Modern application of evolutionary theory to psychology: Key concepts and clarifications

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Darwinian selection has become the centerpiece of biology, and in the last few decades many psychologists and anthropologists have recognized the value of using an evolutionary perspective to guide their work. With a focus on evolved psychological mechanisms and associated information processing features, evolutionary psychology has risen as a compelling and fruitful approach to the study of human psychology and behavior. In this article we review the instrument of evolution: natural selection, the products of evolution, and the impact of evolutionary thinking on modern psychological science. We conclude that as prejudicial barriers are overcome, as more evolutionary psychological work is conducted, and as hypothesized psychological mechanisms are substantiated in other disciplines, evolutionary psychology will emerge as the metatheory for psychology.

Darwin (1859) was not the first to suggest that species evolve. One of the first discussions of evolution predates 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." However, what Darwin provided was a viable working mechanism for 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 using an evolutionary perspective to guide their work (e.g., Barkow, Cosmides, & Tooby, 1992; Chagnon & Irons, 1979; Daly & Wilson, 1983; Symons, 1979). With a focus on evolved psychological mechanisms and associated information processing features, evolutionary psychology has risen as a compelling and fruitful approach to psychological science. This article provides an introduction to evolution by natural selection and its modern application to the study of human psychology and behavior.

Natural selection and sexual selection

Evolution by natural selection is the resultant process when individuals of a population vary in their characteristics, this variation is heritable,

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and individuals reproduce differentially (Darwin, 1859; Mayr, 1982). Individuals can vary morphologically, physiologically, psychologically, and behaviorally; no two individuals are exactly the same (even monozygotic twins vary). Because of 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 from parents to offspring. 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. A classic example of natural selection follows.

The peppered moth (*Biston betularia*) typically is 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 are 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 moths replaced the lighter moths, but in unpolluted areas, more of the light-colored moths 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 caused more confusion than clarification (Gaulin & McBurney, 2001). 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. Therefore, survival functions only to enable individuals to reproduce (directly or indirectly). Second, Spencer's adage suggests that an individual may evolve to be the "fittest." What determines an individual to be "fit" is its functional structure in relation to competing structures 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. In an evolutionary context, fitness 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 directly with reproduction (Darwin, 1871). Darwin

distinguished sexual selection from natural selection, but today most evolutionary scientists include the two concepts under the label *natural selection*. Sexual selection includes the two components of intrasexual competition (competition between members of the same sex for sexual access to members of the other sex) and intersexual selection (differential mate choice of members of the other sex). Under sexual selection, even a trait that is a liability to survival can evolve. When the sexual attractiveness of a trait outweighs the survival costs needed to maintain it, the trait may be sexually selected. The epitome of a sexually selected trait is the peacock's tail. Producing, maintaining, and maneuvering an unwieldy tail is metabolically costly for peacocks, and it is often the target of predators. However, the cumbersome tail evolved because it was attractive to peahens. The mass and brightness of the plumage attract peahens because they signal a lower parasite load (Hamilton & 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 in which 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 via sexual selection, but as mentioned previously, this distinction often is not necessary.

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

Modern synthesis and 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, advances in genetics, systematics, and paleontology aligned Darwin's theory with the facts of genetics (Mayr & Provine, 1980). The Modern Synthesis is so-called because it was the integration or synthesis 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 & Provine, 1980). With a more precise understanding of inheritance, Darwin's theory of evolution by natural selection took flight as a powerful explanatory model.

After 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 classic 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 is naturally selected if it causes an individual's genes to be replicated, regardless of whether the individual directly produces offspring. This addendum to natural selection produced a "gene's eye" view of selection and could 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 provides an overall benefit to those relatives (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."

Products 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 only evolutionary force capable of producing functional organization (Fisher, 1954; Mayr, 1963; Williams, 1966). The creative force of natural selection, acting on random genetic variation, generates three products: adaptations, byproducts of adaptations, and noise.

