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The Altruism Puzzle: Psychological Adaptations for Prosocial Behavior

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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, while those that cared least for their comrades, and lived solitary, would perish in greater numbers. (Charles Darwin in *The Descent of Man*, 1871, p. 105)

Humans are social animals is an often stated phrase, but what exactly does it mean? We are certainly not as solitary as some mammals, such as sharks, foxes, and cats, whose sociability does not stretch far beyond mating engagements (Wilson, 1975). Humans are together for a variety of additional reasons, including joint parental care, territorial and group defense, trade, and the provision of scarce goods like food and shelter (Kenrick, Li, & Butner, 2003; Van Vugt, 1998). At first sight, human sociability pales in comparison with that of bees, ants, and termites that are known to routinely sacrifice their lives to defend their colonies. Self-sacrifice in social insects, however, only occurs within family groups where genetic interests are strongly overlapping (Wilson, 1975). In contrast, humans have an unrivalled capacity to sacrifice themselves for individuals that are not closely related, sometimes in large social groups (Fehr & Fischbacher, 2003; Wilson, 2002).

Examples are abound. Humans invest time and effort in helping the needy within their community and make frequent anonymous donations to charities (Van Lange, Van Vugt, Bekkers, Schuyt, & Schippers, 2006; Van Vugt, Snyder, Tyler, & Biel, 2000). They come to each other's aid in natural disasters (Van Vugt, 2001; Van Vugt & Samuelson, 1999). They respond to appeals to sacrifice themselves for their nation in wartime (Stern, 1995). And, they put their lives at risk by aiding complete strangers in emergency situations (Latané & Darley, 1970).

The tendency to benefit others—not closely related—at the expense of oneself, which we refer to here as altruism or prosocial behavior, is one of the major

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puzzles in the behavioral sciences.¹ For many decades, biologists, economists, and psychologists alike have been telling their audiences that humans are fundamentally selfish: When faced with two behavioral options, individuals will choose the alternative that yields the best immediate personal payoffs. But, as the above examples illustrate, this picture is incomplete at best in explaining human social behavior. We need to rethink the validity of the self-interest model in light of the evidence for the ubiquity of examples of altruism and prosocial behavior in human society.

In this chapter, we pursue this goal in several steps. We first present the archetypical social decision situation that humans have faced throughout evolutionary history, the social dilemma, and explain how this over time may have shaped a prosocial tendency in humans. Second, we discuss two broad evolutionary theories of prosocial behavior, and focus our attention on a simple, yet powerful psychological mechanism of social exchange that can account for a broad range of phenomena that have been observed in social psychological research on altruism and prosocial behavior. The wealth of data supports an adaptationist perspective on social exchange (Cosmides & Tooby, 1992; Schmitt & Pilcher, 2004). Throughout human evolutionary history, the benefits of social exchange were so substantial that it increased the relative fitness of those engaging in altruistic interactions, thus enabling this capacity to spread through the population. But, as we shall see, the potential fitness costs associated with making a risky prosocial move were such that it would only be elicited under well-defined social conditions. The main purpose of this chapter is to identify the social psychological conditions that made the evolution of altruism possible and allowed humans to “adapt” to their (natural and social) environments.

SOCIAL DILEMMAS

Perhaps nothing can illustrate the significance of altruism better than the example of the Prisoner’s Dilemma Game (PDG). The PDG represents a broad class of social decision situations, also known as social dilemmas, in which there is a conflict between an individual’s self-interest and his or her shared interests with other individuals. The assumptions behind the game are relatively straightforward (Dawes, 1980; Van Vugt, 1998):

1. Each individual is better off acting in their immediate self-interest; yet,
2. if all individuals act according to their self-interest, then everyone will be worse off.

Broadly speaking, any situation in which you are tempted to do something, but know it would be a grave mistake if everybody acted like you is likely to be a social dilemma. Take the example of two students, Ann and James, who share a house together. Each of them would be better off if they relied upon the other to clean the house (assuming that for most cleaning is a pain). Yet, if neither of them makes an effort to clean the house, the house becomes a mess and they will both be worse off.

The interdependence structure of this example can be presented in an outcome matrix, like the one in Figure 11.1. The altruistic or cooperative choice (C-choice) in this example stands for cleaning the house, whereas the defecting choice (D-choice) stands for not cleaning the house. If Ann cleans the house by herself, but James does nothing, the outcomes for James are very good (say 10 on a personal-satisfaction scale), but they are poor for Ann (say 0). In game-theoretical terms, James gets the free rider's payoff, whereas Ann earns the sucker's payoff (Komorita & Parks, 1994). In contrast, if James cleans by himself, but Ann does nothing then the outcomes for Ann are good (10), but for James they are bad (0)—here Ann is the free rider or “cheater” and James is the “sucker.” If Ann and James share the cleaning, the outcomes for both of them are moderately good (say 5 each), which is not as good as when the other person does all the cleaning. Yet, and here lies the crux of the social dilemma, if neither Ann nor James cleans the house, their outcomes will be relatively poor (say 2 each), which is worse than their outcomes had they both shared the cleaning (5 each).

What makes the social dilemma paradigm so powerful is that the key properties of the conflict between self-interest and collective interest that underlies the dilemma can be easily extended to situations (1) in which the consequences of noncooperative behavior are much more severe, and (2) there are larger groups of individuals involved. As an example, in a legendary article “Tragedy of the Commons,” the late Garrett Hardin (1968) addressed the preservation of common pasture grounds in 17th and 18th century England. The story describes how a collection of herdsmen raise their cattle on a public pasture (known as the Commons). According to Hardin, the tragedy starts once one herdsman realizes that he is better off adding a piece to his herd. His profits in terms of meat and wool increase, so he argues, whereas the losses of adding a cow or sheep (e.g., grazing space) are negligible, because they will be shared with all herdsmen. As all herdsmen come to the same conclusion at some point—there is no a priori reason why they will not—it all ends in disaster as the commons is being overgrazed. As Hardin (p. 1244) puts it dramatically “Freedom in the Commons will bring ruin to all .”

		James	
		Clean	Don't clean
Ann	Clean	5 / 5	0 / 10
	Don't clean	10 / 0	2 / 2

FIGURE 11.1 An example of a Prisoner's Dilemma Game: keeping the house tidy, whereby “Clean” is the cooperative choice and “Don't clean” the defective choice.

