Evolution and Human Behavior 31 (2010) 231 – 245

Evolution and Human Behavior

Review Article

Communication and collective action: language and the evolution of human cooperation

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Initial receipt 30 June 2009; final revision received 19 March 2010

Abstract

All social species face various “collective action problems” (CAPs) or “social dilemmas,” meaning problems in achieving cooperating when the best move from a selfish point of view yields an inferior collective outcome. Compared to most other species, humans are very good at solving these challenges, suggesting that something rather peculiar about human sociality facilitates collective action. This article proposes that language — the uniquely human faculty of symbolic communication — fundamentally alters the possibilities for collective action. I explore these issues using simple game-theoretic models and empirical evidence (both ethnographic and experimental). I review several standard mechanisms for the evolution of cooperation — mutualism, reciprocal altruism, indirect reciprocity and signaling — highlighting their limitations when it comes to explaining large-group cooperation, as well as the ways in which language helps overcome those limitations. Language facilitates complex coordination and is essential for establishing norms governing production efforts and distribution of collective goods that motivate people to cooperate voluntarily in large groups. Language also significantly lowers the cost of detecting and punishing “free riders,” thus greatly enhancing the scope and power of standard conditional reciprocity. In addition, symbolic communication encourages new forms of collectively beneficial displays and reputation management — what evolutionists often term “signaling” and “indirect reciprocity.” Thus, language reinforces existing forces that favor the evolution of cooperation, as well as creating new opportunities for collective action not available even to our closest primate relatives.

Keywords: Language; Reciprocity; Collective action; Large-scale cooperation

> *Man in the rudest state in which he now exists is the most dominant animal that has ever appeared on the earth. He has spread more widely than any other highly organised form; and all others have yielded before him. He manifestly owes this immense superiority to his intellectual faculties, his social habits, which lead him to aid and defend his fellows, and to his corporeal structure. The supreme importance of these characters has been proved by the final arbitrament of the battle for life. Through his powers of intellect, articulate language has been evolved; and on this his wonderful advancement has mainly depended.* — Darwin (1871, pp. 136–137)

> *Language is our legacy. It is the main evolutionary contribution of humans, and perhaps the most interesting trait that has emerged in the past 500 million years… It enables us to transfer unlimited non-genetic information among individuals, and it gives rise to cultural evolution. — Nowak, Komarova and Niyogi* (2002, p. 611)

1. The problem

All social species face various “collective action problems” or “social dilemmas,” meaning problems in achieving cooperating when the best move from a selfish point of view does not produce the best collective outcome (Olson, 1965). Compared to most other species, however, humans are very good at solving these challenges, thereby often avoiding the “tragedy of the commons,” escaping the “prisoner’s dilemma” and the like. How is this accomplished?

Unlike social insects, humans do not have unusual asymmetries in genetic relatedness and reproductive

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doi:10.1016/j.evolhumbehav.2010.03.001

specializations that facilitate kin selection. Although humans have skills in individual recognition and memory that facilitate conditional reciprocity (Axelrod, 1984), there is no reason to think we are particularly more gifted in this regard than chimpanzees or perhaps even baboons (Byrne, 1996; Seyfarth, Cheney & Bergman, 2005). In any case, conditional reciprocity (a.k.a. "reciprocal altruism") cannot be simply "scaled up" from dyadic interactions to the large-group collective action in which humans excel, as discussed below (see also Boyd & Richerson 1988; Kollock, 1998; McElreath & Boyd, 2007).

Evidence and theory thus suggest that something rather peculiar about human sociality facilitates collective action. This unique ability has been variously ascribed to intelligence, specialized cognitive abilities (e.g., theory of mind, intentionality), cultural inheritance, inter-group competition and language. This article examines the last of these — the capacity for symbolic communication — as a key factor altering the costs and benefits of collective action. Theory and data discussed herein suggest that under many conditions, language significantly lowers the cost of detecting and punishing "free riders," thus greatly enhancing the scope and power of standard conditional reciprocity. In addition, symbolic communication facilitates new forms of displays and reputation management — which evolutionists term "signaling" and "indirect reciprocity" — with collectively beneficial effects. Thus, language reinforces some existing forces favoring the evolution of cooperation, as well as creating new opportunities for collective action not available to even our closest primate relatives.

I explore these issues using simple game-theoretic models and ethnographic examples to illustrate the ways in which the uniquely human faculty of symbolic communication fundamentally alters the possibilities for collective action. Along the way, I review the standard mechanisms for the evolution of cooperation — mutualism, reciprocal altruism, indirect reciprocity, group selection and signaling — in order to highlight their limitations when it comes to explaining human cooperation as well as the ways in which language helps overcome those limitations. To maintain a reasonable length and sufficiently sharp focus, this review of evolutionary theories of cooperation is far from comprehensive; for example, I do not address the role of language in kin selection. Because much of the relevant theory and empirical research surveyed comes from social sciences (such as economics, anthropology and political science), the review illustrates the extent to which interesting research on the evolution of cooperation currently lies at the interface of evolutionary biology and these other fields.

Let me stress that my goal here is not to address why language (symbolic communication) itself evolved (for many arguments on this question, see Buckley & Steele, 2002; Hurford, 2007; and Pinker & Bloom, 1990; among others). Rather, the arguments advanced below are about how and why language, once it evolved for whatever reasons, has major adaptive consequences for collective action.

2. Collective action

Terminology for describing cooperation and social dilemmas has developed somewhat independently in evolutionary biology and in various social sciences. Because these traditions are now undergoing some merging, it is useful to point out equivalent as well as divergent meanings. Here I adopt some key terms (italicized when defined) from social science (e.g., Hardin, 1982). *Collective action* refers to any situation where several or many individuals must cooperate in order to produce some collective good. A *collective good* is any good or service provided to the members of some collective (coalition, village, organization, nation, etc.) through the efforts of some or all of its members. As defined here, collective goods include but are not limited to *public goods* and *common-pool resources*. (Pure public goods are defined as nonrival — meaning consumption by one does not reduce amount available to others — and nonexcludable; common-pool resources are rival but non-excludable; see Ostrom, 2003.) Collective goods abound in every kind of human society. Examples include large game that is widely shared, a community irrigation system, defense against enemy attack, a wide variety of rituals and ceremonies, and scholarly journals. Other social species produce collective goods as well, but if we restrict ourselves to cases where the members of the collective are not closely related (thus ruling out kin selection as the dominant evolutionary force), the number of nonhuman examples dwindles drastically (predator mobbing by birds being an example — see, for example, Krams et al., 2010).

