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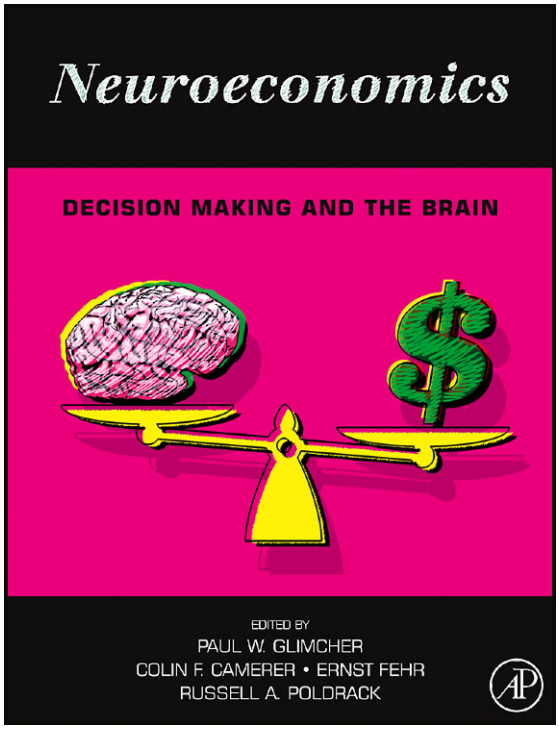

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From: Neuroeconomics: Decision Making and the Brain
Edited by Paul W. Glimcher, Colin F. Camerer, Ernst Fehr and Russell A. Poldrack
ISBN: 978-0-12-374176-9
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CHAPTER

18

Social Preferences in Primates

Joan B. Silk

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When I do good, I feel good; when I do bad,I feel bad, and that is my religion.

Abraham Lincoln

INTRODUCTION

Humans, like all of the other organisms on earth, are the product of evolution by natural selection. Natural selection generally favors traits that enable individuals to survive and reproduce successfully. Success in what Charles Darwin (1859) called "the struggle for existence" often comes at the expense of others, leaving little scope for the kinds of prosocial sentiments that Lincoln expressed. Darwin himself was troubled by the fact that his theory could not explain the altruistic existence of sterile workers in social insect colonies, which spend their lives caring for the offspring of the queen, but never reproduce themselves. In *The Origin of Species*, he wrote that the

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altruism of social insects presented "one special difficulty, which at first appeared to me insuperable, and actually fatal to my theory." This conundrum has engrossed evolutionary biologists for the last 40 years, and has generated a large theoretical and empirical literature on the evolution of altruism. This work shows that altruism is widespread in nature, but is typically limited to kin and reciprocating partners (Crozier and Pamilo, 1996; Dugatkin, 1997; Kappeler and van Schaik, 2006). This literature has also illuminated the gap between humans and other animals. Humans rely on cooperation to a far greater extent than most other animals do, and are able to orchestrate cooperation in substantially larger groups. Moreover, humans are the only animals that regularly provide aid to strangers and impose costly punishment on wrongdoers in anonymous, one-shot interactions (Fehr and Fischbacher, 2003; Boyd and Richerson, 2005; Henrich *et al*. 2006). Cooperation in humans is sustained by a willingness to impose costly punishment on those who shirk social obligations. In humans, altruism seems to be motivated at least in part by social preferences based on empathy, concern for the welfare of others, and a preference for equity (Batson, 1991; Fehr and Fischbacher, 2003; see also Chapter 19 of this volume).

What is the evolutionary source of human prosocial preferences? If our prosocial preferences are based on empathy, which relies on the ability to perceive the thoughts and feelings of others, then comparative studies of the cooperation, cognition, and capacity for empathy in humans and and other primates may provide clues about the origins of prosocial preferences. On the other hand, our prosocial preferences might reflect the evolutionary consequences of the economic importance of cooperation in human societies. If that is the case, then it might be profitable to examine the nature of social preferences in other species in which cooperation plays an important role.

Here, I review what we know about the evolutionary foundation and deployment, of altruism in non-human primate species. I begin with a brief primer on the evolution of altruism, and briefly describe the pattern and scope of altruism among primates in the wild, including the deployment of both beneficent behavior and punishment. Then, I examine what is known about the cognitive capacities that underlie empathy, and evidence for empathy and sympathy in non-human primates. Finally, I review what we know about the nature of social preferences that motivate altruistic behavior in non-human primates, focusing on recent experimental studies that probe the nature of prosocial preferences in chimpanzees.

THE ADAPTIVE CHALLENGE OF ALTRUISM

Biologists define altruism as any behavior that is costly to the actor and beneficial to the recipient. By performing an altruistic behavior, actors incur costs that reduce their own chance of reproducing successfully (fitness), and provide benefits that increase the recipient's fitness. If altruists provide benefits to others indiscriminately, then the benefits will not increase the relative fitness of altruists. However, altruists always bear the costs. The average fitness of a genetic variant (allele) that increases the likelihood of performing the altruistic behavior will therefore be lower than the average fitness of the non-altruistic allele. In order for altruism to evolve, there must be some process that allows altruists to direct benefits selectively with other altruists. In nature, two types of processes can produce this outcome: nepotism and contingent reciprocity.

Kin Selection

Selection can favor altruism toward close relatives because kinship provides a reliable cue of genetic similarity. W.D. Hamilton realized that individuals that are descended from the same ancestors have some probability of inheriting copies of the same genes. In particular, 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 behave altruistically to their relatives, they have some chance of conferring benefits on individuals who also carry copies of the the genes that lead to altruistic behavior. This is the underlying foundation for the theory 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.

If there is limited movement in and out of groups, levels of genetic relatedness will build up over time. When this is the case, group membership can provide a cue for assortative interaction because genes that generate altruistic behavior are disproportionately likely to be shared by other group members. This holds even for individuals who do not share recent ancestry.

Multi-level selection models (Wilson and Sober, 1994) provide an alternative, but equivalent, description of the same process (Dugatkin and Reeve, 1994; Reeve and

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Keller, 1997). In the Hamilton's rule approach, fitness effects are allocated to the bodies in which the genes causing the effects are expressed. In the multi-level selection approach, fitness effects are partitioned into within-group and between-group components. The two approaches are mathematically equivalent, but their heuristic value may vary in different circumstances.

Contingent Reciprocity

The basic logic underlying contingent reciprocity, or reciprocal altruism, is the same as the logic underlying kin selection, but now previous behavior provides a cue about whether others carry alleles that lead to altruistic behaviors. When individuals interact more than once, contingent altruistic strategies (such as tit-for-tat) can arise. (For example, in the one-shot version of the prisoner's dilemma game, two suspects of a crime are apprehended and interrogated separately. Each suspect is offered a reduced sentence if he confesses, and implicates his partner. Not knowing what the other suspect will do, each suspect has a strong incentive to confess. Even though both would be better off if they remained silent, neither can afford to take the chance that the other will confess and implicate him. However, the dynamics of the prisoner's dilemma are altered when two individuals face the same situation repeatedly. Then, contingent strategies may be favored. See McElreath and Boyd (2007) for a more complete discussion of the iterated prisoner's dilemma game.)

