Evolutionary Perspectives on Caring and Prosocial Behavior in Relationships

Lane Beckes and Jeffry A. Simpson

According to popular belief, selfishness is the natural condition of human and animal behavior from the standpoint of most evolutionary theories. Indeed, the premise that nature is "red in tooth and claw," or the idea that nature is highly competitive and vicious, is one of the most common and widespread misconceptions that beleaguer evolutionary approaches to human behavior (Simpson & Beckes, 2010). These incorrect perceptions probably stem at least in part from the lack of a word other than *selfish* to describe the processes by which natural selection leads certain genes to survive across generations and others to disappear (Dawkins, 1976). Richard Dawkins, who wrote the book *The Selfish Gene,* has clarified that "selfish genes" do not necessarily connote selfish and always egocentric people. In fact, selfish genes are often not selfish, yet the myth that nature is invariably competitive and antagonistic persists.

Despite this basic misconception, evolutionary theorists stretching back to Darwin have claimed that social animals must have been selected for prosociality at some level (Darwin, 1871/1981). Most competition, rather than being direct, tends to be indirect, favoring those who are most effective and efficient at securing or managing critical resources. By cooperating with other people in select situations, more cooperative individuals should have been more likely to pass their genes to future generations than less cooperative individuals. In certain situations, evolutionary processes may actually favor cooperation and sometimes even altruism in some species.

Human societies represent a unique example of prosociality in nature. As Boyd and Richerson (1988; Richerson & Boyd, 1998) have discussed, the size and complexity of the societies in which humans live rival those of both the social insects and corals, species whose extensive societies exist in large part because individuals within a hive or colony are genetically identical or very closely related to one another. Human societies, however, are distinct in that their size and complexity are achieved without the high degree of genetic relatedness that characterizes all other "ultrasocial" species. Some of the most important questions that currently exist within the evolutionary sciences revolve around how and why such strong forms of prosociality evolved during human history (see Gangestad & Simpson, 2007). Wilson (Chapter 6, this volume), for example,

Kelly, 1995; Richerson & Boyd, 2005). Thus, one can assume that the human mind evolved within a relational context. Although a few individuals may have occasionally migrated from one tribe or band to another, most individuals probably spent their entire lives within the same group. Strangers were most often encountered during periods of trading or warfare (Wright, 1994). Extended family and other tribal members assisted extensively with the rearing of children (Eibl-Eibesfeldt, 1989). Men, however, did most of the hunting and women did most of the gathering (Richerson & Boyd, 2005; Wood & Eagly, 2002). Given the strong reliance on others and delegation of duties to procure resources and raise children, this living arrangement would have required a high degree of interdependence between tribe members, making extensive cooperation essential for daily living.

Brewer and Caporael (1990) proposed that being an active member of a cooperative group may have been the primary survival strategy adopted by our ancestors. Accordingly, adaptations to group living, willingness to engage in certain cooperative behaviors, and other prosocial interpersonal behaviors should have evolved in humans (Simpson & Beckes, 2010).

Evolutionary Theories of Prosocial Behavior in Humans

Several major theories are pertinent to the evolution of prosocial behavior in humans. *Prosocial behavior* is a general term for any behavior or action that has the effect of helping or assisting another person. Included within this broad term are more specific prosocial behaviors such as *caregiving,* which refers to behavior that is specifically focused on benefitting another's welfare. Often caring and caregiving behavior occur in a parent–child context and thus can be considered, from a gene-centered point of view, forms of helping promoted by selfish or egoistic motives to pass on one's genes. Altruism is a stricter form of prosocial behavior that usually is conceived as requiring nonegoistic or unselfish motivations, and thus it is helping behavior meant to assist another person, even at some cost to the self (Batson, 1991). In this section, we review several evolutionary theories that, collectively, represent the modern evolutionary perspective as well as their relevance to prosocial behavior broadly (see also Chapter 8, this volume). We begin with Darwin's (1859) theory of natural selection.

NATURAL SELECTION THEORY. Charles Darwin (1859) based his seminal theory of evolution on the idea that evolution occurred through natural selection. Through natural selection, only the "fittest" survive, reproduce, and pass their traits on to progeny. Thus, traits that increased an individual's differential reproductive rate and survival across time gradually became a dominant phenotype within a given species. Because of this process, organisms tend to act in their own best interests or risk having their lineage removed from the gene pool. However, Darwin also argued for the evolution of strong prosociality and altruism in humans. The difficulty was that Darwin did not comprehend the exact mechanisms by which certain behaviors and traits evolved and, thus, whether human behavior was truly altruistic versus selfish began to be debated shortly after his theory was introduced.

