CHAPTER TWENTY-THREE

HUMAN COOPERATION

EVOLUTIONARY APPROACHES TO A COMPLEX PHENOMENON

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Humans work together to achieve common goals on larger scales and in a wider variety of ways than do members of any other species. In a word, they cooperate. They do so despite many obstacles to cooperation, which come in two main varieties: (1) collective action dilemmas, which arise from conflicts of interest among would-be cooperators, and (2) coordination problems, which arise from a lack of common knowledge about how cooperation can be achieved. Evolutionary scientists have identified a variety of factors that help people solve these problems. These include kinship, a high likelihood of repeated interactions, an ability to distinguish cooperators from noncooperators and preferentially associate with the former, concerns about audiences and resulting reputations, an ability to send and receive signals regarding individuals' levels of commitment to cooperative enterprises, and the importance of dealing with an uncertain future through risk-pooling arrangements. Although we understand a great deal more about the evolution of human cooperation now than we did a half century ago, when this approach was first developing, much work remains to be done. Some current frontiers in the evolutionary analysis of human cooperation include the study of coordination problems, cultural group selection, coalitional psychology, and a greater appreciation of the institutional and organizational contexts in which most human cooperation occurs.

INTRODUCTION

Humans cooperate with one another on larger scales and in a wider variety of ways than do members of any other species. This fact is all the more remarkable given that they do so despite the many obstacles to cooperation that exist. Such obstacles come in two broad varieties: conflicts of interest and a lack of common knowledge. Conflicts of interest lead to situations in which a public good is either not provided at all or not provided at a desired level (Olson 1965), and to situations in which a common pool resource is not managed in a way that will sustain it for future use (Hardin 1968). In both cases, the reason is what is known as the "free-rider problem": everyone would like to see the public good provided or the common pool resource maintained, but because everyone has limited resources to put into such efforts, everyone also would prefer to contribute as little as possible to these outcomes. This is also known as a collective action dilemma or a social dilemma. These situations are a result of the fact that both public goods and common pool resources have

what is known as "low excludability": it is hard to prevent people from enjoying them, even if they have not contributed to their production or maintenance. In this way, they contrast with private goods, which have high excludability: although theft of private goods certainly does occur, it is relatively easy to prevent people from consuming them without first paying for them. Common pool resources are more problematic than public goods because they also suffer from "high subtractability," that is, one person's consumption of them diminishes the ability of others to also consume them (Ostrom, Gardner, and Walker 1994).

Lack of common knowledge is a problem in situations in which there may be no conflicts of interest—everyone would benefit if cooperation were to take place—but those who would like to cooperate do not all know how to do so. These situations are known as coordination problems or coordination games (Schelling 1960). They are solved through the creation of not only common knowledge about how to cooperate but also common metaknowledge, that is, common knowledge that there is common knowledge (Chwe 2001). For example, if the goal is the safe evacuation of a crowded theater, it helps if everyone knows that this outcome can best be achieved by walking to the nearest exit in a calm and orderly manner. However, even if everyone does know this, such common knowledge will not help achieve the desired outcome if everyone does not also know that his or her fellow theatergoers are also aware of it. Without that common knowledge, everyone may assume that he or she is the only one in the theater who knows the proper procedure, which will lead theatergoers to behave as if they do not know the proper procedure even though they do. The end result may be a rush to the exits that leads to lower numbers of survivors overall (Ullmann-Margalit 1977).

When traditional social scientists have turned their attention to the phenomenon of human cooperation, they have been most concerned with these kinds of obstacles and how they seem to be overcome so infrequently. This attitude was captured succinctly by economist Mancur Olson, who declared that "unless the number of individuals in a group is quite small, or unless there is coercion or some other special device to make individuals act in their common interest, *rational, self-interested individuals will not act to achieve their common or group interests*" (1965: 2; emphasis in original). When evolutionary scientists look at human cooperation, in contrast, they are struck not so much by the difficulties that beset would-be cooperators but rather by the fact that humans cooperate more often, on larger scales, and in a wider variety of ways than do most nonhumans, including our closest primate relatives. Of course, both of these perspectives are perfectly valid—two sides of the same coin, if you will. At the same time that humans cooperate less frequently than would be beneficial in theory, they do cooperate at rates rarely seen among nonhumans. This chapter summarizes some of the major insights that evolutionary scientists have provided to the study of human cooperation and points toward some possible directions for future research on this topic.

DEFINING COOPERATION

Evolutionary scientists often define cooperation in a way that makes it synonymous with altruism. For example, Nowak (2006: 90) defines cooperation as a situation in which "a donor pays a cost and the recipient gets a benefit." Similar definitions have been used by many others (e.g., Henrich and Henrich 2007; Bowles and Gintis 2003; Lehmann et al. 2008). Thus, when evolutionary scientists claim to be explaining something about cooperation, often they are really explaining something about altruism.

Because altruism is already a perfectly good term to use for situations in which one individual does something that is costly to himself or herself in order to provide a benefit to someone else, I instead define cooperation as simply "working together." This much broader definition of the term includes not only situations that may involve altruism but also those that do not, such as coordination problems. This has the additional advantage of being more in keeping with the way the term has traditionally been used in the non-evolutionary social sciences, thus facilitating communication across disciplines (Cronk and Leech 2013).

