CHAPTER 22

Culture and the Evolution of Human Sociality

Alex Mesoudi *and* Keith Jensen

Abstract

Compared to other species, humans are unusual in both our capacity for extensive and cumulative culture and our large, non-kin-based cooperative societies. In this chapter we review recent theories that draw links between these two unusual traits. Theories of indirect reciprocity posit that language allows cooperation to be maintained in human groups through the formation of reputations, and cooperation can also be maintained through altruistic or third-party punishment of noncooperators. The theory of cultural group selection holds that cooperative tendencies arose as a result of competition between internally cohesive cultural groups in human prehistory. We also discuss the role of social emotions in maintaining cooperative societies. Finally, we review recent work that suggests that population size can set limits on the degree of cultural complexity that can be maintained, suggesting a two-way interaction between culture and sociality.

Key Words: Cooperation, culture, cultural evolution, cultural group selection, human sociality, punishment

Introduction

Compared to other species, humans are rather unusual in two respects. The first is our capacity for *culture*. We effortlessly and automatically acquire huge amounts of information from other individuals via imitation, language, and other forms of social learning to a much greater extent than any other species, such that human culture forms a new evolutionary inheritance system in which vast bodies of technological and social knowledge are preserved and accumulated over successive generations. The second is our *sociality*. We live in large and highly cooperative societies in which genetically unrelated individuals frequently and often voluntarily exchange resources and information with one another, from the market-based economies and democratic political systems of many large-scale industrial societies to the smaller-scale trade networks and food-sharing customs of hunter-gatherer societies.

In this chapter we review a growing body of research that has attempted to link these two unusually human traits of culture and sociality. We stress at the outset that these links are far from definitive, and the issues are currently being vigorously debated. Some researchers, for example, have argued that the high fidelity cultural transmission allowed by language permits the formation of reputations, which in turn allows reciprocity-based cooperation to emerge (e.g., Nowak & Sigmund, 2005; Sommerfeld, Krambeck, Semmann, & Milinski, 2007). Others have suggested that the unusually strong cooperation that forms the basis for human sociality has emerged, not by reciprocity, but via a process of cultural group selection, where internally cooperative societies outcompete less internally cooperative societies (e.g., Gintis, Bowles, Boyd, & Fehr, 2003; Henrich, 2004a). It has also been suggested that sociality permits culture; specifically, that complex technological and social traits can only be preserved and accumulated once societies are large enough to prevent the accidental loss of beneficial traits (e.g., Henrich, 2004b; Powell, Shennan, & Thomas, 2009). Before considering these theories, we first review the evidence concerning the unusualness of both human culture and human sociality.

Human Culture

Although the term *culture* was once defined as being unique to humans (e.g., Kroeber, 1948), recent decades have seen a much-needed widening of the concept that has allowed its comparative study. Rather than defining culture in terms of a single Rubicon-like defining characteristic, it is more productive to break the concept down into its constituent processes and examine the evidence for each of these in different species (Laland & Hoppitt, 2003; Whiten, Horner, & Marshall-Pescini, 2003). A basic requirement of culture is that it involves some kind of social learning, that is, the transmission of information from one individual to another nongenetically, via imitation, emulation, stimulus enhancement, or any other social learning mechanism. There is good evidence for social learning in a wide range of species, including mammals, birds, fish and insects (Galef & Laland, 2005; Leadbeater & Chittka, 2007). One step up from a basic capacity for social learning is the existence of stable between-group differences in behavior that result from social learning (rather than being caused by genetic differences or individual adaptation to local ecological conditions). These can be termed cultural traditions. Again, there is good evidence for the existence of cultural traditions in several species, from tool-use traditions in primates (van Schaik et al., 2003; Whiten et al., 1999) to song dialects in birds (Catchpole & Slater, 1995) to schooling sites in fish (Helfman & Schultz, 1984).

Yet humans appear to be unusual in the extent to which we acquire information from other conspecifics nongenetically and the means by which we acquire that information. In a direct comparison of the cultural and physical intelligence of human children, adult chimpanzees, and adult orangutans, Herrmann, Hernandez-Lloreda, Hare, and Tomasello, (2007) found that, although there was little cross-species difference in physical intelligence (e.g., an understanding of quantity or causality), 2.5-year-old human children greatly out-performed the other two species in the cultural tasks (tests of social learning, theory of mind and communication). Other studies have shown that children overimitate, copying the actions of adults even when it is inappropriate to do so (Lyons, Young, & Keil, 2007), in contrast to chimpanzees who default to individual learning in such situations (Horner & Whiten, 2005).

These individual-level differences between humans and other species in the extent and use of social information seem to result in qualitative large-scale differences between human and nonhuman culture. As Tomasello (1999) has highlighted, human culture is uniquely *cumulative*. Beneficial techniques, innovations, ideas, and skills are faithfully preserved and accumulated over successive generations of humans in a way not seen in any other species. Technology such as cars or computers, and knowledge such as quantum mechanics, are the accumulated product of countless people over thousands of years and could never have been invented by a single individual alone (Basalla, 1988; Wheeler, Ziman, & Boden, 2002). Even what we might consider as "simple" technology, such as the bow and arrow of hunter-gatherer groups, features multiple working parts all interacting with one another in a precise manner. For example, the bow and arrow of the San people of Botswana have 1-meter-long bows with strings made of animal tendons, arrow shafts made of reeds, an arrowhead of ostrich bone (or more recently barbed wire) poisoned using beetle larva, and quivers made of tree roots (Henrich, 2008). In contrast, the culturally acquired behaviors of other species, such as chimpanzees' nut-cracking or termite-fishing behaviors, do not seem to have been accumulated over successive generations and could potentially be invented by a single individual.