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This parable could easily lead to a wrong conclusion. Social dilemmas often do not end in collective disaster when they are played out in the real world, especially when individuals can “enlarge the shadow of the [their] future” (Axelrod, 1984, p. 126). Historical evidence shows, for example, that most commons grounds in England and other countries were, in fact, managed very well by local communities (Gardner & Stern, 1996; Ostrom, 1990)—many commons still exist to this day. Even the Cold War, which inspired so much research into social dilemmas, ended peacefully. In addition, findings from experimental social dilemma research involving repeated interactions between strangers suggest that the vast majority of interactions result in mutual cooperation (De Cremer & Van Vugt, 1999; Komorita & Parks, 1994). Finally (and perhaps the most devastating for the self-interest model), even if there is no expectation of future interaction between complete strangers in the laboratory, still around 40–60% of people make an altruistic move (Caporael, Dawes, Orbell, & Vandekragt, 1989; Fehr & Fishbacher, 2003; Van Lange, 1999).

The validity of the self-interest model is also undermined by a simple thought experiment. In the house-sharing example, if neither James nor Ann makes an effort to clean the house, their situation simply becomes unbearable over time. If James does all the cleaning, but Ann systematically refuses, the relationship between the two will deteriorate over time and James will leave the house, forcing Ann to look for a new room mate to exploit who will then also leave until there is no one who wants to share a house with Ann. Thus, the most likely outcome over time is that Ann will go some way in sharing the cleaning duties with James.²

Thus, the notion that people often act altruistically in social dilemmas is suggested by historical, experimental, and anecdotal evidence. Once people are aware that their interests are at least partly overlapping, and that they have some sense of a shared future, they will often act benevolently toward each other (cf. Axelrod, 1984).

THE EVOLUTIONARY APPROACH

So, what are the ultimate, evolutionary origins of the rich patterns of prosocial behavior that we find in human society? Addressing the evolutionary question is important, for at least *three* reasons. First, it may strengthen the validity of social psychological theories of altruism and prosocial behavior (as well as other puzzling human social behaviors) by providing a fuller and richer account of the phenomenon. In this regard, it is important to note that the evolutionary approach complements rather than competes with social psychological analyses of altruism and cooperation. It looks at the question of altruism at a different level of analysis.

Social psychologists are generally interested in studying proximal explanations for altruism, trying to establish which factors decrease or increase the likelihood of altruism toward others through empirical research (the “how” question). In contrast, evolutionary theorists are interested primarily in the ultimate functions of altruism (the “why” question), trying to figure out whether this type of behavior could have been selected for in human evolutionary history—the adaptation question (Schmitt & Pilcher, 2004).

To give an example, social psychological research on empathy—defined in terms of feelings of sympathy, compassion, tenderness, and the like—examines the conditions under which individuals may become altruistically motivated by benefiting another person as an end in itself (e.g., Batson, 1998; Batson, Duncan, Ackerman, Buckley, & Birch, 1981). Evolutionary psychologists look for evidence to suggest that empathy is a psychological adaptation that has emerged through natural selection, such that individuals who possessed the capacity to empathize with others were more successful in propagating their genes into the next generation than individuals without this capacity. Combining the proximate and ultimate levels of analysis can obviously provide a much richer perspective on the origins of altruism than any singular approach can. Unfortunately, many researchers tend to confuse these levels of analysis in their work, failing to make a distinction between proximate and ultimate explanations for social behavior (cf. Barrett, Dunbar, Lycett, 2002).

Second, addressing the evolutionary question may help to resolve particular contradictions and controversies in social psychological research on altruism. For example, it sheds light on the debate whether empathy derives from selfish or unselfish motivations (Batson, Sager, Garst, Kang, Rubchinsky, & Dawson, 1997; Cialdini, Brown, Lewis, Luce, & Neuberg, 1997). The evolutionary perspective makes clear that these views may not be as incompatible as they seem. Rather than looking at empathy from the perspective of the individual actor, one could look at it from the perspective of the actor's genes (Dawkins, 1976). From the perspective of the gene, it makes sense that, under specific circumstances, such as when empathy is aroused, individuals act prosocially toward specific others. So, selfishness at the gene level does not automatically result in selfish behavior at the level of the organism.

Third, an evolutionary perspective facilitates social psychological research on altruism by generating a plethora of new research questions, hypotheses and analyses. These new developments may bridge fields and even disciplines, thereby serving the cumulative function of knowledge. For instance, an evolutionary perspective suggests that altruism cannot be sustained without some form of discrimination between recipients—the costs of altruism are simply too high to be ignored. Thus, the human psychological system is likely to possess particular “protection” mechanisms that act as brakes on altruism. One likely mechanism is the ability to detect and avoid free riders or cheaters, those who try to exploit the benevolence of others. On the basis of psychological research, informed by an evolutionary perspective, there is now growing support for the presence of a cheater-detection system in the human psyche, but much further research is needed to bolster this claim (Cosmides & Tooby, 1992).

HUMAN EVOLUTION AND THE ALTRUISM PUZZLE

So, what do we know about human evolutionary history that may shed light on the selfishness vs. altruism debate? Most experts agree that the roots of human social behavior lie far back in the Pleistocene, a period that started a couple of million

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years ago and continued until the agricultural revolution, some 10,000 years ago (Barrett et al., 2002; Boyd & Richerson, 1985; Dunbar, 1993). There can be little doubt that this interval, which encompasses about 95% of human history, has left deep traces in the human body and psyche. During this period, humans lived predominantly in relatively small and stable nomadic hunter-gatherer groups, with high degrees of mutual dependence and kinship, and relatively minor status and power differences between individuals. Group living provided our hominid ancestors with numerous benefits for survival and reproduction, such as communal childcare, protection against predators, and food sharing, but it also introduced various specific problems that needed to be solved to reap the benefits of group living. Experts agree that many of the more basic problems were, in fact, archetypical social dilemmas (Fehr & Fischbacher, 2003; Kenrick et al., 2003).³

To illustrate, in order to survive in harsh climates, it was essential for our ancestors to obtain a daily nutritious diet of fruits and meat. The daily provision of meat, in particular, was not guaranteed, however, because the returns of hunting were likely to be variable. Furthermore, meat came in packages that were often too large to consume by one family. Hence, there would be days with a food surplus and days with a food shortage. This would open up the possibility to engage in altruistic exchanges, whereby individuals (or families) would share their food with others that were less lucky on that particular day (Hawkes, 1993). These recipients would return this favor at a later day. This resembles the PDG that we sketched in Figure 11.1, which can promote group cooperation, but leaves an individual open to exploitation from cheaters.

