

Introduction to evolutionary psychology: A Darwinian approach to human behavior and cognition

AARON T. GOETZ, TODD K. SHACKELFORD, AND
STEVEN M. PLATEK

Charles Darwin's (1859) theory of evolution by natural selection is among the most important scientific theories and is *the* most important theory in all of the life sciences. Some have even argued that the principles of Darwin's theory can explain the laws of physics and the organization of the universe (e.g., Dennett, 1995). Although Darwin's name is synonymous with evolution (which refers to the modification of traits with descent), philosophers and scholars were thinking about evolution long before Darwin. In fact, one of the first discussions of evolution pre-dates Darwin by two and a half millennia. Anaximander, a Greek philosopher, suggested that "in water the first animal arose covered with spiny skin, and with the lapse of time some crawled onto dry land and breaking off their skins in a short time they survived." Even Darwin's grandfather, Erasmus Darwin, wrote of common ancestry and speciation. What Charles Darwin (1859) provided, however, was a viable working mechanism of evolution: natural selection. Darwinian selection has become the centerpiece of biology, and in the last few decades, many psychologists and anthropologists have recognized the value of employing an evolutionary perspective in their work (for early writings see Barkow, Cosmides, and Tooby, 1992; Chagnon and Irons, 1979; Daly and Wilson, 1983; Symons, 1979). With a focus on evolved psychological mechanisms and their information processing, evolutionary psychology has risen as a compelling and fruitful approach to psychological science. This chapter provides an introduction to evolution by natural selection and its modern application to the study of human behavior and cognition.

The mechanisms of natural and sexual selection

Evolution by natural selection is the resultant process when (a) individuals of a population vary in their characteristics, (b) much of the variation is heritable, and (c) resources are limited so that individuals reproduce differentially (Darwin, 1859; Mayr, 1982). Individuals can vary morphologically, physiologically, psychologically, behaviorally – no two individuals are exactly the same; even identical twins vary. Due to these variations, some individuals may be better able to survive and reproduce in their current environment than other individuals. If the variations are heritable (i.e., if they have a genetic component), the characteristics can be passed down from parents to offspring. Limited resources (e.g., food, available mates) result in a competition between individuals, and those individuals who have inherited characteristics that allow them to compete more effectively will produce more offspring. Thus, all organisms are subject to evolution by natural selection. As long as the ingredients of natural selection are present – variation, heredity, and competition resulting in differential reproduction – organisms will evolve. An example of natural selection follows.

The peppered moth (*Biston betularia*) is typically white with black spots. This coloration provides an effective camouflage for the moths as they rest on certain Birch trees. There exists variation in the coloration of moths so that some are very white and some very black. In a series of studies, Kettlewell (1955, 1956) documented that when the white trees on which the moths rested became dark from industrial pollution, birds ate more of the white moths because they were now conspicuous on the soot-covered trees. In polluted areas, the population of darker, or melanic, moths replaced the lighter form, but in unpolluted areas, more of the light-colored moths had survived. Kettlewell showed that the environment in which the moths were better camouflaged contributed to better survival and reproduction. Kettlewell's work is a classic demonstration of natural selection in action.

Herbert Spencer's summary of natural selection, "survival of the fittest," has, unfortunately, caused more confusion than clarification (Gaulin and McBurney, 2004). Reproduction is a much larger component of natural selection than is survival. If an individual had characteristics that enabled it to survive for hundreds of years, yet it never reproduced, those characteristics could not be favored by selection because without transmission to offspring, characteristics cannot become more common in a population. Survival, therefore, functions only to enable individuals to reproduce (directly or indirectly). Secondly, Spencer's adage suggests that an individual may evolve to be the "fittest." What determines an individual to be "fit" is its design in relation to competing

designs in the current environment. What is fit in one generation may be unfit in another generation. Also, fit is often taken to imply physically fit. Fitness, in an evolutionary context, is an organism's success in producing offspring that survive to reproductive age (Williams, 1966).