INCLUSIVE FITNESS THEORY. The field of evolutionary biology changed radically with Hamilton's (1964) publication of inclusive fitness theory. According to this theory, one of the mechanisms by which prosociality evolved was through kin selection. Because genes are the primary unit of selection, helping one's kin to survive and reproduce also benefits the fitness of one's own genes. This realization solved a longstanding question in evolutionary science, namely, why do some individuals sacrifice their own reproduction in favor of their biological relatives' reproduction?

Hamilton proposed a concept that he termed *inclusive fitness,* which factors in both an individual's own reproductive output along with the total reproductive output of all his or her genetic relatives, adjusted for their degree of genetic relatedness. Because genes are the unit of selection, aiding others who carry the same genes can propagate one's own genetic material into future generations. Consider an example. If a man can save his kin by defending them against predators, he should be willing to sacrifice himself if his own reproductive output is outweighed by the reproductive potential of his relatives. Individuals share on average all their genes with their identical twins; half of their genes with parents, siblings, and children; one quarter of their genes with grandparents, grandchildren, aunts, uncles, nieces, and nephews; and one eighth of their genes with cousins. Thus, one can calculate the degree to which an individual should sacrifice his or her own reproductive output to aid a relative, even if such aid could mean that individual's death.

According to inclusive fitness theory, one can calculate the likelihood of altruistic behavior by determining when the costs of a given altruistic action are less than the benefits of that action times the degree of relatedness of the individual receiving aid. In particular, altruism is expected when $C < Br$, where C = costs, B = benefits, and r = relatedness (see also Simpson & Belsky, 2008). Thus, an individual should be willing to sacrifice his or her life for three siblings (each of whom shares 50% of genes with the individual), but not for three cousins (each of whom shares only 12.5% of genes with the individual). Instead, one would expect a sacrifice only if eight or more cousins could be saved by a self-sacrificial act. This theoretical breakthrough was a critical step in evolutionary science. Indeed, it was the catalyst for several theoretical expansions that have changed our understanding of the evolution of altruism, caring, and prosocial behavior, especially in humans.

As a rule, inclusive fitness theory anticipates more helping and resource sharing with individuals who are genetically more closely related to the self. This hypothesis has been consistently confirmed by studies examining the distribution of financial estates (Judge, 1995), the amount of physical labor offered to others (Berte, 1988), the sharing and procuring of food (Betzig & Turke, 1986), willingness to endure pain for another (Fieldman, Plotkin, Dunbar, Robertson, & McFarland, described in Barrett, Dunbar, & Lycett, 2002), and willingness to assume risks for others (Korchmaros & Kenny, 2001; Kruger, 2003). These effects persist even when statistically controlling for liking, closeness, and empathic concern for the person being aided, suggesting that the degree of genetic relatedness is the critical operative variable.

In addition, Burnstein, Crandall, and Kitayama (1994) manipulated the costs and benefits associated with helping others who have varying degrees of

genetic relatedness. People are more inclined to assist those who are more closely related to them, with the increased likelihood of helping being linearly related to the helper's genetic relatedness to the recipient of help, especially when the recipient's life is in danger. These studies verify that the higher the benefit–cost ratio of helping to recipients, the more likely helpers are willing to assist individuals who share more genes in common with them. In life-or-death situations, people are most likely to assist healthy individuals (Burnstein et al., 1994) as well as people or groups who are more genetically related to them. This suggests that relatives may view themselves as interdependent in terms of survival (see Burnstein, 2005).

RECIPROCAL ALTRUISM THEORY. Trivers (1971) developed reciprocal altruism theory to explain why organisms occasionally behave in a cooperative manner even with nonkin. Trivers argued that under certain recurrent conditions, mutually beneficial long-term exchange relationships emerge that can benefit the reproductive fitness of both parties. Although these conditions do not exist for all species, for some species conditions could have resulted in the evolution of reciprocal altruism.

Trivers (1971) claimed that six conditions must be met for reciprocal altruism to evolve within a species: (a) the species must have long life spans, increasing the likelihood of encountering situations in which reciprocal altruism could be beneficial; (b) the species must have a high dispersal rate, increasing the likelihood that an individual repeatedly interacts with the same set of individuals; (c) the species must be mutually dependent, increasing the probability that individuals can provide help that would increase the fitness of other individuals; (d) the species must have weak dominance hierarchies, such that benefits can be spread fairly evenly throughout the group; (e) the species can benefit from aid in combat, assisting one another by defending against outgroups; and (f) the species must invest heavily in offspring and parental care. Humans meet all of these criteria and, therefore, should have evolved to display selective reciprocal altruism.

A great deal of the empirical evidence for reciprocal altruism theory comes from game theory. Game theory can test the viability of different strategies that are intended to achieve different economic or resource outcomes. One basic strategy is tit-for-tat. Axelrod (1984) demonstrated that strategies in which players respond to positive (prosocial) behaviors with a reward and negative (selfish) behaviors with immediate punishment lead to cooperative behavior that is easy to establish and maintain in two-person experimental games. Such games provide compelling empirical evidence that humans readily enter and maintain exchanges that follow the logic of reciprocal altruism theory.

