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EVOLUTIONARY PERSPECTIVES ON PROSOCIAL BEHAVIOR

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It has often been assumed that animals were in the first place rendered social, and that they feel as a consequence uncomfortable when separated from each other, and comfortable whilst together; but it is a more probable view that these sensations were first developed, in order that those animals which would profit by living in society, should be induced to live together . . . for with those animals which were benefited by living in close association, the individuals which took the greatest pleasure in society would best escape various dangers; whilst those that cared least for their comrades and lived solitary would perish in greater numbers. (Darwin, 1871, p. 80)

As this quotation indicates, Charles Darwin believed that prosocial tendencies probably evolved via natural selection in many species. Indeed, one of the great misunderstandings in the life sciences is the notion that nature is merely “red in tooth and claw” (Tennyson, 1850/1906). Although organisms do compete for valuable and sometimes scarce resources, both against members of their own species and against members of other species, the majority of competition is neither direct nor violent (Trivers, 1985). Most competition occurs indirectly as organisms scramble to find, maintain, and control resources critical to their survival and reproduction. Over time, the most reproduc-

tively successful organisms—those leaving the most descendants across generations—evolve traits and behaviors that help them more efficiently and effectively identify, procure, and control the most valuable resources, which in turn are passed on to their progeny through genetic inheritance.

No one in the evolutionary sciences questions that many species, including *Homo sapiens*, are able and sometimes willing to act prosocially toward others, even total strangers. Humans are the most prosocial primate species and one of the most prosocial of all species, as indexed by the size and complexity of their societies. What is debatable is how and why stronger forms of prosociality (i.e., willingness to incur heavy costs or even death for the welfare of a group) were selected for during evolutionary history. The question of how and why strong prosociality might have evolved in humans is one of the most important ones within the evolutionary sciences today (Gangestad & Simpson, 2007).

The goal of this chapter is to review the major evolutionary theories that are most relevant to understanding whether, how, and why strong prosociality may have evolved via natural selection in humans. As we explain, more recent evolutionary theories and models have become increasingly open to the likelihood that prosociality evolved in humans.

The chapter is divided into four sections. In the first section, we describe the physical and social environments—particularly the most likely obstacles to survival and reproduction—that contemporary humans' ancestors probably had to confront and master during evolutionary history. We begin with this set of issues because one cannot understand how or why strong prosociality evolved without awareness of the primary physical and social conditions in which early humans lived. In the second section, we review major theoretical models relevant to the evolution of prosociality in humans, starting with Darwin's (1859) theory of natural selection and then working through inclusive fitness theory (Hamilton, 1964), reciprocal altruism theory (Trivers, 1971), group-selection models (Sloan Wilson & Sober, 1994), and more recent gene-culture coevolutionary models (e.g., Richerson & Boyd, 2005). In the third section, we review empirical work that has tested evolutionary theories or models of prosociality in humans. In the final section, we integrate the most significant theoretical and empirical work, identify gaps in the current understanding of how and why natural selection may have sculpted certain prosocial tendencies in humans, and suggest that multiple factors linked to different evolutionary theories and processes are all likely to have generated the "ultra" prosocial tendencies that humans often display (see Brewer & Brown, 1998).

STABLE FEATURES OF EVOLUTIONARY ENVIRONMENTS

To understand the distal factors that may be responsible for the development of prosocial tendencies in humans, one must look back to the most

stable features of the environments in which humans probably evolved. During more than 98% of human evolutionary history, our ancestors lived as hunters and gatherers (Hill, 2002; Kelly, 1995), most likely in small, cooperative tribes or bands (Richerson & Boyd, 2005). Many people within a tribe or band were biologically related (Foley, 1992). Complete strangers were probably encountered infrequently, most often during either intertribal trading or war (Wright, 1994). Although some people migrated in and out of their original tribes or bands, most people probably lived in the same group their entire lives. Children were raised with considerable help from extended family members and most likely from the entire tribe or band, and older children, especially older siblings, assumed important roles in socializing and helping to rear younger children (Eibl-Eibesfeldt, 1989). Both genders participated in securing food, with men doing most of the hunting and women doing most of the gathering (Richerson & Boyd, 2005; Wood & Eagly, 2002). As a result, extensive cooperation with other tribe or band members—both kin and nonkin—was essential, particularly given the changing and precarious nature of the climate, competing tribes, and the food supply.

These conditions are ideal for reciprocal altruism to evolve (chap. 1, this volume; Cosmides & Tooby, 1992). Brewer and Caporeal (1990), in fact, suggested that active participation in cooperative groups probably was the primary “survival strategy” of early humans. Willingness to enter and maintain mutually cooperative, long-term alliances with others, therefore, may have been essential for survival, successful reproduction, and adequate parenting. Although some of these inferences are more speculative than others, the human mind most likely evolved to deal with problems that arose in physical and social environments containing these features.