Adaptations are central to the study of evolution. Through the process of natural selection, small and incremental phenotypic changes that enhance an organism's ability to survive and reproduce (relative to competing structures) accumulate to form an adaptation. Adaptations are inherited, develop reliably, usually are species typical, and were selected for because they were economic, efficient, and reliable solutions to adaptive problems (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Thornhill, 1997; Tooby & 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 are not necessarily "problems"; instead, 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 & Cosmides, 1992, p. 62). In sum, natural selection produces adaptations that solve problems associated with survival and reproduction.

The heart, the production of sweat, and sexual arousal are all adaptations produced by natural selection. The heart is an anatomic adaptation that circulates blood throughout an organism's body. The production of sweat is a physiological adaptation that thermoregulates an organism. Sexual arousal is a psychological adaptation that motivates sexual behavior.

Not all products of natural selection are adaptations. Byproducts of adaptations are characteristics of a phenotype that are functionless and do not solve adaptive problems. They are called byproducts because they are incidentally tied to adaptations and are therefore carried along with them. Identifying byproducts is 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 known 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 also is functionless and cannot solve adaptive problems. Noise can be produced by random changes, perturbations in the genetic or developmental environment, or chance mutations. Unlike a byproduct, noise 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 generates three products: adaptations, byproducts, and noise. Adaptations are the product of natural selection and are functionally organized features that contribute to an individual's reproductive success, however indirectly. Byproducts and noise do not solve adaptive problems and are not the direct products of natural selection. In the following section we discuss how the study of psychological adaptations has changed the study of human psychology and behavior.

Evolutionary psychology

Evolutionary psychology 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 in order for them 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 evolutionary psychology.

Because the focus of evolutionary psychology is on describing adaptations, some have charged its practitioners with being hyperadaptationists.

Assuming a priori that a trait may be an adaptation, however, is a heuristic that guides research questions and methods. Biologists have been conducting research this way for more than 70 years. Moreover, byproducts and noise typically are identifiable only after the adaptations of which they are a byproduct or noise have been discovered and described (Tooby & Cosmides, 1990).

Although modern evolutionary psychological theories are new, all psychological theories are evolutionary in nature (Buss, 1995, p. 2): "All psychological theories—be they cognitive, social, developmental, personality, or clinical—imply the existence of internal psychological mechanisms." The only known scientific explanation for complex functional organization—of psychological and physiological adaptation—in turn, is evolution by natural selection.

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 produced behavior that solved a particular adaptive problem (Tooby & 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 particular 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 be either ripe or unripe. Because ripe fruit is more nutritious (i.e., calorically dense) than immature fruit, humans have evolved a preference for ripe fruit. The decision rule regarding the selection of fruit might proceed as follows: "If the fruit tastes sweet, then eat it." If 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 to discard the unripe fruit. This example illustrates the fact that psychological mechanisms can operate without any conscious awareness or formal learning and that we are often blind to their underlying logic. Do you enjoy calorically dense fruit because it provides nutrition needed to carry out activities related to survival and reproduction? Or do you simply enjoy sweet fruit?

Tooby and Cosmides (1992) have noted 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 operates on behavior indirectly,

by selecting genes associated with the psychological mechanisms that produce the behavior. Williams (1966, p. 25) 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]."

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

Not only are there theoretical arguments against a content-independent system, but also myriad empirical evidence for domain specificity comes from, among other areas, evolutionary psychological theory and research (Cosmides, 1989; Cosmides & Tooby, 1994; Flaxman & Sherman, 2000; Pinker & Bloom, 1990), cognitive research (Fodor, 1983; Hirschfeld & Gelman, 1994), studies of animal learning (Carey & Gelman, 1991; Garcia, Ervin, & Koelling, 1966), and the clinical neurological literature (Gazzaniga & Smylie, 1983; Ramachandran, 1995; Sergent, Ohta, & MacDonald, 1992). Practitioners of evolutionary psychology concede that domain-general mechanisms that function, for example, to integrate and relay information between domain-specific mechanisms *may* exist, but the 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. Many have assumed subsequently 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 this is taken as evidence of the domain generality of the proposed mechanism. However, this is incorrect. When referring to a psychological mechanism, a domain is a selection pressure, an adaptive problem (Cosmides & Tooby, 1987). Domain, then, is synonymous with *problem.* That is, a domain-specific mechanism is 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 used instead. Although some psychological mechanisms cut across different domains of life (e.g., face recognition, working memory, processing speed), they still solve specific problems. Working memory, for example, solves the specific problem of holding information in the mind for a brief period of time. 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 (D. M. Buss, personal communication, January 2005).

