Chapter 10
From Grooming to Giving Blood: The Origins of Human Altruism

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Abstract Cooperation plays an important role in the lives of most primates, including ourselves. However, the magnitude and scope of cooperation varies considerably across taxa: callitrichids pool efforts to rear a pairs' offspring, male langurs jointly challenge resident males for access to groups of females, female baboons groom one another equitably, and male chimpanzees exchange support for mating opportunities. All of these forms of cooperation have analogs in human societies, but humans cooperate in more diverse contexts, with a wider range of partners, and at larger scales than other primates. The evolutionary foundations of cooperation in nonhuman primates – kinship, reciprocity, and mutualism – also generate cooperation in human societies, but cooperation in human societies may also be supported by group-level processes that do not exist in other primate species. The human capacities for culture may have created novel evolutionary forces that altered the selective benefits derived from cooperation.

10.1 Introduction

Humans are exceptionally altruistic creatures. We honor promises, make donations to charity, vote in elections, recycle bottles, give blood, participate in political protests, punish cheaters, and go to war. We are moved by prosocial sentiments, such as empathy and compassion, that influence our responses to others in need, and moral emotions, such as a concern for fairness, that shape our judgments about what we should do in particular situations. Although other animals can be altruistic, our species is unusual because our altruistic impulses extend to people who lie outside the circle of close kin and beyond networks of reciprocating partners. This suggests

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that the evolutionary processes that are thought to underlie altruistic cooperation in other animals, kin selection, contingent reciprocity, and biological market processes, may not be sufficient to account for the patterning of altruism in humans.

How were humans transformed from smart, sociable, and cooperative apes into other-regarding altruists? In this chapter, we attempt to provide some answers to this question. We begin with a discussion of the evolutionary processes that underlie altruism in nature, and then review the distribution, scope, and limits of altruism in nonhuman primates. We also review a growing body of data that provides insight about the nature of preferences that underlie cooperation in nonhuman primates. This information provides the context for understanding the similarities and differences among humans and other primates, and for considering the kinds of selective processes that may have played a role in the evolution of altruism in human societies. Then, we discuss the evolutionary processes that may have favored the evolution of altruistic, other-regarding creatures like ourselves.

10.2 The Evolution of Altruism

Evolutionary biologists define altruism as any behavior that reduces the genetic fitness of the actor and increases the genetic fitness of the recipient. There is considerably less consensus among evolutionary biologists about the definition of cooperation. Sometimes, cooperation is used as a synonym for altruism, and sometimes it is used to encompass any type of coordinated mutually beneficial behavior. Here, we will adopt the narrower definition of cooperation as a synonym for altruism, and we will use the terms cooperation and altruism interchangeably.

Natural selection is not expected to favor indiscriminate altruism because altruists always bear the costs of the altruistic behaviors that they perform on behalf of others, so the average fitness of an allele that increases the likelihood of performing altruistic behaviors will be lower than the average fitness of the non-altruistic allele. In order for altruism to evolve, there must be some cue that causes altruists to direct benefits selectively to other altruists. In nature, three types of cues seem important: recent common descent, proximity in viscous populations, and previous behavior.

Selection can favor altruism toward close relatives because recent common descent provides a reliable cue of genetic similarity. Individuals that are descended from the same ancestors have some probability of inheriting copies of the same genes. Thus, individuals who carry genes that are associated with altruistic behavior are more likely to have relatives who carry copies of the same genes than individuals drawn at random from the population. If individuals can identify their relatives and preferentially behave altruistically toward them, they will tend to confer benefits on individuals who also carry copies of the the genes that lead to altruistic behavior. Selection can also favor indiscriminate altruism toward other individuals if limited dispersal in viscous populations causes neighbors to be more closely related than chance would dictate even though they do not share a recent common ancestor.

Both these processes are often lumped together under the heading of kin selection (Hamilton 1964). What has come to be known as Hamilton's rule predicts that altruism will be favored when $br > c$. The quantities b and c represent the benefits and costs associated with the altruistic act. The quantity r measures how much the possession of a particular gene in one individual predicts the presence of the same gene in a second individual. Kin selection relies on the existence of a cue that allows individuals to direct altruism toward kin, and natural selection has produced a variety of mechanisms for kin recognition (rodents: Holmes and Mateo 2007; primates: Widdig 2007; social insects: Gamboa 2004; amphibians: Blaustein and Waldman 1992; birds: Komdeur and Hatchwell 1999).

The same basic logic underlies the theory of reciprocal altruism that was first introduced by Trivers (1971) and later formalized by Axelrod and Hamilton (1981). Reciprocal altruism is a form of contingent reciprocity in which the past behavior of other group members provides a cue about whether they carry alleles that lead to altruistic behavior. When individuals interact repeatedly, contingent altruistic strategies can arise. In the first interaction, an individual who carries the gene that leads to altruistic behavior provides help, and continues to help only if its partner reciprocates. If individuals follow this tit-for-tat rule, then contingent altruists will channel help toward other altruists after the first interaction. These kinds of contingent strategies can be sustained as long as $(1-1/t)\,b>c$, where b is the benefit derived from the other's helpful act, c is the cost of the helpful act, and t is the expected number of interactions between the two. It is not possible to satisfy this inequality when $t = 1$, so multiple interactions are required for contingent reciprocity to be favored. It is also easier to satisfy the inequality when the ratio of benefits to costs is high.