This cumulative characteristic makes human culture an evolutionary process (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Mesoudi, Whiten, & Laland, 2004, 2006; Mesoudi, 2011). Just as genetic evolution involves the selective accumulation of beneficial genetic mutations over successive generations, so, too, human culture involves the selective accumulation of beneficial cultural variants. Once cultural evolution is operating, it can significantly alter evolutionary dynamics (Boyd & Richerson, 1985; Laland, Odling-Smee, & Myles, 2010). Cultural evolution allows new kinds of behavior to evolve (culturally and/or genetically) that would not be possible in its absence, from the fixation of new genes for lactose tolerance as a result of the cultural practice of dairy farming (Beja-Pereira et al., 2003) to the emergence of new polygamous mating systems in response to culturally transmitted beliefs about paternity (Mesoudi & Laland, 2007). Rapid cultural evolution also generates substantial cross-cultural variation to a far greater extent than the cultural traditions of any other species. Whereas chimpanzees exhibit just 39 culturally variable behaviors (Whiten et al., 1999), linguists have documented almost 7,000 languages (Grimes, 2002), ethnographers have documented hundreds of culturally variable customs and beliefs (Murdock, 1967), and cross-cultural psychologists have documented extensive cultural variation in psychological traits (Heine & Norenzayan, 2006).

Human Sociality

The basis of human sociality, like the sociality of any species, is cooperation. Individuals living together in social groups must at the very least tolerate one another's presence, and the more complex forms of sociality require their members to engage in cooperative interactions, such as working together to acquire food and then sharing that food. The vast majority of the cooperative interactions between members of nonhuman species are directed toward kin. In many species, parents care for their offspring and siblings form alliances to secure mates and resources. Most striking of all, eusocial insects form highly cooperative societies containing millions of (genetically highly related) individuals with complex division of labor and collective defense mechanisms.

The reason why cooperation is so often directed toward kin has been understood since the seminal work of W.D. Hamilton in the 1960s. Hamilton (1964) was the first to formally establish that helping one's kin is evolutionarily advantageous because one's kin are likely (specifically, more likely than a randomly selected individual) to share genes that code for kin-directed helping. So helping kin also helps to spread kin-helping genes: from a gene-level perspective, cooperation is entirely self-serving (Dawkins, 1976). The more likely two individuals are to share such genes, the stronger the cooperation. Therefore, two siblings, who have a 50 percent chance of sharing a particular version of a gene, will be more cooperative toward one another than two cousins, who have just a 12.5 percent chance. Eusocial insect societies are so highly cooperative in part because of their unusual haplodiploid genetic system, which means that workers have a 75 percent chance of sharing a particular version of a gene in monogamous species (West & Gardner, 2010).

A few cases of nonhuman cooperation may involve direct reciprocity (Trivers, 1971), where one individual helps another unrelated individual in exchange for a future return. Again, this is consistent with a gene-level perspective because the future return compensates for the immediate loss: the helpful individual receives direct, though delayed, fitness benefits. A classic example of direct reciprocity involves vampire bats (Wilkinson, 1984). Bats that have been unusually successful on a nightly feeding trip have been observed to regurgitate blood into the mouths of unsuccessful neighbors. In the future, when the roles are reversed and the previously altruistic bat is unsuccessful on its feeding trips, the previous recipient will return the favor. However, this example has recently been reinterpreted in terms of kin selection, and robust cases of direct reciprocity are relatively rare in nature; most nonhuman cooperation is kin directed (Hammerstein, 2003).

Humans also preferentially direct help toward genetic kin. Parents expend huge amounts of resources raising offspring, and nepotistic favors toward family members are common (Burnstein, Crandall, & Kitayama, 1994; Madsen et al., 2007; Silk, 1980). People are also quite effective reciprocators, showing a particular talent in detecting potential free-riders who are reneging on reciprocal arrangements (Cosmides, 1989). However, a growing body of research suggests that human cooperation goes beyond that predicted by the theories of kin selection and direct reciprocity. One line of investigation involves experimental games developed by behavioral economists. Like biological "selfish-gene" theories of cooperation, traditional economic explanations of cooperation return to individual benefit: people only ever help others when it ultimately benefits themselves. Yet the behavior of participants in experimental games often violates this prediction: people frequently cooperate with nonrelatives in anonymous, one-shot interactions in which there is no expectation of any future return or reputation enhancement (Fehr & Fischbacher, 2003; Gintis, Bowles, Boyd, & Fehr, 2003). In the Ultimatum game, for example, one player, the "proposer," divides up a sum of money, say $100, between him- or herself and another player, the "responder." The responder then either accepts the split, in which case both players get the determined amount of money, or rejects the split, in which case neither player gets anything. The purely self-interested choices would be for the proposer to offer the smallest possible nonzero amount (e.g., $1) keeping as much as possible (e.g., $99) for him- or herself. A purely self-interested responder, faced with a choice between $1 (if they accept the split) or $0 (if they reject) should choose the former.

Yet people typically make offers of 50 percent of the total amount, and responders routinely reject any offers of less than 20 percent (Camerer, 2003; Fehr & Fischbacher, 2003; Gintis et al., 2003; Güth, Schmittberger, & Schwarze, 1982). This finding—that people behave cooperatively according to some sense of fairness, rather than in a purely self-interested manner—has been replicated in numerous and varied human societies worldwide (Henrich et al., 2005), albeit with some degree of cultural variation (see later). Yet our closest living relative species, chimpanzees, show no sense of fairness in experiments like the Ultimatum game, and they do behave in a purely self-interested manner: proposers do not make fair offers, and responders accept any nonzero offer even when it is unfair (Jensen, Call, & Tomasello, 2007a; see also Silk et al., 2005 and chapter 20 of this volume).

