



ARTICLES

Engineering cooperation in chimpanzees: tolerance constraints on cooperation

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The cooperative abilities of captive chimpanzees, *Pan troglodytes*, in experiments do not match the sophistication that might be predicted based on their naturally occurring cooperative behaviours. This discrepancy might partly be because in previous experiments potential chimpanzee cooperators were partnered without regard to their social relationship. We investigated the ability of chimpanzee dyads to solve a physical task cooperatively in relation to their interindividual tolerance levels. Pairs that were most capable of sharing food outside the test were also able to cooperate spontaneously (by simultaneously pulling two ropes) to obtain food. In contrast, pairs that were less inclined to share food outside of the test were unlikely to cooperate. Furthermore, previously successful subjects stopped cooperating when paired with a less tolerant partner, even when the food rewards were presented in a dispersed and divisible form to reduce competition between subjects. These results show that although chimpanzees are capable of spontaneous cooperation in a novel instrumental task, tolerance acts as a constraint on their ability to solve such cooperative problems. This finding highlights the importance of controlling such social constraints in future experiments on chimpanzee cooperation, and suggests that the evolution of human-like cooperative skills might have been preceded by the evolution of a more egalitarian social system and a more human-like temperament.

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In their natural habitat chimpanzees, *Pan troglodytes*, cooperate in various ways. Most prominently, adult males form long-term alliances within their social groups to coordinate their attacks and dominate rival males (de Waal 1982; Watts 2002). Chimpanzees also 'patrol' the borders of their territory together to avoid being outnumbered by any rival group they might encounter (Watts & Mitani 2001; Wilson et al. 2001; Watts 2002). Patrolling chimpanzees will also occasionally enter the territory of a neighbouring group and coordinate attacks on its members that can be lethal (Goodall et al. 1979; Wrangham 1999; Boesch & Boesch-Achermann 2000; Watts & Mitani 2001; Wilson et al. 2001). In addition, Boesch & Boesch (1989) observed frequent cooperative hunting in which males corral a monkey, seemingly performing different roles (e.g. driving prey versus ambushing) in the process and sharing meat afterwards (see also Watts & Mitani 2002).

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These same kinds of cooperative skills have not been observed in laboratory experiments. Crawford (1937, 1941) tested seven pairs of chimpanzees for their ability to pull a heavy baited box within reach. However, the box could be moved only if subjects pulled simultaneously. After repeated exposures, none of the chimpanzees spontaneously cooperated to obtain the food; they were successful only after being explicitly trained to retrieve it. In addition, once subjects were trained they were unable to transfer their new skill to a slightly modified version of the same task (i.e. subjects had simultaneously to pull ropes from the ceiling instead of the floor). In a similar study, Povinelli & O'Neill (2000) trained a pair of chimpanzees to work together to pull a heavy box and then paired each of the experienced chimpanzees with a series of naïve subjects. Of the 10 possible experienced-naïve pairs, only three were successful in obtaining the food by pulling the ropes simultaneously. Povinelli & O'Neill concluded that the chimpanzees' failure to cooperate was largely because either naïve individuals were unable to imitate the experienced individuals, or experienced individuals were unable to teach the naïve

individuals (e.g. with encouraging gestures). Finally, Chalmeau (1994) and Chalmeau & Gallo (1993, 1996), using a similar task (subjects needed to pull two handles simultaneously to obtain food) within a captive group, found that only two individuals were consistently skilled at working together to retrieve the food, and this only involved one individual waiting for the other to pull his handle. However, in this case the authors concluded that the low levels of cooperation resulted from social constraints on the subordinates. In almost every trial the most dominant individual monopolized the apparatus, preventing others from potentially cooperating.