Evolutionary time lags and the environment of evolutionary adaptedness. Because evolution is an excruciatingly slow process, modern humans and their minds are built for the earlier environments of which they are a product. Our minds were not built to solve most day-to-day problems of modern society but instead were built to solve the day-to-day problems of our evolutionary past. Examples of the consequences of these 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 & 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 do not concede to intercourse indiscriminately even though modern contraception can eliminate the reproductive costs associated with intercourse; and our preferences for sugar and fat were once adaptive because of the scarcity of food items rich in these elements in our evolutionary past but now generate unhealthy food consumption, given the wide availability of these elements in the modern environment. 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 a time in history but a statistical composite of the selection pressures (i.e., the enduring properties, components, and elements) operating on a species, more specifically the adaptations that characterize a species' ancestral past (Tooby & Cosmides, 1990). That is, each adaptation evolved because of a specific set of selection pressures. Each adaptation, in principle, has

a unique EEA, but there probably would have been significant overlap in the EEAs of related adaptations. However, Tooby and Cosmides (1990) and other evolutionary psychologists use the term *Pleistocene* to refer to the human EEA because this time period, lasting 1.81 to 0.01 million years ago, includes the relevant selective periods for many adaptations of *Homo sapiens*.

Although our evolutionary past is not available for direct observation, the discovery and description of adaptations allow us to make inferences about our evolutionary past, and the characterization of adaptations is arguably the most reliable way of learning about the past (Tooby & 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 (Cosmides, 1989; Cummins, 1998; Kurzban et al., 2001; Pinker & Bloom, 1990; Trivers, 1971). The multitude of male psychological mechanisms associated with cuckoldry avoidance tells us that female infidelity was a recurrent feature of our evolutionary past (Buss, Larsen, Westen, & Semmelroth, 1992; Buss & Shackelford, 1997; Goetz et al., 2005; Platek, 2003; Shackelford, Pound, & Goetz, 2005).

However, some adaptations do not make clear (at least upon first inspection) their link with our ancestral past. For example, a mechanism present in the middle ear of humans is able to reduce sound intensity by as much as 30 dB in 50 ms. 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 solution to a problem), 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 feature of our evolutionary past. Thus, by discovering and describing adaptations, we can tentatively characterize aspects of our evolutionary environment.

However, is not to be taken to indicate that the aim of evolutionary psychology is to make inferences about the past. Evolutionary psychology is not post hoc storytelling; its practitioners often 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's [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 typically are stated as tentative until the proposed adaptation has undergone rigorous hypothesis testing (see Schmitt & Pilcher, 2004). However, the inductive approach 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 & Cosmides, 1992).

Ultimate and proximate explanations. Some psychologists seem 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) nonevolutionary (e.g., sociological or cultural) analyses. Such critics fail to recognize that evolutionary and nonevolutionary approaches operate at different levels of analysis (Tinbergen, 1963). Evolutionary scientists typically are 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, nonevolutionary 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 & 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). 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. In contrast, many sociobiologists 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 becomes known only generations later because there is no guarantee that selection pressures remain stable over time. Practitioners of evolutionary psychology have argued that "humans are adaptation executers, not fitness maximizers" (Tooby & 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. 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, anatomic, and genetic evidence indicates that men have evolved solutions to combat the adaptive problem of sperm competition (Gallup et al., 2003; Goetz et al., 2005; Kilgallon & Simmons, 2005; Pound, 2002; Shackelford et al., 2005; Smith, 1984; Wyckoff, Wang, & Wu, 2000). For example, Shackelford et al. (2002) 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. Without an evolutionary lens, this exciting and fruitful line of research would have been missed entirely.