Other evidence comes from real-world observations of people living in traditional tribal settings. Hill (2002) documented that the Ache in Paraguay spend considerable time engaging in behaviors that benefit nonbiologically related tribe members. These activities are often important and sometimes costly. Food sharing, for example, occurs on a need basis rather than on the degree of the recipient's biological relatedness to the sharer, assuming there has been reciprocity in the past. This and other studies suggest that reciprocal altruism is grounded in equity and needs rather than merely genetic relatedness, as

inclusive fitness theory might anticipate. In ecologies similar to those of the Ache, food supplies are often unpredictable and variable, so sharing food with reciprocating others is likely to provide insurance against future hardships.

GROUP SELECTION THEORY. The idea that natural selection can occur at the level of the group rather than the individual has been discussed since the 1960s (e.g., Wynne-Edwards, 1962). This idea was largely dismissed in the subsequent decades until Wilson and Sober reinvigorated interest in the topic in 1994. Group-level selection models posit that, in certain cases, groups that reproductively outcompete other groups can become the primary unit on which selection operates, with highly successful groups eventually displacing less successful groups. To operate, group selection relies on several factors, including (a) the severity of local environments, which increase the need for cooperation; (b) the ability and willingness of group members to sacrifice for the good of the group; and (c) the ability of the group to outcompete outgroups.

Using mathematical modeling, Simpson (1994) found that, whereas group selection may have occurred in isolated cases, the likelihood that it was a major and pervasive selection force is low. The models indicate that costs for individuals must remain low, and the proportion of altruists within the group must remain high for long periods of time. There is currently little convincing evidence for the operation of group-level selection on humans (for some possible exceptions, see Wilson & Sober, 1994), at least as most group selection theorists conceive it. That being said, new ways of conceptualizing the evolution of culture and its potential effects on group-level selection suggest other avenues for thinking about group-level selection. These new conceptualizations indicate that groups may have been a primary unit of selection, especially in modern man.

GENE–CULTURE COEVOLUTIONARY THEORIES. Richerson and Boyd (2005) suggested that group selection has occurred through the coevolution of genes and culture (see also Richerson & Boyd, 1998). The conditions necessary for group selection—extremely low within-group variation and high between-group variation—are rarely witnessed in primates. Richerson and Boyd (2005) solved this problem by showing that gene–culture coevolutionary processes may have provided the opportunity for group-level selection to occur. Specifically, they argued that the climate during the Pleistocene fluctuated rapidly, which should have promoted the evolution of social learning in humans. The greater capacity for social learning probably permitted the development of cumulative cultural transmission, a phenomenon rarely seen in other species. Indeed, humans have vastly superior social imitation abilities than even our most closely related brethren, the chimpanzees (Whiten et al., 1996). Although other species do learn both socially and culturally, human transmission, accumulation, and construction are much more complex, cumulative, and long lasting than is true of all other species. Accordingly, each generation of humans learns and builds upon the knowledge of the previous generation, leading to extremely complex cumulative cultural systems.

Similar to genetic evolution, the process of cultural evolution operates through the transmission of cultural variants (Richerson & Boyd, 2005), which are knowledge, skills, and ideas passed from person to person through social

learning. These variants are themselves subject to natural selection as well as other evolutionary processes, such as mutation and drift. They are, however, also selected through biased transmission processes based on their content (e.g., some cultural variants are easier to remember or more likely to be mimicked), frequency (common variants are more often transmitted), and social use (e.g., high-status members are more likely to be imitated, so variant transmission can be influenced by the social status of their users). For example, skills such as computer programming are currently valued and rewarded within our society, so the skills and knowledge of computer programming are more likely to be "selected" because of social pressures to gain status and achieve financial success. Other skills, such as expertise in ancient languages, require tremendous investment but are extremely uncommon and have relatively few benefits in contemporary America. Thus, fewer people should learn the variants associated with ancient languages relative to those associated with computer programming.

Richerson and Boyd (2005) suggested that three criteria must be met for group-level selection to occur: (a) moralistic punishment must be consistent and widespread within a group, (b) there must be strong, consistent pressure to conform to group rules and norms, and (c) there must be significant and sustained conflict with outgroups. Certain cultural variants could have promoted the development of moralistic punishment norms and conformity norms in certain groups. These groups, having strong cohesion and codes endorsing sacrifice for the good of the group, may have been more successful in intergroup competitions, particularly during war. As a result, cultural variants promoting moralistic punishment and conformity may have significantly decreased within-group variability and significantly increased between-group variability. Group-level selection, therefore, was made possible by stronger forms of prosocial behavior directed toward other ingroup members.

