The Evolution of Altruism in Humans

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Keywords

prosociality, cooperation, conflict, adaptationism, kinship, reciprocity, punishment

Abstract

Humans are an intensely social species, frequently performing costly behaviors that benefit others. Efforts to solve the evolutionary puzzle of altruism have a lengthy history, and recent years have seen many important advances across a range of disciplines. Here we bring together this interdisciplinary body of research and review the main theories that have been proposed to explain human prosociality, with an emphasis on kinship, reciprocity, indirect reciprocity, punishment, and morality. We highlight recent methodological advances that are stimulating research and point to some areas that either remain controversial or merit more attention.

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INTRODUCTION

Humans routinely behave in ways that benefit others across a range of interactions, from mothers nursing their babies to large numbers of individuals sacrificing their lives in the service of group goals. Here we review proposed explanations for these patterns of behavior, with an emphasis on the evolutionary explanations for the properties of the psychological mechanisms that cause these acts.

We first clarify the phenomena we wish to explain. This is necessary because different communities and even different scholars within communities do not always use the same terms to refer to the same phenomenon (West et al. 2007b). Our central interest is in the evolutionary explanation for those psychological systems that are designed to deliver benefits to others. We are interested in explaining the properties of psychological benefit-delivery devices, the computational mechanisms in humans designed to aid others.

Very broadly, evolutionary explanations for benefit-delivery devices come in two varieties. The first variety explains why some organisms have psychological systems designed to aid relatives. These explanations turn on the idea that genes can cause copies of themselves to increase in subsequent generations by causing the body they inhabit to deliver benefits to other individuals who carry those genes (Hamilton 1964). The second variety explains why some organisms have psychological systems designed to aid even those not closely related. These explanations turn on how individuals who aid others can stand (eventually) to benefit as a result of giving aid to others. There are many ways these delayed benefits can be achieved, the most famous means of which

is reciprocity (Trivers 1971), when an organism that helps another individual recoups more than the cost of the help through the process of the mutual, sequential exchange of aid.

Humans help others in a wide variety of ways. Parents nurture their children, friends support other friends in fights, strangers engage in mutually profitable transactions, individuals sacrifice in the service of aiding groups to which they belong, and so on. For many of these categories of behaviors, multiple proposals have been offered for their evolutionary explanation. Here we discuss evidence that speaks to these debates and, in our conclusion, provide some suggestions about how research in this area might profitably proceed.

Phenomena to Be Explained

In this section, we clarify the set of phenomena we wish to explain and also those phenomena that lie outside our scope, excluding from our agenda the ways in which individuals make others better off merely as a side effect of their own actions.

First, and continuous with the rest of the biological world, humans across cultures tend to help those most closely related to them. Parents invest resources of various kinds in their offspring, a pattern of behavior common across many taxa (Davies et al. 2012). Indeed, the delivery of benefits tends to follow the logic laid out by Hamilton (see below), being strongest among close relatives—offspring and full siblings—and diminishing with distance.

A second type of social behavior is exchange. Humans across cultures and over time have exchanged various goods and services, either in simultaneous transactions or in voluntary giving and receiving over time.

A third pattern of benefit-delivering behavior is human "friendship." Like some nonhuman primates and dolphins, humans form relatively long-term nonkin relationships that include significant amounts of cooperation and occasional forms of self-sacrificial behavior, and such friendships constitute an important part of human sociality.

A fourth type of human social behavior, and arguably the most complex, is cooperation in large non-kin-based groups. This includes phenomena as varied as barn raising to large-scale military conflict among modern states. These phenomena are among the most contentious among scholars working in this area.

These four patterns of behavior are not intended to be perfectly mutually exclusive nor are they intended as an exhaustive list of ways in which humans benefit one another.

Exclusions

Because our interest is in systems designed for delivering benefits, we exclude from our focal interest systems designed for some other function but that generate benefits to other organisms as a side effect (West et al. 2007b). Consider, for instance, an elephant eliminating solid waste, which has the effect of providing a home and nutrients for organisms that can consume the nutrients in the dung. These benefits to other organisms come as a side effect or byproduct of the design of the elephant digestive system. No part of the elephant's digestive system's properties can be explained by virtue of the benefits delivered to the organisms that exploit the dung. Our interest excludes such cases.

Excluding beneficial side effects of behavior is important in the context of social behavior because humans are continually affected—positively or negatively—by side effects of others' actions. In addition, we regard altruistic intent in the folk psychological sense—the experienced desire to help another individual—as part of the phenomenon we wish to explain, as opposed to the explanation.

Reciprocity: a type of cooperation that is initially costly but favored because of the mutual exchange of benefits over time

Cooperation: behavior that provides a benefit to another individual (recipient) and that has been selected for because of such benefits

Similarly, we emphasize that conscious altruistic intentions are not required for a mechanism to be a benefit-delivery device in the sense we use the term here. Consider cases of mutualism among plants and the animals that eat their fruits, dispersing seeds in the process. Calorie-rich fruits provide benefits to animals that disperse the sex cells of the plants, and plants have evolved fruit that benefits animals (and, in consequence of animals' transactions with fruits, the plant). Yet, although fruits appear as if they were designed to attract and benefit animals, there is no sense in which individual plants need be conscious of this.

EVOLUTION AND NATURAL SELECTION

Our interest in the evolution of altruism in humans should not be taken to imply a focus on the historical process of evolution. Instead, our interest is in functional traits that deliver benefits to other people. Our modern understanding of Darwin's (1859) theory of natural selection is that genes that increase the fitness of individuals will accumulate in populations, leading to organisms that appear to behave as if they were designed to maximize their fitness (Fisher 1930). Our most general definition of fitness is inclusive fitness, which is the sum of the individuals' influence on their own reproductive success (direct fitness) and that of their relatives (indirect fitness; Hamilton 1964, 1970). The easiest and most common way in which indirect fitness benefits can occur is through helping close relatives; this process is often referred to as kin selection (Maynard Smith 1964).

Increasing one's indirect fitness will sometimes have to be traded off against reducing one's own direct fitness, such as when helping behaviors are costly. Inclusive fitness theory can be encapsulated in a pleasingly simple way by Hamilton's (1964) rule, which states that altruism will be favored by selection when $rb - c > 0$, where c is the fitness cost to the actor, b is the fitness benefit to the recipient, and r is the genetic relatedness between the actor and the recipient. The relatedness term, r, is a statistical coefficient, which measures the genetic similarity between the actor and recipient, relative to the rest of the population (Hamilton 1970).