EVOLUTIONARY THEORIES OF PROSOCIAL BEHAVIOR IN HUMANS

Several major theories are relevant to the evolution of prosocial behavior in human beings. In this section, we begin with an overview of natural selection theory, and then review several theories that, collectively, define the modern evolutionary perspective.

Natural Selection Theory

Darwin's (1859) theory of evolution by natural selection focused on the survival of the fittest and explained why, on the basis of the importance of differential reproduction across time, organisms often act in line with their self-centered interests. *Natural selection* is the process by which organisms in a species that possess traits or characteristics resulting in higher rates of survival and reproduction out-compete other organisms. Organisms that sur-

vive and successfully reproduce pass on these traits or characteristics to their offspring. Over time, traits that are most adaptive—that is, those that are differentially reproduced across many generations—increase in representation within a population, whereas those that are not eventually disappear. Through this process, some traits are naturally selected as organisms compete for resources.

Darwin's theory, however, left room for strong forms of prosociality and even altruism, particularly in humans, a species that was vulnerable to assorted dangers if individuals lived isolated from groups or collectives. Despite the fact that Darwin's theory of evolution was a remarkable intellectual accomplishment, it was incomplete and imprecise in several ways. To begin with, the theory was developed well before Mendel's pioneering work, which unlocked some of the secrets of genes and patterns of inheritance. Second, because Darwin did not conceive of genes as the principal units upon which natural selection operates, he could not explain why some organisms frequently engage in self-sacrificial or nonreproductive behavior. This enigma was solved by Hamilton (1964), who introduced and provided compelling evidence for inclusive fitness (i.e., the process by which differential gene replication drives evolution). Third, Darwin had only a dim understanding of how sexual recombination and genetic mutations provide the variation from which better adaptations and new species are selected. Fourth, like many theorists of his era, Darwin did not fully appreciate the extent to which specific adaptations are associated with both benefits and costs. What is most impressive about Darwin is that he envisioned, without the benefit of this subsequent knowledge, how natural selection is likely to have operated.

Inclusive Fitness Theory

Few significant theoretical advances occurred in the evolutionary sciences for nearly a century after Darwin published his second landmark book, *The Descent of Man*, in 1871. This state of affairs changed rapidly beginning in the mid-1960s. With the development of inclusive fitness theory, Hamilton (1964) introduced the notion of kin selection. By focusing on genes rather than on individual organisms as the primary units on which selection operates, Hamilton solved the biggest problem that eluded Darwin's grasp: In the struggle for reproductive fitness (i.e., an individual's ability to produce fertile and reproductively viable offspring at a rate higher than other organisms in the same species), why do some organisms forego reproduction to assist the reproductive efforts of their biological relatives?

Hamilton (1964) realized that an individual's total (inclusive) fitness depends on his or her own reproductive output (i.e., offspring) plus the total reproductive output of all kin who share some of the individual's genome. To the extent that genes are the units on which selection operates, and that individuals can facilitate the reproductive output of their biological rela-

tives, there are situations in which it pays to sacrifice one's own reproductive output, including one's life, to facilitate the successful reproduction of close relatives. Unlike Darwin, Hamilton was able to calculate the degree to which pairs of individuals share novel genes. On average, parents share half their novel genes with their children, full siblings share half their genes with each other, grandparents share one quarter of their genes with their grandchildren, aunts and uncles share one quarter of their genes with their nieces and nephews, and first cousins share one eighth of their genes.

Armed with this knowledge, Hamilton discerned that self-sacrificial behavior should have been selected in situations in which the costs of engaging in an act were less than the benefits to be gained times the degree to which individuals were biologically related (that is, altruistic behavior should occur when $C < Br$, where C = costs, B = benefits, and r = the degree of relatedness; see Simpson, 1999). For example, although it would make sense to sacrifice one's own life to save at least two biological children (each of whom shares 50% of the parent's genes and has years of reproductive potential left), one would have to save many more nieces or nephews (who carry fewer genes) to achieve the same fitness benefits. Hamilton's intellectual breakthrough marked the dawn of modern theorizing in the evolutionary sciences.

