanation for our confidence in our evaluations is their felt benefit: according to Kitcher (2011), when we collectively resolve moral conflicts within a society, the positive experience we feel may induce the thought that we have discovered a moral truth.

5. IMPLICATIONS FOR NORMATIVE AND APPLIED ETHICS

Let us now turn to specific normative stances about what should or should not be done, and to what extent it is possible to ground our arguments on results and theories from evolutionary psychology. Following Wilson's example (section 1.1), one may simply try to deduce normative prescriptions from knowledge about adaptive social patterns. But that strategy has obvious drawbacks: it is not because a behavior is adaptive that we should consider it moral. For example, parochialism and nepotism are adaptive, but we do not necessarily consider them as moral. Most authors are aware of this difficulty and make use of more subtle strategies. In this section, we will discuss two of them: attempts at weakening moral intuitions with debunking arguments and attempts at rejecting moral theories because they violate the 'ought implies can' principle.

5.1. 'Local' Evolutionary Debunking Targeting Some (but Not All) Moral Intuitions

One lingering question in normative ethics is the way competing moral theories can be justified and defended against their competitors. One traditional method involves the use of moral intuitions as 'tests' for the competing theories. Traditionally, intuitions are considered

to be self-evident (or self-attractive) judgments that bear enough evidential weight to increase or diminish the plausibility of a moral theory. Consider Kant's ethical theory: according to Kant, his theory implies that lying is always wrong (Kant, 1787). Against this claim, Constant gave this famous example: what if a friend of yours was chased by a murderer and found shelter in your home minutes before the murderer knocked on your door and asked whether your friend was in? Would it be wrong to lie to the murderer and answer that you never saw your friend? (Kant and Constant, 2003) Clearly, it would not. But we then have a counter-example to Kant's theory. However, the claim that there would not be anything wrong about lying to the murderer, on the basis of which we reject Kant's theory, is not supported by or derived from any other theory. We just accept it as self-evident enough to ground our rejection – this is why philosophers call it a 'moral intuition'.

The more famous systematization of this method is Rawls' conception of 'reflective equilibrium' (Rawls, 1951). According to Rawls, moral theorizing can be seen as a constant back-and-forth between 'considered judgments' (i.e. intuitions formed in adequate epistemological conditions) and moral principles. Taking our considered judgments as a starting point, we try to systematize them under the form of more general and abstract moral principles, rejecting principles that violate too many of our considered judgments, but also rejecting or revising considered judgments that would prove impossible to systematize or reconcile with other considered judgments. Of course, this method leads one to wonder about the reliability of some of these intuitions or considered judgments. This is why, following Rawls, Daniels (1979) proposed distinguishing a 'wide' from a 'narrow' reflective equilibrium. The difference between the two is that, while a 'narrow' reflective equilibrium only involves a certain equilibrium between moral intuitions and moral principles, a 'wide' reflective equilibrium allows the introduction in ethical

reflection of relevant scientific facts. Among these facts are facts about the origin and reliability of said considered judgments.

This is where evolutionary psychology becomes relevant to philosophical reflection: to the extent that evolutionary psychology might tell us something about the origin and thus reliability of a certain set of intuitions, it might allow us to reject those intuitions that are not worthy of consideration in our theory-building and reflective equilibrium.

Let us take a famous example. Two major families of moral theories are consequentialism and deontology. Consequentialism is a philosophical position according to which the moral value of an action depends on its consequences, and its more famous variant is utilitarianism, according to which the right action is the one that maximizes well-being (well-being being defined either as ‘pleasure’ or as ‘satisfaction of interests’, depending on the version). Deontology, on the contrary, is a family of moral theories according to which certain actions (murder, theft, breaking a promise, incest, etc.) are wrong in themselves, independently from consequences.

One typical objection against utilitarianism is that, more than deontology, it has counter-intuitive implications. For example, it implies that (at least in certain circumstances) it is morally permissible to sacrifice one person to ensure the happiness of several. One famous example is the Trolley Problem (see Cova, 2017 for an introduction and review), a pair of thought experiments that seem to reveal contradictions in our moral intuitions. Take, for example, the case (the *Divert* case) in which a runaway trolley is speeding towards five people working on the tracks. However, you can save these five people by hitting the switch and redirecting the trolley on another track where it will kill only one person. Is it acceptable to divert the train and cause the death of the lone workman to save the five other workmen? In this case, most people say ‘yes’ (Greene, 2001; Hauser et al., 2007). This seems compatible with utilitarian ethics,

because saving five lives at the price of one seems the best way to maximize happiness.

Now take a second case (the *Push* case), in which the five workmen can be saved from the trolley by throwing a large person from a bridge onto the tracks and under the wheels of the trolley, causing it to stop. In this case, most people judge that it is not acceptable to push the person onto the tracks, even if this would save five lives at the cost of only one. Clearly, in this case, our intuition goes against utilitarianism: it does not feel like maximizing well-being warrants taking one life by throwing the stranger to the tracks. On the contrary, some variants of deontology can easily accommodate the fact that we react differently to both cases. For example, a deontologist might point to the fact that, in the *Push* case, pushing the stranger onto the tracks constitutes a necessary means to reach one’s goal while, in the *Divert* case, the death of the lone workman is only a side effect of diverting the train – a distinction that many deontologists consider to be relevant.

So, should we abandon utilitarianism in light of the fact that it feels wrong to maximize happiness in the *Push* case? Not necessarily. Instead, we might try and discard this intuition by arguing that it is unreliable and misguided. This is precisely philosopher and neuroscientist Joshua Greene’s defense (Greene, 2003). Through a series of psychological and neuroscientific studies, Greene developed an influential account of the psychological mechanisms underlying our reactions to such cases: the dual-process model of moral cognition (Greene, 2008). According to this model, utilitarian responses are supported by higher-order cognitive processes, such as mathematical reasoning, while deontological responses are the reflection of automatic emotional responses (Greene, 2016). For example, in the *Divert* and *Push* cases, the thought of killing someone elicits an automatic negative reaction (‘it’s horrible to kill someone’) that is then followed by a slower cognitive response (‘by causing the death of one person, I can save five’). It is

the conflict between these two answers that makes such cases feel like moral dilemmas. However, while the utilitarian, cognitive answer prevails in the *Divert* case, it is often defeated by our emotional answer in the *Push* case, which explains that we reach different verdicts in both cases.

Of course, showing that deontological answers are ‘emotional’ while utilitarian answers are ‘rational’ is not enough to conclude that utilitarian answers are better than deontological ones. After all, many philosophers have argued that emotions and sentiments are a better guide to morality than pure reason (Kauppinen, 2014; Railton, 2014). However, Greene’s theory goes beyond the mere contention that the thought of causing someone’s death elicits stronger negative emotional reactions in the *Push* than in the *Divert* case. It also puts forward an evolutionary explanation for this difference. This explanation is the following: we react more intensely to harm that is caused directly (such as pushing someone) compared to harm that is caused indirectly (such as hitting a switch to divert a train that will then run over someone) because moral cognition evolved in a context in which we had no means of causing indirect harm. To quote Greene himself:

The rationale for distinguishing between personal and impersonal forms of harm is largely evolutionary. ‘Up close and personal’ violence has been around for a very long time, reaching back far into our primate lineage (Peterson and Wrangham, 1997). Given that personal violence is evolutionarily ancient, predating our recently evolved human capacities for complex abstract reasoning, it should come as no surprise if we have innate responses to personal violence that are powerful, but rather primitive. That is, we might expect humans to have negative emotional responses to certain basic forms of interpersonal violence, where these responses evolved as a means of regulating the behavior of creatures who are capable of intentionally harming one another, but whose survival depends on cooperation and individual restraint (Sober and Wilson, 1998; Trivers, 1971). In contrast, when a harm is impersonal it should fail to trigger this alarm-like emotional response, allowing people to respond in a more ‘cognitive’ way, perhaps employing a cost-benefit analysis. (Greene, 2008)

Let us now suppose this explanation is true: the reason why we treat the *Divert* and *Push* cases differently is that our moral cognition evolved in a context in which indirect ‘impersonal’ harm was absent. Had such harm been more prevalent in the ‘ancestral’ context, our moral intuitions might have been radically different: maybe we would have judged utilitarian sacrifice as unacceptable in the *Divert* case as in the *Push* case. Thus, it does not seem that our intuitions are accurately tracking moral truths: rather, our intuitions about such cases are primarily shaped by accidents of our evolutionary history, and not by morally relevant factors. Hence, it is not because most of us react differently to the *Divert* and *Push* cases that we are warranted in doing so.

It is important to note, however, that this argument only works because it already involves a normative, moral premise: that the difference between direct, personal harm and indirect, impersonal harm is morally irrelevant. It is this particular moral assumption that allows us to discard our intuitions about Trolley cases. Moreover, this argument only allows us to draw a negative conclusion: that we should not trust our intuitions about such cases or take them into account in our ethical theory-building. This might help rescue utilitarianism from the objection of counter-intuitiveness, but this does not prove that utilitarianism is better than deontology.

However, Greene’s argument goes one step further: he argues that his account provides good reasons for rejecting deontology. His argument starts from the following observation: traditionally, deontologists are more concerned about sticking to intuitions and trying to justify them than are utilitarians. Utilitarians, on the contrary, have a greater tendency to stray away from everyday intuitions. But we just saw that our moral intuitions could sometimes be the product of psychological mechanisms that do not accurately track moral truths but reflect the accidents and contingencies of our evolutionary

history. This means that deontologists are more likely than utilitarians to engage in a post-hoc rationalization of unreliable intuitions. But because post-hoc rationalization is traditionally considered to be an unreliable way of forming beliefs, this means that we should be wary of deontological theories (on moral rationalization, see Schwitzgebel and Ellis, 2017; however, see Cushman, 2019 for the claim that rationalization might sometimes be epistemically sound).

Because this argument tries to show that some, but not all, moral intuitions are unreliable, it should be distinguished from the arguments presented in section 4.2 that purported to show that *all* our moral beliefs are unwarranted: they are not ‘global’ but ‘local’ evolutionary debunking arguments. Now, local evolutionary debunking is not limited to the deontology *versus* utilitarianism debate. It has also been used in other contexts. Let us consider the case of the reliability of disgust-based moral judgments.

In the past two decades, a growing body of research in moral and social psychology has stressed the importance of emotions in the formation of moral judgment (Haidt, 2001). Among these emotions, disgust has garnered a lot of attention, mostly for the role it seems to play in the condemnation of ‘harmless crimes’ (i.e. actions that are judged morally wrong even though they harm no one, such as consensual incest, having sex with a dead chicken, or cleaning one’s toilets with the national flag) (Haidt et al., 1997). For example, in-lab experimental studies have shown that inducing disgust led participants to judge such cases more severely (Schnall et al., 2008; Eskine et al., 2011). Though these studies should be interpreted with caution (May, 2014) and recent replication attempts have shed doubt on the validity of these experimental results (Landy and Goodwin, 2015), other studies have shown a robust and consistent link between disgust-sensitivity and more conservative moral judgments (Inbar et al., 2012; van Dijke et al., 2018).

Thus, there are good empirical reasons to think that disgust shapes some of our moral judgments (for example, those related to sexual ethics). But some have argued that this is problematic because disgust is not a reliable source of moral knowledge. Indeed, the primary aim of disgust is not to track what is morally wrong: rather, its original function is to protect us against poisoning, parasites, and infectious agents (Kelly, 2011). Even though disgust seems to have been co-opted to fulfil moral functions (such as regulating human social interactions), Kelly argues that this ‘moral’ disgust retains many of the features that allowed original disgust to effectively protect us against poisons and parasites, leading to some mismatch between this emotion and the social issues on which it has been brought to bear. As such, ‘moral’ disgust would track properties of actions that might be relevant to hygiene, but are not relevant to morality. For example, disgust might lead us to morally condemn certain sexual activities not because they are morally reprehensible, but simply because they feel ‘dirty’.

This picture of disgust as an unreliable source of moral evidence can be substantiated by psychological findings on disgust. These findings highlight two key properties of disgust. First, disgust is not cognitively flexible and is hard to revise in light of new evidence; thus, participants are reluctant to eat feces-shaped chocolate, even though they are aware that it is chocolate. Second, disgust follows strange laws of ‘sympathetic magic’, according to which it is enough to have been in contact with a disgusting object – even through the intermediary of a third object – to be perceived as disgusting (Rozin et al., 1986). Taken together, these findings paint a picture of disgust as an emotion that follows irrational principles and is mostly impervious to rational revision. As such, it makes sense not to rely on it when making moral judgments, and to be skeptical of moral judgments that are grounded in it.

5.2. *Limitations of 'Local' Evolutionary Debunking*

Using evolutionary theory and evolutionary moral psychology to debunk a specific set of moral beliefs ('local' debunking) seems to be one way to make evolution relevant to moral theorizing. However, one might question the role played by evolutionary considerations in these arguments. Indeed, the key premise in the 'local' arguments just presented is that the specific set of moral beliefs one sets out to debunk is the product of a psychological mechanism that is sensitive to morally irrelevant factors. It is because deontological intuitions are sensitive to the contrast between direct and indirect harm that we are warranted to reject them, or it is because disgust is shaped by morally irrelevant factors that we are justified in being skeptics about disgust-based moral judgments. Thus, the mere fact that these beliefs are shaped by evolution is not sufficient to reject them: we also have to show that their evolutionary history makes them sensitive to morally irrelevant factors.

In fact, it is not clear that providing an evolutionary origin for these beliefs is necessary for these arguments to work. If it turned out that our sensitivity to the contrast between direct and indirect harm was not the product of evolution, but of learning and acculturation (Nichols et al., 2016), the argument would still be valid: what matters is that our intuitions are shaped by morally irrelevant factors (e.g., the direct/indirect distinction), not the reason why they are sensitive to such factors. For example, we do not need to know whether racial bias in judgments of criminals is grounded in evolution or culture to conclude that judgments that are shaped by such biases are unreliable.

Thus, it seems that, even in such arguments, appeals to evolution carry no argumentative force by themselves. It can easily be shown that moral condemnation of incest is grounded in evolution: we condemn incest because we find it disgusting, and we find it disgusting because it is fitness-enhancing to

prefer mates to whom we are not genetically related. However, by itself, this evolutionary account does not show that this condemnation is dubious or unjustified. After all, one could argue that in this case, our intuitions are sensitive to morally relevant factors (i.e. whether the people we are going to have sex with are genetically related to us).

One could then argue that it is enough to 'debunk' our condemnation of incest to show that it is grounded in evolution, because it is unlikely that evolution tracks moral truths (rather, evolution tracks fitness-enhancing behavior). However, if correct, this argument applies to all moral intuitions for which we can find an evolutionary origin and not only to intuitions about the moral wrongness of incest. Thus, we leave the realm of the 'local' debunking argument and are back to the 'global' debunking argument, according to which widespread skepticism about all our moral judgments is warranted.

This is why 'local' debunking arguments often tread a thin line and are in constant risk of stumbling into widespread moral skepticism: it is indeed not easy to show that evolutionary considerations give us specific reasons to reject some moral beliefs and intuitions, but not all. For example, in order to save utilitarianism, Greene rejects intuitions about the distinction between direct and indirect harm yet maintains intuitions about the value of human life. But we can also find an evolutionary explanation for the latter and Greene does not explain why those explanations do not provide ground for debunking.

This tension has led some philosophers to distinguish between moral intuitions that are shaped by evolution (and thus are unreliable) and other moral intuitions that come from more trustworthy sources. For example, in a paper on 'ethics and intuition', utilitarian philosopher Peter Singer argues that we should not rely on moral intuitions because if 'moral intuitions are the biological residue of our evolutionary history, it is not clear why we should regard them as having any normative force' (Singer, 2005: 331). However, to

avoid falling into widespread moral skepticism, Singer proposes that we distinguish between these unreliable, evolution-based intuitions and ‘rational’ intuitions that we can trust. In a later paper in collaboration with Lazari-Radek (2012), he elaborates on these claims by arguing that certain basic moral intuitions such as the ‘principle of universal benevolence’ cannot be due to evolution. Of course, such claims are debatable.

5.3. Using ‘Ought Implies Can’ to Bridge the ‘Is–Ought Gap’

A traditional reason to resist the use of evolutionary theory in normative ethics is the ‘is–ought gap’: as argued by Hume, one cannot deduce a normative conclusion (X should do Y) from purely descriptive premises (A is B). Contrary to what one might think at first glance, the ‘local’ debunking arguments we just surveyed do not violate this principle: we saw that each of them relied on a normative premise according to which the psychological mechanisms responsible for a certain set of beliefs were sensitive to morally irrelevant factors. Saying that a factor is ‘morally irrelevant’ is already a normative claim: it amounts to saying that we should not take such considerations into account when making a moral judgment.

Another way to bridge the gap between what ‘is’ and what ‘ought’ to be is to rely on the principle according to which ‘ought implies can’. This very intuitive line of thought, often put forward in the literature (e.g., see Wilson in section 1), goes back at least to Kant. It can be summarized in the following way: if a moral theory demands from us actions or attitudes that are beyond our capacities, then this is a reason to doubt its plausibility.

In his book *A Darwinian Left*, Singer (2000) combines this principle with evolutionary theory to advocate for political systems that are compatible with what the theory

of evolution teaches us about human cognition. According to him, ‘to be blind to the facts about human nature is to risk disaster’ (Singer, 2000: 38). For example, he argues that a moral or political system that would ask us to give as much importance to others’ children as to ours would be unfeasible: evolution (and kin selection) has designed us to give more importance to members of our own family. Thus, evolutionary theory, because it tells us about human nature, can help us detect moral or political systems that could not be reasonably implemented.

6. CONCLUSION

In this chapter, we have explored how evolutionary psychology helps us understand the architecture of the moral mind, why moral competencies have emerged, and what their limitations are. We have surveyed how this knowledge may be used for elucidating classical meta-ethical questions (e.g., are there right or wrong moral facts, or is it all in our head?) and for grounding moral norms and prescribing the right decisions. A general impression that emerges from our analysis is that some theories and assertions advocated in moral philosophy (e.g., moral realism) are compromised by empirical knowledge stemming from evolutionary psychology. General debunking arguments seem to be the most promising. Nevertheless, upon close analysis, evolutionary knowledge is less relevant to moral debates than one might think at first glance, especially in the realm of normative ethics. Many debates remain open and await further improvements.

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Evolutionary Literary Theory

Emelie Jonsson

INTRODUCTION: STUDYING LITERARY MEANING

Evolutionary literary theorists treat literature as a product of the evolved human mind. That core premise sets them apart from non-evolutionary literary theorists, but it provides only their most general theoretical ground. After positing that literature is produced by the human mind, and that the human mind is structured by evolved dispositions, literary theorists still face many unanswered questions about their subject: the mental experiences of people who construct and consume verbally conveyed fictional experiences. Literature portrays fictional humans (or human-like characters) from the perspective of authors, as interpreted by readers. The minds of authors and readers are lodged in particular cultural settings, and the fictional minds of characters may be lodged in entirely different cultural settings. Authors and readers have different developmental trajectories

and childhood environments, different mating strategies, and different expressions of basic personality traits such as extraversion and agreeableness. They each construct a life narrative and adhere to some variation of the values available to them within their culture (McAdams and McLean, 2013). The fictional minds of characters – to the extent that they are naturalistically rendered – also display such differences.

Individual differences matter to evolutionary literary theorists because literature is a form of simulated social interaction (Mar and Oatley, 2008; Oatley, 2016). When reading a novel, one is to some degree registering the interaction between the author and the characters. *Does Joseph Heller like Yossarian? How does Jane Austen's attitude differ from Emma's?* One is also registering the interaction between oneself, the characters, and the author: *Why am I sympathizing with Count Dracula when Bram Stoker does not want me to?* If one reads a literary text without characters, one is nevertheless

interacting with authors – distancing oneself or becoming sympathetically absorbed in their outlooks. The total experience comes to a reader through words that convey images and simulate emotions, evoke the memory of other texts, or inspire you to stand back in aesthetic admiration (Jacobs, 2015; Jacobs and Lüdtke, 2017). This verbally artistic experience of perspectival interplay is *literary meaning* (Carroll, 2018a). Evolutionary literary scholars study literary meaning using an explanatory framework from the evolutionary social sciences.

Ideally, an evolutionary literary scholar would always consider the whole process of literary meaning. When approaching a novel, he or she would identify its cross-cultural themes (mate selection, coalitional violence, self-narrative), describe how the themes are expressed in its depicted cultural environment (finding a mate and constructing a self-narrative in the midst of coalitional violence during the Spanish Civil War), analyze the author's perspective using biographical information (early-20th-century American expatriate, male, neurotic but assertive), and study how readers have responded to the novel (critical accolades and condemnations, scholarly consensus and controversies, modern reader response experiments). Going through those steps, each of which involves its own methodological difficulties, would simply identify the particular subject of study (literary meaning in Ernest Hemingway's *For Whom the Bell Tolls*). It would prepare for the questions that can lead toward explanation or meaningful contextualization. *What are the psychological functions and effects of this novel? How does the author use cross-cultural themes for specific cultural and individual purposes? What type of novel is it, and what can it tell us about other novels that are similar or different?*

In reality, individual literary scholars can rarely focus on all aspects of literary meaning at once. But evolutionary literary theory explicitly treats each aspect as part of the whole. There is no text without an author,

no literary experience without a reader, and no literature without the human psychology that has been shaped by evolutionary history. Since the beginning of academic literary study, theoretical schools have centered on one or another aspect of literary meaning: the author (e.g. biographical criticism), the reader (e.g. reader response theory), the text (e.g. narratology), or the world (e.g. new historicism) (Abrams, 1953). Not infrequently, such schools have behaved as if their focus constitutes the whole of literary meaning. They have treated an author's life as the sole key to the text; or claimed that readers create the text while reading; or envisioned the text as an artistic essence detached from author, reader, and world; or reduced author, reader, and text to effects of historical tendencies (Abrams, 1997). Ultimately, all evolutionary literary scholars appeal to biocultural theory for explanation (Boyd et al., 2010). They see humans as products of genes and environments, human environments as fundamentally cultural, and literature as a product of human minds. This conceptual framework helps prevent a myopic focus on the author, the reader, the text, or the world.

Evolutionary literary scholars still focus on one or another aspect of literary meaning. Those who focus on the text use evolutionary psychology and neuroaesthetics to explain the beauty of word-choices, the logic of sentence-length, and the effect of metaphors (Boyd, 2009; Dissanayake, 2000; Dutton, 2009; Easterlin, 2010). They identify cross-cultural themes to account for the staying power of particular literary works (Nordlund, 2007; Kruger and Jonsson, 2019; Saunders, 2015), or they provide evolutionary explanations for archetypal heroes and monsters (Clasen, 2017; Cooke, 2010; Kjeldgaard-Christiansen, 2017). Those who focus on the author use biographical information to trace how an author's core motives, personality profiles, and self-narrative shape his or her literary works (Carroll, 2011; Jonsson, 2013; Saunders, 2018a).

Those who focus on the reader tend to use quantitative methodology, finding patterns of emotional response across hundreds of texts, or measuring how people interact with particular genres (Carroll et al., 2012; Clasen et al., 2018; Gottschall and Nordlund, 2006). Those who focus on the world use biocultural theory to reconstruct particular socio-cultural environments, explaining how those environments gave rise to specific literary works (Gottschall, 2008a). The best work in each category bleeds over into other categories and contributes to the general understanding of literary meaning.

At the most general level, evolutionary literary theory aims to explain why humans create verbal art. Why spend time and effort on simulated social experiences? Why, since it is already so demanding to navigate the real world, create and inhabit imaginative virtual worlds made of words? These questions speak to the broader question of whether the arts have an adaptive function. Among humanists and evolutionary scientists, the answer has sometimes been that the arts are a by-product of complex cognition – a functionless pleasure technology (Cochran and Harpending, 2009: 126–27; Davies, 2012; Pinker, 1997: 524–25; Kramnick, 2011). Evolutionary literary scholars who pursue this question have a different answer. They suggest various adaptive functions for verbal art, but they agree that it is too costly to have persisted as a byproduct. They argue that it requires reliably developing, complex cognitive mechanisms, and that it modifies human behavior in significant ways (Boyd, 2009; Carroll, 2011; Clasen, 2017; Dissanayake, 2000; Gottschall, 2012; Saunders, 2018a; Scalise Sugiyama, 2005).

The rest of this chapter outlines the history of evolutionary literary theory; describes some of its most important achievements, debates, and ongoing research programs; relates it to contiguous fields; positions it within the larger field of evolutionary studies in imaginative culture; and discusses directions for future research.

HISTORY AND INSTITUTIONAL POSITION OF THE FIELD

In the 1970s and 1980s, literary study adopted a ‘blank slate’ view of the human mind and, in that respect, came into alignment with the non-evolutionary social sciences (Abrams, 1997; Pinker, 2002). There was a sharp turn away from cross-cultural patterns and psychological explanation toward cultural variation and ideological argument. Focus increasingly shifted from analyzing literary works to critiquing power structures and empowering marginalized groups (Boyd, 2010; Gottschall, 2008b). Unlike the social sciences, literary study has not turned back toward biology. Literary scholars who publish in the field’s flagship journals still believe that culture is the primary cause of human behavior, that culture is unrestrained by biology, and that science cannot explain literature (Carroll et al., 2017b). This paradigm-level resistance, mirrored in several humanist disciplines, has not prevented scholars and scientists from investigating humanist subjects scientifically. Beginning in the early 1990s, the biological turn in the social sciences was extended to the arts (Dissanayake, 1992; Tooby and Cosmides, 2001). Evolutionary literary theory emerged toward the end of the 20th century (Carroll, 1995; Cooke and Turner, 1999; Storey, 1996). Within the last three decades, the field has produced around 30 books and hundreds of articles (Carroll, 2018b). It has been given different names – literary Darwinism, biocultural literary criticism, biopoetics – but the core premise has remained the same. The field is sufficiently stable and productive to be included simultaneously in handbooks of evolutionary psychology and anthologies on literary theory (Buss, 2016; Corstorphine and Krammel, 2018; Dunbar and Barrett, 2007; Richter, 2018; Turner et al., 2014).

The early years of evolutionary literary theory were marked by manifestos and polemical exchanges (Boyd, 2010; Carroll, 1995, 2008;

Gottschall, 2008b). Evolutionary literary scholars had to stake out a territory between the sciences and the humanities, clarifying their theory and methods. Almost every paper had to include a basic rationale for the field. Though literary interpretations were part of the repertory from the start, the proportion of strong interpretive work has increased within the last decade (Boyd et al., 2010; Carroll, 2011; Carroll et al., 2012; Clasen, 2017; Saunders, 2018a). The field continues to be theoretically conscious. Literature depicts all of human life, and literary experience depends on human capacities that remain hotly debated among evolutionary psychologists and neuroscientists: moral evaluation, narrative imagination, and aesthetic appreciation. Evolutionary literary scholars therefore have a particularly urgent need to stay abreast of scientific developments. Articles often take on a hybrid character – part theoretical synthesis, part literary interpretation; part theoretical argument, part quantified reader response (Carroll, 2015; Clasen et al., 2018; Kruger and Jonsson, 2019). But evolutionary literary scholars no longer take part in frequent polemical exchanges to justify their academic existence.