In such conditions, culture could have been a selective pressure on individuals who promoted the group's welfare. Over time, individuals who rapidly distinguish ingroup from outgroup members, conformed to group norms, and punished anyone who violated group norms should have been more reproductively successful on average, passing on genes that promoted ingroup cohesion and conformity. Richerson and Boyd (2005) suggested that these gene–environment interactions across many generations promoted "tribal instincts" that fostered rapid ingroup–outgroup distinctions, enforcement and adherence to group norms, and complex social emotions such as shame, guilt, and righteous anger.

Many of the predictions that Richerson and Boyd (2005) made about the specific types of social behavior that should be "amplified" by gene–culture coevolution are well supported by empirical evidence, particularly within social psychology. High levels of conformity are very well-documented in humans. Sherif (1936) and Asch (1956), for example, conducted classic studies showing that people conform even in situations when it is obvious that the group is completely wrong about basic perceptual judgments. There is also strong and convincing evidence that humans can and do rapidly distinguish ingroup and outgroup members (Brewer & Brown, 1998). Sherif and colleagues (1954/1961) demonstrated that simply assigning boys to different groups randomly at a summer camp produced immediate ingroup identification with their assigned group and strong intergroup hostility. Social identity theory (Tajfel & Turner, 1979)

and the research it has inspired have confirmed that people rapidly identify and benefit ingroup members over outgroup members, even when group distinctions are arbitrary and meaningless.

Richerson and Boyd's (2005) premise that individuals must be willing to apply moralistic punishment has also been supported by empirical research. For example, Fehr and Fischbacher (2003) noted that humans engage in "strong reciprocity" to a degree not observed in other animals. They are often willing to punish others who violate norms of equity, even at considerable cost to themselves. This form of reciprocity is "stronger" than Trivers's (1971) reciprocal altruism because individuals are willing to enforce reciprocity without receiving any tangible benefits (Axelrod & Hamilton, 1981), ostensibly for the well-being of the group. Ultimatum Game studies have confirmed that people punish those who behave unfairly toward others, even if they lose considerable money in the process of doing so (Fehr & Fischbacher, 2003). When such games are played across generations (i.e., having early players tell later players what strategies work best), altruistic punishments and rewards increase in future generations of players, resulting in greater cooperation over time.

The willingness to sacrifice for the good of the group by engaging in altruistic punishment is essential because free riders and cheaters can destabilize group cooperation quickly and easily (Fehr & Schmidt, 1999). In addition, enforcers may receive indirect benefits by gaining a positive reputation within the group (Alexander, 1987; Nowak & Sigmund, 1998) or by showing that they are highly resourceful and have ample energy and resources to "spend" on enforcing group norms (Gintis, Smith, & Bowles, 2001).

Gene–culture coevolutionary models contend that traditional gene-centered models cannot account for the stronger forms of prosociality witnessed in humans. They also point out that norms and institutions such as sharing food, hunting and gathering, and serial monogamy typically benefit most group members as long as individuals in the group are willing to enforce such norms consistently. These tendencies may have led to evolutionary processes that resulted in the stronger forms of prosociality and altruism seen in humans today. In the next section, we discuss how current evidence from cross-species comparisons and social neuroscience are beginning to shed light on the mechanisms that support novel forms of prosociality in humans. We also speculate about their connection to evolutionary theory, particularly gene–culture coevolutionary models.

Neurobiology, Phylogeny, and Prosocial Behavior

If multilevel selection theorists are correct that more traditional evolutionary models cannot account for human prosociality, what distinguishes humans from other species? Is there evidence for a link between culture and prosociality in humans? If so, what may have promoted that link? In this section, we explore these questions and explain how current studies addressing the neuroscience of empathy, investigations into the evolution of cooperative behavior, and hypotheses concerning the exaptation of caregiving mechanisms are starting to shed light on human prosociality and its deeper implications for interpersonal relationships (see also Chapters 1 and 11, this volume).

Empathy

One of the strongest empirical challenges to selfish explanations of human pro-social behavior grew out of research on empathy. Daniel Batson (1991) argued that empathic concern, or feelings of sympathy and distress for another person, motivates altruistic behavior in a nonegoistic (nonselfish) manner. Batson and his colleagues have demonstrated that adopting the perspective of another person motivates helping behavior (e.g., Coke, Batson, & McDavis, 1978; for a review, see Batson, 1991). In this research, Batson has identified three important antecedents to altruistic behavior: (a) recognizing another person is in need, (b) adopting his or her perspective, and (c) valuing his or her welfare (Batson, Eklund, Chermok, Hoyt, & Ortiz, 2007).

Given the link between empathy and altruistic motivation, understanding the mechanisms that underlie empathy should provide critical insights into the evolution of prosociality in humans. If, for example, empathy and social learning are influenced by similar mechanisms, a connection between prosocial behavior and culture might exist. Such a finding would provide strong support for the link between culture and prosociality, as proposed by gene–culture coevolutionary theorists.