Social dilemmas would have been everywhere in traditional hunter-gatherer societies, not just in food sharing, but also in cooperative hunting, territorial group defense, and the communal care for children. Therefore, it is not at all unlikely that across millions of years, humans have evolved specific psychological and behavioral adaptations to cope with social dilemmas (Nesse, 2001). The benefits of group living, or the costs of solitary living, were simply too large to be ignored. An obvious adaptation that would greatly facilitate group living for any individual would be the emergence of some degree of altruism, targeted toward specific others under specific circumstances.

On the face of it, however, altruism provides a major puzzle for Darwin's theory of evolution. Evolutionary theory assumes that individuals who possess particular traits and behaviors that produce survival and reproductive benefits, leave more offspring than individuals without such characteristics. And, to the extent that these traits and behaviors are inheritable, they will spread through a population. Yet, how can altruism, a behavior that enhances the welfare of others at the cost of the individual, enhance the individual's reproductive success? Darwin struggled with this question, but failed to come up with a satisfactory answer.

Only in the past few decades have evolutionary scientists come up with various plausible evolutionary scenarios for altruism. Unlike Darwin who believed that individuals, or sometimes even groups, were the units of natural selection these scientists argued that basic selection unit is the gene and that our bodies are merely "vehicles for the transmission of genes" (Dawkins, 1976). This gene-eyed perspective of human nature opens up the possibility that, under certain specific

conditions, altruistic tendencies can be adaptive. Which are these theories? And, more important for the present argument, to what extent are they able to account for altruism toward those that are not closely related?

Kin-Selection Theory

According to Hamilton's (1964) theory of kin selection, individuals can promote their own genetic future by making sacrifices on behalf of others who carry copies of their genes. The kin-selection model predicts that individuals engage in altruistic sacrifices on behalf of close relatives, such as offspring, more than distant relatives, such as cousins, and more toward distant relatives than toward genetic strangers. Yet, altruistic behavior only emerges if the costs for the helper are lower than the benefits for the recipient multiplied by the degree of relatedness between the two individuals, which is known as *Hamilton's formula*

$$rB > C$$

where r represents the degree of relatedness, B the benefit to recipient, and C the cost to helper.

There is considerable support for the kin-selection hypothesis of altruism among human samples. For example, Burnstein, Crandall, and Kitayama (1994) found in a number of scenario studies that intended helping increased with genetic relatedness, and, consistent with the kin-selection model, this relationship was particularly strong in life-death situations, such as entering a burning building to save another person's life (see also Neyer & Lang, 2003). Furthermore, a survey among female residents in Los Angeles found that, in times of need, close relatives were a greater source of help than were unrelated individuals (Essock-Vitale & McGuire, 1985).

There is no doubt that the kin-selection model accounts for a considerable portion of sacrifice in our everyday lives (as readers with young children will appreciate), but can it also account for prosocial acts toward individuals that are not closely related, which is so uniquely human? Genetic relatedness declines extremely quickly if we go beyond the nuclear family, so the answer should be negative.

However, an intriguing possibility is that, because humans spent most of their history in small, kin-based groups, no perfect mechanism has evolved for discriminating between kin and non-kin, as this was not particularly necessary within these conditions. Therefore, humans rely on heuristic but imperfect kinship rules as the basis for altruism (Van Vugt, Schaller, & Park, 2004c). Physical similarity, similarity in attitudes or culture, and geographical proximity could potentially all be used as kinship cues. Although these cues are fallible to denote kinship in modern society, they may have been effective throughout much of evolutionary history. This "big mistake" hypothesis for altruism has received some skepticism from evolutionary scientists (Boyd & Richerson, 1985), but initial tests have produced some hopeful results.

For example, there is evidence that fathers favor children that look more like them (Burch & Gallup, 2000). Also, adults report greater willingness to assist unrelated children who have similar facial features (DeBruine, 2004), and they are more likely to help someone who shares their name or speaks the same dialect

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(Barrett et al., 2002). Even something as remote as attitude similarity can apparently elicit a kinship cue. In an ingenious social cognition experiment, Park and Schaller (2005) showed that participants subconsciously linked a target person believed to hold similar attitudes to themselves with word stimuli denoting kinship (e.g., family). Further research is needed to investigate the importance of other possible kinship cues, such as proximity and shared personality traits, and their consequences in terms of prosocial behavior toward strangers.

Social Exchange Theory

Kin selection may have paved the way for a second, and perhaps more powerful mechanism for altruism toward genetic strangers, social exchange. Once the capacity for altruism toward kin had evolved, it became possible to bestow small benefits on those that were around, but were non-kin (Barrett et al., 2002). Unlike kin altruism, however, this system would have been based on a mechanism of social exchange.

Social Exchange Between Individuals The theory of reciprocal altruism (Trivers, 1971) holds that individuals sometimes act benevolently toward others in the expectation of a reciprocal act of kindness in the future. Examples of reciprocity can be found in most social mammals. The blood sharing among vampire bats and the formation of fighting coalitions among chimpanzees are often cited as examples (de Waal, 1996; Wilkinson, 1984). Yet, there is no species in which reciprocity is as common, as varied, and highly developed as among humans. Humans trade in nearly everything that is of value, from food and weapons to information and sex. Furthermore, exchanges can be paid out in a different currency (e.g., sex for money). In this regard, it is perhaps better to use the more generic term of social exchange for this type of altruism rather than reciprocity (cf. Cosmides & Tooby, 1992).⁴

Social Exchange Within Groups In humans, social exchanges are not necessarily restricted to two individuals, but they frequently occur within larger social networks (Alexander, 1987). Generalized exchange networks involve situations where individuals, who act benevolently toward others, do not necessarily expect a return from the recipients themselves but from a third party. For example, an individual A may share his food with individual B, and upon seeing this a third individual C may share his food with A. One of the reasons this system works is that by acting altruistically, individuals develop a positive *reputation* within their group, which increases their attractiveness as potential exchange partners (Alexander, 1987; cf. costly signaling theory; McAndrew, 2002).