Although the logic underlying kin selection is fundamentally similar to the logic underlying contingent reciprocity, the outcome can be quite different because there are multiple equilibria. When the conditions $(1-1/t)\,b>c$ are fulfilled, contingent reciprocity can persist as an evolutionarily stable strategy (ESS), but unconditional defection is also an ESS, as are a variety of other strategies. In a world of unconditional defectors, contingent reciprocators will not prosper because they will invariably encounter partners who do not cooperate. In order for mutually beneficial strategies like tit-for-tat to evolve, there must be some factor that shifts the balance in their favor and makes it more likely that the population will move toward a cooperative equilibrium.

The solution to this problem was provided by Axelrod and Hamilton (1981). When pairs of related individuals interact, the odds of encountering another individual with the same rare strategy are substantially increased. If the benefits obtained over time by a cooperating pair are sufficiently greater than the benefits obtained by two unconditional defectors, then these rare cooperators can compensate for the fact that they do poorly when they are paired with unconditional defectors. Quite small amounts of relatedness may allow reciprocating strategies to invade a population composed of unconditional defectors. Axelrod and Hamilton termed this the “ratchet effect,” because small amounts of relatedness can ramp up cooperation. Although the ratchet effect is powerful, it is also quite restrictive: it only works when groups are small (Boyd and Richerson 1988).

Below, we briefly review empirical evidence which suggests that kin selection and contingent reciprocity have shaped the distribution of altruistic behavior in nonhuman primate groups.

10.3 Kin Biases in Behavior

Primatologists have produced a rich body of information about maternal kin biases in behavior over the last 30 years (reviewed in Silk 2002, 2005; Chapais and Berman 2007). Perhaps the best way to summarize this extensive literature is to say that female primates behave as though they understand the logic of Hamilton’s rule. In nearly every species in which females live in groups with their relatives, there are pronounced nepotistic biases among females in the distribution of altruistic behaviors, such as grooming, coalitionary support, and food sharing. Moreover, the most costly forms of altruism, including reproductive suppression and defense against higher ranking opponents, are limited to very close kin.

The most extreme form of nepotism occurs in cooperatively breeding groups of marmosets and tamarins. Marmoset and tamarins, members of the subfamily Callitrichinae, live in small territorial groups (French 1997; Tardif 1997). Cooperatively breeding callitrichid groups typically contain only one breeding pair, who are assisted by several nonbreeding adults, who may be same-sexed siblings of the breeding pair, and mature offspring from previous litters (Dietz 2004; French 1997; Tardif 1997). Breeding females typically give birth to fraternal twins and can produce two litters per year (in contrast, most other primates give birth to singletons at considerably longer intervals). After females give birth, nonbreeding group members provide extensive help carrying and provisioning infants. In golden lion tamarins, the species for which we have the most complete data in the wild, coresident adult males are generally close kin, but only one male sires offspring (Dietz 2004).

Nepotism is also a pronounced feature of behavior in the well-studied Cercopithecine societies, which include baboons, macaques, and vervets. In these species, mothers support their immature daughters when they are involved in conflicts with members of lower-ranking families, and daughters acquire rank positions just below their mothers (Silk 2002, 2005). Females form matrilineal dominance hierarchies in which all members of one matriline rank above or below all members of other matrilines. This process has long-lasting impacts on females because matrilineal dominance hierarchies are remarkably stable over time. High-ranking females have priority of access to resources, including food and water, and generally reproduce more successfully than lower-ranking females.

Male philopatry characterizes a much smaller set of primate species, including chimpanzees, bonobos, spider monkeys, muriquis, and wooly spider monkeys (Pusey and Packer 1987). Unlike males in most other primate species, males in these species form close ties with one another. For example, chimpanzee males spend a considerable amount of time in parties with other males, and males groom, hunt, share meat, aid, and patrol the borders of their territories with one another (Mitani 2005; Muller and Mitani 2005). In chimpanzee communities, males tend to form close relationships with their maternal brothers when they are available (Nishida 1979; Goodall 1986; Langergraber et al. 2007), but many males do not have brothers in their groups and kinship does not seem to be a necessary ingredient of close relationships among male chimpanzees (Langergraber et al. 2007).

Until recently, analyzes of nepotistic biases in favor of paternal kin were complicated by uncertainties about paternity (at least on the part of observers), which made it impossible to identify the paternal kin. The development of molecular genetic techniques for assessing paternity and noninvasive methods for obtaining genetic material from free-ranging animals now allow primatologists to identify the sires and to study the effects of paternal kinship on the distribution of altruistic behavior in primate groups (reviewed by Widdig 2007).

In baboon and rhesus macaque groups, females are more likely to associate with and groom paternal half sisters than unrelated females (Widdig et al. 2001, 2002; Smith et al. 2003; Silk et al. 2006a). In general, females show considerably stronger preferences for the maternal half sisters than for their paternal half sisters. This may reflect some degree of uncertainty about paternal relatedness or differences in the value of relationships with maternal and paternal sisters. If social bonds reinforce alliances, then maternal sisters may be more valuable allies than paternal sisters. Widdig et al. (2006) found that female rhesus macaques do not selectively support their paternal half sisters in agonistic encounters, but they do avoid intervening against them. Paternal kinship does not seem to play an important role in the distribution of altruistic behavior among adult male chimpanzees (Langergraber et al. 2007), young chimpanzees (Lehmann et al. 2006), juvenile mandrills (Charpentier et al. 2007), or white-faced capuchins (Perry et al. 2008).