In the first interaction, an individual who carries the gene that leads to altruistic behavior provides help, but continues to help only if his partner reciprocates. Thus, after the first interaction, contingent altruists direct their costly help only toward other altruists. 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. Note that the inequality cannot be satisfied when $t = 1$, so repeat business is required for contingent reciprocity to be favored. This repeated process is the foundation of the theory of reciprocal altruism, which was first introduced by Robert Trivers (1971) and later formalized by Robert Axelrod and William Hamilton (1981).

THE DEPLOYMENT OF ALTRUISM IN PRIMATE GROUPS

There is an extensive literature on the form and distribution of altruism in non-human primate groups (see edited volumes by Chapais and Berman, 2004; Kappeler and van Schaik, 2006). The most common form of altruistic behavior in primate groups is social grooming, which has important hygienic and social functions. Other forms of altruistic behaviors that occur in various primate species include coalitionary support, in which one individual intervenes on behalf of another in an ongoing agonistic interaction; alarm-calling, in which one individual signals to others that a predator is nearby; alloparental care, in which group members help to carry, protect, and care for dependent offspring; and food-sharing, which ranges from active donations of food items to passive tolerance of others feeding in close proximity.

In-group Biases

Virtually all of the New World monkeys (which range through Central and South America) and Old World monkeys and apes (which range through Africa and Asia) live in social groups (Figure 18.1). The size and structure of social groups vary considerably across species, to include pair-bonded nuclear family units; polygynous groups composed of one adult male, multiple adult females, and immatures; and larger groups composed of multiple adult males, multiple adult females, and immatures. In most cases groups move as cohesive units, but some species,

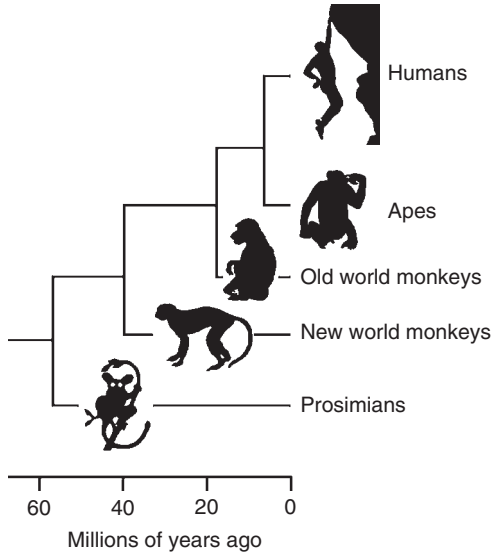

FIGURE 18.1 The primate order is composed of prosimians, New World monkeys, Old World monkeys, and apes. Brain size is generally correlated with body size, but some species have larger brains in relation to their body size than others. In general, apes have relatively larger brains than other primates do.

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including chimpanzees, regularly split up into smaller parties. A few primate species form multi-level societies, in which primary social units are organized into larger aggregations that coordinate their ranging behavior and share sleeping sites (Stammbach 1987). (Orang-utans, however, are largely solitary; females associate with their dependent offspring, and juveniles and subadults may form temporary aggregations, but there are no stable associations among adult orang-utans. Mandrills live in groups that may number hundreds of animals, but it is not known whether all group members are recognized as individuals. Similarly, hamadryas and gelada baboons live in multi-level societies, and it is not known whether individual recognition extends to all members of the larger social units.)

Friendly social interactions are restricted to familiar group members. There are very limited exceptions to this rule. For example, females sometimes mate with males from outside their groups (Goodall, 1986; Palombit, 1994; Cords, 2002). Otherwise, responses to strangers and members of neighboring groups range from passive avoidance to active hostility. Some species actively defend their territories from intruders, while others form home ranges and compete with members of neighboring groups for access to resources in areas of range overlap. There is no evidence of cooperation among members of neighboring groups in the wild.

Nepotistic Biases

Dispersal patterns and mating systems influence opportunities for kin-selected altruism. In many primate species, females remain in their natal groups throughout their lives, while males disperse to avoid inbreeding (Pusey, 2004). In most of these species, females form strong and well-differentiated social bonds, and display pronounced maternal kin biases in behavior (Kapsalis, 2004; Silk, 2005). For example, female baboons are significantly more likely to intervene on behalf of their mothers and daughters than for more distantly related females or non-relatives (Silk *et al*., 2004). They also form longer lasting and more equitable relationships with close maternal kin than with others (Silk *et al*., 2006a, 2006b). In some species, kin biases extend to paternal kin, although the mechanisms underlying paternal kin recognition are unknown (Widdig, 2007). In chimpanzees, males remain in their natal groups while females disperse, and social bonds among males are well-developed (Muller and Mitani, 2005; Duffy *et al*., 2007). Males and females show preferences for close maternal kin (Williams *et al* 2002; Langergraber *et al*., 2007), but maternal kin biases are not as pronounced among male chimpanzees as they are among female monkeys, and paternal kin biases among males are not evident (Langergraber *et al*., 2007).

The most extreme examples of altruism are found in cooperatively breeding species within the sub-family *Callitrichinae*, the family of New World monkeys that includes marmets and tamarins. In these groups there may be multiple adults of each sex, but breeding is limited to the dominant male and female (Bales *et al*., 2000). (Dominant females actively enforce their reproductive monopoly. In several cases dominant females have killed infants produced by subordinate females, and subordinate females are only able to rear litters if they gave birth when the dominant female does not have dependent infants; see Digby, 1995). Mature offspring delay dispersal, and normally do not breed in their natal groups. All group members help to care for infants, regardless of their genetic relationship to them.

Kin selection has probably played an important role in the evolution of cooperative breeding in callitrichids. Groups are mainly composed of closely related family members, and helping behavior contributes to their inclusive fitness. Moreover, callitrichids typically produce twins that share a common placenta and chorion (the membrane the surrounds the growing embryo in the uterus). Stem cells are passed from one twin to the other, a process that is called genetic chimerism (Haig, 1999). It has recently been learned that chimerism extends to all bodily tissues, including the gametes (Ross *et al*., 2007). This means that individuals sometimes pass along their siblings' genes, not their own. Chimerism effectively raises the degree of relatedness within sibling pairs, and may increase the inclusive fitness benefits derived from helping (Haig, 1999).

Altruism Toward Reciprocating Partners

There is considerably less consensus about the role of contingent reciprocity than about the role of nepotism in primate groups (for reviews, see Hammerstein, 2003; Noë, 2005; Silk 2007a). This issue is contentious because it is difficult to demonstrate contingency in natural sequences of behavior.

A series of naturalistic experiments suggest that contingency does influence the pattern of exchanges within dyads. Seyarth and Cheney (1984) showed that 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

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they had not been groomed recently by the same monkey. In contrast, grooming among closely related monkeys did not influence the likelihood of responding to distress calls. Similarly, Hemelrijk (1994) showed that long-tailed macaques were more likely to intervene on behalf of monkeys who had recently groomed them than for monkeys who had not groomed them. In both these experiments, researchers used a within-subject design to assess the effects of recent grooming. This allowed them to exclude the possibility that close associates are simply more likely to groom one another and support one another. There have also been a number of more formal experimental studies of contingent cooperation in several species of monkeys (reviewed in Silk, 2007a). These studies generally suggest that altruism by one individual enhances the likelihood of cooperation by the other, but the behavioral strategies and preferences underlying these contingencies are not well established.

