

Collaboration and Helping in Chimpanzees

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In September 1979, all but one of the Kasakela adult males were traveling in Lower Mkenke Valley when they came upon a female baboon with a tiny black infant. She was feeding in an oil-nut palm and appeared to be quite on her own. Goblin grinned, squeaked softly, and reached to touch Satan. All six males had their hair erect. When the baboon noticed the chimpanzees, she stopped feeding and gazed towards them. . . . Jomeo, moving very slowly, left the other males and climbed a tree close to the palm. At this point the female baboon began to scream but she did not run off. When he had climbed to a branch level with her and about 5 meters away, Jomeo stopped. He stared at her, then began to shake a branch—possibly to try to make her run. She screamed even louder, but apparently no other baboons were within earshot. Two minutes later Figan and Sherry, also moving slowly, climbed two other trees. A male chimpanzee was now in each of the trees to which the baboon could have leaped from her palm; the other three, still looking up, waited on the ground. At this point Jomeo leaped over onto the palm. The baboon made a large jump into Figan's tree, where she was easily grabbed and her infant seized. The mother ran off 6 meters or so, where she remained, screaming, then uttering waa-hoo calls for the next fifteen minutes while the chimpanzees consumed her infant. (Goodall 1986, p. 286)

In many ways the life of a chimpanzee is like that of most primates—a delicate balancing act between out-

competing one's competitors within the group and needing to cooperate with some of those same individuals in defense of oneself and one's kin and allies against threats from other group members, neighboring groups, and predators (Muller and Mitani 2005). What becomes apparent from field research, however, is that male cooperation in chimpanzees is particularly unusual among primates. The males form coalitions and longer-term alliances to overpower group members when competing for food and mating opportunities (e.g., de Waal 1982, Goodall 1986). In some cases they can be completely dependent on one another, since in large groups no single male is able to dominate the group in all contexts. For example, pairs or even trios of males in the Ngogo community have been seen to mate-guard ovulating females, trying to prevent them from copulating with all other adult males. These coalition males have been found to gain higher shares of copulations than could have expected from solo mate-guarding (Watts 1998). Male chimpanzees also reciprocally exchange grooming, meat, and support within and across currencies, and these relationships are still highly significant after controlling for proximity, similarity in rank, age, and kinship within the group (Watts 2002; Mitani 2006).

Chimpanzee males stand out most prominently from other primates, though, in terms of the breadth of forms in which they express these cooperative partnerships. Not

only do they protect a territory as a group, but they also frequently hunt in groups. They support each other during agonistic interactions with other groups and patrol the borders of their territory together. Patrolling chimpanzees, upon detecting members of another group, reportedly react most strongly when discovering isolated individuals. In such cases they will occasionally enter the neighboring territory and coordinate attacks on these strangers that can result in the death of infants or even adults (Boesch and Boesch-Achermann 2000; Watts and Mitani 2001, Wilson and Wrangham 2003). Second, across all sites where groups of multiple males are found living sympatrically with monkeys, chimpanzees are extremely successful arboreal predators; they frequently hunt in groups—primarily red colobus monkeys—and share the meat afterwards (Boesch and Boesch-Achermann 2000; Watts and Mitani, 2002; see also chapter 18). Finally, like other primates they also spend a considerable amount of time grooming kin and other preferred partners (Goodall 1986; Mitani 2006).

While it is male cooperation that makes chimpanzees seem to stand out among primates, it is not the case that females never work together with others. Coalitionary behavior of female chimpanzees does occur—particularly in sites where the costs of sociality are reduced and females can spend time together in larger groups (i.e., Tai: Boesch and Boesch-Achermann 2000). Moreover, in captive situations females have been observed to form coalitions with one another, and in special circumstances they can even dominate males together (de Waal 1982; Wrangham and Peterson 1996).