There are three general points to make here. First, the genetic and individual perspectives are complementary, not competing (Dawkins 1976, Hamilton 1964). Natural selection acts on allele frequencies to produce individuals that appear designed to maximize fitness (Grafen 2007). Second, inclusive fitness is not just a special case for interactions between relatives; it is the modern interpretation of Darwinian fitness in its most general form (West & Gardner 2013). Instead, maximization of individual fitness is the special case, when $r = 0$. Third, Hamilton's rule describes not only when altruism will be favored but also any other trait. Both b and c can be positive or negative, and so Hamilton's rule also predicts when selfish, spiteful, or mutually beneficial traits will be favored.

Evolutionary Versus Mechanistic Questions

In seeking to explain cooperation from an evolutionary perspective, we wish to emphasize that the process of providing explanations from the standpoint of modern biology is not a unitary enterprise. As Ernst Mayr (1961) and Niko Tinbergen (1963) emphasized, because behavior X will have multiple causes, asking why organisms do behavior X really entails asking separate (yet related) questions. One question often at the forefront of evolutionary psychology is about the function of the trait in question. What is the trait for? How did the trait increase inclusive fitness during the course of evolution? A related question has to do with history. What are the phenotypic precursors of the trait? These ultimate questions can be informed by—and can inform—the answers to more proximate questions one can ask about traits. Tinbergen broke these proximate questions into two types. First, the adult phenotype is the result of a process of development, a joint interaction

Altruism: behavior costly to the actor and beneficial to the recipient, measured in lifetime personal fitness consequences

Inclusive fitness: the effect of one individual's actions on everybody's production of offspring, weighted by relatedness; the sum of direct and indirect fitness

Direct fitness: the effect of one individual's actions on his or her own production of offspring

Indirect fitness: the effect of one individual's actions on everybody else's production of offspring, weighted by relatedness

Kin selection: the process by which traits are favored because of their effects on the fitness of relatives

Relatedness: a measure of genetic similarity relative to the population mean

between the organism's genetic complement and its environment. This leads to the question of how a given trait develops during the life course of the organism. And, finally, though not least importantly, is the question about the mechanism by which a trait operates.

We distinguish among these different questions because although they may interact in interesting ways, they are not competing and require different answers (Scott-Phillips et al. 2011). For example, the proximate answer that individuals cooperate because they are afraid of being punished by angry individuals (Fehr & Gächter 2002) does not provide an answer, in itself, to the ultimate question of why cooperation was favored because it does not explain why the costly punishment was favored.

Levels of Selection

In recent years, there has been considerable controversy over the level at which selection operates and the possible role of group selection. Because these issues have been recently reviewed (West & Gardner 2013, West et al. 2008), we provide only a brief overview.

One source of confusion is that the term group selection is used to mean different things by different people. "Old" group selection is the idea that organisms will appear to be designed to maximize group fitness (Wynne-Edwards 1986). As explained above, gene dynamics lead to organisms appearing as if they were designed to maximize their inclusive fitness, so we can also ask when gene dynamics would lead to organisms that appear designed to maximize group fitness. It turns out that this is only the case under restrictive contexts, such as clonal groups or when competition is completely repressed between group members (Gardner & Grafen 2009). For this reason, old group selection was rejected as a generally applicable theory in the 1960s (Leigh 2010, Maynard Smith 1964).

"New" group selection is the idea that there are multiple levels of selection (hence usually termed multilevel selection), which can vary in their importance (Wilson 1975). For example, cooperation could be favored if the benefits at the group level (between-group benefits) outweighed the cost at the individual level (within-group costs). It is sometimes suggested that in situations where kin selection or inclusive fitness could not account for cooperation or altruism, this new group selection approach provided an alternative explanation (e.g., Wilson & Hölldobler 2005).

However, new group selection (multilevel selection) and kin selection are just different ways of conceptualizing the same evolutionary dynamics. Both approaches find that increasing the group benefits and reducing the individual costs favors cooperation. Similarly, group selection theory predicts that cooperation is favored if we increase the proportion of between-group as opposed to within-group genetic variance, but that is equivalent to saying that the kin selection coefficient of relatedness is increased. In all cases, where both methods have been used to look at the same problem, they yield identical results (Hamilton 1975, Lehmann et al. 2007).

HELPING RELATIVES

We now turn from broad theory to the present literature on prosocial behavior in humans, starting with questions surrounding close relatives. Cross-culturally, relationships within the family are a crucial aspect of social life (Brown 1991). Indeed, as Kurland & Gaulin (2005) put it, "Although agreeing on little else, anthropologists acknowledge that kinship is one of the central organizing features of human society" (p. 447). Anthropologists have recognized the key role of kinship for some time (e.g., Westermarck 1921).

Psychology has focused much less on kinship. Lieberman et al. (2007), for instance, noted that the average number of index citations for kinship terms in the relevant textbooks was, surprisingly,

less than two. One possible reason is that the observation that human parents care for their offspring is so prevalent and obvious that it seems to require no explanation (Cosmides & Tooby 1994). From the Darwinian point of view, the explanation is straightforward: The theory of evolution predicts that organisms' features will be designed for survival and reproduction, in the service of maximizing the representation of their offspring (and other relatives) in the next and subsequent generations. Inclusive fitness theory neatly explains why organisms are often designed to help closely related others.

Parents and Offspring

Human parents make a tremendous investment in genetically related offspring, although there is some cross-cultural variability in the details. For human females, this investment is obligatory, including nine months of gestation and then, typically, a longer, more energy-intensive period of nursing. Heavy female parental investment is the rule among mammals, and humans are not overly exceptional in this respect (Hrdy 1999). The milk-delivering mammary glands in humans are clearly designed to deliver calories and other benefits from mother to child, and they represent an obvious example of benefit-delivery systems. Many other behavioral adaptations are designed to cause mothers to care for their offspring (Davies et al. 2012).

In contrast to humans, male parental investment is very small for the vast majority of mammals (Geary 2000). Set against this backdrop, human paternal investment in offspring is remarkably large. Furthermore, male parental care is relatively costly in humans, compared to other animals, in terms of the extent to which care reduces the likelihood of successful breeding in the future (Griffin et al. 2013).