What might explain such discrepancies between observational and experimental studies of chimpanzee cooperation? One hypothesis is that noncognitive factors may have constrained the ability of chimpanzees to cooperate in experimental studies (e.g. Chalmeau 1994). For example, chimpanzee problem solving can be affected by motivational issues related to the experimental context. Hare & Tomasello (2004) found that chimpanzees were more skilful in several cognitive tasks when the task was conducted by a competitive experimenter rather than a cooperative one. Such findings suggest that chimpanzees show their most sophisticated cognitive abilities when emotionally engaged in experimental tasks, in this case while competing against an experimenter (Hare & Tomasello 2004; Hare et al. in press). Similarly, in the case of cooperative problem solving, experiments with other primate species have shown that subjects are most motivated to cooperate when there are high levels of tolerance between potential partners. For example, more tolerant species are reliable cooperative problem solvers (Tonkean macaques, *Macaca tonkeana*: Petit et al. 1992; capuchin monkeys, *Cebus apella*: Chalmeau et al. 1997; Mendres & de Waal 2000; Visalberghi et al. 2000; marmosets, *Callithrix jacchus*: Werdenich & Huber 2002; cottontop tamarins, *Saguinus oedipus*: Hauser et al. 2003). Furthermore, capuchin monkeys are most cooperative in joint food retrieval tasks when their partner is closely related and the food reward is shareable (de Waal & Davis 2003). Finally, chimpanzees are more likely to tolerate receiving a smaller reward than another chimpanzee for the same effort if the two subjects come from a more stable social group (Brosnan et al. 2005). Taken together, such results with chimpanzees and other primates support the idea that noncognitive factors can constrain social problem solving. In the case of cooperative problem solving, levels of social tolerance in particular may explain much of the variance in the ability of primates, including chimpanzees, to cooperate in novel instrumental tasks requiring joint effort.

Have previous experimental paradigms used to examine chimpanzee cooperation allowed for high levels of social tolerance among the chimpanzees tested? First, there have been few, if any, natural observations of chimpanzees working jointly on any type of instrumental task to acquire monopolizable food (e.g. using stone tools jointly; the one exception to this may be the use of 'ladders' by captive chimpanzees; Menzel 1972; de Waal 1982). However, all previous cooperation experiments have required chimpanzees to work together to solve an instrumental task (pushing or pulling an object) to obtain monopolizable food (e.g. a single cherry in Chalmeau 1994). Second, almost all

observations of naturally occurring cooperation in chimpanzees involve two individuals working together to outcompete another individual (heterospecific or conspecific) for a shareable resource (meat, status, mates or territory). In these cases, cooperation can be considered a competitive strategy, like deception, to deal with competition (Kummer 1967; Humphrey 1976; Wrangham 1980; de Waal 1982). This hypothesis suggests that chimpanzees would be most motivated and perhaps even most skilful as cooperators while trying to outcompete a common rival (Hare 2001). Finally, researchers have tested chimpanzees without controlling for tolerance levels between potential cooperative partners, so making it possible that subjects actually viewed their potential 'cooperative' partner as a competitor when attempting to obtain the nonshareable food. Therefore, it seems plausible that an experimental paradigm that controls for levels of tolerance between potential cooperative partners would be most likely to elicit spontaneous cooperation in chimpanzees.

The current study was designed to test this 'tolerance hypothesis' for cooperation in chimpanzees. The tolerance hypothesis suggests that pairs of individuals with the highest levels of interindividual tolerance will be the most successful at solving novel instrumental tasks that require joint effort. Specifically, the tolerance hypothesis predicts that tolerance levels, both in the interpersonal sense (interindividual tolerance levels within a dyad) and in the situational sense (the shareability of the food rewards and the presence of a common competitor), will influence the subjects' tendency to cooperate.

In experiment 1 we investigated all three variables predicted to affect tolerance levels and thus spontaneous cooperation. This included the shareability of the food rewards, interdyad competition and interindividual tolerance levels. For example, by varying the shareability of the food reward, we altered the potential for competition after cooperation (de Waal & Davis 2003). The presence of a common competitor might increase interindividual tolerance levels and the motivation of dyads to work together to defeat the competitor. Therefore, we predicted higher levels of tolerance and more coordinated problem-solving efforts when food rewards were shareable (de Waal & Davis 2003) and a common competitor was present (Hare 2001). In experiments 2 and 3 we focused solely on the effect of interindividual tolerance levels on cooperation. Here we predicted that individuals with the highest interindividual tolerance levels would be the ones most likely spontaneously to solve the novel cooperative task.