Sexual selection is the process that favors an increase in the frequency of alleles associated with reproduction (Darwin, 1871). Darwin distinguished sexual selection from natural selection, but today most evolutionary scientists combine the two concepts under the label natural selection. Sexual selection is composed of intrasexual competition (competition between members of the same sex for sexual access to members of the opposite sex) and intersexual selection (differential mate choice of members of the opposite sex). Under sexual selection, even a trait that is a liability to survival can evolve. When the sexual attractiveness, for example, of a trait outweighs the survival costs to maintain it, the trait may be sexually selected. The epitome of a sexually selected trait is the peacock's tail. Maintaining and maneuvering an unwieldy tail is metabolically costly for peacocks, and it is often the target of predators. The cumbersome tail evolved, however, because it was attractive to peahens. The mass and brightness of the plumage is attractive to peahens because it signals a low parasite load (Hamilton and Zuk, 1982). Peacocks with smaller, lackluster tails have been shown to be more susceptible to parasites and to have a higher parasite load. Thus, the large bright tail feathers are an honest signal of health, and peahens would be reproductively wise to select as mates males with such tails (who sire offspring that share their high quality genes).

In many species, particularly polygynous species where male reproductive variance is high and female reproductive variance is low, sexual selection is responsible for prominent sexual dimorphism. In such species, intrasexual competition between males for sexual access to females is fierce, and a size advantage is adaptive. It is often difficult to establish whether a trait evolved via natural selection or sexual selection, but as mentioned previously, this distinction is not often necessary.

In summary, the core premise of natural selection as a mechanism for evolution is that individual variation exists among traits in a population due to random mutations. Those individuals who have traits that better enable them to survive and reproduce will propagate the genes associated with those traits throughout the population.

After Darwin: the Modern Synthesis and Hamilton's inclusive fitness theory

The details of modern evolutionary theory, or neo-Darwinian theory, are the result of the Modern Synthesis. From the early 1930s to the 1950s,

advancements in genetics, systematics, and paleontology aligned Darwin's theory with the facts of genetics (Mayr and Provine, 1980). The Modern Synthesis is so called because it was the integration or synthesizing of Darwinian selection with Mendelian genetics. R. A. Fisher, J. B. S. Haldane, Sewall Wright, Ernst Mayr, and Theodosius Dobzhansky are considered the primary authors of the Modern Synthesis (Mayr and Provine, 1980). With a more precise understanding of inheritance, Darwin's theory of evolution by natural selection took flight as a powerful explanatory model.

Following the Modern Synthesis, evolution by natural selection was extended once more to include inclusive fitness theory (Hamilton, 1964). Hamilton reasoned that selection could operate through classical fitness (i.e., the sum of an individual's own reproductive success) and inclusive fitness, which includes the effects of an individual's actions on the reproductive success of genetic relatives. That is, a trait will be naturally selected if it causes an individual's genes to be passed on, regardless of whether the individual directly produces offspring. This addendum to natural selection produced a "gene's eye" view of selection, and could now explain the evolution of altruistic behavior (i.e., behavior that is beneficial to others but costly for the actor). Genes associated with producing an alarm call when sighting a predator, for example, may spread throughout a population even when it is detrimental to the caller if the alarm call is emitted in the presence of genetic relatives and has an overall benefit to those relatives (e.g., Sherman, 1977). Hamilton's inclusive fitness theory is considered the most important advance in our understanding of natural selection, so much so that the term "inclusive fitness theory" is synonymous with "evolution by natural selection."

The products and byproducts of evolution: adaptations, byproducts, and noise

Although natural selection is not the only mechanism of evolution (e.g., mutation, migration, genetic drift), it is the primary means of modification and the primary creative evolutionary force capable of producing functional organization (Fisher, 1954; Mayr, 1963; Williams, 1966). The creative force of natural selection, acting on random genetic variation, designs three products: adaptations, byproducts of adaptations, and noise.

Adaptations are central to the study of evolution. Through the process of natural selection, small incremental phenotypic changes that enhance an organism's ability to survive and reproduce (relative to competing designs) accumulate to form an adaptation. Adaptations are inherited, they develop reliably, are usually species-typical, and were selected for because they were

economic, efficient, and reliable solutions to adaptive problems (Buss, Haselton, Shackelford, Bleske, and Wakefield, 1998; Thornhill, 1997; Tooby and Cosmides, 1990; Williams, 1966). An adaptive problem is an obstacle or impediment that was recurrent during a species' evolutionary history and whose solution affected the survival and reproduction (i.e., genetic propagation) of an organism. Furthermore, adaptive problems aren't necessarily "problems," they are the "regularities of the physical, chemical, developmental, ecological, demographic, social, and informational environments encountered by ancestral populations during the course of a species' or population's evolution" (Tooby and Cosmides, 1992, p. 62). In sum, natural selection designs adaptations that solve adaptive problems associated with survival and reproduction. The heart, the production of sweat, and sexual arousal are all adaptations designed by natural selection. The heart is an anatomical adaptation designed to circulate blood throughout an organism's body. The production of sweat is a physiological adaptation designed to thermoregulate an organism. Sexual arousal is a psychological adaptation designed to motivate sexual behavior.