What is also becoming increasingly apparent with the growing data from field scientists is that chimpanzees likely adjust the form of their cooperative behavior depending on socioecological factors (Boesch et al. 2002). This suggests the possibility that they develop cooperative strategies relatively flexibly. For example, the ways in which chimpanzees form coalitions and alliances can vary depending on the stability of the male hierarchy (see Muller and Mitani 2005 for review). Likewise, it has been suggested that their hunting strategies may vary depending on the canopy structure of the forest, since that affects the level of difficulty of catching prey, and thus it may create different pressures for hunters to develop cooperative strategies (Boesch 1994a, 1994b; see also chapter 18). At Tai, three-quarters of the hunts have been described

as collaborative, in which different hunters perform different complementary actions towards the same prey (Boesch and Boesch 1989, Boesch and Boesch-Achermann 2000). Boesch describes how during collaborative hunts individuals coordinate their actions, performing different roles (chaser, blocker) that aim to drive the prey towards locations where they can be caught (by the ambusher). In Gombe, however, collaboration seems to be rare, and group hunts appear to be mostly simultaneous solitary hunts during which hunters do not coordinate their actions and even pursue different animals from the same group of prey (Goodall 1986; Boesch 1994a; see also chapter 18). Boesch (1994b) argued that the canopy structure at Tai makes the cost of pursuing red colobus higher than at Gombe where the trees are shorter and the canopy is broken. Thus, hunting at Tai requires coordinated action between individuals, whereas at Gombe the hunting success of single hunters is already high enough. Corroborating this idea, Gilby et al. (2006) found evidence that even within a particular site (Gombe), the probability and success of hunting are higher in woodland forest (where the canopy is low and broken) than in evergreen forest.

From a cost-benefit analysis perspective, some of these cooperative interactions entail immediate benefits for all participants, whereas in many other cases it is less clear how (directly or indirectly) or when the actor of the behavior will benefit. Perhaps most surprising is that contrary to previous models of male behavior based on kinship, at Ngogo (with the largest male community to be studied to date) coalition and alliance partners have exceptionally low degrees of relatedness. Therefore, instead of benefiting from such cooperative relationships through indirect reproductive benefits, it seems that male chimpanzees must benefit directly through mutualistic or reciprocal rewards—both of which require a careful choice of cooperative partners to maximize benefit and minimize cheating (Langergraber et al. 2007).

The frequency, variety, and adaptability of chimpanzee cooperation suggest that the underlying motivational and cognitive processes could be similar to those of humans. Yet it recently has been proposed that the range and types of human cooperative behavior are unique in the animal kingdom, and that this diversity relies on uniquely derived human cognitive and emotional adaptations (Fehr and Fischbacher 2003; Tomasello et al. 2005; Stevens and Hauser 2004). Therefore, in order to understand the evo-

lutionary roots of human cooperation, it is crucial to investigate the similarities and differences in the proximate mechanisms underlying the cooperative behavior of our closest living relatives, chimpanzees and bonobos. Only then can we identify the traits that are derived and unique in humans, and which might account for our unusual levels of cooperation.

Proximate versus Ultimate Accounts of Cooperation

Experimental studies with captive chimpanzees can make an important contribution to our understanding of the proximate mechanisms underlying chimpanzee cooperation. We use the term "cooperation" in its broadest sense to mean behavior through which both actor and recipient or only the recipient can benefit (van Schaik and Kappeler 2006). In mutualistic cooperative interactions, in which both actor and recipient benefit, the interest from a cognitive point of view is the extent to which the participants might understand the role of the others in the interaction. Do they understand how the different roles interrelate with each other? Do they actively coordinate their actions, and what types of social and communicative strategies can they use to help them do so? Observations like the baboon hunting episode described above illustrate how different levels of understanding about any joint activity can be put forward to explain the behavior. For example, when Goblin squeaked and touched Satan, it is possible that he understood how success depended on Satan's help and was therefore trying to recruit him. But it is equally possible that he was aroused and excited at the sight of a potential prey and that touching Satan simply calmed him down. When Jomeo, Figan, and Sherry climbed three different trees blocking the baboon's potential escape routes, it is possible that they understood how these different escape routes had to be blocked so that they could succeed. Possibly the chimpanzees were taking into consideration the positions and most likely behavior of their partners. However, it is also possible that each of them simply took a position in a free tree anticipating a possible escape route of the baboon, without any understanding of how the others' actions were related to their own chances of success. It is only with careful and controlled experiments in captivity that we can distinguish between these alternative explanations. We use the term *collaboration* to indicate

joint activities that involve active coordination between partners who understand something about the role of the others in the interaction (this would comprise coordination and collaboration as defined by Boesch and Boesch 1989). This is in contrast to *by-product cooperation* in the case of simultaneous actions that are directed towards the same goal, but without coordination or participants understanding how the others' actions relate to one's own actions and potential success (similarity and synchrony sensu Boesch and Boesch 1989).