10.4 Cooperation Among Reciprocating Partners

Until recently, most analyzes of the patterning of cooperation among unrelated individuals were based on the assumption that these interactions were the product of some form of contingent reciprocity. However, some researchers have argued that primates lack the cognitive ability to keep track of interactions with multiple partners across time (de Waal 2000; Barrett and Henzi 2002, 2005) and have cognitive biases, such as a preference for immediate rewards, that constrain the evolution of contingent reciprocity (Stevens and Hauser 2004; Stevens et al. 2005). Skepticism about the plausibility of contingent reciprocity as a strategic option for primates has led to interest in alternative processes, particularly the biological market model (Noë 2005, 2006). In biological markets, transactions are influenced by economic forces, such as supply and demand; trading partners act as buyers and sellers, negotiating prices for commodities based on their value to each party and the availability of alternative trading partners. Because buyers and sellers both obtain immediate benefits from their exchanges, there is no need to develop long-term relationships with partners.

The theoretical foundations of these approaches are quite different, but it is difficult to disentangle these processes empirically. For example, positive correlations between the amount of grooming given and received might be the product of contingent reciprocity or the outcome of trade in a biological market. Similarly, the absence of correlations in the amount of support given and received might mean that contingent reciprocity is not operating, that support is being exchanged for some other commodity (and there is some mechanism for enforcing trades), or that the frequency of interactions provides a poor index of the benefits accrued or costs incurred. Below, we summarize the pattern of interactions among unrelated individuals, although it is not always clear whether these patterns of exchange are the product of contingent reciprocity or market forces.

10.4.1 Patterns of Exchange and Interchange

Monkeys and apes generally spend the most time grooming those from whom they receive the most grooming, although the magnitude of the correlations in grooming given and received varies considerably (Schino and Aureli 2008). In addition, in some species, grooming within dyads is associated with the distribution of other commodities, such as access to infants (Henzi and Barrett 2002) and food (de Waal 1997), and with the distribution of some types of services, including support (Schino 2001; Watts 2002; Schino and Aureli 2008), participation in border patrols (Watts and Mitani 2001), and mating opportunities (Duffy et al. 2007).

Several recent studies indicate that grooming is more evenly balanced across multiple bouts than within single bouts (Frank and Silk 2009a; Gomes et al. 2009; Schino et al. 2009). For example, grooming among pairs of adult female baboons was significantly more evenly balanced over an 18-month study period than within single grooming bouts (Frank and Silk 2009a). These results strongly suggest that monkeys and apes are able to keep track of the distribution of grooming given and received over substantial periods of time.

Several lines of evidence suggest that cooperation may be limited to cooperating partners. First, female baboons and male chimpanzees form the strongest and most enduring social relationships with those that groom them most equitably, and this holds for both related and unrelated females (Silk et al. 2006b; Mitani 2009). We do not know whether equitable grooming relationships are more likely to be maintained across time, or whether relationships among close associates become more equitable over time. Either way, female baboons and male chimpanzees selectively maintain relationships with those that groom them most equitably.

Several factors seem to influence the distribution of cooperation within dyads. Grooming is often directed up the dominance hierarchy in macaque groups, as low-ranking females groom their partners more than they are groomed in return

(Schino 2001). This imbalance may exist because low-ranking females trade grooming for support as Seyfarth (1977) originally suggested. It may also exist because low-ranking females use grooming to appease high-ranking partners and reduce the risk of harassment from them. Barrett and her colleagues have shown that such trades become more imbalanced when the risk of aggression from higher-ranking females increases (Barrett et al. 1999). In some cases, females may use grooming to obtain access to other kinds of resources. For reasons that are not entirely clear, females are highly motivated to handle other females' infants, and often use grooming as a means to this end (Maestripieri 1994; Henzi and Barrett 2002). In some groups, females spend more time grooming mothers of newborns when few other infants are present than when many infants are available (Henzi and Barrett 2002; Manson 1999), but in others, the supply of infants does not seem to influence the grooming behavior (Frank and Silk 2009b). Similarly, female baboons groom higher-ranking mothers more than lower-ranking mothers in some groups (Henzi and Barrett 2002), but not in others (Frank and Silk 2009a).

Several naturalistic experiments have been designed to detect contingencies in cooperative behavior. Wild vervet monkeys were more attentive to the tape-recorded distress calls of unrelated group members if they had been groomed recently by the caller than if they had not been groomed recently by the same monkey (Seyfarth and Cheney 1984). In contrast, grooming among closely related monkeys did not influence the likelihood of responding to distress calls. Similarly, when disputes over food were instigated by researchers, long-tailed macaques were more likely to intervene on behalf of monkeys who had recently groomed them than monkeys who had not groomed them (Hemelrijk 1994). Grooming also enhances feeding tolerance among chimpanzees (de Waal 1997). In this experiment, chimpanzees were provisioned with leafy branches and all food transfers were recorded. In addition, grooming behavior *before* the provisioning event was monitored. The chimpanzees were more tolerant to individuals that had previously groomed them than they were to other individuals, and the effects of previous grooming were most pronounced for pairs that did not frequently groom at other times.