Yet, there is another intriguing possibility for the evolution of prosocial behavior in larger groups, something which Darwin himself recognized in *The Descent of Man*:

A tribe including many members who, from possessing in high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes, and this would be natural selection.

According to this argument, which is often referred to as group selection or multilevel selection (Campbell, 1975; McAndrew, 2002; Wilson, 2002), acting prosocially toward members of your in-group may be beneficial to you as it can ensure that your group is victorious over other groups in an intergroup competition. Although within the group, altruists fare worse than cheaters, groups with many altruists fare better than groups with many cheaters, giving altruists indirect benefits via group selection. The evolution of altruism (and other social traits) may thus be possible via selection at the level of the group rather than the individual. However, this model only works if (1) the between-group selection pressures are stronger than the within-group selection pressures (i.e., intergroup competition overrides intragroup competition), (2) groups frequently disband and individuals have the opportunity to choose with whom they interact, and (3) in- and out-group members can be easily distinguished—these conditions are likely to uphold for humans (Wilson, 2002).

Brakes on Social Exchange The evolution of social exchange required the presence of various social, structural, and biological conditions that acted as brakes on social exchange to reduce the risks of exploitation by an exchange partner (Cosmides & Tooby, 1992; Trivers, 1971). For example, individuals must interact repeatedly with the same individuals, and there must be many opportunities for social exchange during the lifetime of these individuals. Humans' long lifetimes and the presence of small and stable groups during much of evolutionary history would have favored these conditions. In addition, for social exchange to evolve, the human psychological system needs to be equipped with a number of different auxiliary mechanisms. These psychological mechanisms should protect individuals against the risks of exploitation by the recipients of their prosocial acts, and they are likely to have co-evolved alongside the social exchange mechanism to enable individual to reap the benefits of social exchange.

What should an evolved psychological system for social exchange look like and what evidence can we find in the social psychological literature on altruism and prosocial behavior for the existence of these psychological mechanisms? Previously, evolutionary psychologists have been primarily interested in the cognitive adaptations underlying social exchange (e.g., computational and memory abilities; Cosmides & Tooby, 1992). Here, we are primarily concerned with the social and motivational adaptations that gave rise to social exchange. In the next section, we discuss several key properties of an evolved social psychological system of social exchange that, we believe, have allowed humans to reap the benefits of altruistic interactions.

AN EVOLVED SOCIAL PSYCHOLOGY OF ALTRUISM AND PROSOCIAL BEHAVIOR

The theory of social exchange makes a number of powerful predictions about an evolved social psychology of prosocial behavior: Who should we help, why should we help, and when should we help? Below, we review the evidence for several of these hypotheses.

Trust

To reap the benefits of social exchange, there must be a psychological mechanism in place that protects individuals from engaging in interactions with poor exchange partners, i.e., individuals who are either unwilling or unable to reciprocate. One such mechanism should enable individuals to detect free riders and avoid interacting with them, which is also known as a *cheater-detection system* (Cosmides & Tooby, 1992). If individuals are unable to distinguish between potential cooperators and free riders, and interact with both types of people indiscriminately then a social exchange system cannot evolve over time because it is too costly for the individual. There are a number of socio-cognitive capacities that are needed to enable individuals to make decisions about whom they are going to interact with, for example, the ability to recognize many different individuals, and remember the history of interactions with these individuals (cf. cheater-detection system). Ultimately, these revolve around the notion of *trust*—a belief in the trustworthiness and honesty of others (Holmes & Rempel, 1989; Komorita & Parks, 1994; Yamagishi, 1986).

The social psychological literature is quite clear about the benefits of trust. For example, relationships characterized by high-levels trust appear to be more rewarding, enjoyable, and stable over time (Simpson, Gangestad, & Lerma, 1990). Trust also enhances benevolent actions. For example, close relationship partners are more likely to make sacrifices for one another—by giving up leisure time to care for each other—if they expect their partners to do the same for them (Wieselquist, Rusbult, Foster, & Agnew, 1999). Similarly, employees who trust their employers to treat them well are more likely to help out their organization in times of need (Tyler & Smith, 1998). Finally, individuals are more prepared to make sacrifices for their group, if they expect other members to do the same (De Cremer & Van Vugt, 1999; Kramer & Brewer, 1984).

Given the importance of trust for social exchange, it is not all that surprising that humans are fairly good at making decisions about who they can trust or not. To illustrate, after a brief encounter with another student, individuals were able to predict with 75% accuracy whether that person would cooperate or defect in a Prisoner's Dilemma (Frank, 1988). Nevertheless, individuals do sometimes make errors of judgment, but if they find out that they are being cheated upon, they retaliate swiftly and aggressively (Fehr & Fishbacher, 2003; Trivers, 1971) or terminate the relationship altogether (Van Vugt & Hart, 2004).

Negativity Effect

In a related vein, the evolution of social exchange would be facilitated if individuals would attend more strongly to negative impressions than positive impressions about potential exchange partners. A false negative—believing that someone is a cooperator who, in reality, is a defector—is more detrimental to the welfare of the altruist than a false positive believing that someone is a defector who, in reality, is a cooperator. Hence, we should expect humans to show a bias toward negative rather than positive personality information, especially information about the

morality of an exchange partner. Furthermore, the negativity bias should be particularly pronounced when the prosocial act is highly costly (e.g., lending a large sum of money).

These predictions are, by and large, supported by the social psychological literature on person perception (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Reeder & Brewer, 1979; Taylor, 1991). The negativity effect (sometimes also referred to as negativity bias) refers to the phenomenon, whereby relative to positive person information, negative person information elicits more physiological arousal, draws greater attention, and exerts greater impact on judgments and impressions as well as behaviors. Several explanatory mechanisms underlying the negativity effect have been advanced, including neurological mechanisms (e.g., the brain seeks to reduce or suppress all deviations from hedonic neutrality), and several range-frequency explanations (e.g., the novel, the infrequent, and the unexpected draws more attention; Taylor, 1991). At an ultimate, evolutionary level, this bias can be explained by the fact that in social exchange dilemmas it is vital to tell the cooperators from the cheaters, and avoid interacting with the latter category of individuals.