It is important to emphasize that the motivation behind these mutualistic interactions (including collaboration) may be purely selfish. Collaborating partners understand that by coordinating their actions with each other, they increase their own probability of success and their likelihood of increasing their own individual payoffs. This leads to the prediction that collaborating chimpanzees will differentiate between different partners and, if given the choice, preferentially choose to collaborate with those who are more skilled, or with whom they have a more tolerant relationship—and thus the highest chances of obtaining the spoils afterwards.

But is chimpanzee cooperation strictly limited to mutualistic endeavors? Or are chimpanzees also motivated and skilled to help others when it does not entail immediate benefits? In other words, can their behavior be more altruistic in nature? Anecdotes like the following would seem to suggest so.

Washoe spent some time on an island ringed with an electric fence. One day a three-year-old female, Cindy, somehow jumped this fence. She fell into the moat, splashed wildly, and sank. As she reappeared, Washoe leaped over the fence, landed on the narrow strip of ground at the water's edge, and, clinging tightly to a clump of grass, stepped into the water and managed to seize one of Cindy's arms as the infant surfaced again. Washoe was about nine years old at the time; she was not related to Cindy and had not known her for very long. (R. Fouts and D. Fouts, personal communication in Goodall 1986)

Many of the cooperative exchanges reviewed in the previous section (food sharing, support in agonistic encounters, grooming) potentially represent examples of altruistic behavior since they do not seem to bring immediate benefits for the actors (although for alternative mutualistic explanations see Stevens and Gilby 2004 and Gilby 2006,

on meat sharing; Mitani 2006 and Bercovitch 1988 on coalitionary behavior; and Shutt et al. 2007 on grooming). This creates an evolutionary puzzle for anyone attempting to understand these social behaviors at the ultimate level of explanation, since the behaviors potentially increase the recipients' fitness at a cost to the performers (Hamilton 1964). How then, could such behaviors evolve? Ultimate accounts of altruism focus on the mechanisms that have selected for such social behavior because of its inclusive fitness effects on the actor. For example, kin selection explains altruistic behavior that increases the actor's indirect fitness (e.g., Hamilton 1964), and reciprocal altruism (Trivers 1971) explains altruistic behavior directed towards unrelated members that increases the actor's direct fitness in the long term (see Bshary and Bergmueller 2007 and de Waal 2008 for reviews on the topic). However, the major goal of our experiments is to test hypotheses about the proximate processes that make such behavior possible. Specifically, our goal is to empirically investigate the motivational and cognitive mechanisms of behaviors that do not result in short-term benefits (and possibly entail some costs) for the actor. Our research is guided by the following questions: Do chimpanzees know when someone else needs help? In what situations are they willing to help? If so, then how are these prosocial tendencies maintained, and what psychological mechanisms allow individuals to detect and avoid cheaters? For example, it has been argued that although the idea of contingency-based reciprocal altruism is theoretically very compelling, there is scarce evidence for it in nonhuman animals (Hammerstein 2003; Stevens and Hauser 2004). For reciprocal altruism, individuals need to keep track of past interactions with different partners, potentially over long periods of time. This requires memory and learning capacities as well as low temporal discounting rates for delayed benefits. Since cognitive constraints could make the establishment and maintenance of reciprocal altruistic strategies difficult, this could account of the relative rarity of evidence for reciprocal altruism in nonhuman animals.

In the current chapter, we will first review the most instructive examples of experimental work on chimpanzee cooperation which has focused on an individual's ability to solve mutualistic instrumental tasks requiring coordinated actions. We then focus on our own recent work, which also concentrates on the skills of captive chimpanzees in collaborative mutualistic tasks in addition to altruistic

helping. Finally, we reflect on how these findings might inform observations in the wild and contribute to a better understanding of the differences between cooperation in humans and cooperation in nonhuman apes.

Cooperative Problem Solving in the Lab

More than seventy years ago, Crawford (1937) presented pairs of chimpanzees with three different instrumental problems requiring simultaneous joint action. The tasks were all very similar, requiring the chimpanzees to pull two ropes or levers at the same time in order to gain access to food. Although some of the chimpanzees eventually learned to solve each problem, no chimpanzee showed spontaneous skill at solving them. The first task required both chimpanzees to pull a rope in order to obtain a heavy baited box that neither individual could pull alone. The subjects did not succeed until the experimenters intervened and trained them to pull on command. This result was replicated with each new cooperative problem, thus suggesting that the subjects did not understand their partners' role in their success. Such an understanding would have facilitated problem solving, enabling the chimpanzees to coordinate their efforts in very similar mutualistic tasks. The author summarizes his subjects' behavior as follows.