More formal laboratory experiments that were designed to assess how individuals respond to the helpful or unhelpful behavior of their partners have generated mixed results (see Silk 2007a for a review). In some cases, researchers have detected biases that favor partners who have provided help in previous trials (e.g., Cronin and Snowdon 2008; de Waal and Berger 2000; Hauser et al. 2003), while in others little or no evidence of contingency has been detected (Brosnan et al. 2009; Melis et al. 2008).

10.5 Limits of Altruism in Primate Groups

In nonhuman primate groups, cooperative interactions involve relatively small numbers of familiar individuals, often close relatives or reciprocating partners. Grooming involves pairs of individuals, coalitionary aggression may involve several individuals, and sizable numbers of individuals may participate in intergroup encounters.

Responses to strangers and members of neighboring groups generally range from passive avoidance to active hostility (see Crofoot and Wrangham this volume). Members of different groups rarely groom, and there are no reports of groups forming coalitions against other groups. In contrast, even human hunter-gatherer societies can orchestrate cooperative activities involving hundreds, sometimes thousands, of individuals. In market economies, goods and services are traded among strangers.

In human societies, people who violate social norms, break rules, or commit crimes are often punished by other group members. Punishment of this sort is altruistic because the individuals who impose sanctions on transgressors incur costs, while the benefits flow to the entire community. Hauser and Marler (1993a, b) provided the first evidence for altruistic punishment in primate groups. Rhesus macaques give distinctive calls when they find desirable foods. Hauser and Marler hid piles of coconut, a rhesus treat, in the monkeys' home range, and monitored what happened when these caches were discovered. In some cases, the monkeys who discovered the piles of coconut called, and in other cases, they remained silent. Female macaques were more likely to be attacked by other monkeys, particularly young males, if they remained silent after finding food than if they gave food calls. The authors hypothesized that females were being punished for attempting to conceal the location of these prized foods. This could constitute a form of altruistic punishment if the screams of the victim alert other group members to the site of the food, giving many animals an opportunity to profit from the aggressor's actions, or if harassment reduces the likelihood that the victims will remain silent after finding food in the future.

Subsequent work on food calling in white-faced capuchins (Gros-Louis 2004) provides an alternate interpretation for aggression in this context. Capuchins who called after finding food were less likely to be approached by others than monkeys that remained silent. In addition, individuals who gave food calls when they were approached by higher-ranking animals were less likely to receive aggression than monkeys who did not call. Gros-Louis (2004) suggests that food calls may function to establish the ownership of resources and signal the owners' willingness to defend them. This would explain why monkeys are especially likely to call when they are approached by high-ranking monkeys, who might challenge them for possession of food items.

10.6 Motives Underlying Altruism in NHPs

It is easy to perceive similarities between the altruistic behaviors we observe in primate groups and some forms of altruistic interactions in humans. A chimpanzee who is being groomed looks very much like someone getting a good massage – deeply relaxed and contented. When a juvenile baboon nestles in the lap of a male who is defending him from harassment, he seems to be relieved and reassured. Despite these parallels, it is not clear whether the motives and sentiments that underlie altruism are the same in humans and other species. In humans, altruism seems to be motivated at least in part by an understanding of others' thoughts and desires, concern for the welfare of others, and a preference for outcomes that benefit others (Fehr and Fischbacher 2003; Henrich et al. 2006). We may also be motivated by a concern for reputation that makes us want others to think that we are generous, fair, or charitable (Haley and Fessler 2005, Fessler and Gervais this volume). Below, we discuss the evidence for empathy and other regarding preferences in nonhuman primates. For a discussion of the evidence for fairness, see Lakshminarayan and Santos, this volume.

10.6.1 Empathy

Until recently, discussions of empathy in other primates were based on anecdotal reports of one individual helping another or reacting to another animal's distress (Silk 2007b). Although these events are intriguing, anecdotal data present several problems. First, interpretations of singular events are based on subjective impressions of observers, and are very difficult to verify. Second, observers may be more likely to notice and remember incidents that suggest that primates are empathetic than they are to take note when they seem oblivious or indifferent. Third, observers may be more likely to offer more anthropomorphic interpretations of the behavior of some animals, such as apes or dogs, than others.

This has led researchers to try to devise more systematic ways to assess the empathic responses of other primates. One study capitalized on the fact that macaques and baboons display elevated rates of self-directed behaviors, such as scratching, when they are under stress. Rates of self-directed behaviors rise sharply after monkeys are threatened or harassed by other group members (Aureli and van Schaik 1991; Castles and Whiten 1998). If monkeys experience empathy, then mothers would be expected to experience distress when their infants are distressed. However, Japanese macaque females showed no obvious signs of stress when their infants were harassed (Schino et al. 2004). Moreover, mothers did not approach their infants or offer comfort after their infants were victimized.

These results are consistent with the results from a study of mothers' reactions when their infants were exposed to danger (Cheney and Seyfarth 1990). In these experiments, mothers had learned that a dangerous or frightening object, such as a model of a snake, was concealed in a box in their enclosure. Mothers made no effort to stop their infants or warn them of danger when their infants, who were ignorant of danger, approached the box. Maternal indifference in these situations strongly suggests that monkeys may not have the capacity for empathy.