WHAT EVOLUTIONARY SCIENTISTS KNOW ABOUT HUMAN COOPERATION

The last half century has seen tremendous progress in the evolutionary understanding of cooperation. Here I provide a brief summary of this approach's main findings regarding what things matter most when we try to explain the phenomenon of human cooperation from an evolutionary perspective. Although each of these is significant in isolation, explaining any particular real-world case of human cooperation may require an understanding of more than one of them.

KINSHIP

Ever since William D. Hamilton's (1964) development of inclusive fitness theory in the early 1960s, kinship has been the starting point for evolutionary analyses of altruistic behavior. This approach is often referred to as kin selection. The idea is simple: because an organism shares some of its genes with its kin, it can ensure the survival of its genes in future generations not only by reproducing directly but also by doing so indirectly, that is, by helping its kin to reproduce. Hamilton theorized that selection may favor a propensity to help kin even if doing so is costly to the donor (i.e., altruistic) if the cost to the donor in terms of reduced future reproduction is less than the benefit to the recipient in terms of enhanced future reproduction, provided that we also remember to discount the benefit to the recipient by the degree of relatedness between the donor and the recipient. This is now known as Hamilton's Rule.

Applications of Hamilton's Rule have shed light on kin-directed helping behaviors in nonhuman species (e.g., Sherman 1977; Reyer 1980) as well as among humans, particularly in small-scale societies (e.g., Hawkes, O'Connell, and Blurton Jones 1989; Nolin 2010) and within families (e.g., Case, Lin, and McLanahan 2000). However, because relatedness diminishes geometrically with each generational or lateral move away from a focal individual, Hamilton's Rule may be of limited use in explaining altruism or cooperation in large-scale societies or among non-kin. Nevertheless, the underlying psychology of kin favoritism that has been favored by kin selection has the potential to be co-opted by people and institutions trying to foster such behaviors. Thus, the use of such kinship-valenced terms as "brother," "sister," "fatherland," and "motherland" are common in political rhetoric and have been shown to increase the persuasiveness of such rhetoric (Salmon 1988). Similarly, religious organizations that require celibacy often use kin terms (e.g., the Roman Catholic use of such terms as "mother," "father," "sister," and "brother"), and organizations that train suicide bombers use kin terms to manipulate and motivate their recruits (Qirko 2004, 2009). In this same spirit, Maasai pastoralists in East Africa establish dyadic helping and risk-pooling relationships that are referred to by their word for umbilical cord (*osotua*), thus evoking the bond between a woman and her fetus (Cronk 2007; Cronk and Wasielewski 2008; Aktipis, Cronk, and de Aguiar 2011).

REPEATED INTERACTIONS

If two organisms are unrelated to each other, if cooperation is costly in some way, and if interactions among them are unlikely to be repeated in the future, then selection will not favor them engaging in cooperation with one another. However, if those same two organisms are likely to interact in the future, then selection can indeed lead them to engage in costly, cooperative acts. This, in a nutshell, is the main insight to have emerged from the study of reciprocity (Hume 1740; Trivers 1971; Axelrod and Hamilton 1981; Axelrod 1984; Aumann 1981). The importance of repeated interactions was clearly demonstrated by Robert Axelrod's (1984) famous computer tournament involving the Prisoner's Dilemma game. In the Prisoner's Dilemma, two players are given a choice between two options, usually labeled "cooperate" and "defect." If both cooperate, they both get a moderately high payoff. However, if one defects and the other cooperates, the cooperator gets a very low payoff and the defector a very high one. This creates a temptation to defect rather than cooperate. If they both choose to defect, they both get moderately low payoffs. If the game is played for only one round, the best strategy is to defect in order to avoid the very low payoff associated with cooperating when one's partner defects. However, Axelrod's tournament demonstrated that if the game is iterated, then it makes sense for both players to cooperate because doing so allows them to accumulate moderate payoffs round after round. This core finding has since been corroborated, refined, and elaborated upon in dozens of subsequent studies (e.g., Nowak 2006; Aktipis 2004, 2011).

Switching from a one-shot game to an iterated game makes it more like real life. Although interactions with kin may not be as frequent in modern societies as they were among our ancestors, we do interact repeatedly, day after day, with the same unrelated individuals. In short, life is an iterated game. This high likelihood of future interaction has a profound effect on the kinds of cooperative dilemmas we face. Although the Prisoner's Dilemma and many other situations involve conflicts of interest and are therefore collective action dilemmas, if they occur repeatedly then in effect they become coordination problems: it is in everyone's best interests to find a way to cooperate. Consider, for example, subsistence and food-sharing practices in the community of Lamalera on the Indonesian island of Lembata. Lamalerans make a living from the sea, mainly by hunting whales and other large marine animals, which is done cooperatively, and by fishing, which can be done individually. Cooperative hunting is more productive, but before it can occur, the participants in the hunt must overcome a collective action dilemma: Who will receive which parts of the kill? One possible outcome is that this dilemma will never be overcome, in which case Lamalerans would simply fish for their dinners. However, because the situation has occurred for years and will continue to occur in the future, they have instead come up with clear-cut rules that govern what each participant in the hunt will receive if it is successful. Thus, the iterated nature of the situation has turned it from a collective action dilemma into a coordination problem, and the Lamalerans have responded by coming up with a coordination convention that works to foster cooperation (Alvard 2003; Alvard and Nolin 2002).