Not all products of natural selection are adaptations. Byproducts of adaptations are side-effects that may or may not be functional but that were not directly selected. They are called byproducts because they are incidentally tied to adaptations and are therefore "carried along" with them. Identifying byproducts is equally as rigorous a process as identifying adaptations because the hypothesis that a trait is a byproduct requires one to identify the adaptation of which it is a byproduct. The human navel and the whiteness of bone are byproducts of adaptations - they do not contribute in any way to an individual's survival or reproduction. In keeping with our mandate: the human navel is a byproduct of an umbilical cord and the whiteness of bone is a byproduct of the calcium in bones.

The third product of evolution is noise, or random effects. Noise is also functionless and cannot solve adaptive problems. Noise can be produced by random changes or perturbations in the genetic or developmental environment or by chance mutations. Noise, unlike a byproduct, is not linked to the adaptive aspect of a characteristic. The random shape of an individual's navel is an example of noise.

In summary, the evolutionary process produces three products: adaptations, byproducts, and noise. Adaptations are the product of natural selection and are functionally organized features that contribute to a species' reproductive success, however indirectly. Byproducts and noise do not solve adaptive problems and are not subject to natural selection themselves. In the following section, we discuss how the study of psychological adaptations has changed the study of human behavior and cognition.

Evolutionary psychology

Evolutionary psychology (EP) attempts to make sense of current human thought, emotion, and behavior by careful consideration of human evolutionary history. Over our evolutionary history, humans have faced many adaptive problems that needed to be solved to survive and reproduce. Generation after generation, over millions of years, natural selection slowly shaped the human brain, favoring circuitry that was good at solving these adaptive problems of our ancestors. The study of psychological adaptations (or evolved psychological mechanisms) is central to EP.

Because the focus of EP is on describing adaptations, some have charged its practitioners as being hyper-adaptationists. Assuming a priori that a trait may be an adaptation is an experimental heuristic that guides research questions and methodology. Biologists have been conducting their research this way for over 70 years. Moreover, byproducts and noise are typically only identifiable after the adaptations of which they are a byproduct or noise have been discovered and described (Tooby and Cosmides, 1990).

Although modern evolutionary psychological theories are relatively new, all psychological theories are evolutionary in nature (Buss, 1995): “All psychological theories – be they cognitive, social, developmental, personality, or clinical – imply the existence of internal psychological mechanisms” (p. 2). If the internal psychological mechanisms implied in any psychological theory were not the product of the evolutionary process, then they would be, by default, unscientific theories.

Psychological mechanisms as information-processing modules

An evolved psychological mechanism is an information-processing module that was selected throughout a species’ evolutionary history because it reliably solved a particular adaptive problem (Tooby and Cosmides, 1992). Evolved psychological mechanisms are understood in terms of their specific input, decision rules, and output (Buss, 1995). Each psychological mechanism evolved to take in a narrow range of information – information specific to a specific adaptive problem. The information (or input) that the organism receives signals the adaptive problem that is being confronted. The input (either internal or external) is then transformed into output (i.e., behavior, physiological activity, or input relayed to another psychological mechanism) via a decision rule – an “if, then” procedure. An example of the input, decision rules, and output of a psychological mechanism is appropriate.

Fruit can either be ripe or unripe. Because ripe fruit is more nutritious (i.e., calorically dense) than immature fruit, humans have developed a preference for

ripe fruit. The decision rule regarding the selection of fruit might go something like, “If the fruit tastes sweet, then eat it.” Supposing all fruit was maximally saturated with sugar all of the time, then that particular decision rule would not exist. The output associated with this mechanism might be to eat the ripe fruit or disregard the unripe fruit. This example illustrates the fact that psychological mechanisms develop and operate without any conscious awareness or formal learning, and we are blind to their underlying logic. Do you enjoy ripe fruit because it is calorically dense and provides nutrition needed to carry out activities related to survival and reproduction? Or do you simply enjoy sweet fruit?