MIRROR NEURONS. Recent evidence from neuroscience and neurobiological approaches to human behavior has provided intriguing clues to how the development of culture may have influenced the selection of prosociality in humans. In 1992, di Pellegrino, Fadiga, Fogassi, Gallese, and Rizzolatti first reported the existence of mirror neurons. When an individual watches another person, these neurons activate and track observed behavior in the same way they would if the observer was the person actually doing the acting. Much of the early research on mirror neurons placed invasive electrodes in the brains of nonhuman primates to directly measure synaptic firings (e.g., di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). These studies measured mirror neuron activity in premotor areas of the brain to determine whether the same neurons fire when subjects watch another individual take some action as when subjects take the same action themselves (for a review, see Iacoboni, 2009). According to these studies, mirror neurons fire at approximately 50% the rate when an individual is watching another take an action as when the individual is taking action (Gallese et al., 1996). In subsequent human studies, similar results emerged using functional magnetic resonance imaging (fMRI), showing that the same mirror neuron patterns found in monkeys operated in the human ventral premotor cortex and in the rostral portion of the inferior parietal lobe (Iacoboni et al., 1999). Furthermore, blood oxygenation level dependent (BOLD) signal assessed during action observation was approximately 50% of the BOLD signal during action execution, lining up nicely with electrode studies in non-human primates.

Additional research on humans has revealed that when one individual creates an internal representation of another person through mirror neurons, relevant emotion processing areas of the brain become active. For example, Carr, Iacoboni, Dubeau, Mazziotta, and Lenzi (2003) found that imitation of affective facial expressions activated both the insula and the amygdala in participants,

areas known for their roles in affective processing (for a review, see Phan, Wager, Taylor, & Liberzon, 2002). These researchers proposed that the insula acts as a relay from premotor areas to limbic areas. For example, when mirror neurons fire to simulate the actions of others, they signal the insula, which then relays information to other limbic regions leading not only to the internal representation of the observed individual's physical state, but to their internal affective state as well. This connection between mirror neuron systems and affective systems within the brain supports empathic reactions toward other people. Given the importance of empathy in promoting stronger forms of prosocial behavior (for a review, see Penner, Dovidio, Piliavan, & Schroeder, 2005), these functional links between mirror neurons and regions of the brain responsible for affective processing may be essential for stimulating and maintaining prosocial responses to others, particularly when they are distressed.

Mirror neurons, therefore, may be critical for imitating behavior and the enactment of empathic perspective taking (Carr et al., 2003). This has important implications for gene–culture coevolution models. Given that substantial cumulative culture requires extensive imitative capacities, selection for increased mimicking ability through mirror neurons most likely occurred early during human evolution. Furthermore, some of the neural mechanisms that gave rise to an increased capacity for social learning and cumulative culture may also have increased the mental "hardware" needed for empathy and perspective-taking. Selection for social learning may, therefore, have laid a "neural foundation" for the evolution of prosociality in humans. This evidence has the potential to directly connect some of the cognitive mechanisms required for culture with the cognitive mechanisms required for empathy, prosocial motivations, and altruism.

SIMULATION: HOW CAN WE KNOW, AND ARE MIRROR NEURONS NECESSARY? The dominant theoretical approach to neural mechanisms of empathy is simulation theory (e.g., Gallese & Goldman, 1998). According to simulation theory, people use the same neural processes that underlie an embodied representation of themselves to infer the internal physiological and mental states of other people. This feat is accomplished by simulating another person's probable internal states and then drawing conclusions about his or her psychological situation in the same way that individuals understand their own behavior.

Several research programs have tested simulation accounts of empathy (see Hein & Singer, 2008). These studies have found that many of the same brain areas become activated when another person feels pain or is threatened as when an individual himself or herself experiences pain or feels threatened (e.g., Singer et al., 2004). Several studies have documented the important role of the insula in this process (e.g., Lamm, Batson, & Decety, 2007; Singer et al., 2004), showing that the insula simulates the affective components of pain in empathic situations (Lamm & Singer, 2010). These and other studies have also implicated the anterior cingulate cortex (ACC) in empathic processes. Thus, activity in both the insula and ACC correlates with various measures of empathy (Lamm et al., 2007; Singer et al., 2004).

Much research supports the simulation account, but some studies have raised questions about some aspects of it (e.g., de Vignemont & Singer, 2006;

Hein & Singer, 2008). For example, some simulation theorists, such as Iacoboni (2009), have argued that simulation occurs automatically and prereflexively. However, Singer and colleagues have demonstrated that simulation does not occur under certain circumstances, such as when another person does not express pain strongly, or when the empathizer does not have sufficient experience to understand the other's situation (see de Vignemont & Singer, 2006; Hein & Singer, 2008; Singer et al., 2006).