Female macaques may not respond to their infants' distress or protect them from potential dangers because they do not have a well-developed understanding of others' knowledge, feelings, and desires (Tomasello and Call 1997). Apes seem to have a more complete understanding of others' minds, and stronger claims are made about their capacity for empathy (Preston and de Waal 2002; de Waal 2003).

The capacity for empathy might underlie chimpanzees' responses to the victims of aggression. Third-party affiliation after conflicts has been documented in a number of chimpanzee populations (reviewed in Silk 2007a). De Waal and van Roosmalen (1979) hypothesized that these interactions are designed to alleviate the distress of the victims of aggression, and applied the label "consolation." This functional interpretation implies that actors are motivated by empathy for the victim (Palagi et al. 2006; Fraser et al. 2008), but studies designed to evaluate the function and effectiveness of third-party affiliation after conflicts have produced conflicting results. Palagi et al. (2006) found that chimpanzees did not selectively console kin or close associates, as might be expected if consolation is based on empathy. More recently, Fraser et al. (2008) have found that chimpanzees are significantly more likely to offer consolation to valued social partners than to other group members. Consolation effectively reduced self-directed behavior in one group of chimpanzees (Fraser et al. 2008), but not in another (Koski and Sterck 2007). The inconsistency among these results makes it difficult to draw strong conclusions about the function of consolation.

10.6.2 Other Regarding Preferences

The difficulties associated with identifying the sentiments that underlie altruistic behavior have led researchers to borrow techniques developed by behavioral economists to investigate the nature of social preferences in primates. In these experimental studies, subjects are faced with decisions about how to allocate resources to themselves and others. The choices that they make in these situations provide insight about their social preferences.

For example, in one set of experiments, chimpanzees were presented with the opportunity to deliver food rewards to themselves and/or other individuals. To implement their choices, the animals manipulated simple mechanical apparatuses that were baited with food. One of the options provided identical food rewards to the actor and to the occupant of the other enclosure (the 1/1 option); and the other option provided a food reward only to the actor (the 1/0 option). Individuals might prefer the 1/1 option because they have prepotent biases toward larger numbers of rewards (regardless of the distribution), so a control condition was included in which there was no potential recipient present. If individuals are concerned about the welfare of others, they are expected to prefer the 1/1 option over the 1/0 option, and this preference is expected to be stronger when another individual is present than when the actor is alone. Chimpanzees at three different sites, using four different apparatus, were as just as likely to choose the 1/1 option when another chimpanzee was present as when they were alone (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008). It is possible that actors did not choose the 1/1 option more often because they were unaware that their partners preferred this outcome (Warneken et al. 2007). However, Vonk et al. (2008) found that potential recipients made begging gestures before the actor had made a choice in some trials, and clearly directed their begging gestures toward the side of the apparatus from which they would obtain rewards. Begging did not increase the likelihood that the actor would deliver rewards.

These experiments with chimpanzees have been followed with similar experiments in other species. In each case, actors were offered choices with different payoff structures. Capuchins demonstrate prosocial preferences in two different experimental paradigms (de Waal et al. 2008; Lakshminarayanan and Santos 2008), while results for two cooperatively breeding species are mixed. Cooperatively breeding common marmosets, *Callithrix jacchus*, were presented with an opportunity to deliver food to another individual, but received no reward themselves (0/0 vs. 0/1). The marmosets were significantly more likely to choose the 0/1 option when another marmoset was present than when they were alone (Burkart et al. 2007), satisfying the criterion for prosocial preferences. However, different results were obtained for another cooperatively breeding callitrichid, the cotton-top tamarin, *Saguinus oedipus* (Cronin et al. 2009). In this case, cotton-top tamarins did not distinguish between partner-present and partner-absent trials for two different payoff distributions (1/1 vs. 1/0; 0/1 vs. 0/0).

In another experimental study, Cronin and Snowdon (2008) evaluated tamarins' willingness to deliver rewards to their mates when (a) both parties got rewards, (b) both parties were rewarded on alternate days, (c) both parties shared access to a monopolizable reward, and (d) one partner could deliver rewards to its partner in repeated trials. The tamarins were most likely to solve the task, and deliver rewards to their partners, when both got rewards (100% trials), and they were least likely to solve the task when they did not receive rewards themselves (46%). Although helping was not extinguished completely when actors did not obtain rewards, latency to solve the task increased and there was more variability across pairs.

Chimpanzees seem to be more inclined to provide instrumental help to humans and other group members than to deliver food rewards to them. In two sets of experiments, chimpanzees retrieved objects that human experimenters could not reach (Warneken and Tomasello 2006; Warneken et al. 2007), and their performance was not influenced by the availability of food rewards (Warneken et al. 2007). In another experiment, chimpanzees were given an opportunity to provide help to other group members. In this experiment, the door to an adjacent room was fastened by a chain. The actor could remove a peg and release the door, but could not enter the room. The potential beneficiary could not reach the peg, but could enter the room. During experimental trials, a bowl of food (visible only to the potential beneficiary) was placed in this room. In control trials, food was placed in another room that was inaccessible to both chimpanzees. During all trials in which food was placed in the accessible room, potential beneficiaries oriented toward the door of the room, while they oriented toward the door to the other room in only half of the control trials. Moreover, actors were significantly more likely to release the door to the accessible room in experimental trials than in control trials. Thus, actors helped potential beneficiaries get into the locked room, and were sensitive to cues about their desires.