ASSORTMENT

If individuals vary in terms of their willingness or ability to cooperate with others, it helps if cooperative people can find each other and avoid time-consuming and otherwise costly interactions with uncooperative people. In the evolutionary literature on cooperation, this is known as positive assortment. The value of positive assortment of cooperators was dramatically shown by a Prisoner's Dilemma simulation that differed in one important

way from previous simulations using that game: the agents were able to move around in virtual space. The strategy that worked best in this simulation was labeled "Walk Away," which summarizes its advantage over other strategies: if you are dissatisfied with the way your current partner is behaving, walk away and try someone else (Aktipis 2004, 2011). In this way, cooperators can find each other, noncooperators suffer from a lack of partners, and cooperation can thrive.

Assortment's importance has led to a great deal of research on cooperative partner choice in the real world. Some of the earliest research on this topic employed an instrument called the Wason Selection Task (Wason 1966), in which subjects are presented with a logical problem of the "if p then q" variety. Research in the 1960s and 1970s established that most people are quite bad at solving such abstract logical problems, but it was also known that people can perform quite well on such tasks when they are presented in more concrete terms. In the 1980s, evolutionary psychologists Leda Cosmides and John Tooby suggested that such improvements in performance on the task reflect evolved cognitive mechanisms that people use when identifying (and presumably then avoiding) people who cheat in social contract situations (Cosmides and Tooby 2005). In such situations, "cheating" is defined as obtaining some benefit without paying the required cost. For example, if there is a norm that if you borrow my car you must fill the gas tank before returning it to me, but you fail to do so, you are a cheater. The key finding is that although people are generally bad at solving the Wason Selection Task when it is presented to them in the abstract "if p then q" form, they suddenly become quite good at solving it when it is presented to them as a tool for identifying cheaters (e.g., people who borrow cars and return them without filling their tanks). The implication is that selection among our ancestors favored the evolution of this kind of social intelligence because it enabled them to engage in positive assortment. More recent studies have demonstrated additional ways in which we identify cooperators, even at very early ages. For example, a study of six- and ten-month-old infants showed that they preferred to play with toys that had been depicted as behaving in helpful ways to other toys over toys that had been depicted as hindering other toys' efforts to achieve their goals (Hamlin, Wynn, and Bloom 2007).

Audiences and Reputations

One way to avoid noncooperators is to pay attention to how they treat others and to their reputations. This bit of everyday wisdom has been systematized in evolutionary theory under the label "indirect reciprocity" (Alexander 1977, 1987). While true reciprocity involves just two parties who exchange favors, indirect reciprocity is all about the audience: Anne does something nice to Ben because Charlie, who may someday be in a position to help Anne, is watching. Given that we have language, Anne may also be concerned about what Charlie might say to others (Darla, for example) about the way she chose to treat Ben.

This basic insight into human interactions has led to a great deal of research on such issues as the impacts of audiences and reputations on cooperative behavior. For example, a series of studies has shown that simply exposing people to images of eyes—even quite stylized ones—can lead them to behave more cooperatively and generously than when such images are not present (e.g., Haley and Fessler 2005; Bateson, Nettle, and Roberts 2006; Burnham and Hare 2007; Rigdon et al. 2009). Other studies, however, have failed to find such an association (e.g., Fehr and Schneider 2010; Lamba and Mace 2010). This discrepancy was recently explained by a study that made a distinction between brief and lengthy exposure to the images of eyes: brief exposure works to increase cooperativeness, long exposure does not. While brief exposure to such images seems to make people concerned at a nonconscious level about the possible presence of an audience,

long exposure provides people with an opportunity to consciously realize that there really is no audience, leading some to then behave in more calculated and selfish ways (Sparks and Barclay 2013).

One implication of indirect reciprocity is that cooperative behavior itself can serve as a signal, which means that signaling theory can play a role in explaining the forms that it takes. If observers are skeptical about an individual's cooperativeness, then the individual needs to come up with a way to overcome that skepticism. One way to do this is with a signal that only a truly cooperative individual could produce. Such signals are known as "costly" or "hard-to-fake" signals. One well-documented example of a costly signal of cooperativeness comes from the island of Mer, a part of Australia located in the Torres Strait. A favorite food on Mer is the meat of the green sea turtle, *Chelonia mydas*. There are two ways to catch turtles, one easy and one quite difficult. The easy way is simply to collect them off the beaches when they are nesting. The difficult way is to catch them at sea, which requires a great deal of both skill and strength. Interestingly, while turtle meat that is collected the easy way is typically eaten within households and shared privately, turtle meat obtained the hard way is shared in public ceremonies involving, on average, more than a third of the island's population. Thus, hunting turtles the hard way is an excellent way to burnish one's reputation not only as a skillful hunter but also as a generous person, and the attention turtle hunters receive helps them obtain more mates and children than nonhunters (Bliege Bird, Smith, and Bird 2001).