These experimental findings are supported by observational studies of actual human and nonhuman social interactions. People living in hunter-gatherer societies frequently cooperate with nonrelatives when obtaining and sharing food (Hill, 2002). Similarly, interactions within business organizations in industrial societies are driven by fairness rather than pure self-interest (Fehr, Goette, & Zehnder, 2009). Workers, for example, are typically concerned that their pay matches equally skilled workers in similar positions rather than with their absolute wage level. These patterns contrast, again, with nonhuman primate societies, which are characterized by Machiavellian-like competitive interactions (Byrne & Whiten, 1988). Although there is some suggestive evidence that nonhuman animals, particularly monkeys and apes, may be averse to personally disadvantageous inequitable outcomes (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010), the evidence is equivocal (Jensen, in press); the Ultimatum game, discussed later, will serve as an example. When non-kin-directed cooperation does occur within nonhuman primate groups, such as coalitions between pairs of individuals, these typically serve the self-interested function of outcompeting other group members over food or mates. In fact, human societies more closely resemble the aforementioned eusocial insect societies with their vast numbers, cooperative exchange of resources, collective group defense, and division of labor. Yet whereas eusocial insect sociality can be explained by kin selection, as noted earlier (see also Foster, Wenseleers, & Ratnieks, 2006), the highly cooperative sociality of humans remains something of a puzzle.

Indirect reciprocity and reputation building

One way in which cooperation might be maintained between strangers is by *indirect reciprocity*. Whereas direct reciprocity occurs when the recipient of help returns the favor back to the original help giver, indirect reciprocity occurs when help givers have their favor returned by a third individual who was not involved in the original altruistic act (Alexander, 1987; Nowak & Sigmund, 2005). Indirect reciprocity works on the basis of reputation: individuals who regularly help others within a group build up a positive reputation for being altruistic. Individuals, then, only cooperate with group members who have reputations above a certain threshold. Free riders cannot exploit groups of indirect reciprocators because they gain a negative reputation and are consequently shunned. Game theoretical models show that indirect reciprocity can lead to the establishment of cooperation in small groups of unrelated individuals as long as each individual has accurate knowledge of other group members' reputations (Nowak & Sigmund, 1998). This theoretical finding is reinforced by the results of lab experiments. Wedekind and Milinski (2000) had pairs of anonymous participants repeatedly play a game in which each partner could either "cooperate," that is, donate an amount of money that was then increased by the experimenter, or "defect," that is, not donate any money to their partner. Although it is better for both players to cooperate than both to defect because each contribution of the joint cooperators is increased by the experimenter, it is even better to defect against a cooperator because that defector would get the inflated donation from their cooperating partner, plus their original undonated amount. Normally, this temptation to free ride eliminates any initial cooperative tendencies in such games. However, when Wedekind and Milinski (2000) allowed each player to see the anonymous partner's past choices (cooperation or defection), then cooperation was maintained. Players refused to cooperate with other players who had a history of defection, or, in other words, had a negative reputation.

It has been suggested that indirect reciprocity may be particularly potent in humans because our greater capacity for culture, and in particular language-based communication, allows the more effective transmission of reputation-related information. Particularly relevant is *gossip*, which typically concerns past positive or negative social interactions such as cheating or deception (Dunbar, 1996;

Mesoudi, Whiten, & Dunbar, 2006). Whereas nonhuman species must directly observe others' cooperative and noncooperative interactions in order to form and update their reputation-based knowledge, gossip allows people to update their reputation-based knowledge without having to be directly present. For example, if Sally observes Bill cheating Sam out of some money, and later tells Simon about what Bill did, then Simon can update his reputation of Bill without actually observing Bill acting uncooperatively.

To test this idea, Sommerfeld et al. (2007) conducted a version of Wedekind and Milinksi's (2000) cooperation experiment in which participants could additionally gossip about other players, by leaving written messages about previous partners that could be read by other participants. In the same way that direct observation of cooperative or noncooperative interactions maintained cooperation in the original Wedekind and Milinski (2000) study, the ability to gossip about the past behavior of participants also maintained cooperation. Players about whom negative gossip was left (e.g., "nasty miser") were shunned, whereas players about whom positive gossip was left (e.g., "generous player") were rewarded with continued cooperation.

Punishment

Another phenomenon that could potentially maintain non-kin-based cooperation in human societies is punishment. Indeed, the previously discussed rejections of offers in the Ultimatum game and the shunning of misers are special forms of punishment. According to learning theorists/behaviorists, "punishment" can be categorized as either the infliction of a cost (positive punishment) or the withholding of a benefit (negative punishment), both of which serve to decrease the frequency of a behavior's occurrence (Jensen & Tomasello, 2010; Seymour, Singer, & Dolan, 2007). To ecologists, punishment is a negatively reciprocal behavior that benefits the punisher, at a cost to the target, at some point in the future; this definition emphasizes the delay in benefits to distinguish punishment from aggression and other biologically selfish behaviors (Clutton-Brock & Parker, 1995). The "problem" of cooperation, as discussed earlier, is the corrosive influence of free riders and cheats. Punishment is more effective in maintaining cooperation than is direct reciprocity, because the individual costs of punishment decline as the number of free riders declines, whereas the costs of cooperation rise as the number of cooperators increases (Boyd & Richerson, 1992b). The threat of punishment can also be a sufficient deterrent to cheating.