Tooby and Cosmides (1992) have written that the causal link between evolution and behavior is made through psychological mechanisms. That is, the filter of natural selection operates on psychological mechanisms that produce behavior. Natural selection cannot operate on behavior directly, but instead, on the genes associated with the psychological mechanisms that produce the behavior. Williams (1966) spoke similarly, “The selection of genes is mediated by the phenotype [psychological mechanism], and in order to be favorably selected, a gene must produce phenotypic reproductive success [adaptive behavior]” (p. 25).

Psychological mechanisms and domain specificity

The vast majority of psychological mechanisms are presumed to be domain-specific. That is, the mind is composed of content-dependent machinery (i.e., physiological and psychological mechanisms) that is presumed to have evolved to solve a specific adaptive problem. Psychological mechanisms can also be expressed as cognitive biases that cause people to more readily attend to or make sense of some pieces of information relative to others. This presumption of domain specificity or modularity contrasts with the traditional position that humans are endowed with a general set of learning or reasoning mechanisms that are applied to any problem regardless of specific content (e.g., Atkinson and Wheeler, 2004). A system that is domain-general or content-independent, however, is a system that lacks a-priori knowledge about specific situations or problem-domains (Tooby and Cosmides, 1992). Such a system, when faced with a choice in a chain of decisions, must select from all behavioral possibilities (e.g., wink, jump, remember mother, smile, point finger, scream, etc.). This problem of choosing among an infinite range of possibilities when only a small subset are appropriate has been described by researchers in artificial intelligence, linguistics, and other disciplines (see Tooby and Cosmides, 1992 for a review).

Not only are there theoretical arguments against a content-independent system, myriad evidence for domain-specificity comes from, among other areas, evolutionary psychological theory and research (e.g., Cosmides, 1989;

Cosmides and Tooby, 1994; Flaxman and Sherman, 2000; Pinker and Bloom, 1990), cognitive research (e.g., Hirschfeld and Gelman, 1994), studies of animal learning (e.g., Carey and Gelman, 1991; Garcia, Ervin, and Koelling, 1966), and the clinical neurological literature (e.g., Gazzaniga and Smylie, 1983; Ramachandran, 1995; Sergent, Ohta, and MacDonald, 1992). Practitioners of EP concede that relatively domain-general mechanisms may exist, but the vast majority of mechanisms are presumed to be domain-specific.

Some of the controversy surrounding the modularity of the mind seems to be rooted in the use of the term *domain*. Psychologists have often used the term to refer to particular domains of life, such as the mating domain, kinship domain, and parenting domain. Subsequently, many have assumed that labeling a mechanism as domain-specific restricts the proposed mechanism to a particular domain, and if evidence can be garnered to show that the mechanism functions in more than one domain (e.g., the mating domain and the kinship domain), then it is taken as evidence for the domain generality of the proposed mechanism. This, however, is incorrect. A domain, when referring to a psychological mechanism, is a selection pressure, an adaptive problem (Cosmides and Tooby, 1987). Domain, then, is synonymous with *problem*. That is, a domain-specific mechanism refers to a problem-specific mechanism – a mechanism that evolved to solve a specific adaptive problem. So although evolutionary and cognitive psychologists use the term *domain-specific*, perhaps some confusion could be avoided if the more accurate term *problem-specific* were employed instead. Many psychological mechanisms cut across different domains of life. Face recognition is used in all the social domains of life (e.g., mating and kinship domains). Working memory is used in all domains, as is processing speed. Face recognition, working memory, and processing speed still solve specific problems. Working memory, for example, solves the specific problem of holding information in the mind for a brief period of time. So although working memory is used in all domains, it is problem specific (and therefore domain specific) because it solves a single adaptive problem. It has been suggested that evolutionary and cognitive psychologists might be better off avoiding these contentious labels and simply describing the proposed mechanism and its function (personal communication, D. M. Buss, January 2005).

Evolutionary time lags and the environment of evolutionary adaptedness

Because evolution is an excruciatingly slow process, extant humans and their minds are designed for earlier environments of which they are a product. Our minds were not designed to solve the day-to-day problems of our modern society, but instead, were designed to solve the day-to-day problems of our evolutionary past. Examples of evolutionary time lags abound: our difficulty

in learning to fear modern threats, such as guns and cars, and our near effortless learning to fear more ancient threats, such as snakes and spiders (Öhman and Mineka, 2001); children's ease in learning biologically primary mathematic abilities, such as counting and their difficulty in learning biologically secondary mathematic abilities, such as arithmetic (Geary, 1995); women will not concede to intercourse indiscriminately even though modern contraception can eliminate the reproductive costs associated with intercourse; our preference for sugar and fat was once adaptive due to their scarcity, but has now become maladaptive. These few examples illustrate that our modern behavior is best understood when placed in the context of our environment of evolutionary adaptedness.