PRIMATE POLICING AND PUNISHMENT

Punitive action against potential rivals and competitors is common in nature (Clutton-Brock and Parker, 1995). Thus, a female monkey may attack another female who encroaches on her food patch, or a male may threaten a rival who comes too close to a female that he is mate-guarding. In contrast, humans often punish individuals who violate social norms or fail to cooperate, even when they are not harmed directly themselves. In colonies of social insects, workers routinely destroy eggs laid by rogue workers, preserving the stability and productivity of the entire colony (Ratnieks, 1988; Ratnieks and Wenseleer, 2005). This type of "policing" in humans and social insects is altruistic, because the individual who imposes the punishment incurs costs, while the benefits are widely shared by other group members.

The English language does not provide an easy way to distinguish between punitive action that benefits the individual and punitive action that benefits the group as a whole. For clarity, I use the terms *retaliation* for the former and *altruistic punishment* for the latter. This distinction is important to keep in mind, because the evolutionary forces that underlie them are quite different. Individual selection will favor retaliation because it generates direct benefits for actors (Clutton-Brock and Parker, 1995). Kin selection (multi-level selection processes) may favor altruistic punishment in the highly related colonies of social insects (Ratnieks, 1988; Ratnieks and Wenseleer, 2005), while the combination of cultural group selection and indirect reciprocity may lead to the evolution of altruistic punishment in human societies (Boyd *et al*., 2003; Panchanathan and Boyd, 2004; Gintis *et al*., 2007).

Retaliation is widespread in primate groups. The most recent evidence for retaliation comes from experimental work on chimpanzees (Jensen *et al*., 2007a, 2007b). In the first study, one chimpanzee was given the opportunity to respond to the loss of valued food items by pulling a rope which caused a sliding platform to collapse and the food to fall out of reach. In one condition, a human experimenter moved the platform away from the actor and slid it to within reach of another chimpanzee (Jensen, 2007a). In another condition, the experimenter did the same thing, but there was no other chimpanzee present to receive the food. In the third condition, a chimpanzee in the opposite cage was able to pull the platform away from the actor and gain access to the food. The chimpanzees were more likely to collapse the table when they lost food than when they were left alone to eat in peace. However, the chimpanzees were most likely to become aroused and dump the food when they were victimized by other chimpanzees.

In the second experiment, Jensen and colleagues (2007b) conducted a reduced form of the ultimatum game in which a one chimpanzee (Player 1) was able to choose between two different pre-set distributions of rewards. One option always provided eight pieces for Player 1 and two pieces (8/2) for another chimpanzee (Player 2), while the other option provided a distribution of 5/5, 8/2, or 10/0. To make a choice, Player 1 pulled a rod that was attached to a tray that held the rewards for each animal. To accept Player 1's choice, Player 2 pulled another rod which brought the food rewards to within reach of both individuals, and then Player 1 and Player 2 could claim their respective rewards. If Player 2 did not pull the rod, neither individual got any food. Here, Player 2 had the opportunity to retaliate against Player 1 if unsatisfied with the offer. Although individuals taking the role of Player 1 preferentially chose offers that benefited themselves (8/2 over 5/5), individuals who took the role of Player 2 rarely rejected any non-zero offers, and showed little evidence of arousal in any of the test trials.

There is very limited evidence for altruistic punishment in non-human primates. Two anecdotes suggest that chimpanzees might punish individuals that violate social norms. In the Mahale Mountains of Tanzania, a young adult male was brutally attacked by eight members of his own group (Nishida *et al*., 1995). The authors speculated that this young male may have been victimized because he did not conform to social rules – he did not defer to higher-ranking

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males, and launched unprovoked attacks on adult females.

More systematic evidence comes from two field experiments conducted on monkeys. Monkeys sometimes give distinctive calls when they find desirable foods (Hauser and Marler, 1993a). Capitalizing on this observation, Hauser and Marler (1993b) surreptitiously provisioned rhesus monkeys (*Macaca mulatta*) with desirable food. In some cases the monkeys who discovered these caches called, and in other cases they remained silent. Female macaques were more likely to be attacked by other group members if they remained silent than if they gave food calls after finding these items. The authors hypothesized that food calls function to announce possession of a food item, and they interpreted the harassment of females who remain silent as a form of punishment for attempting to conceal the location of food items. This would constitute a form of altruistic punishment because the screams of the victim alerted other group members to the site of the food, and many animals had an opportunity to profit from the aggressor's actions.

Subsequent work on food-calling in white-faced capuchins (*Cebus capucinus*; Gros-Louis, 2004) provides an alternate interpretation for aggression in this context. Like rhesus monkeys, capuchins who called after finding food were less likely to be approached by others in the vicinity than were 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, thus deterring potential competitors from trying to take them. This would explain why monkeys are more likely to call when approached by high-ranking monkeys, who might challenge them for possession, than by lower-ranking monkeys, who are unlikely to do so.

In some species of primates, individuals mediate disputes among other group members (Flack *et al*., 2005). This form of intervention differs from coalitionary aggression, because the actor does not take sides. Impartial mediation may bring disputes to a speedy end, thus reducing the costs incurred by the participants and avoiding the possibility of conflicts escalating. Flack and her colleagues consider mediation a form of policing, and predict that it will only be deployed in species with pronounced asymmetries in power. In these cases, powerful individuals can intervene effectively at minimal cost to themselves. If the costs are negligible, then this form of policing may not represent a form of "altruistic punishment."

COGNITIVE BASIS OF SOCIAL PREFERENCES

In humans, empathy enhances prosocial motivations (Batson, 1991). The capacity for empathy relies on the ability to comprehend the feelings, motives, and thoughts of others, and to appreciate the distinction between one's own thoughts and the thoughts of others (Preston and de Waal, 2002). This, in turn, requires a well-developed theory of mind, a multidimensional construct that includes the ability to attribute perception, attention, desires, goals, intentions, knowledge, and beliefs to others (Call, 2007).

Monkeys and apes have considerable knowledge about social information. For example, they are able to recognize dozens of individuals, identify kin, compute the values of resources and services, keep track of past interactions with group members, make transitive inferences, discriminate between cooperators and defectors, and assess the qualities of prospective rivals, mates, and allies (Cheney and Seyfarth, 2007; Tomasello and Call, 1997). Primates also know something about the nature of dominance, kinship, and affiliative relationships between other group members (Cheney and Seyfarth, 2007).

Monkeys and apes can succeed in tasks that require them to attribute perceptual knowledge to others. For example, chimpanzees use visual gestures selectively when others can see them, and pay particular attention to the orientation of the face (Call, 2007). In experiments in which rhesus monkeys attempt to "steal" food from humans, the monkeys attend to the visual and auditory perceptions of the experimenter (Flombaum and Santos, 2005; Santos *et al*., 2006).