These experiments indicate that chimpanzees understand others' needs and desires, but do not provide unambiguous information about the motivations that underlie their behavior. In these situations, chimpanzees could be motivated by other regarding preferences or expectations of delayed reciprocity.

It is not easy to explain why these experiments lead to prosocial behavior in marmosets and capuchins, but not in tamarins or chimpanzees, and why chimpanzees display prosocial preferences when they are given an opportunity to provide instrumental help to others at some cost to themselves, but not when they are given an opportunity to provide food to others at no cost to themselves. Having a large brain and sophisticated knowledge of others' thoughts and desires is apparently neither necessary nor sufficient for the development of other regarding preferences. Burkart et al. (2007) suggested that cooperative breeding in callitrichids and humans might generate prosocial preferences, but this explanation does not fit the prosocial results for capuchins or the absence of prosocial preferences in tamarins. Warneken and his colleagues (Warneken and Tomasello 2006; Warneken et al. 2007) have speculated that chimpanzees may not display prosocial preferences in these experiments because they perceive food as a limited resource, and are not predisposed to provide food to others. This might explain why capuchins, which are remarkably tolerant of scrounging, display prosocial preferences. But it does not explain why prosocial responses are seen in marmosets, but not in tamarins, as food transfers play an important role in both taxa (Brown et al. 2004). It is possible that chimpanzees view all interactions involving food as zero-sum games because food supplies are limited in nature (Warneken et al. 2007), and have selfish preferences about food. If such preferences biased their behavior in these experiments, they would be expected to show consistent preferences for the 1/0 option; instead they choose the 1/1 and 1/0 option with equal frequencies.

10.7 The Origins of Other Regarding Preferences in Humans

When the human lineage diverged from the great ape lineage 5–7 million years ago, our ancestors were probably something like modern chimpanzees – smart, sociable, and cooperative. They would have been helpful to group members in some situations, and hostile to strangers. They might have exchanged goods, services, and favors with reciprocating partners, but were not unconditionally altruistic and may have had limited capacities for empathy and sense of fairness. To understand the origins and evolution of group-level cooperation and generalized other regarding preferences in humans, we need to consider two related questions. First, why did selection favor the evolution of the group-level cooperation and other regarding preferences in ancestral human populations, but not in other closely related species of primates? What evolutionary processes sustain these other regarding preferences in human groups?

To answer this question, it is useful to consider how the social organization and subsistence strategies of human foraging societies differ from those of other primates. Like the cooperatively breeding callitrichids, humans often get considerable help from others in rearing their offspring (Hrdy 2005; Burkart et al. 2007). Humans make more use of resources that are difficult to obtain and complicate to process than other primates do (Kaplan et al. 2000, 2003). We also rely more heavily on social learning to acquire the knowledge, skills, and information we need to make a living (see Whiten this volume). Finally, warfare has played an important role in the history of human societies (Gat this volume), but lethal intergroup conflict is absent in nonhuman primate groups, with the exception of chimpanzees (Crofoot and Wrangham this volume). All of these factors have been implicated in the evolution of other regarding preferences of humans. Here, we focus on cooperative breeding, complex foraging, and cultural evolution. For a more complete discussion of the role of warfare in the evolution of human societies see Gat (this volume) and Crofoot and Wrangham (this volume).

10.7.1 Cooperative Breeding

Hrdy (2005) hypothesizes that the high costs of producing and supporting slow-growing human children favored the development of extensive allomaternal care networks, which included fathers, grandmothers, and older siblings. In societies with high levels of infant mortality, alloparental care was an integral element of females' reproductive strategies. Hrdy considers humans to be cooperative breeders because multiple individuals contribute to children's care. This definition conflates taxa in which there is only one breeding pair who are assisted by nonbreeding helpers (e.g., wild dogs, meerkats) with taxa in which there are multiple breeding females who share some maternal tasks and may be assisted by other group members (e.g., lions, banded mongoose). We reserve the term cooperative breeders for the former, and use the term communal breeders for the latter. By this definition, callitrichids are cooperative breeders and humans are communal breeders.

Hrdy suggests that the ability to engage caretakers and elicit investment would be advantageous for infants, and this would favor the evolution of cognitive capacities that allow young children to assess the intentions and predict the responses of others. Over the course of our evolutionary history, selection elaborated these capacities to produce empathy and a well-developed theory of mind. According to this argument, delayed maturation and cooperative/communal breeding coevolved, and both of these developments preceded the marked expansion of brain size in humans and the origin of other regarding preferences.

Burkart et al. (2007) have also emphasized the link between cooperative breeding and other regarding preferences in humans and marmosets. They suggest that "...unsolicited prosociality, which arose in the context of provisioning, carrying, and sharing was then generalized toward the sharing of information and psychological states." When unsolicited prosociality was added to the the ape-like brain of our ancestors, it precipitated a "cascade of further developments" including language, teaching, and the development of other regarding preferences and group-level cooperation.

Generalized prosocial preferences in small groups of closely related individuals could evolve through kin selection. Callitrichid groups are typically small and group members are closely related to the infants that they care for. Although there is some evidence that altruistic responses are not limited to kin and not all group members are equally altruistic (Burkart et al. 2007), it is possible that there are few opportunities for prosocial behavior toward nonrelatives in the wild. Thus, group-level cooperation evolved through kin selection.