Economic experiments demonstrate the effectiveness of punishment in discouraging free riding. In the Public Goods game, individuals playing anonymously contribute to a common pool that is later divided equally. Cooperation, as measured by the level of contribution to the common pool, quickly declines over repeated rounds because the highest payoffs come from not contributing while everyone else does. However, allowing players to cause free riders to suffer losses, even though it is costly for the players to do so, stabilizes cooperation (Fehr & Gächter, 2002). People initially prefer playing these games in environments with no punishment—likely because they are averse to being punished—but soon shift to groups that allow it because these have higher levels of cooperation (Gürerk, Irlenbusch, & Rockenbach, 2006).

This do-it-yourself, or second-party, punishment, where cheated individuals directly punish those who have cheated them, can stabilize cooperation, but it is something that stronger and more dominant individuals are in a better position to do. "Cooperation" in this case, therefore, amounts to coercion. For example, cooperatively breeding animals, such as meerkats, have "helpers" that look after offspring that are not their own, thereby forfeiting their own reproduction (Clutton-Brock, 2002). Aggression from dominants suppresses reproduction in these helpers; subordinates remain because they are better off in the group than going it alone. Whether punishment actually targets noncooperative behaviors such as failing to provide food is a matter of some debate (Jensen & Tomasello, 2010). Experimental evidence shows that chimpanzees, particularly dominant individuals, will retaliate against personally harmful behaviors, namely, having food stolen from them (Jensen, Call, & Tomasello, 2007b), and they will selectively choose cooperative partners over noncooperative ones, effectively "shunning" noncooperators (Melis, Hare, & Tomasello, 2006). Although the outcomes of such positive punishment (inflicting a cost) in the former case and negative punishment (removing a benefit) in the latter case are harmful to the targets, it is not clear how effective these are in discouraging free riding. For instance, in the Jensen et al. (2007b) study, theft increased over time while punishment decreased, demonstrating that punishment in this context was not effective at deterring noncooperative behaviors. Some of the most interesting examples of punishment come from cleaner fish which remove parasites from larger fish referred to as clients. The cleaner fish face the temptation to "cheat" by removing mucous from the clients; doing so results in them being chased away by the clients, or by their partners (Bshary & Grutter, 2005; Raihani, Grutter, & Bshary, 2010). All these examples of punishment in animal societies are interesting, but because they are self-serving, it is difficult to discern punitive acts that target noncooperative behavior from other acts of aggression and coercion (Jensen, 2010).

Of particular interest to cooperation are acts of punishment that do not ultimately benefit the punisher. A special form of punishment, called *altruistic punishment*, has the punisher pay a cost to inflict harm on another individual, resulting in benefits for others. For instance, in the public goods studies already described, the punisher never encountered the free rider again, but others playing the game benefited from playing with the reformed individual. Because the punisher incurs costs that lead to cooperative benefits to others, altruistic punishment has been suggested as a challenge to natural selection at the individual level (Boyd, Gintis, Bowles, & Richerson, 2003; Fehr & Gächter, 2002). This is a matter of considerable debate, both because natural selection measures costs and benefits in terms of fitness, and because of the artificial nature of one-shot, anonymous encounters (Hagen & Hammerstein, 2006; West, Griffin, & Gardner, 2007). There is no experimental evidence of altruistic punishment in nonhuman animals, nor is there much to suggest it from their naturally occurring behavior. The one study that addressed this question directly (Jensen et al., 2007b) found that chimpanzees playing a mini-Ultimatum game would not pay a cost to punish unfair outcomes; as long as the responders got something, they would accept it (which is what would be expected from models of rational self-interest). Had they been altruistic punishers, as people often are, responders would have paid a cost in the form of a rejection to modify the subsequent selfish offers of the proposers. That even our closest living relatives did not do this and so make the proposers "play fair" with themselves speaks against the existence of altruistic punishment in species other than humans.

Third-party punishment is a better test of punishment of noncooperative behavior because the punisher has no stake in the interaction and has not been harmed in any way. Therefore, misguided retaliatory (vengeful) responses are less likely than they might be in experimental tests of altruistic punishment. Examples of institutionalized third-party punishment include the police and judicial system. Informally, one can think of numerous examples of impartial punishment, from small acts such as bystanders scolding jaywalkers to headline news in which good Samaritans die in pursuit of criminals. In one amusing anecdote, a would-be gun-wielding thief was scolded for jumping the queue by a bank patron, and left, discouraged (Bryson, 1995). In experimental economics, third-party punishment is seen when an observer witnesses defection in a prisoner's dilemma, for instance, and pays a part of his endowment to punish the defector (Fehr & Fischbacher, 2004). The benefits to cooperation are obvious. Whether the punisher has punitive motives (Price, Cosmides, & Tooby, 2002), experiences moral outrage (Trivers, 1971) or is somehow seeking a reputation as an enforcer (Barclay, 2006), third-party punishment is clearly distinct from self-serving punishment. There is no unequivocal evidence for third-party punishment in animals other than humans, but some observations are suggestive. Social insects like bees and wasps will "police" by destroying eggs laid by "cheats" for the benefit of the remainder of the hive, but kin selection can fully explain this behavior (Ratnieks & Wenseleers, 2008). In nonhuman primates, there are only a handful of examples of intervention in conflicts (de Waal, 1982; Silk, 1992) although it is not possible to rule out direct benefits to the intervener such as reducing the amount of noise in the group—something that can attract predators—or keeping harem females (the male's reproductive resources) from hurting each other (Schradin & Lamprecht, 2000). As yet, there have been no experimental tests of third-party punishment in nonhuman animals; one purported example in cleaner fish is actually a test of second-party punishment because the punishing male benefits directly and there is no third party (Jensen, 2010 Raihani et al., 2010).