When Ross and Bulla were introduced into the situation immediately after individual training with a single rope, their efforts toward moving the box were entirely uncoordinated. There was no suggestion in the behavior of either which would indicate any attempt of one to coordinate its activity with that of the other. While their efforts were directed toward the food-baited box, and while they both made strenuous efforts to draw it in alone, they never, even for an instant, pulled simultaneously. Typically, one animal would pull while the other watched and played about the cage. When the first finished pulling, the other would take the rope, of the same one, and pull while the first animal did something else. Frequently they took a succession of turns at the ropes in this manner (Crawford 1937, p. 21).

Eventually Crawford did see behaviors in one individual that he interpreted as communication used to recruit a cooperative partner, but this interpretation was moderated by the fact that the behavior was rare and occurred only after hundreds of trials. Crawford did see the potential limitations in his experimental approach, however, and he sug-

gested the need for further research with a larger sample of individuals and with tasks perhaps more appropriate for use with chimpanzees. In another attempt several years later with more individuals, Crawford did find that one pair of chimpanzees could learn to coordinate their behavior very quickly (Crawford 1941).

Using a method highly similar to that used by Crawford (1937), Povinelli & O'Neill (2000) trained a pair of chimpanzees to simultaneously pull two adjacent ropes in order to retrieve food from a heavy baited box. Each of the successful cooperators was then paired with a series of naïve subjects. Of the ten resulting pair combinations of experienced and naïve chimpanzees, only three were ever successful in obtaining the food by pulling the ropes simultaneously. Although they were equally constrained by sample size ($n = 7$) and had essentially used the same method that had not worked sixty years before, Povinelli and O'Neill (2000) quickly concluded that the chimpanzees' failure to cooperate was largely due to cognitive constraints that both prevented a naïve individual from learning socially from an experienced partner, and also prevented an experienced partner from teaching a naïve individual (e.g., with encouraging gestures).

Chalmeau and colleagues (Chalmeau 1994; Chalmeau and Gallo 1996) also presented a task that required joint actions (i.e., pull two handles simultaneously to obtain a small amount of food) to another small group of chimpanzees ($n = 6$). Like previous investigations, theirs found very low levels of cooperation, with only two individuals consistently solving the task. The successful cases involved one dominant male coordinating his pulling so that it occurred when a younger female was near the apparatus. On several occasions this dominant individual even coerced the young female into pulling the handle by herding her into the correct location, and in all cases the male was the one to obtain the small fruit rewards. Here the authors were able to draw an important conclusion that would be the basis for future success: they noted that the chimpanzees' cooperative behavior was limited by social constraints on the subordinates. In almost every trial the most dominant individual monopolized the apparatus, thereby preventing others from cooperating, while also eating any food retrieved through joint effort.

Recently Hirata and colleagues (see chapter 20) tested two chimpanzees in a cooperation task similar to the one previously used by Petit et al. (1992) with two species

of macaques. Food was placed in a hole in the ground and covered by a set of heavy stones. Pairs of chimpanzees were required to pull simultaneously on the rings attached to the stones in order to uncover the hole. Although both chimpanzees pulled the stones, they almost never did so at the same time, and therefore never succeeded in moving them. In observations similar to those made by Crawford (1937), Hirata et al. report that each chimpanzee rather seemed to avoid pulling at the stones when the partner was pulling them.

These experiments on cooperation, together with other repeated findings that chimpanzees fail tasks in cooperative-communicative contexts (see Tomasello et al. 2003; Hare and Tomasello 2004; Hare 2007) have led researchers to propose that the sophisticated cognitive abilities of nonhuman primates might be best demonstrated in competitive rather than cooperative contexts (e.g., Hare 2001; Tomasello et al. 2005). It is possible, however, that just as competitive paradigms engage chimpanzees particularly well in certain cognitive tasks, there are cooperative paradigms that can engage them as well. In fact, it is possible that in previous problem-solving experiments requiring cooperation chimpanzees interpreted the situation not as potentially cooperative, but as competitive. In order to tease apart the psychology that underlies what seems to be flexible chimpanzee cooperation in the field, we sought to elicit spontaneous cooperation in captivity and investigate key factors that may cause this phenomenon to be relatively scarce in captive settings.