Evolutionary literary theory has had greater success outside than inside its literary home discipline. It has been featured in social science handbooks and journals, drawn attention from the media, and appeared frequently at the conferences of the *Human Behavior and Evolution Society*. But it has not been widely embraced by academic literary study. Though a few non-evolutionary literary scholars have softened their tone over the years – supposedly no longer ‘Against Literary Darwinism’ (Kramnick, 2011) so much as requiring ‘Another Literary Darwinism’ (Fletcher, 2014) – there is an epistemological disagreement at the heart of this conflict. Literary study still considers culture a force independent of biology (Carroll et al., 2017b). Evolutionary literary theorists consider culture a crucial part of the human niche, but one that is ultimately constrained by evolved

psychological dispositions (Boyd, 2009; Carroll et al., 2017a; Saunders, 2018a). For evolutionary literary theorists, nothing in culture makes sense except in the light of human psychology. For non-evolutionary literary theorists, in contrast, psychology should be treated with suspicion – especially if it claims to identify ‘timeless themes’ or ‘deep themes that fascinate us in fiction’ (Kramnick, 2011: 346, 338). To quote Jonathan Kramnick (2011: 338), the most influential critic of evolutionary literary theory: ‘Academic literary criticism of course recoils from this sort of thing and for good reason’. Kramnick does not articulate the reason. Part of it is most likely ideological, since some agendas for social reform seem more plausible if culture is a force unrestrained by biology (Lewontin, 1980; Lewontin et al., 1984). Another part may be institutional inertia – the unwillingness of scholars to abandon their theoretical assumptions and master new methodologies. Regardless of its causes, the academic literary establishment’s belief in the autonomy of culture is incompatible with the biocultural perspective of evolutionary literary theory.

The contrast between evolutionary literary theory and conventional literary theories mirrors broader contrasts between the sciences and the humanities. It shows two fundamentally different ideas about how to study subjects in the humanities. Non-evolutionary literary theorists study the interaction between culture and literature: a meeting between cultural discourses and cultural artefact without clearly conceived causal direction. Evolutionary literary theorists study literature as imaginative experience in human brains, explicable through science. These two ideas of the subject produce different research goals. Non-evolutionary literary theorists aim to show multiple interpretations of literary works, to uncover their ideological affiliations, or both (Richter, 2018). They frame their social contribution as agitation – moral and political enlightenment – rather than explanation (Gottschall, 2008b). Evolutionary literary theorists aim to explain

the psychological functions and effects of literature. They may have individual moral and political values, but those values are subordinated to the purpose of explanation. They test their ideas against data collected by themselves and others. As in any field, there are also literary scholars less concerned with theory, who focus on categorization and analytic description. *Which Victorian novels mention Darwinian evolution? How does Webster's Duchess of Malfi allude to King James's court?* Evolutionary literary theorists can use the work of such literary scholars. But to the extent that analytic description is done within the theoretical paradigm of literary study, it is shaped by literary study's attitude to science.

Attitudes to science are the fundamental difference between evolutionary literary theory and its home discipline. Conventional literary theorists may adopt concepts from the sciences, but those concepts are chosen ad hoc, and treated as if they were part of any other cultural discourse (Kramnick, 2011; Fletcher, 2014; Grubbs, 2016). Where there is contradiction, scientific concepts are subordinated to humanist concepts, such as Foucauldian social theory (all hierarchies are oppressive) or the gender philosophy of Judith Butler (sexual identity is entirely cultural). Evolutionary literary theorists take the opposite approach. They may adopt concepts from the humanities, but where there is contradiction, they use scientific data to correct humanist concepts. They assimilate information from the evolutionary social sciences, envisioning a research program that is coherent, cumulative, and explanatory.

MAIN ACHIEVEMENTS, DEBATES, AND CURRENT RESEARCH PROGRAMS

The Adaptive Function of Literature

Debates about the adaptive function of literature have perhaps been the most visible part

of evolutionary literary theory. Hypotheses have been advanced, or discussed, in books that reach beyond Academe (Boyd, 2009; Dissanayake, 2000; Dutton, 2009; Gottschall, 2012). Biologists and evolutionary psychologists have addressed the question in non-fiction bestsellers (Cochran and Harpending, 2009; Miller, 2000; Pinker, 1997; Wilson, 1998). Critics of evolutionary literary theory have protested with particular vigor against the idea that literature has an adaptive function (Davies, 2012; Kramnick, 2011), and one skeptical fellow traveller has declared it the most interesting idea in evolutionary literary theory (Harpham, 2015). Given how fundamental the adaptive function of literature is to how literature should be conceived and studied, such attention is not unreasonable. Evolutionary literary theory would still remain viable if literature were a functionless byproduct. Biologists find it worthwhile to study functionless structures and vestigial traits or to analyze the susceptibility of functional structures to non-functional uses. But the research questions one asks about literature are profoundly affected by whether or not one envisions literature as adaptively functional. Moreover, which functions one attributes to it – social cohesion or sexual display, cognitive flexibility or motivational structures – influences how one interprets new data. Any scientific endeavor involves an interdependence between theory and empiricism. For evolutionary literary theory, adaptationist debates are at the heart of that interdependence.

What does it mean for literature to have an adaptive function? Evolutionary literary theorists who argue that it does have an adaptive function often refer to Tinbergen's four levels of analysis: phylogeny, ontogeny, mechanism, and function (Carroll, 2012a). Such theorists suggest that storytelling appeared around the time of behavioral modernity, that human infants reliably develop an appreciation for it, that it depends on complex neurological mechanisms, and that it solves some problem related to human fitness (Boyd,

2009; Carroll, 2018b; Scalise Sugiyama, 2005). They do not argue that humanity evolved a cognitive module for the Victorian three-volume novel. They frame today's printed and visual storytelling as intricate, culturally specific expressions of ancient narrative impulses (Gottschall, 2012). Several strands of data support this fundamental hypothesis: storytelling can be found in every known human culture, including the hunter-gatherer populations used as proxies for ancient populations (Brown, 2010; Smith et al., 2017); behavioral modernity coincides with a globularization of the brain, affecting areas involved in the 'brain's default mode network', which is activated when reading and writing stories (Carroll, 2018a; Jacobs and Willems, 2018); particular folktales can be traced thousands of years into the past (Graça da Silva and Tehrani, 2016; Tehrani, 2013); storytelling is a time-consuming activity in which humans engage relentlessly from a young age; and stories appear to affect human behavior (Gottschall, 2012).

Evolutionary literary theorists still debate how literature contributes to human fitness, but they tend to argue that it solves problems specific to the human niche. One hypothesis suggests that stories help maintain social cohesion in the vast and complex human social world (Dissanayake, 2000). Another suggests that stories are a medium for sexual selection, displaying the cognitive power and mental flexibility crucial to human survival (Dutton, 2009). Several hypotheses center on the idea that stories are a technology for mental simulation. In one version, storytelling is an extreme form of play, honing human cognitive flexibility and pattern recognition the way other animals hone hunting and evasion (Boyd, 2009). In another version, stories are a safe way to convey environmental information across generations (Scalise Sugiyama, 1996). In a third version, stories create an arena for case-based reasoning – a flight simulator for piloting human life, allowing us to act out possible scenarios without facing real-world consequences (Clasen, 2017;

Pinker, 2010; Tooby and Cosmides, 2001). Finally, one hypothesis suggests that literature helps produce a sense of meaning, guiding human values and self-images (Carroll, 2018a; Wilson, 1998). Some of these hypotheses have been in conflict over the years. For instance, the idea of a prosocial function has been critiqued by advocates of literature as sexual display, on the grounds that authors often turn against society and promote anti-social forms of individualism (Dutton, 2009). The idea of sexual display has been critiqued, in turn, on the grounds that storytelling is a communal behavior that begins long before pubescence (Dissanayake, 2000). Despite these conflicts, there is obvious room for the hypotheses to complement each other. Many evolutionary literary theorists subscribe to some version of the hypothesis that literature helps produce meaning (Clasen, 2017; Jonsson, 2018; Saunders, 2018a). That hypothesis can incorporate other functions like social cohesion, sexual display, cognitive play, environmental information, and case-based reasoning.

Human Life History Theory and Literary Universals

From the first, evolutionary literary theorists have been concerned with 'human universals': traits and behaviors that appear in all known human cultures (Brown, 2010; Carroll, 1995; Hogan, 1997). Such cross-cultural features have clear implications for what tends to engage human attention and emotions – and thus, what tends to be the subject of literature across time. In order to turn human universals into an explanatory framework, evolutionary literary theorists have sometimes recruited human life history theory (Boyd et al., 2010; Kruger and Jonsson, 2019; Saunders, 2015, 2018b). Life history theory identifies the patterns of behavior that arise from a species' reproductive cycle. In the case of humans, the reproductive cycle involves an extended dependent

childhood, socialization into sustenance systems that require high degrees of technology and cooperation, romantic pair-bonds embedded in complex sociocultural environments, and cooperative parenting developing into grandparenting. Evolutionary literary theorists use this model of human nature to analyze literary themes like romantic love, social status, and survival (Boyd, 2009; Clasen, 2017; Nordlund, 2007; Saunders, 2015; Winkelman, 2013). Carroll (2012b) identifies a set of core literary themes: survival, growing up, love and sex, family life, social life, aliens and enemies (outlaws, ethnic conflict, war), and the life of the mind (the arts, science, religion). These themes arise out of the phases and main social relationships of human life. Taken together, they can be used to measure an author's scope in depicting human experience.

The life history model allows evolutionary literary theorists to analyze each universal theme in relation to specific cultural and individual systems of value. For instance, many authors take the romantic pair bond as a central theme. That theme reflects a cross-culturally important human motive. But no human motive exists in isolation. Across cultures, the romantic pair bond is tied to the separate range of motives involved in parenting; it is lodged within networks of extended kinship, non-kin social structures, and systems of sustenance; it is riddled with conflicts and partly in conflict with other bonds, or with other individual motives; and it is given varying cultural meanings. Evolutionary literary theorists can ask how a particular author depicts the nature and relative importance of the romantic pair bond. How is it related to the organization of family and networks of extended kinship? How is it related to the economic organization of a given society? How is it integrated into those aspects of socio-sexual identity that vary from culture to culture? How does it compare with the values attached to romantic pair bonds in the author's culture? If an author has religious beliefs, in what way is

the romantic pair bond integrated into a cosmic religious vision?

Literature does not, of course, exclusively deal with reproduction that is successfully achieved or tragically unattained. Nonetheless, literary works build on the emotional and cognitive apparatus that has evolved around the human reproductive cycle. Some works do that by celebrating reproductive unions embedded in prosocial environments, like the folk tales recorded by the Brothers Grimm, the comedies of Shakespeare, and many British novels from the early 19th century. Others do it by portraying the breakdown of every human attachment, from families to societies, like the tragedies of Sophocles or the dystopian novels of the 20th century. Oscar Wilde's *The Picture of Dorian Gray* does it by depicting a supernaturally perpetuated youthful pleasure-seeking in conflict with Christian morality. Charlotte Perkins Gilman's *Herland* does it by valorizing maternal care to the exclusion of all other motives. Many works build on evolved human psychology by pushing its boundaries. The Marquis de Sade's *120 Days of Sodom*, for instance, eroticizes cruelty and mocks every type of human relationship. Evolutionary literary theorists use life history theory to understand all of these different perspectives on human life.

The themes from human life history explain the psychological foundations of literary genres. Classic comedy tends to affirm universal human relationships, while tragedy tends to evoke their fragility and inherent conflicts (Boyd, 2009; Carroll, 2012b; Nordlund, 2007). Romance novels and pornographic literature reflect female and male mating psychology respectively, focusing on mates who are either exaggeratedly powerful and romantically committed or exaggeratedly beautiful and sexually accessible (Salmon and Symons, 2010). Horror literature draws on ancestral threats like homicidal humans, predators, parasites, contagion, and darkness (Clasen, 2017). Gothic and 19th-century realist novels often center on mate choice

and mate guarding, portraying characters who choose wisely or disastrously, and characters who represent faster or slower mating strategies (Carroll et al., 2012; Kruger et al., 2003; Saunders, 2015). Dystopian literature portrays dysfunctionally rigid social systems that suppress human needs like pair bonding and privacy (Cooke, 2010). Utopian literature extrapolates from human preferences for social stability and environmental control, depicting worlds without social and ecological conflict (Jonsson, 2019). Postapocalyptic literature portrays the failure of human society – sometimes the end of the human species – and often contains visions of utter social isolation (Clasen, 2019). Starting from the broad psychological effects of genres, evolutionary literary theorists can pinpoint the particular effects of individual literary works.

Agonistic Structure

Agonistic structure – the division between protagonists and antagonists – is one main way in which authors convey their perspectives. Readers are expected to root for the protagonists and feel antipathy for the antagonists, who are the protagonists' enemies. The utility of this concept can be indicated by the interpretive questions it raises. How clearly do authors signal agonistic structure to readers? What personality factors characterize protagonists and antagonists? What emotional consequences follow from the victory or defeat of a protagonist? What implications do preferences for characters have for the value structure implicit in any given work? How are those value structures implicated in the depictions of personal identity, basic human motives, social organization, and world views?

Though the terms 'protagonist' and 'antagonist' have been used in literary study from its birth as an academic discipline, they have not been subject to much investigation. Evolutionary literary scholars have approached them through theoretically

rationalized reader response studies. The most ambitious study of agonistic structure in the field collected data from around 500 readers responding to characters in over 100 novels from the 19th century (Carroll et al., 2012). Respondents answered questions in three categories: (1) the characters' agonistic role (protagonist, associate of protagonists, antagonist, or associate of antagonists), (2) the characters' personal identities (age, personality, attractiveness, motives, and criteria of mate selection); and (3) the respondents' subjective responses to the characters (wanting them to succeed or fail; basic emotional responses like anger, sadness, or interest). These measures tested whether protagonists and antagonists can be separated into recognizable patterns of motives, personality traits, and emotional effect. The study hypothesized that protagonists would form cooperative communities geared toward constructive goals, and that antagonists would exemplify dominance behavior (Carroll et al., 2012: 8). That hypothesis was robustly sustained. In fact, antagonists tended to be *exclusively* motivated by a desire for dominance, with little concern even for sex (Carroll et al., 2012: 40–3). Protagonists tended to 'care about friends and family, respond to romantic attractions, and become readily absorbed in cultural pursuits' (Carroll et al., 2012: 55). The domineering antagonists represented the opposite of these positive absorptions. They displayed 'dominance striving devoid of all affiliative dispositions' and 'sex-neutral egoism'; they were 'emotionally isolated' and 'incurious' (Carroll et al., 2012: 43, 55). On the basis of these data, the study's authors argue that agonistic structure mirrors the human egalitarian syndrome: the tendency of cooperators to band together and suppress dominance behavior in individuals. They also argue that agonistic structure in literature, like gossip, fulfils an adaptive function by enhancing social cohesion (Carroll et al., 2012: 10).

The long-overdue quantification of agonistic structure opened up a new avenue of

research for evolutionary literary theorists. The study concerned itself only with British novels from the 19th century, but it is unlikely that no other body of literature features distinctions between protagonists and antagonists that draw on evolved human sociality. Nineteenth-century novels in different genres and styles, written by authors as distant in personality, values, and life experience as Jane Austen and H. G. Wells, all used the same pattern to elicit positive and negative responses to their characters. Against the background of that pattern, it is possible to clarify agonistically complex characters – characters like Victor Frankenstein and his monster or Cathy and Heathcliff from *Wuthering Heights* – who do not fit smoothly into either the protagonist category or the antagonist category (Carroll et al., 2012: 22–3, 91). Such characters tend to combine protagonistic traits like openness, cultural absorption, and romance with antagonistic dominance behavior. The theoretical framework derived from this study has been used to explain modern anti-heroes and villains in film (Kjeldgaard-Christiansen, 2016, 2017). Evolutionary literary theorists have used the same framework to approach questions about 20th-century and 21st-century literature: how horror novels create emotional investment through their portrayal of sociality and dominance (Clasen, 2017), and how popular science and adventure stories shape evolutionary history into agonistic structures (Jonsson, 2018).

Literary Form

Evolutionary literary theorists consider literary form an integral part of literary meaning (Boyd et al., 2010). *Literary form*, in this sense, means the aspects of literary texts that have to do with structural organization: ‘from individual words, with their evocative sounds and connotational resonance, through the rhythm of sentences and paragraphs, up to the largest features in the organization of time, representational mode, and manner of

narration’ (Carroll, 2018a: 142). These aspects function as the medium of literary art. Authors do not convey their perspective on characters, behaviors, and ideas simply through declarative statements, but through choices of adjectives and metaphors, through rhetorical repetition and symbolic juxtaposition, producing effects like allegory, allusion, satire, or tragic irony. Readers do not usually experience formal features separately from the semantic contents of a literary text. As suggested by the early-20th-century Shakespearean A. C. Bradley (1965: 14), that would be like experiencing the lines of a smile as something separate from the feeling conveyed by the smile: ‘Just as there the lines and their meaning are to you one thing, not two, so in poetry the meaning and the sounds are one’. Nevertheless, the formal features of literature can be studied with concentrated attention, the way one can study the muscles and environmental cues of a facial expression.

Though evolutionary literary theorists acknowledge the importance of literary form, they have not yet produced many studies that focus on it. Instead, discussions of style and structure have been included as part of the most ambitious interpretive analyses. Several evolutionary analyses of Shakespeare discuss the effect of his language (Boyd, 2009; Carroll, 2010; Nordlund, 2007). There have been articles and book chapters in the field that deal specifically with poetry (Boyd, 2009; Easterlin, 2010; Kruger and Jonsson, 2019; Saunders, 2018b, 2018a: 61–77, 175–203; Winkelman, 2013). These studies have tended to foreground themes, depicted content, and authorial self-presentation. For instance, Easterlin explains William Wordsworth’s celebration of mother-infant bonds using developmental psychology (against a tradition of Freudian interpretations), and Winkelman analyzes the intricate romantic self-advertisement of John Donne using evolutionary accounts of sexual display. However, none of these studies of poetry entirely omits discussions of formal features. Easterlin supports

her argument by analyzing word choice, rhetorical repetition, and compositional structure (Easterlin, 2010: 354–57). Winkelman largely bases his argument on Donne's word choices and metaphors. Saunders (2018a) combines her evolutionary analysis of Edna St. Vincent Millay's sexual identity with a constant attention to her sonnets' allusions, analogies, hyperbolic wit, lyrical alter egos, and satirical narrative structures (175–203).

CONTIGUOUS FIELDS

Psychology of Fiction

'Psychology of fiction' is a broad term for the psychological study of literature and narrative thinking. The field's main premise is that fiction engages real emotions through mental simulation (Oatley, 2016; Oatley et al., 2012). Psychologists who subscribe to this idea tacitly identify literary experience as a special form of cognitive activity. They relate fictional experience to the brain's default mode network and speculate about the function of literature (Jacobs and Willems, 2018; Oatley, 2016). In order to investigate the cognitive mechanics of reading, they use a variety of experimental tools: questionnaires, personality profiles, textual manipulation, lexical databases of emotional valence, eye-tracking, heart-rate measures, skin-conductance response, and neuroimaging (Barnes, 2018; Carney and Robertson, 2018; Carney et al., 2014; Jacobs, 2015; Mar and Oatley, 2008).

There are obvious lines of convergence between the psychology of fiction and evolutionary literary theory. Both fields attempt to understand fiction psychologically, subordinating their theoretical ideas to empirical data. Indeed, evolutionary literary scholars have often collaborated on empirical studies with psychologists (Carroll et al., 2012; Clasen et al., 2018; Kruger and Jonsson, 2019). To the extent that psychologists measure the

real process of literary experience, evolutionary literary theorists can use their data (Carroll et al., 2012; Oatley et al., 2012). To the extent that evolutionary literary theorists synthesize scientific information, psychologists can use their theoretical ideas (Jacobs, 2015). The two fields have the potential to improve each other directly. Evolutionary literary theory can have its hypotheses tested using the sophisticated experimental tool kit of psychologists. Its theoretical ideas can be refined by the detailed accounts of emotional and aesthetic engagement provided by empirical reader response studies. Psychologists, in turn, can use evolutionary literary theory to guide their reader response studies. They can use the concept of literary meaning created by evolutionary literary scholars to develop the 'ecological validity' of their experiments (Jacobs, 2015). Most importantly, they can provide an explanatory framework for their research through biocultural accounts of literary experience, life-history models of literary themes, and hypotheses about the adaptive function of the arts.

Cognitive Literary Study

'Cognitive literary study' covers a multitude of perspectives. In some uses, it describes an assimilation of scientific information into literary study that is consistent with evolutionary literary theory and even overlaps it (Fisher et al., 2013; Hogan, 2003; Winkelman, 2013). Cognitive literary scholars in this camp tend to use the word *evolution* sparingly but still strive for a cross-cultural understanding of literature: universal narrative structures, literary engagements of basic emotions, cognitive biases, and theory of mind. They may collaborate with – or at least have dialogues with – researchers from the psychology of fiction (Oatley et al., 2012). Overall, their approach resembles that of cognitive scholars in film studies and performance studies (Bordwell, 2010; McConachie, 2008; Smith, 2017). These scholars aim in

some way to build new theoretical frameworks for literary study based on psychology and neuroscience. However, in other uses, cognitive literary study simply means appropriating scientific concepts to currently conventional literary theories (Richardson, 1999; Spolsky, 2008; Zunshine, 2014). Cognitive literary scholars in this camp display beliefs and deploy methods like those of non-evolutionary literary scholars: emphasizing the subjectivity and ideological biases in science, subordinating scientific information to literary theories, and criticizing scientists for not deferring to humanist perspectives on literature (Grubbs, 2016; Carroll et al., 2017b; Spolsky, 2008). Such cognitive literary scholars gain the approval of literary scholars who oppose evolutionary literary theory (Fletcher, 2014; Kramnick, 2011).

The heterogeneity of cognitive literary study makes it hard to say how constructively it can interact with evolutionary literary theory. Literary scholars who call themselves 'cognitive' may or may not acknowledge the epistemological authority of science. They may use quantitative methodology or resist it, strive for theoretical coherence or champion theoretical pluralism. Similar classification problems apply to related literary schools that absorb scientific concepts. For instance, 'ecocriticism' includes both evolutionary literary analysis that focuses on the environment and non-evolutionary literary analysis that treats nature as a victim of ideological oppression (Glotfelty and Fromm, 1996; Helsing, 2017; Love, 2003). In a critical light, the amorphousness of these schools resembles a parasol: a way for scholars who want to use psychology and neuroscience to avoid censure from colleagues, and a way for scholars who want to resist scientific literary study to claim science as an ally. More generously, one might view the amorphousness as a sign of paradigmatic transition. Cognitive literary study and related schools could possibly introduce cautious literary scholars to scientific information and experimental methodologies. Its precise effect on

interdisciplinary collaboration is open for investigation. However, after nearly two decades of cognitive literary study, the most prominent journals in literary study still resist scientific approaches to literature (Carroll et al., 2017b).

Evolutionary Studies in Imaginative Culture

'Evolutionary studies in imaginative culture' is not so much a contiguous field as it is an overarching field. It is roughly equivalent to the 'evolutionary humanities': research that uses the evolutionary social sciences to analyze imaginative behavior like musical arts, visual arts, plastic arts, performance, religion, ideology, and philosophy (Carroll, 2017). Evolutionary literary theorists ultimately aim to explain verbal art within the total context of evolved human behavior. The subjects of the humanities are important forms of human behavior. Moreover, literature often interacts with other types of imaginative culture. Across cultures, verbal art is combined with images, music, and performance; stories inspire sculptures; religious and philosophical systems are pervaded by fables, allegories, metaphors, and rhythmically organized words (Brown, 2010; Dissanayake, 2000; Dutton, 2009; Gottschall, 2012). Research in each subject in the humanities can be greatly facilitated by an understanding of the others.

Evolutionary scholars have long attempted to provide evolutionary explanations that account for all of the arts (Asma and Gabriel, 2019; Boyd, 2009; Dissanayake, 2000; Dutton, 2009). Given the connection between different artistic behaviors, approaching them as a collective riddle is reasonable. Discussions about the adaptive function of literature often include discussions of other arts (Dissanayake, 2000; Gottschall, 2012). That makes particular sense for some hypotheses. For instance, if literature serves to promote social cohesion,

or if it helps create world views that guide our behavior, that is probably true also of related arts like figurative painting and song (Carroll, 2012a; Dissanayake, 2000; Zaidel, 2017). Nevertheless, different arts may have different evolutionary origins and multiple adaptive functions. The neurological health benefits of music have been linked to bipedal movement and complex coordination as well as to social cohesion (Meehan et al., 2017). The origin of figurative painting has been attributed to the close observation and empathetic projection required by human hunting techniques (Coss, 2017; Hodgson, 2017). Narrative psychology has connected verbal self-narratives to the evolution of self-consciousness and identity (McAdams, 2019). The origin and adaptive function of religion have been vigorously debated, with hypotheses ranging from cognitive byproduct to motivational regulator (Lawson, 2019; Wood and Shaver, 2018). These behaviors all form part of the human experience that literature depicts, but they can also illuminate literature as an art form. If literary theorists understand the evolution of rhythm, they are in a better position to understand meter, rhyme, and rhetorical repetition. If they understand the mechanisms of visual imagination, they can better understand verbal imagery. If they understand the adaptive functions of religion and self-narrative, they can get new insights into how literature shapes personal and collective world views. Research about the other arts, in turn, can gain by incorporating the main achievements of evolutionary literary theory: the model of literary meaning, the range of universal literary themes, the explanatory account of agonistic structure, and hypotheses about the adaptive function of verbal art.

CONCLUSION

Evolutionary literary theory has existed for nearly three decades, but the evolutionary

study of literature is only beginning. Literary meaning is not a subject that lends itself easily to scientific explanation. Even a scientific description of it requires high degrees of specificity about controversial, multi-variable phenomena like human sociality and personality differences. Psychologists who study fiction employ complex experimental methodology simply trying to measure the experience of reading and writing literature (Jacobs, 2015). Evolutionary literary scholars use intricate biocultural models to interpret single literary works or authorships. Much of this work is still being done in isolated pockets. Individual literary scholars can be informed to a greater or lesser extent about current developments in psychology, and psychology labs can develop their own eclectic theoretical frameworks (Carroll, 2018a; Jacobs, 2015). One goal for the future of evolutionary literary theory is to cooperate systematically and achieve theoretical integration with the psychologists who study fiction. That goal is related to the perpetual need for quantification and hypothesis testing. But there are many areas within the field that are open for theoretical development.

Literary form and historical specificity are the two most obvious areas of development for evolutionary literary theory. The field's early stages necessarily focused on the big picture – epistemology and scientific theory, literary universals, the adaptive function of literature, and the basic elements of literary meaning. Now there is need for more detailed studies of the verbal medium and cultural variations. All evolutionary literary scholars could gain from studies that theorize rhetorical rhythm and imagery, narrative structure and symbolic interplay. The study of historical specificity is an even greater opening. Each human population organizes human life history in somewhat different ways, through their specific modes of sustenance, social systems, marriage practices, child-rearing habits, and gender relations – all of which affect literary expression. The scientific study of literature from different periods can do a lot to

illuminate the values and preoccupations of those periods. For instance, one might envision studies of agonistic structure that replicate the study of 19th-century literature for other cultural and historical periods (Carroll et al., 2012). The original study found variation even within the database of 19th-century British fiction: a decrease in happy endings around the turn of the century. How would these patterns compare to British literature from the 18th or 20th century, or to American literature from the same periods – or to different periods in Chinese, Polish, or Italian literature? Such large-scale studies might be complemented with more case studies that interpret the imaginative structure of literary works that have been particularly influential throughout history.

Though much remains to be done, recent progress is encouraging. Book-length studies published in the last few years suggest that the explanatory framework of evolutionary literary theory can integrate, correct, and improve upon previous literary scholarship (Clasen, 2017; Saunders, 2018b). Evolutionary literary scholarship has occasionally been praised by high-profile non-evolutionary literary scholars (Cain, 2019; Harpham, 2015). As has been indicated in this chapter, evolutionary literary scholars and psychologists have already been engaging in collaboration, but the scope of possible collaborative work is immense. Progress in other fields has also improved the position of evolutionary literary theory. Evolutionary social theory now allows for vastly more nuanced interpretations of human sociality than it did during the 1990s – with detailed accounts of prosocial dispositions and cooperative networks, leadership, norm-internalization, and moral emotions (Carroll, 2015). Culture has itself received increasing attention from evolutionary scientists (Henrich, 2015; Richerson, 2017). Until recently, evolutionary literary theorists had to work without any sense of the brain mechanisms involved in imaginative experiences. We now know that the brain's default mode network is activated in daydreaming, moral

evaluation, mental time-travel, autobiographical memory, and literary experience (Jacobs and Willems, 2018). These advances can help immensely with the tasks of theorizing literary form and historical specificity.

