Evolutionary Social Psychology

Adaptive Predispositions and Human Culture

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The conventional wisdom in the social sciences is that human nature is simply the imprint of an individual’s background and experience. But our cultures are not random collections of arbitrary habits. They are canalized expressions of our instincts. That is why the same themes crop up in all cultures—themes such as family, ritual, bargain, love, hierarchy, friendships, jealousy, group loyalty, and superstition... Instincts, in a species like the human one, are not immutable genetic programs; they are pre-dispositions to learn. (Ridley, 1996)

Social psychologists have generated a wealth of fascinating empirical findings on topics ranging from altruism and aggression through stereotyping and xenophobia. Yet a recurrent criticism of the field is the lack of a cohesive theoretical framework to incorporate these diverse snapshots of empiricism. Part of the appeal of an evolutionary perspective is its capacity to organize these findings, and to integrate the insights of psychology, sociology, and anthropology with those of the other life sciences. Another part of its appeal is its ability to provide answers to interesting questions that are not easy to address from traditional social science perspectives. For example: Why is the distinction between “Us” and “Them” universal? In selecting a mate, why are men generally more attuned to physical attractiveness and women to social status? Why do age preferences in mate choice over the lifespan violate the homogamy principle in a patterned and
universal way? Why are stories about “wicked step-parents” found in many different cultures? Why are some characteristics universally treated as stigmas? Why is investment by fathers, normally rare in mammals, found in all human societies?

In spite of its theoretical promise and an increasing body of empirical research, evolutionary social psychology remains misunderstood. This chapter provides an overview of current research and theory on evolutionary psychology, explores some implications for research on cultural and group processes, and addresses some recurrent criticisms and misconceptions.

**GENERAL PRINCIPLES OF EVOLUTIONARY MODELS**

Evolutionary theorists assume that human beings share certain characteristics with other animals by virtue of either common descent (e.g., with great apes such as chimpanzees) or common ecological demands (e.g., with other groups of living mammals such as wolves or baboons). Observations across the spectrum of living organisms have yielded a number of powerful general principles, which are now being used to expand our understanding of human social behavior. In this section, we summarize the concepts of natural selection, inclusive fitness, life history strategies, differential parental investment, and sexual selection.

**Natural Selection: Morphology and Behavior by Adaptive Design**

Darwin’s (1859) original theory of natural selection was based on three interlinked concepts: variability within a species, inheritance of traits by offspring, and differential reproduction. Within any species, individuals vary in traits relevant to survival and reproduction. For example, a trait that helps an animal run faster than others of its same species will assist in escaping predators, and therefore living longer and producing more offspring than others without that trait.

Physical innovations such as a whale’s flipper or a bat’s wing only help the animal survive and reproduce because they co-evolved with central nervous systems capable of producing particular behaviors adapted to the animal’s particular environment. Imagine a whale trying to hunt flying insects at night, or a bat trying to sift plankton from the ocean, for instance. Besides their wings, however, bats have inherited complex neural machinery designed to fit a particular behavioral repertoire. Because they must locate moving prey in the dark, bats have a large portion of their brains dedicated to analyzing the sonar-like echoes of the specialized sounds they emit. On the other hand, humans have brain mechanisms specially designed to analyze binocular color vision, which assists in locating and tracking prey or estimating ripeness of fruit on a distant limb.

Despite the very different ecological demands on whales, bats, and humans, they also share certain behavioral programs by virtue of common descent and common ecological pressures. For example, all mammalian females nurse their young. Most species of whales and bats, like humans, congregate in large groups, a behavioral adaptation that has some adaptive advantages—avoiding predators or searching for scattered food sources, for example, but also some disadvantages—such as increased intraspecies competition and disease (Alcock, 1998). Group aggregation, like most behavioral tendencies, is found when advantages outweigh disadvantages (more likely in prey than in predator species, e.g., and less likely in species who eat food that can be defended in small territories). Besides those adaptations shared by
common descent or common ecological demands, some are uniquely designed to solve particular problems encountered by a given species (e.g., flying ability in bats, but not in other mammals).

Modern evolutionary theorists assume that many features related to human cognition, motivation, and behavior were designed through natural selection. For example, much as the bird of paradise has inherited dazzling plumage and associated courtship displays, humans have inherited a larynx along with a brain designed to easily learn to communicate using language (Pinker, 1994).

From an evolutionary perspective, the first question one asks about a morphological or behavioral feature is: What is its function? A baby’s crying would have served to alert its mother to the child’s immediate needs, and its smiling and cooing to cement the mother–infant bond, for example. From the mother’s perspective, the bond would have served to increase the survival rates of her offspring (Zeifman & Hazan, 1997).

Because humans have lived in small, kin-based groups for over three million years (Foley, 1989), it is assumed that many features of human cognition and behavior were designed to solve the problems of living in such groups (Kenrick, Sadalla, & Keefe, 1998). For example, humans around the world have well-articulated vocabularies for describing the extent to which another person is cooperative or dominant, and it has been suggested that this is because our ancestors’ survival and reproduction would have been served by knowledge of those who were reliable allies or leaders (White, 1980). Similarly, people are very good at solving normally difficult logical problems when they are framed in terms of detecting cheaters in social situations, and it has been suggested that this ability was likewise well-fitted to the demands of living in human ancestral groups (Tooby & Cosmides, 1992).

It is important to note that evolutionary theorists do not assume that humans or other organisms inherit some capacity to determine in advance which behavioral strategy will be adaptive, and thereby proceed through life as “fitness-maximizing” machines. Instead, it is assumed that organisms inherit specific behavioral mechanisms designed to increase the probability of solving recurrent problems confronted during the ancestral past. For example, animals whose ancestors ate fruit are sensitive to sweetness, and find it reinforcing; animals whose ancestors were purely carnivorous do not. Generally, sweetness sensitivity led our human ancestors to eat ripe, rather than unripe, fruit (the latter having less nutritional value, and higher toxin content). While evolutionary psychologists typically begin by investigating a behavior’s function, it is not always assumed that the particular behavior in question continues to be adaptive in the human-altered modern world. Because natural selection operates over the long haul, whereas human culture and technology can change rapidly, modern humans likely possess some characteristics that are less than perfectly suited for current environments. For a diabetes-prone individual with unlimited access to chocolate bars and ice cream, the sweetness-seeking mechanism might shorten his or her lifespan; however, it would, on average, have helped his or her ancestors survive to reproductive age.