Successful collective action is not achieved as readily as its benefits might suggest; this is due to two broad reasons. There may be logistical or informational constraints on getting the relevant individuals to act in concert — what game theorists term a coordination problem; or there may be insufficient incentives to motivate individuals to contribute. Both situations are examples of a *collective action problem* (CAP for short); in the second case, individuals have an incentive to engage in "free riding" — that is, benefiting from a collective good without paying the costs of providing it. These basic insights, and many subtle variations on them, were developed initially in classical game theory. In recent years, analysts (even many in the social sciences) increasingly use evolutionary game theory (Gintis, 2000; Maynard Smith, 1982) to move from the language of decision theory, and its concern with motivation and incentives, to a focus on fitness payoffs and evolutionarily stable strategies.

Formal models in both classical and evolutionary game theory suggest that CAPs should be quite resistant to cooperative solutions, particularly in groups containing more than a handful of members (as discussed below). Yet humans seem to be very good at solving CAPs, even for larger group sizes (though size does matter). Furthermore, as already noted, in great contrast to other species, kinship (as measured by r, the coefficient of genetic relationship) often plays a minor or negligible role in human collective action. Indeed, it can be argued that the rapid spread of *Homo sapiens* over the planet, and our ability to survive in varied ecological conditions (and indeed to refashion habitats to our liking), is due in large part to our success in large-group (n>5) low-relatedness (r<0.1) collective action. Solving CAPs under such conditions marks an important evolutionary innovation in the hominin line (Henrich & Henrich, 2007; Richerson & Boyd, 1999; Smith, 2003).

3. Explaining collective action

Evolutionary theorists have developed several distinct approaches to explaining collective action. Key explanatory frameworks include mutualism, conditional reciprocity, indirect reciprocity, (cultural) group selection and honest signaling. Kin selection is of course another key mechanism for the evolution of cooperation; although crucial for understanding many cooperative patterns in human society, it is of limited relevance to the large-group collective action that is the focus of this review. I do not discuss either the view that large-n, low-r collective action is a maladaptive outcome of traits that evolved in past environments characterized by small groups (see critique by Fehr & Henrich, 2003).

3.1. Collective action and game theory

In the growing convergence between social-science and biological analyses of behavior, game theory has come to play an important role in providing a common language and basic analytical framework bridging these rather separate traditions. The normal-form payoff matrix of game theory is a simple but convenient way to represent social interactions, used here to illustrate various ways of viewing CAPs and their possible solutions (Table 1). In such a matrix, strategies employed by the focal player's strategies (labeled "Ego") are listed on the left (row), the other player(s) strategies are listed on top (column) and payoffs are shown for Ego/row only, under the assumption that payoffs to any given strategy pair are symmetrical. For simplicity, I represent payoffs in dyadic form even for n-player games; this is reasonable if payoffs are linear in n.

Conventional labels denote payoffs to each strategy combination (R if all cooperate, etc.); these labels facilitate concise statements of the conditions needed for strategy equilibria. In this convention:

R=Reward from mutual cooperation (collective action)
T=Temptation to free ride
S=Sucker's payoff
P=Punishment from mutual defection (failure to provide collective good)

For many CAPs, the payoff rank order=T>R>P>S, which is the main defining feature of the infamous "prisoner's dilemma" (on which we will have more to say).

Table 1
Payoff matrix for generalized collective action game

	Others contribute	Others shirk
Ego contributes	R: Mutual cooperation	S: Unilateral cooperation
Ego shirks	T: Free riding	P: Failure of CA

Table 2
Mutualism payoff matrix (integers indicate ordinal values of payoffs, not numerical values; higher values mean larger payoffs)

	Others contribute	Others shirk
Ego contributes	R=4	S=2 or 1
Ego shirks	T=3	P=1 or 2

3.2. Mutualism

Perhaps the simplest model of collective action is mutualism. It applies whenever mutual cooperation yields higher payoffs than free riding (unilateral defection) — that is, R>T (Table 2).

Mutualism comes in two forms, depending on the relative payoffs to the other two strategy pairs (S and P). If unilateral cooperation has a higher payoff than mutual defection (S>P), then Ego does best to contribute regardless of what other players do, a condition termed "byproduct mutualism." (For example, suppose that constructing an irrigation canal will boost one's crop production, but also improve yield in neighboring fields.) On other hand, if it is better to defect if others defect (P>S), this more fragile form is termed "synergistic mutualism" (an "assurance game" in the language of classical game theory).

Alvard and Nolin (2002) argue that human cooperative hunting often has a synergistic mutualism payoff structure, rather than one posing a greater chance of defection (such as a prisoner's dilemma). They present data on traditional whaling in Lamalera, Indonesia, to support this claim (Table 3). When Lamalerans cooperate in whaling, they get a higher per capita payoff than when they engage in solitary fishing (R>P). As long as the whaling crew is big enough (n>8), there is no gain from defecting to fishing (R>T), and hence no real opportunity for free riding. But if individuals cannot coordinate on whaling and try to go whaling on their own (or indeed in a crew of less than eight), they get nothing. Thus, the payoffs do conform to synergistic mutualism, a game of assurance (or a "stag hunt," after Rousseau — see Skyrms, 2004). There is congruence between what is any individual's best move and what is

Table 3
Lamaleran whaling-fishing payoffs (after Alvard & Nolin, 2002)

	Others hunt whales	Others fish
Ego hunts whales	R>0.39 kg/h	S=0
Ego fishes	T=0.32 kg/h	P=0.32 kg/h

collectively beneficial, but it requires that individuals cooperate to produce this collective good.

Although the mutualism argument offers a promising way to account for some forms of collective action, it may overlook some significant complications. First, if there are more than a handful of players, coordinating on the highest-payoff option can be extremely difficult (Chaudhuri, Schotter & Sopher, 2009). Second, if we dig below the surface we often find that mutualistic payoffs depend upon a set of underlying norms for division of the joint product, and perhaps enforcement of those norms against potential defectors. Thus, in the case of Lamalera, the high payoffs from whaling depend on a complex division of labor in the hunt itself (e.g., a harpooner and a steersman as well as ordinary crewmen) as well as in preparation for it (e.g., boat carpenters). The payoffs also depend on a prescribed division of the catch (including shares to some not even present on the hunt, such as boat carpenters and sail makers); the sharing rules minimize transaction costs (reducing or eliminating squabbling over shares) and guarantee that each participant will find it worthwhile to contribute to production of the collective good. While all of this is clearly described by Alvard and Nolin, and intuitively comprehensible, it raises challenges that may be rather more difficult to solve than those definable as synergistic mutualism. Put simply, the harvest and sharing of whales in cases like Lamalera is a social institution (McElreath et al., 2008); such institutions necessitate development and enforcement of norms that prevent self-interested “cheating” (e.g., withholding shares from the boat owner or the carpenter). These second-order CAPs — so called because the solution to one CAP poses its own CAP — simply push the explanatory problem back one level (Heckathorn, 1989).