Experimental studies also provide evidence that chimpanzees have some understanding of others' knowledge and intentions, and can use this information in strategic ways. Hare and colleagues (2000, 2001) created an experimental protocol in which a subordinate chimpanzee was paired with a more dominant group member. The experiment relies on the fact that subordinate individuals are normally reluctant to challenge dominant individuals over access to food rewards. In a central enclosure, food rewards were hidden behind barriers, so that both rewards were visible to the subordinate but only one was visible to the the dominant chimp. The subordinate saw the food being placed in the enclosure, but the dominant did not (Figure 18.2). After the foods were hidden, the chimps were given access to the central enclosure, and the researchers monitored each chimp's movements. They predicted, of course, that the dominant would head directly for the food reward that was visible to it.

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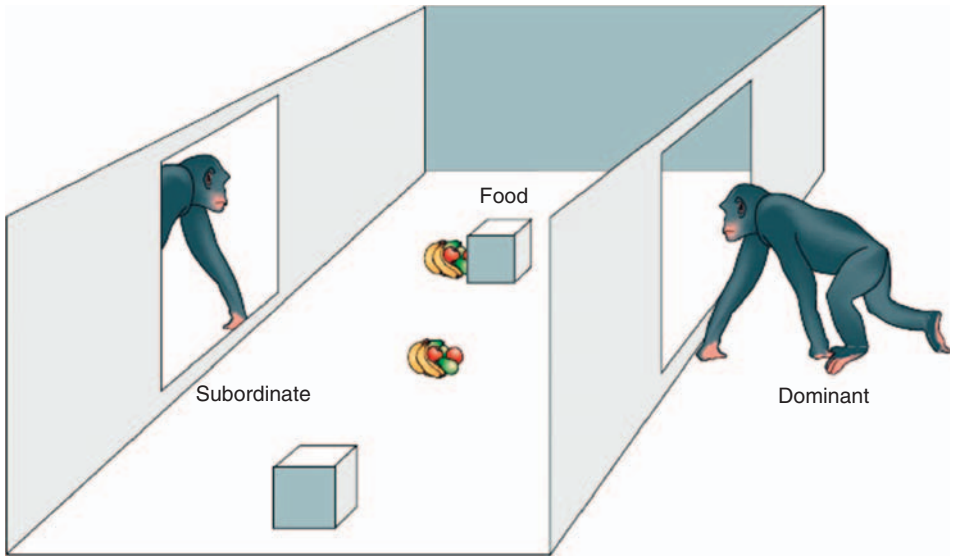

FIGURE 18.2 In this experiment, food rewards were placed in the central area and on one side of an opaque barrier, making both visible to the subordinate (on the left) but only one visible to the dominant. The dominant chimp's knowledge and beliefs about the location of food rewards were varied systematically.Reprinted from Ghazanfar *et al*. (2004), with kind permission of *Nature Review Neuroscience*.

If the subordinate chimp knew what the dominant saw, then it was expected to take advantage of this knowledge and head for the reward that was hidden from the dominant. This is just what the chimpanzees did. So, chimpanzees evidently knew what others knew about the location of food items (see Karin-D'Arcy and Povinelli, 2002, for an alternative interpretation). Capuchin monkeys do not succeed in the same task (Hare *et al*., 2003).

Comparative studies of apes and children suggest that there are substantial differences in social cognition. While chimpanzees, bonobos, and orangutans do as well as two-and-a-half-year-old children on tasks that require physical cognition (e.g., tracking a reward after it has been moved, using a tool to retrieve a reward that is out of reach), human children are much more successful than apes in tasks that rely on social learning, communication, and knowledge of others' minds (Herrmann *et al*., 2007). There are also differences in the ways that apes and children solve problems that rely on collaboration. Although chimpanzees are able to solve collaborative tasks effectively (Melis *et al*., 2006a, 2006b), the means they use to achieve success are different from the means that children use. Chimpanzees do not develop the kinds of joint attention skills that are seen in young children (Tomasello and Carpenter, 2005), and they do not perform well in tasks that build upon this capacity (Wyman and Tomasello, 2007). Chimps coordinate individual goals and their accompanying actions, while "children form shared goals and achieve them through the adoption and reversal of designated roles" (Wyman and Tomasello, 2007: 230).

EMPIRICAL EVIDENCE FOR EMPATHY AND SYMPATHY

Knowledge of others' thoughts, intentions, and desires may give chimps the capacity for empathy. In order to feel sympathy, chimps must also be concerned about the welfare of others. The literature on empathy and sympathy in other primates consists of a number of singular accounts of unusual events, descriptions of several types of common behaviors, and a very small number of systematic analyses and experiments (for a more complete discussion of this body of evidence, see Silk, 2007b).

Conclusions derived from anecdotes are problematic, because they cannot be tested systematically against alternative hypotheses. (To provide a concrete example of this problem, consider the case of Binti Jua. Several years ago, a small child fell into the gorilla enclosure at the Brookfield Zoo in Chicago. Binti Jua, then a young adult female, picked the unconscious child up cradled him to her chest, and eventually turned him over to the zoo staff unharmed. This event was recorded on amateur video, and Binti Jua became an instant celebrity. Some have cited this incident as evidence for empathy and sympathy in apes, arguing that Binti Jua was motivated by compassion

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and concern for the welfare of the child (Preston and de Waal, 2002). However, other facts need to be considered. Binti Jua was hand-reared by humans, after being rejected by her own mother. Concerned that Binti Jua might become a neglectful mother herself, the zoo staff used operant training methods to guide the development of appropriate maternal skills. One of the things that she was trained to do was to retrieve a doll-like object and bring it to the front of the enclosure, where zoo personnel could inspect it (C. Dimitrios, personal communication). This raises the possibility that Binti Jua's response reflected her training, not her understanding of the child's plight and concern for his welfare.) Compilations of anecdotes suffer from the same problem that plagues all *ad libitum* data collection schemes – they are subject to various sorts of bias (Altmann, 1974; Sarringhaus *et al*., 2005). For example, observers may be more likely to notice and remember incidents that seem to indicate that monkeys or apes are empathetic or sympathetic about the welfare of others than they are to take note when they seem oblivious and indifferent.

Some forms of common behaviors have been interpreted as evidence of empathy and sympathy. These include wound-cleaning (Boesch, 1992) and consolation (O'Donnell, 1995; de Waal, 1996). Non-human primates often lick and groom others' wounds, and this may play a role in keeping the wounds clean and preventing infection. Boesch (1992) conjectures that wound-cleaning in chimpanzees is based on awareness of the needs of the wounded individual and sympathy for the discomfort that the other is suffering. This conjecture could be correct, but it is also possible that chimps perform this behavior without conscious awareness of others' needs, or because they like the slightly salty taste of blood.

Consolation behavior occurs when bystanders approach, embrace, touch, and groom the victims of aggression, particularly after episodes that include aggressive vocalizations or physical contact (de Waal and Aureli, 1996). Consolation behavior has now been described in several groups of chimpanzees and bonobos (Arnold and Whiten, 2001; Wittig and Boesch, 2003; Palagi *et al*., 2004). De Waal and Aureli (1996) suggest that chimpanzees console victims of aggression because they empathize with their pain and distress, and are concerned about their welfare. This interpretation implies that consolation will provide an effective means to relieve victims' distress after conflicts. In primates, self-directed behaviors, such as scratching and body shake, are correlated with cortisol levels, and provide an external index of stress levels (Aureli and Smucny, 2000). In a group of captive chimpanzees, consolation did not reduce the rates of self-directed behavior in the victims of aggression (Koski and Sterck, 2007). These data cast doubt on the link between consolation behavior and empathy for the victims of aggression.