The environment of evolutionary adaptedness (EEA) is not a place or time in history but a statistical composite of the selection pressures (i.e., the enduring properties, components, and elements) of a species', more specifically the *adaptations* that characterize a species', ancestral past (Tooby and Cosmides, 1990). That is, each adaptation evolved due to a specific set of selection pressures. Each adaptation, in principle, has a unique EEA, but there likely would have been significant overlap in the EEAs of related adaptations. Tooby and Cosmides (1990) and other practitioners of EP, however, use "Pleistocene" to refer to the human EEA because this time period, lasting 1.81 to 0.01 million years ago, was appropriate for virtually all adaptations of *Homo sapiens*.

Although our evolutionary past is not available for direct observation, the discovery and description of adaptations allows us to make inferences about our evolutionary past, and the characterization of adaptations is arguably the single most reliable way of learning about the past (Tooby and Cosmides, 1990). Some adaptations provide unequivocal information about our ancestral past. Our cache of psychological mechanisms associated with navigating the social world tells us that our ancestors were a social species (e.g., Cosmides, 1989; Cummins, 1998; Forgas, Haselton, and von Hippel, 2007; Kurzban *et al.*, 2001; Pinker and Bloom, 1990; Trivers, 1971). A multitude of psychological mechanisms associated with cuckoldry avoidance tell us that female infidelity was a recurrent feature of our evolutionary past (Buss, Larsen, Westen, and Semmelroth, 1992; Buss and Shackelford, 1997; Goetz and Shackelford, 2006a; Platek, 2003; Shackelford, Goetz, McKibbin, and Starratt, 2007).

Some adaptations, however, do not make clear (at least upon first inspection) their link with our ancestral past. There exists, for example, a mechanism present in the middle ear of all humans that is able to reduce sound intensity by as much as 30 decibels in 50 milliseconds. The attenuation reflex, as it is known, acts by contracting muscles that pull the stirrup away from the oval window of the cochlea, preventing strong vibrations from damaging the inner

ear. The attenuation reflex meets the characteristics of an adaptation (e.g., economic, efficient, reliable), yet it is not obvious what selection pressures drove the evolution of this adaptation. That is, what specific noises did our ancestors recurrently hear that would create this noise reducing mechanism? That the muscles appear to contract as we are about to speak suggests that our own loud voices might have been the impetus for this adaptation. Moreover, sound attenuation is greater at low frequencies than at high ones (and humans speak at low frequencies), also suggesting that ululating was a recurrent (enough) feature of our evolutionary past. Thus, from discovering and describing adaptations, we can tentatively characterize aspects of our evolutionary environment.

This is not to be taken to indicate, however, that the aim of evolutionary psychology is to make inferences about the past. Evolutionary psychology is not *post hoc* storytelling; its practitioners typically use a deductive approach, moving from theory to data. That is, evolutionary psychologists make predictions derived from hypotheses based on middle-level theories – e.g., Trivers' (1972) parental investment theory – then collect data to test their predictions. For example, Buss *et al.* (1992) tested the hypothesis proposed by Symons (1979) and Daly, Wilson, and Weghorst (1982) that the sexes would differ in their reactions to a romantic partner's sexual and emotional infidelity. Buss and his colleagues did not happen to collect the appropriate data, analyze the results, and develop a *post hoc* explanation for what they observed. Furthermore, claims of adaptations are typically stated as tentative until the proposed adaptation has undergone rigorous hypothesis testing (see Schmitt and Pilcher, 2004). The inductive approach, however, should not be disregarded. Moving from data to theory is a common practice in all scientific enterprises (e.g., cosmology, geology, physics) and is known as "explanation" (Tooby and Cosmides, 1992).