Linguistic communication may not eliminate these challenges, but it can certainly be of great help (Alvard & Nolin, 2002). First, language greatly facilitates complex coordination, such as is involved in forming a whaling crew and establishing a productive division of labor (e.g., captain, paddlers, sail tenders, harpooner, coordination with other boats). With language, people can coordinate so as to plan cooperative actions at precise future times and locations (“Meet the three of us plus Joseph and his brothers at the boat house tomorrow at sunrise, and we will paddle out to hunt sperm whales that have been sighted to the west”) in ways that even very intelligent nonlinguistic creatures such as chimpanzees cannot hope to attain. Recent models of “cheap talk” (e.g., Demichelis & Weibull, 2008; Skyrms, 2002, 2004) as well as various experiments (summarized in Camerer, 2003, pp. 356–62, 403–4) generally support this point.

Second, some form of symbolic communication is essential for defining norms, sharing rules (division of the collective good) and the like. Rather than waste time and effort quarreling over the spoils of cooperation, as carnivores and nonhuman primates so often do, human groups usually rely on established norms that are quite effective (even in the absence of third parties such as police or courts). As social scientists have long noted, such norms and rules greatly reduce conflict and other “transaction costs” involved in collective action (e.g., Acheson, 2002; Ostrom, 1998, 2000; Taylor & Singleton, 1993), and such norm coordination could play a key role in forms of collective action such as ethnic solidarity (McElreath, Boyd &Richerson, 2003).

Both of these effects — facilitating coordination and establishing norms to guide division of collective goods — greatly increase the potential payoffs from cooperation. This payoff enhancement should provide behavioral incentives as well as selection differentials that encourage the evolution and stability of cooperation. Indeed, economic historians and others have noted the frequent development of such norms and conventions as well as other linguistically mediated coordination devices when new opportunities and problems have arisen (e.g., Ellickson, 1991; Ensminger & Knight, 1997; McAdams, 1997; see also Boyd & Richerson, 2002; Kaplan, Gurven, Hill & Hurtado, 2005).

3.3. Conditional reciprocity

Conditional reciprocity (sometimes termed “reciprocal altruism” or “direct reciprocity”) has long been the most prominent approach to evolution of cooperation. The defining feature of conditional reciprocity is that Ego cooperates if other participants do too, but otherwise withholds cooperation. As formulated by Trivers (1971), and extended by Axelrod and Hamilton (1981) and many others, conditional reciprocity is meant to solve the CAP presented by a prisoner’s dilemma payoff structure (or its multiplayer equivalent, a linear public-goods game). (The prisoner’s dilemma is formally defined by a payoff structure where $T>R>P>S$ and $(S+T)/2<R$, as in Table 4.)

The dilemma here is a difficult one, since mutual defection (and hence complete failure to produce the collective good) is always an equilibrium, and, indeed, the unique equilibrium. This is easy to see in the static, one-shot (single interaction) version represented in Table 4. Here, no matter what strategy the other players follow, Ego always does best by shirking (defecting); if others contribute, Ego gets the maximum possible payoff by free riding ($T>R$), while if others shirk, Ego avoids the sucker’s payoff by shirking too ($P>S$).

Things get more interesting when interactions are repeated, as Axelrod and Hamilton (1981) famously

Table 4
The one-shot, two-person prisoner’s dilemma

	Others contribute	Others shirk
A. Ordinal version		
Ego contributes	$R=3$	$S=1$
Ego shirks	$T=4$	$P=2$
B. Parameterized version		
Ego contributes	$b-c$	$-c$
Ego shirks	b	0

demonstrated. Suppose two actors have fixed probability w of engaging in future prisoner's dilemma interactions and thus have no way of knowing when such interactions will cease to occur. The payoff matrix of this game (Table 5) is now modified, because players who mutually cooperate will reap long-term rewards that can overcome the temptation to shirk or defect. Thus, as long as w (Axelrod's "shadow of the future") is large enough (specifically, $wb>c$), mutual cooperation is evolutionarily stable (though mutual defection remains so as well).

A host of proposed solutions to the prisoner's dilemma via conditional reciprocity have been proposed, of which the best known (but not necessarily the most robust) is tit-for-tat (cooperate on the first move, subsequently match the other player's move). In highly simplified situations, such a strategy can spread by selection once established in sufficient frequency (or sufficient clustering) in the population. But tit-for-tat and its cousins turn out to have a number of perhaps crippling limitations. First, it is highly vulnerable to errors of perception (mistakenly classifying a response as defect) and of commission (accidentally violating the reciprocity rule), either of which can lock tit-for-tat players into an endless sequence of mutual defection (Boyd & Lorberbaum, 1987; Nowak & Sigmund, 1992; Selten & Hammerstein, 1984). Once widely established in a population, conditional reciprocity strategies are also vulnerable to replacement by toothless imitators (e.g., unconditional cooperation) that can spread by drift until the population becomes vulnerable to an invasion of ruthless defectors. Third, it is easily undermined by delays (due to temporal discounting of future rewards relative to current temptations) or low probability of future interaction (Axelrod & Hamilton, 1981; Stephens, McLinn & Stevens, 2002).

More germane to the present essay, there is the troubling fact that no one has been able to develop a convincing model for the evolution of cooperation in an n-player prisoner's dilemma using conditional reciprocity. There are two main reasons for this. First, conditional reciprocity becomes very difficult to sustain as soon as the number of players gets beyond two or three, because conditional reciprocators can only respond to a defection by one member of the group by withholding cooperation from all, thus inciting defection all around (Boyd & Richerson, 1988). It is possible that this limitation can be remedied by models with strategies other than the binary all-or-none "trigger strategy" of cooperate or defect, but that is speculative.

A more fundamental problem in the collective-action context is that conditional reciprocity can only be stable if the collective good that results is unavailable to nonreciprocators (i.e., free riders can be excluded from the benefits of collective action). This requirement rules out certain types of nonexcludable goods (e.g., collective military defense) and requires effective and often costly means of monitoring and enforcement for many other collective goods (Hawkes, 1992; Olson, 1965; Ostrom, 1990). As a result, conditional reciprocity is difficult to evolve outside of small groups with stable membership (Boyd & Richerson, 1988), and even there may require solving the second-order collective-action problem of punishing free riders (Boyd, Gintis, Bowles & Richerson, 2003).