In an even stronger challenge to simulation theory, Jacob (2008) suggested that mirror neurons may be unnecessary for understanding another's intentions or internal psychological states. Rather than providing information about the other's intentions and current state, mirror neurons may represent a prediction of the other's future movements and, thus, are not related to understanding the other's intentions, feelings, or thoughts. In this case, mirror neurons need not be necessary for understanding other people, but their action is a function of other neural processes that have already decoded a person's intentions to predict his or her future tendencies.

Jacob (2008) also argued that simulation theory implies a form of simulation in which the simulator adopts a psychological state that duplicates or produces an internal state similar to that experienced by the other person. This is in contrast to simulation as it is meant in other domains, in which simulation is simply construed as a calculation or modeling process designed to predict, but not duplicate, the simulated object or situation. This begs the question of what fMRI studies of simulation in empathy are detecting and whether standard methods can answer the questions being posed.

The standard approach to determining whether people rely on the same regions of the brain to simulate another person's experience as they use when processing their own experience is *conjunction analysis* (Friston, Holmes, Price, Buchel, & Worsley, 1999). Conjunction analysis identifies which specific regions of the brain are significantly active in two distinct experimental conditions. In neuroscience investigations of empathy, conjunction is taken as evidence that self-related processing and other-related processing are supported by the same neural mechanisms. Users of this approach often imply, either explicitly or implicitly, that conjunction indicates simulation in the duplication or similarity sense.

An alternative interpretation suggests that it is impossible to discern whether shared activation in such regions is duplication (similarity-based simulation) or calculation. Such a distinction can be important because a duplication interpretation implies viewing the other as a "part of the self" in a neural sense. The calculation interpretation suggests no self–other inclusion. Instead, similar brain substrates make calculations about the self and others, which may or may not inform the observer's experience directly. Thus, a calculation process may inform but not necessary produce empathy, whereas a duplication process ought to directly produce an empathic response toward the other. If individuals are simulating another person's situation in a manner congruent with how they process their own situations, one would expect not only activation in the same brain regions in self-related and other-related experimental conditions but also significant correlations within those regions between self-related processing and other-related processing. Such evidence

would indicate that people are interpreting the other's experience through their own experience.

Conjunction evidence is not the same as correlational evidence, even though the two are often interpreted similarly. Whether simulation stems from duplication or calculation is potentially quite important, especially for relationship scholars who are interested in the evolution of empathy. For example, a number of relationship theories propose that people incorporate others (i.e., their relationship partners) into their self-representations, thus blurring the distinction between self and other. If this is true, people ought to use a duplication form of simulation when simulating the experiences of close others. However, they could be more likely to use a calculation-based form of simulation when simulating the experiences of strangers. Such a finding would provide support for both Aron and Aron's (1996) self-expansion theory and Andersen and Chen's (2002) relational self theory. It would also provide potential bridges for integrating current social psychological theories of relationships with theories of human evolution and neurobiology.

Aron and Aron (1996) claimed that love is related to the fundamental human motivation to expand the self. From this perspective, falling in love is a self-expansion process in which an individual begins to include his or her partner into the self-concept and sense of self. This theory, originally introduced as a metaphor, may be less metaphorical than originally believed. If people include others in the self in a neural sense as implied by the duplication sense of simulation, such a process may be critical for empathic responding and relationship processes.

Andersen and Chen's (2002) notion that the self is integrated into a relational context, and that self-related cognition is relationship dependent given that people usually think of themselves in relation to important others, may also be supported by the duplication concept of simulation. In fact, the duplication form of simulation could be a basic mechanism that links the self with other cognitive structures. Achieving a better understanding of these mechanisms might provide critical insights into how the self is constructed in relational contexts.

Such findings may also be useful in integrating relationship theory with theories from neuroscience. If this integration is to occur, the first step is to determine whether self-related activation is correlated with (and not simply conjoined with) other-related activation. Deeper integrations with evolutionary perspectives may also be fruitful. For example, gene–culture coevolutionary processes may have created conditions that promoted cognitive structures allowing for the overlap of self–other representations, further facilitating prosocial tendencies in humans. Alternatively, such cognitive structures may have evolved from evolutionary pressures to produce cooperation, launching the adaptations that were necessary for gene–culture coevolution to emerge. Understanding these links could shed light on the ways in which evolution has prepared humans to manage, repair, and dissolve different types of relationships. Before such integration is fully realized, however, several questions must be answered. Is there a functional link between imitation, culture, and empathy? If so, what is the nature of this link? And are there behavioral differences between humans and other apes that might illuminate such a link?

Phylogeny, Cooperation, and Interspecies Differences

Michael Tomasello and his colleagues believed that the concept of shared intentionality holds important clues to how human evolution diverged from that of other primates (Tomasello & Carpenter, 2007). They suggested that ecological changes that required increased cooperation promoted the evolution of cognitive mechanisms that facilitated the sharing of attention, cognition, and motivation with other people. These resultant changes in social behavior and cognitive ability could have fueled the development of culture and cooperative behavior in humans, providing a critical link between the evolution of prosociality and the evolution of social learning mechanisms.