Inclusive Fitness: Why Humans Everywhere are Concerned with the Distinction between Kin and Non-Kin

While Darwinian theory revolutionized the natural sciences, its focus on individual reproductive success could not account for the persistence of behaviors in which one individual sacrificed his or her reproductive success for the sake of another individual. Altruistic acts such as sacrificing one’s life for a child, or refraining from mating in order to help care
for the offspring of others (common among many social insects), would seem likely to be replaced by more selfish behaviors that led to successful reproduction. This dilemma was resolved when biologists began to understand processes of genetic inheritance. W. D. Hamilton (1964) explained that any gene in an individual may be propagated by that individual directly or by a related individual who shares that gene. More closely related individuals are more likely to share the gene and are also more likely to exhibit altruistic behaviors towards each other. Because closely related individuals share common genes, altruistic inclinations could be selected if on average, they led organisms to act in ways that maximized the genetic payoff (e.g., risking one’s own life to save three brothers). While classical fitness had been calculated based only on the number of offspring an individual produced, inclusive fitness is calculated in terms both of direct reproduction and indirect replication of genes gained through assistance to kin. The biological literature abounds with descriptions of altruistic acts among related animals (Alcock, 1998; Trivers, 1985). This does not mean that humans, or any other animals, consciously decide to assist kin because it maximizes their own fitness. Proximate mechanisms such as familial love incline people to help relatives; inclusive fitness theory merely explains how such a behavior could develop and be sustained in a species.

Alarm calls in various rodents offer good examples of kin altruism (Hoogland, 1983; Sherman, 1977). Upon sighting predators such as hawks, ground squirrels risk their own lives by making an alarm call that warns neighbors to take cover. However, their alarm calling is socially contingent, and from a genetic perspective, actually selfish: It is much more likely when the animals are in the vicinity of close kin as opposed to unrelated squirrels. Another common example of kin altruism is known as “helping at the nest”—a phenomenon in which adult offspring help care for relatives’ offspring. For example, when they are unable to find a suitable location to mate on their own, white-fronted bee-eaters delay mating to help both younger siblings and more distant relatives who inhabit the same communal nest. The likelihood that a bird will aid a relative can be modeled with extreme precision to Hamilton’s laws of inclusive fitness. Full siblings are the most likely to be helped; distant relatives are the least likely. Emlen (1997) notes that over 90% of bird and mammal species living in multi-generational families show this cooperative breeding behavior.

In humans as well, resources and assistance are often provided by close kin. According to kin selection theory, we should help siblings, parents, and offspring (who share on average 0.50 of our genes) more often than aunts and uncles or nieces and nephews (all sharing about 0.25 of our genes). Aunts and uncles (especially on the mother’s side) tend to invest effort in helping a woman raise her children (Gaulin, McBurney, & Brademan-Wartell, 1997). Grandparents, again more so on the maternal side, are particularly likely to invest in children (Euler & Weitzel, 1996). There is, in general, a propensity to support relatives of many types, although close relatives are usually favored over more distant ones. The fact that helping is more likely from a mother’s relatives is also consistent with notions of inclusive fitness: Paternity always carries some degree of uncertainty, so although the mother’s relatives can always be certain they are helping kin, the father’s cannot.

In times of real need, it is often kin, and not friends, that people call upon for assistance and support. In a series of experiments, Burnstein, Crandall, and Kitayama (1994) asked participants to imagine that they were in a burning building and given a choice of which one family member to save. Grandparents were more likely to be helped in everyday situations, but in life-and-death situations, helping for grandparents as well as cousins decreased in favor of more assistance for siblings who were not past the age of reproductive viability (younger siblings). Under the collective threat of war, people rely increasingly on relatives rather than
the friends or neighbors they turn to for everyday support (Shavit, Fischer, & Koresh, 1994). In a multicultural study, there were some cultural differences in the composition of support networks, but regardless of ethnicity, the person most likely to care for a mentally ill person was a female relative (Guarnaccia & Parra, 1996).

On the other side of the equation, non-relatives often suffer neglect and abuse. Anderson, Kaplan, and Lancaster (1997) found that genetic children were 5.5 times more likely than stepchildren to receive money for college expenses. Of even greater concern, children living with a stepparent are approximately 40 times more likely to suffer physical abuse than those living with two genetic parents (Daly & Wilson, 1985) and 40–100 times more at risk of homicide (Daly & Wilson, 1988). These figures hold even when controlling for factors such as socioeconomic status. In short, social relationships in humans, like those in other animals, are greatly influenced by genetic relationships between the actors.

**Life History Strategies: When and How to Reproduce?**

A life history is a genetically organized plan for allocating resources over the lifespan. Individual animals have a finite amount of time and energy to invest in growth, maturation and reproduction before they die. Life history theory assumes that natural selection operates on the timing of allocation of effort to these processes (Crawford & Anderson, 1989; Stearns, 1976). For example, an animal could invest all its energy over a prolonged period into somatic effort (bodily growth and maintenance) while delaying expenditures of energy for reproductive effort (mating and parenting). If the animal, therefore, becomes larger, stronger, and healthier than competitors, it may eventually leave more offspring, and its developmental gamble would have then paid off. On the other hand, in a different environment, those rivals who begin reproducing right away might leave more offspring than the animal who delays reproduction and dies before leaving viable offspring.