COMMITMENT

Signaling theory can also help explain how people overcome one of the most basic and pervasive problems facing would-be cooperators: how can they tell that their fellow cooperators are truly committed to the task at hand (Nesse 2001)? Organizations often overcome this problem by requiring people who want to join them to pay some sort of cost that demonstrates their commitment. Recent research has shown that religious groups are particularly successful at obtaining signs of commitment from their members that then lead to higher levels of cooperation among group members (Irons 2001; Sosis and Alcorta 2003). An interesting demonstration of this comes from an analysis of historical data on communes in nineteenth-century America. Such communes were quite numerous, and while some of them were based on secular ideologies, others were very religious. All of them demanded that their members pay various sorts of costs, ranging from minor things like not drinking coffee or alcohol to more serious things like giving up control over one's own sex life. On average, the religious communes lasted longer than the secular ones. Furthermore, while religious communes lasted longer when their leaders added additional costly requirements for membership, the same effect was not found among secular communes, suggesting that there is something special, though still not well understood, about religious signals of commitment (Sosis and Bressler 2003). Subsequent studies of specific religious communities have corroborated and elaborated upon this finding. For example, levels of cooperation in an experimental game were higher among men belonging to religious kibbutzim in Israel than among men belonging to secular kibbutzim (Sosis and Ruffle 2003). Similarly, but in a very different cultural setting, levels of cooperation in an experimental game played by members of an Afro-Brazilian religion called Candomblé correlated with cooperative behaviors outside the game (Soler 2012). Some critics have argued that findings like these may also be explained by a fear of supernatural punishment for failing to cooperate rather than the hypothesized relationship between signals of commitment and cooperation. Because Candomblé is a religion that does not include a doctrine of supernatural punishment, that study clearly

demonstrates the merit of signaling theory in explaining the ability of religious rituals to serve as signs of commitment.

UNCERTAINTY, RISK, AND NEED

Uncertainty about the future is one of the most common and enduring features of the environments in which humans live. Will we be able to find food? Will we have enough water to drink? Will there be a drought, flood, or other calamity? Will our property be stolen by others? Humans have found a variety of ways of dealing with the risk created by such uncertainty (Dorfman 2007). Risk retention consists of accepting risk and absorbing any resulting losses. Examples include storing resources in anticipation of future shortages and self-insurance by institutions. Risk avoidance involves reducing one's dependence on high variability outcomes. For example, focusing one's foraging efforts on reliable plant foods and small game rather than on unpredictable returns from big-game hunting is a way of avoiding risk. Risk reduction includes efforts to lower the probability of loss or to reduce the size of losses, such as by buying bonds as well as stocks. Finally, risk transfer is the exchange of risk from one individual or group to another. Risk transfer does nothing to reduce the overall amount of risk, but it allows people to exchange the possibility of a catastrophic loss for the certainty of small, manageable losses. In our society, buying an insurance policy is a common way to transfer risk, but humans have been transferring risk for much longer than insurance companies have been around, primarily by risk-pooling, also known as risk sharing (e.g., Barr and Genicot 2008; Fafchamps and Lund 2003). Because risk transfer, including risk-pooling, is the only one of these four strategies to necessarily involve cooperation, understanding it is an essential part of the evolutionary analysis of human cooperation.

Although many evolutionary scientists have considered risk-pooling to simply be a type of reciprocity (e.g., Gurven 2004), it differs considerably from the sort of back-and-forth, account-keeping, tit-for-tat arrangements for which the theory of reciprocity was originally designed. In reciprocity, relationships are maintained by extensions of credit that create debt that is then repaid. If debts are not repaid, such relationships end. The relationship is thus similar to that between a banker and a lender. Risk-pooling does not work like that. Instead, in risk-pooling systems, favors are provided in response to the recipient's need and with an eye toward the establishment of a partnership that the donor may find useful in the future because of its inherent unpredictability. The relationship is less like that between a banker and a lender and more like that between an insurance company and a person who buys a policy. The person who buys the policy pays the premiums not because he or she is hoping to one day suffer a loss and thus be entitled to a payment. Instead, he or she hopes never to suffer such a loss, making all of the premiums a complete waste of money. But the future is unpredictable, so he or she pays the premiums anyway. Similarly, people who participate in risk-pooling arrangements agree to help others who happen to be in need, not because they are hoping that they themselves will someday be in need but rather because they recognize the very real possibility of such an event.

Risk-pooling partnerships have been documented ethnographically in many African pastoralist societies (e.g., Almagor 1978; Gulliver 1955; Dyson-Hudson 1966). This reflects the fact that pastoralists typically live in marginal areas prone to drought. Livestock are also vulnerable to a variety of diseases and theft. Among Maasai and other Maa-speaking pastoralists in Kenya and Tanzania, such partnerships are referred to as "umbilical cord" (*osotua*) relationships. Such relationships are imbued with a deep sense of responsibility and respect. Within osotua relationships, gifts are given only in response to requests that are based on genuine need. In contrast to relationships governed by the

principle of balanced reciprocity, such gifts do not create debt and are never referred to as payments (Cronk 2007; Cronk and Wasielewski 2008). Computer simulations of osotua relationships both in dyads (Aktipis, Cronk, and de Aguiar 2011) and in networks (Hao et al., forthcoming) show that they help livestock owners maintain their herds for longer periods despite the volatile ecology of the region.