Tolerance as a Prerequisite

One possible explanation for the poor performance of chimpanzees in previous experimental studies on cooperation is that their low levels of social tolerance constrained their ability to cooperate in food-retrieval tasks (e.g., Chalmeau 1994). Experiments with other primate species have demonstrated that the ability to cooperate to produce mutually beneficial outcomes is likely not just a product of complex cognitive abilities, but also a result of tolerance between potential cooperative partners. For example, species with the highest level of tolerance (low dominance asymmetries) are generally more reliable cooperative problem solvers (Tonkean macaques: Petit et al. 1992; capuchins: Mendres and de Waal 2000; marmosets: Werdenich and Huber 2002; cotton-top tamarins, Cronin

et al. 2005). Moreover, capuchin monkeys have been found to be most cooperative in a joint food-retrieval task when their partner is closely related (i.e., one with whom they have more a tolerant relationship) and the food reward is sharable (de Waal and Davis 2003).

To systematically investigate whether or not social tolerance plays a significant role in chimpanzee cooperation, we conducted a set of studies in which we measured both the tolerance level and the problem-solving performance of chimpanzee dyads (Melis et al. 2006a). Subjects were 32 unrelated chimpanzees from Ngamba Island Chimpanzee Sanctuary in Uganda. We found that levels of social tolerance (measured as the tendency of a pair of individuals to share food) predicted the dyad's likelihood of solving a cooperative problem. In the tolerance test that was conducted prior to the cooperation test, we allowed the two subjects to enter the testing room and feed from a baited tray that was placed outside the room but within their reach. The baited tray was placed against the metal bars of the subjects' test room (figure 21.1). We measured the level of sharing within and across several trials in which we also varied the amount and distribution of the food. Each dyad obtained a sharing score and participated after this phase in the cooperation test. As in previous studies, the cooperation problem was a food-retrieval task in which two individuals were required to pull simultaneously on two ends of a rope in order to obtain a tray of food that had been placed outside the testing room and out of their reach. The pulling mechanism (originally conceived by Hirata and Fuwa 2007; see chapter 20) consisted of a single rope threaded through loops fixed on top and across the length of the tray (figure 21.1a). Both ends of the rope were extended into the testing room through the metal bars. The rope's two ends were too far from each other for one chimpanzee to pull both ends simultaneously. If one chimpanzee pulled only one end of the rope, it would simply slide out of the loops on the tray. Thus, to pull the tray and food within reach, subjects had to cooperate to pull both ends of the rope simultaneously. This cooperation test consisted of six trials in which, to facilitate the emergence of cooperation and reduce possible situational tolerance constraints, we made the food rewards extremely sharable: an abundance of sliced banana pieces on two separate dishes.

All 16 dyads (32 individuals) showed a positive correlation between the tendency to share food in the tolerance

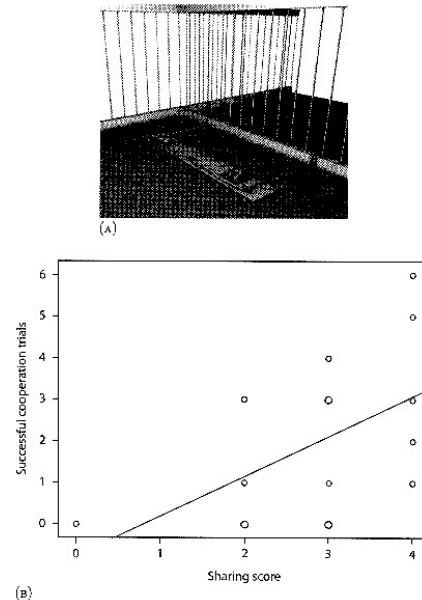


Figure 21.1 (a) The cooperation apparatus from the Melis et al. 2006a and 2006b experiments. Two food dishes 2.7 m apart were baited with fruit pieces. The two ends of the rope were 3.4 m apart. Metal bars separated the testing room, where the subjects were located, from the room where the tray was located. (b) Correlation between the score obtained in the food-sharing tests and the number of successful trials in the cooperation tests ($r_s = 0.56$, $N = 16$, $P = 0.02$). Larger circles represent two data points. From Melis et al. 2006a.