Organisms show an amazing array of life history patterns. One small mammal from Madagascar begins reproducing a few weeks after birth (Quammen, 1996). Elephants, on the other hand, take decades to reach sexual maturity, and then carry each fetus for over a year (Daly & Wilson, 1983). Variations in rate and timing of maturity, and relative amount of effort invested in somatic versus reproductive effort are related to ecological conditions in a species' evolutionary past. For example, animals whose newborns are subject to heavy predation, like wildebeests, may reproduce en masse on one day of each year, thus reducing their individual risk of losing individual offspring to predators, who can only attack a few of the helpless offspring at one time.

Primates in general reach sexual maturity later and live longer than other mammals of similar size. Compared with other primates, humans have four unique life history characteristics: (1) a very long life span, (2) an extended period of offspring dependence, (3) reproductive support by older post-reproductive individuals, and (4) male help in caring for offspring (Hill & Kaplan, 1999). Hill and Kaplan (1999) argue that species such as humans, whose food is varied and difficult to obtain, delay reproduction to acquire the knowledge and skills needed to successfully forage. In hunter-gatherer groups, older females who are slightly more vigorous, despite declining fertility, often provide foods such as tubers and berries to enhance the survivorship of grandchildren while allowing the mothers of those offspring to begin a new pregnancy sooner (Hawkes, 1999).

Another characteristic of human life-history is lifelong relationships between related individuals of both sexes. Among our closest relatives, the chimpanzees (Pan paniscus),
females disperse from the group at sexual maturity, and have no further contact with related individuals with whom they grew up. In all human societies, individuals of both genders maintain relationships with kin of both genders, even if they are not in physical proximity (Rodseth, Wrangham, Harrigan, & Smuts, 1991).

Life-history theory offers insights into a number of social psychological phenomena. For example, in a wide variety of human societies, the long delay in reproduction is more pronounced for males, who must generally accumulate status and resources before attracting a mate (Hill & Kaplan, 1999). This may be associated with a general female tendency to prefer older rather than younger partners. A sex difference in the age of preferred mates, in fact, appears in all human cultures examined thus far (Kenrick & Keefe, 1992; Otta, Queiroz, Campos, daSilva, & Silveira, 1998). The general pattern is that females of all ages generally prefer older males, whereas males change their relative preferences as they age. Young men are attracted to women older than themselves, men in their twenties are attracted to women their own age, and older men are interested in younger women (Kenrick, Yabrielidis, Keefe, & Cornelius, 1996). It appears that women in the years of peak fertility are attractive to men in all cultures (Kenrick & Keefe, 1992). Because of intrinsic differences in the costs of reproduction for males and females, some of the most theoretically important within-species differences cut along the lines of sex, a topic to which we now turn.

Differential Parental Investment: Sex Differences and Similarities in Reproductive Strategy

The question of how much to invest in offspring is a key part of the life-history strategy. Resources invested in one offspring exact costs to the parent’s ability to invest in others (Trivers, 1985). In reptiles, birds, and mammals, there is an initial sex difference in parental investment stemming from the fact that eggs are more nutritionally expensive than sperm. In most mammals, the initial expense of producing a large nutritionally rich egg (as in reptiles and birds), are drastically increased because the fertilized egg develops inside the mother’s body (in most mammals). After birth, mammalian females invest further by nursing their young for some time—a year or more in some species. In over 95% of mammalian species, males invest no more direct nutritional resources than the calories required to produce and deposit sperm (Clutton-Brock, 1991).

Parental investment is correlated with selectivity in choosing a mate. Because females generally tend to invest more, they are generally more demanding shoppers in the mating marketplace. Consider spending money from a bank account as an analogy for investing resources in reproduction (Kenrick & Trost, 1996). Imagine men and women each have bank account balances of $1,000 when they reach reproductive age. Women are required to spend at least $100 on every child they bear, while men can spend as little as 10 cents or as much as $100. For a man, the low cost (or 10 cent) option involves only as much energy as it takes to have sex. Under this circumstance, a male need not be selective about partners, because he has almost nothing to lose by mating with anyone. Contrast this with the woman, whose minimum required investment is $100, which is a significant portion of her total bank account. She is not likely to spend that $100 on just anyone. In return for her higher investment, she will demand a mate of high quality, to ensure that her few precious offspring have a good chance at survival and reproduction. When men decide to invest more than the minimum in their offspring, their choices follow the same pattern as women: men desire a high quality partner in
return for larger investments (Kenrick, Sadalla, Groth, & Trost, 1990; Kenrick, Groth, Trost, & Sadalla, 1993).

Given an opportunity to make the minimum investment in offspring, a man could afford to be less selective in choosing partners. But most men will find few takers for such a low offer. Because females are selective, a male must demonstrate qualities that make him a better deal than other males. These might be better genes than his competitors, signaled by a relatively more robust and symmetrical physical appearance, or extraordinary skills (Gangestad & Thornhill, 1997; Miller, 1999). Or the male might show a willingness to match some of the female’s investments with investments of his own, such as nest building and providing her with nutrition.

There are species in which males invest in the offspring as much as, if not more than, females. The male seahorse carries the fertilized eggs in a pouch and then cares for the newborns, freeing the female to invest energy in a new family. Like male humans who invest $100 rather than a dime, male seahorses are more selective about the females with which they will mate, and females in such species may compete with one another for the male’s attentions (Trivers, 1985).

Thus, parental investment leads to at least two general regularities in animal behavior. First, there is a direct link between the amount of resources invested by a given sex and that sex’s selectiveness in choosing mates. Second, to the extent that members of one sex make investments, and are therefore selective, members of the other sex will compete with one another, and hence show sexually selected traits. For example, in monogamous species, males and females tend to be similar in size and appearance. In polygynous species, where one male mates with several females, males tend to be larger and to possess decorative or defensive features, such as peacocks’ feathers or bucks’ antlers. The reason for this is related to the principles we discussed previously. Males in monogamous species make high investments of effort and resources in the offspring, often matching those of the females. Males in polygynous species make less direct investment in any given female or her offspring, and hence are subject to strong sexual selection pressures, as females pick males with traits suggesting superior genes. Polygynous males must, therefore, make higher investments in features that females find attractive.