Cultural Group Selection

Indirect reciprocity and altruistic punishment appear to be mechanisms by which cooperation can be maintained in groups. However, there are still shortcomings with these theories. Even with the added benefit of language-based gossip, indirect reciprocity is still limited in the size of the groups in which cooperation can be maintained. Humans still engage in cooperative one-shot interactions with complete strangers (e.g., giving to charity) about whom we have no reputational information, whether via direct observation or via gossip. On the face of it, altruistic punishment would appear to be able to maintain non-kin-based cooperation in large human groups. However, theoretical models show that although this is indeed possible, in fact altruistic punishment can stabilize *any* behavioral norm, not specifically cooperative norms (Boyd & Richerson, 1992b; Panchanathan & Boyd, 2004). If a norm requires everyone to, say, wear a bowler hat, and to punish people who do not wear bowler hats, then bowler-hat wearing will be maintained in the population (as long as the cost of being punished exceeds the cost of wearing bowler hats). Punishment can even stabilize norms that are harmful to the group. If a norm emerged for executing people suspected of being witches (which, for the accuser, may be individually beneficial, but is detrimental to the group as a whole) and failure to follow this norm was punished, then the witch-hunting norm would be maintained in the group. Another process that can stabilize group norms is conformity, where people adopt whatever behavior is most common in their group voluntarily, without the threat of punishment for nonconformity (Henrich & Boyd, 2001). However, again, conformity does not favor cooperation specifically; it simply favors whatever norm is most common, whether it is beneficial, detrimental, or neutral with respect to the group. So according to these models, some additional process is needed to favor the cooperative norms over the noncooperative norms.

Several researchers have argued that *cultural group selection* might be one way in which cooperative, group-beneficial behavior (as opposed to neutral or detrimental behavior) can evolve (Boyd & Richerson, 1985; Gintis et al., 2003; Henrich, 2004a; Richerson & Boyd, 2005). Recall that one of the hallmarks of human culture is the extensive between-group cultural variation that can emerge due to the rapid, cumulative quality of cultural evolution. As detailed earlier, this between-group variation can be maintained by punishment and conformity. Cultural group selection occurs when those groups that are characterized by more highly cooperative norms, such as norms for patriotism, collective defense, and self-sacrifice, are more likely to persist and outcompete groups that are characterized by less cooperative norms, such as norms for free riding and desertion (or, as in the preceding example, witch-hunting). This between-group competition can be direct, via warfare and violent conquest, resulting in the extinction of less cooperative groups. Or the between-group competition can be more indirect, such as when members of less-cooperative groups preferentially migrate to more-cooperative groups because they find the latter's norms, such as lower crime or welfare for the sick, more attractive (Boyd & Richerson, 2009). Alternatively, people living in less-cooperative societies might preferentially copy the attractive norms of more-cooperative societies, without themselves physically migrating (Boyd & Richerson, 2002). The result of all of these processes is a human sociality in which people cooperate with other group members (although not with members of other social groups) who are not necessarily genetically related to them, and who may not directly reciprocate that cooperation. According to Richerson and Boyd (2005), this culturally group-selected human sociality first emerged around 100,000 years ago during the late Pleistocene. At around this time, evidence for large-scale cooperative human groups and large-scale intergroup conflict can first be observed in the archaeological record, for example, in the form of symbolic group markers. They also argue that cultural group selection favored the genetic evolution of hard-wired prosocial emotions, such as guilt, as explored in the next section.

It is important to distinguish this process of cultural group selection from genetic group selection. The latter occurs when genetic traits are favored that benefit unrelated groups of individuals. Although theoretically possible (Price, 1970; Sober & Wilson, 1998), genetic group selection is unlikely to act in reality without the cultural processes already detailed. This is because groups of unrelated individuals are unlikely to persist over time such that group-beneficial (but individually costly) traits can be selected. Selfish free riders can easily invade such groups, shifting selection to the individual (and ultimately gene) level. Cultural group selection, however, does not have this problem: cultural groups *do* persist over time and may be selected as whole units, because they are bound together by punishment and conformity, as was already noted. Migration is also a big problem for genetic group selection: in many group-living species one sex typically disperses out of the group, reducing between-group genetic differences. In humans, however, migrants often acquire the social norms of their new cultural group, maintaining between-group cultural variation and consequently allowing cultural group selection to act.