Parr (2001) measured the physiological responses of three adult chimpanzees who were shown images of hypodermic needles and dart guns, chimpanzees being darted or injected, and chimpanzees being chased by a veterinarian with a dart gun. Scenes from the home environment (including activity by caretakers, unfamiliar chimpanzees in neutral activities, cage mesh, and transport boxes) were used as control stimuli. Using skin temperature to measure arousal, Parr found that the chimpanzees responded strongly to the images of other chimps being injected and darted, and to images of the dart gun and needles alone. However, the needles and dart guns created as strong a response as the images of chimpanzees being injected or darted. If the chimpanzees' responses were influenced by an understanding of other individuals' feelings or desires, and if they were concerned about the welfare of others, they would have been more strongly affected by the images of other chimpanzees being injected or darted than by the needles or dart guns alone.

SOCIAL PREFERENCES IN PRIMATES

To investigate the nature of social preferences in primates, researchers have recently devised a series of experiments in which animals are presented with opportunities to provide benefits to others at little or no cost to themselves. The choices that they make in these experiments provide insight about their social preferences. The results of this body of work are not fully consistent. Some works suggest that chimps are indifferent to the welfare of other group members, while other works suggest that chimps are motivated to provide benefits to others. Below, I describe these experiments, and then evaluate possible explanations for why the chimps behave differently in different contexts. To help readers keep track of this body of work, a brief synopsis of the experiments is provided in Table 18.1.

Chimps Display Indifference About the Welfare of Other Group Members

My colleagues and I presented chimpanzees from two different captive facilities with the opportunity to provide food rewards to other individuals and to themselves (Silk *et al*., 2005). To implement their choices, the chimpanzees manipulated experimental

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TABLE 18.1 Outline of chimpanzee experimental protocols

Source	Location	Payoff structure Reward for actor/recipient Option 1		Option 2	Reward type	Recipient status	Subject ages (mean years)	Subject Sex (M, F)
Silk *et al.*, 2005	Louisiana	1/1	or	1/0	Food	Group member	15	1, 6
	Texas						28	3, 8
Jensen *et al.*, 2006	Leipzig	1/1	or	1/0	Food	Group member	19	2, 9
	Leipzig	0/1	or	0/1	Food	Group member		
	Leipzig	0/1	or	0/1	Food	Group member		
Vonk *et al.*, 2008	Louisiana	1/0	and	0/1	Food	Group member	15	1, 6
	Texas					Group member	28	3, 8
Warneken and Tomasello, 2005	Leipzig	0/1	or	0/0	Non-food	Familiar human	4	1, 2
Warneken *et al.*, 2007	Uganda	0/1	or	0/0	Non-food	Unfamiliar human	10	15, 21
		0/1	or	0/0	Non-food	Group member		
		0/1	or	0/0	Non-food	Group member		

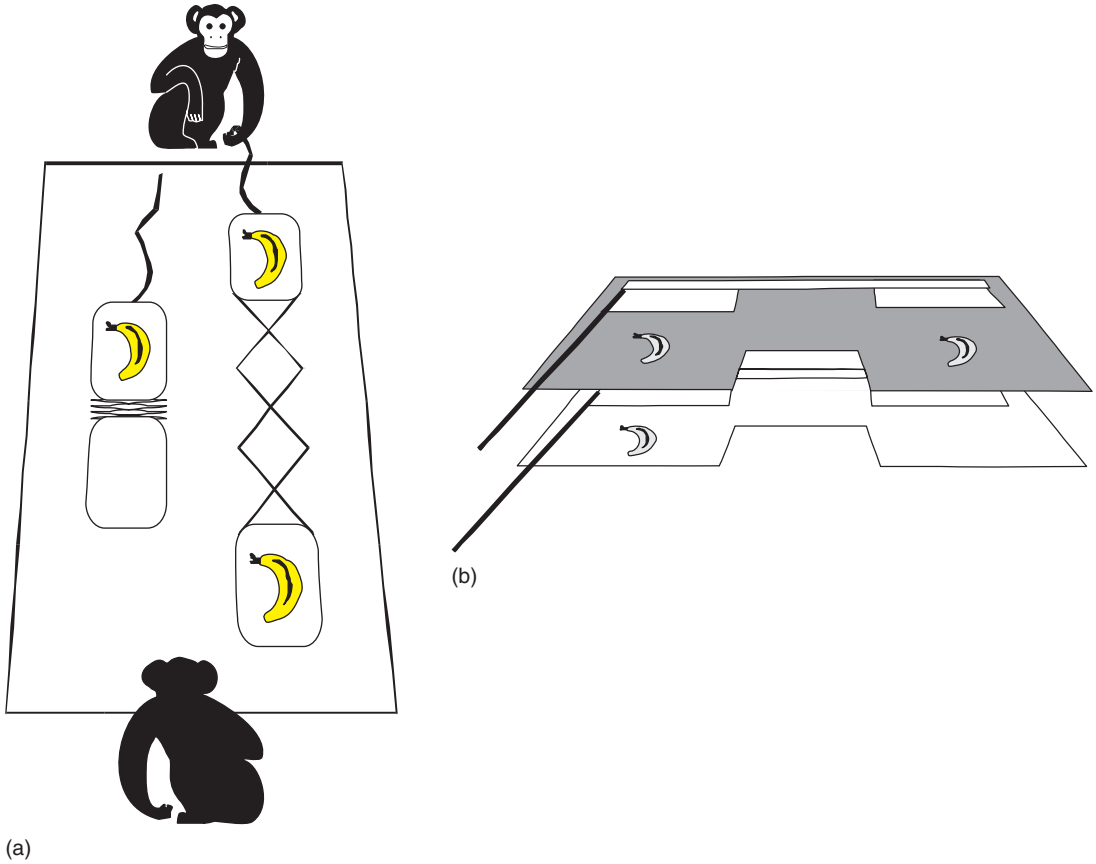

FIGURE 18.3 (a) The actor pulled a rope to expand the device and bring food trays to within reach of its own enclosure and the enclosure on the opposite side. The actor and potential recipient were able to see how the trays were baited, and could also see one another. (b) The actor pulls on one of the two hoses, which sweeps the food forward. When one hose is pulled, the other sweeper is locked in place. Figures drawn by Ruby Boyd.

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apparatuses that were baited with food. At one site, the chimps used an expanding device that was positioned between two food trays. When a rope was pulled, the device expanded and one food tray moved to within reach of the actor while the other tray moved to within reach of a chimpanzee (when present) in the opposite enclosure. Two of these devices were placed side by side in a central enclosure (Figure 18.3a). At the other site, the chimpanzes manipulated a two-tier bar pull device. On each tier, a hose was attached to a bar, and when the hose was pulled the bar moved forward and swept food rewards to the front of the platform (Figure 18.3b). One side of each platform was accessible to the actor; the other side was only accessible to the occupant of the adjoining enclosure. At both sites, the location of the potential recipient's food rewards was counterbalanced (right/left, top/bottom) across trials.