Because humans are mammals, there is a large initial discrepancy in parental investment. Consistently, there is abundant data that men given the opportunity are, compared with women, more likely to accept a low cost sexual opportunity (e.g., Buss & Schmitt, 1993; Clark & Hatfield, 1989; Kenrick et al., 1990). But unlike 95% of other mammals, human males often invest heavily in their offspring, with long-term marriage bonds being universal across human societies (Broude, 1994; Daly & Wilson, 1983). Parental investment theory would lead to the prediction that males will have minimal criteria for engaging in casual sexual relationships, but will become increasingly selective about partners for long-term relationships (Kenrick et al., 1990). Consistently, males surveyed about criteria for one-night stands expressed standards considerably below those of females, and were willing to have sex with a partner whose intelligence was considerably lower than they would require in a dating partner. However, males’ minimum standards for marriage partners were much more similar to those of females (e.g., both sexes insisted on someone considerably above average in intelligence for a spouse).

With regard to criteria such as status and wealth in a mate, however, men’s standards are still lower than those of women, and for characteristics related to physical attractiveness, men sometimes have higher standards than women. These differences are consistent with research and theory on sexual selection, to which we now turn.
Sexual Selection: Mate Choice, Status, and Attractiveness

Sexual selection was a concept advanced by Charles Darwin to explain the evolution of sex-based characteristics that did not, at first glance, seem to make sense from the perspective of natural selection. Traits such as peacock's feathers seem to directly reduce survival. Large colorful male animals are likely to die earlier: Their showy displays are not only physiologically costly to maintain, but are also like neon signs that draw the attention of hungry predators. If selection favors characteristics well suited to survival, how could such traits have ever evolved? The answer is that these characteristics helped ancestral animals acquire more mates than their less colorful or smaller-antlered competitors. The bottom line of selection is not survival, but reproduction. Traits that predispose an individual to live long without reproducing do not get replicated. Alternatively, traits that enhance successful mating, even if they impose a potential survival cost, can be selected if the mating enhancement is enough to compensate for their costs on longevity.

Sexual selection can be further divided into intrasexual and intersexual selection. Intrasexual selection refers to competition within one's own sex for mates, and encompasses features such as large size or weapons of defense such as large antlers. In many species, physically dominant males are disproportionately successful in leaving offspring (Hrdy, 1999). In some species, such as elephant seals, Mirounga angustirostris (Stewart & Huber, 1993), only the strongest male in a particular group gets to mate at all. Intersexual selection, also known as mate choice, refers to success in attracting members of the opposite sex.

Darwin believed sexual selection most commonly results from female choice of males. For example, a female fruit fly chooses her mate by his dancing ability. Dancing ability is a proxy for overall health and vigor, so those male fruit flies that can't keep up with her elaborate dance are not chosen as mates. Females' choices therefore influence not only their own reproductive success but also the evolution of males (Maynard Smith, 1955).

There is evidence that female choice operated in human evolution. Adult males are about 30% heavier, due in part to larger upper body muscles and in part to longer bodies (males are about 10% taller). Male and female humans also mature at different rates. Although both sexes delay maturity for over a decade, males typically reach puberty later than do females, and continue to grow for several years longer. Knowing nothing else about this species, a biologist would observe these physical differences as the marks of sexual selection (Geary, 1998). The extent of the discrepancies suggests a species whose ancestors were somewhat polygynous, and in which males competed with one another for females. However, human males are not immensely larger than females, as is found in highly polygynous species, like elephant seals and baboons, where males are several times larger. The degree of difference instead suggests a species that was only mildly polygynous (Daly & Wilson, 1983).

In species in which males invest in the offspring, male choice may also exert sexual selection pressures on females. As we noted earlier, men are indeed selective when it comes to choosing long-term mates. Given that each sex would be expected to choose partners on characteristics that enhanced reproductive success, some of the selection criteria should be the same for both sexes. For example, both men and women preferentially choose partners manifesting traits (such as symmetry) that are correlated with "good" genes, often indicating longevity, reproductive viability, and parasite resistance (Gangestad, 1994; Thornhill & Gangestad, 1994). However, human males and females contribute different resources to the offspring, and would be expected to value potential correspondingly different traits. Because females contribute direct physical resources, carrying the fetus and nursing the offspring, males would be expected to value characteristics that tend to be correlated with fertility, such
as health and physical traits typical of women who have reached puberty but not yet borne children (Cunningham, Druen, & Barbee, 1997; Kenrick & Keefe, 1992; Singh, 1993). Because males contribute indirect resources, such as material goods and protection, females would be expected to place more emphasis on characteristics associated with financial success and social status (e.g., Sadalla, Kenrick, & Vershure, 1987). Consistent with these expectations, research conducted across different cultures has shown that females place more importance on the status of a mate while males place more value on a mate’s attractiveness (Broude, 1994; Buss, 1989; Townsend & Wasserman, 1998). Some of the cues linked to successful reproduction are behavioral, and may require inferences about underlying personality traits, such as fidelity or agreeableness (Kenrick & Trost, 1996).

**MIND, LANGUAGE, AND CULTURE**

It is a rare social scientist who rejects Darwinian theory as an explanation of whale’s flippers or bat’s wings, yet many still question its relevance to human social behavior. Some believe that an evolutionary approach provides an incompatible alternative to the cultural, cognitive, or learning-based approaches most familiar to social scientists. Others believe that biological and social approaches are not actually incompatible, but represent different “levels of analysis” which, like a topographical map and a subway map, are appropriately explored independently of one another. Still others grant that an evolutionary analysis is relevant and useful when applied to some “simple behaviors” such as initial attraction and aggression, but fail to see its relevance to complex group level phenomena such as intergroup stereotyping, social identity, or culture. In this section, we argue that an evolutionary perspective is neither incompatible with, nor independent of, the study of culture, learning, or cognition. Instead, these perspectives are mutually informative and all essential to a full understanding of the roots of human social behavior. The characteristics that make humans unique, including the capacity for language, thought, and the creation of culture, can be fully understood only in light of the powerful evolutionary forces that shaped human nature. What humans are inclined to learn, what humans are inclined to think about, and the cultural norms that humans create are all indirect products of the adaptive pressures that shaped the human mind. In this section, we first consider the evidence for adaptive biases in learning, then we consider human language as a model of how genetic and cultural forces mutually construct and constrain one another. We also consider some ways in which evolutionary analyses may be applied to other group-level phenomena, including social identity and intergroup relations.