Although debate continues about the reason for this unusual pattern among humans, attention has often focused on the fact that human babies, compared to our close relatives, are born immature and dependent on investment for a substantial period of time. Indeed, in many places, human offspring could not easily make it to reproductive age without tremendous transfers of energy to them, usually by parents and often by other close relatives (Kaplan et al. 2000). This means that the benefit of paternal care may be especially large. Another factor that may be important in humans, relative to other animals, is that female promiscuity is relatively rare; thus, males are unlikely to waste investment in offspring that are not theirs (Griffin et al. 2013). Variation is sure to exist in the degree of male parental investment both within cultures (Geary 2000) and between cultures (Marlowe 2000).

This is not to say that all interactions within families are cooperative. Casual observation and data from developmental psychology reveal that they are not (Buunk et al. 2008, Fouts et al. 2005, Kim et al. 2001, Schlomer et al. 2010). Trivers's (1974) parent-offspring conflict theory (POCT) explains why (reviewed by Mock 1994). Consider the simple case of a parent with two offspring that are full siblings. The conflict derives from the fact that each of the two offspring is related to itself by $r = 1$ but shares only half its genes with its sibling ($r = 0.5$). Therefore, all else being equal, any particular allele will only benefit half as much from parental investment when that investment is allocated to the sibling instead of the allele's host. This creates a conflict of evolutionary interest, as each of the two offspring should "prefer" an allocation of maternal resources that favors itself.

Furthermore, the parent's optimal allocation of resources among offspring may often differ from what is optimal for each individual offspring, leading to parent-offspring conflict, which may even be fought out within the womb (Haig 2010). Relatively little work has been done on parent-offspring conflict in humans. Indeed, Schlomer et al. (2011) recently referred to POCT as "barely known within psychology," noting that Trivers's (1974) famous paper had been cited only

14 times in major psychology journals. As such, the topic remains a fertile ground for additional research (see also Pollet & Hoben 2011).

One area where POCT has informed research has been in the conflict between parents and offspring in terms of mate preferences, especially the ways in which parents might try to influence their offspring's mate choices (e.g., Perilloux et al. 2008). Although both parents and offspring benefit when offspring choose mates with good genes and resources, under many circumstances there is conflict, with parents preferring a tradeoff more weighted toward resources. Perilloux and associates (2011) recently found this pattern, with parents valuing earning capacity more than attractiveness (an index of genetic quality) in their offspring's mates, whereas the offspring showed the reverse preference (Buunk & Solano 2010).

Generally, relatedness will increase cooperation and decrease conflict, a pattern seen clearly in findings that children have a much greater risk of abuse or even infanticide when they live in households with nonrelatives, such as stepparents, compared to genetic relatives (Daly & Wilson 1988). Recent studies have continued to document the increased risks faced by children living with stepparents, especially stepfathers (Daly & Wilson 2007, Tooley et al. 2006), though debate on this issue continues (Temrin et al. 2011).

Beyond Parents and Offspring

A wealth of data from anthropology shows that humans generally aid relatives rather than strangers and closer relatives rather than more distant ones. For instance, among the Ifaluk, chiefs share food as a positive function of relatedness (Betzig & Turke 1986), a pattern that is observed among a number of groups studied by anthropologists (e.g., Nolin 2010, Patton 2005, Wiessner 2002), though the details vary cross-culturally (e.g., Allen-Arave et al. 2008 regarding the Ache; for a discussion, see Gurven 2004). Anthropologists have provided substantial evidence that cooperation among kin plays important roles in additional contexts, such as alliance formation (Marlowe 2010) and the raising of offspring (Flinn 2011). Such patterns of kin discrimination are common in birds and mammals (Griffin & West 2003).

There are some data on kin-directed behavior in the psychological literature as well. In one early set of studies using self-report questionnaires, Burnstein et al. (1994) found that people said they would be more inclined to help a relative who was closely (e.g., a full sibling) rather than more distantly (e.g., a cousin) related across a range of conditions. A number of studies have yielded results consistent with these findings using self-report of actual previous help (Neyer & Lang 2003), hypothetical vignettes (Korchmaros & Kenny 2006, Osiński 2009, Stewart-Williams 2007), and experimental techniques (Madsen et al. 2007). People also report being more willing to engage in morally wrong behavior to benefit those who are closely related to them (Kurzban et al. 2012) and tend to pass wealth on after their deaths in a way that is weighted toward those who are most closely related (Judge & Hrdy 1992). This is not to say that people always favor kin over nonkin, particularly when the latter are close friends (Stewart-Williams 2008).

Recent work has focused more narrowly on possible proximate mechanisms underlying kin-directed behaviors (Batson 2010), especially on the emotional systems that produce feelings of emotional closeness and that seem to play a key role in motivating helping behavior (Neyer & Lang 2003). Work that explores the details of these proximate (emotional) systems represents an important and promising route for research in this area. For instance, Burton-Chellew & Dunbar (2011) investigated how the frequency of contact affected emotional closeness and found that even though people may feel emotionally close to their in-laws, to whom they are not genetically related, they do so in a way that aligns with their inclusive fitness interests.

In terms of the proximate mechanisms underlying helping behavior toward kin, recent work has illuminated the ways that people make use of particular cues, that is, features of the environment that reliably correlate with genetic kin. For instance, Lieberman et al. (2007) documented how particular cues available during early development have important psychological effects. In particular, the tendency for directing altruism toward a sibling seems to depend positively on the length of coresidence with that sibling and observations of the sibling's perinatal association with the same mother.

COOPERATION AMONG NONKIN

Cooperation and the exchange of benefits is not restricted to relatives. Non-kin-based friendships, for instance, play a central role in human social life cross-culturally (Brown 1991). Furthermore, people are often generous to relative strangers and make sacrifices for others, especially those seen as belonging to the same group (Allport 1954). This section reviews candidate explanations for these phenomena.

Direct Exchange

For psychological systems to evolve that are designed to aid others outside one's immediate kin (see previous section), the costs of aid have to be (probabilistically) recovered over the long term, such that the actor gains a net direct benefit from aiding, or the systems could not have been selected for. The best-known evolutionary route to such recovery is Trivers's (1971) theory of reciprocal altruism. We refer to this as reciprocity because it can only be selected for if it is beneficial to the actor in the long term; hence, it is not altruistic (West et al. 2007a,b). Reciprocity has been discussed in detail elsewhere (e.g., Trivers 1971, 2006), so here we very briefly sketch the logic.