Risk-pooling is also the logic behind central place food sharing, a practice common among hunting and gathering peoples (Winterhalder 1986; Cashdan 1985; Wiessner 1982). That such sharing is an example of risk-pooling is demonstrated by the fact that unpredictable foods, particularly large game, are typically much more widely shared than foods that come in small, predictable packages, such as small game, honey, and plants (e.g., Hames 1990; Gurven et al. 2000; Kaplan and Hill 1985; Kaplan, Hill, and Hurtado 1990). Among the Hadza of Tanzania, sharing is maintained by a strong normative expectation. According to Woodburn (1998), the individual Hadza hunter "has no choice about whether he shares the animal he kills. It has to be redistributed" (62). Woodburn also points out that back-and-forth exchange "with other Hadza is reprehensible" (54). Sharing is so important among the Hadza that they even use the notion of indebtedness to differentiate themselves from neighboring groups: "'We have no debt,' they say. Only the general right to share is carried forward over time. Specific claims are not" (54; see also Marlowe 2010). Recently, the effects of variance in resource acquisition on sharing patterns were explored through the use of a computer game in a laboratory setting. Participants rarely shared while foraging in low-variance virtual patches, but considerable sharing took place among foragers in high-variance virtual patches (Kaplan et al. 2012). Similarly, a risk-pooling simulation involving virtual herds rather than foraging found that participants commonly used risk-pooling rather than reciprocity strategies, particularly if they had read brief descriptions of real-world risk-pooling practices before playing the game (Gazzillo et al. 2013). Thus, the logic of risk-pooling through sharing seems to come easily even to people who do not themselves have any personal experience with such systems or the environments and subsistence practices that lead to them.

Need is also the starting point for another explanation for why people sometimes share food and other resources known as tolerated theft (Blurton Jones 1984, 1987) or tolerated scrounging (Isaac 1978). In tolerated theft, one shares one's resources in order to avoid the cost of defending them rather than as a sort of insurance policy. The fact that much sharing in hunting and gathering societies is in response to aggressive requests, a pattern labeled by ethnographers as "demand sharing" (Peterson 1993), shows the value of the tolerated theft model as an explanation of some instances of sharing. As suggested by Blurton Jones (1987), tolerated theft may have been a starting point for exchanges that later developed into a way of reducing day-to-day variance in food intake.

FRONTIERS IN THE EVOLUTIONARY STUDY OF HUMAN COOPERATION

Because human cooperation is such a large and diverse phenomenon, there is still much that we do not understand about it. The rest of this chapter briefly describes a few areas of inquiry that have recently received increasing attention from evolutionary scholars.

COORDINATION PROBLEMS

The bulk of the theoretical literature on cooperation has concerned collective action dilemmas, that is, situations in which cooperation is stymied by the problem of free riders. This has led to a comparative neglect of coordination problems. Recently, many evolutionary scientists have begun to advocate a shift of focus in the direction of coordination problems and how they are solved as a crucial aspect of the human success story

(e.g., Alvard 2001; Tomasello 2009). This partly reflects a realization that coordination problems are in many ways more fundamental than collective action dilemmas. After all, in order for a collective action dilemma to exist, there already must be some degree of common understanding among the potential participants in the collective action regarding what constitutes participation and what does not (McAdams 2008). If the goal is to bring home a piece of whale meat, as in the Lamaleran example given earlier in this chapter, does one need to actually harpoon the whale, or can one simply bail or pull on one of the boat's oars? Before the collective action dilemma can be overcome, these kinds of common understandings must first be established.

Given the value of solutions to coordination problems, it is not surprising that evolutionary scientists have suggested that humans may possess a variety of both physical and psychological adaptations designed to help us find such solutions. For example, humans are much better than nonhuman primates at following each other's gaze (Wyman and Tomasello 2007), and it has been suggested that this may be made easier by a couple of unusual morphological features of the human eye. First, the sclera or "whites" of our eyes are indeed white, rather than blending in with the iris and surrounding skin, as is the case with most other primates. Second, our eye openings are also unusually elongated horizontally compared with those of most nonhuman primates. Both of these characteristics may make it easier for us to tell what others are looking at and also to signal to others what we are interested in simply by looking at it (Kobayashi and Kohshima 1997, 2001). This shared *attention* may be a step to shared *intention* (Tomasello and Carpenter 2007), which may in turn be a step toward full-blown theory of mind (Premack and Woodruff 1978). Also known as mentalizing, theory of mind is the ability to imagine the mental states of others and to understand that those mental states may differ from one's own. This mind-reading ability is something at which cognitively normal humans excel. Based on studies of its development in children and of people who lack it in adulthood, theory of mind is an ability that evolved due to selection pressure specifically for its usefulness in social coordination rather than simply as a side effect of our high general intelligence (Baron-Cohen 1995; Baron-Cohen et al. 1995; Emery 2000).

Of course, language is the ultimate coordination norm. Without language, human culture and society as we now know it could not exist. If anyone wants a one-word explanation for why humans are so much more successful at cooperation on both small and large scales than most other species, here it is: *language* (Smith 2010). Language's role in social coordination may also be a good starting point for understanding its evolution. Consider, for example, linguist Derek Bickerton's hypothetical scenario for the emergence of language (Bickerton 2009; Bickerton and Szathmáry 2011; see also Cronk 2004a). Bickerton sees the key difference between language and animal signaling systems as displaced reference: while animal signaling systems are largely limited to references to things that are actually present (e.g., alarm calls that refer to predators), language allows us to refer to things that are not present. Bickerton thinks that displaced reference developed as a way of coordinating the cooperative, aggressive scavenging that some paleoanthropologists see as having been a precursor to social hunting (e.g., Blumenschine 1987). Thus, the first instances of displaced reference—and thus the thin edge of the wedge that separated language from its precursor in animal signaling—may have been efforts to recruit others to help scavenge large kills made by other predators.