Reciprocal Altruism Theory

In 1971, Trivers introduced the theory of reciprocal altruism, which explains why organisms that have inherently "selfish" genes should, at times, behave in a cooperative manner with certain nonkin. *Altruism* is defined as any "behavior that benefits another organism, not closely related, while being apparently detrimental to the organism performing the behavior, benefit and detrimental being defined in terms of contribution to inclusive fitness" (Trivers, 1971, p. 35). The theory suggests that recurrent situations may have arisen during evolutionary history in which nonkin who forged mutually beneficial long-term exchange relationships could have helped one another, facilitating each individual's survival and reproductive output. Trivers identified several special conditions under which selective reciprocal altruism should have enhanced an individual's inclusive fitness and, therefore, might have evolved.

According to Trivers (1971), reciprocal altruism is more likely to have evolved in species that (a) have longer life spans (which increases the probability that an individual will encounter others in altruistic situations), (b) have a higher dispersal rate (which increases the likelihood that an individual will interact repeatedly with the same people), (c) are more mutually dependent (which increases the probability that others could facilitate an individual's survival and successful reproduction), (d) have weak dominance hierarchies (i.e., social structures in which more people can potentially ben-

efit from each other), (e) can benefit from aid in combat (whereby more individuals can assist one another during conflicts with outgroups), and (f) invest heavily in offspring and parental care (in terms of the quantity and the quality of resources directed to children). All of these conditions were met by human groups throughout most of their evolutionary history (Trivers, 1985).

Group Selection Theory

In 1994, Sloan Wilson and Sober reintroduced a model of group selection that revitalized interest in this topic. According to group selection perspectives, there may have been instances in which specific groups of people, rather than individuals, were the primary units of selection in evolutionary history. If certain groups were highly skillful, inventive, or productive across extended periods of time relative to other groups, the members of “successful” groups would have been more reproductively successful than members of less viable groups, on average. Because individuals in successful groups would have needed to be contributing and cohesive group members over time, greater prosociality directed toward all members of the group—including even nonkin—should have been selected for (for related analyses, see chap. 1, this volume; Sloan Wilson, 2002; Sloan Wilson & Sober, 1994). From an evolutionary standpoint, the probability that group selection occurred should have depended on several factors, including the severity of local environments requiring extensive cooperation within a group, the ability and willingness of group members to act self-sacrificially for the good of the group, and the nature and resourcefulness of competing outgroups.

According to Sloan Wilson and Sober’s (1994) model, the probability that group selection evolved in certain cases hinges on three parameters: (a) the amount of personal costs associated with making sacrifices for the group, (b) the amount of personal benefits associated with doing so, and (c) the proportion of altruistic versus nonaltruistic members within the group. Simpson (1994) modeled these parameters to estimate the likelihood that group selection would have evolved. The results revealed that although there may have been isolated cases in which group selection emerged, they were probably atypical, aberrant, and unlikely. Specifically, the ratio of personal costs to benefits must have remained very low and the percentage of altruists within the group must have been quite high for extended periods of time to ensure that a group was stable enough to facilitate strong altruism. Although there may have been select cases in which group selection operated (e.g., the Hutterites in North America; see Sloan Wilson & Sober, 1994), these cases were probably rare.

Gene–Culture Coevolutionary Theories

Most recently, Richerson and Boyd (2005) proposed that group selection could have occurred through the joint operation of genetic and cultural

evolution. To occur, group selection requires minimal within-group variation in a trait or characteristic critical to the reproductive fitness of individuals within a group, along with a great deal of between-group variation on that trait or characteristic. These conditions are rarely witnessed in primate species because of intergroup migration (Richerson & Boyd, 2005) and the absence of proper conditions (Simpson, 1994). Richerson and Boyd (2005) contended, however, that the evolution of culture may have created special conditions under which group selection could have emerged via gene-culture coevolutionary processes.

During the Pleistocene (1.8 million years ago to approximately 9600 B.C.E.; Lourens, Hilgen, Shackleton, Laskar, & Sloan Wilson, 2004), climate change may have been rapid enough for social learning to become very beneficial, an event that allowed our ancestors to develop novel abilities that supported rapid and diverse social learning. To the extent that social learning facilitated the rapid acquisition of adaptive skills, behaviors, and abilities, it could have been preferentially selected. These skills and abilities most likely spawned the development of cumulative culture, a phenomenon rarely seen in nonhuman societies (Richerson & Boyd, 2005). Not only are humans excellent social imitators but our imitative abilities are also far superior to even the most clever and social of other species, including chimpanzees (Whiten, Custance, Gomez, Teixidor, & Bard, 1996). Although Richerson and Boyd (2005) acknowledged that cultural and social learning occurs in species other than humans, they contended that cumulative knowledge and information is uniquely transmitted from generation to generation in human cultures, which are then built on by subsequent generations. No other species has such a complex cumulative cultural system.