Because evolutionary literary theorists remain at odds with the paradigm that governs academic literary study, they still face the problem of institutional resistance within the humanities. That makes publication more difficult for established scholars, but more importantly, it limits the number of doctoral students who can pursue evolutionary literary theory. The open vistas of research require nothing so much as manpower. If evolutionary literary theorists are to pursue the study of specific literary periods, they will need experts in those literary periods. If they are to produce case studies of influential authors, they will need scholars who have spent months or years studying those authors. Theorizing literary form will require scholars who are deeply immersed in poetic meter, rhetorical traditions, and modes of allegory or allusion. Single scholars cannot achieve total literary expertise, any more than single biologists can specialize in every species. The field needs to grow numerically as well as theoretically and methodologically.

Scholars who publish in prestigious humanist journals do not tend to believe that science can explain aesthetic and subjective experience. Literary scholars are among the most extreme disbelievers in this proposition (Carroll et al., 2017b). Thus, their perspective on literary meaning remains essentially unchanged since A. C. Bradley's declaration in 1901: 'It is a spirit. It comes we know not whence. It will not speak at our bidding, nor answer in our language. It is not our servant; it is our master' (Bradley, 1965: 28). Evolutionary literary theorists do believe that literary meaning can be explained by science. In fact, they are slightly more emphatic in that belief than evolutionary psychologists (Carroll et al., 2017b). Evolutionary literary theorists believe that literature can be understood from neurological mechanism

to evolutionary function – from the level of basic communicative processes, universal themes, and agonistic structures to the expressions of every particular cultural ethos, down to the world views and stylistic decisions of individual authors. But no evolutionary literary theorist believes that this will be easy. We have only just begun.

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Evolutionary Psychology and the Study of Religion

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INTRODUCTION

The contentious relationship between Darwinian evolution and religion dates back to the very beginning of the field. The publication of *On the origin of species* set things in motion, with the Thomas Huxley/Bishop Wilberforce debate at Oxford being the most famous public dispute; it continued throughout the next century, playing out in schools, courthouses, and political campaigns – particularly, but not exclusively, in the United States. There is also a long history of attempts to present a more conciliatory model of evolution and religion, for example, theistic evolution, in which the Darwinian processes work their way through natural history but as instantiations of a transcendental design – that is, God working his will through natural laws discovered by Darwin. This approach seemed to offer an effective détente to the often volatile clashes between evolutionary and religious world-views and allowed theistically-inclined

scientists and scientifically-informed believers alike to compartmentalize these aspects of their intellectual life into ‘non-overlapping magisteria’ (Gould, 1999).

A new phase of the evolution–religion issue began, however, with the development of the field of evolutionary psychology. While Gould desired to draw a clear dividing line between empirical facts about the natural world (evolutionary science) and values, meaning, and purpose (religion), evolutionary psychology, by bringing all things ‘mind’ within the domain of the natural sciences, effectively rules out any such neat and simple division of labor. Evolutionary science may have nothing to say about whether there is a God working through the evolutionary process; evolutionary psychology, however, does have something to say about *the belief* that God is working in this way – for example, about the cognitive processes that underlie the formation and maintenance of religious beliefs, behaviors, and emotions, and about

the environmental conditions that served as selection pressures during the earliest stages of human evolution – selection pressures that may have shaped cognitive functions in such a way as to lead to the evolution of those religious-belief generating processes. These are the foundational tasks of a new approach to the study of religion. Whether it is referred to as the cognitive science of religion (CSR), the bio-cultural study of religion, or, more simply, the evolutionary study of religion, a guiding principle of this general approach is that religion is grounded in cognitive/emotional processes that have an evolutionary history.

Before proceeding, it is important to clarify some of the terms in the claim that this is a ‘new approach to the study of religion’. In one sense, taking a broad view of what constitutes an evolutionary approach to religion, it is not ‘new’ at all. There is a lineage of evolutionary approaches to religion. Both anthropology and sociology have long treated religion within a naturalistic framework, with evolutionary overtones: Emile Durkheim’s (1912) *Elementary forms of religious life* and Guy Swanson’s (1964) *The birth of the Gods: The origins of primitive beliefs* are prominent examples. Sigmund Freud (1927) famously theorized that religion arose from the mind’s attempt to deal with evolutionary challenges, for example, in *The future of an illusion*. Centuries before these social scientific approaches, David Hume (1757) attempted to write a natural history of religion, and almost two millennia earlier, we find an account of a proto-evolutionary Epicurean theory of religion, presented by Lucretius (2001) in *On the nature of things*. The contemporary evolutionary approach to religion is just the most recent example of an established tradition in the study of religion. Still, there is something ‘new’ about this approach.

What is most distinctively ‘new’ about the contemporary approach is that it is grounded in a more advanced, better empirically

supported, science of the mind. Those earlier attempts, for all the insight and inspiration they contributed, were limited by the lack of a truly scientific understanding of the processes and mechanisms that give rise to, shape, constrain, and distort cognition. It was only in the latter part of the 20th century, with the development of evolutionary psychology and its incorporation into cognitive science, that it became feasible to construct a natural history of religion – one that could study religious ideas, behaviors, emotions, and values in an empirical and (at times) experimentally testable manner.

The other element of the contemporary evolutionary study of religion that is, in some sense, ‘new’ (at least relative to the sort of historical studies mentioned above) is the broader, more nuanced, conception of ‘religion’ that it works with – and here we address the second definitional qualification. Defining ‘religion’ is one of the most contentious issues within the academic study of religion, so much so that many scholars have given up searching for a set of characteristics that may be defining of religion and instead stipulate what aspect of religion, or things we typically ‘deem religious’ (Taves, 2009), is being considered. However, this is distinctive of late-20th-century religious studies. The study of religion from the 19th through much of the 20th century was marked by a search for just such a definition. In fact, it was the failure of such approaches that has led to the contemporary resistance to treating religion as if it were a natural kind that could be neatly distinguished from other aspects of socio-cultural phenomena.

It is now widely recognized by scholars of religion that the study of religion, at least as it has been conducted in the West throughout the Modern era, is flawed. The flaw is the typically unacknowledged assumption that the proper model of ‘religion’ is that of modern, Western Christianity, most often Protestant Christianity. This has been the implicit model of religion used

to draw distinctions between what is truly religion and what is merely primitive ideation, magic, or superstition. It is this model which allowed scholars to differentiate stages of religious development, creating a spectrum from primitive to advanced. Abandoning this model allows us to recognize the continuity, even the integration, of things deemed religious and other aspects of human experience and social practice. Adopting a more contextualized, fluid, and nuanced understanding of religion not only makes the evolutionary study of religion more legitimately a study of religion, it also allows it to become more legitimately an evolutionary study.

The 'evolutionary' aspect of earlier sociological and anthropological theories was contained in the assumption that societies and their religions progressed and did so following some linear path. That is, these theories started from the misconception that evolution equals progress – from lower to higher, from simple to complex, to better from worse. This, of course, is not consistent with a Darwinian conception of evolution. Each species is assessed, not in relation to what came before, but in relation to its fit within its own environment. We can speak of a species, or an organism, being 'better' than others in terms of its fit to its environment but not because of its perceived state of advancement over previous species or its complexity. As natural history demonstrates regularly, such ostensibly superior characteristics can quickly become an organism's, and a species', downfall in the face of ecological disruption.

The 'new' evolutionary study of religion, then, is new (and we might claim, better) in terms of being grounded in a deeper understanding of the workings of the mind, a more nuanced, less Western-biased conception of religion, and a more accurate model of evolutionary thinking, than any previous studies. With those qualifications set, we are prepared to explore just how evolutionary psychology impacts the study of religion.

In the next section, we consider the model of the religious mind as it is being developed by an evolutionary cognitive science. The general contours of that model present religion as a cultural practice that answers the challenges of increasingly complex social formations, specifically those tasks concerned with social exchanges and cooperation strategies. While this model sees religion functioning as a cultural solution, it is a solution to challenges that arose from the needs of particular organisms (i.e. *Homo sapiens*), with a particular evolutionary history, to adapt to shifting ecological conditions, employing cognitive resources shaped by natural selection. Gaining an understanding of the evolutionary history of those cognitive resources sheds light on the particularities of religious beliefs and behaviors and provides insight into the role of religion, both historically and today.

We then turn to the archaeological record: what evidence might there be in support of the claim that elements of religious belief and behavior have an ancient evolutionary history? How might an evolutionary understanding of the mind shed light on the evidence we do have of ritual, burial, or visual representations of supernatural beings?

Finally, we examine some of the philosophical and theological implications of this field of study. As noted, the relationship between evolution and religion has been complex and often contentious. How do the findings and models coming out of an evolutionary psychology of religion affect that relationship? This is a subject of much debate within the field, with some arguing that this new approach undermines, or debunks, religious claims, while others argue that, on the contrary, not only may an evolutionary approach to religion be compatible with religious beliefs, it might even strengthen the argument for having religious beliefs. Avoiding polemics, this final section will take a careful look at how the new evolutionary study of religion updates these perennial debates.

THE EVOLUTION OF THE RELIGIOUS MIND

In setting out an evolutionary psychological account of religion, we must distinguish two phases of the development of religion as a cultural solution to evolutionary challenges. In order to understand how religious beliefs and behaviors came to function as a cultural solution, we first need to understand how those beliefs and behaviors may have arisen. Here we will focus on one particularly important religious belief: belief in gods. In what follows, we will use the term ‘gods’ to refer to any of the panoply of supernatural beings – for example, spirits, ghosts, demons, revered ancestors, etc. The issue at hand is not what leads any particular individual to believe in gods, but what are the evolved cognitive mechanisms that equipped *Homo sapiens* to be capable of conceiving of gods? What were the natural selection pressures that shaped the cognitive capacities that allowed our ancestors to believe in beings that possessed traits so distinct from more familiar beings in their environment?

While these ‘god-generating mechanisms’ (Shults, 2014) are posited to be the results of natural selection, it does not follow that belief in gods was selected for by Darwinian processes, or that these mechanisms were selected for in order to make belief in gods possible. God-beliefs are outputs of cognitive mechanisms that were selected for their contribution to ancestral survival and reproduction. They are, in the parlance of the field, by-products of naturally selected mechanisms (which should not be taken to mean that they did not play an important role in human evolution).¹ The work of this first phase of an evolutionary study of religion is to identify these mechanisms and their evolved function(s).

In tracing the history of the evolution of brains capable of conceiving of gods, there is no natural starting point. The Upper Paleolithic period seems a reasonable starting

point since the earliest artefacts that can be interpreted as representing gods are dated to this time, as we will see below. However, the cognitive mechanisms required to produce such objects must predate their production. How much further back must we go? A recent work, arguing that ‘the emergence of religion among humans is the outcome of selection on the basic great-ape anatomy and neuro-anatomy over millions of years of evolution’ (Turner et al., 2018: p. 49), starts the story 30 million years ago, with the appearance of an early anthropoid ancestor, *Aegyptopithecus*. This species possessed an expanded parietal lobe, resulting in a sensory-dominance shift from olfactory-based to visual-based, and ‘a mammal with dominant visual receptors... that are geared mostly to the reception and understanding of the external world’ (Turner et al., 2018: p. 52). This paved the way for symbolic representation of the world, without which religion would not be possible (Turner et al., 2018: pp. 52–54).

A more complete evolutionary account of religion would need to fill in the gap between this late Eocene development and the Paleolithic evidence for religion,² but such an account is beyond the scope of this chapter. Instead, we will focus on the cognitive processes that must have been present during the Upper Paleolithic in order to make possible the production of distinctively religious objects, and associated religious beliefs and behaviors, without concerning ourselves with dating the initial appearance of such processes.

A seminal work in this field is Stewart Guthrie’s (1993) *Faces in the clouds*. Aside from the theoretical contributions made by Guthrie, perhaps his key insight is that ‘perception is interpretation’ and that this interpretative strategy is driven by inferential potential. Perception is never simply a passive matter of registering what is presented by the environment but, rather, is an active process on the part of an organism to detect order and patterns in the service of successful action. In situations of uncertainty and

urgency, when the need to interpret under-determined stimuli cannot wait for careful investigation, we bring to bear the model that provides the most useful information in terms of deciding how to act. In a common example, when walking through the woods and seeing movement up ahead, or hearing rustling in the bushes, the ‘best bet’ perceptually is to interpret these stimuli as the actions of an agent, as evidence of intentional behavior of, for example, a predator. As Guthrie (1993: 45) writes:

If perception requires choosing among interpretations and therefore requires betting, and if the payoff is discovering significance, then the first bets to cover—those with the biggest payoff—are bets as high on the scale of organization as possible. The discoveries of order they yield are those we most need. Some such bets are built into perceptual systems genetically.

This is the ‘best bet’ as it has the highest cost/benefit ratio, even if mistaken (i.e. better to mistake the action of the wind for a tiger than a tiger for the wind). Being able to detect agents in the environment – particularly predators and potential prey – is essential to survival. Given the cost/benefit ratios, natural selection would have favored a mechanism that tended toward false positives, as opposed to false negatives. That we often detect agency when there is no agent present is not a malfunction of the mechanism involved, it is a necessary design feature. Such a cognitive mechanism would have been so advantageous that evolution produced an exquisitely sensitive propensity toward detecting agents, equipping us with a ‘hyperactive agency detection device’ (Barret, 2004).³

Guthrie argued that the most significant model we could bring to bear is often that of the human. Other humans were the most significant part of our ancestral environments, the most dangerous, and the most stealthy of threats that our ancestors faced on a regular basis, and so when encountering an urgent situation of perceptual uncertainty, the ‘best bet’ was to bring the model of the human to

bear – this is the origin of anthropomorphism (Guthrie, 1993). Later developments in the literature see anthropomorphism as a specific form of a more generalized agency detection strategy, but it is particularly salient in understanding the genesis of god-beliefs.

While being able to detect the activity of an agent is a vital skill, it is, in itself, insufficient. It does not help to detect an agent – an organism that acts with intention – without also having some insight into its possible intention. Detecting that an agent may be lurking in the bushes does not guide action unless we have some sense of why an agent might lurk. That is, we need to ascribe some motivation, some desire or intention, to the agent in order to decide how to act: is it hiding its presence in order to protect itself from me, or is it lying in wait in order to attack me? In order to enrich our interpretation of the detected agent, we must possess a Theory of Mind (ToM) – that is, we must be able to ascribe mental states to other beings (Atran, 2002; Barrett, 2004; Boyer, 2001). While we can discuss agency detection and ToM as distinct processes, these are not, in practice, distinct steps in the interpretive process. To interpret some stimuli as being caused by an agent is to already bring ToM to bear – to detect an agent is to detect a being that acts with intention – that is, a being with mental states.

For our earliest ancestors, struggling to successfully navigate a dangerous and uncertain environment, the cognitive capacity to detect the presence of agents, and to discern their intentions and thereby successfully predict the best course of action, would have occasioned advantages over less cognitively-endowed competitors. Agency detection and ToM are two manifestations of this cognitive capacity, but they may be aspects of a more general cognitive strategy to distill meaning from patterns in nature. Pattern detection is a basic strategy driving perception: being able to recognize regular relationships between stimuli allows us to perceive distinct features of the environment (Mattson, 2014). Patterns

not only provide information about the environment, but they also can provide information about the presence, action, and, therefore, intentions of agents. Patterns of markings in the dirt interpreted as hoof-prints provide information about the intentional actions of certain animals; recognizing an arrangement of sticks and leaves as a nest provides us with strategic information about the behavior of the animal doing the arranging. Coming to understand what certain patterns may tell us about agents in the environment – that is, interpreting them as evidence of purposeful action – would have contributed to more successful navigation of the environment.

A general interpretive strategy to actively search for the purpose or meaning behind the patterns we detect has been termed Promiscuous Teleology (Kelemen, 1999a, 2004). Kelemen and her associates posit a general cognitive strategy to search for possible meanings and signs of purpose. They conducted a number of experiments with children, and later with adults, that provide evidence of this psychological mechanism and argue that it had adaptive value to our ancestors (e.g., Kelemen, 1999a, 2004; Kelemen and Rossett, 2009; Kelemen et al., 2013).

Hominins equipped with a cognitive system that actively searched for meaningful patterns in the environment, with a sensitivity to detecting the presence of agents, and a predisposition to ascribe intentional states to those agents, would have had an advantage in the struggle for resources, survival, and successful reproduction. These psychological mechanisms did not evolve to enable humans to detect the presence of gods, but they constitute the cognitive conditions that allowed god-beliefs to arise among *Homo sapiens*.⁴ Hominin minds equipped with these cognitive systems scanned their environment searching for meaning in the events they encountered, to detect the activity of agents whose presence was not always readily detectable, and to intuit the intentions behind their activity. These systems often produced false positives,

an acceptable cost paid to avoid missing critical information. However, it was not always possible to recognize when a perceptual interpretation constituted a false positive; not all interpretations were falsifiable – for example, the belief that natural events, such as storms or death, were the acts of agents acting with intentions. The fact that the physical presence of such agents was never perceived did not constitute counter-evidence to such interpretations. As Guthrie points out, there are agents in the natural world that can act at a distance, successfully disguise themselves, or hide their presence (Guthrie, 1993: 64). If the interpretation of agency or purposeful action provided coherence to experience, and was not positively contradicted by other strategic information, such beliefs could be sustained and transmitted, from individual to individual, and from generation to generation.

That it was possible for prehistoric humans to conceive of gods does not explain why such conceptions came to be such an ubiquitous element of belief systems across the world and throughout human history, at least since about 40,000 BP (before present)⁵. In order to understand this, we need to flesh out the processes by which gods came to be relevant to human societies. This is the second stage of development.

RELIGION AND THE EVOLUTION OF COOPERATION

One of the challenges to evolutionary psychology is understanding how humans, endowed with a moral psychology evolved to function within small, relatively homogeneous groups, were able to develop systems of cooperation and effective social exchanges that allowed for the development of large, complex societies, comprising large numbers of not only non-kin, but strangers. There is a robust literature that argues religion played a significant role in this process (Atran and

Henrich, 2010; Henrich, 2009; Henrich et al., 2010; Johnson and Bering, 2006; Johnson and Kruger, 2004; Lahti, 2009; Norenzayan, 2013). In general, this account views religion as ‘an adaptive complex of traits incorporating cognitive, neurological, affective, behavioral, and developmental elements ... that supports extensive human cooperation and coordination’ (Sosis, 2016: 221). We have explained how it was that humans came to have minds capable of conceiving gods. What we need to understand now is how the human mind constructs god-beliefs that are able to serve as a valuable social resource.

As noted, a key move in responding to the presence of an agent is to determine, or ascribe, the mental states of that agent: what might it want? How might it behave? What responses might be most effective in dealing with this particular agent? In other words, how do humans conceive of the minds of gods? To this task humans bring the same strategy employed in interpreting underdetermined stimuli: apply the model that brings the greatest inferential richness, namely, the model of the human mind (Atran, 2002; Boyer, 2001; Purzycki and Sosis, 2011; Purzycki et al., 2012). While the minds of gods are modeled on human minds, there are some notable distinctions. For example, Pascal Boyer (2001: 155) states that while we conceive of humans as ‘limited-access strategic agents’ (i.e. they have imperfect access to the minds of others), gods are often conceived as ‘full-access strategic agents’. It is important to note that ‘full-access’ is not the same thing as omniscience, which is a later theological concept. Gods across numerous cultures are often presented as having limited knowledge in a variety of domains (Purzycki, 2011). However, there is one domain in which gods often are portrayed as having supernatural cognitive powers: gods often have special access to information relevant to social exchanges – that is, the motivations, desires, etc. of humans (Purzycki et al., 2012).

This is not surprising, given the vital role that negotiating social relationships plays in

the pursuit of inclusive fitness for humans. Determining who can be trusted and who cannot, who is contributing (or not) to the common good, how to encourage cooperation and discourage antisocial behavior, how to repair damaged relationships, etc., are regular, and fitness-relevant challenges that have faced humans and other animals throughout evolutionary history. Indeed, it has been argued that the need to manage the cognitive challenges of negotiating a complex social environment was a driving force in the expansion of the human brain (Dávid-Barrett and Dunbar, 2013; Dunbar, 2009). As these tasks constitute a major function of our mental activity, it is natural to conceive of gods as having comparable concerns – beings with special access to socially strategic information are particularly well-suited to assume a role in the development of human social organization.

A socially shared belief in gods who are concerned with social exchanges makes those beings morally relevant to society. This is not to suggest that they are necessarily conceived of as morally concerned beings who care about the ethical behavior of humans – most gods throughout history decidedly did not care (Baumard and Boyer, 2013). However, these gods were still relevant to the moral behavior of the societies that believed in them (Teahan, 2016). While gods may not have been concerned with the moral doings of humans, as social agents they did have expectations about how humans were to act toward them. Gods were widely seen to expect, for example, sacrifices, burnt offerings, that humans avoid certain sacred areas or treat those areas with specific behaviors, etc. In other words, gods were concerned with ritual behavior, and it was an intuitive inference, given the model of social exchange that defined the minds of gods, that if gods were disappointed or offended they would respond as other agents would – with anger and possibly violence (they could, of course, also respond with favors if they were pleased). If, as was often the case, that anger

was directed at the group as a whole, and not solely at individual actors, then the correct performance of ritual behavior became a concern of the entire group. Participation in collective rituals and the proper performance of rituals then become targets of moral evaluation by other group members – the gods become morally relevant to the group (Teehan, 2016).

In the evolutionary study of religion, religious ‘behaviors, badges, and bans’ (Sosis, 2006) (and eventually beliefs) are seen as signals of commitment (Irons, 2001): they are means of communicating – not to the gods, but to other members of the group – that one is invested in the group and committed to its social code. This helps to explain the seemingly irrational and idiosyncratic, not to mention at times painful, nature of religious rituals. The costlier the ritual, the more reliable is the signal. In fact, studies show that extreme rituals not only promote prosociality, they can even lead to identity fusion, in which the individual sees their own identity as integrated into the group identity (Swann et al., 2012; Whitehouse, 2018; Xygalatas et al., 2013). Religious rituals function to bind the group into a moral community and promote extensive prosociality, equipping such groups to better meet the needs of resource acquisition and self-defense – religion, then, becomes a culturally adaptive system (Purzycki et al., 2014).

While much of the literature on religion and signal theory focuses on costly or extreme rituals, it is also the case that even minimal signaling can promote in-group solidarity and contribute to the extension of prosociality (Shaver and Bulbulia, 2016; Teehan, 2016; Teehan and Shults, 2019). Participating in a collective ritual, wearing distinctive garb, performing simple religious actions can all serve as signals of in-group membership, even when not costly. Totemism and magic, common practices that may be deemed religious, also were well suited to play this role (Palmer et al.,

2008, 2010). Research on empathy indicates that the brain’s empathy systems are sensitively attuned to signals of in-group membership, and such signals trigger a wide range of prosocial behaviors and attitudes (Avenanti et al., 2010; Hein, et al., 2010; Phelps et al., 2000; Van Bavel et al., 2008; Xu et al., 2009).

Religion can assume a role in the evolution of cooperation, as gods that do care about the moral code of the group certainly appear in the historical record, and such gods can be valuable moral resources for a group. As evolutionary accounts of morality attest, the detection and punishment of cheaters and defectors is key to promoting cooperation (Boyd et al., 2003; Fehr and Gächter, 2002; Price et al., 2002; Vanneste et al., 2007). In the small groups characteristic of our hunter-gatherer ancestors, our evolved psychology functioned effectively to address such challenges. However, as groups became larger, and group membership more anonymous, the complexity of these tasks became cognitively untenable. Cheating and defecting then became less costly, and so cooperation became more costly, undermining the coherence of the group.

Shared belief in a morally concerned god, one conceived to have supernatural access to socially strategic information, helps to address this challenge. The supernatural punishment hypothesis posits that individuals effectively off-load the task of keeping track of cheaters and defectors to their gods, whose ability and reliability in terms of meting out punishment change social calculations and promote prosociality (Atkinson and Bourrat, 2011; Bering and Johnson, 2005; Bering and Shackelford, 2004; Johnson, 2005; Johnson and Bering, 2006; Johnson and Kruger, 2004; McKay et al., 2011; Shariff and Norenzayan, 2007). Early versions of this hypothesis stressed the importance of ‘high gods’, creator gods who are concerned with moral transgressions (Norenzayan, 2013; Shariff and Norenzayan, 2011). However, more recent cross-cultural evidence indicates that

small gods (who are not creator gods and are mainly concerned with ritual misdemeanors) also have a positive effect on prosocial behavior (Watts et al., 2015).

Another proposed means by which religion functioned to strengthen the moral bonds of the group is the practice of ancestor worship. In honoring the ways and values of a set of shared ancestors, the community effectively became an extended kin group. This reinforced the moral code of the group and tapped into the evolved mechanisms for kin altruism (Coe and Palmer, 2008; Coe et al., 2010; Steadman and Palmer, 1994). Belief in the post-mortem influence of ancestors in the life of the group is an ancient and widespread phenomenon (Steadman et al., 1996), adding further support for the thesis that religion played a vital role in human cultural evolution.

The advantages of group living drove the evolution of social mammals. Selection pressures on the hominin line led to increasing brain size, with increased capacity for dealing with social complexity, ecological novelty and diversity, and eventually to the appearance of *Homo sapiens*. The adaptive value of large, cooperative groups served as a selection pressure for cultural systems that allowed for the extension of evolved mechanisms that facilitate prosociality. Religion is one of those complex adaptive systems. It is not the only cultural practice that may have served this role (Baumard et al., 2015; Henrich et al., 2010), but given its antiquity and ubiquity, it is one of the most important. The argument set out here is that religions, as cultural systems, were able to play this role, and at such an early stage of human cultural history, because they are built on beliefs, emotions, and behaviors that arose from the natural functioning of evolved psychological mechanisms that have their origins in the earliest stages of the human evolutionary story. We may find evidence for this evolved 'religious' psychology by looking at what some of our early ancestors left behind.

ARCHAEOLOGICAL EVIDENCE FOR THE ANTIQUITY OF RELIGIOUS BEHAVIOR/COGNITION

In exploring the evolutionary origins of the cognitive building blocks of religion, we noted that there is no natural starting point for this process. We claimed that these god-generating mechanisms were almost certainly in place by the Upper Paleolithic, given the appearance of artefacts and other evidence from this period which are plausibly interpreted as serving a religious function. The archaeological record provides evidence for the antiquity of religious cognition and supports the thesis that religion (e.g., rituals) has been particularly well positioned to play a significant role in human evolutionary history.

Evidence for Ritual

Archaeological evidence for religious behavior and cognition may afford means for empirically testing hypotheses about the evolutionary origins of religious beliefs and practices. The earliest archaeological evidence for behavior that might be interpreted as religious is for ritual. The cave of Wonderwerk, Canteen Kopje (South Africa) has well-preserved layers of Early Stone Age (ESA, 3.3 million years BP–300,000 BP) and Middle Stone Age (MSA, 320,000–30,000 BP) hominin occupation. There is no evidence for accumulated ochre in the ESA layers of this cave, but starting about 300,000 BP, there are abundant concentrations of red ochre deep in the cave (Watts et al., 2016). Similar concentrations of pigments, including yellow, blue, and even sparkling purple, have been found in Central African sites such as Twin Rivers, Zambia, at around 266,000 BP (Barham, 2002). Evidence of pigments that were transported over large distances was also uncovered in eastern Africa, at Olorgesailie Basin, southern Kenya, dated 320,000–305,000 BP (Brooks et al., 2018).

In South Africa, from about 170,000 BP, we can see the concentration of red ochre in virtually every rock shelter – rock shelters were used as home bases by prehistoric hunter-gatherers (Watts et al., 2016).