A nice illustration of the negativity bias comes from research on sex differences in reading the intentions of potential mates. Because the costs of a sexual encounter with an unreliable mate are much higher for females than for males, Haselton & Buss (2000) argued that it would be in a woman's interest to underestimate the commitment of men in order to avoid a false negative (mistaking a cheater for a cooperator). Their results confirmed this prediction, thus supporting our evolutionary argument about the adaptive benefits of judgment biases in targeting prosocial behavior.

Commitment and Loyalty

Altruism based on social exchange can only evolve if individuals themselves are not too opportunistic in entering and leaving reciprocal relationships. Hence, the capacity for commitment, defined in terms of strong desire to continue the relationship, long-term orientation, and feelings of attachment. Commitment, sometimes also referred to as loyalty, improves the functioning of a social exchange system by mechanisms that are conceptually linked to altruism and prosocial behavior, and therefore can be viewed as a psychological adaptation for social exchange (Nesse, 2001; Rusbult & Van Lange, 2003; Van Vugt & Hart, 2004).

For example, commitment enables individuals to maintain an exchange relationship that was rewarding in the past, but for some reason, is not quite as rewarding now. Commitment thus gives exchange partners a little bit of credit in reciprocating the investments that an individual has made in the relationship. These investments would, of course, be lost if individuals were to leave relationships impulsively. Commitment would also serve as a signal to the other party that the relationship is likely to endure, despite the temporary decline, which makes altruistic exchanges between partners further possible (Rusbult, 1983). Finally, there may be indirect benefits to expressions of commitment. Showing

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commitment may enhance the reputation of an individual in the eyes of a third party, and may therefore make the individual a more attractive exchange partner in the future (Frank, 1988).

It may come as little surprise that commitment is the main predictor of satisfaction and stability in close relationships (Rusbult, 1983) and in groups (Van Vugt & Hart, 2004). It is also predictive of cognitive and behavioral activities to maintain relationships, such as derogating or driving away tempting alternatives (Johnson & Rusbult, 1989). Furthermore, commitment enhances positive illusions about the relationship, serving the belief that their own relationship is better than—and not as bad as—others' relationships (Murray, Holmes, & Griffin, 1996; Rusbult, Van Lange, Wildschut, Yovetich, & Verette, 2000; Van Lange & Rusbult, 1995). Perhaps most importantly, loyalty and commitment promote tendencies toward altruism and cooperation, such as willingness to sacrifice, engaging in extra-role behaviors in teams and organizations, and responding constructively (rather than destructively) to another's destructive behavior (Rusbult, 1983).

Forgiveness

To evolve, a system of social exchange would have to be sufficiently flexible to deal with minor deviations from strict reciprocity. In the social dilemma literature, social exchange is often conceptualized in terms of a tit-for-tat strategy (mimicking the partner's choice). Whereas tit-for-tat has been shown to promote altruistic exchanges, more so than unconditionally altruistic or defective strategies (Axelrod, 1984), it has an important limitation. This limitation derives from the fact that tit-for-tat becomes trapped in a cycle of noncooperative interaction, once an accidental or nonaccidental noncooperative choice is made. The only way out of this so-called echo effect (or negative reciprocity) is that one individual initiates a unilateral, risky altruistic move.

Forgiveness (responding altruistically to a partner's noncooperative choice) is an important psychological mechanism that may keep social exchange going in such situations. Thus, we believe that human tendencies to be forgiving may have evolved for this particular purpose. Computer simulations and laboratory studies on social dilemmas have both shown that forgiveness overcomes the detrimental effects of unintended errors in non-cooperation (Bendor, Kramer, & Stout, 1991; Van Lange, Ouwerkerk, & Tazelaar, 2002). Similarly, there is evidence from close relationship research that acts of forgiveness facilitate the stability and satisfaction of close relationships through tendencies related to prosocial behavior (Fincham, 2000; Karremans, Van Lange, Ouwerkerk, & Kluwer, 2003; McCullough, Worthington, & Rachal, 1997).

Without some degree of forgiveness it is hard to imagine how individuals could continue to reap the benefits from social exchange, especially in situations when intentions cannot be perfectly communicated—which is often true in social dilemmas in everyday life (e.g., arriving late for a meeting because of an unforeseen traffic jam; accidentally saying the wrong thing). The act of forgiving is probably so important for the functioning of groups that it is one of the cornerstones of almost every society, religious or nonreligious (Wilson, 2002)—see social norms.

Social Emotions

Empathy The evolution of social exchange would greatly benefit from the existence of a psychological system that enables individuals to quickly assess if and how much other persons require aid. If this is true, then humans should be sensitive to any cues that yield information about the cost and benefits of helping so that altruists know how much help is required and recipients know how much they should reciprocate. People are indeed very attuned to the costs and benefits of altruism (Penner, Piliavin, Dovidio, & Schroeder, in press). But, it is often a complex calculation and the ability to put oneself in another person's shoes or "perspective taking"—a main component of empathy—can be viewed as a heuristic rule for making a calculated decision. Furthermore, empathy should be stronger the greater the victim's need, because this increases the potential benefit of helping to the victim and therefore their gratitude.

There is substantial evidence that empathy promotes altruism toward complete strangers (e.g., Batson, 1987; Batson et al., 1981). Empathy increases helping, even if there are substantial costs in money, time, and effort associated with the helping act (Batson et al., 1981, 1997). In contrast, needy people are much less likely to receive aid in the absence of empathic concern. Although some critics argue that empathy is really a selfish emotion—based on a merger between the images of the self and the other (Cialdini et al., 1997)—there is no denying the fact that strong feelings of empathy can give rise to altruism toward complete strangers.

Then, why are individuals selective in who they empathize with? According to Batson et al.'s (1981, 1997) experiments, individuals empathize more with people who are similar to them. One evolutionary explanation for this finding may be that helpers have less difficulty in assessing the amount of aid victims need if they are similar to themselves. Another intriguing possibility, however, is that people are more likely to help similar people, because similarity may be used as a cue for kinship—the big mistake hypothesis (Park & Schaller, 2005; Van Vugt, Jepson, Hart, & De Cremer, 2004b). Thus, helping a similar (i.e., kin) person would be less costly because it contributes indirectly to their individual fitness—via the kin-selection route. Whether empathy as an adaptation is ultimately shaped by kinship psychology or social exchange psychology remains to be seen, but there can be little doubt about the role of this prosocial emotion in regulating helping behavior.