In this experiment, the chimps were provided with two options. One option provided identical food rewards to the actor and to the occupant of the other enclosure; the other option provided a food reward only to the actor. These are referred to here as the 1/1 and 1/0 options, respectively (the actor's payoff is given on the left, the recipient's payoff is given on the right). The chimps could choose one of these two options, or do nothing. We realized that chimps 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 no potential recipient was present. If individuals are concerned about the welfare of others, we would expect them to prefer the 1/1 option over the 1/0 option, and this preference to be stronger when another individual is present than when the actor is alone. Alternatively, if individuals view potential recipients as rivals or competitors, they may be motivated to deprive them of resources. If so, we would expect them to prefer the 1/0 option over the 1/1 option, and this preference to be stronger when another individual is present than when the actor is alone. Finally, if chimps are indifferent to the welfare of others, we would expect them to choose at random, and their choices not to be affected by the presence of conspecifics.

At both sites, the chimps were as likely to choose the 1/1 option when another chimpanzee was present as when they were alone. Moreover, they were more strongly influenced by the location of the food rewards (left/right, top/bottom) than by the presence of the potential recipient. Based on these findings, we concluded that chimpanzees were indifferent to the welfare of other group members.

Interestingly, cooperatively breeding marmosets showed clear prosocial preferences when they were tested using the same basic protocol that was used in Silk *et al*. (2005). In this experiment, actors were presented with a choice between 0/1 and 0/0, so they did not benefit directly from either choice. The marmosets were significantly more likely to choose the 0/1 option when another marmoset was present than when they were alone (Burkhart *et al*., 2008).

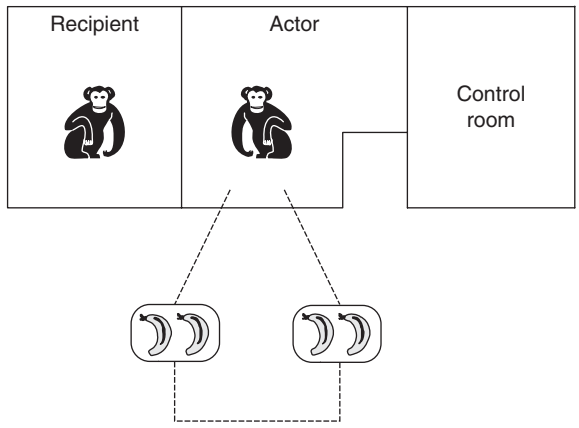

FIGURE 18.4 The actor is confined to the middle room, and can pull a rope that moves the two tables. When one table is pulled forward, the other moves out of reach. The room on the left is occupied by a potential recipient (another chimp from the same group), and the room on the right is always empty. When the door between the actor's room and the potential recipient's room is closed, the actor can only obtain food from its own side of the table. The actor and the potential recipient can see one another, and both can see how the trays are baited. Redrawn from Jensen *et al*. (2006), with permission.

Jensen and colleagues have conducted a different series of experiments to evaluate social preferences in chimpanzees. In this experiment, there were three adjacent enclosures (Jensen *et al*., 2006; Figure 18.4). Two tables were located outside the enclosure, out of the chimps' reach. When one table was pulled forward, the other moved away. When the table on the left side of Figure 18.4 was pulled forward, the inner food cup was accessible to the actor and the outer food cup was accessible to the occupant of the enclosure on the left. When the table on the right side of Figure 18.3 was pulled forward, the inner food cup was accessible to the actor but the outer food cup was not accessible to the occupant of the enclosure on the right. Food cups were positioned on the tables so that only one cup could be reached by the actor. In each trial, the actor was able to move one of the two tables or do nothing, but could not move both tables.

To make sure that the chimps understood that food on the left side was accessible, a set of trials was conducted in which the door between the actor's room and the recipient's room was left open. All four cups were baited, and the chimps were allowed to move only one table. The chimps were significantly more likely to choose the left table (thereby obtaining two

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food items) than the right table (which provided only one food item), suggesting that they understood that food was accessible from the table on the left, but not from the table on the right. The chimps were tested with members of their social groups with whom they had long-term social relationships.

In test trials, the potential recipient was in the room on the left, and could obtain food if the left-hand table was pulled forward. In control trials, the potential recipient was in the room on the right, and was unable to reach food when the right-hand table was moved forward. The chimps strongly preferred the table on the left. However, they were just as likely to choose the table on the left in the test and in control conditions. Thus, their responses were not affected by whether another individual would profit from their actions. As in the experiments described above, the chimps' were apparently indifferent to the payoffs other chimps obtained.

Jensen and colleagues also tested the chimps' preferences when they did not receive any food themselves. In this experiment, only the outer cups were baited; the actors were able to pull one of the two tables forward, or do nothing. In test trials, the left enclosure was occupied; in control trials, the right enclosure was occupied. The absence of rewards for themselves substantially reduced the chimps' motivation to pull the tables forward. When the inner cups were baited, the chimps pulled one of the tables forward in about 85% of all trials; when the inner cups were empty, the chimps' response rate dropped to about 50%. The actors' preference for the table on the left also declined. When the chimps did make a response, they were as likely to choose the table on the right as the table on the left. Thus, they showed no preference for the option that provided rewards to other individuals.

The same reward distribution was used in the third experiment, but this time the actor had a chance to *prevent* the chimp in the left enclosure from obtaining food. If the actor did nothing, the table on the left would automatically be delivered to the chimp in the enclosure on the left. However, if the actor pulled on a rope, the table on the right would be pulled forward and the recipient would be deprived of food Again, the chimps were most likely to do nothing, and they did not differentiate between the two tables.

In another group of experiments using food rewards, Vonk *et al*. (2008) tested the same chimpanzees that were tested by Silk *et al*. (2006). In this experiment, one choice delivered a reward to the actor, but nothing to the potential recipient (1/0). The other choice delivered an identical reward to the potential recipient, but nothing to the actor (0/1). The actors had the opportunity to choose 1/0 only, 1/0 and 0/1, or 0/1 only, or to do nothing. At one site, the chimps had to use a pole to dislodge a food reward, which rolled down a ramp to the actor or toward the potential recipient (Figure 18.5). At the other site, we used the same two-tiered platform shown in Figure 18.3, but in this case the chimps were able to manipulate both levels. As before, we compared the chimps' responses when another chimp was present in the opposite or adjacent enclosure, with when they were alone.

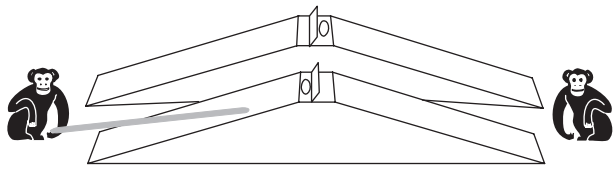

FIGURE 18.5 In this experiment, the actor can use a pole to dislodge a transparent capsule containing a food reward. After it is dislodged, the capsule rolls down the ramp to within reach of the actor or the other chimpanzee (when present). A mesh barrier at the apex of the ramp prevents the food reward on the actor's side from rolling down the ramp toward the potential recipient, and prevents the potential recipient's reward from rolling down the ramp toward the actor.