EXPERIMENT 1

In this experiment, we measured the tendency of six pairs of chimpanzees to share food that was already within their reach. We then presented subjects with a novel food retrieval task, which required cooperation (i.e. simultaneously pulling two ropes) to obtain food. We manipulated subjects' interindividual tolerance level by: (1) presenting dispersed or clumped food rewards and (2) sometimes presenting subjects with a conspecific competitor who could prevent them from obtaining the food reward. Our hypothesis was that the highest level of cooperation would

occur when pairs of subjects who readily share compete against a third party for shareable food. Since we predicted higher tolerance levels among mother–offspring dyads than nonrelated subjects (de Waal & Davis 2003), we tested only mother–offspring (and one father–offspring) dyads.

Methods

Subjects

We studied 12 chimpanzees housed at the Wolfgang Köhler Primate Research Center at the Leipzig Zoo, Germany (Table 1). They lived in a stable group of 18 individuals (one adult male, six adult females, seven adolescents of 7–11 years and four youngsters of 6 months to 4 years), which have been housed together for over 12 years. Chimpanzees at the zoo spend the day in a 4000-m² outdoor area, and a 400-m² indoor area, both of which have natural vegetation, climbing structures, trees, streams and other natural features, as well as enrichment facilities such as spinning treat logs and artificial termite mounds. At night they stay in a series of sleeping rooms (about 47 m²). The chimpanzees are fed a variety of fruits, vegetables and cereals several times per day. Subjects were tested in dyads in their sleeping rooms with a familiar experimenter. We tested one father–son pair and five mother–offspring dyads (Table 1). The subjects were never food deprived and water was available ad libitum. Subjects could choose to stop participating at any time. They had never before participated in an experiment requiring them to cooperate. This experiment was conducted between October 2002 and September 2003.

Apparatus

The apparatus consisted of a long, flat food platform (50 cm × 2.25 m) attached to metal tracks allowing it to slide freely across the width of a central room (Fig. 1). Two ropes could be attached either at opposite ends of the platform or together in the centre of the platform (2.2 m or 38 cm apart) extending through the wire mesh into the test subjects' room on one side. Additional ropes could be attached at the other side of the platform extending into the competitor's test room, opposite the two test

subjects' room. Only when the two ropes were positioned in the centre of the platform was it possible for a single individual to move the platform. Subjects could reach through the wire mesh to obtain the food once the food platform was adjacent to their room.

Experimental treatments and procedure

Tolerance tests. We tested each pair for their ability to share food. The food platform was placed against the wire mesh adjacent to the subjects' test room. Food was baited in one of three ways. (1) Dispersed–divisible: both food boxes (2.2 m apart) were each baited with approximately 350 g of sliced fruit. (2) Clumped–divisible: a single food box was baited with approximately 700 g of sliced fruit. (3) Clumped–solid: only one food box was baited with two fruit pieces. Once the food boxes were baited, we released the subjects into the test room to retrieve the food. Each dyad participated in two trials of each of the three conditions ($N = 6$ trials). We tested dyads in the morning and each dyad participated in only one trial per day. The order in which the conditions were presented was randomized within and across dyads.

Familiarization. Before the cooperation test, each subject was individually introduced to the cooperation apparatus. The food platform was placed outside the subjects' test room, out of reach of the subjects, and baited with food. Two ropes were attached to the centre of the platform (38 cm apart) so that a single individual could pull the food platform within reach. Subjects were given 5 min to pull the food platform within reach. If subjects did not succeed in pulling the food within that time, they were again moved to the holding room until the next trial. Subjects had to succeed in at least one of three trials to participate in the cooperation tests. If a subject did not pull in three consecutive trials but already had a partner who did pull, this subject received no further experience and the cooperation tests started.

Cooperation test. In the cooperation test, the food platform was positioned in the centre of the room and the two ropes were attached 2.2 m apart so that the two subjects had to work together to retrieve the food. Subjects participated in the following test conditions (Fig. 1), which differed in the monopolizability of the food rewards and the presence of a common competitor.

(1) Dispersed food: two food boxes (2.2 m apart) were each baited with approximately 350 g of sliced fruit.

(2) Dispersed food with competitor: as in condition 1 but in addition an adolescent female (kept together with another young female) could pull the platform in the opposite direction away from the test dyad.

(3) Clumped food: one food box was positioned in the centre of the platform and baited with two whole fruit pieces.

(4) Clumped food with competitor: one food box was baited as in condition 3 and there were competitors as in condition 2.