An evolutionary approach also has encouraged reevaluating and rethinking old topics in psychology. Tomes of nonevolutionary psychological research argued that people encode automatically the race of individuals they encounter. However, Kurzban, Tooby, and Cosmides (2001) 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. However, considering that the mind consists 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 use new techniques to study this phenomenon (Keenan, 2005; Stevens, Guise, Kelly, & Keenan, 2005).

Evolutionary psychology's future. Although this modern approach to human cognition and behavior is young—about 25 years old—evolutionary psychology's impact already is permeating all areas of psychology and is being applied successfully to fields as diverse as medicine (Nesse & Williams, 1994) and law (Jones & Goldsmith, 2005). Evolutionary psychology's current merit and bright future also are demonstrated in the fact that the number of empirical publications using an evolutionary psychological approach is growing exponentially (Durrant & Ellis, 2003). Some have even suggested that, in the foreseeable future, the psychological equivalent to *Gray's Anatomy* will be possible, cataloguing and describing evolved psychological mechanisms, their information processing features, and their neural substrates (Tooby & Cosmides, 1992).

Because an evolutionary perspective can be applied to all areas of psychology, new research programs have emerged and will continue to emerge. One exciting future direction is the development of evolutionary cognitive neuroscience. Using functional neuroimaging technologies (e.g., functional magnetic resonance imaging, functional near-infrared spectros-

copy, and transcranial magnetic stimulation), evolutionary cognitive neuroscience combines evolutionary psychology and cognitive neuroscience to identify the neural substrates of psychology and behavior. Evolutionary psychologists have proposed psychological mechanisms associated with self-awareness, deception, kin recognition, and sexual attraction, and now evolutionary cognitive neuroscience is locating these mechanisms in the brain (Keenan, Wheeler, Platek, Lardi, & Lassonde, 2003; Platek, Keenan, Gallup, & Mohamed, 2004; Platek, Keenan, & Shackelford, 2006).

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 (Bjorklund & Pellegrini, 2002; Hernández Blasi & 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 & Pellegrini, 2000; Ellis & Bjorklund, 2005; 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 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 & Shackelford, 2004; Stone, 2005; 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 evolutionary psychology, as evolutionary psychology's empirical harvest grows, as the cross-cultural efforts of the International Sexuality Description Project continue (Schmitt et al., 2003), as findings from genetics corroborate findings from evolutionary psychology (Cherkas, Oelsner, Mak, Valdes, & Spector, 2004), as the neural substrates underlying hypothesized psychological mechanisms are discovered (Platek, Keenan, & Mohamed, 2005), and as cross-disciplinary frameworks of evidence are used (Schmitt & Pilcher, 2004), evolutionary psychology will emerge as *the* metatheory for psychological science.

Conclusion

In this article, 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 features, evolutionary psychology has risen as a compelling and fruitful approach to the study of human psychology and behavior. Because the brain owes

its functional organization to a natural, evolutionary process, an evolutionary psychological approach is a logical framework on which to base all psychological theories. Evolutionary psychological theories specify the problems our psychological mechanisms were built to solve, thereby providing important information about their likely features. 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).

This was article was intended to be a broad overview of the modern application of evolutionary theory to human psychology and behavior. For a more detailed overview of this approach, see Buss (2004, 2005), Barkow et al. (1992), Gaulin and McBurney (2004), and Pinker (1997, 2002). It is possible to do research in psychology with little or no knowledge of evolution. Most psychologists do. But without an evolutionary perspective, psychology becomes a disparate set of fields. Evolutionary explanations pervade all areas in psychology and provide a unifying metatheoretical framework within which all of psychology can be organized.

Notes

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References

Alcock, J. (2001). *The triumph of sociobiology.* New York: Oxford University Press.

Atkinson, A. P., & Wheeler, M. (2004). The grain of domains: The evolutionary-psychological case against domain-general cognition. *Mind & Language, 19,* 147–176.