Other Emotions The benefits of social exchange are so substantial that we would expect prosocial behavior to be evoked not just by empathy, but also by a range of other emotions. For example, the experience of a self-conscious emotion, like *guilt*, in response to one's own cheating makes individuals less likely to transgress next time, thereby maintaining the quality of their exchange relationship (Haidt, 2001). Guilt should also increase altruism. Research on the negative state-relief hypothesis (Cialdini & Futz, 1990) provides support for this claim.

Similar benevolent acts are expected if people experience other self-conscious emotions, such as shame and embarrassment, for failing to reciprocate. In contrast,

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emotions that people experience in reaction to free riders, such as *anger*, *contempt*, and *envy*—the so-called other-condemning emotions (Haidt, 2001)—should result in a decline in prosocial behavior. These are testable propositions.

Social Norms

So far, we have reviewed evidence for the existence of psychological adaptations that can explain the emergence of prosocial behavior at the dyadic level, such as empathy and trust. This is perhaps an easier task than trying to understand prosocial behavior within larger groups where the problem of cheaters is likely to be much greater. For example, why would people contribute to team performance, why would they volunteer for a job, or pay their taxes if they fear that there will be people who free ride on their sacrifices (Van Vugt et al., 2000)? Earlier, we have offered two evolutionary models for understanding prosocial behavior in large groups, (1) reputations (Alexander, 1987) and (2) group selection (Wilson, 2002). Both are likely to have played a role in shaping prosocial tendencies in humans. Altruism at the group level, however, could have evolved only under a narrow set of social and structural conditions. Once these were in place, individual could reap the benefits from investing in larger groups.

For most of history, humans lived in relatively small and stable groups (Barrett et al., 2002). This condition opens up the possibility for the evolution of social exchange on the group level, in addition to the interpersonal level. Group-based altruism (based on generalized exchange) can be beneficial particularly in cooperative situations with highly uncertain payoffs that involve more than two individuals (e.g., hunting large game, group defense). The evolution of generalized social exchange would not be possible without the support of *social norms* to regulate cooperative exchanges between the individual and the group. Thus, social norms may have found a place in human society as a way to promote cooperation and deter free riding in large groups.

Norms about *fairness* and *morality* are examples. They regulate social exchanges between members of groups and are designed to promote group harmony and ensure that everyone gets what they deserve, whatever that may be (Tyler & Smith, 1998). Justice is so strongly engrained within the human psychological system that we are prepared to punish cheaters, even if they have not done us any harm personally—moralistic aggression (Fehr & Fischbacher, 2003; Van Vugt & Chang, 2004; de Waal, 1996).

There is much evidence for the importance and prevalence of these moral norms in human societies (Krebs & Janicki, 2002). Most societies have *decency norms* in place to promote cooperation and coordination between individuals, for example, not interrupting a conversation, giving up seats to elderly people, and acknowledging the receipt of a gift. Societies also have *obedience norms* (e.g., respecting your parents) and *solidarity norms* in place (e.g. defending your country), which help to foster group cohesion. Most societies also work on the basis of strict *fairness rules* that promote altruistic exchanges by prescribing how scarce resources and goods ought to be divided between the group members. For example, it is universally accepted that wealthy individuals in a group should contribute

more to the common good than the poor—in modern society this principle is enforced through a progressive tax system.

Failure to adhere to these moral and fairness norms often evokes strong expressions of anger, rage, condemnation, and sometimes even revenge (cf. retributive justice; Tyler & Smith, 1998). Social disapproval, ostracism, prison sentences, and death penalties are but a few examples of the widespread tendency in human societies to engage in cheater punishment.

Group Identification and Xenophobia

Social exchange within groups could only come about if there was a mechanism in place that allowed groups to create, preserve, and adhere to group boundaries to serve as a guide to whom prosocial activities should be directed to. Hence, it would have been vital to know who is an in-group member and who is an out-group member. This is especially important in intergroup competitions in which helping a person from a rival group would harm one's own group, which is likely to have been the situation during much of human history (Alexander, 1987; Van Vugt & Hart, 2004). Thus, we would expect humans to have evolved capacities to attend very carefully to information about group memberships (Campbell, 1975), and form deep emotional attachments to in-groups (in-group identification) as well as strong resentments against out-groups (xenophobia).

There is a considerable body of social psychological research to confirm the existence of intergroup bias. Individuals are much more likely to act altruistically toward in-group members rather than outgroup members even when group categorization is based on a completely random event, like the flip of a coin (Tajfel & Turner, 1986), and the categorization cuts across friendship groups (Sherif & Sherif, 1953). In addition, humans have a propensity to identify themselves quickly and spontaneously as group members rather than as unique individuals (Brewer, 1979). Group identification promotes self-sacrificial behaviors for the benefit of groups, for example, in a resource crisis or intergroup conflict (De Cremer & Van Vugt, 1999; Kramer & Brewer, 1984). Group identification also creates a strong sense of individual loyalty toward groups, which further enhances group-based altruism (Levine & Moreland, 2002; Van Vugt & Hart, 2004).

Group Size

Generalized social exchange systems must have evolved in conjunction with adaptations to regulate the size of groups. Obviously, the larger the group the more difficult it becomes to detect free riders. Yet, larger groups also yield better protection against predators and rival groups (Alexander, 1987). Hence, we would expect humans to have the capacity to create flexible group arrangements in response to different types of environmental threats and opportunities (e.g., fission–fusion societies; Barrett et al., 2002). For example, in-group settings in which the costs of free riding are huge, such as in highly interdependent work teams, we would expect individuals to have a preference for keeping group sizes relatively small.

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There is a good deal of evidence suggesting that people prefer to work in smaller groups of five to eight people. This “dinner-party” size has been observed by anthropologists studying interactions, exchange, and culture in tribes, organizational psychologists studying teams and self-organizing groups, and game theorists analyzing the mathematics of interpersonal decisions (Gallucci, Van Lange, & Ouwerkerk, 2004). Social dilemma researchers, too, have observed that cooperation declines with increasing group size, and that such decline sets in when groups constitute of more than eight individuals (Liebrand, 1984).