**Adaptively Prepared Learning**

For decades, social scientists were mired in the nature–nurture controversy, wed to the idea that “learning” and “instinct” were alternatives—that animals either learned their habitual behaviors or inherited them in programs written before birth. Researchers in the field of learning and cognition have, in recent decades, shed these old dichotomous ways of thinking. One of the most useful constructs to emerge from this controversy is the notion of “preparedness”—the idea that organisms are often predisposed to learn some associations more easily than others (e.g., Ohman & Mineka, 2001; Rozin & Kalat, 1971; Seligman & Hager, 1972). The best-known example comes from research on food aversion. Rats exposed to novel foods and later made nauseous learn in one trial to avoid those foods in the future.
This aversive learning is difficult to extinguish, and does not follow normal principles of classical conditioning. For example, it does not require multiple trials and it can occur when the novel taste stimulus and the nausea response are separated by hours (rather than the usual milliseconds required for "normal" classical conditioning). Furthermore, rats cannot learn to associate nausea to visual stimuli, but only to taste stimuli. Human beings likewise are subject to one-trial conditioning when novel tastes are followed by later nausea (Seligman & Hager, 1972). Animals such as rats and humans, who sample widely from a range of potentially toxic plant substances, are "prepared" to quickly learn associations between novel tastes and nausea, in order to protect them from eating potentially poisonous foods more than once.

Ohman and Mineka (2001) review evidence that fear responses involve just such an innate prepared system. For example, the lower brain centers associated with fear have a powerful directive effect on cortical processing, and are difficult to override consciously (most people have difficulty picking up a snake, for example, even after they have been convinced it is non-poisonous). But although some of the triggers for fear responses may be innate (snakes, wasps, or large spiders), most of them are learned (the face of the neighborhood bully, or the characteristics of members of "enemy" groups). Importantly, this fear learning is itself "prepared," in that it is markedly easier to learn, and harder to extinguish, avoidance responses to some cues than others (e.g., angry as opposed to happy faces, dogs as opposed to flowers).

Preparedness applies to more complex forms of learning as well. For example, the human brain is particularly prepared to learn a spoken language. Infants are born especially sensitive to human vocal patterns, and predisposed to emit all the phonemes of human language. During the first few years of life, despite their generally undeveloped state of cognitive development and lack of formal training in grammar, they learn the local argot to a level of perfection that will not be possible at any later time in life (Pinker, 1997). Highly intelligent adult Americans who move to Germany still speak the new language with noticeable imperfections decades later, while their 4-year-old children, barely able to tie their own shoelaces or learn simple addition and subtraction, manage to converse in complex and fluent German prose.

As in the case of language, evolution-based sex differences in behavior need not be "hard-wired" at birth. Instead, the sexes may be simply be "prepared" to have different learning experiences. For example, simple differences in size, upper body development, and testosterone levels, may combine to make aggressiveness more appealing and rewarding for males than for females. And differences in estrogen and oxytocin levels may combine to make close social relationships more rewarding for females. Thus, even though some gender differences in social behavior are found across a wide array of animal species, this does not imply that they arise "independent" of experience. The sexes may simply enter the world biologically prepared to experience slightly different events, and the societies constructed by adult members of this particular species may further reinforce, channel, and facilitate those differential learning experiences.

The Construction of Culture

Evolutionary theorists would not deny that humans have complex cultures, and that these vary from time to time and place to place. Furthermore, some of the variations are the products of arbitrary historical accident, such as whether one eats with a fork, chopsticks, or one's left
hand. However, an evolutionary analysis of culture begins with the assumption that many important cultural norms are not arbitrary, but products of an interaction between flexible evolved psychological mechanisms and local ecological conditions. Evolved preferences and capacities simply influence the menu of likely cultural practices (Fiske, Kitayama, Markus, & Nisbett, 1998). Language provides a perfect model—no one argues that there is an evolved genetic tendency to speak Italian as opposed to Dutch—if two Venetian newlyweds move to Amsterdam, their children will speak perfect Dutch. Yet, no other species is capable of conversing in any human language, and human languages the world over share many features, such as similar levels of grammatical complexity (Pinker, 1997). Thus, human language is best understood as an innate predisposition to absorb certain kinds of cultural information. Without either the innate predisposition or the cultural context, language could not exist.

Part of the evolutionary program has been a search for common features that link human cultures the world over (Brown, 1991; Rosch, 1973). For example, all human cultures have systems for reckoning kinship, and norms for differential treatment of individuals according to kinship status (Daly, Salmon, & Wilson, 1997). All human cultures have long-term marital bonds between males and females who share parenting responsibilities (Broude, 1994; Daly & Wilson, 1983). The latter fact is neither necessary nor obvious, in that it does not apply to 95% of other mammalian species (Geary, 1998). Older men in all human cultures are attracted to women who are younger than themselves (Harpending, 1992; Kenrick & Keefe, 1992; Otta et al., 1998). Adult males are more likely to kill one another than are adult females in all human societies (Daly & Wilson, 1988). Mothers spend much more time in childcare than do fathers in all human societies (Geary, 1998). All human cultures also have status hierarchies, divisions between ingroups and outgroups, and many other common features (Brown, 1991). And facial signals that communicate anger and disgust are recognized by people in all cultures (Ekman & Friesen, 1971).