CULTURAL GROUP SELECTION

Say the term "group selection" in a room full of evolutionary scientists and you are likely to get reactions ranging from delight to abject horror. The reasons for this divide go back to 1962, when evolutionary biologist V. C. Wynne-Edwards proposed that the differential

survival and reproduction of entire groups of organisms rather than that of individual organisms may be responsible for many aspects of animal behavior. Wynne-Edwards's claim was quickly challenged by John Maynard Smith (1964, 1976), George Williams (1966), and others on the grounds that unless groups are isolated and experience frequent extinctions, selection at lower levels, such as that of individual organisms and the genes they possess, will usually have a greater impact than selection at the group level on how selection designs organisms. The result was that most subsequent research on animal behavior, including work on humans conducted within that tradition, rejected the group selectionist framework and focused instead on selection at lower levels. Today, most evolutionary scientists accept the idea that selection can work at multiple levels, but differences of opinion remain regarding its relevant strength at various levels. Particularly in the study of human behavior, group selection continues to have its fans and advocates (e.g., Sober and Wilson 1998).

The situation when we study humans is made more complicated by the fact that groups may be defined either in biological terms (e.g., populations of organisms) or in cultural terms (e.g., tribes, religions, and other groups that share some body of knowledge). This distinction is crucial because, despite their similar names, biological group selection and cultural group selection are quite different processes (Richerson and Boyd 1998). They resemble each other only in that they both involve groups. The actual mechanisms involved in the two processes can be quite different. For example, although biological group selection is weakened when individuals move from group to group, cultural group selection can actually be strengthened by such movement, provided that migrants adopt the culture traits of their adopted groups. Because many such culture traits are social coordination norms, it often makes good sense for the individuals involved to conform to them. This kind of "voting with your feet" may sometimes be a major determinant of which groups fail and which succeed.

The between-group cultural differences that make cultural group selection possible may exist for a variety of reasons, but one of the most interesting arises from the fact that coordination problems can often be solved in a variety of ways. In the United States and much of the rest of the world, people drive their cars on the right side of the road, but traffic flows just as well in countries where people drive on the left side. English is a very effective means of communication, but of course so are French, Urdu, Swahili, and so on. Electrical plugs in the United States have flat prongs, while those used in much of Europe have round ones. Because different coordination norms can perform equally well so long as everyone in a particular location knows about and follows them, groups of people can end up with very different coordination norms. McElreath, Boyd, and Richerson (2003) used a computer simulation to explore the power of coordination games to create between-group differences. Players in the game had two options, and they scored the most points when paired with another player who chose the same option. Players were also endowed with marker traits (a zero or a one) and a propensity to prefer interactions with players with whom they shared a marker. Just as a person's language, accent, clothing, religion, and so on can be reliable indicators of the social coordination norms that he or she is most likely to use, over time the marker traits became reliable indicators of who was playing which game (see also Efferson, Lalive, and Fehr 2008).

For a good real-world example of cultural group selection, one need look no further than competition among companies in a market economy (Johnson, Price, and Van Vugt 2013). Even if they provide the same product or service, companies differ from one another, and those differences are clearly cultural (i.e., due to social learning), not genetic. Furthermore, those cultural differences lead to differential success among companies,

with some surviving and others failing and shutting their doors. Of course, companies also have characteristics that make them somewhat unusual among the wide variety of culturally defined groups that humans form. First, competition among them is intense, with companies being founded and dying out with great frequency. Second, companies are normally quite discrete from one another, with occasional mergers or acquisitions duly noted as important exceptions to this rule. Third, companies are functionally integrated and have clear corporate structures. In contrast, other culturally different groups might better be thought of simply as categories, that is, people who share some common characteristic but do not interact in an interconnected set of roles or within any sort of corporate structure (Keesing 1975). Consider ethnic "groups," for example. Particularly in nonstate societies, such "groups" are really just categories, that is, people who share a bundle of culture traits (e.g., a common language) but do not necessarily have any sort of functionally integrated corporate structure.

These differences among different kinds of culturally defined groups may lead to different kinds of cultural group selection. Selection among companies (e.g., Arthur 2012), political interest groups (e.g., Baumgartner et al. 2009; Gray and Lowery 1997), organized religions (e.g., Stark 1996), descent groups (Keesing 1975; Cronk and Gerkey 2007; Gerkey and Cronk 2014) or other corporate, functionally integrated groups will largely be on culture traits that influence their ability to achieve their group-level goals, possibly at the expense of their constituent individuals. Let's call this "hard cultural group selection." When cultural group selection occurs among "groups" that are really just categories lacking functional integration, such as those shaped by shared ethnicity (Barth 1969), spirituality (e.g., Fuller 2001), and nationality (Anderson 1991), then no such traits exist. Instead, such groups differ in terms of the extent to which the culture traits that are prevalent within them help their members to survive and reproduce. Let's call this "soft cultural group selection." To understand the distinction between hard and soft cultural group selection, it might help to recall the contrast George C. Williams (1966: 16) drew between a "fleet herd of deer," in which fleetness is a characteristic of the herd, and a "herd of fleet deer," in which fleetness is a characteristic of the individual members of the herd and the fleetness of the herd as a whole a mere side effect. Between these two extremes lies what we might call "firm cultural group selection": selection among groups based on characteristics that provide less functional integration than is seen in corporate groups but more than is seen in categories.