If organisms interact repeatedly over time, and the benefits of receiving cooperation are greater than the cost of performing it, then helping can be favored if individuals preferentially cooperate with those that have aided them previously (Axelrod & Hamilton 1981). Very broadly, we expect natural selection to favor psychological mechanisms that meet cooperation with cooperation and defection with defection.

Humans are good candidates for having such psychological systems because our ancestral lifestyles were likely to have consisted of a large number of repeat interactions with the same individuals, with various goods and services that could be exchanged (Cosmides & Tooby 1992). The hypothesis that there are psychological systems designed around reciprocity makes a number of empirical predictions regarding the existence of specialized computational machinery to enable reciprocal exchange, many of which have been examined (reviewed by Delton et al. 2011). For example, a requirement for reciprocity is that individuals be able to identify when the reciprocal exchange has been violated, with a transaction partner taking a benefit but not reciprocating appropriately. Cosmides and colleagues, not uncontroversially (Sperber & Girotto 2003), have gathered evidence over the past 20 years for just such a specialized psychological system (Cosmides & Tooby 2008).

Reciprocal exchanges of benefits require a substantial number of additional proximate computational mechanisms—none of which need be conscious—including the ability to compute what counts as a cost or benefit to the self and others, the ability to recognize others and remember one's past transaction with them, and emotional systems designed to take advantage of the opportunities for potential gains in trade (see, e.g., Cosmides & Tooby 1992, p. 177).

These emotional systems have recently received increasing attention. Perhaps foremost among these emotions is empathy, which has long been known to be related to helping behavior (e.g.,

Batson 1991). If help is likely to be reciprocated, then those in need of help represent potentially important opportunities. That is, those who are (temporarily) in some sort of distress are sources of potential gains in trade because helping in their moment of need might produce reciprocal aid in the future. This might explain why those in need elicit sympathy and empathy, as they represent long-term fitness opportunities. Of course, in modern environments many people in need elicit these emotions even though the probability of return help is exceedingly slim (Hagen & Hammerstein 2006).

The emotion of guilt might play a similar role in reciprocity. Ketelaar & Au (2003) showed not only that people reported experiencing guilt when they defected in a bargaining game, but also that those who experienced guilt—whether as an endogenous reaction or through experimental induction—were more likely to cooperate in a subsequent experimental game (see also Nelissen et al. 2011). These results imply that guilt might be designed to restore a previously damaged exchange relationship.

Along similar lines, anger appears to play a role in exchanges. In particular, people report experiencing anger and the concurrent desire to impose costs when a potential exchange partner has not delivered the benefit seen by the actor as appropriate, or if a partner has failed to reciprocate appropriately (reviewed by McCullough et al. 2013). These feelings of anger motivate revenge, which can be thought of as (roughly) meeting defection with defection in the context of the prisoner's dilemma game. The emotions that motivate initial helping (empathy), harming others who do not help (anger), and restoring damaged reciprocal relationships (guilt) are components of a set of complex, interrelated systems supporting reciprocity.

Beyond Direct Reciprocity

Trivers's (1971) ideas have frequently been invoked to account for friendship: strong, enduring, social bonds among nonkin. [For excellent treatments and critiques, see Seyfarth & Cheney (2012) for nonhuman friends and Hruschka (2010) for human friendships.] However, there are reasons to doubt that reciprocity can fully explain all aspects of human friendships (DeScioli & Kurzban 2009b, Silk 2003). First, people explicitly deny that they view friendships as exchanges, and, indeed, keeping track of reciprocal obligations undermines, rather than strengthens, friendship ties (Silk 2003, Xue & Silk 2012). Second, friends help friends when they have suffered a catastrophe, exactly a moment in which return benefits are least likely (Tooby & Cosmides 1996) and reciprocity models predict abandonment. Third, reciprocity doesn't explain phenomena such as friendship jealousy; if you are my exchange partner, I am not necessarily worse off if you exchange with others (Archer & Coyne 2005).

One alternative to the idea that friends are used to reap gains from exchange is that friendship is a kind of social insurance (Tooby & Cosmides 1996). This proposal begins with the observation that when people are most in need, they are the worst investment from the standpoint of reciprocity and so least likely to be chosen as a reciprocal exchange partner. To buffer against this problem, individuals cultivate associations with other people who will come to value them, specifically, because of their particular talents, abilities, history, and so forth, so that when the individual suffers a reverse, those people will be motivated to come to their aid. The social insurance view might help to explain why people don't keep very close track of immediate costs and benefits.

A second, related alternative is that friends are used as allies, individuals who will provide support when conflicts arise (DeScioli & Kurzban 2009b). Although conflicts in many nonhuman species are limited to dyads, human conflicts can consist of many individuals, with victory more likely to go to the side with the larger number (Adams & Mesterson-Gibbons 2003). Cultivating allies, then, even if immediately costly, can be repaid through alliance support in the future. The

Prisoner's dilemma: a game used to illustrate the problem of cooperation; in the one-shot game, each player maximizes payoff by defecting rather than cooperating

alliance model predicts that a key variable for friendship is where one lies in others' friendship rankings because this indexes how likely they will be to support you (DeScioli & Kurzban 2009b). This prediction was borne out in a recent analysis of data from a social networking site, which showed that people's choice of best friend—the most valuable slot for an ally—is predicted by partners who rank the focal individual higher than others (DeScioli et al. 2011).

Indirect Reciprocity and Signaling

Another way that incurring a cost to benefit someone today might bring return benefits tomorrow is via reputation and the actions of third parties (Alexander 1987). In indirect reciprocity models, it is assumed that agents meet one another and that in such meetings one agent can help the other at some cost that is less than the benefit bestowed. Now, if others in the population choose to help those who they have seen helping others, or those who have a good reputation, then helping can, under appropriate parameters, be evolutionarily stable (e.g., Nowak & Sigmund 1998).

Recent years have seen a proliferation of such models, with varying assumptions, especially surrounding how third parties evaluate the actions of others. For instance, does helping an agent who has previously been selfish—helping a nonhelper—give one a "good" or "bad" reputation (Uchida & Sigmund 2010)? In models that use the notion of "standing," refusing to help a non-helper preserves one's favorable reputation from the point of view of subsequent third parties (Leimar & Hammerstein 2001, Panchanathan & Boyd 2003). Theory suggests that the possibility of indirect reciprocity is greatest when agents take account of whether helping or not helping is justified by the target's reputation (Ohtsuki & Iwasa 2006).