Tomasello and Carpenter (2005) demonstrated one key difference between human behavior and that of other primates by testing whether human children and chimpanzees both share attention with others. Young chimpanzees are similar to human children when it comes to basic attentional cognitions, such as following eye gaze and intention reading. The two species differ, however, in that human children engage in "shared attention," that is, turning attention to others in order to share interest in an external object. This difference suggests that humans are prepared to share information and attention with others in a way that chimpanzees are not and that they may also be motivated to do so.

Similar differences between human children and other young primates also exist in communication (see Call & Tomasello, 2005). For example, humans often communicate to inform other people in ways that help other people reach their goals. Moreover, human infants can understand when an adult is communicating to help them, whereas young chimps are often unable to decode communicative behaviors that are intended to assist them (Behne, Carpenter, & Tomasello, 2005). As a rule, young chimps communicate to manipulate others, whereas humans have added a communicative repertoire that involves helping others as well (Liszkowski, Carpenter, Henning, Striano, & Tomasello, 2004). Furthermore, young chimps are less prepared and cognitively able to engage in collaborative tasks than are human toddlers (Warneken, Chen, & Tomasello, 2006), and young humans engage in more complex social and instructive learning than young chimps do (Carpenter, Tomasello, & Striano, 2005; Tomasello & Carpenter, 2005).

Tomasello and Carpenter (2007) suggested that this research shows that humans are prepared to share psychological states to support and facilitate cooperative behavior. Similar to research on the neuroscience of empathy, this work supports the notion that social learning, shared psychological states, and cooperative behavior may be outgrowths of human evolution and that these tendencies may be specific to humans. These mechanisms might also explain connections between human prosociality and the development of culture as proposed by gene–culture coevolutionary theories.

This perspective may also have important implications for how we understand social support and interpersonal responsiveness processes (see Chapter 4, this volume). For example, perceived partner responsiveness (Reis, 2007) could be an outgrowth of shared intentionality processes. To the extent that humans are motivated to share psychological states with close others, responsiveness might be construed as the degree to which another person shares or is adopting

one's own thoughts, feelings, and motivations. When a partner does not do so (or is perceived as not doing so), this should be disruptive and stressful. Alternatively, if psychological states are shared or adopted, individuals should feel connected to and supported by their partners.

Caregiving and the Exaptation of Oxytocin Mechanisms

Several theorists have argued that mechanisms supporting prosociality in humans may have been partially exapted from mechanisms that had already evolved to promote infant–parent bonding and caregiving, given the vulnerability of human infants (e.g., Goetz, Keltner, & Simon-Thomas, 2010). Such evolved features include sensitivity to neotenous characteristics and distress vocalizations (e.g., Berry & McArthur, 1986; Bowlby, 1969/1982). Neotenous stimuli make people more careful in their movements, improving fine motor performance presumably to respond better to vulnerable infants (Sherman, Haidt, & Coan, 2009). Neotenous stimuli also motivate caregiving behavior in adults (Glocker et al., 2009). Moreover, distress vocalizations tend to promote caretaking behavior in a variety of species (Panksepp, 1998). Adaptations such as these that facilitate the care of altrical young could have been coopted by evolution to promote more extensive caregiving behavior directed toward nonkin and perhaps even competent adults who request or clearly need assistance.

One mechanism implicated in both parent–infant bonding and prosocial behavior more generally is the neuropeptide oxytocin (see also Chapter 5, this volume). Oxytocin receptors cluster in areas of the brain associated with social and caregiving behavior, such as the bed nucleus of the stria terminalis, the hypothalamic paraventricular nucleus, the central nucleus of the amygdala, the ventral tegmental area, and the lateral septum (Francis, Champagne, & Meaney, 2000). Indeed, direct injection of oxytocin into a variety of different species rapidly initiates maternal behaviors, providing clear evidence for the powerful role of oxytocin in caregiving behavior (Keverne, & Kendrick, 1992; Pedersen, Ascher, Monroe, & Prange, 1982). Thus, there is strong evidence that oxytocin is involved in a variety of caregiving behaviors, but what about prosocial behavior more generally?

Although most evidence for oxytocin's role in social behavior comes from studies of infant–parent interaction and pair bonding, recent evidence suggests that oxytocin also plays an important role in nonkin and nonreproductive relationships. Kosfeld, Heinrichs, Zak, Fischbacher, and Fehr (2005), for example, found that administering oxytocin through a nasal spray substantially increases prosocial behavior during a trust game. In this game, one participant is an investor, and the other participant is a trustee. Each round, the investor must decide how much money to give the trustee with the understanding that (a) investing money in the trustee increases the total amount of money available to both parties, and (b) the trustee is under no obligation to return any of the money. If both players cooperate, they can earn much larger sums of money. If, however, the investor gives money to the trustee, there is a risk that the trustee will not reciprocate, meaning that investors must take risks in order to trust the trustee in this game. In the Kosfeld et al. (2005) experiment, participants

in the oxytocin condition were more than twice as likely as those in the control condition to entrust the maximum amount of money to the trustee. Administered oxytocin, therefore, instilled greater trust in investors, promoting prosocial and possibly even altruistic behavior.