Several interesting and plausible psychological explanations have been advanced to account for the group size effect in social dilemmas. For example, anonymity increases with group size, whereas perceptions of personal efficacy (e.g., the feeling of making a difference) and feelings of personal responsibility or identity tend to decrease with group size. Also, a series of computer simulations of social dilemmas have shown that small groups do very well in terms of maintaining cooperation. Moreover, individuals spontaneously form groups of sizes that are not much larger than five (Gallucci et al., 2004). Thus, one could argue that group formation decisions may ultimately (and at least partially) be rooted in adaptations for social exchange.

Group Stability

The theory of social exchange would also predict that humans have an evolved psychology for group stability—keeping the group together. The costs of altruism are such that individuals are unlikely to engage in cooperative exchanges within groups if they are not confident that the group will stay together for a while in order for individuals to get a return from their investment. Hence, individuals should be sensitive to information about the duration of their group membership. Moreover, once they have invested in a group, they should want to engage in activities to keep the group together, and react negatively to forces that undermine group integrity.

There is some evidence to suggest that individuals carefully attend to cues about the longevity of group membership. For example, individuals cooperate more in groups with a fixed membership than in groups with a fluid membership, primarily because they trust each other more (Van Vugt, Hart, & Chang, 2004a). In addition, individuals often defect on the last trial of a social dilemma—thus, when the termination of the group is eminent (cf. endgame effect; Murnighan & Roth, 1983). Finally, group members often treat newcomers with some distrust, and they do not immediately accept them as full members (Moreland & Levine, 1982).

The social psychological literature is also quite clear about a link between investment size and loyalty—a powerful mechanism to keep groups together. The more individuals invest in their group or relationship, the more committed they are to maintain it, thereby foregoing attractive exit options (Rusbult, 1983; Van Vugt & Hart, 2004). Furthermore, the loss of a group member—a threat to group stability—often evokes strong negative reactions from current members. Current members often treat departing members with some disdain, presumably out of

fear that they may set an example to others. And, leavers are especially disliked if they join a rival group (Levine & Moreland, 2002; Van Vugt & Chang, 2004). Finally, the departure of a member often gives rise to ceremonial activities to strengthen the bonds of the group (e.g., farewell parties, funerals; Moreland & Levine, 1982). Thus, it is perhaps not too far-fetched to argue that prosocial behavior systems rely upon a broad range of activities that humans display, which may have been designed for keeping large groups together (Wilson, 2002).

Individual Differences in Altruism and Prosocial Behavior

Research has found considerable individual differences in prosocial inclination. Altruism, for example, is more prevalent among individuals who score consistently higher on scales of agreeableness, prosocial values, trust, communal orientation, collectivism, and moral development (e.g., Clark & Mills, 1979; Penner et al., 2005; Triandis, 1994; Van Lange, Otten, De Bruin, & Joireman, 1997; Van Vugt, Meertens, & Van Lange, 1995; Yamagishi, 1986). On a measure of social value orientation, usually around 60% individuals can be classified as individuals who are primarily concerned with maximizing mutual gains (i.e., prosocials), while 30% are primarily concerned with maximizing absolute personal gains (i.e., individualists), and 5–10% with maximizing relative personal gains (i.e., competitors). Together these latter two orientations are sometimes referred to as proselfs (Van Lange & Kuhlman, 1994). How does this fit with an adaptationist perspective on social exchange and prosocial behavior?

First, social-value orientation is a better predictor of behavior in one-shot dilemmas than in repeated dilemmas. In repeated social dilemmas, behavior is also importantly influenced by the strategy of the partner (McClintock & Liebrand, 1988; Van Lange, 1999). Both results are in agreement with an evolutionary theory of social exchange. It is not surprising that many individuals would start with an altruistic move on their first encounter with a stranger—provided that the act of benevolence is not too costly—because generosity builds trust (Van Lange et al., 2002).

Then why do some people defect on their first choice? We believe that differences in prosocial behavior at least in part, arise from early interaction experiences and childhood environments that channel an individual's development toward pursuing different adaptive strategies (Penner et al., in press). For example, analyzing the family background of a large sample of individuals, one of us found that prosocials, relative to proselfs, came from families with more siblings, particularly sisters, and they also had a more secure attachment style (Van Lange et al., 1997). Also, prosocials were less likely to be first-borns. It might be interesting for further research to look into other developmental differences shaping altruistic orientations, such as, age differences between siblings, children, and family stability (Sulloway, 1996).

Furthermore, it is possible that social-value orientations are affected by present social circumstances that activate either a cooperative or competitive strategy. For example, in a relatively stable working environment it pays to cooperate with someone on a first encounter as you may meet that same person again. In contrast,

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in settings characterized by many short-term exchanges with strangers, like in the car-sale or estate-agency business, it may pay to cheat every now and then. In the same way, cross-cultural differences in altruism (Triandis, 1994) may be traced back to differences in the stability of the social environment, which may favor a particular behavioral strategy. For example, encountering an extended family member is more likely to happen in a collectivistic culture than in an individualistic culture, and it therefore pays not to cheat so as to avoid damaging one's reputation (Moghaddam, 1998).

Finally, it is possible that individual differences in altruism can be sustained, to some extent, through *frequency-dependent selection* (Mealey, 1995). This is particularly relevant for the competitive orientation, which is found among only 5–10% of the population. As long as the frequency of individuals who constantly cheat is sufficiently small, this strategy may be sustained in a population, because the costs of fully eradicating this strategy are higher than the damage it does. Once this strategy spreads through a population, however, the benefits of cheating decrease because there would be more pressure on the evolution of protective mechanisms to detect and punish cheaters.

Thus, the existence of individual differences in altruism is compatible with an evolutionary theory of social exchange if we assume that social exchange is an inherently flexible system sensitive to environmental cues. Interactions between childhood and adulthood experiences as well as minor variations in genetic material probably determine whether individuals approach social dilemmas with more selfish or selfless intentions. Yet, such minor personality differences can have profound effects on the outcomes of any social exchange, as shown in prisoner's dilemma research (Kelley & Stahelski, 1970).

THE INDIVIDUAL WITHIN SOCIETY

Humans are Social Animals

This is a true, but incomplete statement. Unlike members of other social species, humans have evolved a unique capacity to act prosocially toward genetic strangers, sometimes in very large groups. To explain the rich patterns of altruism and prosocial behavior, in this chapter we have gone back to the ancestral world of the Pleistocene where humans spent 95% of their history living in highly interdependent nomadic hunter-gatherer bands, presumably of around 50–200 individuals (Barrett et al., 2002). To reap the numerous benefits of group life (e.g., group defense, food sharing), our ancestors had to come up with various cooperative solutions to a range of social dilemmas that they encountered on a daily basis (Kenrick et al., 2003; Van Vugt, 1998).