Such strategies entail nontrivial cognitive requirements, including recognizing when others have helped or harmed, keeping track of others' reputations, and combining these two pieces of information in the service of making one's own decision about helping when the opportunity arises. Everyday experience—as well as laboratory evidence dating back 50 years (Rapoport & Chammah 1965)—suggests that humans are interested in, closely attend to, and condition their behavior on others' history of helping when the opportunity arises.

In addition, an increasing amount of empirical work has been aimed at investigating possible psychological mechanisms for indirect reciprocity in humans. One prediction of indirect reciprocity models—though perhaps not unique to them—is that people should be more likely to behave cooperatively, and less likely to behave antisocially, when they believe that their behavior is observed and the actor is identifiable. This prediction is borne out by a long tradition of research in social psychology (Diener et al. 1976). Furthermore, even relatively low-level cues that one is being observed, such as the presence of eyes or eye-like stimuli, can increase prosocial behavior (Bateson et al. 2006, Burnham & Hare 2007, Ernest-Jones et al. 2011; reviewed by Nettle et al. 2013), suggesting the sensitivity of these decision-making systems to context. Field experiments have yielded supporting evidence (Yoeli et al. 2013).

In some cases what may matter for either direct or indirect reciprocity is not just whether individuals help, but also how much they help relative to others (Roberts 1998). Barclay & Willer (2007) investigated the influence of the amount of cooperation for indirect reciprocity in a laboratory study with two phases. In the first phase, participants had to choose a level of cooperation in a continuous version of the prisoner's dilemma game. In the second phase, observers of the interaction in the first part were paired with one of the participants, either randomly or by virtue of their choice. When observers could choose, participants in the first round transferred more money in the initial prisoner's dilemma game, suggesting that people were using their decisions strategically.

More generally, some have proposed that generosity acts as a signal of one's intentions or traits, which in turn improves one's outcomes (e.g., Smith 2004, Smith & Bliege Bird 2006).

Miller (2000) has proposed that human altruism systems might have been selected because they reliably signal properties of the altruist, increasing the altruist's outcomes on the mating market.

Delivering Benefits to Avoid Costs

The preceding section discusses how costs of helping are recouped in the future by a number of routes to subsequent benefits, including reciprocity, gains that result from a positive reputation, and so forth. Recently, increasing attention has been focused on another explanation for prosocial behavior: the possibility that antisocial behavior will be met with costs.

Much of this work has followed in the tradition of Boyd and Richerson's early pioneering work, which used analytical models to understand the evolution of cooperation in groups. Boyd & Richerson (1992) showed that cooperation can evolve in populations in which agents punish noncooperators. In fact, these early models showed a strong result, that essentially any behavior—cooperative or not—could evolve in a world in which punishment was possible. The upside of avoiding punishment, in essence, outweighed the costs of engaging in the behavior. Recent years have seen refinements and elaborations of these models (e.g., Boyd et al. 2010, Henrich & Boyd 2001).

In large part motivated by these ideas, a body of research has recently explored the effect of punishment on cooperative behavior in laboratory settings. Much of this research uses a public goods game (PGG), which pits individual interests against group interests. Participants, usually in groups of between three and six, are given an allocation of resources to be divided between two accounts, one that benefits only them, and one that benefits the group as a whole. Resources contributed to the group account increase in value but are split equally. Contributions to the group account, then, entail a cost to help other group members.

Early work in this area suggested that when players know that others in their group can impose costs on them for their (non)contribution behaviors, people make larger contributions to the group account than when no such punishment mechanism is available (Yamagishi 1986; see also Ostrom et al. 1992). More recently, Fehr & Gächter (2002), for instance, had subjects play a repeated PGG, with subjects in one condition able to punish other members of their groups. Their results showed that punishment had effects over time, with players increasing their contributions after rounds of punishment even though players changed groups each round. Subsequent research confirmed the finding that punishment led to increased contributions, especially when punishment was relatively cheap (Egas & Riedl 2008, Nikiforakis & Normann 2008) and when interactions were repeated (Gürerk et al. 2006, Walker & Halloran 2004). Although variability exists, results are similar when investigated in non-Western cultures (Hermann et al. 2008; reviewed by Chaudhuri 2011).

The results of such experiments have been interpreted as supporting a link between punishment and the evolution of cooperation in groups, but debate continues regarding these findings. First, in these studies, people can punish with impunity; that is, subjects cannot take revenge on the person who punished them, a feature that deviates from many real-world situations. When subjects who are punished are permitted to punish the punishers, there is both less punishment and, consequently, less contribution to the public good than when people can punish with impunity. When counter-punishments are possible, cooperation is no longer stable (Nikiforakis 2008; see also Nikiforakis & Engelmann 2011).

Furthermore, although the availability of a punishment option increases players' contribution decisions, aggregate welfare—overall payoffs—is typically reduced: The cost of punishment to the punisher and the punished outweigh the gains from increased rates of contribution (Ambrus & Greiner 2012, Dreber et al. 2008), although this is not always the case (Nikiforakis & Normann 2008), especially if the game is played for a large number of rounds (Gächter et al. 2008; but

see Ambrus & Greiner 2012). Relatedly, nontrivial amounts of punishment are "perverse," directed not at low contributors but rather at high contributors (Cinyabuguma et al. 2006). Intriguingly, some recent work suggests that simply sending messages about how much players should contribute can, perhaps briefly, increase cooperation rates without the imposition of actual costs (Andrighetto et al. 2013).

An additional complexity arises in interpreting PGG results because low contributors have simultaneously (*a*) behaved in a way that harms—or, at least, does not help—fellow group members and (*b*) violated an implicit norm to contribute as much as others. Punishment, then, might be driven, proximately, by (*a*) a revenge motive—to hurt those who have hurt the self (Kurzban & DeScioli 2013, McCullough et al. 2013), (*b*) a desire to punish norm violators (Boyd & Richerson 1992), or (*c*) an instrumental desire to increase noncontributors' contributions in subsequent rounds (Fehr & Gächter 2002).

Additional work is needed to distinguish among these possibilities, but some evidence already exists. For instance, people punish in one-shot games and in final rounds (Anderson & Putterman 2006, Fehr & Gächter 2002, Page et al. 2005), undermining the instrumental interpretation. In addition, in a one-shot PGG, Carpenter & Matthews (2012) investigated people's punishment behavior when they could impose costs on members of groups to which they did not belong, taking away the revenge motive (and instrumental motives), comparing punishment in such cases to a treatment in which people could punish members of their own group. In the key condition, few (10% of subjects) punished outside the group, and those that did punished relatively little. Still, punishment was nonzero, leaving the matter open.