Table 5
The repeated prisoner's dilemma

	Others contribute	Others shirk
Ego contributes	$(b-c)/(1-w)$	$-c$
Ego shirks	b	0

Presumably as a consequence of the problems just noted, conditional reciprocity has received surprisingly little empirical support in studies of nonhuman behavior (Hammerstein, 2003; Stevens, Cushman & Hauser, 2005). However, humans appear to be much better at playing this game than other vertebrates. I propose that linguistic communication is a key to why this is so, for several reasons. First, language is very useful for defining agreements and perhaps crucial for communicating the precise sanctions for violating them (as exemplified by various legal codes, whether transmitted orally or in writing, found in many cultures). This ability of language to more precisely specify the scope and reasons for punishment could be critical in the conditional reciprocity context and would allow punishment to be effective even if considerable time has elapsed since free riding occurred. It would also help distinguish between justified and unjustified punishment (as well as justified and unjustified defection), thus reducing the cycles of retaliatory defection that plague many reciprocity strategies (including tit-for-tat). A host of experimental studies of cooperation (cited in Cardenas, Ahn & Ostrom, 2004) support the generalization that face-to-face communication greatly enhances individual cooperation rates in social dilemmas, thus raising collective payoffs (Kollock, 1998; Kopelman, Weber & Messick, 2002; Ledyard, 1995; Ostrom & Walker, 1991; Sally, 1995). Even a small amount of pregame communication can increase trust and cooperation in the prisoner's dilemma and other games, as reviewed by Cook and Cooper (2003, p. 228f), who cite six experimental studies that obtain this result (see also Crawford, 1998).

Second, language might help overcome one of the major stumbling blocks for extending the dyadic logic of conditional reciprocity to n-player contexts. Thus, instead of having to respond to a defection by a single player in a collective (e.g., a food-sharing network) by withdrawing cooperation from the entire group — the so-called grim trigger strategy usually assumed in n-player prisoner's dilemmas (Boyd & Richerson, 1988; Kollock, 1998), a victim of free riding could withhold it only from the defector and communicate exactly this consequence to the defector as well as to third parties. Language is not required for this selective reciprocity, but communicating one's intention to follow such a strategy, and advertising the fact that one has done so to past defectors, should reduce the frequency with which defections will occur. Indeed, with language one could even lobby others to follow the same rule. This is similar to the two-stage process of collective action followed by dyadic reciprocity developed by Panchanathan and Boyd (2004), to be discussed below. And it matches empirical evidence that sharing networks are restricted in scope in larger communities (Gurven, Allen-Arave, Hill & Hurtado, 2001), easing the information-management problem, as well as experimental evidence for selective cooperation reviewed in the following two sections.

Third, language can greatly reduce the costs of monitoring and enforcement, as a cooperator need not observe a defection event herself to find out from other observers that a given individual has failed to uphold a social contract. This leads us directly to the next mechanism for the evolution of cooperation, indirect reciprocity.

3.4. Indirect reciprocity

Indirect reciprocity is a term coined by Alexander (1987) to describe cases where cooperators are preferentially chosen as partners by third parties who learn of their cooperative interactions with others. The concept can be seen as an attempt to extend the reach of reciprocity beyond the narrow bounds of dyadic repeated interactions which is the standard purview of conditional reciprocity (and indeed Trivers speculated on just this point in his classical 1971 article on reciprocal altruism). Thus, in the basic formulation of indirect reciprocity, the actions of Individual A (cooperate or defect) in relation to Individual B become known to Individual C, who can then decide whether or not to cooperate with (trust) A.

Indirect reciprocity has become a hot topic for evolutionary game theorists recently and has been modeled in two basic versions. In the "image score" version (Nowak & Sigmund, 1998), Ego's reputation as a cooperator is enhanced if she cooperates (with any other player) and reduced if she defects. In the "standing strategy" form (Sugden, 1986), Ego's actions are judged in relation to the status of her recipient: Ego's reputation as a cooperator is enhanced if Ego is nice to cooperators and reduced if Ego defects with cooperators, but Ego's interactions with defectors are not counted.

Although the image score version of indirect reciprocity is simpler (both analytically and in terms of the cognitive mechanisms it presumes), analysis indicates it is not evolutionarily stable (Leimar & Hammerstein, 2001; Panchanathan & Boyd, 2003). The basic reason for this is that those who defect against defectors are penalized and are thus hung on the horns of a dilemma, since cooperating with defectors, while enhancing a cooperator's image score, contributes to the evolutionary success of defectors. The standing strategy avoids this contradiction, penalizing an individual's standing only when she defects against cooperators. However, there is active debate on which version (standing, image score or some other strategy) best matches human behavior empirically.

Because models of indirect reciprocity generally preserve the dyadic structure of standard reciprocity, they are not immediately suitable for analyzing collective action. Nevertheless, indirect reciprocity has the potential to define a set of reciprocators who can be relied on to cooperate (as well as a set of defectors to avoid), which could provide an initial step towards solving CAPs. But first, let us consider the dyadic case. A simple way to represent this is outlined in the payoff matrix shown in Table 6 (after Nowak, 2006). Here, the parameter q represents the probability that Ego knows the standing (cooperative history) of any potential partner and uses this knowledge to decide whether or not to engage in cooperative interactions with others. Analytical results (Nowak, 2006; Panchanathan & Boyd, 2003) indicate that such a system of indirect reciprocity is evolutionarily stable as long as q, the information used in discriminative cooperation, is sufficiently large (specifically, $qb>c$). The equivalence of q to r (relatedness) in Hamilton's rule for kin selection, and to w in Axelrod and Hamilton's formulation of direct reciprocity (see above), is noteworthy. These three parameters are alternative measures of positive assortment — the degree to which cooperators can identify each other and direct beneficial interactions accordingly.

Thus, a general finding of indirect reciprocity models is that the possibility of reaching or maintaining a cooperative evolutionarily stable strategy is directly dependent on the knowledge any cooperator has of other group members, measured by q. In small, stable populations, one might expect that the average individual will be able to develop observation-based estimates of the cooperative standing of a large fraction of others with whom she might interact. But as population size (or inter-group mobility) increases, such direct estimates become too limited in scope. Communication with third parties about the past behavior of others — in a word, gossip — could potentially fill this gap (Mohtashemi & Mui, 2003; Nowak, 2006, p. 1561; Ohtsuki & Iwasa, 2004; Panchanathan & Boyd, 2003, p. 119; Smith, 2003, p. 419).

In contrast to nonverbal communication, language can provide extremely detailed and precise information about cooperative behavior and its contexts — past, present and future. For example, failure to participate in collective action can be justified (e.g., "Jane didn't show up to help today because she's too sick."). Linguistic tenses and syntax are also critical for distinguishing past, present and future (expected) patterns of cooperation, thereby helping to quantify the amount of cooperation various individuals have contributed., as well as to determine which patterns of cooperation are ongoing or have ceased.