To point out common cultural features is not to imply that humans construct their cultures robot-like, according to a rigid genetic program. These cultural similarities exist alongside many cultural variations. Consider the case of the Tiwi. In this aboriginal Australian group, a young man often marries a much older woman (Hart & Pillig, 1960). Among traditional Tiwi, all women were required to be married. Widows re-married at their husband's gravesites, and infant girls were betrothed at birth. Men were not required to be married, and because the society was polygynous, many men remained single for a good portion of their lives. There were two ways for a man to get a wife—to have an older married man betroth his infant girl to cement an alliance, or to marry an older widow to gain her resources, while cementing an alliance with her sons. As it turns out, traditional Tiwi men married older women not because of a reversal of normal attraction preferences, but as a pathway to gaining the younger wives, they found most desirable (Hart & Pillig, 1960). Rather than being completely arbitrary, Tiwi mating patterns manifest an interplay between general human mating preferences and a particular social ecology.

Indeed, some of the most interesting questions at the interface of evolutionary biology and the social sciences involve a search for the precise ecological conditions under which cultural practices will vary. For example, most human marriages are monogamous, although a majority of cultures permit polygyny (one man and more then one wife), and a few permit polyandry (one woman and more than one husband). When biologists find variations across species in behavior, they search for correlations with ecological factors (Alcock, 2001). These include factors relevant to survival and reproduction, such as the type and spatial distribution of food resources, population density and distribution (e.g., small groups, large herds, isolated mating pairs), proximity to kin, and sex ratios of mating age adults. For example, polyandry
in birds is often found under conditions of extreme resource scarcity, and males who share a partner are often brothers (Daly & Wilson, 1983). Similarly, one can search across human cultures for ecological factors associated with variations in cultural practices, such as marital arrangements. This search has yielded some interesting regularities (Crook & Crook, 1988). For example, polyandry, though rare, is associated with conditions of extreme resource scarcity (as found in the high Himalayas) under which survival rates for children of single males and their wives are low. In Nepal and a few other places, several brothers often combine their resources and marry a single wife, increasing survival rates for resultant children. On the other hand, extreme polygyny (harems) is correlated with ecological conditions including: (1) steep social hierarchy, (2) generally rich environment allowing higher status families to accumulate vast wealth, (3) occasional famines so lower status families face possibilities of starvation (Crook & Crook, 1988). Under these circumstances, a woman who absorbs the cost of sharing a wealthy husband reaps a survival insurance policy for herself and resultant children.

Due to warfare, migration, and random historical and geographic variations, there are sometimes relatively more available females than males in the pool of eligible mates, or the converse. Guttentag and Secord (1983) found that a surplus of women (putting men in a "buyers' market") is associated with later marriage, more divorce, and permissive sexual norms. A surplus of men, on the other hand, is associated with male commitment to more stable monogamous relationships. Again, variations in ecological circumstances (sex ratios) seem to interact with innate predispositions (sex differences in inclinations toward unrestricted mating) to result in meaningful patterns at the societal level. By searching for interactions between local conditions and individual-level predispositions, we may develop a fuller picture of the emergence of cultural practices (Gangestad & Buss, 1994; Kenrick, Li, & Butner, 2003). Following ecological research in biology and anthropology, it might be profitable to begin the focus on large-scale factors directly related to survival and reproduction (distribution and abundance of resources, kin proximity, population density, sex ratios of mature adults in the local environment, and so on).

Intra- and Intergroup Relationships

Anthropological and archaeological data suggest that the context for human evolution has always involved small groups of related individuals. Data from historical and modern hunter-gatherers suggest that these groups were comprised of 20–30 individuals at the lower end, up to a few hundred individuals in richer environments (Barnard, 1999). While hunter-gatherer bands might may coalesce into larger groups seasonally, small groups are and were more often the norm. The typical size for hunter-gatherer bands is about 50–80 people (Maryanski & Turner, 1992). These bands occupy relatively large and exclusive territories through which they migrate to exploit resources. Compared with agricultural and industrial societies, life in hunter-gatherer bands is characterized by relatively less steep social hierarchies (although mature adults and males tend to hold relatively higher status positions across human societies). Ties of kinship (whether actual or fictive) are extended to almost all in the local band (Barnard, 1999; Maryanski & Turner, 1992).

While our human and proto-human ancestors foraged (or at least scavenged) for several million years, plant cultivation is, in evolutionary perspective, a recent phenomenon, beginning only about 10,000 years ago (Maryanski & Turner, 1992). Modern, industrial, anonymous society represents only a small slice of our evolutionary history. In the ancestral world, an unknown
individual was a potential enemy—perhaps someone encroaching on our band’s hunting and gathering territory. Although some traditional groups do establish cordial exchange relationships, trading goods with members of other groups, outsiders may also bring increased threats of kidnapping, rape, or, homicide (Chagnon, 1988; Radcliffe-Brown, 1913).

The data on hunter-gatherers has led some to suggest that humans are cognitively inclined to divide other people into “in-group” and “out-group” (Krebs & Denton, 1997; Wilson, 1978). Because out-group members did not always pose threats, and could sometimes offer rewards, a simplistic inclination to reject and avoid such individuals under all circumstances would have not have been as adaptive as a more flexible response system. Schaller (2003) and his colleagues have conducted a series of studies suggesting that circumstances associated with increasing danger in ancestral environments can enhance group stereotypes associated with threat. For example, Canadian students showed exaggerated perceptions of the hostility and untrustworthiness of Iraqis and African Americans, and less favorable attitudes toward immigration, when rating the out-group members in a darkened room (likely to have been associated with increased danger in the ancestral environment). Darkness increased stereotyping only for threat-relevant characteristics (e.g., dangerous), and not for other stereotypical traits (e.g., lazy). This research is typical of recent evolutionarily inspired work—rather than presuming inflexible mechanisms “hard-wired” at birth, this modern work posits cognitive mechanisms that respond in adaptive and flexible ways to environmental variations (c.f., Kenrick, 1994; Kenrick, Neuberg, Zierk, & Krones, 1993).