The chimps were strongly motivated to obtain food for themselves, and did so on virtually every trial in which they made any response. At both sites, the chimps nearly always obtained their own reward first. The chimps sometimes chose the 0/1 option as well, but the presence of a potential recipient did not affect the likelihood that they would do so.

These seven experiments, conducted with four different apparatuses, in three different populations of chimpanzees, generated strikingly similar results. The chimps who participated in these experiments were strongly motivated to obtain rewards for themselves, but did not take advantage of the opportunity to provide food rewards to others at little or no cost to themselves.

It is important to emphasize that in these experiments, the bar for prosocial responses was deliberately set very low. Actors incurred virtually no costs when they behaved prosocially, and they did not have to sacrifice their own rewards to provide rewards to others. This means that other-regarding sentiments did not conflict with selfish motives to obtain rewards, because actors' choices had no effect their own payoffs. In addition, the experiments involved familiar group members, not strangers. Actors might have behaved generously toward group members with whom they cooperated outside the experiment, even if they lacked genuine concern for the welfare of their partners. But the *absence* of prosocial behaviour toward familiar group members implies that actors do not have prosocial preferences about the distribution of food rewards.

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Chimps Respond Positively to the Needs of Others

Warneken and Tomasello (2006) showed that young chimpanzees took advantage of opportunities to provide instrumental assistance to familiar human experimenters in some situations. In these experiments, a familiar human trainer tried to accomplish a task, but was unable to do so for various reasons. For each task, a control condition was included in which no help was needed by the experimenter – for example, a book slipped off a stack of books as the adult attempted to place it on top of the stack (experimental), or he placed it next to the stack (control). While human children consistently helped more in the experimental condition than the test condition in four different situations, young chimps only helped consistently in tasks that required retrieving an object that was out of reach. However, they did distinguish between the test and control conditions in several different versions of the reaching/retrieval tasks. Thus, these chimps seemed able to perceive that the human experimenter needed assistance in some situations, and were motivated to provide help.

In a follow-up study, Warneken *et al*. (2007) examined chimps' willingness to extend instrumental help to less familiar humans, and their willingness to help other chimpanzees. In the chimp–human experiments, the subject observed two people struggling over a stick, and one person gaining possession. The victor then placed the stick out of the loser's reach. The loser stretched his arm toward the object (experimental), or simply looked at the object (control). In half of the trials of each condition, the chimps were shown a piece of food which they were given after retrieving the object. Two-thirds of the chimps helped on at least one trial, and they were significantly more likely to help in the experimental condition than in the control condition. However, the presence of a reward did not affect the chimps' behavior.

In a follow-up to this experiment, the chimps were required to exert more physical effort to retrieve the stick; they had to climb 2.5 m up into a passageway. In this experiment, the chimps retrieved the object about half the time. However, they did not distinguish between the experimental and control conditions. Chimps that helped most often in the previous experiment also helped most often in this experiment, suggesting that their failure to distinguish between the test and experimental conditions was "likely due to a carry-over effect from experiment 1 in which subjects had possibly learned that the experimenter wanted the object" (Warneken *et al*., 2007: 1416).

In the third and most compelling experiment in this study, chimps were given an opportunity to provide help to other chimps. In this experiment, the doors to two rooms were fastened by chains held in place by a peg (Figure 18.6). When the peg was removed, the door could be opened. The subject was confined to the room with the pegs. The subject could then remove a peg and release the door on the right side, but could not reach the peg on the left. The chimp in the middle room could not reach the pegs. The door to the room on the left could not be opened by either chimpanzee. In experimental trials, food was placed in the room on the right. In control trials, the food was placed in the room on the left. Nine chimpanzees served as subjects in this experiment, and three unrelated chimps served as recipients.

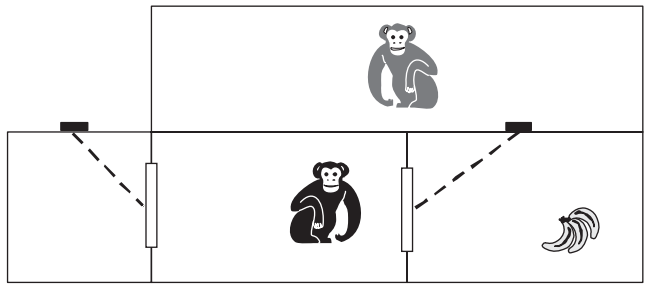

FIGURE 18.6 The actor occupies the room at the top of this diagram. The potential beneficiary occupies the middle room, which is connected to the other two rooms by doors. In order for the potential beneficiary to open these doors, a peg must be released. The actor can reach the peg that releases the door to the room on the right, but cannot reach the peg that releases the door to the room on the left. Food rewards are placed in one of the two connecting rooms, and are visible to the potential beneficiary but not to the actor. Redrawn from Warneken *et al*. (2007), with permission.

The recipients approached the door to the room on the right in every experimental trial, but oriented toward the door to the room on the left only about half the time in control trials. The actors were significantly more likely to release the door in the experimental condition than in the control condition; the difference in the chimps' responses in the experimental and control conditions increased over the course of the experiment. Actors might have been helpful because they expected to share in the rewards obtained. However, the actors never begged for food after the door to the room on the right was opened, and never received food. Thus, these results suggest that the actors were responsive to the needs and desires of other chimps.

Reconciling the Results

These two bodies of experimental work lead to seemingly incompatible conclusions about social preferences in chimpanzees. No serious methodological flaws have been detected in any of the experiments,

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and both bodies of work are based on multiple experiments that generate internally consistent results. In all of these experiments, appropriate controls for things like location preferences, prepotent biases, and dominance rank were implemented in the design of the experiment or the statistical analyses. Therefore, it seems that we must proceed under the assumption that the results of these experiments are reliable and robust. Below, I examine several possible explanations for the discrepancy in the results obtained by Silk/Jensen/Vonk and by Warneken and colleagues.

1. The chimps do not display prosocial biases because they do not understand the way the apparatuses work

It is possible that the Silk experiments did not elicit prosocial responses because the chimps simply did not understand how the experimental apparatuses worked, and did not realize that they could use the apparatus to deliver rewards to other individuals. This criticism implicitly assumes that chimps have prosocial preferences, and the experiments failed to elicit their true preferences.

This objection cannot explain the results obtained by Jensen and his colleagues, because they allowed the chimps access to the enclosure on the left side of the apparatus. When they were allowed to enter the room on the left, the chimps showed clear preferences for the table that delivered rewards that could be recovered by the occupant of the left enclosure over the table that delivered rewards to the other room. Thus, there is little doubt that the chimps knew how the apparatus used in these experiments worked.