Table 6
The prisoner's dilemma with indirect reciprocity

	Other cooperates	Other defects
Ego cooperates	$(b-c)$	$-c\ (1-q)$
Ego defects	$b\ (1-q)$	0

To date, little theoretical effort has been devoted to this potentially crucial role of language in human cooperation. Enquist and Leimar (1993) modeled a finite population where gossip is exchanged about the "reliability" (cooperative history) of individuals and concluded that this process can be very effective in countering free riders, such that "with gossiping cooperation is stable even in very dense populations" (p. 751). Nakamaru and Kawata (2004) modeled the conditions under which evolution of rumors will effectively detect not just defectors, but defectors who lie about their past history. Bergstrom (2009) and colleagues (Lachmann, Szamado & Bergstrom, 2001) discuss how deceptive linguistic information, despite being "cost free" in production (unlike a peacock's tail), can be kept at bay through socially imposed costs of dishonesty (much in the same way that honesty in low-cost "status badges" in some sparrow species is enforced); put simply, false advertisers are punished once discovered, and if the costs of punishment exceed the benefits of deception the incentive for dishonesty is undermined.

The experimental literature on the role of language in reputation formation is somewhat richer. It has long been known that face-to-face conversation prior to actual experimental interaction will enhance cooperation dramatically (review in Ostrom, 2003). Evidence that the cooperation-enhancing effect of communication is not just a matter of establishing a personal relationship comes from experiments that involve third parties as conduits of written communications (Mohlin & Johannesson, 2008) or that involve computer-mediated "chat room" interactions (Bochet, Page & Putterman, 2006). Ellingsen and Johannesson (2008) used one-shot dictator games to show that allowing anonymous written feedback induced a substantial increase (ca. 40%) in the size of shares offered by the allocator and an increase in the number of allocators who shared equally (from 30% without feedback to almost 50% with it). A similar study by Xiao and Houser (2007) found a smaller but also positive effect on generosity with anonymous feedback from recipients to allocators. Piazza and Bering (2008) used an experimental variation that mimicked gossiping in social networks, running anonymous one-shot dictator games in which recipients could inform third parties how much the allocator had shared. When the allocator had previously given the third party some personally identifying information, allocations increased by 30%. The researchers conclude that "concerns about being identified and gossiped about play an important role in promoting prosocial behavior" (Piazza & Bering, 2008, p. 178). Complementary effects of communication in enhancing trust have also been demonstrated experimentally, notably in a series of experiments by Bolton, Katok and Ockenfels (2005). Interestingly, linguistic feedback may even substitute for materially expensive means of punishing selfish behavior: Xiao and Houser (2005) found that recipients who could send anonymous written feedback after ultimatum games were less likely to reject "unfair" offers.

This use of linguistic communication (gossip and related forms) for learning about the past behavior (and hence expected future likelihood of cooperation in social dilemmas) is the very lifeblood of reputation management and encouragement of cooperation in small-scale social groups, whether these be hunter–gatherer bands (Wiessner, 2005) or task groups in large-scale agrarian or industrial societies (e.g., business associates, academic departments). However, posing such a crucial role for communication raises problems of honesty (information manipulation) and accuracy (erroneous rumors). As Fehr and Fischbacher (2003, p. 789) put it, "we can use our language to tell the truth or to lie. Thus, what ensures that individuals' reputations provide a reasonably accurate picture of their past behaviours?"

It would be naïve to deny that such factors reduce the value of linguistically derived information and reputation (Nettle, 2006). Nevertheless, language likely provides some net gain in knowledge about who cooperated with whom, or else why would people so avidly seek out such information (Nakamaru & Kawata, 2004). There are in fact several tactics that people use to increase the accuracy of second-hand information, including cross-checking it via multiple independent sources, weighting statements of observers over second-hand sources and discounting statements from parties with personal interests in the third parties involved (Hess & Hagen, 2006; Smith, 2003, p. 419; Sommerfeld, Krambeck & Milinski, 2008). However, the effectiveness of indirect reciprocity is sensitive to error rates (Panchanathan & Boyd, 2003), and much work remains to be done on this problem. More generally, we can agree with Nowak and Sigmund (2005, p. 1295) that "the co-evolution of human language and cooperation by indirect reciprocity is a fascinating and as yet unexplored topic."

3.5. Signaling strategies

Signaling theory is a relatively new approach to analyzing collective action and provides an interesting alternative to reciprocity-based accounts of cooperation. There are various ways in which honest signaling can be evolutionarily stable (Maynard Smith & Harper, 2003), but here I am primarily concerned with costly signaling.

The basic requirements for a costly signaling dynamic can be summarized as follows (Bliege Bird & Smith, 2005; Johnstone, 1997):

(1) Individuals vary in one or more socially relevant attributes ("quality") that are difficult to perceive directly (e.g., immune competence, cognitive abilities, social network size);
(2) Signal costs or benefits are quality dependent (e.g., lower quality signalers pay higher marginal signal costs);
(3) The best move for signal observers is to respond in ways that also benefit the signaler (e.g., forming alliances with high-quality signalers, choosing them as mates or deferring to them in competitive contexts).

Note that variation in signaler quality need not be genetic; for example, wealth could be inherited by an adopted child, yet signaling extraordinary wealth (e.g., through conspicuous consumption or high levels of philanthropy) could still yield social benefits that translate into fitness gains. Do such cases still lend themselves to evolutionary analyses? Yes, because the linked strategies of signaling more when one's quality is high, and responding in mutually beneficial ways to such signals, are plausibly products of genetic or cultural evolution.

To apply signaling theory to collective action, we can introduce a signaling dynamic into a standard *n*-player prisoner's dilemma (public goods) interaction. Suppose that if an individual provides some collective good, this constitutes an honest signal of high quality — for example, of productive efficiency, wealth or social network size. Suppose this signal induces one or more observers to behave favorably towards the signaler: choosing Ego as ally or mate, or deferring to Ego in a contest over status or resources. Such a response boosts the signaler's expected payoff from collective action by an amount s, as shown in Table 7. Depending on the effect s has on the relative payoffs of different strategies, signaling can make cooperation the best move for a high-quality player (Gintis, Smith & Bowles, 2001). Specifically, even unilateral cooperation (the sucker's payoff in a standard prisoner's dilemma) can be stable if R>T and S>P, which in this case reduces to $s>c$ (Table 7); in other words, signaling dissolves the dilemma as long as the benefit of signaling exceeds the signaler's cost of producing the collective good.

Although several authors (beginning with Zahavi, 1977) have suggested that honest signaling logic could apply to cooperative acts (Boone, 1998; Roberts, 1998; Smith & Bliege Bird, 2000), Gintis et al. (2001) were the first to formally model how a signaling dynamic could be extended into an *n*-player collective goods context. Analysis of the model shows that honest signaling via providing a collective good can be stable if standard conditions for honest signaling are met: the cost of providing the public good is less than the benefit of being chosen as an ally for high-quality but not for low-quality types, and there is a net benefit from allying with high-quality rather than with low-quality types (Gintis et al., 2001).