Barkow, J. H., Cosmides, L., & Tooby, J. (1992). *The adapted mind.* New York: Oxford University Press.

Bering, J. M., & Shackelford, T. K. (2004). The causal role of consciousness: A conceptual addendum to human evolutionary psychology. *Review of General Psychology, 8,* 227–248.

Bjorklund, D. F., & Pellegrini, A. D. (2000). Child development and evolutionary psychology. *Child Development, 71,* 1687–1798.

Bjorklund, D. F., & Pellegrini, A. D. (2002). *Origins of human nature: Evolutionary developmental psychology.* Washington, DC: American Psychological Association.

Buss, D. M. (1995). Evolutionary psychology: A new paradigm for psychological science. *Psychological Inquiry, 6,* 1–20.

Buss, D. M. (2004). *Evolutionary psychology: The new science of the mind* (2nd ed.). Boston: Allyn & Bacon.

Buss, D. M. (2005). *The handbook of evolutionary psychology.* New York: Wiley.

Buss, D. M., Haselton, M. G., Shackelford, T. K., Bleske, A. L., & Wakefield, J. C. (1998). Adaptations, exaptations, and spandrels. *American Psychologist, 53,* 533–548.

Buss, D. M., Larsen, R., Westen, D., & Semmelroth, J. (1992). Sex differences in jealousy: Evolution, physiology, and psychology. *Psychological Science, 3,* 251–255.

Buss, D. M., & Shackelford, T. K. (1997). From vigilance to violence: Mate retention tactics in married couples. *Journal of Personality and Social Psychology, 72,* 346–361.

Carey, S., & Gelman, R. (1991). *The epigenesis of mind.* Hillsdale, NJ: Erlbaum.

Chagnon, N. A., & Irons, W. (1979). *Evolutionary biology and human social behavior.* North Scituate, MA: Duxbury.

Cherkas, L. F., Oelsner, E. C., Mak, Y. T., Valdes, A., & Spector, T. (2004). Genetic influences on female infidelity and number of sexual partners in humans: A linkage and association study of the role of the Vasopressin Receptor Gene (*AVPR1A*). *Twin Research, 7,* 649–658.

Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition, 31,* 187–276.

Cosmides, L., & Tooby. J. (1987). From evolution to behavior: Evolutionary psychology as the missing link. In J. Dupre (Ed.), *The latest on the best: Essays on evolution and optimality* (pp. 277–306). Cambridge, MA: MIT Press.

Cosmides, L., & Tooby. J. (1994). Origins of domain specificity: The evolution of functional organization. In L. A. Hirschfeld & S. A. Gelman (Eds.), *Mapping the mind: Domain-specificity in cognition and culture* (pp. 85–116). New York: Cambridge University Press.

Crawford, C. (2000). Evolutionary psychology: Counting babies or studying information processing mechanisms. *Annals of the New York Academy of Sciences, 907,* 21–38.

Cummins, D. D. (1998). Social norms and other minds: The evolutionary roots of higher cognition. In D. D. Cummins & C. Allen (Eds.), *The evolution of mind* (pp. 30–50). New York: Oxford University Press.

Daly, M., & Wilson, M. (1983). *Sex, evolution, and behavior* (2nd ed.). Boston: Willard Grant.

Daly, M., Wilson, M., & Weghorst, S. J. (1982). Male sexual jealousy. *Ethology and Sociobiology, 3,* 11–27.

Darwin, C. (1859). *On the origin of species.* London: Murray.

Darwin, C. (1871). *The descent of man and selection in relation to sex.* London: Murray.

Durrant, R., & Ellis, B. J. (2003). Evolutionary psychology: Core assumptions and methodology. In M. Gallagher & R. J. Nelson (Eds.), *Comprehensive handbook of psychology: Vol. 3, Biological psychology* (pp. 1–33). New York: Wiley.

Ellis, B. J., & Bjorklund, D. F. (Eds.) (2005). *Origins of the social mind: Evolutionary psychology and child development.* New York: Guilford.