Ultimate and proximate explanations

Some psychologists seem to be hostile to the idea of applying evolutionary theories to human behavior. One cause of this unwarranted hostility is the misconception that evolutionary analyses are incompatible with (or less important than) non-evolutionary (e.g., sociological or cultural) analyses. Such critics fail to recognize that evolutionary and non-evolutionary approaches operate at different levels of analysis (Tinbergen, 1963). Evolutionary scientists are typically interested in causation at the ultimate (or distal) level. An ultimate explanation refers to the evolved function of a trait, behavior, or mechanism. This is in contrast to proximate explanations. Proximate explanations refer to the immediate, non-evolutionary causes of a trait, behavior, or mechanism (e.g., the genetic or cellular causes). In our example of the input, decision rules, and

output of a psychological mechanism associated with ripe fruit, one could correctly note that humans prefer ripe fruit because it is perceived to be sweet (proximate cause) and because it provides needed calories to perform duties related to survival and reproduction (ultimate cause). Although the explanations are fundamentally different, they are compatible and equally important (Sherman and Alcock, 1994). But it is also possible and not uncommon to have competing explanations at the same level of analysis (e.g., competing evolutionary psychological hypotheses); such debate is a healthy feature of science.

Evolutionary psychology's relationship with sociobiology

Those less familiar with evolutionary psychology often construe the approach as “sociobiology reborn.” Although sociobiology, ethology, behavioral ecology, and evolutionary psychology share evolution as a guiding framework, the programs are conceptually distinct for at least three reasons (see also Buss, 1995; Crawford, 2000). First, evolutionary psychology investigates a broader array of phenomena than sociobiology. Sociobiology is the study of plant and animal social behavior. Evolutionary psychology’s research agenda includes the social domain but it also addresses all other domains of life and all areas of psychology (e.g., consciousness, memory, sensation, perception, motivation, etc.). Second, the focus on evolved psychological mechanisms and their information processing is a unique and defining feature of evolutionary psychology. The input, decision rules, and output of psychological mechanisms are central to the analysis. Third, evolutionary psychologists do not measure individuals’ direct reproductive output (i.e., number of children) or fitness. Many sociobiologists, in contrast, have advocated measuring an individual’s reproductive success to understand the adaptive value of behavior. Evolutionary psychology questions the premise that measuring fitness in a recent or current environment provides information about the evolutionary history or selection pressures that caused the evolution of the psychological mechanisms that motivate the particular behavior. The information needed to measure fitness correctly only becomes known generations later, because there is no guarantee that selection pressures remain stable over time. Practitioners of evolutionary psychology have argued that “humans are adaptation executors, not fitness maximizers” (Tooby and Cosmides, 1990, p. 420). Whether a subdiscipline of or a separate field from sociobiology, evolutionary psychology and sociobiology share evolution as a guiding framework (Alcock, 2001).

Discovering new topics and rethinking old topics

The modern application of evolutionary principles to the study of human psychology and behavior has opened up new lines of research and has

shaken up old topics in psychology. In this section, we discuss the recently developed area of human sperm competition (with an emphasis on the evolutionary cognitive neuroscience of human sperm competition) and the rethinking of racism and self-deception in light of evolution.

With the recognition that female infidelity was a recurrent feature of our evolutionary past has come the development of a unique field within human mating: sperm competition. A form of male-male postcopulatory competition, sperm competition occurs when the sperm of two or more males simultaneously occupy the reproductive tract of a female and compete to fertilize her egg (Parker, 1970). Males must compete for mates, but if two or more males have copulated with a female within a sufficiently short period of time, sperm will compete for fertilizations. Psychological, behavioral, physiological, anatomical, and genetic evidence indicates that men have evolved solutions to combat the adaptive problem of sperm competition (Gallup *et al.*, 2003; Goetz and Shackelford, 2006a; Goetz *et al.*, 2005; Kilgallon and Simmons, 2005; Pound, 2002; Shackelford and Goetz, 2007; Shackelford, Goetz, McKibbin, and Starratt, 2007; Shackelford *et al.*, 2002; Smith, 1984; Wyckoff, Wang, and Wu, 2000). Shackelford *et al.* (2002), for example, documented that men who spent a greater proportion of time apart from their partner since the couple's last copulation – therefore, facing a high risk of sperm competition – report that they find their partner more sexually attractive, have more interest in copulating with her, and believe that she is more interested in copulating with him (effects were independent of the total time since last copulation and relationship satisfaction). These perceptual changes may motivate men to copulate as soon as possible with their partner, thereby entering their sperm into competition with any rival sperm that may be present in her reproductive tract.