Given the necessity of group living, it is not unlikely that, through evolutionary time, humans evolved a specific psychological and behavioral system that enables them to solve such dilemmas. An example of such a system is *social exchange*, which makes it possible for humans to engage in altruistic exchanges with other individuals in dyads or larger groups. We have reviewed the social psychological

literature on altruism and cooperation for evidence that humans possess an evolved psychology of social exchange. This review has highlighted a range of social psychological adaptations that could have been in place to make social exchanges between individuals and within groups possible. Trust, forgiveness, empathy, social norms, group identification, and group stability are but a few examples of such social psychological mechanisms, which protect altruistic individuals, at least to some extent, against the dangers of cheating and free riding.

The Function of Society

Before closing, we wish to address a final peculiarity of human social behavior, the ability to cooperate in extremely large social units, sometimes comprising millions of individuals working together—as in the example of nation states or mass social movements (Van Vugt et al., 2000). Can an evolved psychology of social exchange, which is rooted in adaptations for small group interaction, account for this? For various reasons, we believe it can.

First, one should realize that these large social units consist of many levels of groupings that are hierarchically linked. For example, a country is divided into regions, which in turn are divided into cities, city areas, streets, and so forth. Because of the interrelations between these levels, what seems to be an altruistic act on the level of society (e.g., engaging in water conservation) may, in fact, be motivated by the fear of social sanctions within a much smaller community (Van Vugt, 2001).

Second, the pressures on humans for operating in flexible social exchange units have made it possible for humans to form emotional attachments with social groups in addition to forging interpersonal bonds. The capacity for group identification may have resulted from this selection pressure. Once the capacity is there, it can be easily extended to social organizations on a much larger scale, such as identifying with one's local football team, the members of one's social class or country.

Third, humans possess a unique mechanism of information exchange, language, which makes it possible to identify cheaters and free riders more effectively, and on a much larger scale than for other social animals. Computer simulations show that if individuals can exchange information about free riders then it becomes much harder for free riders to invade a population of cooperators (Enquist & Leimar, 1993). Reputational concerns mushroom if individuals have the opportunity to gossip about each other (Dunbar, 1993). Social dilemma research also shows that cooperation rates in larger groups increase dramatically when individuals have the opportunity to talk to each other (Dawes, McTavish, & Shaklee, 1977). In this regard, it is not surprising that some theorists have argued that the language capacity and a large brain size, in general, evolved for the specific purpose of fostering cooperation within large groups (i.e., the social brain hypothesis; Dunbar, 1993).

Finally, large-scale cooperation can be sustained in the presence of moral norms, another unique feature of the human psyche (but see de Waal, 1996). In small groups, altruists can punish cheaters by themselves, however, in large

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groups the altruists must rely on others to do the sanctioning for them. Selection pressures on increasing group size—possibly for the purpose of improving group defense against either predators or rival groups (Alexander, 1987; Barrett et al., 2002)—may have created pressures to evolve a moral system whereby penalties were not just imposed on cheaters but also on individuals who failed to punish cheaters (Fehr & Fishbacher, 2003). Such moral norms, which are in today's society conveyed through the state or the church ("Thou shall not steal"), can be an effective means of sustaining prosocial behavior on societal scale (Wilson, 2002).

CONCLUSION

This chapter outlined an evolutionary perspective on human altruism and prosocial behavior. We argued that prosocial tendencies have evolved (at least in part) to reap the benefits of social exchanges in order to adapt to social dilemmas and related conflicts between the interests of two or more individuals. We have specified a range of conditions under which an evolved psychology of prosocial behavior (based on social exchange) could emerge and reviewed the social psychological literature for evidence. Research on a range of interpersonal processes (e.g., empathy, negativity effects, and forgiveness) and group processes (e.g., group identification and xenophobia) is generally consistent with hypotheses derived from an evolutionary theory of social exchange.

This chapter suggests (at least to us) that the search for social psychological adaptations underlying altruism and prosocial behavior is a worthwhile enterprise. We hope that the readers of this chapter will take up the challenge to conduct further research on altruism, which connects social psychological and evolutionary perspectives. Only then will we move toward a more complete understanding of one of the great puzzles of human behavior, altruism.

ACKNOWLEDGMENT

The first author was supported by a grant from the Leverhulme Trust Foundation (F/00180/L).

NOTES

1. The social psychological literature draws a distinction between altruism and prosocial behavior (Batson, 1998; Penner et al., in press). Prosocial behavior refers to any kind of action that benefits others and is motivated by a variety of interpersonal motives, including pursuit of various self-rewards. In contrast, altruism refers to the underlying motivation to increase the welfare of others. In this chapter, we will use these terms interchangeably, because we are primarily interested in understanding actions in which there is an underlying *intention* to help others. If that is not the case, there is not much interesting to be explained. For example, a pedestrian on a zebra crossing who accidentally steps in front of a car, thereby injuring himself, but

saving another person's life is helping the other person. But this is not a case of altruism, and therefore requires no theoretical explanation. Only if the pedestrian steps in front of the car *for the purpose* of saving the other's life are we dealing with a case of altruism, which needs to be explained.

2. This example is reminiscent of the well-known hawks and doves example in the evolutionary biological literature, where over time the outcomes of peaceful interactions between doves exceed the outcomes of repeated interactions between hawks and doves, or hawks-hawks interactions (Maynard-Smith & Price, 1973).
3. This is not to deny that there were no other social problems than social dilemmas in the ancestral world. Numerous important social problems revolve around coordination (e.g., leader-follower problems) or competition (e.g., status and dominance). Undoubtedly, these problems have also shaped the human psychological system. But they are unlikely candidates for the emergence of altruism.
4. This theory should not be confused with exchange theories that were once popular within the social sciences (Homans, 1950). These theories advocated the self-interest model by arguing that social interactions are rational exchanges whereby individuals attempt to minimize the costs and maximize the rewards of their interaction. Such theories have a hard time explaining spontaneous help toward strangers in emergency situations. In contrast, by adopting a selfish-gene model, an evolutionary-based theory of social exchange can explain why individuals sometimes relinquish their immediate interests to help a needy stranger.

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