We tested subjects in 12 test sessions each of which included five test trials (5 min each; $N = 60$ trials). Within

Table 1. Sex, age, rearing history and kin relation of the subjects in experiment 1

Dyad	Name	Sex	Age (years)	Rearing history	Kin relation
1	Ulla	Female	27	Nursery/peers	Mother
	Fifi	Female	11	Mother	Daughter
2	Fraukje	Female	28	Nursery/peers	Mother
	Jahaga	Female	11	Mother	Daughter
3	Robert	Male	29	Nursery/peers	Father
	Patrick	Male	7	Mother	Son
4	Corry	Female	28	Nursery/peers	Mother
	Truddy	Female	11	Mother	Daughter
5	Natascha	Female	24	Nursery/peers	Mother
	Frodo	Male	11	Mother	Son
6	Riet	Female	27	Nursery/peers	Mother
	Sandra	Female	11	Mother	Daughter

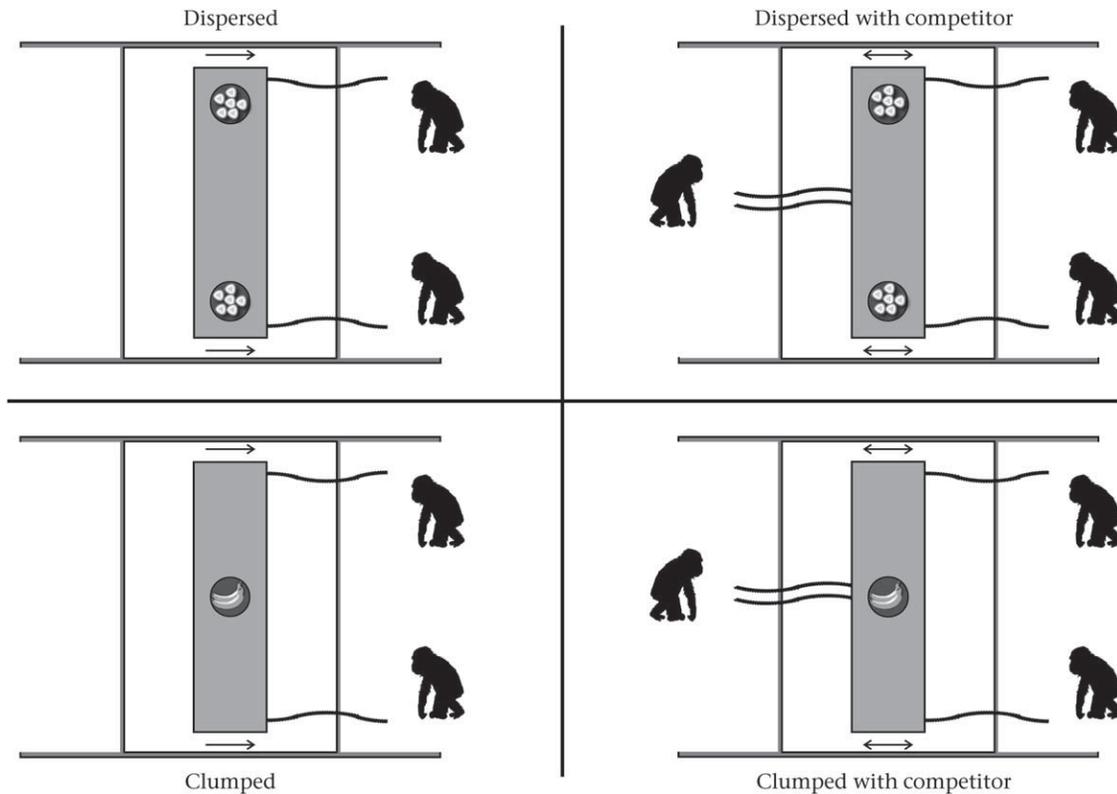


Figure 1. Experimental set-up of the four conditions in experiment 1. Dispersed: two food boxes (2.2 m apart) were baited with fruit slices. Clumped: one food box in the centre of the platform was baited with two pieces of whole fruit. In both conditions with a competitor an adolescent female could pull the platform in the direction opposite from the test dyad. The two ropes on the test dyad's side were always 2.2 m apart. Arrows indicate the direction in which the platform could move.

each session only one of the four test conditions was administered. The order in which the four conditions were administered was counterbalanced within and across dyads. In each session we conducted an additional motivational trial by attaching the ropes to the middle of the food platform, and detaching the ropes of the other party (e.g. the competitor) so that the previously unsuccessful party could retrieve the food at least once within each of the 12 test sessions. No individual, including the female competitor(s), participated in more than one session per day.