Moralistic Psychology

Although debate continues surrounding the interpretation of PGGs with and without punishment, there seems to be relatively strong agreement that, cross-culturally, humans are moralistic, evaluating others' actions on the right/wrong dimension, usually accompanied by a desire that wrongdoers be punished (Brown 1991). This feature of human psychology is important because of the possibility described above that punishment psychology was selected because it reduced antisocial behavior.

However, certain features of moral psychology are puzzling from this point of view. Perhaps the oddest aspect of moral psychology is the very wide breadth of categories of behavior that are moralized across cultures, including actions that do no harm or, even more puzzlingly, produce benefits (DeScioli & Kurzban 2009a). Lending money, for instance, is a mutually beneficial transaction, yet historically was proscribed and punished.

More generally, a pervasive property of human moral judgment is nonconsequentialism, that whether acts are right or wrong does not depend only on their (intended) consequences. Human moral judgments are frequently nonconsequentialist (Hauser 2006), perhaps most famously in the context of "trolley problems," in which people judge pushing one person off a footbridge in front of a runaway trolley in order to save five to be morally wrong, despite the saving of four (net) lives (Hauser et al. 2008). As reviewed above, the experimental literature suggests that punishment often reduces rather than increases group welfare. In short, if moralistic psychology is designed to prevent harmful acts, then the fact that it prevents mutually beneficial acts, or harmless acts, is an unusual empirical pattern (DeScioli & Kurzban 2009a).

A possible explanation for this is that moral psychology has a role in choosing sides during conflicts, termed the bandwagoning model (DeScioli & Kurzban 2013). Humans engage in multi-individual coordinated conflict, and although people do build relatively stable alliances, human coalitions can shift as contexts change (Kurzban et al. 2001, Pietraszewski et al. 2014), producing a

complex strategic problem. A potential solution is to join the side of the conflict that more people are joining (DeScioli & Kurzban 2013), even if friends are on the other side (Kurzban et al. 2012). If all third parties use such a strategy, then each party's costs are minimized because conflicts with large power asymmetries are relatively cheaply resolved (Davies et al. 2012). Morality—the assignment of certain sets of actions as wrong and deserving of punishment—provides a mechanism to do this, allowing all third parties to take the same side in emerging conflicts.

The bandwagoning model sees moral rules as coordination devices and so can explain why moral rules can take very different forms and change over time (DeScioli & Kurzban 2009a). Therefore, epidemiological considerations might be important for understanding how moral contents emerge, spread, and diminish (cf. Sperber 1996). This returns us to the work of Boyd & Richerson (1992). If certain moral regimes lead to better group-wide outcomes, then these regimes might spread at the expense of less group-wide beneficial regimes in a process of cultural group selection or through some other epidemiological process (Richerson & Boyd 2008). An important direction for future work is to continue to try to understand the epidemiological issues associated with moral contents.

Cultural evolution: changes in groups of people's norms, beliefs, practices, etc., over time

SUMMARY AND FUTURE DIRECTIONS

In this concluding section, we briefly sketch some of the avenues that we believe will be productive for future research. We touch on innovations in theory and methods and the benefits of cross-disciplinary integration, and we discuss some specific areas in which exciting work is beginning to be done (especially in development and neuroscience) and some areas of research that surprisingly have been neglected.

Theoretical Advances

It is an exciting time for theoretical work on the evolution of cooperation. Previously, a great deal of theoretical development focused on simple games such as the famous prisoner's dilemma. This narrow emphasis, although useful, limited the applicability of the models derived from these games. Similarly, the historical reliance on computer simulations made it difficult to move from model to mechanism. A new set of techniques referred to as neighbor modulated fitness methods are both broadly applicable and relatively straightforwardly linked to actual biological systems (Rouset 2004, Taylor & Frank 1996). Another perennial difficulty is modeling multiple traits at once; so-called multilocus methods have been developed to solve this problem and are particularly useful for investigating how traits such as cooperation and punishment interact as they evolve together (Gardner et al. 2007, Lehman et al. 2007).

In addition, many old debates have been resolved, freeing up time and resources to address new and often more interesting questions. For example, we now know that the different theoretical frameworks, such as kin or multilevel selection, are just different ways of dividing up the dynamics of natural selection and are not competing hypotheses. These frameworks all give the same results, predicting that individuals should appear as if they were designed to maximize their inclusive fitness (West & Gardner 2013). This allows us to focus on a new set of problems. For example, unlike in the genetic evolution framework, many fundamental questions remain with respect to cultural evolution (Boyd et al. 2011, El Mouden et al. 2014). Debates continue about cultural evolution in part because predictions made from the framework are not necessarily as straightforward as are predictions from the framework of genetic selection. Still, issues arising from genetic selection remain, such as how competitive altruism models differ from indirect reciprocity models in the service of generating empirical predictions.

New Methods

In the same way that theory has advanced, empirical work on cooperation has benefitted tremendously from methodological innovations that have enabled researchers to ask questions and find answers that were previously out of reach. Although many such innovations are now at researchers' disposal, here we focus on those in just three areas: neuroscience, physiology, and genetics.

The emerging and growing field of neuroeconomics (Glimcher & Rustichini 2004) has begun to illuminate, through neuroimaging techniques such as electroencephalography, positron emission tomography, and functional magnetic resonance imaging, the neurophysiological structures involved in decision making (Declerck et al. 2013). For instance, there is evidence that acquiring a good reputation (Izuma et al. 2010), successfully cooperating (Fehr & Camerer 2007), or punishing (Seymour et al. 2007) activates the regions of the brain that have been well documented to be active when experiencing reward. This last element holds particular promise for distinguishing among different mechanisms for prosocial behavior. To the extent that imaging shows that prosocial behavior in a particular context is rewarding, as indexed by activation in these regions, one can argue that the proximate mechanism bears a stronger resemblance to a taste for prosociality as opposed to a more strategic explanation. Additional work might well help to illuminate these issues further.