test and the level of success in the cooperation test (figure 21.1b). That is, levels of food sharing between members of a dyad predicted spontaneous success or failure in the cooperation task. We even found that social tolerance was a better predictor of success than was the subjects' understanding of the task's physical properties. However, an alternative explanation for these findings could be that it was not necessarily the dyad's level of inter-individual tolerance but rather some characteristic of the individuals themselves that determined their success at cooperating. Therefore, to provide further evidence that the level of tolerance was indeed the critical factor enabling cooperation, we conducted another experiment in which we attempted to turn cooperation on and off by systematically varying the level of tolerance between members of a pair. We tested whether a previously unsuccessful subject would succeed in the cooperation test when paired with a more tolerant partner and, conversely, whether a previously successful subject would fail when paired with a less

tant partner. Confirming the earlier results, we found that previously unsuccessful subjects were immediately successful when paired with partners with whom they had a more tolerant relationship—but even when subjects knew how to solve the pulling task, they stopped working earlier when paired with less tolerant partners. This appears to be clear evidence that the level of tolerance was in fact the causal factor in these situations (Melis et al. 2006a, experiment 3).

Low levels of inter-individual tolerance constrained chimpanzees' tendency to cooperate or act simultaneously on the apparatus even when the tray had been baited with dispersed and shareable food and the working space between the partners had been maximized. Interestingly, unsuccessful dyads typically did not show any aggressive behavior in the cooperation test. Instead, individuals seemed to avoid approaching or manipulating the apparatus in the presence of certain partners. This suggests that the individuals were inhibited by some partners since they probably knew from their experience outside the experimental setting that approaching and/or manipulating the baited tray in the presence of that more dominant partner could lead to a negative response (aggression, or lack of sharing afterwards). Not only do these results demonstrate that chimpanzees can spontaneously cooperate when their tolerance level is high, but they also help to interpret the failure of chimpanzees in previous studies (Crawford 1937; Povinelli and O'Neill 2000; Chalmeau 1994; see also chapter 20) in which the social tolerance between individuals was not controlled and dyads were presented with highly monopolizable food rewards (often in a small reduced working space). These results suggest that high levels of social tolerance within a social group may be an important prerequisite for certain forms of cooperation to appear. Only if individuals are tolerant enough to approach and manipulate objects or food items that are in possession of others are they likely to find a cooperative solution to a problem and share the rewards of the joint effort afterwards.

Collaborative Chimpanzees

Although lifting tolerance constraints in chimpanzees allowed us to elicit spontaneous cooperation between individuals, it was still not possible to distinguish between *collaboration*, in terms of individuals actively coordinat-

ing their actions to those of their partners, and *by-product cooperation*, in which two individuals act simultaneously without each having any understanding of, or behavioral coordination with, their partner's actions. Since in the previous experiment both subjects entered the room simultaneously to participate and both were attracted to the baited tray, it was possible that their success was due to their simultaneous but independent actions taken toward the same tray (by-product cooperation)—and thus we were left with the question of what each chimpanzee understood about their partner's contribution to the task, and to what extent they coordinated their actions with those of their partner.

To investigate these questions, we presented a subset of chimpanzees from the previous study with several variations of the same cooperation task described above. After an individual introduction to the pulling task, in which each subject could learn about the physical properties of the pulling mechanism (see Melis et al. 2006b; online material), subjects participated in the partner delay test, which consisted of allowing one individual in each pair to enter the testing room first while the other waited in an adjacent room. The baited tray could not be pulled within reach by a single subject since, as described above, the length of the rope ends inside the testing room were too short and too far apart for one chimpanzee to reach both simultaneously. Therefore, the subject who entered first had to wait for the partner (thus inhibiting pulling the rope out of the loops), who was allowed to enter after increasingly long delays of 5, 10, 20, and 30 seconds. Once subjects were able to wait for the partner without pulling the rope out, and were successful in obtaining the food on two consecutive trials at a given delay, we increased the delay. This test ended when all subjects were able to wait 30 seconds for their partner. In order to move to a longer delay, subjects first had to wait for the partner and successfully obtain the food on two consecutive trials at a given delay. Two test subjects made no mistakes, two subjects made three to four mistakes respectively, and the other four subjects made between 12 and 28 mistakes before completing two consecutive successful trials at all of the delays. These results suggest that half of the subjects understood from the very beginning the need to wait for their partner, whereas the other half needed additional experience to learn to inhibit the impulse to manipulate the rope before the partner's arrival.