Richerson and Boyd (2005) believed that this process operates through *cultural variants* (i.e., cultural knowledge, skills, and ideas), which are transmitted both between and across groups and also across generations, via social learning, and which are subject to selection pressures in the same general way that genes are. According to Richerson and Boyd, cultural variants that enhance survival and reproduction are more likely to continue within a culture due to selection-like processes, and they are also influenced by evolutionary forces such as genetic mutation and drift. However, cultural variants are also vulnerable to biased transmission in which certain variants become more successful because of their content (being easier to remember than that of other variants and thus more likely to be mimicked or used), their frequency (commonness within a population), and the people who model them (group leaders versus followers). For example, for difficult-to-attain knowledge, such as academic expertise, people must choose among many alternatives to decide what to learn. As a result, people may be prone to choose easier subjects, or subjects that are more common, because they are easier to learn or it is easier to find people from whom relevant skills can be learned.

Under the assumptions that cultures evolved and were adaptive for our ancestors, Richerson and Boyd (2005) proposed that cultural variants contain certain properties that make group selection much more likely to have evolved. If certain conditions were met during evolutionary history—if moralistic punishment was consistent and widespread within a group or culture, if pressures to conform to important group rules and norms were constant and strong, and if there was significant and sustained intergroup conflict—group selection could have evolved. More specifically, to the extent that important group rules and norms were consistently enforced by ingroup members, ingroup members remained motivated to conform “for the good of the group” to norms and rules, and sustained conflict existed between competing groups, within-group variability in terms of behaving in line with important ingroup norms and rules should have decreased and between-group variability should have increased. These factors could have created the necessary conditions for group selection to occur (see Richerson & Boyd, 2005). When these conditions coalesced, ancestral groups that encouraged self-sacrifice for the greater good of the group should have out-competed rival groups, and stronger forms of prosocial behavior toward ingroup members should have emerged.

Once this happened, genetic evolution may have been influenced by culture insofar as individuals who regularly behaved in ways that promoted the welfare of the group (e.g., recognizing ingroup members and distinguishing them from outgroup members, habitually conforming to basic group norms or rules, being willing to punish anyone who violated critical group norms or rules) became more reproductively successful (see also Haidt, 2007). This interaction between genetic and cultural evolution may have resulted in the evolution of what Richerson and Boyd (2005) called *tribal instincts*. These instincts encompass three attributes: (a) psychological predispositions (i.e., psychological mechanisms) that encouraged the enforcement of important group norms and rules; (b) psychological mechanisms that permitted easy and rapid discrimination between groups, especially ingroup versus outgroup members; and (c) emotional capabilities that permitted the experience and expression of certain complex social emotions, such as guilt and shame, which may have facilitated stronger forms of prosociality.

The Expansion of Prosociality in Evolutionary Theories

Over time, evolutionary theories have focused greater attention on the evolution of prosocial tendencies in humans. This trend, shown in Figure 2.1, can be depicted as a series of expanding circles, beginning with Darwin’s (1859) theory of evolution by natural selection at the core.

Although Darwin was sympathetic to the idea that humans evolved to be highly prosocial, he focused on survival and reproduction at the level of the individual and could not fully explain how strong forms of prosociality