Similarly, the past decade has seen advances in the role that hormones play in various aspects of social behavior. Early work in this area investigated how trusting another subject—or being trusted by another subject—affected hormone levels, especially oxytocin. This work on how hormone levels are affected by interactions in the laboratory has now been supplemented by exciting work investigating how hormones affect behavior (de Dreu 2012). Recent results have suggested that hormone administration—oxytocin and testosterone—affects decision making in prisoner's dilemma games (Rilling et al. 2012), trust games (Baumgartner et al. 2008), bargaining games (Eisenegger et al. 2011), and public goods games (van Honk et al. 2012). A challenge for future work is to determine how these hormones interact with experience (Veenema 2012) and how these results can be profitably linked to the ultimate explanations for cooperation.

In addition to the research described above, investigators are now identifying genetic variants associated with altruism (Thompson et al. 2013). However, linking genotype and phenotype remains exceptionally challenging, especially as we expect most adaptations to be constructed by the interaction of many (>100) genes, most of which will have only a small effect. Still, work in genetics has the potential to explain some of the variation in measures of altruism (Anacker et al. 2013).

Innovative Experimental Treatments

The use of innovative control treatments and null models has helped overturn conventional wisdom, forced a reevaluation of the answers to old questions, and opened up new questions. For example, as discussed above, in PGGs, in which not cooperating at all maximizes each individual's financial gain, numerous researchers have observed that individuals do indeed voluntarily contribute. This result has been taken to imply that humans have prosocial preferences, and based on that inference, a huge literature has emerged.

However, in most studies, any contributions to the group that are made for whatever reason—including, for instance, confusion regarding the incentives—have prosocial consequences and therefore have been counted as prosocial. Consequently, in the absence of some other methodological fix (cf. Laury & Holt 2008), it is important to add appropriate control treatments. When such treatments are carried out, individuals cooperate at lower levels than would maximize their own personal financial gain (Kümmerli et al. 2010). Specifically, even in scenarios in which 100% cooperation would maximize income, average cooperation is considerably less than 100%. Such

results imply that contribution behavior in PGGs derives not only from prosocial preferences but also from uncertainty, bet hedging, boredom, or cognitive errors.

Such results raise the question of what is the appropriate null model to use when evaluating the results of economic experiments. Burton-Chellew & West (2013) investigated a behavioral null model by having individuals play a PGG in which participants were told that they were contributing to a metaphorical black box computer program that determined their payoffs in an unknown but systematic way. The surprising result was that individuals playing in this asocial black box treatment cooperated at levels that were not significantly different from those of individuals who knew they were in a PGG. This result implies that knowledge of the benefit to others had negligible effects on game play.

Attention to the relationship between the tools one is using and the inferences being drawn opens up a slew of new questions. What factors beyond prosocial preferences might cause people to play experimental games in ways that deviate from standard economic predictions? More specifically, how might, for instance, reputational concerns (Barmettler et al. 2012), demand characteristics and affective forecasting (Pedersen et al. 2013), as well as confusion and uncertainty (Burton-Chellew & West 2013, Kümmerli et al. 2010) account for variation both within and between experimental treatments? The present context of critical self-assessment in experimental psychology (Pashler & Wagenmakers 2012) provides an excellent framework to revisit common paradigms and assess what they can and cannot teach us about prosocial preferences.

Cross-Field Cross-Fertilization

Recent years have seen exciting cross-fertilization of ideas from one field to another. The combination of neuroscience and economics, discussed above, is one example. Another especially fruitful cross-pollination of disciplines has been the importation of methods used by behavioral economists into anthropological field sites with populations of small-scale societies, including pastoralists and hunter-gatherers (Apicella et al. 2014, Henrich et al. 2010a, Thomae et al. 2013). In a pioneering study, Henrich et al. (2001) had people across the globe play a number of standard games for which a vast amount of comparison data had already been gathered, predominantly in the industrialized West. These games and subsequent related work included methods used to investigate various aspects of cooperation and prosocial behavior, such as the ultimatum game, dictator game, third-party punishment game, and public goods game.

This work has opened up new research possibilities by bringing the virtues of laboratory experiments to settings in which these techniques historically have been lacking. These methods have revealed large variation across cultures in measurements of the disposition to trust, cooperate, and punish others for noncooperation. At present, one proposal is that a key factor is the extent to which a group engages with institutions on a large scale, such as markets; groups that are more integrated show more prosociality (Henrich et al. 2010a) and/or more market-adapted behavior in general (Apicella et al. 2014).

More generally, this growing database of results allows researchers using similar methods to measure prosocial behavior using the same techniques, which facilitates rich comparisons between groups. Perhaps most significantly, bringing these techniques into these field sites has allowed a look at the extent to which results in the West can be understood to generalize to other populations (Henrich et al. 2010b). In addition, this body of work offers considerable potential for discriminating among alternative explanations. For example, there is an ongoing debate about the extent to which culturally inherited norms on the one hand or differences in ecological conditions on the other might best explain variation in play and variation in real-world behavior (Lamba & Mace 2011).

A related area of substantial potential is research moving out of the lab and into the field in industrialized settings (e.g., Dean & List 2007). Although such work inevitably sacrifices some internal validity to gain external validity, recent years have produced a number of interesting findings. For example, Bateson et al. (2006) showed that an image of human eyes above an "honesty box" could more than double people's contributions to offset the costs of a university coffee room. Similarly, Ernest-Jones et al. (2011) found that human eye images could reduce rates of littering in a university canteen. Collaboration among human behavioral ecologists, psychologists, and economists offers substantial promise for understanding what factors influence cooperative behavior in the real world.

Current Debates and Promising Directions

In this final subsection, we highlight a small number of areas that we believe would benefit from increased research attention, either because an area is important but understudied or because it is at present a source of intense scholarly debate.

Development. A perennial debate in discussions of cooperation surrounds the question of the extent to which people acquire the disposition to engage in prosocial behavior as a result of social learning, and the extent to which these dispositions develop independently of such learning processes. As a proximate matter, that is, do prosocial dispositions require modeling or some other sort of input from the social world to structure the details of how they unfold?

This question has focused attention on measuring prosociality in young children, who—given their minimal experience with and exposure to social norms—can help to illuminate the degree to which social learning processes play a key role in the development of prosocial behavior and preferences. In turn, research with children has been aided through methodological innovation and creative techniques that have coaxed interesting results from a group that historically has been challenging to study.