Further evidence for the possible exaptation of oxytocin mechanisms to support general forms of prosociality comes from research on social emotions. If Richerson and Boyd are correct, older affective mechanisms should be involved in both basic forms of social behavior (e.g., maternal behavior, sexual reproduction) and in more complex social–emotional processes. This would suggest that exaptations of mechanisms that originally evolved to govern primitive social affect now govern complex social affect as well. Such evidence has recently been marshaled by Silvers and Haidt (2008), who found that the neuropeptide oxytocin is involved in feelings of moral elevation (a complex social emotion) when breastfeeding mothers watch an uplifting video versus a control (neutral) video. Silvers and Haidt then took an indirect measurement of oxytocin levels by determining the amount of milk letdown the women experienced while watching each video. Oxytocin is both a critical peptide in breastfeeding (Gabay, 2002) and important in the milk letdown process, and it also promotes pair bonding and bonds between mothers and their young children (Carter, 2005). Thus, the Silvers and Haidt study suggests that oxytocin's role in maternal behavior and pair-bonding processes might have been exapted to govern other complex social emotions. This represents indirect but intriguing evidence for Richerson and Boyd's (2005) hypotheses about the evolution of complex social emotions.

Integration and Conclusions

As this review of evolutionary theories of prosocial behavior indicates, more recent evolutionary approaches tend to explain increasingly stronger forms of prosocial and altruistic behavior, particularly in humans.

Despite the tendency for popular culture to depict evolution as "red in tooth and claw," evolutionary theorists dating back to Darwin himself have argued that cooperative group living is a likely by-product of evolution as much as selfish and competitive behavior is. Determining how and why strong prosocial traits and behavioral tendencies were selected has been a challenge for evolutionary theorists. Early attempts to resolve this issue focused on a purely gene-centered approach (e.g., inclusive fitness theory) to explain how and why individuals behave in a prosocial and sometimes altruistic manner toward genetic kin. Fairly compelling evidence supports these models, particularly the tendency for individuals to be willing to make major sacrifices for those who are more genetically related to them, especially in life or death situations.

Reciprocal altruism theory was developed to account for how and why individuals should at times assist nongenetically related others. By showing that certain long-term reciprocal alliances can occasionally increase the reproductive fitness of each partner, this theory extended evolutionary models of prosocial behavior to nonkin. The benefits of reciprocal alliances are particularly likely in harsh and variable environments, similar to those that probably

existed early in human evolution, during which allies work together and provide "insurance" for each other in difficult and unpredictable conditions.

Most recently, multilevel selection models, such as gene–culture coevolutionary models (e.g., Richerson & Boyd, 2005), have suggested how and why more extreme forms of prosociality and altruism could have evolved. Complex, cumulative culture might have produced boosts in inclusive fitness to individuals who were productive and contributing members in highly successful and stable groups. This could have led to the survival of groups that adopted cultural practices that enforced group-promoting norms, resulting in the evolution of the "tribal instincts" and opening the door for more extreme forms of prosocial behavior.

Contemporary approaches to the psychology of prosocial behavior, including neuroscience and cross-species comparative research, have the potential to shed new light on how prosocial behavior evolved in humans. For example, approaches examining oxytocin have documented connections between the evolution of mechanisms that originally supported parent–infant and pair bonds with broader forms of prosocial behavior and moral emotions. This provides evidence that evolution may have exapted older mechanisms to support broader forms of prosociality in humans. Neuroscience techniques are beginning to suggest that empathy and perhaps altruism are undergirded by neural mechanisms that process the experiences of other people in a manner similar to self experiences. Comparative approaches to interspecies differences are beginning to indicate that humans are unusually cooperative and that cooperative behavior is based in part on the ability to share intentions and psychological states with others. In addition, the evolution of prosociality, and ultimately ultrasociality in humans, may be best explained by multilevel models that incorporate the development of cumulative culture into the wider view of human evolution.

Human ultrasociality has to be explained. Few species possess the level of complexity, cooperation, and sheer size of communities witnessed in human societies. Those that do, or that come close, are composed of highly genetically related individuals, meaning that inclusive fitness theory is all that is necessary to understand and explain the prosocial tendencies of these species. Human societies, however, require theories and models that move beyond purely gene-centered approaches and include multiple levels of selection. Without these additional models, human societies cannot be fully understood through evolutionary theories. Ultimately, new evidence must be gathered to refute or support the many untested predictions that flow from multilevel evolutionary models.

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