Scoring and analysis

All tests were videotaped, with the food dishes and the entire test room visible on the tape. In the tolerance tests, all trials were coded from videotape for whether the two subjects in a dyad were able to feed together or obtain part of the food reward from the food platform (de Waal 1997). A trial started when the first subject entered the room and finished when the baited dish or dishes had been emptied. The following types of food acquisition (i.e. sharing) were coded: (1) subjects fed together at the feeding site(s), reaching through the bars and obtaining the food reward simultaneously; (2) one subject obtained part of the food reward before being displaced by the partner; (3) one subject fed on scraps left by the partner. In the condition with two dishes we used a more conservative criterion, so that trials in which one individual was able to monopolize

both dishes were not considered as 'sharing trials', even if one of the subjects fed on some scraps left by the partner. In the cooperation tests, all trials were coded for whether the test dyad successfully retrieved the food platform, so that at least one of the subjects could feed. To test each successful dyad for differences between number of successful and unsuccessful trials across conditions, we used Fisher's exact test on a 2×2 contingency table. Successful pairs' efficiency was measured by comparing, with Mann-Whitney U tests, latencies to pull the food tray within reach. The performance of each dyad was considered as an independent test and we used the method specified in Rosenthal (1991) to calculate a combined P value. Of the trials in the tolerance and cooperation tests, 20% were randomly selected and coded for reliability by a second coder who was blind to the conditions and hypotheses being tested. There was 100% agreement between coders with respect to sharing behaviour and success in the cooperation tests (Cohen's Kappa = 1.00). All P values reported in this and the following experiments are two tailed.

Results and Discussion

Three dyads, two of them with the highest sharing scores (Ulla-Fifi: 6; Fraukje-Jahaga: 4; Robert-Patrick: 3) spontaneously solved the cooperative pulling task with no

explicit training. These successful dyads solved the task within their first test session (five trials), and one dyad was successful in its first trial (even though one individual in the dyad, Fraukje, never pulled the rope in the introduction to the apparatus). The other three dyads (sharing scores: Corry–Truddy: 3; Natasha–Frodo: 3; Riet–Sandra: 2) remained unsuccessful throughout the experiment. This bimodal performance (i.e. success versus no success) suggested a possible link between cooperation and tolerance levels. The failure of three dyads to cooperate is unlikely to have been caused by a lack of motivation, since these same subjects, as individuals, were successful in obtaining the food reward in the motivational trials that were included in each test session. Other factors such as age, sex and dominance rank do not seem to have contributed to the differences in performance. The ages and sexes of the two best cooperative dyads and two of the unsuccessful dyads were identical (Table 1) and the two highest-ranking individuals in the group (Robert and Riet) were successful and unsuccessful, respectively.

Among the three successful dyads, there was no evidence that the presence of a competitor improved the subjects' tendency to work together (overall $Z = 1.08$, $N = 3$, combined $P = 0.14$, Rosenthal 1991). On the contrary, subjects appeared to be somewhat less successful in her presence (Fig. 2). A possible interpretation of this result is that the additional pulling of the competitor in the other direction increased the difficulty of the task, thus preventing dyads from succeeding in this condition, regardless of whether they were motivated to cooperate. However, this explanation seems unlikely since dyads were equally efficient in terms of speed at moving the food platform within reach in both conditions (Mann–Whitney test for all the three dyads: NS; overall $Z = 0.58$, $N = 3$, combined $P = 0.72$, Rosenthal 1991). Nevertheless, subjects could have been more motivated to work together in the presence of the competitor but unwilling to invest the higher level of effort the competitor imposed.