What evidence is there for cultural group selection having shaped the unusually strong non-kin-directed cooperation that underlies human sociality? First, social psychologists have amassed decades of experimental research showing that people readily identify with their particular social group, and discriminate against other groups (Mesoudi, 2009; Tajfel, 1982). Such psychological tendencies would act to maintain cultural variation and foster intergroup competition. As with the behavioral economics experiments discussed previously, this occurs even when there is no direct benefit to the individual or even to the group as a whole. In the minimal group paradigm, for example, participants assigned to entirely arbitrary groups (e.g., "red" groups and "blue" groups) preferentially allocate points to ingroup members over outgroup members, even when these points fail to translate into monetary payoffs (Tajfel, Billig, Bundy, & Flament, 1971). This ingroup favoritism also appears to show specific characteristics that are consistent with a cultural-group-selection origin, such that levels of ingroup favoritism increase when the ingroup is perceived to be under threat from an outgroup (Rothgerber, 1997), or that ingroup favoritism emerges during development at around the same time, 7 to 8 years of age, as do general nonkin altruistic tendencies such as inequality aversion (Fehr, Bernhard, & Rockenbach, 2008). Second, Henrich et al. (2005) found substantial cross-cultural variation in offers and rejection rates in the Ultimatum game, consistent with the requirement that there exist between-group cultural differences in cooperation that cultural group selection can act upon. Third, Soltis, Boyd, and Richerson, (1995) used ethnographic reports to estimate the rates of extinction of societies in New Guinea prior to Western contact. As noted earlier, extinction due to intergroup conflict is one way in which internally cooperative groups can outcompete less internally cooperative groups. Extinction rates were estimated to be around 10 percent per 25 years, rates that are consistent with cultural group selection (albeit slowly, over several hundred years). Fourth, Turchin (2003) has modeled the rise and fall of empires in Europe during the last few thousand years, finding historical dynamics consistent with a process whereby empires initially expand due to increasingly cooperative internal norms (e.g., collective defense), followed by contraction and conquest due to a weakening of those norms as the empire overstretches itself. Models that did not assume a role for within-group cooperative norms, in contrast, did not generate realistic historical dynamics.

More direct links have been drawn between cultural group selection and the punishment findings discussed in the previous section via the phenomenon of "strong reciprocity" (Gintis, 2000). Strong reciprocators are individuals who are motivated to cooperate and willing to punish those who do not. A minority of strong reciprocators in a group creates a cooperative culture. Because one's own social group is the cooperative environment, strong reciprocators should be more likely to punish noncooperators within the group than outgroup members. This "false- friends" effect was supported in a gift-giving game in which stingy ingroup members were more likely to be punished than scrooges from other groups (Shinada, Yamagishi, & Ohmura, 2004). However, if an outgroup member harms someone within one's group, then the outsider will be punished (Bernhard, Fischbacher, & Fehr, 2006). Cultural forces, and possibly cultural group selection, are clearly relevant to both human cooperative and punitive behaviors.

Social Emotions

One of the chief proximate mechanisms that govern human sociality are social emotions, and these may well have been shaped by the evolutionary processes outlined earlier, such as direct reciprocity, reputation-based indirect reciprocity or cultural group selection. Emotions have classically been regarded as the enemies of reason and have long been ignored when discussing prosociality. However, in the absence of emotions, people have a difficult time making decisions (Damasio, 1995). There is more to social judgments than pure reason (Frank, 1988); emotions act as commitment devices, inducing individuals to action and signaling this to others. For instance, the threat of acting irrationally (i.e., spitefully rejecting money) in an Ultimatum game will make the responder's actions difficult to predict, leaving the proposer little option but to make a fair offer. Socially mediated emotions also bridge the gap between the act of helping and later tangible gains, as required by direct and indirect reciprocity, as well as later costs such as punishment for defecting (Richerson & Boyd, 2005). Mediating psychological mechanisms also decrease the costs of rewards and sanctions; guilt is less damaging to the sufferer and ostracism is less demanding for the punisher than physical assault. Evolution would select for social emotions to allow for cooperation to work when fitness benefits—or costs—are not immediate (Fessler & Haley, 2003).

Social concerns are emotions that are influenced by the welfare of others, namely, their emotions (e.g., happiness) or outcomes that would lead to these feelings (e.g., winning a lottery). Also called fortunes-of-others emotions (Ortony, Clore, & Collins, 1988), having emotions that are sensitive to the emotions and states of others can clearly motivate prosocial behaviors. Feeling happy at another's happiness (symhedonia) can provide emotional rewards for acts of helpfulness and generosity, even though personally material benefits will not be immediately forthcoming, as in direct reciprocity. This is sometimes called warm-glow altruism (Andreoni, 1990) or attitudinal reciprocity (Brosnan & de Waal, 2002). Likewise, feeling unhappy about the misfortunes of others will also motivate helpfulness.

Empathy and sympathy are the prototypically prosocial concerns. Having the emotions appropriate to the circumstances of another individual involves some degree of putting oneself in the position of others (affective perspective taking). This distinguishes empathy and sympathy from emotional contagion, a reflexive response that is likely to lead to self-oriented actions to alleviate personal distress, such as when a child retreats to her mother's arms when seeing someone else harmed (Eisenberg, Shea, Carlo, & Knight, 1991). Empathy appears early in humans, by at least 18 months of age (Vaish, Carpenter, & Tomasello, 2009), but its evolutionary origins are a matter of some debate (Koski & Sterck, in press; Parr, 2001; Preston & de Waal, 2002). The greatest difficulty lies in distinguishing empathy from emotional contagion, some form of which is even shown by mice (Langford et al., 2006), which are not noted for their cooperative behavior. Empathy is an other-oriented emotion of relevance to human sociality that would plausibly have been honed through cultural group selection processes that may not have antecedents in nonhuman species (Silk, 2007; although see de Waal, 2008).

Guilt is another other-oriented emotion that motivates prosociality. It does so by making the transgressor of norms suffer, even if he is not caught and punished. Such self-induced suffering decreases the likelihood of behaving amorally (Tangey, Stuewig, & Mashek, 2007). Individuals who feel guilty for having behaved noncooperatively in an experimental game subsequently become more cooperative (Ketelaar & Au, 2003). If the opportunities for relationship repair are not available, individuals will punish themselves (Nelissen & Zeelenberg, 2009). Guilt, then, can prevent harmful, noncooperative behaviors from occurring in the first place due to the anticipated negative feelings. It is an internal sanction that enforces normative behavior even in the absence of external sanctions, and could theoretically have arisen through cultural group selection (Gintis, 2003).