Selection among companies, states, or any other functionally integrated corporate groups will suffice as an example of hard cultural group selection. For an example of soft cultural group selection, consider the possibility that some ethnic groups may succeed and others may fail because some happen to have culture traits that help their bearers survive and reproduce but have nothing to do with the group's ability to work as a unit. I have documented one instance of soft cultural group selection among the Mukogodo of Kenya, who learned to emulate the ethnic identity of a much larger, wealthier, and more successful group, the Maasai, to a point where they have almost totally lost all markers of their previously quite distinct ethnic identity, including not only their language but also their subsistence practices and religion (Cronk 1989, 2002, 2004b). As for "firm cultural group selection," consider selection acting on characteristics that provide some functional integration but not as much as that seen in corporate groups. Again, consider the Maasai. Although Maasai society has never been fully functionally integrated in the manner of a chiefdom or state, they do have other institutions that provide a limited degree of functional integration at local and regional levels. These include a descent system, an age-set system, and the more diffuse osotua risk-pooling system mentioned earlier in this chapter

(Cronk 2007; Cronk and Wasielewski 2008; Aktipis, Cronk, and de Aguiar 2011), all of which may have helped the Maasai succeed in competition with neighboring groups. Firm cultural group selection might be implicated in some episodes of religious conversion, as well. For example, Ensminger (1997) has argued that the spread of Islam in Africa was aided by the fact that it brought with it an innovative system of organizing trade. Finally, although corporate groups and categories are quite different, they may be closely related to one another in a functional sense. "People who manufacture and sell Hondas" is a corporate group, while "people who own Hondas" is a category. They are related in that the ability of the corporate group to attract people to the category determines its success in competition with other corporate groups. Similarly, "clergy and other officials of the United Methodist Church" is a corporate group that is dependent for its success on how many people consider themselves to be in the category "Methodist."

COALITIONAL PSYCHOLOGY

What impact might cultural group selection have on our evolved psychology? To date, most advocates of cultural group selection (e.g., Henrich 2004) have answered this question with a list of the same kinds of characteristics that would be favored by biological group selection: altruism, other-regarding preferences, prosociality, and so on. In some instances of cultural group selection, this must be true. Hard cultural group selection, for example, may involve some sacrifice on the part of the individuals in a group, which could provide selection pressure that rewards individual tendencies toward altruism and other prosocial behaviors. The research described earlier in this chapter on the greater longevity of religious than secular communes and its association with the costs they impose on their members may be a case in point. However, most culturally defined groups have more flexible memberships and fewer barriers to membership than religious communes, and their success often depends less on the costs they impose on their members than on the benefits they provide to them (Clark and Wilson 1961). Given that people can often move from group to group and that such movement can enhance rather than undermine the power of cultural group selection, its main effect on human psychology may have been to enhance our ability to deal with coalitions rather than to make us generally prosocial.

Depending on the type of cultural group selection that is operating, cultural group selection may favor different sorts of characteristics in individuals. When soft cultural group selection acts on categories, it will favor an ability to correctly predict the impact of membership in different categories on one's own success. By itself, this would not necessarily favor prosociality or cooperativeness. Although some categories of people may be more successful than others because they have found ways to be more cooperative, others may have succeeded by finding ways to avoid costly social entanglements. Hard cultural group selection among corporate groups, in contrast, should favor individual characteristics that enable entire groups to function well as integrated wholes. Individuals play specific and important roles in such groups, and group members need to know that everyone involved is committed to playing those roles. This should lead to individuals who become emotionally attached and committed to such groups and who send convincing signals to their fellow group members regarding those attachments and commitments. Paradoxically, selection on individuals to move from less successful to more successful groups would also favor an ability to shift loyalty from one group to another. The perfect person in this scenario would be one who feels and signals an honest commitment to the groups to which he or she belongs but who can also switch loyalties to other groups and then send equally convincing signals of his or her newfound commitments. Obviously, such "perfection" may be difficult to achieve. Our actual coalitional psychology may be

a suboptimal mixture of these two abilities, involving considerable anguish and internal conflict in the face of uncertain, conflicting, and shifting loyalties.

Evidence of our flexible coalitional psychology can be found in the existing social psychological literature. For example, it has long been known that people find it surprisingly easy to form attachments even to quite arbitrary and temporary groups. For example, Tajfel, Billig, and Bundy (1971) had people rate paintings by Klee and Kandinsky and then divided them into two groups based ostensibly (but not actually) on their preferences. Subjects who then had to divide a sum of money between members of their own group and the other group gave more to members of their own group. More recently, social psychologists in England focused on the coalitional psychology of football (soccer) fans, in particular fans of Manchester United (Levine et al. 2005). Subjects who had already been identified as fans of Manchester United were given a series of questionnaires to heighten their sense of identification with the team and with their fellow fans. They were then taken across campus for the second part of the study. As they were walking across campus, a confederate playing the role of a jogger fell down and shouted as if in pain. The experimental condition was in which of three shirts the jogger was wearing: a Manchester United shirt, a plain shirt, or a shirt branded with the logo of MU's bitter rival, Liverpool FC. All but one of the subjects who saw a fellow Manchester fan fall down came to his aid, but they helped the runner in the plain shirt only a third of the time, and they helped the Liverpool fan even less often. In a follow-up study, the researchers again recruited Manchester United fans, but this time they gave them questionnaires that primed their sense of being football fans in general rather than Manchester fans in particular. This time, both the Manchester United and the Liverpool FC shirts elicited high rates of helping compared with the plain shirt, thus demonstrating the ease with which people's group identifications can be manipulated.