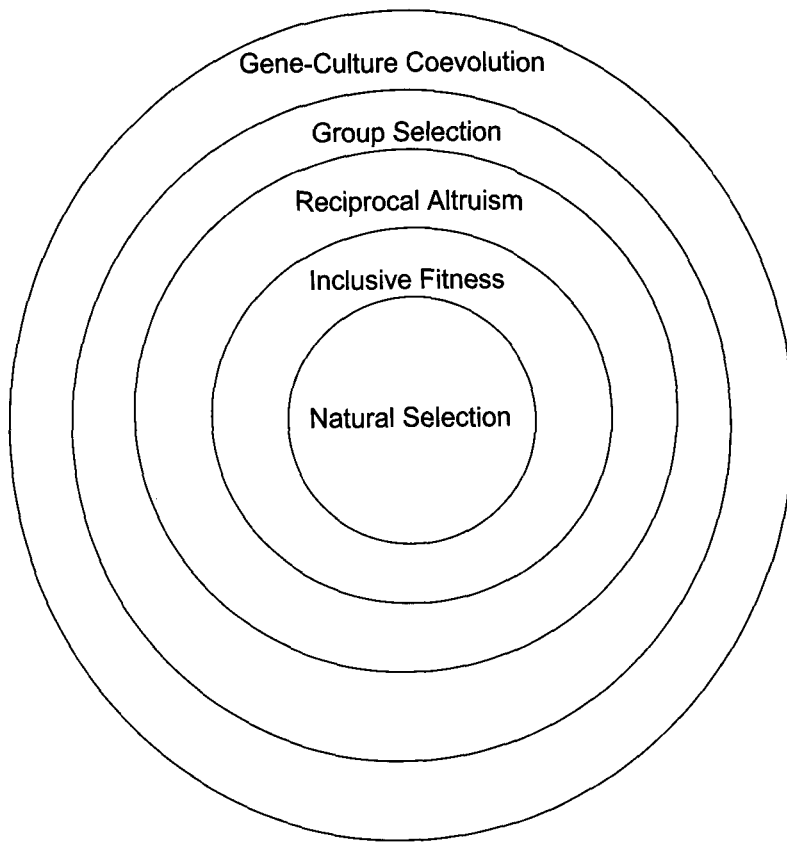


Figure 2.1. Major evolutionary theories relevant to prosociality in humans.

evolved in humans. Inclusive fitness theory (Hamilton, 1964) greatly expanded the evolutionary foundations of strong prosociality by documenting how and why organisms would have benefited by making sacrifices for biologically related relatives who carried a portion of their genes. Reciprocal altruism theory (Trivers, 1971) moved beyond a purely “gene-centered” perspective by indicating how and why long-term, mutually cooperative, and reciprocal exchanges with nonkin could also have evolved, especially in humans. Group selection models (e.g., Sloan Wilson & Sober, 1994) then directed attention to special cases in which strong prosociality in humans might have been amplified by the differential reproduction of individuals in highly cooperative, cohesive, and productive groups, compared with those in less cooperative, cohesive, and productive groups. Gene–environment coevolutionary models have substantially expanded the possible evolutionary foundations of strong prosociality in humans. These recent models have provided additional compelling reasons for how and why strong prosociality should have evolved. These most recent models were developed in response to both new theorizing (e.g., Boyd & Richerson, 1988; Brewer & Caporael, 1990)

and anthropological evidence (e.g., Cronk, 1999; Kelly, 1995) suggesting the extremely interdependent, complex, and role-governed division of labor that characterizes existing hunter-gatherer tribes and, most likely, the majority of human groups during evolutionary history.

EMPIRICAL EVIDENCE FOR EVOLUTIONARY THEORIES OF PROSOCIAL BEHAVIOR

In this section, we review research that has tested evolutionary theories, models, or principles of prosociality in humans. Some of this work has tested gene-centered theories of evolution, particularly inclusive fitness theory. Other research inspired by coevolutionary models has investigated the conditions under which individuals are willing to display strong prosocial tendencies, including the willingness to punish cheaters for the good of a group at considerable cost to the self.

Inclusive Fitness Theory

Most of the research on gene-centered models of the evolution of prosociality in humans has tested predictions derived from inclusive fitness theory. Much of this work has investigated the conditions under which the degree of genetic relatedness between *helpers* and *recipients* of help is associated with how resources are distributed to close biological relatives, to more distant kin, and to nonbiologically related others.

According to inclusive fitness theory, people should be biased on average to distribute a larger percentage of assistance and resources to kin with whom they share more genes. For example, individuals ought to preferentially benefit persons with whom they share half their genes (e.g., full siblings), compared with more distantly related kin (e.g., half siblings, first cousins) or nonkin (e.g., good friends). Regardless of whether one examines financial estates (Judge, 1995), physical labor (Berte, 1988), or procuring food (e.g., fishing catches; Betzig & Turke, 1986), resources are almost always distributed preferentially to closer biological relatives. This nepotistic bias also extends to the willingness to endure pain for closer relatives. Fieldman, Plotkin, Dunbar, Robertson, and McFarland (described in Barrett, Dunbar, & Lycett, 2002) found that people are more willing to endure a painful physical task for longer periods of time if the money they will receive for doing so is given to closer biological relatives rather than more distant biological relatives or close friends. This willingness to endure greater pain for closer relatives does not depend on how much individuals like or spend time with their closer relatives; only the degree of genetic relatedness accounts for this effect. Moreover, when they asked how willing individuals would be to engage in risky behavior that would benefit other people,

Korchmaros and Kenny (2001) found that individuals are more willing to assume greater risks to help closer biological relatives, an effect that is only partially mediated by the degree of emotional closeness to closer relatives. Similar results have emerged when “empathic concern” (chap. 7, this volume) is treated as a mediating variable (Kruger, 2003).

Viewed together, these studies suggest that costly forms of assistance (altruism) are preferentially directed toward closer biological relatives and that these effects are not driven by greater psychological closeness, attachment, or connection with closer biological relatives. The degree of genetic relatedness appears to be the most parsimonious explanation of these effects.