Fisher, R. A. (1954). Retrospect of the criticisms of the theory of natural selection (pp. 84–98). In J. S. Huxley, A. C. Hardy, & E. B. Ford (Eds.) *Evolution as a process.* London: Allen & Unwin.

Flaxman, S. M., & Sherman, P. (2000). Morning sickness: A mechanism for protecting mother and embryo. *Quarterly Review of Biology, 75,* 113–148.

Fodor, J. A. (1983). *The modularity of mind: An essay on faculty psychology.* Cambridge, MA: MIT Press.

Gallup, G. G., Burch, R. L., Zappieri, M. L., Parvez, R. A., Stockwell, M. L., & Davis, J. A. (2003). The human penis as a semen displacement device. *Evolution and Human Behavior, 24,* 277–289.

Garcia, J., Ervin, F. R., & Koelling, R. A. (1966). Learning with prolonged delay of reinforcement. *Psychonomic Science, 5,* 121–122.

Gaulin, S. J. C., & McBurney, D. H. (2004). *Evolutionary psychology* (2nd ed.). Upper Saddle River, NJ: Pearson.

Gazzaniga, M. S., & Smylie, C. S. (1983). Facial recognition and brain asymmetries: Clues to underlying mechanisms. *Annals of Neurology, 13,* 536–540.

Geary, D. C. (1995). Reflections of evolution and culture in children's cognition: Implications for mathematical development and instruction. *American Psychologist, 50,* 24–37.

Goetz, A. T., Shackelford, T. K., Weekes-Shackelford, V. A., Euler, H. A., Hoier, S., Schmitt, D. P, & LaMunyon, C. W. (2005). Mate retention, semen displacement, and human sperm competition: Tactics to prevent and correct female infidelity. *Personality and Individual Differences, 38,* 749–763.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology, 7,* 1–52.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science, 218,* 384–387.

Hernández Blasi, C., & Bjorklund, D. F. (2003). Evolutionary developmental psychology: A new tool for better understanding human ontogeny. *Human Development, 46,* 259–281.

Hirschfeld, L. A., & Gelman, S. A. (1994). *Mapping the mind.* New York: Cambridge University Press.

Jones, O. D., & Goldsmith, T. H. (2005). Law and behavioral biology. *Columbia Law Review, 105,* 405–502.

Keenan, J. P. (2005). *The selfish brain.* Paper presented at the 17th Annual Meeting of the Human Behavior and Evolution Society, Austin, TX.

Keenan, J. P., Wheeler, M. A., Platek, S., Lardi, G., & Lassonde, M. (2003). Self-face processing in a colostomy patient. *European Journal of Neuroscience, 18,* 2391–2395.

Kettlewell, H. B. D. (1955). Selection experiments on industrial melanism in the Lepidoptera. *Heredity, 9,* 323–342.

Kettlewell, H. B. D. (1956). Further selection experiments on industrial melanism in the Lepidoptera. *Heredity, 10,* 287–301.

Kilgallon, S. J., & Simmons, L. W. (2005). Image content influences men's semen quality. *Biology Letters, 1,* 253–255.

Kurzban, R., Tooby, J., & Cosmides, L. (2001). Can race be erased? Coalitional

computation and social categorization. *Proceedings of the National Academy of Sciences, 98,* 15387–15392.

Mayr, E. (1963). *Animal species and their evolution.* Cambridge: Harvard University Press.

Mayr, E. (1982). *The growth of biological thought.* Cambridge: Harvard University Press.

Mayr, E., & Provine, W. B. (1980). *The evolutionary synthesis.* Cambridge, MA: Harvard University Press.

Nesse, R. M., & Williams, G. C. (1994). *Why we get sick.* New York: Times Books Random House.

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review, 108,* 483–522.

Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews, 45,* 525–567.

Pinker, S. (1997). *How the mind works.* New York: W.W. Norton.

Pinker, S. (2002). *The blank slate: The modern denial of human nature.* New York: Viking.

Pinker, S., & Bloom, P. (1990). Natural language and natural selection. *Behavioral and Brain Sciences, 13,* 707–727.