Because in-group members would have been connected by genetic relatedness and long-term reciprocal exchanges, relationships within groups in traditional human societies would have been more trusting, and characterized by communal exchange of goods rather than market-like reciprocal exchange (Fiske, 1992). Evolutionary analyses of social stigmatization processes have suggested that stigmas often involve threats to group welfare, with particular distaste for individuals who violate principles of fair sharing or group welfare, such as cheaters, free riders, sociopaths, and carriers of communicable pathogens (Kurzban & Leary, 2001; Neuberg, Smith, & Asher, 2000). Consistent with this analysis, a series of experiments by Cosmides and Tooby (1992) suggest that people are especially good at solving otherwise difficult logical problems if the problems are framed so they involve catching cheaters on social contracts.

Besides this nascent work on stereotypes and intergroup relations, there have been evolutionary analyses of other topics relevant to group researchers, including cooperation, leadership, and sexual harassment in organizations (e.g., Brewer, 1997; Caporael & Baron, 1997; Kenrick, Trost, & Sheets, 1996). Unlike the research on aggression or mating strategies, evolutionary analyses of group processes have only begun to explore the implications of adaptationist thinking, and a great deal more research is required. However, the human mind was designed in the context of group living, and increased understanding of any cognitive or learning biases that affect processes within and between groups could have socially important implications.

WHY DON’T SOCIAL SCIENTISTS TAKE FULLER ADVANTAGE OF MODERN EVOLUTIONARY THEORY?

An evolutionary approach to social behavior is based on a pair of rather unremarkable premises. First, animals’ physical and behavioral structures evolved through the process of natural selection. Second, human behavior can be better understood if the social scientist’s empirical
and theoretical toolbox included the sorts of functional analyses that have proved so useful in understanding the social arrangements of ants, bee-eaters, and chimpanzees. Indeed, it would be quite remarkable if *Homo sapiens* were the one species to which evolutionary theory is irrelevant. The evolutionary perspective has already yielded increased understanding of a number of human behaviors, such as nepotism and gender differences in sexual selectivity, and we believe many more insights would follow if students were better trained in evolutionary principles, and more research efforts were directed toward understanding the interaction of genes, culture, and cognition. Yet, as we indicated earlier, many social scientists continue to be reluctant to incorporate evolutionary perspectives into their models (Badcock, 2000; LoPreato & Crippen, 1999). Lee Ellis (1996) goes so far as to suggest that many social scientists suffer from “biophobia.”

There are a number of concerns and misconceptions that have kept social scientists from taking full advantage of an evolutionary perspective, and these have been addressed in great detail elsewhere (Alcock, 2001; Buss & Kenrick, 1998). In this section, however, we consider five important concerns about evolutionary theory: that it is reductionistic; that it implies that evolved mechanisms are unchangeable; that it implies that evolved mechanisms are “natural” and therefore good or moral; that its hypotheses are untestable; and, that its explanations are post hoc.

The concerns about reductionism stem from a perception that the aim of evolutionary analyses is to isolate the particular genes for various social behaviors. This misconception is perhaps understandable in light of the fact that natural selection indeed operates on genetic predispositions (Alcock, 2001). One of the most popular books on sociobiology was in fact titled *The Selfish Gene* (Dawkins, 1989). While it is true that evolutionary analyses assume cross-generational transmission of genetically based traits, it does not follow that most evolutionary researchers (1) assume single genes for each and every social behavior, (2) assume that genes (singly or in combination) do not interact with the environment, or (3) are more interested in studying genes than in studying the environments within which genetic predispositions unfold. By analogy, consider that, although any cognitive psychologist interested in memory must assume brain cells capable of storing information, most have absolutely no interest in locating the neurons wherein memories are stored. Most evolutionary researchers who study behavior are curious about the functional relationships between behaviors and changes in the environment, and are in fact no more interested in particular genes than cognitive psychologists are interested in particular neurons (c.f., Alcock, 2001). For example, a researcher interested in sexual selection and its relation to differential parental investment would examine the correlation between male parental care and female competition over males (Geary, 1998). A researcher interested in inclusive fitness and prosocial behavior might examine the correlation between helping in communally nesting birds and the relatedness between helping providers and recipients (Emlen, Wrege, & DeMong, 1995).

Even Richard Dawkins, author of the *Selfish Gene*, has been quite explicit in explaining that single genes do not determine anything except in interaction with other genes and developmental experience (Dawkins, 1982, 1989). Genes interact with other genes to produce cells, which interact with other cells to produce organs, which interact with other organs to produce organisms, which interact with one another to produce emergent social structures such as ant colonies, chimpanzee dominance hierarchies, the Bon Jovi fan club, and the European Union. We believe that individual social traits can only be fully understood when considered in light of emergent group phenomena, and that conversely, emergent group phenomena can only be understood in light of the characteristics of the individuals involved. Indeed, one of us has elsewhere argued for an integration of evolutionary psychology with the
insights and methods of complexity theory, which, as the study of emergent phenomena, is anything but reductionist (Kenrick et al., 2003).

Related to the concern about genetic reductionism is the assumption that to admit a behavior is linked to evolved mechanisms is to say it is unchangeable. But as we discussed, the model of psychological mechanisms held by evolutionary psychologists and biologists is not one of determinism, but rather of “if-then” decision-rules that are inherently flexible and dynamically linked to the environment (Alcock, 2001; Kenrick, 1995; Kenrick et al., 2003). As discussed earlier, evolved fear responses and poison-avoidance mechanisms are characterized not by inflexibility, but by especially rapid learning (Garcia & Koelling, 1966; Ohman & Mineka, 2001).