Antisocial concerns, or negative social preferences, would seem to be, at best, undesirable evil twins of prosocial concerns. This may be the case, but having emotional motivations that lead to harming others can be valuable. Most obviously, taking pleasure in the misfortunes of others (*schadenfreude*) can motivate harmful acts, but also group beneficial ones. For instance, when subjects in an fMRI watch someone (more specifically, the hand of someone) receive a painful stimulus, brain regions associated with empathic pain are activated; however, if that hand belonged to someone who had previously cheated the subject in a prisoner's dilemma, pleasure centers of the brain light up, at least in men (Singer et al., 2006). Taking pleasure in the misfortunes of others, then, can make punishment psychologically rewarding, despite the possible immediate costs. Altruistic punishment is an interesting case because the actor does not receive material benefits for harming a noncooperator whereas others in the group do. Although it might be tempting to conclude that altruistic punishment is motivated by prosocial sentiments or group-focused emotions, such as social pride at righting wrongs, this does not seem to be the case. People who are cheated in economic games report being angry and they show the appropriate physiological and neurological responses (de Quervain et al., 2004; Fehr & Gächter, 2002; Pillutla & Murnighan, 1996; van't Wout, Kahn, Sanfey, & Aleman, 2006). Altruistic punishment may not be prosocial, as implied by its name, but rather antisocial (Herrmann, Thöni, & Gächter, 2008). The motivation of the individual is spiteful rather than altruistic, and the emotions underlying it would include an aversion to inequity—envy is a crude form of this—and *schadenfreude*. Yet the end result would be benefits for others in the group. Cultural group selection could conceivably have fashioned altruistic behaviors out of antisocial, as well as prosocial sentiments. It is speculative to propose that cultural group selection, as opposed to selection at the individual level (e.g., direct reciprocity), produced social emotions, but the existence of so-called *corporate emotions* (Fessler & Haley, 2003), in which one feels anger, pride, shame, gratitude, and so on for the actions of one's group does suggest that some form of group-level process sculpted these emotions.

Large Societies Support Cultural Complexity

The previous sections concern how cultural processes, such as reputation building, third- party punishment, social emotions, conformity, and cultural group selection, may have led to the emergence of large, highly cooperative human societies. A complementary line of research has examined how large, cooperative societies may, in turn, permit the emergence and persistence of complex cultural traits. A model of cultural evolution constructed by Henrich (2004b) explored the relationship between group size and cumulative cultural evolution. In this model, individuals living in groups could acquire a cultural trait (e.g., a skill or technology) of varying complexity from successful members of the previous generation. This cultural transmission was assumed to be imperfect, such that occasional errors in learning changed the skill in some way. These errors usually decrease the complexity of the trait, but occasionally may lead to chance improvements. Henrich (2004b) showed that a global increase in cultural complexity—cumulative cultural evolution—occurred only above a certain group size. Too few individuals meant that transmission errors prevented the preservation and accumulation of beneficial cultural traits. In large enough groups, however, the effects of preferentially copying successful members of the previous generation plus occasional beneficial copying errors outweighed the effect of detrimental copying errors. In other words, culture accumulates only in large enough social groups.

Powell and colleagues (2009) recently used this model to explain the emergence of complex cultural traits in human prehistory. The archaeological record indicates that a set of complex cultural traits, such as systematically produced stone tools, symbolic cave paintings, decorative body ornaments, hunting technology such as spear-throwers and nets, the long-distance transfer of raw materials, and musical instruments, first appeared together around 45,000 years ago in Europe and Western Asia, around 40,000 years ago in Africa, and 20,000 years ago in southern and eastern Asia and Australia (Powell et al., 2009). The appearance of these complex cultural traits does not appear to be consistent with a single genetic adaptation, given that early *Homo sapiens* migrated across Europe, Asia, and Australia *before* these complex traits appeared. Moreover, some of the traits appeared sporadically in sub-Saharan Africa much earlier, around 100,000 years ago, yet did not spread until much later. Powell et al. (2009) suggested that the emergence of complex cultural traits was made possible by an increase in group size in each of the aforementioned regions such that traits were not lost due to transmission error. Simulations using estimated population sizes of prehistoric human groups during the late Pleistocene supported this idea, finding that the appearance of complex cultural traits as determined from the archaeological record coincided with estimated increases in group size. Henrich (2004b) similarly showed that the loss of various cultural traits such as bone tools and hunting techniques from Tasmanian society, beginning around 10,000 years ago, coincided with Tasmania becoming cut off from mainland Australia. This isolation would have reduced the effective population size of early Tasmanians and prevented complex cultural traits from being maintained and further accumulated on the island, unlike on the Australian mainland where cultural traits did accumulate.