In contemporary hunter-gatherer cultures, ochre and other pigments are mostly used in ritual contexts, in which they are employed to color the skin. These pigments emphasize visual similarity of the participants, which is further enhanced by synchronous movements such as dance. Synchronous action enhances within-group cooperation and has a positive effect on pain tolerance (Reddish et al., 2013). The prehistoric ochre chunks have marks of rubbing and scraping, suggesting that pigment coloration may have been used during this period. Ochre also has non-ritual usage, such as being part of mastic in composite weapons (for example, to glue the stone tip and the shaft of an arrow together). However, high concentrations of ochre cannot easily be explained by purely utilitarian use. For one thing, hominins in South Africa hafted stone tips on spears about 500,000 BP, but this was not associated with significant concentrations of ochre (Wilkins et al., 2012). Moreover, the pigment-rich cores that are found in rock shelters across South Africa yield many different colors (see above), and it is hard to see why people would want their glues to have different colors.

Archaeologists have formulated hypotheses to explain this increased use of ochre for body decoration. For example, Knight and colleagues (1995) associate the use of red ochre with rituals performed by women, surrounding fertility and the menstrual cycle: women simultaneously faking their menstruation would thereby maximize attention of potential mates (as menstruation is a sign of imminent fertility) while also maximizing long-term investment in them and their offspring. Kuhn (2014), by contrast, sees body decoration as a cheap but honest signal of collaborative intent. Kuhn speculates that the earliest rituals were not high-stakes costly rituals, but relatively cheap: they were used

by people whose interests were already well-aligned to signal cooperative intent. This is consistent with recent work (see above) that suggests that even minimal signaling can have a positive impact on prosocial behavior (Shaver and Bulbulia, 2016; Teehan and Shults, 2019).

Archaeological evidence indicates that costly rituals – indicated first by beads and then sculptures, cave paintings, and other forms of art – only emerged later in the Pleistocene, as we will see below. Thus, archaeological evidence suggests a gradual shift from the earliest rituals as cheap signaling to more costly expressions of religiosity over time.

Along with ochre, beads can be used as a form of body decoration, likely for a variety of purposes, including rituals and signaling group membership. The earliest beads appeared during the MSA and consisted of perforated shells of marine mollusks, sea snails, and bivalves. They were found in Israel (Skhul) and Algeria (Oued Djebbana), dated to about 135,000–100,000 BP (Vanhaeren et al., 2006) and a bit later in Ifri n’Ammar, Morocco (83,000 BP) and Blombos Cave, South Africa, around 75,000 BP (d’Errico et al., 2009). Shells need to be transported from the beach; if found significantly far away from the coast, they either need to be carried in person or exchanged between neighboring groups. For example, bivalves found in a grave in Qafzeh, Israel (ca. 92,000 BP) were transported approximately 22 miles from the coast. They did not require much work to fashion as they were naturally perforated. They were strung and covered in ochre (Bar-Yosef Mayer et al., 2009). If these shell beads were used in ritual context, wearing them aligns with the cheap signaling hypothesis. Body decoration becomes more expensive over time, for example, basket-shaped mammoth ivory beads commonly found at Aurignacian (c. 41,000–30,000 BP) European sites required at least one hour, and perhaps up to three hours, to carve, by an experienced artisan (White, 1993).

Mortuary Practices

Grief among non-human animals is common, with ample examples of birds and mammals showing caring behavior toward dead conspecifics. The interpretation of these behaviors as expressions of grief is somewhat contentious as one cannot know whether they experience a sense of loss, but given that nudging and carrying around of dead bodies occurs mainly in social animals, the idea that adaptations for attachment and affiliation would lead these animals to experience grief at the death of a close, possibly related conspecific is plausible. However, mourning – the purposeful burial of group members and associated rituals – is uniquely human. It is also fairly recent. There is no solid evidence for burials before 120,000 BP, but even after that date, burials are few and far between. For example, the Sima de los Huesos hominins (*Homo heidelbergensis*) lived around 500,000 BP in Atapuerca, in northern Spain. Their fossils are well preserved (so exceptionally in fact that ancient DNA could be extracted from them), but archaeologists agree that their preservation is the result of an accidental, rather than purposeful, burial (De Castro et al., 2004). For the period of 92,000 to 50,000 BP, there are only 58 burials; of those, 35 appear to be Neanderthals (but not all archaeologists accept Neanderthal burials, see, e.g., Gargett, 1999 for an overview). Burials become more common in *Homo sapiens*, gradually at 120,000 BP and even more so around 28,000 BP. Group burials with dozens, or even hundreds of individuals appear at the end of the Ice Ages, after 12,000 BP, such as in Lepenski Vir in Serbia (Hovers and Belfer-Cohen, 2013).

Stiner (2017) notes several interesting observations about burials before 28,000 BP: most Pleistocene *Homo neanderthalensis* and *Homo sapiens* who were purposefully buried were adults; given that child mortality was very high, this suggests not everyone was buried, although taphonomic processes can also play a role here. (Due to their size

and composition, the bones of young children do not fossilize as readily as those of adults.) There was also a skew toward adult males, with about two thirds of buried individuals identified as male. These sex and age skews might indicate that burying the dead had a symbolic meaning and was not merely done out of hygienic considerations (getting rid of unsightly and smelly bodies). However, selective burials do not necessarily point toward religious beliefs. Perhaps burial by Neanderthals and *Homo sapiens* merely expressed social significance or respect for the dead.

The presence of grave goods makes the inference to religion more straightforward, as it makes sense to offer gifts if one thinks the deceased could make use of them. It makes less sense as a mere commemorative act, as these goods are lost to the organizers of the burial, though the loss of the goods may be a form of costly signaling. But note that costly signaling does not in itself exclude a religious interpretation. One coherent explanation is that *Homo sapiens* and *Homo neanderthalensis* who offered grave gifts had a ToM similar to ours, which generates spontaneous inferences about other's mental states. Upon the death of a person, these inferences continue, and this may have given rise to afterlife beliefs (see De Cruz and De Smedt, 2017 for an overview).

As we have seen, an early *Homo sapiens* burial in Qafzeh, Israel (around 92,000 BP) has grave gifts, including ochre and perforated bivalves. The distance to the coast and the lack of other marine resources in this site (e.g., fish bones) make it likely that these shells were obtained through exchange with neighboring groups (Bar-Yosef Mayer et al., 2009), indicating some social function of the bivalves, such as signaling that the deceased is still a member of the social group. A later burial with grave gifts is the triple burial from Sungir, Russia (about 34,000 BP), with one male adult and two adolescents of unclear sex (Sikora et al., 2017). Their bodies are covered in ochre and dressed in parkas covered with

thousands of mammoth ivory beads, buried alongside spears and bracelets. These objects were made of rare, difficult to obtain materials and required extensive work to produce – as we have seen earlier, mammoth ivory beads take up to three hours each to carve, burying them is thus an intriguing and telling act, plausibly pointing to belief in an afterlife.

Symbolic Representations and Music

The earliest evidence for symbolic art and music appears relatively late in the archaeological record, in the form of sculptures, cave paintings, and musical instruments. There has been a long tradition to interpret cave art religiously, particularly in the 19th and the first half of the 20th century, when cave paintings in France and the Iberian Peninsula were interpreted as hunting magic or totemistic signs (de Beaune, 1998). This interest in cave art can be situated in a wider intellectual climate where turn-of-the-previous-century anthropologists and archaeologists became increasingly aware of the religious beliefs and practices of non-Western, small-scale societies, for example, the Australian aborigines and their use of art in representing the Dreaming (e.g., Tylor, 1871). The end of the 20th century brought a revival of the use of anthropological parallels of small-scale societies to interpret cave art. Notably, Lewis-Williams (2002) uses evidence from historical southern African societies (the San), for example, their shamanic rituals and the representations they made of these, and draws parallels with visual representations in Paleolithic caves. According to Lewis-Williams, European Paleolithic caves such as Chauvet, Lascaux, and Altamira show visual representations of the successive stages of hallucination. Shamans, cross-culturally, use hallucinogens to elicit visions, which they interpret and communicate to other members of the group. The earliest stages of hallucination are characterized by seeing zigzags,

lattices, dots, and other elementary geometric shapes (so-called entoptic signs), which are often depicted on cave walls. During later stages of altered states of consciousness shamans experience more vivid visual and auditory hallucinations, morphing into complex scenes. This interpretation has given rise to a debate on whether prehistoric imagery could be interpreted in other ways, for example, Dronfield (1996) has provided cross-cultural evidence to show that not all entoptic signs are produced in ritual shamanic contexts.

More direct evidence for religion is the depiction of human-animal hybrids. For example, the southwestern German Aurignacian has yielded two mammoth ivory figurines that look like a human-lion hybrid. The larger one (about 31 cm in height) comes from the Hohlenstein Stadel cave and is dated to 41,000 BP (Kind et al., 2014); the smaller one (only about 2.5 cm in height) comes from Hohle Fels, is less detailed but has a similar, rigid, upright pose and ear shape, with arms held stiffly to the side (Conard, 2003). There are a few later representations of human-animal hybrids, mostly dating to the Magdalenian or more recent (i.e., 17,000 BP or later), including a painting of a figure with a bison head and human body playing a musical bow from Grotte des Trois Frères, France (de Beaune, 1998). A cladistic analysis of hunter-gatherer religious beliefs has found that hunter-gatherers historically did not espouse beliefs in high gods (Peoples et al., 2016), so with that in mind it is unlikely the lion man and other early religious representations depicted high gods. However, it is difficult to further pin down what the function of these figurines might have been.

Intriguingly, the oldest musical instruments date from the same period as the earliest visual religious representations. These Aurignacian flutes, made from mammoth ivory and griffon bone (Conard et al., 2009) may have been used in religious rituals.

In summary, then, the evidence for religious rituals and beliefs emerges gradually

in the archaeological record. The earliest evidence is for cheap signaling, presumably during rituals, using ochre as a form of body decoration in various African MSA sites. Burials appear much later, at around 92,000 BP, and first are selective (e.g., mostly male adults), with few, if any, grave goods, and later, starting 28,000 BP, become more common, sometimes with lavish grave gifts. The first visual representations of supernatural beings appear around 41,000 BP, alongside the earliest musical instruments. Together, this shows a gradual evolution of religious beliefs and practices, with costly, more time-consuming religious practices only appearing late in prehistory.

IMPLICATIONS FOR PHILOSOPHY OF RELIGION

While the contemporary evolutionary psychology of religion may be a ‘new’ approach, it has attained sufficient theoretical development and empirical support to make in-roads into the larger field of religious studies. Religious studies is a multi-disciplinary field and so there are numerous ways that the evolutionary approach may impact it. This final section will look at one particular sub-field where this approach is gaining attention and generating controversy, namely the philosophy of religion.

Broad-Brush Approaches

While many philosophers of religion might not be concerned with, or be aware of, CSR and other evolutionary approaches to religion, there is an increasing willingness to engage with this material (see, for example, the papers collected in De Cruz and Nichols, 2016). This fits within a broader, emerging approach in philosophy to consider empirical evidence, either gathered specifically for the purpose of testing philosophical claims

(experimental philosophy), or, indirectly, by considering empirical work that might be relevant for one’s philosophical claims (empirically informed philosophy). Knobe (2015) notices that this tendency is robust across different philosophical traditions: while 62% of a sample of highly-cited philosophy papers up to the late 1990s used only a priori methods (armchair reasoning, thought experiments), only 12% of papers from the late 1990s to the mid-2010s purely relied on such methods – the vast majority at least mentioned some empirical evidence to support philosophical claims. Philosophy of religion might be relatively late in this trend (compared to, say, philosophy of mind), but it is certainly not immune to it. As a result, an increasing body of work in philosophy of religion engages with evolutionary approaches to religion.

One of the main questions of empirically informed philosophy of religion is whether the study of the evolutionary origins of religious beliefs has any implications for their epistemic status – that is, does knowing about the evolutionary origins of religious beliefs and practices cast a negative or positive light on their justification? Some authors (e.g., Kahane, 2011; Wilkins and Griffiths 2013) have approached this question in an abstract way, wondering whether the fact that religious beliefs and practices have an evolutionary origin casts any doubts on their justification without going into the specifics of any religious beliefs. For example, Kahane (2011) constructs a general recipe for evolutionary debunking arguments along the following lines:

Causal Premise: S’s belief that p is explained by evolution through natural/sexual selection.

Epistemic Premise: Evolution is an off-track process (i.e., evolution is not a truth-tracking process).

Conclusion: Therefore, S’s belief that p is unjustified.

For example, if it can be argued that religious belief, such as belief in gods, can be explained

as resulting from evolutionary processes, then such beliefs would be unjustified.

Other authors have questioned whether we can paint with such broad brushstrokes. In particular, *companions in guilt arguments* (e.g., Das, 2016; Rowland, 2016) aim to show that if we debunk beliefs in a given domain (often religion or morality), then, using an analogous form of reasoning, we would also need to be skeptical about beliefs in domains we would rather not be skeptical about: for example, if we dismiss religious beliefs as unreliable because they arise as by-products of certain cognitive adaptations, then scientific beliefs that have arisen in a similar way would likewise have to be rejected. Wilkins and Griffiths (2013) try to avoid this global, undesirable skepticism by building a so-called ‘Milvian bridge’ that would connect an evolved propensity to form beliefs in a given domain with its truth value. They propose that such a bridge can be constructed between the cognitive capacities that give rise to commonsense and scientific beliefs, but not between similar cognitive capacities that give rise to religious and moral beliefs. However, Wilkins and Griffiths rely on controversial claims about the unreliability of agency detection. As we have seen, religious beliefs, such as god beliefs, are the result of complex interactions between evolved cognitive capacities (e.g., agency detection) and specific cultural settings (e.g., societies in which god-beliefs function as social controls). It is difficult to make principled claims about the justification or warrant of religion, in general, or about god-beliefs, in particular, without undermining a host of other beliefs. In this case, a debunker would risk undermining any belief that relates to agency detection, which is not restricted to the formation of religious beliefs, but which we use in a wide variety of everyday circumstances. General arguments that aim to debunk religious beliefs based on their evolved origins run into a problem: they have a difficult time insulating certain other beliefs from their general debunking strategy, notably the

scientific beliefs on which the debunking is based. Hence, we need to look at specific CSR claims and specific religious claims and evaluate the plausibility of the latter in the light of the former.

Evaluating Specific Philosophical Claims Using Specific CSR Theories and Findings

Once we get into specifics, the discussion becomes messier, but also more interesting. In order to have fruitful discussions on science and religion, we need to move away from broad and indistinct categories such as ‘science’ and ‘religion’, instead focusing on how specific scientific claims impact specific theological positions (Perry and Ritchie, 2018). So, for example, rather than focus on whether science makes religious claims untenable, we can consider what quantum mechanics has to say about action and causation and then consider how divine action might be conceived within these scientific parameters (e.g., Murphy, 2009). The more specific scientific and religious claims are, the more productive such an engagement might be. One can evaluate a religious claim in terms of various epistemic values, including parsimony, fruitfulness, and empirical adequacy. This approach can be used both by people who are part of the religious tradition they want to reflect upon and by outsiders. This science-engaged theological approach has an important methodological advantage: since CSR authors disagree about the relative importance of specific cognitive biases in generating religious beliefs, and about whether religion is produced by adaptation or as a byproduct of other adaptations, considering the philosophical implications of CSR as a whole is too daunting a task. It is not necessary to consider the implications of CSR for religion as a whole (which is pluralistic and diverse), rather, one can consider a particular CSR theory, and investigate how this impacts a particular religious claim

(see, for example, De Smedt and De Cruz, 2020, for several case studies).

To give an example, Clark and Barrett (2010) have argued that CSR provides support for the *sensus divinitatis* as posited in Reformed epistemology. According to Reformed epistemologists, humans are endowed with a *sensus divinitatis*, an untutored sense of the divine, which generates religious beliefs under a wide range of conditions. Plantinga (2000) takes this Reformed starting point to argue for a range of philosophically substantial points. In particular, he outlines an externalist epistemology where beliefs can have warrant if they are the outputs of reliable cognitive processes that operate in a proper environment: if people have a *sensus divinitatis* and it operates under the right environmental conditions, then, according to Plantinga, they can have warranted religious (including and especially Christian) beliefs without having to formulate any arguments in favor of these beliefs. Clark and Barrett take the presence of agency detection, ToM, and existential theory of mind (E-ToM, basically, the quest for meaning and teleology in life events) as forming the *sensus divinitatis*. However, to evaluate this idea, we need to not only consider how CSR agrees with Reformed epistemology, but we also need to investigate points of divergence between them. Like CSR, Reformed epistemology offers an explanation for why belief in a monotheistic god is not universal. CSR proposes that people are prone to believe in a wide range of supernatural beings; it views belief in a monotheistic god as the product of exceptional cultural factors, including literacy and living in a large-scale society. Reformed epistemology, by contrast, posits the noetic effects of sin (Plantinga, 2000): due to the Fall, the *sensus divinitatis*, as well as other cognitive capacities, is marred in such a way that it no longer produces correct outputs. Such corrupted outputs include belief in theologically incorrect religious beings (at least according to Christianity, such as impersonal religious principles

and polytheistic pantheons) or lack of religious belief (atheism). However, the danger of this strategy is that it undermines the positive claims of Reformed epistemology, namely that we can have warranted religious beliefs without marshalling any arguments or evidence in their favor (Teehan, 2014). Moreover, there is no scientific support for an actual historical Fall with large cognitive consequences, as posited by Reformed epistemologists (De Cruz and De Smedt, 2013). This does not mean that the claims of Reformed epistemology are unsalvageable, but rather that, in order to be properly empirically informed, concepts such as the noetic effects of sin and the *sensus divinitatis* will have to be carefully spelled out in scientific terms that CSR can help evaluate. Such empirically grounded theological concepts can then be gauged in terms of their internal coherence and fruitfulness.

Broadening the Scope of Philosophy of Religion

The evaluation of specific theological positions using specific CSR hypotheses has several advantages: it gets us out of an unproductive broad-brush discussion of science versus religion that quickly becomes mired in generalities, and it provides a genuinely new way to engage with theological claims. CSR can also provide avenues to consider religious views that have not received much attention in the philosophical literature. Philosophy of religion, as practiced in Western philosophy departments, has been narrowly focused on Christianity or a kind of thin Anselmian omnitheism, where God is an abstract omniscient, omnipotent, and omnibenevolent entity (De Cruz, 2020; Schilbrack, 2014). When the claims go beyond Anselmian omnitheism, such as Plantinga's Reformed epistemology, they almost exclusively derive from Christianity. Because CSR is not focused on Christian religious views, it can help philosophers

escape this parochialism and thus help them consider other religious traditions.

The connection between teleology and religious beliefs and practices can provide a concrete example of how CSR can help expand philosophical investigations. As we have seen, CSR authors such as Kelemen (e.g., 1999b, 2004) have noted that people have an intuitive tendency to see teleology in the natural world for example, young children tend to assume that clouds are for raining, and they prefer this explanation to alternative mechanistic accounts, such as that clouds are formed by evaporated water. Kelemen (2004) argues that this evidence shows that young children are intuitive theists, as their preference for teleological explanations for natural phenomena goes together with an increased tendency to see God as the creator of natural objects. CSR evidence also suggests that Western education can diminish teleological reasoning – for example, Romani adults who were not regularly enrolled in school reason more teleologically than Romani adults who were (Casler and Kelemen, 2008), and PhD holders in sciences or humanities reason less teleologically than people who have only a bachelor's degree (Kelemen et al., 2013). On the face of it, these studies seem to support the idea that theism and teleology are connected, and that scientific education lessens this connection. But cross-cultural research on teleology and CSR suggests a different, more nuanced picture. Teleological thinking persists in low-religiosity populations, such as in China (Rottman et al., 2017), and also correlates positively with non-theistic religious practices. Chinese participants who self-identify as atheists but who engage in practices such as ancestor worship and *feng shui* show increased teleological thinking compared to compatriots who do not engage in these practices, and endorse claims that natural objects such as mountains and maple leaves were made by a being (Järnefelt et al., 2019). American PhD holders with Gaia beliefs (the belief that the Earth is a purposeful agent who self-regulates) also have

a greater tendency to reason teleologically (Kelemen et al., 2013). Moreover, the idea that Western education is needed to 'correct' mistaken teleological beliefs has recently been challenged by Ojalehto and colleagues (2013), who argue that teleological reasoning can be useful for indigenous communities to make sense of ecological relationships. For example, 'trees grow for birds to build their nests in' may reflect an awareness of an ecosystem, appealing to a relationship between birds and trees, where birds nest in trees, protect them by eating harmful insects, and help them reproduce by dispersing their seeds (e.g., by caching seeds and forgetting about their location). By focusing on cognitive tendencies across cultures and how they relate to local religious beliefs, we can obtain a more nuanced picture of teleology as not only figuring in design arguments for God, but as a broader cognitive tendency that correlates with a wider range of religious beings and that is ecologically relevant.

CONCLUSION

The 'new' evolutionary study of religion has in its short history provided a distinct paradigm for an empirical, naturalistic approach to religion. It has already produced an impressive body of research, and has opened up fertile paths for future research that will allow the field to develop, refine, and – more importantly – correct and revise the model of religion presented here. There are a growing number of specialized journals devoted to the field, and a number of graduate programs and specializations that will continue to train the scholars who will move the field forward. It has already become a major player in the professional field of religious studies – a field, thus far, dominated by cultural theorists.

At the end of *The origin*, Darwin (1859: 488) predicted: 'In the distant future I see open fields for far more important researches.

Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation'. While he, himself, made an early contribution to this project in his 1871 book, *Descent of man* (in which he speculated on the natural history of religion), evolutionary psychology is the coming-to-fruit of that prediction, and the contemporary evolutionary study of religion, grounded in evolutionary psychology, is further evidence of the perspicacity of Darwin's vision.

Notes

- 1 There is a debate within CSR about the status of religious beliefs as by-products (Atran and Norenzayan, 2004; Boyer, 2001; Guthrie, 1993) versus adaptations (Bulbulia, 2004; Johnson, 2005; Johnson and Kruger, 2004; Sosis, 2006). The details of this debate are not salient to this discussion; a compelling case has been made that even if religious beliefs originated as by-products, as part of religion as a complex adaptive system, they came to assume an adaptive role (Crespi and Summers, 2014; Sosis, 2016).
- 2 Turner et al. (2018) provides one of the most complete evolutionary accounts to date.
- 3 'Device' is the term given to such evolved cognitive mechanisms in the literature. Its use here does not commit us to cognitive modularity.
- 4 It is important to be clear on what is being claimed about these mechanisms. It is not asserted that any individual comes to believe in gods because of these evolved psychological mechanisms, rather, the claim is these mechanisms made it possible for the notion of gods to be conceived by humans at some point in our evolutionary history. Once it is possible for humans to conceive of such beings and communicate these ideas, they become potential social resources.
- 5 BP stands for 'before present'. To avoid the problem of an ever-shifting present, it is conventionally put at 1950, but for the timescales involved, this does not matter.

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Evolution and History

Laura Betzig

In one of the last paragraphs of his book *On the Origin of Species*, Darwin closed with this prophecy: 'Much light will be thrown on the origin of man and his history'. He liked having thought of that so well that he said it again, in the first paragraph of his book on *The Descent of Man*. 'Much light will be thrown on the origin of man and his history' (Darwin 1859: 488; 1871: 1).

Like every other species on earth, *Homo sapiens* evolved to reproduce. Almost every aspect of our behavior is shaped by adaptations that helped our ancestors get genes into the next generation. Over the past few decades, Darwin's theory has thrown light on biology and anthropology, on psychology and the arts. And it's started to inform how we study the human past.

Much of that work has been done by historical demographers. They've looked at the *Peditura Lusitana*, a 15th- and 16th-century genealogy of the Portuguese nobility; they've looked at the *Ortssippenbücher*, or clan records, collected for over three centuries in

early modern Germany; they've looked at the Demographic Database from 18th- and 19th-century Sweden; they've looked at 15 generations of parish registers from rural Finland. And they've found Darwinian answers to questions about, among other things, marriage and fertility, childcare and inheritance strategies, disease and longevity, migration and mortality.

Other work has incorporated different sorts of historical sources. Architecture and artefacts, laws and administrative documents, personal letters and annals, anatomic and genetic evidence have all been used to test Darwinian hypotheses on comparative history. Light has been thrown on, among other things, political and scientific revolutions, the oppression of women and children, the rise and fall of empires, and the rise and fall of the Church.

HISTORICAL DEMOGRAPHY

Demographic historians have culled census data from Roman tomb inscriptions and

Carolingian polyptyques, from genealogies and pedigrees, from wills and estate surveys, from tax records and parish registers, in order to reconstruct how populations reproduced in the past. All have used quantitative methods, and a few have used evolutionary theories. They've studied child births and child survival in 18th-century Lancashire (Hughes, 1986, 1988) and in 18th- to 20th-century Norway (Røskft et al., 1992); polygynous marriage in 19th-century Utah (Josephson, 1993); migration in 19th- and 20th-century Ireland (Strassmann and Clarke, 1998); lethal conflicts in 9th- to 11th-century Vikings (Dunbar et al., 1995; Palmstierna et al., 2017) and the English nobility (Johnson and Johnson 1991); and patterns in the demographic transition (Borgerhoff Mulder, 1998; Sear, 2015; Sear et al., 2016; Burger, Lee and Sear, 2020).

Some of those databases have been analyzed for years. They include the pedigrees of medieval Iberian nobles; clan registers on early modern German laborers and farmers; records on early modern Swedish landowners and business owners; and parish registers on early modern Finnish fishermen and farmers. Those studies have offered insights into the effects of status on marriage, fertility, and mortality; the importance of grandparents; primogeniture bias; and differential investment in daughters versus sons.

THE PEDITURA LUSITANA

The archaeologist Jim Boone worked on excavations in Morocco at Qsar es-Seghi, a small castle in the Strait of Gibraltar captured by Portuguese forces in 1458. Then in Lisbon, he looked into the *Peditura Lusitana*, an 11-volume, 17th-century manuscript that holds the carefully compiled genealogies of hundreds of Portuguese noble families. Data on over 3,700 people from the *alta nobreza*, or high nobility, were collected, and descendants of the 25 highest houses, or *linhagens*,

born between 1380 and 1580, were sorted into four status groups.

The first class was made up of the royal family, and lineages of dukes, counts, marquises, viscounts, and barons. The second class included the royal bureaucracy, holders of mostly hereditary offices. Third was the *senhorial* class, a cadet aristocracy with hereditary titles to their estates. The fourth class included the descendants of men with no known title. Some were *cavaleiros*, or knights, who often campaigned abroad; others were supported by the houses of greater nobles. If they survived foreign wars, they could be granted a career pension in the form of a stipend or lands, and that could be passed on to their children.

Boone found a linear relationship between social status and reproductive success. Men in the first class (holders of primary titles) reported more children than men in the second class (the royal bureaucracy), who reported more children than men in the third class (*senhorial*), who reported more children than fourth-class men (military or untitled).

He found another strong relationship between social status and son bias. Holders of primary titles (the first class) were most likely to send their daughters off to nunneries; military or untitled men (in the fourth class) were least likely to do that. The opposite was true of their brothers. Sons of men in the fourth class (military or untitled) were most likely to get sent away to die in a war; and sons of men in the first class (with primary titles) were least often sent off.

Boone found another linear relationship between birth order and marital status. Firstborn men and women married more often than second children, who married more often than third children, who married more often than fourth or laterborn children.

And he found evidence of parents' bias in favor of their firstborn daughters and sons. Oldest sons were less likely than other sons to die in a war in Morocco, and they were much less likely to die far away in an Indian

war. Oldest daughters were less likely to become nuns (Boone, 1983, 1986, 1988).

The evolutionary advantage of biased investment in sons or daughters was worked out by the biologist Robert Trivers, with help from Dan Willard, his mathematician friend. Successful sons, in most species, outreproduce successful daughters, but unsuccessful daughters outreproduce unsuccessful sons. So parents in poorer condition should bias their investment towards daughters, but parents in better condition should bias their investment towards sons (Fisher, 1958; Hamilton, 1967; Trivers and Willard, 1973; see too Dickemann, 1979a, 1979b and Hartung, 1976, 1982).