Perhaps stemming from this concern about inflexible genes is the naturalistic fallacy—the error of jumping from what is to what ought to be. But a moments’ reflection refutes that line of reasoning. For example, natural selection has led to viruses that destroy their host’s immune systems and to insects whose offspring, after hatching from eggs laid inside paralyzed prey, eat their way out. Biologists indeed view such behaviors as products of natural selection, but certainly do not claim they are therefore “good.” Likewise, to say that past evolutionary pressures contributed to the tendency for humans to be xenophobic, or for males to be relatively more violent than females, is not to imply that prejudice or male violence should be encouraged. To understand the roots of a behavior is not to condone it, but to be in a better position to intervene. An excellent example comes from research on PKU, a disease in which a genetic predisposition leads to an inability to metabolize certain proteins present in milk, and consequent mental retardation. Understanding these links led not to passive acceptance, but to a simple intervention—removing milk from these childrens’ diets effectively prevents retardation (Alcock, 2001).

One application of the naturalistic fallacy is the belief that evolutionary explanations of sex differences are sanctions for a social system in which women are oppressed. Besides the fact that such a belief confuses causal explanation with prescription, the sexism accusation is worth re-examining for other reasons (Gowaty, 1997; Kenrick, Trost, & Sheets, 1996). Indeed, according to most evolutionary models, many gender differences in behavior and morphology are driven by female choice—selective females choose amongst males, who compete amongst themselves for the attentions of those selective females. Studies of other primates, for example, suggest that females have at least as much power as males in making reproductive decisions, and in influencing the course of evolutionary history (Hrdy, 1999; Small, 1993). As compared to a view of females as helpless pawns of norms created by powerful males, the evolutionary model may be, contrary to popular opinion, more flattering to both sexes.

Another concern is that evolutionary hypotheses are not falsifiable. Part of the concern here can be clarified by considering the distinction between research predictions and the underlying theoretical assumptions on which they are based (Alcock, 2001; Buss, 1999; Schaller & Conway, 2000). For example, based upon evolutionary assumptions regarding an association between parental investment and selectiveness in choosing mates, one of us predicted that men and women would differ greatly in their standards for short-term sexual partners (where the two sexes differ greatly in expected parental investment), but would become increasingly similar in their standards for long-term relationship partners (where the two sexes differ less in expected parental investment) (Kenrick et al., 1990, 1993). That research prediction could very easily have been disproved. The fact that the data were consistent with the hypotheses, on the other hand, does not prove every step in the underlying logic. Perhaps the observed sex difference was due to sex-role socialization processes unique to the Western
society in which the data were collected, for example. To address that alternative possibility, cross-cultural data would be necessary (see Kenrick & Keefe, 1992, for an example of this approach). However, even cross-cultural data do not definitively prove or disprove broad underlying theoretical assumptions. Broad theoretical notions, such as differential parental investment, generate diverse predictions and rest upon nomological networks of different sources of data (such as developmental findings, physiological research, and cross-species comparisons of species in which males and females vary in their relative amounts of parental investment, Geary, 1998). Those broad assumptive networks ultimately stand or fall to the extent that scientists find them useful for generating new predictions, parsimonious in integrating existing findings, and so on (Ketelaar & Ellis, 2000).

A related and final concern is that evolutionary hypotheses are simply post-hoc re-explanations of obvious social phenomena (such as sex differences in mate preferences). But evolutionary models have in fact been useful in leading researchers to look beyond the obvious. Consider one supposedly well-known sex difference—females generally marry relatively older males; males generally marry relatively younger females. Evolutionary theorists explained this apparent discrepancy in terms of a sex difference for desired commodities in partners. Because ancestral females contributed bodily resources to their offspring, and males contributed indirect resources, females were selected to value male partners for their resources, which generally increase with age; males were selected to value females for fertility, which generally decreases with age (Symons, 1979). A reasonable alternative explanation is that such sex differences result from cultural norms—men prefer younger women because they should prefer younger and less powerful mates (e.g., Deutsch, Zalenski, & Clark, 1986). If children could be socialized to follow such a seemingly obvious norm, why posit evolutionary explanations that assume pressures from a past that we cannot directly observe? Part of the answer is that an evolutionary life-history perspective leads to novel predictions (Kenrick & Keefe, 1992). For example, that model assumes that age-linked changes in mate choice will be the same across cultures, because females in all cultures bear the children and go through an age-linked decline in fertility (terminating in menopause), whereas males in all cultures contribute indirect resources, which tend to increase with age. Another differential prediction from an evolutionary perspective is that males will change their age preferences as they age; with the preference for relatively younger females pronounced only amongst older males (for teenage males, older females are more fertile). Because younger males tend to be more attuned to sex-role norms (Deutsch et al., 1986), the evolutionary prediction that younger males will show less of the “sex-typed” preference for younger (and less powerful) partners is at odds with a perspective focusing on sex-role socialization in our culture. Across a number of societies, these evolutionary predictions were corroborated—males’ tendency to prefer younger females becomes more pronounced with age (Kenrick & Keefe, 1992), and teenage males are strongly attracted to females above their own age (Kenrick et al., 1996). Thus, the presumed common knowledge of normative sex differences in age preference was erroneous, and an evolutionary perspective led to a better understanding of the phenomenon.

CONCLUSION

We have argued that the evolutionary perspective to social psychology is not untestable, not reductionist, not a theory about rigid genetic determinism, not a justification for the status quo, and not incompatible with sociocultural or cognitive analyses. What it is, instead, is a set of ideas that have proved quite useful in generating novel hypotheses, and parsimoniously
connecting findings from very different domains ranging from mate choice and family relationships to aggression and intergroup relations. Adopting an evolutionary perspective can help us appreciate not only the common threads that bind the people in our culture to those in other cultures, but also, beyond that, to the other species with which we share the earth. Taking this broad perspective, however, also makes us aware of the vast reaches of our own ignorance. As yet, we know very little about how evolved psychological mechanisms inside individuals develop, or how they influence, and are influenced by, the complex cultures that humans construct. Bringing light to these questions will require a fuller integration of all the different theoretical perspectives on human social behavior.

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