Our results contrast with the slower learning process described by Hirata and colleagues (Hirata and Fuwa 2007; chapter 20) using the same cooperative task. In that study, subjects began to show waiting behavior only after 90 to 170 trials, even though they had already participated in a long learning phase of 600 trials in which the rope ends had been increasingly shortened. It is possible that this difference between studies is due to individual differences (as evidenced by the fact that some Ngamba subjects made no mistakes whereas others made up to 28 mistakes in the partner delay test). Alternatively, it is possible that this difference is due to the different methods we used to familiarize the subjects with the task. Hirata and Fuwa (2007) report several treatments in which subjects actually did not need to cooperate since both ends of the rope could be reached simultaneously by a single individual (and, in fact, that is what subjects often did). Thus, when confronted with the crucial tests, subjects might not have fully understood the impossibility of solving the task without a partner, and instead might have been very motivated to continue pulling by themselves (thus trying to find an individual solution to the task). Furthermore, it is possible that subjects were not highly tolerant of each other and therefore tended to avoid pulling simultaneously from the rope. In our introduction to the pulling task, on the other hand, subjects experienced that they could not solve the problem alone, since they could not reach both ends of the rope—and if they pulled one end of the rope, they experienced how the rope came out of the loops. After that, they were paired with highly tolerant partners, with whom they experienced successful cooperation. This different method may have accelerated the learning process in our test.

Although our results from the partner-delay test were evidence of the chimpanzees' ability to synchronize their actions with that of their partners in order to obtain a common goal, we reasoned that a further test of their level of understanding about the partner's role would be if they were allowed to recruit a collaborative partner when they either did or did not need help in solving the problem. Specifically, they could choose to let another chimpanzee enter the testing room to collaborate on the task with them. For this purpose, we showed subjects how to remove a "key" (wooden peg) that locked a sliding door between the testing room and an adjacent room (see online material in Melis et al. 2006b). All subjects learned very quickly that upon removing the key, they could open the door and

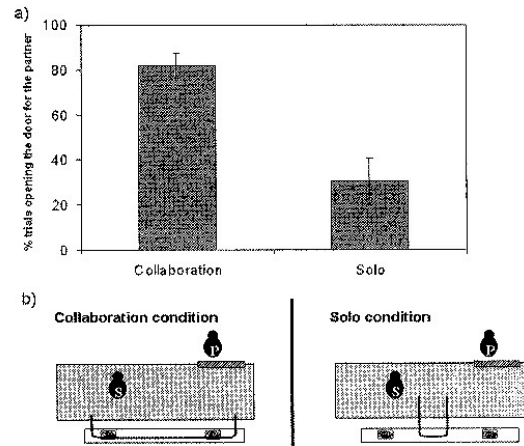


Figure 21.2 (a) Mean percentage of trials (\pm SEM) in which subjects opened a door for the potential partner. Subjects unlocked the door to recruit their partner significantly more often in the collaboration condition, when they needed assistance to obtain the food, than in the solo condition, when they did not ($t = 7.27$, $df = 7$, $P < 0.001$, paired t test). As individuals, seven of eight subjects recruited significantly more in the collaboration condition than in the solo condition. From Melis et al. 2006b. (b) Set-up of the collaboration and solo conditions: the subject was released from an adjacent room into the testing room, while the partner was "locked" in another adjacent room that only the subject could open with a key from inside the testing room. The rooms were separated by metal bars so that the subjects could see each other.

enter the adjacent room. In the collaboration condition of this test (figure 21.2) the tray of food could not be pulled within reach unless two individuals pulled simultaneously, as the ends of the rope were too far apart. Therefore, the first subject had to open the door to the adjacent room to recruit their partner and initiate the collaborative activity. In the control (solo) condition, however, the two ends of the rope were placed close to each other so that a single individual could simultaneously reach both ends and did not need to recruit a partner. The results showed that individuals recruited a partner significantly more often when solving the problem required collaboration (figure 21.2). Furthermore, this preference for recruiting a collaborator when needed appeared relatively fast, with five of eight subjects doing so within the first twelve trials.