The evolutionary advantages of primogeniture were worked out at around the same time. Other things being equal, older children should be bigger and stronger, more immunocompetent and more experienced; they should do better in competition with members of other species, and with conspecifics, including their younger siblings. They should be able to help their parents, as foragers or caregivers, sooner; and their waiting time to direct reproduction should be shorter. Their reproductive value should be higher (Hamilton, 1964, 1972; Trivers 1972, 1974; see discussions in Daly and Wilson, 1980, 1988 and Hrdy and Judge, 1993).

THE ORTSSIPPENBÜCHER

The anthropologist Eckart Voland studies the demography of the Krummhörn population, a group of farmers and landless laborers from north of the River Ems. His database, the *Ortssippenbücher*, or local clan registers, reconstructed from 18th and 19th-century tax lists and parish records, includes vital and social data on 120,852 individuals from 34,708 families in 33 contiguous parishes. Voland's collaborators have included economists, epidemiologists, geneticists, psychologists, and zoologists. They've worked on this

database for over 30 years. And they've looked at, among other things, sex ratios, mate choice, child mortality and grand-mother effects.

Most women have their last baby in their 30s or 40s, but they often live on into their 70s or 80s. It isn't obvious why. The evolutionary biologist, George Williams, suggested that mothers might do better to care for the children they've already born, rather than risk bearing new ones. 'A termination of increasingly hazardous pregnancies would enable her to devote her whole remaining energy to the care of her living children, and would remove childbirth mortality as a possible cause for failure to raise these children' (Williams, 1957: 407). The biologist, William Hamilton, added that post-reproductive *Homo sapiens* could be helpful as grandmothers. 'It inevitably suggests a special value of the old woman as mother or grandmother during a long ancestral period, a value which was for some reason comparatively little shared by the old male' (Hamilton, 1966: 37; see discussions in Hawkes et al., 1998 and Sear and Mace, 2008).

In Ostfriesland, over the last couple of centuries, children with mothers did better. Almost a quarter of all children who lost a parent before their first birthday died, and almost half who lost a parent before their 15th birthday did. Mortality in the first month of life was about twice as high after the loss of a mother than of a father; after that, fathers closed the gap. But across age categories, fatherless children did better than motherless ones (Voland, 1988).

Children with grandmothers did better, too. Women in poorer, landless families who had their mothers around were able to get married younger, to start their families sooner, to live longer, and to have more children in the end. And women in richer, landed families tended to do better when their mothers-in-law were nearby. They married younger, started their families sooner, and were less likely to die young (Voland, 2005; Johow and Voland, 2012; Johow et al., 2018; Willführ et al., 2018).

THE SWEDISH DEMOGRAPHIC DATABASE

The ecologist Bobbi Low made many trips to Umeå, where she analyzed records in the Swedish Demographic Database – a computerized file put together from church examination registers, birth and baptismal registers, marriage registers, migration registers, and death and burial records. With the demographer Kenneth Lockridge and the environmentalist Alice Clarke, she analyzed samples from seven parishes. She's sorted them into five status groups, and looked for effects on reproductive success.

Upper-middle-class men owned large businesses, or large amounts of land, and had several servants. Lower-middle-class men owned small businesses, or were artisans or professional soldiers, and seldom had servants. *Bönder* were farmers who owned land they could pass on to their descendants; *torpare* had a lifelong interest in the land they farmed, but were unable to will it. *Statare*, or migrant farm laborers, and a proletariat made up of household servants and the indigent poor, made up the last status group.

Low found that women across status categories married earlier than men. A full 96% of them married at or before peak reproductive value: wives averaged 25.0 years at marriage, husbands averaged 27.5. Women who married young had more children overall. So did women who married rich men.

For men, occupational status and land ownership were strong predictors of reproductive success. In all, 64% of men of the lowest status, migrant laborers and the proletariat, never married at all. Men of higher status married younger women, and the age differences increased when men married more than once. For first marriages, women were almost half a year older than their husbands on average. For second marriages, husbands were over a decade older, on average, than their wives. Men who remarried had significantly more children, and more surviving children, than

men who married just once. They averaged 3.0 children born by their first marriages, with another 2.9 births by their second wives. 'The bottom line? Even in socially monogamous, late-marrying, egalitarian Sweden, and even during the demographic transition, wealth augmented fertility' (Low, 1991; Low et al., 1991; Low and Clarke, 1992; Clarke and Low, 2001; Low, 2015: 132).

The evolutionary logic behind men's marriages to younger women is obvious. Younger women have their childbearing years ahead of them; older women may not have children at all (Williams, 1957; Hamilton, 1966). It makes evolutionary sense, too, that both women and men should choose partners with whatever resources to raise whatever children they have (Williams, 1966; Trivers, 1972).

RURAL FINNS

The biologist Virpi Lummaa, with help from a group of interdisciplinary collaborators, has spent decades sorting through Finnish parish registers. That data set includes over 100,000 18th and 19th-century Finns, living in eight farming and fishing populations, with full life histories of up to 15 generations. They've found that in early modern Finland, as in early modern Portugal, there was evidence of a primogeniture bias: having an older brother or sister of the same sex was associated with lower reproductive success. They've found that in early modern Finland, as in early modern Germany, parents with mothers around to help were more reproductively successful than parents without. And they've found that in early modern Finland, as in early modern Sweden, adults with high status raised more children than adults of low status. Just 74.7% of the women in this population, and just 65.7% of men, reproduced: reproductive variance among women remained smaller than reproductive variance among men.

Like early modern Portuguese nobles, early modern Finnish fishermen and farmers practiced primogeniture. Older sons did better than their younger brothers; and older daughters did better than their younger sisters. Women with older sisters were less likely to marry, they were less likely to marry a landowner, and they were less likely to have children. The same sorts of biases affected their brothers. Every extra older brother lowered their probability of becoming a father, and lowered their overall reproductive success. As usual, heirs were more likely to become fathers, and fathered bigger families, than their younger brothers (Nitsch et al., 2012).

The Finnish grandmothers who lived in these parishes were philopatric: they tended to live in the same house with at least one of their grown children, and near most of them. More than the patrilocal Germans studied by Eckart Voland, they would have been able to help. Impressively, for every 10 years that a grandmother stayed alive after her 50th year, she left an additional two grandchildren, compared to grandmothers who died. Their sons and daughters had children at younger ages – on average, almost 2.5 years earlier, they had children at shorter interbirth intervals – on average, about three months shorter, at least for their first three births; they reproduced for longer; and their children were more likely to survive (Lahdenperä et al., 2004; Chapman et al., 2019).

Finally, for these mostly monogamous Finns, as for their mostly monogamous Swedish neighbors, reproductive variance was higher for men than for women. Neither marital success (number of wives or husbands) nor reproductive success (number of children) was much affected by status: landowners had more children than the landless, but the differences were small. Sex made more of a difference than status. More women married at least once: 88% of them did, compared to 82% of men; but more men married at least twice: 14% of women remarried, and 19% of men. Most of those men married reproductive-aged women (Courtiol et al., 2012).

BIG HISTORY

Big historians have consulted a wider variety of sources, from biographies and autobiographies, to bathhouse burials and hospital artifacts, to climate data and Gini coefficients, to chronicles and parliament rolls, in order to answer evolutionary questions about the broad sweep of the past. They've tackled, among other things, warfare (Gat, 2006); technology (Russell, 2011); religion (Hagar, 1992; Hill, 1999; Betzig, 2019); lineage formation (Kroll and Bachrach, 1990; Hill, 1999); inheritance (Judge and Hrdy, 1992; Judge, 1995; Shenk et al., 2010); marriage (Betzig, 1992a, 1992b, 2009, 2013, 2020; Herlihy, 1995; Scheidel, 2009a, 2009b, 2014); childhood (Konner, 2010); and the seclusion of women (Dickemann, 1979a, 1979b, 1981, 1997). Many have used comparative methods, and some have made a big impact. In his book, *Guns, Germs and Steel*, and its sequel, *Collapse*, the geographer Jared Diamond has reinterpreted the rise and fall of states, as effects of the use and misuse of natural resources (Diamond, 1997, 2005). In *The Better Angels of Our Nature* and *Enlightenment Now*, the psychologist Steven Pinker, who's written authoritatively on the evolution of language and the evolution of mind, has shown that wars, homicides, terrorism and genocide are on the decline, but that health, safety, peace, and prosperity are on the rise – not just in the West, but worldwide (Pinker, 1994, 1997, 2011, 2018). And in *Sapiens* and its follow-up, *Homo Deus*, the historian Yuval Noah Harari has made a case for how storytelling has contributed to our success as a species (Harari, 2014, 2016). Among other things, we've become readers and writers of history.

Other Darwinian historians have tested hypotheses about birth order, maternal behavior, apocalypses and social inequality. They've produced *magna opera* on political, religious, and scientific revolutions; the history and prehistory of child abuse and

neglect; the collapse of civilizations; and the evolutionary origins of injustice.

Born to Rebel

Frank Sulloway has spent the better part of a lifetime studying the work of Charles Darwin. He started out making films about Darwin's *Beagle* voyage to the Galápagos Islands and writing articles about Darwin's 'conversion' to evolution; he's studied Darwin's finches and Galápagos ecology for decades (Sulloway, 1982). Along the way, he devoted over a quarter century to the massive research project that became one of the first Darwinian histories, *Born to Rebel*. Its subtitle suggests its contents: *Birth Order, Family Dynamics, and Creative Lives*. Sulloway's database includes information on 3,890 scientists in 28 scientific revolutions; on over 700 men and women involved in the Protestant Reformation; and on 893 members of the National Convention who took part in the French Revolution. He's drawn from over 20,000 biographical sources. And he's found that revolutions – scientific, religious, democratic – overwhelmingly have been supported by younger daughters and sons (Sulloway, 1995, 1996).

Darwin, who was the fifth of six children, and the second of two sons, was never a fan of primogeniture. He once made fun of it in a letter: 'Primogeniture is dreadfully opposed to selection; suppose the first-born bull was necessarily made by each farmer the begetter of his stock!' (Letter to J. D. Hooker, January 25, 1862, in Darwin, 1985). As he later complained in the *Descent of Man*: 'Eldest sons, though they may be weak in body or mind, generally marry, whilst the younger sons, however superior in these respects, do not so generally marry' (Darwin, 1871 :170). But he never explained why.

Sulloway has been explicit about the Darwinian logic that makes parents favor their eldest. Again, other things being equal, older children should be in a better position

to win competitions with predators, parasites, their parents, and their younger sisters and brothers. They should be the first to become producers of resources, and they should be the first to help out as caregivers; they're more likely to survive to adulthood, and they're most likely to reproduce first. 'Firstborns are like "blue chip" securities. Their younger siblings are more like "penny stocks"' (Sulloway, 1996: 65; see, too, Hamilton, 1964, 1972 and Trivers, 1972, 1974).

To that, Sulloway has added a Darwinian theory of personality. Not long before he published the *Origin*, Darwin hit upon an idea about why species branch off from each other. He called it adaptive radiation, or the principle of divergence. As he put it to the American botanist, Asa Gray: 'The varying offspring of each species will try (only few will succeed) to seize on as many and as diverse places in the economy of nature, as possible' (Letter to Asa Gray, September 5, 1857, in Darwin, 1985). Darwin's finches are a wonderful example: they occupy different ecological niches, which helps them to coexist. That principle can be extended to families. In Sulloway's words: 'As children grow up, they undergo adaptive radiation in their efforts to establish their own niches within the family' (Sulloway, 1996: 86; Sulloway, 2010). Laterborns are open to ideas and experiences; firstborns are set in their ways.

Galileo, Kepler, Newton, Lyell, Einstein, Pauling, Crick and Watson: Scientific revolutions occasionally have been born of oldest sons. But many innovators, like Darwin, came lower in the birth order, and the vast majority of their supporters have been laterborn. Sulloway found that younger children were 4.4 times more likely than oldest children to support evolutionary theory. And that the same liberal bias could be extended to another 27 innovations – from Copernicus' heliocentrism, to Newton's theory of gravity, to Lyell's uniformitarianism, to Einstein's relativity. Of scientific revolutions classed as radical, technical, or controversial, laterborn

support has exceeded support by firstborns, by ratios of 4.8:1, 2.2:1, and 3.5:1. 'Firstborns tend to reject new ideas', but 'laterborns are inclined to take risks', and as a result 'Most innovations in science, especially radical ones, have been initiated and championed by laterborns' (Sulloway, 1996: 53, 112).

The same bias extends to the Protestant Reformation. On 31 October of 1517, Martin Luther posted 95 theses on the door of his Wittenberg church. Soon afterward, he was ordered by pope Leo X to be tried for heresy in Rome; instead, the Reformation began. Luther, like his staunch supporter, Philipp Melanchthon, was a firstborn; but the vast majority of reformers were younger daughters and sons. Jean Calvin, the French theologian; Huldrych Zwingli, the Swiss pastor; John Knox, the Scottish minister; William Tyndale, the English translator: all came second or later in birth order. In a sample of 718 individuals who played prominent parts in the Reformation, drawn from across ages and social classes, Sulloway found that laterborns generally endorsed Protestantism, but that firstborns endorsed the pope. All 24 of the religious martyrs in his sample were executed for their Protestant convictions, and 23 of them were younger daughters or sons (Sulloway, 1996: 268).

The French Revolution was no different. Like revolutions in science, and like revolutions in religion, revolutions in politics have been resisted by firstborn children and supported by laterborns. After an assault on the palace, Louis XVI and his family ran away from Paris in the summer of 1792. France would be governed by a number of factions, and some of those factions would be more open-minded than others. Sulloway found that the Girondins, who took over soon after the royalists lost power, tended to be liberal and laterborn. But that on the Committee of Public Safety, which rolled more than 10,000 heads in their Reign of Terror, seven out of 10 were eldest sons. 'France once again experienced political domination by firstborns.' *L'enfant terrible*, Louis-Antoine

de Saint-Just; *le tigre*, Collot d'Herbois; *le monstre*, Jean-Paul Marat; *l'incorruptible* Robespierre: All were at the top of their birth orders (Sulloway, 1996: 314).

Mother Nature

Decades before she wrote a book about the history of mothers, Sarah Blaffer Hrdy went to India to study the Hanuman langurs on Mount Abu. She found that whenever a male took over a troop, he tried to kill all the infants. Infanticide turned out to be common across taxonomic groups, from mammals to birds to fish; and mothers could be the perpetrators, as well as fathers. Mother nature has not made us all loving parents. In bad times, we resorb, or abort, or abandon our young; in good times, we lavish hours and resources and affection on them. Across seven countries, and over more than 30 years, as she put together her *History of Mothers, Infants, and Natural Selection*. Hrdy drew on documents from founding home records to DNA from old Roman skeletons, and on fields from ethology to history. She made a case that our instincts to nurture or abandon our children have been molded by natural selection. In her words: 'For better or worse, I see the world through a different lens than most people. My depth of field is millions of years longer, and the subject in my viewfinder have the curious habit of spontaneously taking on the attributes of other species: chimps, platypuses, australopithecines' (Hrdy, 1980; Hrdy, 2000).

In her preface to *Mother Nature*, Hrdy quoted Darwin. At the end of his chapter on 'Difficulties of the Theory' in his book *On the Origin of Species*, he wrote: 'Maternal love or maternal hatred, though the latter fortunately is most rare, is all the same to the inexorable principle of natural selection' (Darwin, 1859: 203). As early as his voyage aboard the *Beagle*, in journal notes on the Tahitians, Darwin remembered bloody wars in which their children had not been spared.

And much later, in whole sections devoted to infanticide in his book on *The Descent of Man*, Darwin considered the practice common among early human parents, an effect of the difficulty of supporting their children (Darwin, 1871:1.134-135, 2.363-364).

Modern evolutionary theorists have had more to say on the subject. William Hamilton once suggested that, across species, abandonment or infanticide followed the birth of offspring whose prospects were hopeless; and Robert Trivers added that investment in offspring should rise as their prospects improve. The condition of parents and the condition of children, the availability of grandparents and other ‘alloparents’, should contribute to genetic representation in descendant generations (Hamilton, 1964, 1966; Trivers, 1972, 1974). Across social animals, ‘allomothers’, or animals other than the mother, help raise the young. *Homo sapiens* are no different. As Hrdy put it: ‘Whether or not a female produces offspring depends on her age, status, and physical condition. Whether or not, and how much, she commits to such offspring as she bears depends on her circumstances, and – in cooperative breeders like humans – on who else is around to help’ (Hrdy, 2000: 79; Hrdy, 2009).

Lacking that sort of help, children have often been abandoned. Church and court records, civil and religious laws suggest that, from late antiquity to the Renaissance, infants were left without mothers in great numbers. Many *expositi*, or exposed infants, undoubtedly died. At the *Ospedale degli Innocenti*, or ‘Hospital of the Innocents’, founded in Florence in 1419, just 95 foundlings were left in the first year; but 15,000 were abandoned between 1755 and 1773. Two out of three died before their first birthday. Orphans fared no better elsewhere. In foundling houses at St. Petersburg and Moscow, established by the enlightened Catherine the Great, death rates were 80–90%; at the state-supported *Hospice des Enfants Assistés* in Bourbon Paris, infants whose destitute mothers left the

building on their birthdays had a 50:1 chance of abandonment; and at a home for deserted children in Hanoverian London, 15,000 children were left behind over a period of four years, and mortality rates soared. Residents of Brescia proposed a motto for the foundling home gate: ‘Here children are killed at public expense’ (Hrdy, 2000).

Lacking help, other infants were put to death. On pain of excommunication, nurses in 15th-century Florence were ordered to use *arcutios* – wooden cages meant to prevent suffocating a baby in bed. Later, 18th-century doctors advised Londoners to adopt those *arcutios*, to little effect: as a result of ‘over-laying’ between 1855 and 1860, almost 4,000 infants died. Across cultures, rich parents – like nobles in the *peditura Lusitana* – discriminated against their daughters. But in some cases, infanticide was son-biased. DNA from 14 of 19 of the days-old skeletons excavated from a bathhouse in ancient Roman Ashkelon was male. The Greek inscription, ‘Enter, enjoy’, was found on the walls: these mothers were professionals.

The Great Leveler

Walter Scheidel has studied classical demography for decades, and was the first classical historian to ask Darwinian questions. He’s written on politics and economics, slavery and the peasantry in ancient societies; and he’s advocated historical tests of Darwinian hypotheses about mate preferences, sex bias, and kin selection. ‘Many of these claims can—and must—be tested against the archival record’ (Scheidel, 2009a, 2009b; Scheidel, 2014: 10). He is, in other words, eminently well-qualified to ask one of the most important questions of our time: What makes societies more or less egalitarian? His answer: The Four Horsemen of the Apocalypse. Wars, revolutions, political collapse, and pandemics have accounted for most if not all of the leveling across history. In eight tables and

48 figures, with evidence from over two millennia and across all five inhabited continents, he makes that case. As populations crashed, egalitarianism went up, and reproductive equality followed. ‘Material inequality routinely translated into reproductive inequality’: leveling worked both ways (Scheidel, 2017: 59).

Roughly a year into the *Beagle’s* trip around the world, Darwin stopped at Tierra del Fuego, where he saw natives on a ledge overhanging the sea, shouting and waving rags. They slept on the ground coiled up like animals and seemed the most miserable people in the world. ‘I could not have believed how wide was the difference between savage and civilized man’ (1839:12/17/1832, with nostalgia on 10/2/1836). The better part of a lifetime later, Darwin returned to those savages in his book on *The Descent of Man*, where he suggested that sedentism may be a prerequisite for civilized life:

‘Nomadic habits, whether over wide plains, or through the dense forests of the tropics, or along the shores of the sea, have in every case been highly detrimental. Whilst observing the barbarous inhabitants of Tierra del Fuego, it struck me that the possession of some property, a fixed abode, and the union of many families under a chief, were the indispensable requisites for civilisation’ (Darwin, 1871:1.167).

Roughly a century later, evolutionary biologists came to a similar consensus. In saturated habitats, where mobility is low, animals with high status – usually bigger and stronger – tend to take more than their share of resources, and animals with low status – usually smaller and weaker – tend to settle for less. Reproductive differentials, or ‘skew’, is the result. Animals with high status become breeders; and animals with low status become helpers. As the biologist Stephen Emlen has pointed out: ‘An individual will remain as a helper in its natal unit only when it is forced to do so by the prohibitive costs of the alternative option of early dispersal and independent breeding’. Where habitats are less saturated, and mobility is easy, those differences even

out (Emlen, 1982a: 32; Emlen, 1982b). In the biologist Sandra Vehrencamp’s words:

‘Dominants within groups can bias resources or fitness in their favor to the limits established by the subordinates’ options outside the group. Ecological factors, such as the cost of dispersing and relative benefit of group living compared to solitary living, determine the subordinates’ options and greatly affect the degree of bias the dominant can impose’ (Vehrencamp, 1983a, p. 667; Vehrencamp, 1983b).

Revolution and international conflict, plague and political collapse should relieve population pressure. Habitats should open up, and hierarchies should fall as a result.

Consider wars. Over the course of human history, most wars had winners and losers. Inequality was flattened for the vanquished; but for the conquerors, it almost always went up. The first civilizations were products of conquest: smaller, more equal polities were swallowed up, and the big polities that swallowed them were almost always despotic. In Rome, millions of slaves were the spoils of wars, and wealth differentials exploded: the largest reported fortunes went up over 10 times from the end of the republic to 300 years later, when the capital was relocated to Constantinople. But where casualties in battle have been high enough, opportunities have presented themselves. After the massive mortality of the two World Wars, progressive taxation, trade unions, and the franchise expanded, but income shares of the top 1% shrank. Territories emptied out, and equality went up. Though over the past few decades, those trends have reversed.

Or consider revolutions. The data tend to blur as we go back in time, but most successful rebellions seem to have amounted to regime change. New bosses mobilized the impoverished and overworked; old bosses were slaughtered and their property was confiscated. Most uprisings were flashes in the pan. There were as many as 269 peasant revolts in China, over the more than two millennia from the fall of the Qin to the fall of the Qing; and peasants revolted all over Europe

in the Middle Ages – in Germany, over 200 times. The consequences of the 20th-century Communist revolutions seem to have been greater and to have lasted longer: through redistribution, and the slaughter of as many as 100 million people, Gini coefficients and other measures of inequality dropped. Mass leveling was the product of mass violence.

Many lose when states fail, but the affluent have farther to fall. Around the world, and across millennia – from Old Kingdom Egypt, to Harappa in the Indus River Valley, to Mycenaean Civilization, to the Classic Mayans – environmental degradation, agricultural pests, climate change, and seismic activity all led to what Scheidel calls Ozymandian collapse. It made everybody worse off, nobody more than the rich.

But there is no better leveler than plague. Genoese ships had carried the *Yersinia pestis* bacterium from the Crimea to the Mediterranean by 1347. Caravan routes that crossed central Asia – the trade that came with the Crusades – had carried the fleas. Papal secretaries counted 23,840,000 casualties across Europe in 1351; and by the time the disease had run its course, an estimated 25–45% of the population was lost. Massive human suffering dispossessed the rich; but among the poor, the survivors were noticeably better off. Hundreds of years of dis-equalization were wiped out overnight. Other plagues from Mesopotamia to the New World have leveled economies in more or less the same way. But as populations recovered, so did wealth differentials (Scheidel, 2017; see too McNeill, 1998).

The Badge of Lost Innocence

The king of Ashanti, or Asantehene, was credited with 3,333 women. Anybody so much as suspected of adultery with any one of those women did the dance of death. Led by a thorny creeper threaded through his naval septum from chieftdom to chieftdom, his left leg was abraded, his left ear was cut off,

his right shin bone was scraped, and he was led into the shade of an atopere tree: ‘Here he is compelled to dance all day.’ After dark, his arms were amputated at the elbows and his legs at the knees, his buttocks were incinerated, and his head was cut off (Rattray, 1927: 88, 95).

In her first book, *A Darwinian View of History*, the anthropologist, Laura Betzig, established a strong connection between despotism and differential reproduction in a sample of 104 politically autonomous groups (Betzig 1982, 1986). She followed up with studies of sex and politics in the first civilizations, the Hebrew Bible, the Roman Empire, the Middle Ages, England after 1066, and the United States (Betzig, 1992a, 1995, 2002, 2005; Betzig and Weber, 1993, 1995). Then she looked at the reproductively suppressed: the celibate helpers and sterile workers who fed and defended other men’s women and children (Betzig, 2009, 2014, 2018, 2019). In the context of world history, with a focus on the history of Europe, *The Badge of Lost Innocence* shows how political and reproductive inequality rose and declined, and why.

Darwin worried most of his life about sterile castes. He sent a letter to his ‘Bulldog’, Thomas Henry Huxley, to say: ‘Bees offer in one respect by far my greatest theoretical difficulty’. And he wrote to Charles Lyell, his ‘Lord High Chancellor in Natural Science’, to confess: ‘I fairly struck my colours before the case of neuter-insects’ (Letters to Huxley of December 9, 1845 and Lyell of September 30, 1859 in Darwin, 1985). As early as his *Beagle* voyage, after a stop at the Falkland Islands, Darwin had made a footnote in his journal about *Apis mellifera*:

‘The bee could not live by itself. And in the neuter, we see an individual produced which is not fitted for the reproduction of its kind – that highest point at which the organization of all animals, especially the lower ones, tends – therefore such neuters are born as much for the good of the community, as the leaf-bud is for the tree.’

In *The Origin of Species*, he referred to the special difficulty that had seemed fatal to his

theory. 'I allude to the neuters or sterile females in insect-communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind' (Darwin, 1839:3/16/1834; Darwin, 1859: 238).

At one end of the continuum of animal societies, workers are obligately, or permanently, sterile. They stay on their natal territories for life, and work to help others reproduce. At the other end of the continuum, helpers are facultatively, or temporarily, sterile. They help out on their natal territories, but disperse after empty habitats open up. Wherever prey is abundant and predators are scarce, animals live together in groups. Some breed prolifically; others are reproductively suppressed (Alexander et al., 1991; Sherman et al., 1995; Betzig 2013, 2014, 2018, 2020).

When, at the beginning of our era, Marc Antony lined up his ships against the future emperor Augustus, he was abandoned by Cleopatra, his fifth wife. Antony sailed away with her withered eunuchs to Egypt, where he put a sword in his gut. Other eunuchs would work under the emperors in Rome. *Cubicularii* – or bedchamber attendants, customarily castrated – overheard Augustus regret his successor, or were commemorated in the tomb of his third wife. Over three centuries later, when Constantine left Rome for Constantinople, he took soft and effeminate, long-sleeved and tiara-wearing eunuchs along. Hives of castrated servants ran the palace in Constantine's time; eventually, a *castrensis sacri palatii*, in charge of the treasury, would manage the imperial household, and a *praepositus sacri cubiculi*, or prefect of the sacred bedchamber, would run the empire. But the emperors bred. Antony remembered Augustus as a philanderer, whose friends pimped for him: 'They would strip mothers of families, or grown girls, of their clothes, and inspect them as though they were for sale' (Suetonius, 1979). And Maximinus Daia, who opposed Constantine's edict of toleration towards Christians, said he had the

same habit of procuring women. 'Eunuchs and panders made search everywhere, and no sooner was any comely face discovered, than husbands and parents were obliged to withdraw' (Lactantius, 1984).

After the castrates moved east, celibates took over out west. At the end of the 3rd century, when Aurelius Augustinus sailed from Carthage to Rome, he was looking for a wife. 'I aspired to honors, money, marriage and you laughed at me', the bishop of Hippo Regius would write. 'Look into my heart, Lord. In obedience to your will I recall this and confess to you' (Augustine, *Confessions* 6.9). Many men much younger than Augustine would become *oblates*, or offerings, given up to monasteries by their parents, and some of those *caelibes*, or celibates, would run governments across the continent. They became counts of the stables (*comites stabuli*), chamberlains (*camerarii*) and counts of the palace (*comites palatii*). But lords would fill those palaces with women. Charlemagne's heirs had access to women's quarters and women's rooms on hundreds of estates, where children were born and brought up. Charlemagne's son, Louis the Pious, hoarded trollops in his Rhine River palaces, and his 17th-generation descendant, Frederick II, was excommunicated by a pope for sexual excess. 'Carefully examine the head, the middle, and the lower parts of this beast Frederick, the so-called emperor; and, as you find only abominations and wickedness in his words, arm your sincere hearts with the shield of truth' (Matthew Paris, *English History*, 1852: 1239).