Some of the most elegant tests of inclusive fitness theory have been conducted by Eugene Burnstein and his colleagues. Burnstein, Crandall, and Kitayama (1994), for example, performed several scenario studies in which they experimentally manipulated different sets of variables relevant to inclusive fitness theory, such as the benefits versus costs of helping a particular person, and the recipient’s age, gender, and degree of kinship with the helper. In both the United States and Japan, the reported likelihood of giving assistance increases linearly with the degree of genetic relatedness between the helper and the recipient, especially when help might save the recipient’s life. These findings support a central prediction based on inclusive fitness theory: The larger the ratio of benefits to costs of help to recipients, the more helpers should be biased to offer more help to closer biological relatives. The willingness to offer assistance also depends on the age of recipients, with the oldest and the youngest closer relatives—individuals who are most likely to be outcome dependent and least likely to reciprocate help—usually receiving more reported assistance than middle-aged closer relatives. By aiding the most vulnerable and outcome dependent, helpers might be “advertising” their benevolence and/or their ability to provide help and still remain resourceful (e.g., Grafen, 1990), either of which could lead to receiving fitness-enhancing benefits from other group members in the future.

Burnstein et al. (1994) also found that helpers are willing to give more assistance to healthy kin than to nonhealthy kin in life-or-death situations, whereas the reverse is true in everyday, nonthreatening situations. And when deciding how much to help members of different groups (e.g., kin groups versus nonkin groups), helpers strongly favor groups that are more likely to provide a better *reproductive return*, defined as the sum of the group members’ degrees of genetic relatedness to the helper. Particularly in life-or-death situations, therefore, biological relatives tend to view themselves as a social unit that lives or dies together (Burnstein, 2005).

Reciprocal Altruism Theory

According to reciprocal altruism theory (Trivers, 1971), if two biologically unrelated individuals provide mutual benefits to one another that are

greater than the costs each individual incurs by providing the benefits, both individuals ought to benefit through the economic principle of gains in trade. As a result, genes that led our ancestors to recognize and selectively enter mutually beneficial transactions with nonkin, such as long-term tit-for-tat exchanges with highly resourceful and trustworthy partners, could have been selected.

Axelrod (1984) established that tit-for-tat strategies, in which positive partner overtures are immediately rewarded and negative ones are immediately punished, tend to develop quickly and remain stable as long as interaction partners continue to make cooperative choices in two-person experimental games. All of the conditions necessary for the evolution of reciprocal altruism in humans—important benefits can be given to others, individuals have repeated interactions with the same people, individuals can remember to whom they have given benefits and from whom they have received benefits, and exchange decisions are based on the outcomes of earlier interactions with specific people—were probably present in evolutionary history.

Indeed, Hill (2002) documented “altruistic cooperation” in the Ache, a remote tribe that lives in the rugged mountains of Paraguay. Ache men and women spend approximately 10% of their foraging time engaged in activities that benefit biologically unrelated individuals in the tribe, often at noteworthy costs to themselves or their families. Furthermore, food sharing is based more on a person’s current need than on his or her degree of genetic relatedness to the individual who secured the food if the needy person has assisted or shared with others in the past. These findings suggest that principles of equity and need rather than genetic relatedness alone govern food sharing decisions in the Ache. This makes sense when one considers the unpredictable and variable pattern of the Ache’s food supply; sharing surplus food with cooperative and well-intentioned others is likely to be beneficial because currently needy individuals should be more likely to share food or other valuable resources when they have them in the future. Reciprocal altruism, therefore, may provide some measure of insurance against inevitable hardships and limited resources in the future.

Kurzban (2003) believed that the need for cooperative hunting could have been one of the major selection pressures that jump-started reciprocal altruism and strong prosociality in humans. Delayed exchanges of goods and resources may have been more common in evolutionary environments than simultaneous (immediate) exchanges, requiring that trust in others be carefully and judiciously placed. The successful use of a tit-for-tat strategy requires a willingness to trust partners and be cooperative on the first “move” (trial), after which decisions are based on whether partners have behaved cooperatively or noncooperatively on subsequent trials. Clutton-Brock and Parker (1995) proposed that spite—the inclination to punish or ostracize defecting or uncooperative individuals, even when such actions are costly to the self—may have evolved to “back up” prosocial orientations or expectations if

partners renege on important promises. And Tooby and Cosmides (1990, 1992) have conjectured that specialized cognitive abilities in humans (e.g., cheater detection, superior memory for faces) should have evolved to help individuals identify and envision new ways in which valuable resources could be exchanged, further fueling the evolution of reciprocal altruism in humans.