Platek, S. M. (2003). An evolutionary model of the effects of human paternal resemblance on paternal investment. *Evolution and Cognition, 9,* 189–197.

Platek, S., Keenan, J. P., Gallup, G. G., & Mohamed, F. (2004). Where am I? The neurological correlates of self and other. *Cognitive Brain Research, 19,* 114–122.

Platek, S. M., Keenan, J. P., & Mohamed, F. B. (2005). Neural correlates of facial resemblance. *NeuroImage, 25,* 1336–1344.

Platek, S. M., Keenan, J. P., & Shackelford, T. K. (2006). *Evolutionary cognitive neuroscience.* Cambridge, MA: MIT Press.

Pound, N. (2002). Male interest in visual cues of sperm competition risk. *Evolution and Human Behavior, 23,* 443–466.

Ramachandran, V. S. (1995). Anosognosia in parietal lobe syndrome. *Consciousness and Cognition, 4,* 22–51.

Schmitt, D. P., & 118 members of the International Sexuality Description Project. (2003). Universal sex differences in the desire for sexual variety: Tests from 52 nations, 6 continents, and 13 islands. *Journal of Personality and Social Psychology, 85,* 85–104.

Schmitt, D. P., & Pilcher, J. J. (2004). Evaluating evidence of psychological adaptation: How do we know one when we see one? *Psychological Science, 15,* 643–649.

Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. *Brain, 115,* 15–36.

Shackelford, T. K., LeBlanc, G. J., Weekes-Shackelford, V. A., Bleske-Rechek, A. L., Euler, H. A., & Hoier, S. (2002). Psychological adaptation to human sperm competition. *Evolution and Human Behavior, 23,* 123–138.

Shackelford, T. K., Pound, N., & Goetz, A. T. (2005). Psychological and physiologi-

cal adaptation to human sperm competition. *Review of General Psychology, 9,* 228–248.

Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. *Science, 197,* 1246–1253.

Sherman, P. W., & Alcock, J. (1994). The utility of the proximate–ultimate dichotomy in ethology. *Ethology, 96,* 58–62.

Smith, P. K. (2005). Play: Types and functions in human development. In B. J. Ellis & D. F. Bjorklund (Eds.), *Origins of the social mind* (pp. 271–291). New York: Guilford.

Smith, R. L. (1984). Human sperm competition. In R. L. Smith (Ed.), *Sperm competition and the evolution of animal mating systems* (pp. 601–660). New York: Academic Press.

Stevens, S., Guise, K., Kelly, K., & Keenan, J. P. (2005). *Self-deception and the brain: Using transcranial magnetic stimulation (TMS) to investigate the evolutionary origins of deception.* Poster presented at the 17th Annual Meeting of the Human Behavior and Evolution Society, Austin, TX.

Stone, V. E. (2005). Theory of mind and the evolution of social intelligence. In J. Cacciopo (Ed.), *Social neuroscience: People thinking about thinking people* (pp. 103–130). Cambridge, MA: MIT Press.

Symons, D. (1979). *The evolution of human sexuality.* New York: Oxford University Press.

Thornhill, R. (1997). The concept of an evolved adaptation. In G. R. Bock & G. Cardew (Eds.), *Characterizing human psychological adaptations* (pp. 4–22). West Sussex, England: Wiley.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20,* 410–433.

Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology, 11,* 375–424.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York: Oxford University Press.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology, 76,* 35–57.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man: 1871–1971* (pp. 136–179). Chicago: Aldine.

Trivers, R. (2000). The elements of a scientific theory of self-deception. *Annals of the New York Academy of Sciences, 907,* 114–131.

Williams, G. C. (1966). *Adaptation and natural selection.* Princeton, NJ: Princeton University Press.

Wyckoff, G. J., Wang, W., & Wu, C. (2000). Rapid evolution of male reproductive genes in the descent of man. *Nature, 403,* 304–308.

Wynn, T. (2002). Archaeology and cognitive evolution. *Behavioral and Brain Sciences, 25,* 389–402.