One interesting aspect of the costly signaling approach to collective action is that signaling by providing collective goods increases "broadcast efficiency" (Smith & Bliege Bird, 2000): sharing food at a feast attracts a larger audience than sharing the same amount of food with your neighbor, and fighting valiantly in a major battle broadcasts your quality to many more people than fighting in a duel. Thus, for appropriate settings and signals, the potential for signaling to solve CAPs increases with group size — the opposite of the usual case.

Table 7
The effect of signaling on payoffs to collective action

	Others contribute	Others shirk
Ego contributes	$b-c+s$	$s-c$
Ego shirks	b	0

The parameter s represents the gain to Ego from signaling by contributing to a collective good (assumed here to be the same whether cooperation is mutual or unilateral, although it will be higher for unilateral cooperation, if this is more costly and thereby signals higher quality).

To date, there are few empirical studies of the role of signaling in collective action. One in which I have been involved analyzed why sea-turtle hunters among Meriam islanders of Torres Strait, Australia, provide their catch to communal feasts (Bliege Bird, Bird, Smith & Kushnick, 2002; Bliege Bird, Smith & Bird, 2001). We argue that turtle hunting signals qualities such as vigor, risk taking, foraging ability and knowledge, cognitive skills, and leadership. By doing so, successful and frequent turtle hunters begin reproducing earlier, average a higher number of mates, have mates of higher average quality, obtain higher reproductive success at all ages and end up with more than twice as many surviving offspring as nonhunters (Smith, Bliege Bird & Bird, 2003). Benefits to observers are hard to measure, but may include reproductive gains (to mates, and to parents who prefer to arrange marriages with successful hunters), political gains (from alliance) and avoiding more costly forms of competition (among male peers). Similar findings have now been reported for Indonesian whalers (Alvard & Gillespie, 2004), Micronesian fishermen (Sosis, 2000) and generous hunters among the Ache (Gurven, Allen-Arave, Hill & Hurtado, 2000) and Tsimane (Gurven & von Rueden, 2006).

Signaling via providing collective goods has also been reported or hypothesized for several noneconomic arenas, particularly various forms of religious ritual (Boone, 1998, 2000; Irons, 2001; Sosis, 2003; Sosis & Alcorta, 2003; Sosis & Bressler, 2003; Sosis, Kress & Boster, 2007; Wilson, 2008). Hagen and Bryant (2003) have proposed that even secular rituals involving communal dancing and song may have been selected as signals of group solidarity that could attract allies and deter competing groups.

A recent flurry of experimental studies of collective action explicitly or implicitly invoke honest signaling. Milinski, Semmann and Krambeck (2002) ran an experiment in two parts, where subjects whose identities were "known" (via pseudonyms) to other members of a small group first chose how much to donate to a prominent relief organization and then engaged in further within-group interactions. Those who donated more to charity received increased allocations from the members of their group and were more likely to be elected to represent their group. Milinski et al. concluded that charitable "donations may thus function as an honest signal for one's social reliability." Barclay (2004) showed that participants in a public-goods game contribute more when they are told they will play a dyadic trust game afterwards and that participants do tend to trust public-good donors more than nondonors. Further experiments demonstrated that participants in a public-goods game with an option for punishing free riders rated punishers as being more trustworthy and worthy of respect than nonpunishers; only punishment directed at free riders brought monetary benefits, suggesting that people distinguish between justified and unjustified punishment and only respond to punishment with enhanced trust when the punishment is justified (Barclay, 2006). Similarly, Nelissen (2008) found that those who paid higher costs to punish noncooperators received greater trust in subsequent dyadic interactions.

Barclay and Willer (2007) used a dyadic prisoners dilemma game with varying opportunities for partner choice and signaling of cooperative intent for future rounds with observers; they found that subjects were more generous when they stood to benefit from being chosen for cooperative partnerships, and the most generous subjects were correspondingly chosen more often as partners. Similarly, Bereczkei, Birkas and Kerekes (2007) demonstrated that subjects were more willing to make charity offers in the presence of their group mates than in anonymous situations and that those donors received significantly higher scores than others on scales measuring sympathy and trustworthiness. Albert, Güth, Kirchler and Maciejovsky (2007) obtained similar experimental results and also found that high donors achieved higher-than-average payoffs by cooperating predominantly with other high donors, indicating that signaling can serve as a device for positive assortment of cooperators. Hardy and van Vogt (2006) extended these findings by showing that as the cost of cooperating in public-goods experiments escalated, the status gains for contributors increased.

Thus, the signaling account of collective action thus has both theoretical and empirical support. Yet important limitations need mention. First, the ethnographic and experimental evidence that collectively beneficial “altruism” can serve as a costly signal which will garner status benefits for the signaler does not mean that all, or even most, such prosocial action is produced by costly signaling dynamics. The widespread existence of norms and practices for detecting and punishing free riders in myriad systems of collective action and common-property regulation (e.g., Fehr & Gächter, 2002; Ostrom, 1990; Price, 2003) shows that signaling alone cannot solve all CAPs and that reciprocity and punishment are equally or more important.

Second, skeptics have rightly asked why high-quality individuals should signal by providing collective benefits rather than some more “selfish” displays that would also yield nonsignaling benefits. For instance, why do Meriam turtle hunters not have their turtles (i.e., capture them as a signal) and then eat them too or even burn them on the beach? One answer is that people everywhere do sometimes engage in costly displays that are selfish or wasteful. However, there are several reasons why signals that provide collective benefits will sometimes be favored over those that are collectively neutral or even harmful. First, signaling via providing collective benefits may attract more observers (enhance “broadcast efficiency”), as discussed above; this in turn increases the gains from signaling whenever there is an advantage in broadcasting widely (Smith & Bliege Bird, 2000). Second, contributing to collective goods may reliably signal qualities that are intrinsically valuable to potential allies or mates, such as productive ability, cooperativeness or political savvy (Gintis et al., 2001; Smith & Bliege Bird, 2005). Third, group selection among multiple equilibria (Boyd & Richerson, 1990) may favor those signaling strategies that enhance the success of the signaler’s social group in competition (direct or indirect) with other groups.

The role of language in costly signaling is not well understood. On the one hand, signaling is a theory of communication, and thus language should be amenable to signaling analyses; yet “talk is cheap” and thus appears to fall outside the costly signaling framework. Appearances can deceive, however: although language has low production costs, dishonest language — like experimentally altered status badges of sparrows — has high social costs (Bliege Bird & Smith, 2005; Lachmann et al., 2001). Although language can be used to deceive, the reputational costs of being considered dishonest are likely to be severe in many social ecologies. This assertion, however, needs empirical verification.