Gene–Culture Coevolutionary Theories

Gene–culture coevolutionary models (sometimes termed *multilevel selection models*) were formulated in response to the fact that gene-centered evolutionary models cannot fully explain the pervasiveness and depth of human altruism and prosociality. Establishing evidence for gene–culture coevolution requires convergent findings that meet the necessary conditions specified by theorists such as Richerson and Boyd (2005). If their model is correct, people should have evolved (a) strong tendencies to conform to important group rules and norms, (b) the clear ability to distinguish ingroup members from outgroup members, and (c) the propensity to punish persons who violate important group rules and norms.

These core propositions have been supported by classic research in social psychology as well as recent findings in the group decision-making area. The tendency for people to conform to group norms and pressures has been extensively documented (for a review, see Cialdini & Goldstein, 2004). The power and pervasiveness of group conformity effects was initially demonstrated by Sherif (1936) and Asch (1956). Asch's classic studies, for example, showed that individuals report blatantly incorrect evaluations of stimuli in easy judgment tasks in order to agree with group members who see things differently than they themselves do. However, social psychologists have only recently attempted to interpret conformity effects from the vantage point of evolutionary thinking (see, e.g., Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006).

Multitudes of studies have confirmed the powerful and almost automatic tendency for ingroup members to distinguish between and discriminate against outgroups (for a review, see Brewer & Brown, 1998). Tajfel and Turner's (1979) social identity theory and subsequent research, for instance, has demonstrated how easily and quickly people identify ingroup members, even when groups are based on arbitrary or meaningless attributes, and how willing they are to benefit ingroup members with valuable resources, often at the expense of outgroup members. Sherif, Harvey, White, Hood, and Sherif (1954/1961) revealed the powerful tendency of boys at a summer camp to immediately identify with their randomly assigned group and then to engage in hostile intergroup conflict with boys in another group, following only minimal provocation. Indeed, Brewer and Caporael (2006) have now recast some of the major principles of social identity theory within an evolutionary framework.

Other recent research supports the third component of Richerson and Boyd's (2005) model, the willingness of group members to engage in moralistic punishment. Humans are unique among species in their ability and willingness to display *strong reciprocity* (Fehr & Fischbacher, 2003). Strong reciprocity is witnessed when individuals take on the costs of rewarding or punishing others in situations in which cooperation is required to secure vital resources or good outcomes, even if "enforcers" receive no personal benefits or sometimes incur great costs. Unlike reciprocal altruism, which presumes that individuals should reward or punish others only if tangible benefits are likely to be received (Axelrod & Hamilton, 1981), strong reciprocity indicates that individuals are willing to enforce important social rules or norms to ensure that cheaters and noncooperators do not destroy cooperation and goodwill within groups. Laboratory studies using the ultimatum game have confirmed that individuals closely monitor and quickly punish those who behave unfairly (e.g., who cheat or fail to reciprocate cooperation) or who offer others unfair outcomes, even if providing sanctions harms their own rational self-interest (Fehr & Fischbacher, 2003). Research using intergenerational ultimatum games (i.e., games in which different players interact over time) has also confirmed that receiving advice from previous players increases altruistic punishments and rewards enacted by current players, and that players who receive advice usually achieve greater cooperation from other players across time.

What explains this clear willingness to make personal sacrifices in order to maintain cooperative norms and behavior within groups? The answer probably lies in how easily cooperation can disintegrate. Because a very small percentage of free riders or chronic cheaters can destroy cooperation in most groups, cooperative systems often fail unless a large majority of group members vigilantly monitor and sanction norm violators, even if they have no personal stake or investment in a given interaction (Fehr & Schmidt, 1999). Individuals who regularly police and enforce important rules and norms, however, may also gain personal benefits through being seen as highly altruistic, which could enhance their reputation within a group (Alexander, 1987; Nowak & Sigmund, 1998) or signal that they are sufficiently resourceful to endure the costs of engaging in altruistic, self-sacrificial acts (Gintis, Smith, & Bowles, 2001).

Advocates of gene-culture coevolutionary models have questioned whether tit-for-tat strategies could have been responsible for the evolution of reciprocal altruism in humans. Even though the results of repeated two-person interaction studies indicate that tit-for-tat strategies can develop quickly and remain stable (Axelrod, 1984), these strategies become less stable in *n*-person Prisoner's Dilemma games unless virtually all group members cooperate on each experimental trial (Boyd & Richerson, 1988). Moreover, tit-for-tat paradigms typically stipulate that individuals cannot "leave the game" (exit) and that third parties cannot intervene unless they can person-

ally benefit from rewarding fair players or punishing unfair ones. These conditions rarely exist in most real-world settings (see Boyd & Richerson, 1988; Richerson & Boyd, 2005).