However, there was evidence that successful dyads were more cooperative when the food rewards were dispersed

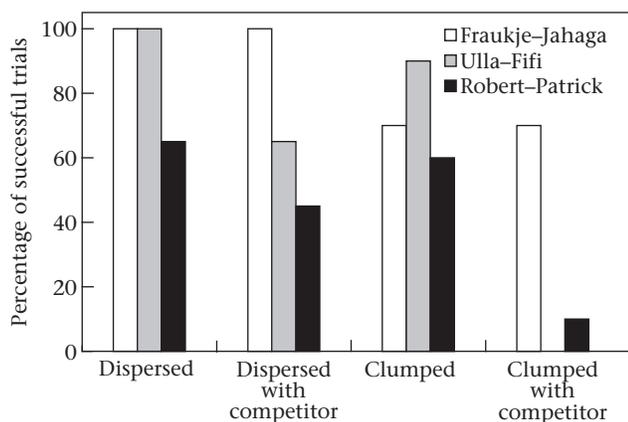


Figure 2. Percentage of successful trials for the three successful pairs in each of the four conditions in experiment 1. Food was dispersed or clumped, with or without a competitor present (see Fig. 1).

than when they were clumped (overall $Z = 3.5$, $N = 3$, combined $P < 0.01$, Rosenthal 1991; Fig. 2). Each of the three cooperative dyads retrieved the food platform not only more often but also faster when the food was dispersed (Mann–Whitney test for all three pairs: $P < 0.05$; Fraukje–Jahaga: $U = 179$, $N_1 = 40$, $N_2 = 16$, $P = 0.01$; Ulla–Fifi: $U = 56.5$, $N_1 = 35$, $N_2 = 11$, $P < 0.001$; Robert–Patrick: $U = 30$, $N_1 = 22$, $N_2 = 7$, $P = 0.015$). In all three dyads both individuals ate food on every trial of this condition. When the food was easily monopolizable (clumped and solid), each subordinate offspring initially continued to cooperate with its dominant parent in pulling in the food platform. However, the parents in these dyads almost never (4% of the trials) allowed their own offspring to obtain any of the food reward, which finally led the offspring to abandon the rope before the food platform was within reach.

The results of this experiment suggest that the highest levels of joint effort to retrieve the platform occurred when tolerant partners were presented with dispersed and divisible food (the two successful and tolerant mother–daughter pairs also had a close relationship outside the test setting). This set-up was designed to facilitate cooperation and avoid competition between the partners over the food. However, even in such a situation, three pairs (one of them with the lowest sharing score) were unable to work together successfully. These results suggest a possible relation between interindividual tolerance levels and ability to solve a problem cooperatively. However, given the small sample size, this relation needed to be explored further with a larger group of chimpanzees.

EXPERIMENT 2

Chimpanzee dyads in experiment 1 did not cooperate more in the presence of the competitor and three of the six dyads (one of them with the lowest sharing score) were unsuccessful even when the food rewards were dispersed and shareable. Therefore in experiment 2 we did not manipulate either of these two variables (competitor and shareability of the food reward) and instead focused on the relation between interindividual tolerance and cooperation success. We presented 16 chimpanzee dyads with a novel cooperation pulling task (Hirata 2003) and compared their performance with their tendency to share food outside the cooperation setting. Since successful dyads from experiment 1 were significantly more likely to cooperate in a condition with dispersed and highly shareable food rewards (as did the capuchins in de Waal & Davis 2003), subjects in experiment 2 were presented only with this condition. We hypothesized that subjects who more readily share food (i.e. are more tolerant of each other) would be more likely to succeed in the cooperation task.

Methods

Subjects

Of 39 chimpanzees living in Ngamba Island Chimpanzee Sanctuary, Uganda, 32 participated in experiment 2.

Ngamba is in Lake Victoria, 23 km from the mainland. The sanctuary was established in 1998 to care for orphaned, confiscated chimpanzees in Uganda. All subjects were unrelated. Each day, a group of 19 adults is released on to the 40-ha island to roam freely and forage from a primary forest, while the juveniles ($N = 20$) spend the day in a smaller forest enclosure (4000 m²). In the juveniles' enclosure, additional enrichment facilities, such as wooden platforms and artificial termite mounds, are available. Twice a day, juveniles are allowed to go to the 40-ha forest with human caregivers and females from the adults' group. At night all chimpanzees sleep in a large holding facility (4 m high and approximately 140 m²) consisting of seven rooms with interconnecting raceways. The chimpanzees are fed four times a day with fruits, vegetables, posho (maize flour cake) and millet porridge. We tested subjects in pairs in one of the rooms of the holding facility (15 m²). The subjects were never food deprived and water was available ad libitum. They could choose to stop participating at any time and had never before participated in an experiment requiring them to cooperate. This experiment was conducted between September and October 2004.