Finally, Mesoudi and O'Brien (2008b; see also Mesoudi, 2008; Mesoudi & O'Brien, 2008a) used agent-based simulations to show how group size limits the emergence of adaptive technological traits even assuming error-free cultural transmission. Computer-generated individuals ("agents") in groups each designed a technological artifact—an arrowhead—with different arrowhead designs giving different hunting payoffs. Rather than assuming a single optimal arrowhead design, it was assumed that there were multiple locally optimal arrowhead designs, some of which gave higher payoffs than others (i.e., a multimodal adaptive landscape: Wright, 1932). During an initial period of individual learning, agents independently explored the design space and converged on one of the locally optimal designs. Some agents discovered good arrowhead designs, giving them relatively high payoffs; other agents discovered poor arrowhead designs, giving them relatively low payoffs. Then, there followed a period of cultural transmission during which agents could copy the arrowhead designs of other group members. During this latter period, agents who had discovered relatively poor arrowhead designs, and thus had relatively low payoffs, copied agents with higher payoffs who had discovered better arrowhead designs. Consequently, most agents converged on the best arrowhead design discovered in the group. This effect was mediated by group size. During the initial individual-learning phase, larger groups could, collectively, explore more of the arrowhead design space, and so one of their members was more likely to discover the best possible (globally optimal) arrowhead design. During the cultural transmission phase, other group members all copied this best possible arrowhead design (Mesoudi & O'Brien, 2008b). Echoing the previous findings of Henrich (2004b) and Powell et al. (2009), then, larger group sizes increased the likelihood of the group acquiring adaptive cultural traits, not because of the loss of beneficial traits due to copying errors but due to the greater ability of larger groups to better explore the design landscape and discover high-fitness peaks. Multimodal adaptive landscapes are likely to be a common characteristic of real-life technological evolution (Boyd & Richerson, 1992a; Mesoudi & O'Brien, 2008a).

Conclusions

In this chapter we have reviewed recent research that has linked human sociality to our capacity for cumulative cultural evolution. Gene-culture coevolution researchers have argued that, by shifting the main route by which adaptive information is acquired from genetic to cultural evolution, new forms of cooperation and sociality have been made possible in humans. In contrast to other species, human sociality is based on extensive non-kin-directed cooperation, perhaps due to some process of cultural group selection by which more internally cooperative groups outcompete less internally cooperative groups. Large, cooperative societies, in turn, allow more complex technological and social traits to culturally evolve because such traits are more likely to be discovered, more likely to spread, and less likely to be lost as a result of transmission errors. Cumulative cultural evolution and cooperative sociality can, therefore, be seen as mutually reinforcing: the former creates distinct cultural groups from which the more cooperative ones are selected, which leads to larger societies, which increases the rate and scope of cultural evolution, and so on.

Recent work has extended this gene-culture coevolution scenario to modern social institutions. Cordes, Richerson, McElreath, and Strimling (2008) have argued that modern business firms are built on the unusually cooperative human sociality discussed earlier, and competition between firms can be seen as a further process of cultural group selection between groups of varying levels of internal cooperation. Henrich et al. (2010) showed that cross-cultural variation in cooperation in behavioral economic experiments correlates with market integration and, to a lesser extent, participation in a world religion. However, exactly how modern institutions such as economic markets and world religions interact with psychological traits and social emotions that may have emerged over several thousand years of human evolution remains unclear.

It should be noted that the cultural group selection hypothesis is not uncontroversial in the human evolutionary behavioral sciences. An alternative explanation for cooperative human sociality is a version of the "environmental mismatch" hypothesis popular among evolutionary psychologists, in which cognitive processes that originally evolved to deal with adaptive problems in ancestral environments may not be adaptive in novel, modern environments. Specifically, it is argued that human cooperative behavior evolved during a period when the vast majority of social interactions were with either kin or familiar individuals with whom people regularly interacted. Kin selection, direct reciprocity, and indirect reciprocity would have favored extensive cooperation under such conditions. Our much larger contemporary societies feature regular interactions with strangers and nonkin, yet our ancestrally adapted cognition maladaptively triggers cooperation with these individuals (West, et al., 2007). A related criticism of the cultural-group-selection hypothesis pertains specifically to the behavioral economic games such as the Ultimatum game discussed earlier, which is that anonymous, one-shot interactions are so unrepresentative of ancestral human environments that the results of such studies tell us little about the evolutionary origins of human cooperation (Hagen & Hammerstein, 2006; Johnson, Stopka, & Knights, 2003).

These alternative hypotheses and criticisms certainly have merits, and it is difficult to disentangle such issues from limited historical/archaeological data and often ambiguous contemporary human behavior. However, one flaw in the mismatch hypothesis is that it assumes an unrealistically inflexible view of human cognition that is unable to keep track of kin relations, reciprocal arrangements, and reputations. The experimental findings reviewed earlier, in which kin relations and reciprocal exchanges *do* influence people's tendencies to cooperate, would seem to count against this assumption. Indeed, a recent experimental study showed that people are sensitive to anonymity in economic games (Lamba & Mace, 2010), and another study showed that people behaved the same in the well-known lost-letter paradigm regardless of whether they knew they were taking part in an experiment (Fessler, 2009). On the other hand, the cultural-group-selection hypothesis is vulnerable to a similar criticism. In modern environments, people often cooperate with members of different groups, such as donating money to famine or earthquake victims from a different society that speaks a different language, holds different religious beliefs, and so on. If our psychological traits evolved to favor ingroup members, it is hard to explain altruism toward outgroup members. These issues underline the many unanswered questions that remain in this field.

Future Directions

1. Is human sociality the result of a novel process of cultural group selection, or simply an extension of noncultural evolutionary processes such as kin selection or direct reciprocity?
2. To what extent does cooperative behavior in laboratory experiments such as the Ultimatum game reflect cooperative behavior in real life?
3. What role do social emotions play in human cooperation, and to what extent are these genetically hard-wired?
4. When and how do children acquire the cooperative norms of their local community?
5. To what extent are modern social institutions such as business firms built on (genetically and/or culturally) evolved cooperative tendencies?
6. Why do people cooperate with outgroup members?

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