Although there is accumulating evidence that males engage differential psychological strategies that appear to be designed as a response to female infidelity, the neural correlates of such strategies have only recently been investigated. If, as documented above, men's sexual interest in their partners is related to perceptions of infidelity, then two recent studies suggest a network of brain substrates that, in the context of sperm competition, might be implicated in the neural control of physiological changes. Rilling, Winslow, and Kilts (2004) used positron emission tomography (PET) to measure brain activation when male rhesus macaques were allowed to observe their exclusive female mating partner engaging in copulation with a rival male. In this situation, activation was observed in the right superior temporal sulcus (STS) and amygdala. Rilling *et al.* (2004) suggest that activation of these areas might relate to similar reports of humans experiencing increased vigilance and anxiety under conditions of purported sexual infidelity by their partners. A similar study

conducted in humans documented similar activation (right amygdala) in men who were asked to read sentences that depicted their partner engaging in sexual infidelity (Takahashi *et al.*, 2006). Because the amygdala is highly innervated with androgen receptors, increased anxiety and vigilance about partner infidelity could subsequently activate a system designed to respond to possible sperm competition. This hypothesis was partially supported by Rilling *et al.* (2004), who also demonstrated increases in circulating testosterone levels when macaques were challenged with the situation described above.

In fact, this neural response system might be “on line” in men prior to any observation or suspicion of infidelity. Shackelford *et al.* (2002) found that perceptions of mate attractiveness increase as a function of time spent apart from a partner; recent research shows that such perceptions of attraction correlate with increased activity in the amygdala (Winston, O’Doherty, Kilner, Perrett, and Dolan, 2007). Similarly, Winston *et al.* (2007) found increased anterior cingulate cortex (ACC) activation in men during rankings of attractiveness, and these authors relate the differential in ACC by sex activation to differences in arousal stemming from internal monitoring. In other words, a man might employ this substrate as part of a mechanism enabling him to make appropriate arousal valuations under circumstances when he suspects or has directly observed his partner’s infidelity. This arousal might then lead to increased execution of sperm competitive behaviors and, possibly, to prudent sperm allocation.

Some data are accumulating that implicate the STS in decisions about social interactions (e.g., Frith and Frith, 1999). Thus, the STS activation reported by Rilling *et al.* (2004) and Winston *et al.* (2007) might reflect the degree to which evaluations about infidelity and trustworthiness are made. Processing associated with social evaluation might also feed into the ACC. Platek, Keenan, and Mohamed (2005) identified a sex difference in activation of the ACC in response to children’s, but not adults’, faces that share the subject’s facial resemblance. Because facial resemblance appears to serve as an indicator of paternity (Platek *et al.*, 2002, 2003, 2004), this finding suggests that the ACC might serve as a broad scale evaluation substrate for fidelity judgments.

Although further research is necessary to understand fully how the neural networks cause sperm competition responses – behaviorally, physiologically, and psychologically – preliminary evidence suggests that the networks will involve several key neurocognitive mechanisms: (1) social evaluation of partners on the basis of presumed propensity towards trustworthiness and fidelity (STS), (2) decisions about attractiveness and relation to internal monitoring, or decisions about belief in suspicions (ACC, STS, medial prefrontal cortex), and (3) automatic response generators (amygdala) that serve to moderate prudent

sperm allocation and behaviors to “correct” a suspected or discovered partner infidelity (e.g., semen displacement, forced in-pair copulation, violence, or defection from pair bond). This network, apparently specific to men, may be quickly called into action during all phases of anti-cuckoldry tactics (mate guarding, sperm competition, and parental investment decisions; see Platek and Shackelford, 2006).

An evolutionary approach also has encouraged re-evaluating and rethinking old topics in psychology. Tomes of non-evolutionary psychological research argued that people encode automatically the race of individuals they encounter. Kurzban, Tooby, and Cosmides (2001), however, proposed that human psychology did not evolve specifically to encode race but, instead, that the encoding of race is a byproduct of adaptations for detecting coalitional alliances. By varying cues of coalitional affiliation and race, so that the two did not correspond, Kurzban and his colleagues were able to reduce (and in some cases remove) the extent to which people categorize others according to race. Subsequent research on racial prejudice and discrimination will benefit from this work.