Apparatus

The cooperation apparatus (Hirata 2003) consisted of a long, flat food platform (17 cm × 3.4 m), outside the subjects' test room (Fig. 3). Food could be placed on wooden dishes (17 × 27 cm) on the ends of the food platform. A rope (7.6 m) could be placed through loops on top and across the length of the platform, so that both ends of the rope extended from the platform through the metal bars into the test room. Pulling from only one end of the rope was ineffectual because the rope would come out of the loops and thus lose its connection to the platform. Thus, subjects could pull the food platform within their reach and obtain the food on the food dishes only

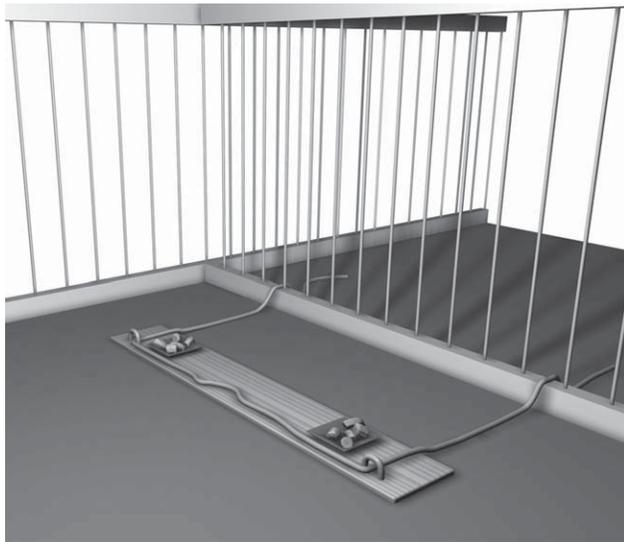


Figure 3. The cooperation apparatus from experiments 2 and 3. Two food boxes (2.7 m apart) were baited with fruit pieces. The two ends of the rope were 3.4 m apart. From Melis et al. 2006. Reprinted with permission from AAAS.

by pulling both ends of the rope simultaneously towards their room (or by pulling one end while holding the other one). Once the food platform was close enough to their room, they could reach through the metal bars and obtain the food.

Procedure

Food-sharing tests. We tested each pair for their ability to share food. The food platform was placed against the metal bars of the subjects' test room. Food was baited in one of three ways. (1) Dispersed-divisible: both food dishes (2.7 m apart) were each baited with approximately 0.25 kg of sliced fruit. (2) Clumped-divisible: one food dish was baited with 0.5 kg of sliced fruit. (3) Clumped-solid: one food dish was baited with two pieces of whole fruit. Once the platform was baited, subjects were released into the test room to retrieve the food.

Familiarization. Before participating in the cooperation test, each subject was individually introduced to the cooperation apparatus. The food platform was placed outside the subjects' test room, out of their reach, and baited with food. The rope was placed in one of three positions, which differed in how far the two ends of the rope were from each other: (1) together; (2) 18 cm apart; (3) 1.4 m apart. A single subject was always able to reach both ends simultaneously. If the subject did not succeed in retrieving the food platform, a trial ended either when the rope had been pulled out of the loops or after 5 min from the start of the trial if the platform had not been pulled in. All subjects participated in one session of six trials (two trials per condition) and these were presented to all subjects in the same order (ends of the rope together, then 18 cm apart, then 1.4 m apart). Since success in this individual introduction to the task was not a prerequisite for participating in the cooperation test, variability in performance during this session was analysed only as a possible factor contributing to cooperation success.

Cooperation test. After the individual introduction to the apparatus, each dyad participated in the cooperation test. The food platform was placed outside the subjects' test room, out of reach of the subjects, and both dishes (2.7 m apart) were each baited in view of the subjects with approximately 0.25 kg of sliced fruit. The two ends of the rope were now 3.4 m apart. The length of each end of the rope extending into the subjects' room was set arbitrarily at 1.3 m. We started a trial by allowing the test dyad to enter the test room. If the dyad was unsuccessful, a trial ended either when the rope had been pulled out of the loops or after 5 min from the start of the trial if the platform tray had not been pulled in. At the end of each trial, the subjects were moved back into the holding room until the apparatus was reset for the next trial.