People shipped east after the Crusades; people shipped west after Columbus. And the inequalities leveled out. A common council of bishops and archbishops, abbots, earls and greater barons met at Runnymede on a June day in 1215, and the Great Seal was impressed on the Great Charter. A generation later, the first writs were sent out to elect lawful and discreet knights (or *milites*), citizens (or *civibus*), and burgesses (or *burgensibus*) to air their grievances at Westminster. They wanted parliaments to be summoned every

September, February, and June, to treat the common business of the realm. *A remembrer fet del hostel le rei et la regine amender*: and they made a note to amend the households of the king and queen (*Provisions of Oxford*, 1258). Monarchs suffered the consequences if they ignored those orders. Incurable and without hope of amendment, Edward II was presented with Articles of Accusation in January of 1327 and abdicated in favor of his son; in October of 1399, Richard II, who governed his household as he saw fit, had to quit; Henry VI, whose civil servants were less like Mars than Dionysius, was usurped in March of 1454 by the duke of York; and on a cold day of January in 1649 – ‘for the advancement and upholding of the personal Interest of Will and Power, and pretended Prerogative to himself and his Family, against the Publick Interest, Common Right, Liberty, Justice, and Peace of the People of this Nation’ – Charles I was hauled off to Whitehall, where his head was cut off (Rushworth, *Historical Collections* 7.1416; Betzig, 2020).

THE FUTURE OF HISTORY

On 22 October, 2004 BC, the universe began. So thought James Ussher, the archbishop of Armagh and Primate of All Ireland, who attended the execution of Charles I. First there was light and darkness; then there was heaven and earth; then came the sun and the moon; then came Adam and Eve. It took six days.

But in the centuries after Ussher finished his book on our beginnings, the bottom fell out of history. Suddenly there were new cosmologies and geologies and paleontologies. Scientists discovered deep time. Historians were slow to catch up. The names in their narratives changed, but their chronologies stayed the same. The 6,000 years of sacred history became 6,000 years of secular history; the Garden of Eden became the fields of Mesopotamia, where farming began; the

birth of Adam and Eve became the birth of Civilization. God gave light to the world; history gave the written word.

The historian, Daniel Lord Smail, has eloquently and repeatedly suggested that we have to do better. We need to pull history back into Africa, and extend it back hundreds of thousands of years. We need to consult fossils and artifacts, animal and vegetable remains, phonemes and DNA, behavior patterns and the brain. We need to do history at multiple time scales. And we need to give up on the idea that culture emancipated us from biology. We’ve altered and been altered by our environments, we’ve taught and learned, for as long as we’ve been human. Culture, in those respects, is as old as life. ‘Shallow history was predicated on the idea that at a certain moment in time, humanity broke through nature’s chains, gained mastery, and through the conquest of nature took the momentous step into history’: better excavation is in order (Smail, 2012b: 4; Smail, 2008, 2012a; Shryock and Smail, 2011; Smail and Shryock, 2013).

Occasionally, deep histories are being written as historical demographies. Anthropologists, archaeologists, biologists, ecologists, and their interdisciplinary teams of collaborators are looking at the *Peditura Lusitana* from medieval Portugal, at the *Ortsippenbücher* from early modern Germany, at the Demographic Database from early modern Sweden, and 15 generations of rural Finns. They’re testing evolutionary hypotheses about primogeniture and patriline, the effects of serial monogamy, the importance of grandparents, and relationships between status and reproductive success.

Other deep histories are panoramic. The Classical historians and historians of science, primatologists and anthropologists who are writing big histories are asking Darwinian questions about revolutions, cooperative breeding, economic and political egalitarianism. They’re looking at hospital records and economic documents, saints’ lives and literary masterpieces. And they’re coming

to conclusions about the manifestations of birth order, the malleability of the maternal instinct, the leveling effects of population crashes, and the causes of political and religious injustice.

The first books of history were written as moral documents. The vast majority of history has been written as political propaganda. After the 19th century, there were materialist histories. In the 21st century, human history is being written as natural history.

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Evolutionary Psychology and the Performing Arts

Nicholas Bannan

INTRODUCTION

This chapter explores an evolutionary approach to the phenomenon of human performative culture. In attempting to ‘reverse-engineer’ capacities that we find to be universal in human society, we first consider what these may represent: a range of aptitudes and characteristics, and the relationships evident between them. A suite of practices embraces music, dance, mime, and drama, together with combinations and extensions of these (e.g., puppetry, pageant, opera, religious observance, some spectator sports) informed by the diverse contexts of play, ritual, and narrative presentation. Performances work on audiences in varied ways: on memory, anticipation, social cohesion, emotion, and cognition. The performing arts exploit language and are commonly rehearsed and responded to with recourse to this medium. But not only can music, mime, and dance be practiced and transmitted independently of language, their complementary

status in relation to verbal interaction points to the possibility of their being considerably older behaviors that predate the emergence of speech.

The timescale we need to invoke for the development of the performing arts is thus one that reaches into deep prehistory for us to discern patterns of origin in traits possessed by other species with which *Homo sapiens* share common ancestry. In parallel with analysis of divergent evolution on these lines will be a consideration of the adaptations to changing environmental challenges that permit modern humans to survive across the globe. A role is evident for inter-species mimicry that may have been shaped by hunting practices and predator avoidance which have left their mark on spirituality and ritual.

The animal origins of expressive representation and communication underpin the genetically-determined, instinctive behaviors of each individual. These become capable of release and intentional exploitation through cultural transmission that depends

on collective interaction. A candidate model for capturing this relationship is recapitulation theory (Gould, 1977), tracing parallels between phylogeny and ontogeny. While modern humans are bipedal, they pass through a significant quadruped phase in infancy in which their four-footed gait presents similarities to that of mammal quadrupeds (Righetti et al., 2015; Zehr et al., 2009). Descent from tree-dwelling ancestors has left vestiges of the instinct to brachiation evident in newborn humans (Futagi et al., 2012); though without special training (gymnasts, acrobats, circus performers; Pennock, 2013), few of us successfully transcend the upright ambulant locomotion of our modern evolved anatomy. Nevertheless, the specialized role of human limbs, divided between the function of the legs in bipedal locomotion and the arms and hands in a sophisticated capacity for independent manipulation, presents the anatomical resources for complex patterns of movement in dance, contrasting modes of employment in work, and instrumental performance that exploit these evolved characteristics to the full. The recapitulation of phylogeny in ontogeny features in a variety of ways in the modeling of how the performing arts have emerged.

A range of facial expressions, correlating with specific emotions which motivate instinctive vocal utterance, corresponds to a set of timbral characteristics that supply the vowel sounds on which language depends (Bannan, 2008; Manén, 1974). The means by which vocal learning permits these to be controlled confers advantages both in the capacity for speech, and in the medium of coordinated wordless song. In terms of vocal range, human children of both sexes share with their mothers an average octave difference from adult males in both speech and song; male adolescents undergo a rapid transformation through which the voice deepens to conform to their fathers' range (Puts et al., 2006; Cooksey, 1997). The consequence of this acoustic arrangement, for the family and tribe, is the capacity for harmonic

reinforcement through which the entire group performs resonantly to its mutual benefit and well-being (Bannan, 2012b).

The story of the performing arts is complex, and its disentanglement on evolutionary grounds somewhat provisional. This chapter therefore proposes trajectories that may inspire further research, drawing on existing work in disciplines such as archaeology, anthropology, semiotics, neurology, vocal acoustics, audiology, child development, and social psychology, in order to illuminate the principal issues that can inform future investigation.

MODELS FOR EVOLUTIONARY THINKING: DARWIN'S LEGACY

In exploring their perspective on the origin of the performing arts, Darwin's evolutionary theories, variously extended and interpreted since their original presentation in the second half of the 19th century, provide convincing proposals for the origins of traits and abilities that have given rise to culture. A sequence of three publications presented the foundations of the evolutionary approach to be explored in this review. The principal of Natural Selection was proposed in *The Origin of Species* (1859); Sexual Selection as the mechanism of characteristics that govern reproduction was propounded in *The Descent of Man* (1871); and the key focus on communication was the theme of *The Expression of the Emotions in Man and Animals* (1872).

Darwin's achievement immediately inspired responses from his contemporaries, spreading the influence of his theories into other disciplines as their potential lent itself to elaboration. Variant interpretations unrepresentative of Darwin's own thinking have complicated a clear understanding of the implications of his work, and inhibited acceptance of its application to fields such as music (Kivy, 1959). For instance, Spencer's (1857) account of the origins of music saw

it as derived from emotionally heightened speech, whereas Darwin's own conclusion (1871) was that musical vocalization occupied a developmental stage between animal communication and language:

We must suppose that the rhythms and cadences of oratory are derived from previously developed musical powers. We can thus understand how it is that music, dancing, song, and poetry are such very ancient arts. We may go even further than this, and ... believe that musical sounds afforded one of the bases for the development of language. (Darwin, 2004: 638–9)

The 'survival of the fittest' tag (Spencer, 1864) illustrates a preoccupation among post-Darwinian commentators (Galton, 1869) with intra-species competition, whereas Darwin's preferred focus was more on the adaptive nature of cooperation. The meme even arose in the biographical literature that Darwin was himself 'tone deaf', a description entirely at odds with his early interest in music and its significance in his attraction to Emma Wedgwood (Healey, 2001), let alone his employment of music in his experiments with animals and infant humans, his informed observations of the musical performances encountered while on the *Beagle* voyage, and his lasting contribution to speculation on the purpose and origins of the arts (Bannan, 2017).

Tylor's *Primitive Culture* appeared in 1871, in the same year as *The Descent of Man*, and from the same publisher, John Murray. Tylor (1871: 152, 223) cites Darwin's eyewitness accounts of religious ceremonies and performances from the *Beagle* Journal (Darwin et al., 1839). The fledgling field of anthropology thus emerged out of an evolutionary approach to humankind and the manifestations of culture. An aspect of this perspective, and a source of contention both within the discipline and in contemporary politics, was the concept of universality: the principle that all members of the species *Homo sapiens* share the same inherited characteristics and therefore an equivalent capacity

for cultural expression¹. The Berlin School of Ethnomusicology led by Curt Sachs and Erich von Hornbostel based the development of their approach upon fieldwork and the analysis of recordings informed by the scientific application of acoustics, psychology, and anatomy (Hornbostel and Sachs, 1914). The German-language original of Sachs's *World History of the Dance* was published in 1933, its author escaping to the USA, where universalism proved less unacceptable than in Nazi Germany. The book opens:

The dance is the mother of the arts. Music and poetry exist in time; painting and architecture in space. But the dance lives at once in time and space. The creator and the thing created, the artist and the work are still one and the same thing. (Sachs, 1937: 3)

Parallels to the universalist approach to dance and music emerged in Carl Jung's (1919) idea of the collective unconscious and the expressive archetypes that derive from it, Lévi-Strauss's (1962) analysis of myth and narrative, and Bowra's cross-cultural investigation into the texts of *Primitive Song* (1962).

A convincing adaptationist account of the role and origins of music and the performing arts did not fully emerge until the last quarter of the 20th century, in a series of publications that included Livingstone (1973), Wallin (1991) and Mithen (2005). While writers such as Pinker (1997) have argued against an evolutionary explanation for the phenomenon of music, let alone for its claimed role as a precursor to language, a growing consensus across several disciplines has moved this topic from the periphery towards a central position in accounting for the nature and attributes of human culture (Ball, 2010; Bannan, 2012a; Changizi, 2011; Levitin, 2006; Morley, 2013; Tomlinson, 2015; Wallin et al., 2000).

The framework for the research trajectory that made possible this new focus on the adaptive nature of the arts has drawn extensively on earlier interpreters of Darwin in creating the synthesis that has informed speculation and research. For instance, the American

scholar Baldwin (1896) accomplished a significant application of Darwinian thinking to psychology, proposing that behavioral response to a changed environment shapes natural selection. Podlipniak (2017) proposed on Baldwinian lines a theory of the development of the role in perception and production of the pitch center that accounts for the phenomena of both musical tonality and prosody in language (see, also, Bannan, 2012b). The evolutionary term *exaptation* (Gould and Vrba, 1982) captures the means whereby a characteristic that evolved in response to one set of circumstances could prove useful for a different purpose in a changed environment (c.f. Changizi's (2011) concept of an existing trait 'harnessed' to new purpose). These modifications of classic natural selection are particularly suitable to theorization concerning the arts and their significance. Of special consequence to the story of human culture is the nature of collective reinforcement in dance and song: the capacity for precise coordination in three-dimensional movement (Garfinkel, 2010; Large, 2000) and the musical parameters of pitch, duration, amplitude, and timbre that constitute unison singing (Bannan, 2020; Merker, 1999). A further variant of natural selection, *group* or *kin selection* (Hamilton, 1971), has featured in explanation of the crucial behavioral trait represented by simultaneous performance in both sound and movement. While there is growing evidence of the physical and psychological benefits of coordinated group engagement consistent with adaptive origins (Dunbar et al., 2012; Koch et al., 2014), these are generally viewed as specialized outcomes of natural selection.

However, if artistic expression is adaptive (Morris-Kay, 2009), then we need to understand the process by which instinctive responses carried in our genes form the basis for learning and exchange mediated, accelerated, and recorded by cultural transmission. Tinbergen (1951) posed four questions to determine whether and in what way a trait or ability is instinctive:

- 1 How has the capability evolved in the species?
- 2 How do individuals within the species develop the capability?
- 3 What happens in the nervous system when the capability is exercised?
- 4 Why is the capability exercised in a particular circumstance?

These questions divide into two pairs: 1 and 2 represent the investigation of ultimate explanations ('why?'); 3 and 4 deal with proximate ('how?') (Scott-Phillips et al., 2011). In sifting through the evidence associated with the development of the performing arts, whether in the fossil record, the material legacy, the recorded accomplishments of historic and living humans, or comparisons between animal and human behaviors, we remain guided by Tinbergen's approach, and aim to discriminate between ultimate and proximate interpretations.

Examples of ultimate evolutionary causality which may have given rise to aspects of the performing arts include:

- mate attraction and retention;
- understanding of the minds of conspecifics;
- understanding of and capacity to mimic and exploit other species;
- capacity to exchange information through vocal, gestural, and imitative means;
- capacity to engage in collective activity, including work, defense, and hunting;
- the protection and nurture of infants.

By contrast, examples of proximate explanation include:

- the assumption of tokens of role and hierarchy (crowns, weapons, uniforms);
- the mnemonic abilities conferred by performative and artistic media;
- activities that permit and convey measurement, its recall, and its role in prediction and planning;
- play and ritual as rehearsal for work, defense, hunting, and parenting;
- activities oriented to instruct or encourage others;
- self-recognition and self-consciousness;
- sacrifice, and the presentation of altruism.

These categories represent abstract or theoretical applications of Darwinian analysis in preparation for a closer consideration of real-life examples that are consistent with a variety of evidence.

'REVERSE-ENGINEERING' THE ANATOMICAL PREREQUISITES FOR THE PERFORMING ARTS

Reconstructing the means by which artistic traits may have emerged in human culture relies on evidence and its interpretation in two principal research fields. The first is that of modern human anatomy, including its consequences for psychology; the second is the material record of human culture – the use of fire, of tools and ornaments, and of spaces in which performances may have been enacted. Investigation of the fossil record illustrates the extent to which analysis of these two forms of evidence combines as traces of cultural behavior began to accompany the deposit of human remains.

Consideration of anatomical features of the evolved prerequisites for art and culture (Bannan, 2003; Morley, 2013) commences with the senses and their integration in perception. The aural system presents a means of spatial location suitable for life in dense forest or the tall grass of tropical savannah, capable of detecting direction and speed of movement through Doppler analysis (Changizi, 2011) and of discriminating timbre and its combination through an instinctive response to harmonicity (Bannan, 2012b; Podlipniak, 2017). Hearing is the first system to commence laying down memories, which it does in the three months *in utero*, prior to birth (Woodward, 2019). Indeed, Prochnow et al. (2017) compared the intonation of German and Swedish babies to suggest that the precise shape of the infant's first cry is influenced by the sound of its mother-tongue perceived in the womb. The human visual system perfectly complements the aural, the

forward-facing, binocular presentation of the eyes working in tandem with hearing to locate the origin of sound sources and track speed and direction of movement. Both hearing and sight gather stimuli from a position near to the vertical maximum of an upright posture oriented to optimum exploitation of the vestibular system on which bipedal locomotion depends (Bannan, 2003; Morley, 2013). The senses of taste and smell involve receptors in the mouth and nose that interact with the digestive and respiratory tracts, respectively. Receptors for these four senses – hearing, sight, taste, and smell – are located within the mid-to-forward section of the skull and, in their connection to the brain, exhibit a degree of overlap, especially where one sense primes for the expectation of perception in another. The tactile sense receives information to differing extents from all over the surface of the body, with a concentration of sensitivity in the feet and hands, and especially the fingertips.

Learning and discrimination proceed as extensions of instinctive responses related to basic needs and their emotional expression. These are exhibited from the first hours of life. Hunger and thirst, discomfort in relation to temperature or wetness, and separation from the provider of care and attention lead to stress that, on its alleviation, may be accompanied by pleasure or relaxation. Disgust sends a signal, as well as registering the need for avoidance. Interaction with carers lays down the means by which instinctive responses can be captured as the bases for communicative behaviors in sound and gesture, involving mimicry and repetition that enables learning and voluntary control.

A bridge between perception and production is evident in several examples of instinctive response to stimuli that provide an early indication of how the senses may be primed for social interaction and learning. Meltzoff and Moore (1977) presented evidence for the instinctive imitation of tongue protrusion and manual gestures in newborns, while Kessen et al. (1979) recorded aural-oral responses

between infants and mothers in the matching of precisely pitched vocalizations. A walking or stepping reflex is exhibited soon after birth, the child supported by a carer in an upright position, and it can form the basis for training that encourages and accelerates the eventual achievement of independent locomotion (Forssberg, 1985; Yang et al., 1998).

A set of physical reflexes elicited by clinical staff as a means of checking for neural abnormalities provides insight into the ontogeny of human locomotion (Futagi et al., 2012). The palmar and plantar grasp reflexes can be elicited in utero by the 25th week of pregnancy. Ernst Moro (1918) described a reflex that now bears his name, also observable *in utero*. Once born, infants continue to exhibit these reflexes in response to specific stimulation. The palmar grasp involves the infant wrapping its fingers around the finger of an examiner who lightly touches the infant palm (Futagi et al., 2012: 2). The grasp reflex in newborns is sufficiently strong for them to support their own body weight (Futagi et al., 2012: 7). The plantar grasp is an equivalent response in the infant foot, involving the flexion and adduction of the toes. Both of these reflexes decline and disappear by the age of six months (palmar) and 12 months (plantar), as the infant begins voluntarily to employ the hands to grasp, and the feet to stand, and to practice locomotive and manipulative functions that require the limbs to be under intentional control.

The Moro reflex (Futagi et al., 2012: 5) is a response to surprise that may take the form of a sudden sound or movement, sensation of cold on the chest or stomach, or change to the sense of support of the head. The response of the infant comprises abduction of the arms at the shoulders coupled to extension of the forearms at the elbows, together with extension of the spine and retraction of the head. The Moro reflex also usually disappears by around six months. Futagi et al. (2012: 8) speculate on the phylogenetic origins of these responses as having been essential to the survival of the young in arboreal

predecessor species. Interestingly, the Moro reflex has also been observed in infant apes and monkeys (Katona, 1998), and evidence that the palmar reflex inhibits the Moro reflex may suggest that it played a role in interaction with the mother as a form of protection against falling (Futagi et al., 2012: 9). What is clear in the interaction between human mothers and infants is that mediation of these instinctive responses plays a part in bonding and socialization involving multi-modal emotional engagement arising out of the infant's trustful dependence on a carer.

Perception and instinctive response provide the basis for infants' expressive employment for learning of their increasingly familiar anatomy as cognition engages with the vocal system and limbs in communicative production and generativity that is uniquely human. Rhythmic entrainment to musical stimuli interacts with the rehearsal of locomotion, which depends on precisely repeated patterns that lend themselves to play and elaboration. Musical responses in the movement of the limbs parallel the acquisition of vocal control (Bannan, 2003), rehearsed by solitary infants but strongly related to interaction with carers. The hands develop the independent abilities that confer interaction with the extrasomatic environment (grasping, holding, placing objects) and of communicative potential (pointing, gesturing). Voice and gesture interact with facial expression, which commences instinctively as an honest signal prior to control being acquired to permit artificial representation (play-acting; the 'poker face') and deception. These co-opt muscular responses arising from specific emotions that can be recalled and expressed both instinctively and as learned patterns. As upright posture is achieved, it completes a functional array of bodily positions (lying, kneeling, sitting, squatting, standing) in which songs, games, and narratives can enact movement between one position and another. Songs and movement games rehearse bodily self-knowledge ('Heads, shoulders, knees and toes', etc.). Enculturation accelerates bodily

self-knowledge in the kinesthetic and vocal domains.

The anatomical and sensory advances through which communication develops are made possible by the large and complex brains with which human infants are endowed. Especially significant to the relationship between emotion and cognition that enables artistic expression and language is plasticity (Hrvoj-Mihic et al., 2013). We are well equipped to deal with changing circumstances:

human life history is characterized by an extended period of offspring dependency compared to chimpanzees, delayed onset of reproductive maturation, and long post-reproductive life-span, enabling prolonged cognitive maturation, acquisition of skills necessary for survival, and their transmission across generations. (Hrvoj-Mihic et al., 2013: 1)

Plasticity provides ‘selective advantages to hominins in unstable conditions’ (Hrvoj-Mihic et al., 2013: 2). The capacity for learning is multi-modal, conferring the advantages of both specialized skills and their integration. Thought can be organized, represented, and expressed through recursion both within and between learned abilities, a capacity that only humans possess that is dependent on a sophisticated ability to lay down, sort, and retrieve memories (Hurford, 2004).

Recursive thought and its role in learning emerge from the developmental interdependence between genetically inherited abilities and cultural transmission that is most strongly evident in mother-infant interaction (Trevvarthen, 1998). The literal physical attachment to its mother in the womb involves the fetus in hormonal exchange associated with aural and movement stimuli, an environment that changes radically at birth. Nevertheless, there is continuity in both dependence and perception, a vital component of infant well-being. Bjorklund (2006) reviewed the evolutionary nature of this developmental phase and its crucial role in the expression of behavioral plasticity.

He illustrates the epigenetic relationship between genetic and phenotypic factors: ‘developmental mechanisms responsive to both genetic and environmental influences produce phenotypic variation that selection might then act upon’ (Bjorklund, 2006: 214). What might we then learn from considering the evidence for the nature of the environments into which human infants and their ancestors have been born in widely separated parts of the globe?

Human cognitive plasticity has led to cultural practices that allowed people to adapt to widely different climatic and environmental conditions involving varied diets, contrasting lifestyles (settled, nomadic), and diverse employment of clothing and bodily adornment. The evidence of these in the fossil record allows speculation on the role of the performing arts in early societies and permits comparisons to be drawn with cultural practices that have survived into modern times. A variety of material evidence informs speculation on the relationship between ultimate and proximate evolutionary explanation. Among these are:

- Fire: the husbanding, creation, and control of fire provides for warmth, protection, hunting, shaping the environment, and food preparation (Archibald et al., 2012; Pascoe, 2018). Hearths and remains located close to them provide insight into social organisation and cultural practice. While there is evidence of hominin control of fire from 1 million years ago, creation of fire is traceable to c. 350,000 BP (Shimelmitz et al., 2014). The hearth may be a location for performance (Gamble, 2012).
- Bodily adornment: among the earliest evidence of material associated with bodily adornment (Iliopoulos, 2016) are ochre (Wreschner et al., 1980), shells, and beads made from them (by Neanderthals, Zilhão et al., 2010; by modern humans, d’Errico et al., 2005); and feathers (Finlayson et al., 2102) – materials that are still employed in bodily adornment today, often in circumstances that relate to dance or ritual performance.
- Clothing for warmth: Gilligan (2007) considered the role of clothing in the capacity of modern

humans to survive climate change that may have led to the demise of the Neanderthals during the period 50,000–30,000 years BP. While clothing itself has not survived from such a distant past, buttons to secure clothes and eyed needles to manufacture them have done, and clothed humans are depicted in art from towards the end of the period. Genetic evidence of the divergence between head and bodily lice (Toups et al., 2011) illustrates that clothing may have been in use as early as 170,000 years BP and regularly so by 83,000 years BP. As remains the case today, clothing for practical purposes (warmth, specific tasks, uniformity) conveys the intention to adorn for special purpose (social ceremony, specific role) or to assert rank or status, as well as emphasizing gender and sexual attractiveness.

- Cave art both depicts dance and musical performance and may represent the designed or adapted location for them. The geographically widespread production of hand stencils is itself a performative act that leaves a trace (Dobrez, 2013), and painting using the breath both creates an image and employs a sound-producing instrument (Gheorghiu, 2019). In a tradition with a long prehistory, dance associated with trance states and healing features clearly in San rock paintings from Southern Africa (Lewis-Williams 2010: 139–41). In Gobustan, near Baku, a petroglyph of line dancing from 6,000–7,000 years BP in the Beyukdash rocks resembles others that depict men hunting and inspires present day enactment of the 'yally dance' (Farajova, 2011). Rock art may equally represent the location at which performance took place. Acoustic measurements at sites of depictions and decoration have demonstrated their enhanced response to musical sound (Rifkin, 2009; Till, 2014).
- Weapons and evidence of their use: tools for killing prey are equally capable of being turned on other humans, as the forensic analysis of the cause of death illustrates in buried corpses. Evidence for cannibalism is also consistent with the butchery of human remains. Spears, clubs and bows, slings, and cutting edges represent the means of survival, and their descendants in the arms race of human history have acquired symbolic significance associated with performance and ritual: military bands, ceremonial maces, depictions on flags and coats of arms. Sword and quarterstaff dances exist in a variety of cultures, and a performative ritual frequently both trains for and precedes involvement in a variety of martial arts. Brazilian males dancing capoeira are sublimating an aggressive martial art in cooperative action (Downey, 2008).
- Musical instruments have survived intact as well as in artistic depiction. Excavated at Hole Fels in Southern Germany, flutes crafted from the wing bones of birds have been dated to over 35,000 years ago, as well as one at Geißenklösterle, more painstakingly carved from mammoth ivory (Conard et al., 2009). Other surviving prehistoric musical instruments have included whistles and bullroarers (Morley, 2013). Stockmann (1986) reviewed evidence from European and Mediterranean sites for drums and drumming, including artistic depictions of performance. In accounting for these earliest appearances of surviving instruments, one assumes that where the bone, ivory, and pottery from which they were made has survived, precursors or templates made from wood or bamboo would not have done. There are no prehistoric bark trumpets or didgeridus: but the prevailing ingenuity of craftsmen around the world in making musical instruments from a wide variety of local materials convinces that there could have been equivalents (Espí-Sanchis and Bannan, 2012). A further consideration would be the technological similarity between the design of instruments and those of weapons. Which came first, the end-blown flute or the blowpipe? The sling or the bullroarer? A clue exists in the two different forms of bow on which music is made by the Xhosa people of Southern Africa. The men's hunting bow has a musical equivalent that is played as a resonant bass percussion instrument; women also play, in a more genteel fashion, a scaled-down version that could do no harm to anything, held in the left hand resting on the lap while it is bowed with a stick held in the right hand (Dargie, 2011). Both male and female versions accompany and interact with song within the vocal range of the player.
- Pottery can be employed to make the bodies of drums over which skin can be stretched. It is also an ideal medium for decoration. Garfinkel (2010) proposes that the repeated patterns of human figures on the rims of pottery vessels from several locations in the Eastern Mediterranean and Mesopotamia depict the act of massed dancing that coincides with the kind of large-scale

organisation of labor necessary to devise the irrigation systems and crop husbandry required for the development of agriculture.