The more relevant issue here is what effects language (symbolic communication) has on the prevalence and evolutionary fate of collectively beneficial signals. These effects might be several, but one important effect is in efficiently disseminating the identity of signalers (as well as slackers) widely. A Meriam hunter who provides turtles for an island-wide feast is observed doing so by just a handful of people, but his identity rapidly becomes known to dozens of feast attenders and becomes general knowledge throughout the island within a few days. “Word of mouth” is very effective at spreading information about public displays of generosity, bravery and other collective goods. Put simply, language amplifies the “broadcast efficiency” of a given signal and hence can dramatically increase the potential reward to the signaler, thereby enhancing the motivation for such signals.

3.6. Group selection

The final explanatory approach to collective action discussed here involves multilevel selection, specifically cultural group selection. Owing to the unsettled nature of the debate over the importance of group selection (Boyd & Richerson, 2007; Gardner & Grafen, 2009; Leigh, 2009; West, Griffin & Gardner, 2007; Wilson & Wilson, 2007) and the paucity of empirical tests of cultural group selection models, this section will be brief.

As in most analyses of the evolution of cooperation, a key aspect of group selection models is the positive assortment of cooperators. What process can result in cooperators mostly interacting with each other, thus reaping sufficient fitness benefits from cooperation to counter the costs of cooperation and the diversion of greater net benefits to defectors (free riders)? Unlike other approaches, with multilevel selection the general assumption is that selection within groups will favor defectors, thus requiring higher-level selection to stabilize (costly) collective action. Thus, positive assortment of cooperators must generally hold at the local group (e.g., deme) level, not simply in dyads or coalitions of actors. For genetic group selection, this generally requires rather special forms of population structure with very low migration rates (gene flow) between demes. Although some recent models and empirical estimates have argued for this possibility in human evolution (Bowles, 2006, 2009), the models reviewed here involve culturally transmitted variation in strategies.

One special property of cultural transmission that can facilitate group selection is *conformism*; unlike the genetic case, immigrants who bring uncooperative strategies into a local group with high frequencies of cooperators may often adopt the local cultural variant. In some models, this is simply an innate feature of social learning, presumably favored (in past genetic evolution) because conformists were able to reap advantages through adopting local cultural variants when the costs of evaluating alternative variants were high and the chances were good that local variants were adaptive due to recent cultural evolution. Such conformist psychology can help reduce within-group variance, even if countered by innate propensities to pursue self-interest over collective interest (Boyd & Richerson, 1985; Henrich & Boyd, 1998). Although language is not needed for conformism, it is clear that linguistic codification and instruction would facilitate learning complex behavioral norms and rules (e.g., "In our group we do not allow men to marry their father's sister's daughters") when immigrating into a new group. This would greatly increase the range of group-beneficial practices that could be transmitted, as well the accuracy of such transmission.

Other models of cultural group selection posit active *inducements* to cooperation. These can involve punishment of nonconformists (including noncooperators) or rewarding of conformists (cooperators). Costly punishment (Fehr & Gächter, 2002) is one candidate for stabilizing large-group cooperation. However, it poses higher-order CAPs: punishing free riders is both individually costly and collectively beneficial, and hence could itself require enforcement (punishment of nonpunishers, and so on in infinite regress). Analytical and simulation models suggest that cultural group selection could plausibly solve these higher-order CAPs, by making altruistic collective action sufficiently common that punishment is rarely required, reducing the within-group fitness cost of enforcement to levels low enough to be maintained by modest amounts of conformism and cultural group selection (Boyd et al., 2003; Henrich & Boyd, 2001).

What role could language play in facilitating punishment-enforced collective action? Clear and widely understood norms of sanctioning noncooperators could induce self-interested cooperation; language might play a large role in achieving both clarity and common knowledge. Experimental evidence shows that if people are informed that noncontribution in a public-goods game can be punished, they are much more likely to do punish and to prefer this over a nonpunishing environment in which collective action is unstable (Gürerk, Irlenbusch & Rockenbach, 2006). Of course, this presupposes that such group-beneficial norms exist; for this, some form of equilibrium selection may well be needed (Boyd & Richerson, 1990, 2009).

Reward-based inducements to collective action are of course integral to costly signaling and indirect reciprocity explanations, as reviewed above. Their role in group-selection models is less prominent. One model developed by Boyd and Richerson (2002) involves payoff-biased imitation across group boundaries: if one social group happens to have developed institutions or norms for solving collective-action problems, thereby increasing average payoffs, members of a neighboring group may selectively imitate them and adopt these institutions or norms. Language might sometimes facilitate this process: a traveler might return to his home group and explain how foreigners have come up with a beneficial custom or institution. On the other hand, language barriers between groups could impede between-group transmission of such solutions to CAPs, making it unclear what the net effect of language on such a process would be.

Language can also be employed in a more instrumental fashion, to reward those who contribute to collective action. This includes oral and written praise for cooperators that is disseminated publicly as well as in private conversation: gossip can be used to enhance the reputation of cooperators in the same way that it can be used to denigrate that of free riders. Kniffen and Wilson (2005) analyzed the role of gossip in small social groups producing collective goods (sports teams) and found that both forms (denigrating free riders, praising contributors) were prevalent. However, it is not clear to me that this process, nor payoff-biased imitation across group boundaries (Boyd & Richerson, 2002), exemplifies what most researchers would define as group selection.

In sum, the role of language in processes of multilevel selection is under-theorized, nor has it undergone much empirical analysis. At this point, little can be concluded about the effect of language on this potentially important mechanism for the evolution of collective action.

4. Synthesis: how can language help solve CAPs?

Having surveyed a range of explanations for how humans might evolve solutions to CAPs, and various evidence bearing on these explanations, let me bring the central points of my argument together. What I hope to have shown here is that in a variety of payoff environments, ranging from coordination games to conditional or indirect reciprocity to signaling interactions, linguistic communication can play a critical role in favoring the evolution of collective action.

Specifically, the human capacity for high-volume, fine-grained symbolic communication:

(1) simplifies otherwise difficult or intractable coordination problems, especially those involving many players and/or planning of future events;
(2) reduces costs of monitoring and enforcing adherence to collectively beneficial norms, in various ways (see Table 8);
(3) enhances the broadcast efficiency of signals, including those which provide collective goods;
(4) facilitates positive assortment of individuals who adhere to similar norms and conventions.