My colleagues and I did not explicitly test the chimps' understanding of the apparatuses that we used in our experiments by allowing them to obtain rewards from the recipients' enclosure. Instead, we relied on preliminary tests which demonstrated that the actors (a) understood that they were able to obtain rewards from one side/level of the apparatus, but not the other; (b) were able to counteract strong location biases when it affected their payoffs; and (c) were attending to the distribution of rewards. At the site where the expanding apparatus was used, all of the chimps participated in the experiments as actors and recipients, giving them a chance to experience both roles. The two-tiered platform device that was used at the other is quite similar to one used in many other studies of cooperation in monkeys and apes, and was not expected to present cognitive difficulties for the chimps in our experiments. Moreover, in the experiments conducted by Vonk *et al*. (2008), the likelihood of choosing the other reward declined across trials, suggesting that the chimps understood that they would not obtain the reward delivered to the other enclosure. Finally, the positive results obtained with marmosets, whose cognitive abilities are considerably more limited than the cognitive abilities of apes, suggest that it is unlikely that the chimps did not understand the way that the apparatus worked.

2. Tasks involving food rewards do not produce prosocial responses in chimpanzees because chimps perceive others as competitors over access to limited quantities of food (Warneken and Tomasello, 2006; Warneken et al., 2007)

This explanation focuses on the selective pressures that shape the evolution of social preferences. Chimpanzees live in a more individualistic world than callitrichids, and this corresponds to differences in their performance on the prosocial task (Burkardt *et al*., 2008). But it is not clear that this explanation fits the chimps' performance on the tasks devised by Silk/Jensen/Vonk. These tasks all involved small food rewards, such as one slice of banana. If chimps perceived other chimps as competitors and rivals over access to limited quantities of food, then they would be expected systematically to deny others access to food, not to ignore them. The chimps didn't behave this way. For example, in the Silk/Jensen experiments, the chimps did not systematically prefer the 1/0 option over the 1/1 option. Instead, they behaved as if they were indifferent to the presence of others.

3. The prospect of obtaining food for themselves might have made the chimps oblivious to the needs and desires of other chimpanzees

When chimps were faced with a choice between 1/1 and 1/0 options, they may have been absorbed by their own food rewards and ignored the effects of their choices on others. However, the responses of the chimps were essentially the same when they did not obtain any food rewards themselves. Recall that Jensen and his colleagues conducted two experiments in which actors were unable to obtain food for themselves. The chimps were considerably less motivated to respond in this situation, suggesting that they understood that they would not obtain rewards themselves. Nonetheless, even when the prospect of obtaining food was eliminated, the chimps did not show prosocial preferences. Similarly, in Vonk *et al*. (2008), there was a long latency between dislodging the two rewards. After dislodging and consuming their own rewards, the chimps had considerable time to attend to the needs of their partners.

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4. Chimps respond to direct requests for help, but do not take advantage of opportunities to provide unsolicited assistance

Prosocial responses might not have been observed in the Silk/Jensen experiments because the actors "were preoccupied with retrieving food for themselves, and the recipient did nothing to indicate any need for help" (Warneken *et al*., 2007). However, this is not entirely correct. Potential recipients could and did use gestures to attract the actor's attention and request food in some trials in the Silk/Vonk experiments. As noted earlier, Vonk and colleagues showed that potential recipients gestured before actors had delivered food rewards to them in over half the trials. These gestures ought to have attracted the attention of the actors, and alerted them to the recipient's presence and desires. However, gestures by potential recipients had no significant impact on the likelihood of receiving rewards.

We have also reviewed the videotaped records of the behavior of potential recipients in the experiments presented in our earlier experiments (Silk *et al*., unpublished data). During these trials, we coded the recipient's behavior before actors had had a chance to make a choice between the 1/1 and 1/0 options. Recipients gestured toward the actor and food trays before the actor was able to make a choice in about one-third of all trials. Recipients nearly always gestured toward the 1/1 side of the apparatus. When recipients gestured before a choice was made, actors chose the 1/1 option 60% of the time. When recipients did not gesture before a choice was made, actors chose the 1/1 option 56% of the time. Again, gestures by potential recipients did not have a consistent impact on the actor's behavior.

5. Differences in the chimps' responses reflect variation in their socialization experiences, rearing histories, age, or sex

Efforts have been made to assess the effects of age and sex on variation in performance within experiments (see, for example, Warneken *et al*., 2007), but it is also worth considering the possibility that demographic factors, socialization experiences, or rearing histories generated variation in performance across experiments. All of the subjects were members of bisexual social groups and were maintained in captive facilities. The chimps tested by Warneken *et al*. (2007) were born in the wild, but subsequently orphaned and confiscated by wildlife authorities. They now live together in a well-maintained 95-acre sanctuary in Uganda.

The chimps that participated in the Silk/Jensen/Vonk experiments were substantially older than most of the chimps tested by Warneken and his colleagues (Table 18.1). Chimpanzees reach sexual maturity in their teens (Muller and Mitani, 2005), so the majority of subjects tested by Silk/Jensen/Vonk were adults, while the majority of chimps tested by Warneken and his colleagues were juveniles or adolescents. We know nothing about the ontogenetic development of cooperative behavior in chimpanzees or other primates, leaving open the possibility that differences in performance on these experimental tasks reflects differences in the maturity of the subjects.

CONCLUSIONS

It is more difficult to demonstrate that help is based on prosocial preferences than to demonstrate the absence of prosocial preferences in a particular experimental setting. This is because the existence of altruism is not necessarily evidence for prosocial preferences. Altruistic behavior occurs in species that lack a well-developed theory of mind and the capacity for empathy. Altruism even occurs in social microbes that don't have brains at all (Robinson *et al*., 2005). This means that the motives and social preferences that underlie altruistic behavior must vary across species, and may differ among humans and other primates.

The experiments conducted by Warneken *et al*. (2007) show that chimps are sometimes willing to provide instrumental assistance to others, but the motives that underlie behavior in these experiments are not clear. Actors might provide instrumental assistance toward group members with whom they have cooperative relationships based on reciprocity outside the experiment, even if they lack genuine concern for the welfare of their partners. In contrast, chimps did not demonstrate prosocial preferences in any of the experiments that involved food rewards. If chimps do have other-regarding preferences, these preferences are clearly muted among adult chimps when food is present.

Although the discrepancy between the results obtained in experiments that were designed to examine chimps' social preferences may seem like an unfortunate complication, it provides us with an important opportunity. If we can work out the reasons that the results of these experiments differ, we may gain deeper insights about the complexity and nature of chimps' social preferences. For example, the presence of food rewards might compete with selfish motives about food. If that is the case, then the chimps who were indifferent in the Silk/Jensen/Vonk experiments might behave prosocially in the protocol used by Warneken and his colleagues, and *vice versa*. Moreover, it would be straightforward to modify the experimental procedures used by Warneken and colleagues to examine

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chimps' willingness to retrieve food items for humans or other chimps. To move the discussion forward, we need to make systematic efforts to explain why individuals make different choices in different settings.

Acknowledgments

My work on prosocial preferences was conducted in collaboration with Joe Henrich, Sarah Brosnan, Jennifer Vonk, and Daniel Povinelli, and was funded by a grant from the MacArthur Preferences Network. I thank Ruby Boyd for preparing the figures, and Robert Boyd for comments on an earlier draft of this paper.

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