The result of this recent work is a body of growing evidence that suggests that intricate and potentially important aspects of strategic social behavior develop precociously. For instance, research with children as young as four years old indicates that in dictator-like games using stickers as the endowment, even young children choose to give at least some of their stickers to another child (Benenson et al. 2007). In work with very young children, Sloane and colleagues (2012), using a looking-time paradigm, were able to show that even 19-month-olds expect that when an adult is dividing up toys among others, they will do so fairly; these young subjects look longer (i.e., showed surprise) at unequal allocations. Perhaps even more strikingly, these authors also found that infants younger than two years old have intuitions about how benefits are allocated depending on effort (see also, e.g., Schmidt & Tomasello 2012). In related work, Shaw et al. (2014) pursued the question of whether children are fair for its own sake or are fair simply in the service of cultivating a reputation for being fair. In a series of clever studies, they showed that, not unlike adults, six- to eight-year-old children seem to be more interested in the appearance of fairness than in its substance.

Methodological innovations and creative techniques are now available to begin to track the development of various aspects of prosocial motives and behavior from even young ages. This work might be very helpful in distinguishing among candidate models, in particular insofar as cultural transmission assigns a large role for social learning in the acquisition of prosocial norms. To the extent that such norms emerge in the absence of—or at least with only minimal input from—social experience, the scope for such models is potentially reduced.

Parents and Offspring. As indicated above, kinship in general has been somewhat neglected in psychology, and when it has been investigated, the emphasis has been, reasonably enough, on cooperation. However, theory (Trivers 1974) predicts that there will be cases in which interest among even close kin will diverge, leading to conflict between siblings or between parents and offspring. There is a tremendous amount of evidence of adaptations designed around such conflicts in nonhumans (Mock 2004), yet, with the exception of parents' preferences regarding their offspring's mates (Perilloux et al. 2011) and how conflict may have driven the evolution of female menopause or differential grandparental investment (Lahdenperä et al. 2012), this idea has received very little attention. Along those lines, intergenerational transfers also represent an emerging and potentially promising line of inquiry (Coall et al. 2014).

Punishment. As indicated above, debates continue regarding the role of punishment in the evolution of and maintenance of cooperation (Boyd & Richerson 1992). First, the theoretical issues are far from settled, and debates continue regarding punishment's role in stabilizing cooperation (e.g., Rand et al. 2010). In a similar vein, there is still a lack of consensus regarding the use of terms in this area. Although the expression "altruistic punishment" has propagated since its first use (Fehr & Gächter 2002), whether the punishment so labeled is properly considered "altruistic" remains the subject of debate (Kurzban & DeScioli 2013, West et al. 2007b).

Similarly, debates continue surrounding the empirical work in this literature. Why is there "perverse" punishment, harming those who have cooperated? If punishment evolved for stabilizing cooperation, then why does punishment often lead to worse, rather than better, outcomes in aggregate (Dreber et al. 2008)? If people have a "taste" for punishment, then why does punishment decrease under conditions of anonymity (Kurzban et al. 2007)? How much of punishment observed in the lab is due to demand characteristics (Pedersen et al. 2013)? How much punishment is better understood as revenge as opposed to moralistic enforcement (McCullough et al. 2013)? Answering these empirical questions will be important for clarifying the theoretical issues that are still very much at stake.

CONCLUSIONS

In *The Descent of Man*, Darwin (1871) anticipated that explaining human prosociality would turn out to be a formidable task, writing that "the circumstances, leading to an increase in the number of those thus endowed [with moral virtues] within the same tribe, are too complex to be clearly followed out" (p. 156). Indeed, the forms of human prosocial behavior are diverse, ranging from the parent/child dyad to the multiparty cooperation among nonkin at very large scales. Reflecting this diversity, the past quarter of a century has seen an efflorescence of research in the search for explanations for the panoply of human social behaviors. This article has reviewed some of this research, but much has been omitted owing to space limitations. Still, we have tried to convey the flavor of where major branches of research have been going.

One set of advances is the distance theorists have come in expanding ideas beyond kin selection and reciprocity. In some ways, these moves were anticipated by Darwin, who suggested that "... another and much more powerful stimulus to the development of the social virtues, is afforded by the praise and blame of our fellow-men" (Darwin 1871, p. 156). Work on ostracism, assortment, indirect reciprocity, and punishment has yielded important theoretical and empirical gains and appears to be identifying promising avenues for additional development. There has been increasing attention to the effects of these forces in stabilizing cooperation, and early models (e.g., Boyd & Richerson 1992) have been supplemented with substantial new ideas and data.

Work on cooperation has also been applied to important real-world issues. For example, Milinski et al. (2008) used economic games to address how people respond to the threat of climate change, showing that individuals could cooperate to avoid simulated dangerous climate change provided the risks were sufficiently certain and sufficiently high. The coming years will likely witness additional real-world-themed research.

None of which is to say that there is not more work to be done. As we have emphasized, debate continues regarding the most basic forms of prosociality, including friendship, morality, and, of course, nonkin group cooperation. The fact that work on these issues has been going on for so long and yet disagreement remains points to the complexities of the issues at stake.

Having said that, the important new tools that have been brought to bear on these issues hold tremendous promise. The tools used by behavioral economists were barely known to evolution-minded researchers 30 years ago, but now they are omnipresent. Related new techniques in developmental psychology, neuroscience, and other fields are buttressing the research efforts directed at these questions. Although recent years have witnessed tremendous advances in our understanding of why—both proximately and ultimately—humans behave prosocially, much fundamental work remains to be done.

SUMMARY POINTS

1. Evolution explains why biological organisms have traits that cause them to aid close relatives. Humans are no exception.

2. One way in which adaptations for cooperation can evolve is through the mutual exchange of benefits at a cost over time. Humans engage in many such (reciprocal) transactions.

3. Recent models of the evolution of cooperation suggest that individuals can benefit from cultivating a reputation for being generous, which in turn elicits aid from others.

4. Signaling that one is generous can lead to benefits for the person signaling, such as being chosen as an exchange partner, friend, or mate.

5. A crucial issue in the evolution of cooperation is the role of punishment. In populations in which certain behaviors are punished, people are better off if they resist engaging in these behaviors, even if doing so is in their short-term interests.

6. Across cultures, people punish others who have violated moral norms, even when the violation leads to people being better off rather than worse off. Debates continue on the explanation for this human moralistic psychology.

7. Advances in theory and methods have continued to elucidate the ultimate and proximate explanations of prosocial behavior. Much work remains to be done, aided by increasing cross-disciplinary efforts.

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