Given the finding that chimpanzees recruit collaborators when needed, a second experiment was designed to test whether they can also learn to choose the more effective of two possible partners to recruit. The testing procedure was identical to that in the collaborative condition from the previous experiment, with the exception that now two potential collaborators were in the separate

rooms adjacent to the testing room and each of the doors that led to the testing room was locked with a key. The subject could open either door from inside the testing room (figure 21.3b). The two potential collaborators—both males—had previously demonstrated very different levels of success in pulling the food tray with others, and on this basis they were designated by the experimenters as the “more effective” and the “less effective” partner. Since the subjects had not interacted with these potential collaborators in this context, they first participated in an introductory session in which they were allowed to recruit either collaborator—by choosing whose door to open—in six consecutive trials. In the test session, occurring on a later day, subjects were again released into the testing room for another six trials and allowed to choose which of the two partners to recruit for the collaboration task (the positions of the two potential partners were counterbalanced across trials). In the introductory session the subjects had

chosen both partners with equal frequency, but in the test session they almost exclusively chose the more effective partner (figure 21.3a). A trial-by-trial analysis revealed that the subjects were basing their recruitment choices in a given trial on the outcome of the preceding trial. If subjects succeeded in a trial, they tended to stay with the same partner on the next trial, whereas when they failed they shifted partners on the next trial (known as a “win-stay, lose-shift” strategy). Overall, subjects were significantly more successful in retrieving the baited tray with the “effective” partner than with the “less effective” partner, which explains the development of a preference for the latter: subjects preferred the partner with whom they were more successful in retrieving the tray. This experiment revealed that after minimal experience, chimpanzees could identify and remember their more skillful and less skillful collaborators, choosing to collaborate preferentially with the partner who led them to higher benefits and avoiding the individual with whom they experienced more failures.

Taken together, these results show that chimpanzees can learn extremely quickly, and without any extensive training, to collaborate with others in reaching a common goal. Furthermore, they show that chimpanzees not only coordinate their actions with those of their partners, but also understand the role a partner plays in joint activity, as evidenced by the fact that they actively recruited the most effective partners for solving a problem that required collaboration. However, several prerequisites are necessary if any potential collaboration is to emerge between chimpanzees in a food-retrieval task. First, the two individuals in a dyad need to be very tolerant towards each other. Second, the food rewards for the task must be sufficiently sharable, and, if possible, distributed widely enough in space, to reduce the potential for competition between the partners. Finally, subjects first need to experience and understand that they cannot solve the problem by themselves. During all of our tests, and often before recruiting their partner, subjects repeatedly checked the apparatus to make certain that the tray of food could really not be pulled successfully by a single chimpanzee. Nearly all subjects employed various means searching for nonsocial solutions to the problem (e.g., tool use, or attempts to fix one end of the rope to the bars). Thus, it seems as though they tried their best to solve the problem alone and were not particularly motivated toward collaboration (most likely

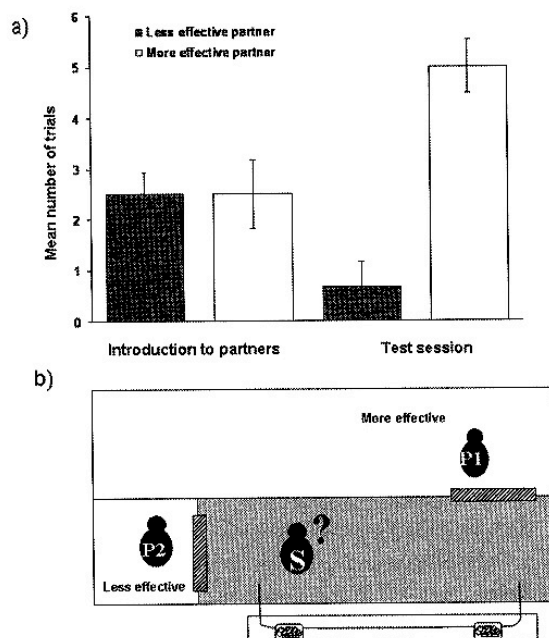


Figure 21.3 (a) The mean number of trials (\pm SEM) in which the subjects chose the less or more effective partner in the introductory and test sessions of the second recruitment experiment of Melis et al. 2006b. Subjects preferred the most effective partner in the test session only ($F(1,5) = 9, P = 0.027$). From Melis et al. 2006b. (b) The two potential collaborators were locked in two rooms adjacent to the testing room. Each door was locked with a key that only the subject could remove from inside the testing room. All three rooms were separated by metal bars so that subjects could see the partner behind the door before opening it. The position of the potential collaborators was counterbalanced across trials.