The principles of evolutionary psychology have even managed to solve a philosophical debate. Known as the paradox of self-deception, many philosophers have argued that self-deception – the active misrepresentation of reality to the conscious mind (Trivers, 2000) – cannot occur because it is impossible to be, simultaneously, the deceiver and the deceived. Considering, however, that the mind is comprised of many information-processing mechanisms, some highly interconnected and some connected to just a few other mechanisms, a self-deception mechanism could evolve if the mechanisms responsible for conscious experience were unconnected to the mechanisms responsible for ultimate intentions. Without being consciously aware of particular ultimate intentions or goals, we may be better able to deceive others in order to reach such goals. Self-deception research from an evolutionary psychological perspective is in its infancy, but is growing as we employ new techniques to study this phenomenon (e.g., Keenan, 2005; Stevens, Guise, Kelly, and Keenan, 2005).

Evolutionary psychology's future

Although this modern approach to human behavior and cognition is relatively young – about 25 years old, EP's impact is already permeating all areas of psychology and opening up lines of research missed entirely by previous psychologists. EP's merit and future are also demonstrated in the fact that the number of publications using an evolutionary psychological approach is growing exponentially (Durrant and Ellis, 2003).

Moreover, evolutionary psychology's influence on cognitive neuroscience is on the rise. Using quantitative methods, Webster (2007) has documented a strong

positive trend in the “evolutionizing” of neuroscience. The observed growth of evolutionary cognitive neuroscience is consistent across several neuroscience journals. Webster notes that “evolution’s penetration into evolutionary cognitive neuroscience has increased at a rate that is roughly equivalent to its penetration into personality and social psychology over the last two decades; however, its penetration into neuroscience in general appears to have happened at an even faster rate” (p. 529). It’s clear from Webster’s analyses, and this volume in particular, that cognitive neuroscientists are recognizing the utility of an evolutionary perspective.

Another promising direction of future work is signaled by the emergence of evolutionary development psychology. The subdiscipline of evolutionary developmental psychology considers how natural selection might have influenced human psychology and behavior at all stages of development (e.g., Bjorklund and Pellegrini, 2002; Hernández Blasi and Bjorklund, 2003). Hypothesizing functions for humans’ extended development, children’s cognitive immaturity, and children’s play behavior, for example, evolutionary developmental psychology asserts that development is as much an influential factor on psychology and behavior as evolution (Bjorklund and Pellegrini, 2000; Smith, 2005).

A future task of evolutionary psychology will be to describe the phylogenetic origins of mental traits. Phylogenetics – an area in biology dealing with identifying and understanding the evolutionary relationships between species and traits – is not well represented in the evolutionary psychological literature, but some have discussed the emergence of some adaptations (e.g., Bering and Shackelford, 2004; Marcus, 2006; Wynn, 2002). Incorporating phylogenetic studies into evolutionary psychology may help to clarify a proposed mechanism’s relative domain-specificity or generality.

As new psychologists are impartially introduced to EP, as “traditional” (i.e., anti-evolutionary) psychologists retire, as EP’s empirical output grows, as findings from genetics corroborate findings from EP (e.g., Cherkas *et al.*, 2004), as the neural substrates underlying hypothesized psychological mechanisms are identified (e.g., Platek, Keenan, and Mohamed, 2005 and this volume) and as cross-disciplinary frameworks of evidence are utilized (Schmitt and Pilcher, 2004), EP will emerge as *the* metatheory for psychological science.

Conclusion

In this chapter we introduced evolutionary theory and its modern impact on psychological science. We discussed how, with a focus on evolved psychological mechanisms and their information processing, evolutionary psychology has risen as a compelling and fruitful approach to the study of human behavior and cognition.

Because the design of the mind owes its functional organization to a natural, evolutionary process, an evolutionarily psychological approach is a logical framework on which to base all psychological theories. Evolutionary psychological theories specify what problems our cognitive mechanisms were designed to solve, thereby providing important information about what their design features are likely to be. In other words: “Is it not reasonable to anticipate that our understanding of the human mind would be aided greatly by knowing the purpose for which it was designed?” (Williams, 1966, p. 16).

It is possible to do research in psychology with little or no knowledge of evolution. Many psychologists do. But without an evolutionary perspective, psychology becomes a disparate set of fields. Evolutionary explanations pervade all fields in psychology and provide a unifying metatheoretical framework within which all of psychology can be organized.

Note

Portions of this manuscript were reproduced from Goetz and Shackelford (2006b).

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