- Tools: flint-knapping involves musical listening of a precise kind if fault lines and striking points are to be efficiently detected (Cross et al., 2002). It also leaves a trace on the listening ear in terms of rhythmic iteration and the evaluation of acoustic properties (Blake and Cross, 2008). Where work is to be engaged collectively, it may be achieved to the beat of a drum or to the self-accompaniment of song. Tools – blades, awls, scrapers – would have been essential to the production of musical instruments, while their potential for sound production also gave rise to modified versions of them being employed by performers as musical instruments themselves. There are musical saws and hammers that are still required for the performance of works of art.
- Toys: children's playthings tend to mimic the associated items of the adults of their gender. Boys play-fight with objects resembling weapons. Girls tend to objects that they care for as if nurturing an infant. Songs may accompany these activities, and the narratives arising in relation to them can form a rehearsal for presented drama.
- Burial and funerary goods: the burial of the dead is near-universal in human culture and involves ritual that may comprise musical and oratorical performance. Tolbert (1990) investigated the key role that women's funeral lamenting plays in the musical practice of Karelia. Where people gather to mourn, there is music, and an appropriate rate and quality of movement.
- The adapted environment: in widespread parts of the globe, natural lithophones exhibit shaped surfaces and evidence of wear that illustrates the exploitation of their acoustic properties. These include sculpted stalagmites and stalactites (Díaz-Andreu and Mattioli, 2016); free-standing rocks (Boivin, 2004); and instruments assembled from component pieces of natural stone (Blench, 2006; Espi-Sanchis and Bannan, 2012) – a process that may have formed the template for the development of subsequent technologies for the crafting of tuned instruments from less durable materials. The field of acoustic archaeology proposes that we listen to the acoustic potential of both natural and man-made spaces and the decorations painted or inscribed upon them as a component of understanding their

wider significance (Ouzman, 1997; Rifkin, 2009). In particular, one may speculate on the kinds of performative behavior, including specialized clothing and ritual enactment, that may have been associated with the cultural function of such environments (Watson and Keating, 1999; Till, 2014), and the times of year and season in which their relation to astronomical markers was of special significance.

This brief summary of the proximate interpretation of evidence that has come down to us from prehistoric cultures presents parallels with our own modern responses to the acoustic properties of special environments, the playing of instruments fashioned from a wide range of available materials, and the nature of occasions on which performances take place. It provides a foundation for thinking about how such properties are exploited in the wide range of ways through which the performing arts are engaged in today, both in traditional societies and contexts and in the new media that modern technology provides.

A conceptual bridge between prehistory and modern practice has been constructed in the work of archaeologists and anthropologists who have been able to work alongside traditional culture-bearers. This kind of collaboration illuminates the relationship between ancient and more recent artefacts as both contributing to continuing cultural significance. A complementary approach to the analysis of cultural development traces possible continuity between the ancient – surviving artefacts and the impact on the environment of historic and prehistoric ancestors – and the modern, as the use or interpretation of prehistoric evidence is sustained in the practices and lore of recent or current descendant populations. This form of chronologically presented, comparative interpretation is particularly associated with the archaeological practice pioneered in southern Africa by David Lewis-Williams, especially in application to the artistic heritage

of the Khoisan (Lewis-Williams, 2010). A similar collaborative agenda for the exploration, preservation, and interpretation of Australian cultural material is set out in the work of Griffiths (2018) and Pascoe (2018). Reference to models of this kind permits an insight into the examples of ritual behavior that may be associated with artistic performance in the wide variety of cultural practices that have emerged in the radically contrasting environments and climatic conditions of the world.

Two aspects of the practice of the performing arts are associated with the kinds of evidence that have given rise to our understanding of the role of music and dance over deep time: their capacity to act as mnemonic media for the recall of information that represents ‘who we are’, and the array of material objects on which artistic performance has come to depend.

The mnemonic function in song transmits knowledge from one generation to another. Children have their own repertoires, sometimes created or adapted by them as an alternative to the models endowed by adult teaching (Bannan and Woodward, 2008), including danced and body-percussion components (Chagall, 2014). Bowra (1962) reminds us that ancient texts such as The Bible and Homer came into being as written records arising from oral transmission of far greater age, a process for which he sought parallels in the song literature of indigenous Australians. The song lines of Australia illustrate how a repertoire committed to memory can represent knowledge of geographical relationships, sources of water and sustenance, and degrees of relationship with other people, as well as spiritual explanation for the world as the individual comes to know it as a privileged initiate (Blair et al., 2002, Norris et al., 2014).

A similar kind of repertoire has come down to us in the Psalms of David – poetry intended for sung performance – since it includes instruction on when and with what enthusiasm to sing it, and, in the case of

Psalm 150, with precise directions for the accompaniment of instruments. The Psalms combine historical and geographical information with religious instruction and the provision of emotionally varied texts suitable for different occasions. The Psalms formed the performative bedrock of monastic liturgy within the Christian tradition that inherited this Jewish literature as a pattern for living, performed in their entirety over the cycle of worship of the religious orders (Zieman, 2008). One particular psalm carries an additional element beyond its Hebrew verbal origins, even despite translation into Latin and English. Psalm 114 (in the Anglican Prayerbook numbering) can still be sung to a melody, the *Tonus Peregrinus*, a mode of musical performance markedly different to the tonal conformity of the Gregorian Chant through which the psalms were intoned for over a millennium. Instead, the lines of Psalm 114 (‘When Israel came out of Egypt/And the House of Jacob from among the strange people’) are sung predominantly to two alternating reciting-notes, a practice that has been traced to the earlier tradition of performance in the Jewish temple itself (Lundberg, 2004). Both text and music represent a recorded version, now translated into most of the world’s languages, of an originally oral tradition. But in this case, the trace of the means of melodic performance would seem to have survived alongside the text.

The mnemonic role of the Psalms took on a more elaborate role as composers in the European monasteries, colleges, and cathedrals adopted their texts and melodic intonation as the basis of increasingly extravagant musical works. Initially adding complementary voice parts weaving their way around the traditional chant, composers from the 13th century onwards employed the potential of music notation to record in written form music of a complexity that could not have been conceived or transmitted orally. The setting of psalm texts played a significant part in the output of composers as diverse as Josquin, Palestrina, Monteverdi,

Schütz, Handel, Bach, Mozart, Bruckner, Stravinsky, and Britten, as well as the many widely known hymns based on their texts rendered in metric form, and a song, *By the Waters of Babylon*, by the rock gospel performers Boney M. Within the two millennia of the Judaeo-Christian tradition, spanning the world through colonization, vocal performance of the psalms represents a songline of a scale unmatched by any other.

A curious instance of the mnemonic properties of music transmitted inter-generationally that illustrates the uniquely human, cross-modal nature of this form of information encoding and retrieval is provided by the case of vocal learning in a species other than our own. A farmer in rural New South Wales found that the music by J. S. Bach he was performing on the flute was being learned by a young lyrebird (Powys et al., 2013). The lyrebird's performance was uncannily accurate both in sound and content. Does this make it the equal of human music? The lyrebird went on to 'teach' this repertoire to subsequent generations. While the results may have been recognizable to an extent as versions of Bach's music, their survival in the form of a bird's repertoire of song is a quite different phenomenon to that of human music retaining reference to preceding times and places in human experience – not least the crafting of the instrument for which Bach wrote his music.

The cross-modal aspects of human musical performance are often more evident in the cultures of, for instance, Africa and the South Pacific than within the European tradition in which notation has influenced the means by which repertoire is learned. Movement and dance play a part in the embodied structure of song, the interaction between performers, and the relationship of performers to the space in which performance occurs. If a performed songline can achieve a navigational function equivalent to that of a visually presented map, what in origin may have been the relationship between these two modes of encoding and retrieval? Might there

have been interaction between performance (vocalization, stepped movement in specific patterns, mimed direction) and visual media – for example the first rock engraving to be claimed as a map (Deleito, 2019)? If this is not a map, what is it? When is an artefact art, let alone a pointer to performance? If this is not the first map so far discovered, then what alternative candidates are there?

In examining the mnemonic properties of performance, we have indicated some features of culture that exemplify its purpose. An alternative field of enquiry is to consider the role of artefacts as components of performance, whether as adornments of the performer, or as tools and prosthetics that extend the range of the human body in visual, spatial, or acoustic dimensions. In turning to the function of material objects and the evidence for their role in performance from prehistory to the present, we can approach their use as augmentations or decorations of the body. Extrasomatic resources for artistic representation and communication include prosthetics such as: stilts, which permit the enlargement of the human frame and the depiction of beings with qualities that may range from either the comical and amusing to the superhuman and disconcerting; masks, which similarly distort, conceal, or amplify the facial repertoire of the wearer; and puppets, which stand in for their human manipulators through a variety of means (including: shadow projection; suspended from strings, as with a marionette; moved with rods; worn like a glove, brought to life through movements of the fingers; held in front of the performer like a smaller projection of their natural movements).

Musical instruments are tools for the controlled production of sound. They can be crafted from a wide variety of available material – bone, ivory, skin, hair, wood, bamboo, silk, stone, metal – and can be grouped by the manner in which they are played: aerophone, chordophone, membranophone, or idiophone (Hornbostel and Sachs, 1914). While designed principally to provide for effective

performance, they may also be highly decorated, and be considered works of art in their own right. The sounds of instruments may have iconic, referential roles in dramatic performance, from Chinese Opera to film music, and also in providing the accompaniment to specific genres of dance, religious processions, military marching, and social events.

Fire has had a role in ritual and performance, both as a source of light – whether the candles of religious ceremony or the blazing torches of open-air events – a symbol of cleansing, in the form of incense, or a supplier of heat, whether that of the hearth around which dancing and music could be performed and tales told into the night, or with the purpose of ritual burning, including animal sacrifice. The *auto-da-fé* of the Inquisition was a public spectacle involving music, costume, incantation, and a fiery conclusion. Since the development of safe means of lighting buildings in the 19th century, stage lighting has become an art-form in its own right through the medium of *son-et-lumière*, and lighting plays a vital role in creating the atmosphere of theatrical, ballet, and opera performances. Our response to the colors and intensity of light in achieving such affects have their origins in our experience of the natural world.

Other external artefacts that convey or enhance performance include vehicles – such as those built for street processions, pageants, and carnivals (and which are replaced by decorated boats in places such as Venice and the Pacific islands where transport is normally on water) – or effigies that are carried publicly to celebrate supernatural beings, such as the Madonnas of Catholic Europe or the juggernauts of Hindu festivals in India. Large-scale outdoor events such as these employ banners and flags that carry text or motifs appropriate to or explanatory of the occasion.

These features present proximate examples of the ways in which people observe performance practices, the places in which they do so, and the means they employ. What may be the evolutionary origins of these characteristics?

THE ANIMAL ORIGINS OF EXPRESSIVE REPRESENTATION AND COMMUNICATION

Comparative observation of animal and human behavior suggests that the origins of the performing arts may have represented a bridge shaped by two principal selective mechanisms: mate attraction and retention, and the development of a theory of mind that permits understanding of the intentions and emotions of conspecifics and which empowers collective action. Geoffrey Miller (2000) argues strongly for the role of sexual selection in shaping behaviors such as performance, citing the attractiveness of musicians and dancers in myth, history, and contemporary media coverage. He proposes that art and music were ‘conspicuous display behaviors’ (Miller, 2000: 5) and cites Zahavi’s Handicap Principle (Zahavi, 1975) as a means of explaining the biological basis of altruism whereby prominence in protecting and providing for others is a desirable trait. The contribution to survival made by superior genes coming together through such a mechanism may well explain courtship rituals and anatomical adaptations such as the relative lack of body hair in females and the octave difference between adult male and female voices. However, sexual selection, while playing a definitive role in the development of human characteristics, is insufficient to explain our lifelong engagement in performative interaction: for instance, it does not account for the instinct of infants to respond to music and participate in dance and play-acting (Dissanayake, 2018).

Collective interaction presents a different form of achievement. Robin Dunbar (1998) modeled the birth of language as a focused and efficient form of grooming that permitted larger-brained hominins to keep track of social relationships in groups of increasing size and went on to demonstrate the measurable social benefits of collective laughter (Mehu and Dunbar, 2008), choral singing

(Dunbar et al., 2012), and dance (Tarr et al., 2016). The integration of independent adaptive traits over the thousands of generations, in which our ancestors met and survived changing environmental pressures, indicates that an iterative mosaic of psychological and cultural factors has been at work.

Donald (1991) proposed *mimesis* as an adaptive stage between animal communicative behavior and human culture, including the later emergence of speech. Links between animal behavior and human cultural practice remain prevalent, for a variety of reasons. We are from childhood fascinated by animals: those we relate to as pets, those that we encounter in everyday life such as birds, those we see in zoos or in safari parks, those familiar from wildlife documentaries, and those brought to life by CGI such as dinosaurs and extinct megafauna, or in their anthropomorphic representation in animations such as those made by Disney. The imitation or mimicry of animals plays a role of great significance in human cultural practices. The depiction of animals is one of the oldest and most universal themes in the visual arts (Clark, 1977).

Imitation of animal behavior informs cultural practices from children's songs and games to ritual enactments and spiritual representation (Lewis, 2009). A song structure that invites participants to mimic animal sounds, such as *Old McDonald had a farm*, has widespread parallels around the world (Durojaiye, 1977; Gammon, 2011). Adolescent Watussi girls in Zaire imitate the mating dance of the crowned crane (Wosien, 1974: 86–87), a behavior consistent with material evidence and depictions of similar rituals in prehistoric Çatalhöyük (Russell and McGowan, 2003) and found in cultures throughout Europe and Asia (Armstrong, 1943). Notably, cranes are, like swans that also feature strongly in artistic depiction and narrative, a pair-bonding species.

Ridington (1993) described the relationship between animal imitation and hunting practices in the pre-Columbian Salish of

Pacific Canada, including the dancing that accompanied feasting. Individual hunters identified closely with the species which they acquired the special expertise and ritual approbation to kill. Similar beliefs and practices have been found in hunter-gatherer societies in South America, Africa, and Australia, illustrating close connections between the management of food sources, religious systems, and ritual enactment in performance (Nadasdy, 2007).

The interdependence of mankind and animals presents impressions of both ultimate and proximate evolutionary processes. In the former case, man shares instinctive responses and anatomical functions with distant ancestors that shape behavior and interaction with the environment; in the latter, specific attributes of culture are transmitted intergenerationally as the means whereby infants acquire the skills to survive and, eventually, to reproduce. Zlatev et al. (2005) reviewed the influence of Donald's (1991) staged adaptive sequence for the emergence of human culture, drawing on a range of literature concerned with child development, semiotics, and theory of mind to propose *mimesis* as 'the missing link' in human cognitive evolution. The synthesis presented draws on Vygotsky's (1962) proposal for how infants assimilate cultural competence, first on the social (interpsychological) level, and secondly within their own minds (the intra-psychological level). This represents a mediation between social and cognitive intelligence (see Gardner, 1983 or Mithen's, 1996 'chapels of the mind') that proceeds from imitative interaction to generativity. Grice's (1969) formulation for recursive, intentional communication guides evaluation of the sequence whereby complex, multi-modal transmission emerges from simple imitative origins. This is exemplified in Zlatev et al. (2005: 5) in four stages: *Proto-mimesis* (facial expression, bodily synchronization); *Dyadic mimesis* (shared attention, imperative pointing, mirror self-recognition, do-as-I-do imitation); *Triadic mimesis* (joint attention, declarative pointing, pantomime);

and *Post-mimesis* (signed language). In cognitive terms, this model clearly conveys a hierarchical sequence that captures the stages which distinguish human from animal capacities, consistent with the implications of Vygotsky's (1962) Zone of Proximal Development. In Vygotskian terms, *tri-adic mimesis* could be viewed as a stage of development achievable with human intervention in apes, as with parental support in children; but this is the peak of what the ape can achieve, whereas it is a springboard for continued normal development in human infants (Zlatev et al., 2005). This is the point at which the capacity for the performing arts takes flight.

One nagging doubt, however, accompanies consideration of the model explored by Zlatev et al. (2005): why the implied silence of our ancestors ('pantomime'; 'signed language')? It is an issue that troubled Steven Mithen (2003, 2005), motivating his speculation on the musicality of the Neanderthals, and his depiction of early modern humans as dancers, singers, and players of instruments. Aside from the evidence of acoustic archaeology (Ouzman, 1997; Rifkin, 2009), it seems illogical to imagine a cognitive bridge in which the noisy interactions of our nearest genetic relatives did not continue and adapt in parallel fashion to connect with our modern capacity for controlled vocalization, and its combination with other communicative modes. Especially if one considers the necessity of sonic communication where dense vegetation and the long grass of the savannah offer concealment, early human capacity for elaborate and appropriately controlled vocalization – including animal imitation – would seem to offer a survival strategy.

In this respect, a multi-modal Gricean formulation provides a model for the emergence of the performing arts. Intentionality and theory of mind are thus evident not merely in language, but also in other media – music (Livingstone and Thompson, 2009) and dance (Chaplin and Norton, 2015), as well as the mimesis envisioned by Donald (1991).

Visual representation of physical processes (such as the cartoon-form instructions that illustrate how to assemble flat-pack furniture without employing language) assumes a similarly shared vocabulary.

In summary, modes of representation and communication such as music, dance, mime, and language permitted humans to employ each other collectively as means for external symbolic storage prior to the development of extrasomatic systems such as writing and depiction. Human bipedal locomotion defines a rhythmic gait, building on an initial quadrupedal stage, onto which elaborate independent employment of the limbs can develop in response to the playing capacities associated with a variety of tools. Instruments such as the piano, the church organ, and the drum-kit require simultaneous, integrated control of all four limbs, as do dance and performances and rituals that involve the carrying of objects while moving – coffins, sculptures, flags, palm leaves, weapons, and the maneuvers of marching bands together with the actions of the drum-majors who direct them or perform choreographed accompaniments through baton-twirling.

Some properties of the principal modes of artistic performance that emerged universally from ancient origins thus include:

Music: meaningful employment, including in synchrony with others, of control of duration, pitch, timbre, and loudness;

Dance: control of stasis, rate of movement, pattern of steps, employment of the arms either independently of the movements of the legs, or in coordination with them; synchronisation with others and/or to music;

Mime: poise; focused imitation of external models including work, the movement patterns of animals and machines; communication of emotion.

While many of these properties are shared by and arguably traceable to those of non-human species, their integration into the encoded cultural practices of humans have unique characteristics of embedding and referentiality, and aspects of these have been

captured in ancient rock art and cave paintings indicating that behaviors of this kind have a long history. Music, dance, and mime may be combined with language in dramatic representations. But all three modes of performative representation and communication can be viewed as alternatives to speech and as founded on animal behaviors that clearly predate the emergence of language in our species.

EVOLUTIONARY PATHWAYS TO HUMAN CULTURE: LEARNING PROCESSES, REPRESENTATION, AND COMMUNICATION

In the diverse contexts of play, ritual, and narrative presentation, the animal origins of a range of behaviors can be discerned. The context in which physical interaction takes place in human culture relies on the development of the human brain as a multi-modal processor capable of metaphorical and recursive thought (Corballis, 2007). This has enabled instinctive responses traceable to pre-human origins to be ‘harnessed’ (Changizi, 2011) to representational or communicative purposes. For instance, a repertoire of gestures can be observed in chimpanzees that remain central to behaviors arising from physical interaction. These include the adult tickling of infants (Plooij, 1979), the equivalent in humans of which is the kind of play-assault in song-games such as *Round and round the garden* (Dissanayake, 2018), and its adult-to-adult continuation in sexual foreplay and copulation (Tutin and McGrew, 1973).

Provine illustrated the communicative power of two adaptive behaviors that are ‘contagious’ in humans: yawning (Provine, 1989) and laughter (Provine, 1996). Human yawning, an ‘honest’ sign of weariness, triggers the desire to yawn in others. Laughter also sets up a chain reaction, eliciting responses even when participants are not aware of the

source of amusement. Lacrimose crying is a further emotional signal unique to humans (Provine et al., 2009). These biological expressions form the basis for shared emotional experience, open to amplification in the structures of communicative media such as music and drama in which the continuity, variation, and pace of emotional affect can be controlled as a function of the storyteller’s art. They give rise to metaphorical elaboration: in the case of yawning, the calm before the storm as much as the depiction of readiness for sleep; and to presentation that, in the case of laughter or crying, can range from the authentic to the artificial or duplicitous, from the truly funny or sad, to mocking laughter, *schadenfreude*, and crocodile tears.

Deacon (1998) illustrated the cognitive outcomes of contagious social interactions and their capacity to recruit shared emotional states. The powerful forces involved in religious ceremony (‘We believe ...’), oaths of allegiance, and the like, draw on this human trait and have entered the repertoire of dramatic performance where crowds and choruses are swayed in support of a cause. The nature of such collective behavior is quite different to that of animal species which may appear to resemble it. Vervet monkey ‘language’ – the specific acoustic and kinaesthetic response to threats from snakes, eagles, and leopards – presents both similarities and differences to human artistic performance (Seyfarth and Cheney, 1980). Notably, vervet communication is multi-modal: while sound alerts those out of sight to the presence of a threat, the behavior it accompanies is physically uniform – a dance-like response oriented to the required secure outcome. However, the calls are not so much ‘words’ referential to perceived visible stimuli as signals that initiate a fixed-action response: ‘This is what we do when one of us makes this noise’.

Within the constellation of the performing arts, drama poses a special problem due to its embrace of language and, in the many instances that survive in widespread cultures, its dependence on literacy. Since

language is a uniquely human trait, we should perhaps view drama as a blend of mimesis and language, able to represent in a heightened manner the narratives that may previously have been transmitted by oral tradition around the campfire.

Kidd et al. (2016) proposed a means of investigating the role of storytelling in the acquisition of theory of mind. Certainly, narrative has a mnemonic function that parallels those we have assigned to dance, mime, and music. Drama, as a performative presentation of existing work, whether transmitted orally or recorded in writing, permits the intensification of the experience and its communication to increased audiences.

Oatley (2001) attributed to the simulation of emotion a key role in the cultural phenomena of storytelling and drama: 'Emotions in the individual are types of readiness for certain repertoires of action' (Oatley, 2001: 27). He focused particularly on three emotional states that are open to depiction and elicitation: attachment-based anxiety, assertion-based anger, and affection-based happiness. The means by which narrative and its presentation transmit these attributes onstage to the audience 'transforms our vision of an aspect of reality' (Oatley, 2001: 30). Oatley's analysis of how this is achieved in drama accords with Scherer et al.'s (1991) investigation of the ways in which actors in radio plays adapt their voices in order to communicate the emotional correlates of their lines.

MORTALITY, CONSCIOUSNESS, AND THE CYCLE OF LIFE

What may have been the adaptive Rubicon crossed by the human species which conferred the additional layer of recursive thinking, linking emotion and cognition (Damasio, 1994) in biographic memory and culturally informed response? Harvey (2017) suggests that the step through which humans attained the modern mind capable of language,

metaphor, planning, and multi-modal thought and communication was associated with recognition of our own inevitable demise. Addressing the unthinkable motivated the complexity of thought as consciousness of mortality demanded ritual response to allow us to deal with the death of our loved ones, and by extension, of the gods we imagined inhabiting the extended reality that lies beyond death, as well as the perilous destination that each of us faces alone. Young (1992) found in early literature themes that he took to represent a spiritual response not only to death, but to cannibalism and the expiation of guilt. The role of the afterlife in many religions, of reincarnation, and the elaborate rites associated with the appropriate disposal of the dead, illustrate a valuing of human life consistent with understanding that the struggle for existence is played out in a special manner.

Where death is the ultimate separation, we first experience fear of loss in our dependence on care in the long helplessness of human infancy. Maternal separation and separation from the family play a part in the narrative structures of dramatic performances, in which long journeys (Odysseus, Sinbad), periods of living incognito or as an outcast, or lives lived unknown to biological parents are resolved in the emotional release of catharsis and the desire to 'live happily ever after'. Each of us identifies with the hero or heroine whose experience is captured in the narrative: whether the 'Everyman' of medieval drama whom we are invited to consider standing in for us so that we learn from his trials, or the more ancient and colorful figures of legend – Hercules, Hamlet, Joan of Arc, Sita, Robin Hood, Cleopatra, or Pocahontas – whose triumphs and disasters we map evenly onto the shifting emotions of our own lived experience. In doing so, we imagine the achievement of our personal survival, or its equivalent in the commemoration of a glorious death. Art documents the process of human individual and collective continuity: 'Kilroy was here' is writ large and creatively,

from hand stencils on cave walls to a graffito on trees and buildings, and from campfire song to grand opera or a Broadway hit.

PSYCHOLOGICAL FEATURES OF ARTISTIC PERFORMANCE

The infinite generative complexity of the human mind gives rise to artistic products that work on us at many levels. They invoke memory, permitting the anticipation of outcomes and intensifying the emotions we associate with them. They both promote and challenge social cohesion. They intersect with the cycles of seasons and life, reflecting by way of preparation and initiation or recall and explanation the parallels to our own biography of the imaginative worlds to which we are exposed. They achieve this through processes that elevate and make distinctive. Drawing on his application to the origin of language of the *developmental stress hypothesis*, whereby singing birds that make the greatest sacrifices in exhibiting complexity and stamina in song bouts attract the mates through which this trait is reproduced, Merker (2018) proposes that human culture arose through the phenomenon of extravagance: the valuing of the special, that which inspires awe. Aesthetic judgment thus evolved, as Darwin (1871) suggested, on the lines of sexual selection. But it exhibits in the earliest phases of life, in the attraction of infants to the shiny, colorful, pretty-sounding, well-proportioned, and impressive. Dissanayake (2018) views this as related to the patterns of ritual and developing out of the play behaviors through which children interact with the world around them, including ‘dressing up’.

We can set out, therefore, a listing of the means by which behaviors are endowed with extravagant or elevated qualities (Table 23.1). This rudimentary set of examples demonstrates processes that link the small-scale, polite, and meaningful affordances and gestures of everyday life to the major

Table 23.1 The instinct to embellish and adorn everyday behaviors

<i>Everyday Category</i>	<i>‘Elevated’ Category</i>
Eat	Feast
Drink	Toast
Bury (dispose of dead)	Commemorate
Use of fire	Fire festival
Promise	Oath
March	Goose-step
Awaken	Enact dawn ceremony

undertakings that bind audiences and congregations to elaborate events which depend on expensive and meticulous preparation with the intention to impress.

Aesthetic judgement is founded on emotional responses associated with the attainment of comfort and security from the last trimester in the womb and through responses to the discovery of the self, the world, and other people in infancy (Falk, 2004; Parncutt, 2009). Trevarthen (1998) described the conventions through which *infant semiosis* arises from the intersubjectivity that develops between child and mother, and Street et al. (2003) illustrated that new mothers who did not see themselves as musical became expressively able to communicate through song via the releasing mechanism of caring for a first child. The mother-infant dyad transmits the capacity for performance within both generations, the form of the lullaby arising universally and sung by men as well as women (Nelson, 1997). Play continues its educative and enculturating functions as children attain greater independence. Winnicott (1971) illustrated the key role of the *transitional object* – a favorite toy or security blanket – that stands in for the carer as an imagined source of affection, a metaphorical application open to the youngest mind. Romet (1992) traced the process whereby young children begin to prefer playing with each other, acquiring through singing-games knowledge of rule-based systems that govern turn-taking and social interaction with peers. Cook (2000) argued the importance of such experiences

for the acquisition of language – the ultimate rule-based system – as much through play (songs, chants, altered voices, games) as through more formal processes. The special nature of children's games as a private world exchanged without adult intervention was analyzed internationally by Opie and Opie (1985; see, also, Bannan and Woodward, 2008; Chagall, 2014). Such games and role-play teach anticipation and primed response (Bettelheim, 1987), preparing the player for the appropriate action when required: fight or flight, dodge and counterpunch, serve and volley, parry-riposte. As such, they are adaptive, contributing to survival, while at the same time allowing bonding with peers and membership of the group as learning leads to belonging, and initiation to acceptance.