It is more difficult to invoke the same argument for the evolution of other regarding preferences in humans. Contemporary human foragers live in larger and more complex groups than cooperatively breeding monkeys do. Allomaternal care in such groups is typically nepotistic, and grandmothers are the most common caregivers for children (reviewed by Hrdy 2005). Male provisioning and direct care of infants may be a form of parenting effort or mating effort (Anderson et al. 1999a, b; Marlowe 1999a,b); in both cases, mens' contributions to childcare linked to their own fitness benefits. Selective pressures favoring allomaternal care and communal breeding in human groups have not produced indiscriminant altruism toward children, and it seems difficult to link communal breeding directly to the emergence of other regarding preferences in human groups.

The similarity in the responses of marmosets and humans in the prosocial task may arise because group-level cooperation is favored in both taxa, not because both species are cooperative/communal breeders. Kin selection may favor group-level cooperation in marmosets while other forces may generate group-level cooperation in humans. Below we consider two possible mechanisms underlying group-level cooperation in human societies.

10.7.2 Complex Foraging

The cooperative breeding hypothesis does not explain why humans mature more slowly in relation to their body size than other primates and why human infants require so much more care than the infants of other primates. Kaplan and his colleagues suggest that humans mature slowly because it takes a long time to acquire the knowledge and skills that human food foragers need to make a living (Kaplan et al. 2000, 2003). Human foragers rely heavily on complex foraging skills, including hunting and extractive foraging, and exploit a much wider range of resources using a larger repertoire of tools and techniques than other primates do. Comparative data indicate that extracted and hunted foods account for about 5% of chimpanzee diets, while these types of food account for about 90% of the diet of human hunter-gatherers. Kaplan and his colleagues emphasize the fact that humans specialize on resources, such as meat, roots, and nuts, that are rare and patchy, but provide rich sources of nutrients.

The reliance on complex foraging techniques may have favored economic interdependence within families and groups. If foraging skills are difficult to master, it makes sense to develop foraging specializations. Such diversification, by sex, age, or ability, will pay off if specialists share the products of their foraging efforts. Sexual division of labor is a universal feature of human foraging societies, as men mainly hunt and women mainly gather. Sharing may also buffer the economic risks associated with hunting (Winterhalder 1986). On some days, hunters return with carcasses large enough to feed many people, but on other days, they come back empty-handed. Sharing provides one way to insure against such risks. Sharing networks that extend beyond family or household, buffer risk even further (Gurven 2004).

According to this argument, the importance of complex foraging techniques in human subsistence strategies may have favored delayed development, extended periods of parental provisioning, division of labor within families, and the formation of extended sharing networks. In hunter-gatherer groups, resource exchanges are influenced by the dynamics of contingent reciprocity, as well as by the norms of fairness (Gurven 2004, 2006). To explain the origins of prosocial preferences, however, we need to take the argument one step further, and consider the role of cultural evolution.

10.7.3 Cultural Evolution

Complex foraging strategies may be linked to the evolution of social learning and the capacity for culture. Early Pleistocene hominins occupied a considerably wider range of habitats than any contemporary apes do today. The knowledge and subsistence technology required for complex foraging varies greatly from one habitat to another, and it would have become more and more difficult for individuals to acquire this information on their own. Social learning allows human populations to gradually accumulate useful knowledge as individuals learn from others, make modest improvements, and pass this accumulated knowledge on. This kind of cumulative cultural change can give rise to complex habitat-specific adaptations much more rapidly than genetic evolution can (Boyd and Richerson 1985, 1996, McElreath this volume). Although we may have underestimated the social learning capacities of chimpanzees and other primates in the past (Whiten this volume), there is no doubt that humans rely on social learning to a much greater extent than any other primates do.

The cultural transmission of information may have been especially important for our ancestors during the Middle and Upper Pleistocene. During this period, world temperatures fluctuated widely. At some points, average world temperatures changed as much as 10°C in 1,000 years (Richerson et al. 2001). In this kind of world, the ability to make rapid adjustments to changing conditions would have provided strong selection for the evolution of cultural capacities.

Social learning may have enabled humans to adapt to changing conditions, but it also had the potential to generate considerable cultural variation among groups. Social interactions commonly give rise to multiple adaptive equilibria. (a nonbiological analog of this process would be conventions about which side of the road to drive on: it is equally efficient to drive on the right or the left, but essential that everyone follows the same rule.) Systems of reciprocity, reputation management, and punishment can stabilize a vast range of behaviors including ones that lead to large-scale cooperation (Axelrod 1986; Boyd and Richerson 1992; Nowak and Sigmund 1998; Henrich and Boyd 1998; Panchanathan and Boyd 2004). Adaptive processes, including both individual learning and the tendency to imitate successful individuals which generates conformist biases, will cause local populations to evolve toward different equilibria. This tendency will be counteracted by the flow of ideas between groups, just as genetic variation among groups is counteracted by migration. However, if individuals adopt the ideas and traditions of their new groups, then cultural variation among groups will be maintained. Cultural adaptation can proceed much more quickly than genetic adaptation, so it is likely that as cultural adaptation became more and more important, the amount of variation in behavior and social organization among human groups also increased (Richerson and Boyd 2005).