In summary, gene–culture coevolutionary models contend that traditional purely gene-centered selection models do not and cannot fully account for the evolution and maintenance of strong reciprocity, whereas gene–culture coevolution theories can. These more recent models suggest that certain norms and institutions, such as sharing food, hunting and gathering, and serial monogamy, could have been maintained to benefit most members of a group to the extent that everyone monitored and was willing to sanction norm or rule violators. This propensity may have spawned widespread strong forms of prosociality, including altruism, in humans.

INTEGRATION AND CONCLUSIONS

According to Darwin, organisms that “profited” by living in society should have lived and worked together and doing so should have increased their reproductive and inclusive fitness. Early gene-centered models of evolution (e.g., inclusive fitness theory) focused on how and why strong forms of prosociality and altruism directed toward kin could have evolved. Indeed, research has begun to document the specific conditions under which individuals are willing to make major sacrifices for other people, often in line with the percentage of genes the helpers share with those in need. These effects are strongest, however, when closer biological relatives face life-or-death situations and immediate help may save their lives.

Later evolutionary theories, such as reciprocal altruism theory, showcased how and why individuals could also have experienced greater reproductive and inclusive fitness by entering certain long-term, mutually beneficial exchange relationships with nonrelatives who had skills, resources, or abilities that enhanced an individual’s well-being. Particularly in harsh, difficult, or demanding environments in which resources were scarce or difficult to secure, or competition for them was keen, preferences for selective reciprocal alliances are likely to have evolved to solve basic challenges of daily living.

The most recent approaches, particularly gene–environment coevolutionary models (e.g., Richerson & Boyd, 2005), have extended the possible evolutionary bases of prosociality in humans even further. These models outline how and why the emergence of complex, cumulative culture could have differentially increased the reproductive and inclusive fitness of individuals who were members of highly stable, cooperative, and productive groups or collectives. Richerson and Boyd (2005) believed that the three “tribal instincts” evolved in part to solve chronic problems associated with competition with other local groups and/or the benefits that were gained from resid-

ing in a group that enhanced the average group member's reproductive and/or inclusive fitness.

Darwin left intellectual room for all of these subsequent theories and models, each of which focuses on slightly different adaptive problems that our ancestors probably recurrently faced. Extreme forms of prosociality (e.g., saving someone's life) may have evolved to protect one's inclusive fitness when close relatives who had years of reproductive potential ahead of them required immediate assistance in order to live. More routine and mundane forms of prosociality (e.g., assisting or trading with nonrelatives on a regular basis) may have increased reproductive or inclusive fitness, especially when resources were limited, sporadic, or difficult to obtain, or when competition for them was intense. Other forms of prosociality (e.g., helping all members of one's group, even if a reciprocal alliance has not been established) might have further increased reproductive or inclusive fitness through the benefits of cumulative culture and living in a highly cohesive and productive group. Given the many daunting obstacles to survival, reproduction, good parenting, and good grandparenting that our ancestors faced (see Buss, 2005), humans should have evolved to take advantage of all opportunities that would have enhanced their inclusive fitness.

In conclusion, human society is difficult for evolutionary theories to fully explain. The degree of cooperative, prosocial behavior displayed within human groups and societies is rare within the animal kingdom. Only a few species, such as colonial invertebrates (e.g., corals) and social insects (e.g., *Hymenoptera*), develop societies and social structures that come anywhere close to rivaling the size and complexity of human groups and cultures. No other species has ever developed such large and complex societies that involve such an array of nongenetically related individuals (Richerson & Boyd, 1998). For species such as *Hymenoptera*, the puzzle of how prosocial "selfless" behavior could have evolved is easily solved by inclusive fitness theory, given that most organisms in a hive or colony are highly genetically related and sometimes genetically identical. To account for the extreme levels of prosociality witnessed in humans, one must draw on different evolutionary theories that address multiple levels of selection pressures.

Human prosociality is most likely the result of multiple selection pressures and multiple evolved mechanisms, all of which have pushed human evolution in an increasingly cooperative and prosocial direction relative to most other species. This premise—that multiple forces and selection pressures probably favored cooperation and caring during human evolutionary history—runs counter to the common misperception that evolution entails fierce direct competition and that nature is "red in tooth and claw." Each of the evolutionary theories we have reviewed indicates when, how, and why an individual's inclusive fitness could have been enhanced if he or she selectively acted in a cooperative and caring manner toward others in certain recurrent social contexts. Far from being competitive and antagonistic, our

most reproductively successful ancestors may have been among the most cooperative and resourceful individuals within their groups.

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