Because coalitions are flexible, people should be able to pick up cues that are easily changed, such as clothing and jewelry, as well as those that are more fixed, such as accents and physical similarities. To explore this, Kurzban, Tooby, and Cosmides (2001) showed people photographs of members of two rival basketball teams and told them to form impressions of the individuals on the teams. Each picture was paired with a statement that the person had supposedly made about the teams' rivalry. The actual pairing of sentences with photos was randomized across subjects. Subjects were then given a surprise memory test involving matching statements with photos. Because this was a difficult task, they made a lot of errors, and the patterns in the errors reveal that they used statements associated with faces along with other cues, such as the basketball jersey colors, to identify coalitions. One of this study's most interesting findings is that flexible cues such as the statements people make and the clothes they wear swamp the effects of race as a coalitional cue. This makes sense in light of how our ancestors lived. Given that their mobility was limited by how far they could walk, they were very unlikely to have encountered people as physically different from themselves as we routinely do now, and it would make little sense for us to have an evolved tendency to focus on race when determining coalitions. Kurzban, Tooby, and Cosmides's conclusion is that racism may simply be a misfiring of a psychological mechanism designed to pick up on more flexible coalitional cues. The encouraging conclusion of the study is that race's importance as a way to sort people into groups is greatly diminished when it is disconnected from actual coalitions.

INSTITUTIONAL CONTEXTS

Most human cooperation takes place not in a vacuum but rather within existing institutional and organizational structures. The evolutionary approach to human cooperation

might be greatly enhanced through greater attention to such structures and how they interact with our evolved psychological propensities. What exactly is meant by the word "institution" has been the subject of much debate, with some scholars focusing on formal organizational structures and others using the term to refer to any "stable, valued, recurring patterns of behavior" (Huntington 1968: 12). Philosopher John Searle (2005) captured what makes institutions special: they have the power to assign people and objects to statuses that allow them to do things that they would not be able to do solely by virtue of their own inherent properties. Thus, paper and round bits of metal are just that—paper and round bits of metal—but money is an institution that facilitates economic cooperation. Similarly, my ability to teach classes and assign grades stems from the fact that I am employed by a university as a professor, not from any personal characteristic of mine. Searle's definition is useful because it captures what is special about both formal organizations and informal norms and conventions.

Although social scientists have devoted an enormous amount of work to the study of human institutions, little has been done on the ways in which such institutions interact with our species' evolved psychology. A recent exception was provided by anthropologist Drew Gerkey (2010, 2013), who examined the relationship between cooperation and institutions among the Koryak, a reindeer-herding and salmon-fishing people who live in the northern part of the Kamchatka peninsula in the far east of Russia. One of Gerkey's main research tools was the public goods game, or PGG. In a PGG, people are divided into small groups, usually of four. The group memberships and actions of the individuals are known only to the experimenter. Everyone is given an initial endowment (in this case, two hundred rubles) and the opportunity to contribute any portion of it, including none at all, to a common pot. The experimenter then doubles the pot and divides it equally among all people in the group. Players go home with whatever they kept from their initial endowments plus whatever they received from the common pot. Because everyone may be tempted to hold back on their donations to the pot for fear that others won't contribute to it, the PGG effectively captures the problem of free riders.

Gerkey's PGGs yielded two interesting findings. First, his participants were the most generous ever recorded among the dozens of PGG studies that have been conducted around the world, with many of them giving all of their endowments to the common pot. The reason appears to have to do with the issue of risk and uncertainty discussed earlier in this chapter. The physical environment in which the Koryak live is a difficult one with an extremely severe climate. As a result, they have become accustomed to helping each other out. One of his interviewees explained the situation this way: "In the North . . . a loner doesn't survive. That's why we support each other. We help each other" (Gerkey 2010: 141). Even participants who expected others to give less still often gave their entire endowment to the common pot. Second, in addition to using standard PGGs, Gerkey also had his participants play games framed with references to two institutions that all Koryak know well: the modern descendant of a Soviet-era collective farm, called a *sovkhoz*, and a post-Soviet collective institution called an *obshchina* that is meant to harken back to traditional cooperative structures. Although those institutions exist to foster cooperation, when the games were framed with references to those institutions, contributions to the common pot actually went down rather than up. The framing seems to have the effect of making the games more real by tying them to institutions that, as the participants well know, do not always work as well to enhance cooperation in the community as their members might like.

CONCLUSION

Early applications of evolutionary theory to the problem of human cooperation stayed close to the approach's roots in animal behavior studies, focusing on such trans-specific phenomena as kinship, assortment, and the likelihood of future interactions. From there, evolutionary scientists moved on to consider things that are more important or unique to humans, such as audiences, reputation, language, signs of commitment, and risk-pooling. The frontier areas described above follow this basic trajectory. For example, although the presence of culture and thus of group-level differences attributable to culture has been documented in other species (e.g., Rendell and Whitehead 2001; Whiten et al. 1999), it is safe to say that the impact of cultural group selection has been felt most powerfully among humans. As evolutionary scholars focus more of their attention on aspects of human cooperation that do not have good nonhuman analogs, they will need to master not only the evolutionary literature on cooperation but also the large existing literature on the topic generated by social and behavioral sciences.

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