More generally, language allows efficient communication about spatially and temporally remote events (Hauser, Chomsky & Fitch, 2002; Pinker & Jackendoff, 2005), which greatly expands the type and scope of collective action, be it economic or military. In addition, language greatly facilitates the creation and propagation of conventions (such as rules for dividing a collectively produced good) that both clarify individual gains and responsibilities in collective action and greatly reduce the transaction costs involved in arriving at these conventions. Finally, language is probably critical for conversion from one set of norms to another. Norms governing myriad facets of daily life are of course a pervasive feature of human society, and in certain domains they require consensus and coordination in order to function properly. For example, norms governing marriage (who is eligible to marry whom, where do the newlyweds live, what property is transferred between the families of the bride and groom, etc.) must be shared within a community in order for marriages to be contracted: a family believing in bridewealth cannot agree on marriage arrangements with a family practicing dowry traditions, and so on. As ecological and social conditions change, however, a community may find itself "stuck with" a set of norms in some domain that are Pareto-inferior (yield lower collective benefits) to some alternative set (Panchanathan & Boyd, 2004); for example, new modes of subsistence might favor a shift from communal land ownership to kin-group ownership, but require a shift in norms of property rights in order to realize these potential gains. Language, used persuasively to articulate the gains to be had, could play a crucial role in building consensus for a shift to Pareto-superior norms and in facilitating collective action to overcome the enforcement of old norms (Hardin, 1995; Kaplan et al., 2005).

There is another effect of symbolic communication that is rarely addressed in the evolutionary literature on group cooperation: technological developments that allow potentially massive increases in the benefits of collective action. The role of technological innovation in the growth of economic production and demographic expansion is of course a central issue in various social sciences and lies at the center of Marx and Engel's classic theory of historical materialism (Cohen, 1978). As technology develops, it often opens up new possibilities for production that require solving various CAPs; large-scale irrigation (Lansing & Miller, 2005), subsistence whaling (Alvard & Nolin, 2002) and fixed-facility salmon fishing (Donald & Mitchell, 1994; Langdon, 2006) are just three examples that come readily to mind. Language plays a crucial role here not only through the various mechanisms of cooperation (reciprocity, etc.) discussed earlier, but by serving as a medium for transmission of cultural information that makes cumulative technological development possible (Boyd & Richerson, 1996). Language thus serves as a midwife to the elaboration of technology and, indeed, may be said to provide much of the cognitive basis for it.

Viewed in this light, technological abilities dramatically increase the potential gains from collective action (i.e., the difference between cooperative and noncooperative outcomes) and hence the incentive to find solutions to CAPs. Coupled with the ways language expands the evolutionary feasibility of various solutions to CAPs (through enhanced monitoring and enforcement, reputation effects and the other means discussed above), the unprecedented scale of large-n, low-r cooperation in *Homo sapiens* becomes much easier to understand.

Table 8
Summary of ways in which language can facilitate evolution of collective action

Effect of language	Payoff environment[a]
Simplify or clarify coordination problems	M
Define norms, rules and punishments, and commitments to these	CR, GS
Reduce costs of monitoring compliance (detecting free riders)	CR, IR
Amplify costs of defection and benefits of cooperation (via reputation effects)	IR
Enhance broadcast efficiency of signaling	HS
Coordinate low-cost collective punishment	All
Facilitate assortment of those with similar norms and conventions	All

[a] CR=Conditional reciprocity; GS=group selection; HS=honest signaling; IR=indirect reciprocity; M=mutualism.

5. Conclusions and prospects

Humans are extraordinarily successful at solving CAPs, even in large groups, and even when relatedness is low. Although there remains disagreement, mounting evidence strongly suggests that conventional explanations for the evolution of cooperation — conditional reciprocity, kin selection and mutualism — are insufficient to account for the pattern and scale of collective action in the human species. At the very least, we need to recognize the ways in which symbolic communication augments these standard evolutionary mechanisms, providing powerful tools for solving CAPs in ways not available to other species.

Theory and data strongly suggest that coordination problems increase dramatically with group size, as do transaction costs (e.g., deciding how to produce and then allocate a collective good). Under many conditions, language facilitates complex coordination and is essential for establishing explicit norms and allocation rules that motivate people to cooperate voluntarily in large groups. Language also significantly lowers the cost of detecting and punishing free riders, thus greatly enhancing the scope and power of standard conditional reciprocity. In addition, symbolic communication encourages new forms of collectively beneficial displays and reputation management — what evolutionists often term “signaling” and “indirect reciprocity.”

Symbolic communication also creates new ways to benefit from collective action, involving technology as well as communication about events at times and places beyond the here and now. These factors can greatly amplify the potential gains from group cooperation and hence increase the incentives (fitness payoffs) for solving CAPs. In sum, language is a novel adaptation that opens up new niches for our species. As noted in the introductory section, I am not claiming that the capacity for language evolved *because* of its usefulness in solving CAPs (though this claim is plausible — see Hurford, 2007, for a recent review). I simply argue that once some system of symbolic communication came into being, it could be used to increase the scope and intensity of collective action; this in turn would increase selective pressures to improve the efficiency and accuracy of communication — a positive feedback dynamic or co-evolution of language and collective action. In sum, the theory and empirical evidence reviewed herein strongly suggest that language amplifies some existing forces favoring the evolution of cooperation, while also helping to create new opportunities for collective action not available even to our closest primate relatives.

Language has not been a central focus of research on cooperation in either social science or evolutionary theory. Social science analyses of collective action have naturally assumed human communication abilities, taking human exceptionalism for granted. Evolutionary theorists have aimed at crafting models of the evolution of cooperation with sufficient generality to apply to a broad range of species and thus naturally avoided any assumptions about specialized communicative abilities. Thus, both traditions — each for their own reasons — have generally overlooked a key element that allows large-*n*, low-*r* collective action to flourish in our species.

There remain many important problems for future research on language and the evolution of cooperation. One major issue is the prevalence of lies and half-truths. I have briefly addressed the issue of what keeps language (partially) honest above. Language itself can be seen as a form of large-*n*, low-*r* cooperation, in the sense of a shared system of meanings, thus raising the same CAPs that lie at the heart of this essay (Nettle, 2006). In any case, we clearly could benefit from more realistic models of the evolution of human cooperation, ones that directly incorporate language and the social processes with which it is closely connected. Evolutionists interested in *Homo sapiens* have much to explore at the intersection of cooperation and communication.

Acknowledgments

This article began as a plenary address to the Human Behavior and Evolution Society in June 2003; I thank Ray Hames and the other meeting organizers for inviting me. A version was also presented to the joint Anthropology, Biology, and Psychology colloquium series at the University of New Mexico (February 2004), and I thank Jim Boone for inviting me and for several stimulating discussions on the topics discussed herein. For comments on the manuscript, I am grateful to Pat Barclay, Carl Bergstrom, Ed Hagen, Richard McElreath, Daniel Nettle and Karthik Panchanathan.

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