Neoteny exhibits in humans (Gould, 1977) in two principal ways: the relative similarity of our adult form to a proportionally enlarged version of the infant, and the extension into adulthood of infant behavioral traits. Chisholm (1999) viewed this as a process of self-domestication – the lifelong extension of the 'play window' which closes in other species as they emerge into sexual maturity. Chisholm's formulation provides a convincing model for an evolutionary account of the origins of the performing arts. Recent work on the role of artistic stimulation in patients with Alzheimer's disease demonstrates that media other than language may remain available for communication and affect where speech is inhibited. But the capacity to sing (Bannan and Montgomery-Smith, 2008) or dance (Karkou and Meekums, 2017) in old age needs to have been primed through experience in childhood. Under such circumstances, the arts remain available to us lifelong. An instinctive inclination to interact with the newest generation remains present to the end of our days (St John, 2012).

This perspective on the cycle of life recalls Harvey's (2017) proposal that music (and by my interpretation, the arts more generally) presents the process whereby we cope with

the certainty of our own mortality. Such a role for the arts clearly developed alongside the practice of religion, the enhanced emotional responses of awe and wonder giving rise to spirituality and ritual prior to the belief system that depends on language and sacred texts. Oubré (1997) imagined a religion without words that paralleled music as a bridge between animal behavior and language; and a framework for the evolutionary origins of religion (Atran, 2004; Boyer, 2007; Lewis-Williams, 2010) represents a synthesis that transcends the opposition of evolution and belief. The gods and Muses may, according to our literature and repertoire of song and drama, have conferred the capacity for the arts and inspired their practitioners. An evolutionary account of human behavior embraces both worlds.

OUR EVOLUTIONARY FUTURE: THE NEW ENVIRONMENT OF AI

An evolutionary perspective on the performing arts would be incomplete without speculation on what the future may bring. One might hope to see the policies of education providers become informed by the position outlined in this chapter, consistent with the view that the arts are essential to human well-being.

A new influence on human cultural development has arisen since the capacity became available at the turn of the previous century to record artistic products through mechanical and electronic means. During the last 50 years, advances in digital technology have accelerated the employment of devices for the storage, manipulation, creation, and retrieval of images, sounds, and recorded information. Computer generated imagery can enthrall, amuse, and deceive. The artistic history of the world is rapidly becoming accessible at the touch of a button. The medium of music, for instance, has become open to analysis on evolutionary lines adopting the process

of memetics (Dawkins, 1973), to account for growth and change within and between works and styles (Jan, 2007). Parallel to this analytical and philosophical agenda, musical creativity has been synthesized in Artificial Intelligence applications capable of a range of compositional achievements (Chamberlain et al., 2018; Miranda, 2003). Image, plot, and music combine together in the worlds of computer gaming (Kirke, 2018) and Alternative Reality (Men and Bryan-Kinns, 2018). It remains to be seen whether innovations in the generation and presentation of artistic performance represent a continuation of the evolved continuity reviewed in this chapter, or a novel phenomenon that will define a new relationship between the genetically endowed capacity for artistic response and participation and the cultural environment with which this interacts.

Note

- 1 Darwin had himself been misled by the claimed research of Sir Duncan Gibb (1869) into reporting that the 'different races' of man have different larynxes. This remained an uncorrected viewpoint regarding the range and capacity of the singing voice as recently as the 1970 edition of the Harvard Dictionary of Music.

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Evolutionary Psychology and the Visual Arts

Richard Hickman

INTRODUCTION

My first university qualification was in Fine Art, specialising in painting; I have been professionally involved with art, education, and art education for over half a century. While my professional interests have revolved around visual art and, to a lesser extent, developmental psychology, my personal interests lie elsewhere: natural history, particularly ornithology and palaeontology. In attempting to address the difficulties of maintaining an academically rigorous argument, I draw upon my personal and subjective experiences of over 50 years of practical and theoretical work within the art world. I position myself, therefore, as an artist with an active interest in evolutionary psychology, rather than as an evolutionary psychologist with an active interest in art. As an academic artist, I have read many texts written by the latter and have been aware of the tendency among such authors to adopt a simplistic view of the nature of art and art-making.

In this chapter, I hope to avoid the tendency to make assertions about disciplines that are beyond my area of expertise and use my theoretical and practical art experiences to inform the present text. While autoethnography could not be considered to be a reliable source of information in discussions about evolutionary psychology, in the present instance, some degree of introspection on my part could prove useful, so I shall draw upon some of my own experiences as an artist and educator to inform my argument.

As a student, and also in my capacity as an educator visiting many different schools in different regions, I noticed that there was often, if not always, someone in each class who was 'good at art' – this usually meant someone who was skilful in representational drawing. In my own case as an eight-year-old, I was a prolific scribbler, and when I was praised and eventually rewarded with my first 'gold star', I scribbled all the more. This extrinsic reward of praise created a 'virtuous circle' of practice/reward/practice/greater fluency/reward, etc.

An early memory was my parents discussing with other relatives where my alleged artistic ability ‘came from’, with one aunt recalling that one of my uncles was ‘good at art’. My early ability in representational drawing was not simply a social, learned phenomenon but arose more or less spontaneously and was fostered through social interactions. Everyone can learn to be more skilled in a particular activity; while skills can be developed, some people appear to have a higher level of innate skill and a greater predisposition to skilfulness in certain areas. On the basis of my observations, not everyone is capable of producing art work of great merit (however we define it), nor is everyone capable of making highly refined aesthetic judgement, but in both cases – that of making and appreciating art – all are capable of getting more skilled as a result of tuition and practice. If one accepts this, then it follows that all humans have an inborn capacity for some kind of artistic ability – of being skilled in artistic representation and making aesthetic judgement – but the level of such skill varies. Of crucial importance is the notion that whatever one’s starting point, we can become more skilled through instruction.

DEFINING ART

We should not underestimate the difficulties associated with the topic of evolutionary psychology and the visual arts. The concept of art is contested, while evolutionary psychology as a discipline is relatively young and by its nature is subject to conjecture and assertions based on circumstantial evidence. As noted by Dissanayake (1995a: 101), it is only when we have an ‘adequately defined’ definition of art that we can proceed with any discussion pertaining to its role in human evolution.

So, what do we mean by ‘art’? The ‘we’ in this instance refers to 21st-century, educated English-speaking readers. I have noted at

length elsewhere (Hickman, 2010) that there are at least 14 different senses of the word ‘art’ as it relates to skill (as opposed to, for example, the old English phrase ‘thou art’). It is interesting to note that only one of these is in the sense of what is often referred to as ‘Fine Art’. No English dictionary before 1880 defined art in the sense of having an association with the creative and the imaginative; this association, as a means of classification, dates from the late 18th century.

A current commonly accepted notion of what art-making behaviour involves can include the concepts of skill, expression, and imagination; to these, we can add the ability to make aesthetic judgment. Art-making, or rather, as Davies puts it, ‘art-behavioral competence’ (2012: 51), can be seen to be the ability in humans to bring together skill, expression, and imagination. It is noteworthy that Gardner (1999), in his influential work on multiple intelligence, identifies several types of ‘intelligence’, including musical intelligence, but does not identify an ‘art intelligence’. This points us to the notion that ability in art may not be one single competence but a group of competencies. I suggest that a suitable term to replace ‘art-making’, one that is broad and inclusive of cultural difference, is ‘creating aesthetic significance’. However, because involvement in visual art involves judgement and appreciation, my preferred term is the more comprehensive ‘creating *and* conferring aesthetic significance’. This term is useful in that it can be related to making (as in ‘creating’) and forefronts the concept of aesthetic judgement, which is central to any discussion about ‘art’ phenomena. Moreover, the word ‘significance’ is useful in highlighting the notions of value and meaning or indeed being special (see Dissanayake, 1995b, and the following section).

The available literature is wide ranging and draws upon several disciplines, including ethology, archaeology, and anthropology. Further to this, De Smedt and De Cruz (2010: 698) asserts that cognitive neuroscience

can offer useful insights and can 'address the proximate causal mechanisms that are involved in artistic behavior, in particular the brain structures that are responsible for art production and appreciation'.

Geoffrey Miller (1999), writing from the perspective of an evolutionary psychologist researching sexual selection, is at the forefront of those proposing that humans have inherited instincts to display social status and that this gives a reproductive advantage. The corollary of this is that art-making, and, presumably, its acquisition, confers such status and is heritable.

Seghers (2015) posits that artistic behaviour might be centred in just one brain area, a suggestion promulgated by Miller (1998). However, it seems reasonable to look for several abilities, each associated with different areas of the brain, that together enable the creating and conferring of aesthetic significance. Pinker (1997) employs what he terms a 'mental toolbox' metaphor to argue that human minds contain a range of tools that can be used, or building blocks that can be assembled, to achieve different behavioural outcomes such as the creating of artefacts. Studies in cognitive neuroscience (e.g. Pearce et al., 2016; Solso, 2000) show that mental features incorporated in artistic behaviour are widely distributed and scattered across the brain. I propose that practical skill, evident in refined hand-eye co-ordination, combined with the ability to give expressive form to imagination, are principal components of art behaviour. These two facilities are likely to be associated with different brain functions that together give us the ability to create and confer aesthetic significance. I shall now comment on the evolutionary dimension of these facilities.

TECHNICAL SKILL

During the past 150 years or so, there has been a gradual move away from valuing

technical skills in the visual arts – in particular, craft skills – towards a greater concern for the idea behind the work rather than the physical work itself. Put simply, the advent of photography and the availability of new technologies and media have led to an emphasis on experimentation and novelty, with practical skill, particularly with regard to verisimilitude, being downplayed. In view of this, I propose that much of what passes for contemporary art can be seen to be a perverse blip in the long line of human creative endeavour. Dutton (2001, 2003, 2009) notes that technical artistic skill is one of seven 'universal signatures' associated with art-making. In advocating a biologically evolved (rather than a socially constructed) conception of art, Dutton identifies six other characteristics: non-utilitarian pleasure, stylistic rules, appreciation and interpretation, imitation, special focus, and, importantly, imagination. A flaw in Dutton's argument, from the perspective of the contemporary artist and from people working in the contemporary art world, is the notion that 'imitation' has anything to do with art as currently conceived. Moreover, from a modern or indeed post-modern perspective, the assertion that art-making is universal appears to be simplistic. Dutton nevertheless asserts that art forms are found everywhere, regardless of culture, and that art's universality suggests that it is connected with prehistoric psychological adaptations. Dutton (2009) uses a larger set of criteria (a 'cluster' definition) for designating a phenomenon as 'art', demonstrating art's cross-cultural and historical universality to give weight to his argument that the instinct to make art is universal. The notion that 'art' is universal flags up again the issue of definition; if we use my preferred term, concerned with aesthetic significance, then we can more easily acknowledge some kind of universality across human culture, especially if we consider such things as concern for one's appearance – hairstyles, for example – the appearance of food, and the desire to have a particular kind of order in our

immediate environment, perhaps reaching its apogee in the creation of gardens.

Proficiency in visual perception is undoubtedly a faculty that helped our Pleistocene ancestors survive on the savannah. A particular skill, one that I have found central to my own artistic practice, is the simple act of *noticing*. Artists tend to notice things, like paint flaking off an old door – revealing a palimpsest of previous incarnations – chimney pots, coins in the gutter, or inebriated wasps rolling around inside rotting apples. Such a facility would undoubtedly have served the Pleistocene hunter-gatherer well.

GIVING EXPRESSIVE FORM TO IMAGINATION

Effective communication is facilitated by the quality of the mode of transmission. In visual culture, the aesthetic quality of the visual form is often highly valued and is usually dependent on the technical skill of the communicator. Mithen (1996, 1999, 2000, 2005), writing as a cognitive archaeologist, postulates an organically based cognitive development model in which the previously separate domains of the mind became accessible to one another. He argues that the brain domains devoted to, for example, technical understanding, social interaction, and natural history have over time blended together; out of this blend there emerged a new range of creative cognitive activity. The notion of ‘creativity’ is a key consideration here: Mithen argues that modern humans differ from their ancestors in that they are capable of original, creative thinking, characterised by what he terms ‘cognitive fluidity’. This refers to the mechanism whereby the modular primate mind evolved into the modern human mind (i.e. after 50,000 years before the present) by combining different ways of processing knowledge. Mithen (1996) further asserts that through the use of metaphor and analogy, modern humans are able to have original

thoughts that can facilitate creative behaviour and in this respect are different from our ancestors. Cognitive fluidity therefore is seen by Mithen as a key element of human consciousness. Mithen (1996) uses the metaphor of the Swiss Army knife to describe the domain-specific nature of the archaic human mind, suggesting that *Homo neanderthalensis* and *Homo erectus* operated in the social, material, and natural worlds by way of a series of largely isolated cognitive domains. According to Mithen, the cognition of modern humans appears to have become less compartmentalised and more fluid.

THE OLDEST ART

Dates for the earliest art forms, or at least evidence of symbolic meaning-making, are contentious, with earliest dates moving back in time as new discoveries are made. At the time of writing, the earliest evidence of non-utilitarian hominin activity that might have some symbolic meaning is in the form of cupules incised into rock. Cupules are depressions in rock surfaces that resemble the shape of a spherical cap or dome, made by direct percussion with hand-held hammer-stones, and are considered the world’s most common rock-art motifs. The fact that they are found on vertical and sloping rock panels in addition to horizontal planes suggests that they were not created for utilitarian purposes, such as grinding seeds. Van Peer et al. (2003) report that seven small pits in a sandstone slab from Sai Island, Sudan, can be dated as being around 200,000 years old. A much older age range has been claimed for numerous cup marks reported from Auditorium Cave and Daraki-Chattan, two sites in the extensive Bhimbetka complex in central India; Malotki and Dissanayake (2018: 73), however, note that this has been refuted by rock-art experts who have since examined the site (e.g. Blinkhorn et al., 2012).

It is possible that hominins other than *Homo sapiens* created forms of aesthetic significance. The lithic figures of what are known as the Venus of Berekhat Ram and the Venus of Tan-Tan, found on the Golan Heights between Syria and Israel during the summer of 1981 (Bednarik, 2003), contain marks suggestive of the head, body, and arms of a female human. The Venus of Berekhat Ram was possibly created during the Stone Age Acheulean culture, which lasted from 500,000 to 300,000 years ago. While the artefact's oldest estimated age has been given as up to 700,000 years old, its provenance is disputed because it was found sandwiched between an upper layer of volcanic residue that is dated to be as 'young' as 230,000 years old and a lower layer dated to much earlier. Nevertheless, it is probably the oldest example of an artefact of its type recorded to date. Of particular significance is that it might have been created by an early hominin such as *Homo heidelbergensis* or *Homo erectus*, as these early humans were alive during the Acheulian period. There is some dispute as to whether they were capable of the symbolic thought processes necessary for creating art, but this 'Venus', together with the morphologically similar Venus of Tan-Tan, give some compelling evidence of very early aesthetic phenomena.

The 'Lion Man' is a prehistoric ivory sculpture discovered in the Hohlenstein-Stadel – a German cave – in 1939 (Kind et al., 2014). It is believed to be about 40,000 years old and has been considered the earliest evidence of religious belief found in an artefact. However, pieces of red ochre found in the Blombos Cave in South Africa, with deliberately engraved designs, are currently said to be the oldest known evidence of the creation of a complex image. Henshilwood et al. (2009) dated the latter finds to be from at least 77,000 years ago. The pieces are carved with a pattern of crossed lines; one can speculate that this shows that humans had a capacity for abstract thought, and use of symbols, tens of thousands of years before they spread from Africa to Europe. Neanderthals inhabited

Europe and western Asia between 230,000 and 29,000 years ago, and archaeologists have found various objects used by them, notably items found in the Fumane cave, near Verona in Italy (Morin and Laroulandie, 2012). Evidence obtained from this cave shows that there was a clean break between Neanderthals and modern humans, both in their culture and lifestyle. Fogliazza (2011–2012), a palaeoartist, recreated a model of a Neanderthal male, based on finds from the Fumane cave showing the use of ornamental feathers and other signs of conferring aesthetic judgement: the ears are pierced and the neck is wrapped in fox fur, from which eagle claws hang; the face is painted with red and black pigments. While it seems that Neanderthals did not use complex tools, they had mastery of fire and built shelters, and it is thought that they had language and a complex social structure, living in small family groups (Wynn and Coolidge, 2004). It is not known why Neanderthals became extinct, but one theory is that they were outcompeted by modern humans – *Homo sapiens* (Flores, 2011). *Homo neanderthalensis* painted caves in what is now Spain before *Homo sapiens* arrived in Europe (Hoffmann et al., 2018). The finding suggests that the extinct hominins, once assumed to be intellectually inferior to *Homo sapiens*, may have been artists with complex beliefs. Neanderthals had larger brain cavities than modern humans (for lucid discussions on brain size in early hominins and the development of metacognition, see, for example, de León et al., 2008; Mithen, 2000). As a side issue, it is interesting to conjecture that modern human's stereotype of an unsophisticated, simple-minded, or even thuggish person often refers to the physical appearance of a typical Neanderthal (at least in the West).

ART BY NON-HUMANS

I have heard it said on several occasions that 'art is what makes us human'. This assertion

is challenged by some who point to examples of animals other than humans making 'art'. It looks increasingly likely that our attitude to non-humans will change over the course of time as we realise that the organisms with which we share this planet are capable of much more than we currently give them credit for. Non-human primates, such as chimpanzees, for example, have given some indication of an ability to make aesthetic decisions. The anthropologist and painter Desmond Morris (1958) worked with a chimpanzee (*Pan troglodytes*) named Congo, who learned to paint abstract paintings. Other primates, such as orangutans, have also produced images that are reminiscent of abstract expressionist art, for example those of Baka, a Sumatran orangutan (*Pongo abelii*) at the Cheyenne Mountain Zoo. The zoo claims that there are 'unique benefits' for orangutans' engagement with art, asserting that painting enriches the orangutans' lives and stimulates their minds. The training process is described thus:

By giving small treats (reinforcing) each time the artist dipped their brush into the paint, and each time he or she then touched the brush to the paper, the orangutans quickly caught on to the process. (Cheyenne Mountain Zoo, n.d.)

This statement, however, indicates that the inclination of orangutans to produce paintings is not innate; it can be equated with training a non-human to do any party trick, through standard behavioural approaches – that is, through positive reinforcement. It should be noted, however, that the chimpanzee Congo was not 'trained' in this way.

Among non-primates, the activities of the male bowerbird (*Ptilonorhynchus violaceus*) are of interest in this matter and are often referred to in the literature (e.g. Borgia, 1985; Endler, 2012; Uy and Borgia, 2000). It is not unknown for other birds to decorate their nests – for example, Benson (1965: 29) noted that the nests of European Goldfinches (*Carduelis carduelis*) are sometimes deliberately decorated: 'I have seen one draped

with fresh forget-me-nots'. However, bowerbirds take this to another level: male bowerbirds create and decorate a structure called a bower; it is not a nest – the important feature of the bower is that it is used only for attracting and mating with females. After mating, females make their own nests elsewhere and raise their offspring by themselves. Males that build superior bowers can mate with up to 10 different females per day; inept bower-builders attract no females (e.g. Miller, 2001). Darwin's (1871) view was that bowers evolved as courtship ornaments, through sexual selection by female choice. Miller (2001: 23–24) asserts that this is evidence of the heritability of aesthetic judgement and aesthetic skill – bowers attract females to copulate by advertising male fitness, and they have no other survival function. The aesthetic quality of a bower is clearly an indicator of heritable skill, and so females have evolved the aesthetic discernment to judge bowers in order to get the best genes for their offspring (Miller, 2001: 23–24). Endler (2012: 282), in putting forward the notion that bowerbirds are artists that have an 'innate aesthetic sense', bases his assertions on his own definition of art: 'visual art can be defined as the creation of an external visual pattern by one individual in order to influence the behavior of others'. This, to my mind, is a compelling but not convincing argument, owing to the somewhat narrow if not simplistic definition of art and art-making behaviour.

ART AS AN ADAPTATION

Pinker believes that art is a byproduct of three other adaptations; namely, the hunger for status, the aesthetic pleasure of experiencing adaptive environments, and the ability to design artefacts to achieve desired ends. Pinker (in Boyd et al., 2010: 128–129) famously asserted that while humans enjoy strawberry cheesecake, it is not because we evolved a taste for it:

of agreeable stimuli which we concocted for the express purpose of pressing our pleasure buttons. Pornography is another pleasure technology [...] I will suggest that the arts are a third.

Dissanayake (1995a, b, 2008) argues eloquently that (an adequately defined concept of) art behaviour can be shown to be adaptive – that is, evolved. She coined the term ‘making special’ in order to define those aspects of human behaviour that are concerned with what we might loosely call art activities. Her principal argument revolves around the notion that ‘making special’ is an aspect of human behaviour, which, in communal, multi-modal performance of ceremonial rituals, evolved to serve the survival needs of both the individual (allaying anxiety) and the group (fostering group cohesiveness). In doing so, she rejects the idea that art is an evolutionary byproduct or ‘spandrel’.

It is important to note that for ‘art’ to be considered an adapted trait in hominins, it should have a demonstrable function that adds reproductive or survival value that is heritable. If we consider ‘art’ to be the bringing together of skill, expression, and imagination, then storytelling is one area that could be seen to be adapted. I offer the theory here that storytelling, which is said to be universal, is usually accompanied by visual form, perhaps through dance and spectacle, but more often perhaps through illustrations. I suggest it highly unlikely that the images found at Lascaux, for example, and many other much earlier sites, were independent of any other activity. Imagination can be associated with the capacity for symbolic thinking. It is thought that such thinking evolved in early hominins, evidenced by such things as ritual burials and, more obviously, in petroglyphs and cave paintings. Miyagawa et al. (2018) examined the relationship between symbolic thinking and the emergence of language with reference to prehistoric cave paintings. They note that certain genes are implicated for externalised communication forms in mice and songbirds and for speech in humans, but only modern humans have art and language.

They ask if there is a genetic basis for this, noting that there is a gene variant absent in early hominins such as Denisovans and only occurring in modern humans; we can speculate that similar genetic change may have given rise to the multi-modal art that occurred all over the world alongside language.

Tooby and Cosmides have written extensively on aspects of evolutionary psychology; of interest here is their 2001 article addressing evolutionary aesthetics, which focuses, among other things, on how humans have evolved to engage in play and how we can distinguish between fictitious and non-fictitious material. This is a useful area to explore as it relates directly to the notion that art-making in one form or another evolved. They argue that

the human mind is permeated by an additional layer of adaptations that were selected to involve humans in aesthetic experiences and imagined worlds, even though these activities superficially appear to be nonfunctional and even extravagantly nonutilitarian. (Tooby and Cosmides, 2001: 11)

In doing so, they underline their position that the various phenomena that constituent art behaviour and aesthetic awareness are in some way evolutionary adaptations. Seghers (2015), in his critical review of the evolutionary psychological study of art, contends that in categorizing art as an adaptation, one needs, in principle, to assume that the ability to make art has a genetic basis. Implicit within Seghers’ review is the notion that the current state of genetic research does not allow for much speculation about adaptations, as there is very little clarity about which traits are, supposedly, adaptive.

Anthropological research on contemporary hunter-gatherers has found evidence to support the idea that imaginative storytelling may help to solve so-called ‘problems of co-ordination’ in hunter-gatherer societies, in order to promote cooperation. Smith et al. (2017) proposed that storytelling may function in hunter-gatherer societies as a way of communicating and promoting social

norms, thereby co-ordinating social behaviour and promoting cooperation. They tested whether the presence of skilled storytellers in a Filipino hunter-gatherer population known as the Agta predicted levels of cooperation, through comparing at least 18 separate groups. They found that overall levels of cooperation were higher in camps with a greater proportion of skilled storytellers. More importantly, as far as the present argument is concerned, skilled storytellers were found to be preferred social partners, both in terms of being selected as future campmates and receiving resources in the cooperative game. The research group found that skilled storytellers were preferred as social partners over skilled foragers, despite the fact that food-sharing is an everyday occurrence in Agta society.

Skilled storytellers were found to have increased reproductive success relative to unskilled storytellers, with an average additional 0.5 living offspring. By demonstrating that skilled storytellers receive more social support and have increased reproductive success, the research of Smith et al. (2017) provides some support for the notion that imaginative creative activity is adaptive and that one of the adaptive functions of storytelling among hunter-gatherers may be to facilitate cooperation.

INDIVIDUAL DIFFERENCES

From my experience as an artist and informed by my observations of others in my capacity as an educator, I contend that art-making or at least creating aesthetic significance is an innate, heritable, human trait. When making art or when involved in some making activities, one draws upon a range of faculties, dispositions, experiences, and skills; I suggest that these inherited traits are brought together to a greater or lesser extent according to individual differences. Broadly speaking, art behaviours – creating and conferring

aesthetic significance – appear to be universal; this being so, such behaviours may be the result of evolved characteristics. Morris-Kay (2010: 158) notes that:

creation of images from the imagination, or ‘the mind’s eye’, required a seminal evolutionary change in the neural structures underpinning perception; this change would have had a survival advantage in both tool-making and hunting.

She continues with the assertion that while the cognitive ability to create art forms that are separate from the body originated in Africa, this ability may have begun at different times in genetically and culturally distinct groups around the world. Importantly, she states that at all stages in the evolution of artistic creativity, stylistic development must have been due to rare individuals with particular skills. She draws attention to the development of individual humans:

Babies, like human ancestors, are born with a greater or lesser potential for artistic creativity. As they grow older, some would never even try if not taught, whereas others are precociously gifted. (Morris-Kay, 2010: 174)

Those advocating the notion that art-making evolved as a result of sexual selection do so on the basis of taking a particular view of the nature of art; this brings us back to the importance of having an appropriate and adequate working definition. There might be some merit in the notion that an individual who displays, among other things, skill and creativity would be preferred as a sexual partner over someone who did not possess such skills. However, to assert that art-making capacities evolved as a result of adaptation may be over-simplifying a view of complex and inter-related phenomena.

IMPLICATIONS FOR EDUCATION

It would be remiss of me, as someone who has spent many years actively involved in

education in different capacities, to not consider how the foregoing might have some impact upon educational policy. The academic study of education has, not surprisingly, strongly resisted ideas relating to heritability and any notion of individuals being born with differing cognitive abilities. Nevertheless, developments in neuroscience and other disciplines have shown, as Pinker (2003) eloquently argued, that humans are not born as a 'blank slate'.

My contention is that the capacities to create and confer aesthetic significance are characteristics we are all born with. This being the case, it is incumbent upon those responsible for organising state education to facilitate through curriculum design the means by which young people can fulfil their natural creative desires. As I have noted elsewhere (Hickman, 2016), where opportunities for creating and conferring aesthetic significance are curtailed, downplayed, or absent, people will be variably frustrated and unfulfilled. A nation's education curriculum is a hotly contested area, with these and other academic subjects vying for more time and resources. There is no shortage of vocal advocates for the arts, with some citing spurious research about the cognitive benefits of arts education or, more sensibly, advocating a balanced educational diet. What is clear to me is that people, especially the young, need opportunities to make, to create, and to appreciate and engage with, in an informed way, their aesthetic environment.

While we cannot be certain about the evolutionary basis of what is known as 'art', we can say with some certainty that hominins have had the capacity to create and confer aesthetic significance for a very long time. Creating aesthetic significance involves a search for truth and as such is one of the highest forms of organisation that involves a physical act into which emotive meaning has been inserted and that can be drawn out by another intelligent being – this being the case, the act of visual meaning-making encapsulated by the concept 'art' remains, for the

time being, a uniquely human activity. In due course, we may discover that our ancestors developed aesthetic consciousness at a much earlier stage than we currently understand; of greater importance is the prospect that other creatures with whom we share this planet will also be understood to have the capacity for what we, in shorthand, can term 'art'.

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