Increased variation between groups could have had important effects on the cultural evolution of group-beneficial traits. To understand the why, it is helpful to adopt the formulation derived by Price (1970) which partitions genetic evolutionary change into two components:

$$\Delta p \propto \underbrace{V_{\mathrm{G}}}_{\text{between groups}} \beta_{\mathrm{G}} + \overline{\underbrace{V_{\mathrm{w}}}_{\text{within groups}} \beta_{\mathrm{w}}}$$

The effect of selection on the change in frequency of a gene, Δp, is proportional to the amount of genetic variation between groups (V_{G}) and the amount of genetic variation within groups (V_{W}). Behaviors are beneficial to the group when the behavior increases group fitness, or $\beta_{\mathrm{G}} > 0$. If it is costly to the individual, $\beta_{\mathrm{W}} < 0$. When behaviors are beneficial to the group and costly to individuals (as is the case for altruistic traits), then the outcome will depend on the relative magnitude of the variance within and between groups. When groups are large, selection is weak, and rates of migration are not too low, V_{W} will greatly exceed V_{G} (Rogers 1990), and group selection cannot overcome opposing individual selection. These conditions often hold in nature, and group selection is generally not thought to be an important force.

Group selection can play a more important role when there are multiple stable equilibria. To see how this works, consider a situation in which there are two alleles, A and B, and homozygotes have higher fitness than heterozygotes ($W_{\mathrm{AA}} > W_{\mathrm{BB}} > W_{\mathrm{AB}}$). This means that when A is common, B will not be able to invade because $W_{AB} < W_{AA}$; when B is common, A will not be able to invade because $W_{AB} < W_{BB}$. In this situation, there is a paradoxical result: when B is common, individual selection will not favor the A allele, even though it confers a fitness advantage. However, group selection can lead to the spread of the B allele when there are multiple stable equilibria. Imagine that a large population is divided into a number of separate groups: A is common in some groups, and B is common in other groups. There is little variance within groups, so V_W will be low. Selection favors A in some populations and B in other populations, so the average value of β_W across groups will also be small. This means that the within-group component of the Price equation will approach zero, and selection within groups will have little impact on the frequency of A and B. If the A allele has higher average fitness, then group selection can favor the spread of the A allele. The A allele may spread if carriers of the A allele are more successful in forming new groups, or if groups with lower frequencies of the A allele are more likely to become extinct and are replaced by individuals carrying the A allele (Boyd and Richerson 2002). Thus, when there are multiple stable equilibria and selection is strong compared to migration, selection will preserve the variation among groups and favor the evolution of traits that increase group fitness.

Although the Price equation was formulated to describe the effects of selection on genetic traits, the same basic logic applies to cultural variants. When there are multiple stable equilibria, processes that reduce the amount of cultural variation within groups will reduce the within-group component of variation and strengthen the forces of selection among groups. This will favor the evolution of group-beneficial cultural traits that increase the competitive ability of groups. Competition between groups will favor the spread and elaboration of cooperative cultural norms that makes groups larger, more productive, and more successful in conflicts with neighboring groups. Cooperative cultural norms may be maintained by concerns about reputation, desire to maintain reciprocity, or fear of costly sanctions. This, in turn, may have favored the development of new prosocial emotions, such as compassion, guilt, and shame. Individuals who lack these new social emotions would have violated the prevailing norms more often, and as a result they may have been punished, denigrated, denied access to community resources, or ostracized. Cooperation and group identification in intergroup conflict may have set up an arms race that drove social evolution to progressively greater extremes of in-group cooperation. Eventually, human populations came to resemble the hunter-gathering societies of the ethnographic record. These societies are egalitarian and political power is diffuse. People readily punish others for transgressions of social norms, even when their own personal interests are not directly at stake.

These new motivations did not replace the motivational biases that we inherited from our primate ancestors. We still care strongly about our own welfare, are biased in favor of our relatives, and place special trust in reciprocating partners. However, we are also moved by broader loyalties to clan, tribe, class, caste, and nation. In some cases, these loyalties conflict: we wince when we pay our taxes, although we realize that our taxes support schools, hospitals, and other worthy institutions.

10.8 Conclusions

In the last 5 million years or so, a smart, sociable, and cooperative forest ape was transformed into a slow growing, highly adaptable, technologically sophisticated, other-regarding altruist. Although much of the ancient ape remains within us, we differ from other apes in our exceptionally slow life history, our reliance on social learning and cultural adaptations, and in our development of group beneficial social norms and social preferences. Our understanding of this transformation is based on work from many academic disciplines. Primatologists have accumulated a wealth of information about the distribution of altruistic behavior in primate groups, which provides a broad comparative framework for understanding the roots of cooperation. Evolutionary theorists have developed a rich body of theory about the evolution of altruism and cultural evolution, which has enabled us to understand the dynamics of these processes in a more rigorous way. Finally, developmental psychologists, behavioral economists, human behavioral ecologists, and evolutionary psychologists have contributed a diverse set of methods and extensive empirical evidence about motivations, preferences, and behavior of contemporary people. This body of work has helped us to define the continuities in the behavior of humans and other primates, and to illuminate the gaps. It is clear that our understanding of the origins of human altruism is incomplete, but we have begun to get some traction on the problem.

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