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

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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.

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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

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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,

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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 by products 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.

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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

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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

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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

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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