Design

Each dyad participated in six food-sharing trials administered in two sessions (one session before the cooperation test and the second session afterwards). In each test

session dyads received one trial of each of the three conditions. The order in which the trials were presented was randomized within and across dyads. Dyads received six cooperation trials within one test session. No individual participated in more than one session per day.

Scoring and analysis

All tests were videotaped, with the food dishes and the entire test room visible on the tape. In the food-sharing tests all trials were coded from videotape for whether the two subjects in a dyad were able to feed together or obtain part of the food reward from the food platform (as in experiment 1). We also measured whether sharing occurred across trials, by looking at whether subjects alternated in monopolizing the food. The sharing score was calculated by adding the number of trials in which both subjects fed to the number of trials in which the subordinate individual monopolized the food (the subordinate was defined as the individual that monopolized the food in fewer trials). If both subjects monopolized the food in an equal number of trials, we added that number of trials to the number in which both individuals fed (since in this case no individual was a clear subordinate). Thus, the sharing score also reflects whether the two individuals in a pair were equally able to monopolize the food across different trials, that is, the dominance asymmetry within the pair. In the cooperation tests all trials were coded for whether the test dyad successfully pulled the food platform within reach, so that at least one of the subjects could feed. We randomly selected 20% of all trials and a second coder who was blind to the conditions and hypotheses being tested coded them for reliability. There was 100% agreement between the two coders (Cohen's Kappa = 1.00).

Results

We combined the results of the two food-sharing test sessions to calculate a sharing score for each dyad since no change was detected in the sharing tendency of the dyads before and after participating in the cooperation test (Wilcoxon signed-ranks test: $T = 6$, $N = 16$, $P = 0.3$). The average sharing score was 2.75 of a possible 6 (range 0–4).

In the familiarization session all subjects except one manipulated the rope to retrieve the food platform. On average, subjects were able to retrieve the platform by pulling both ends of the rope on 4.2 trials (range 0–6 trials). Nearly all subjects were able to obtain the food when both ends of the rope were close to each other (the first two conditions or first four trials received) and 12 of the 32 subjects succeeded at least once in the last two trials, in which the ends of the rope were further apart (1.4 m).

Of 16 pairs, 11 succeeded in at least one trial of the cooperation test, when the two ends of the rope were too far apart for one individual alone to manipulate them simultaneously. Although four of five unsuccessful dyads consisted of two adults, the average age of the dyad did not correlate with the level of success in the cooperation test (Spearman correlation: $r_s = -0.40$, $N = 16$, $P = 0.12$).

The ability of dyads to solve the pulling task cooperatively was, however, significantly correlated with their tendency to share food as assessed in the food-sharing tests ($r_s = 0.56$, $N = 16$, $P = 0.02$; Fig. 4). However, since only 12 of the 32 subjects had shown an understanding of the physics of the pulling task in the familiarization session, the success or lack of it could have also been a consequence of the dyads' different levels of understanding of the task. To test this, we calculated an average score of the level of understanding per dyad (or mean number of successful trials during the familiarization session) and analysed whether this factor was related to their success in the cooperation test. The average level of understanding of the pairs did not correlate with their success in the cooperation session ($r_s = -0.1$, $N = 16$, $P = 0.7$). A partial correlation that controlled for subjects' level of understanding revealed that success in cooperation remained significantly correlated with the sharing score ($r_s = 0.6$, $N = 16$, $P = 0.002$).

Discussion

The results of experiment 2 support the hypothesis that interindividual tolerance levels are related to the ability to solve a cooperative task. A dyad's level of success in the cooperation task was significantly correlated with the extent to which individuals in the dyad would share food outside the cooperation setting. Pairs with high sharing scores were more likely to succeed in the cooperation task than were those with low sharing scores. We also found no relation between dyads' cooperation success and their level of understanding of the pulling task. In fact, many of the individuals with the highest scores in the individual familiarization session were unable to succeed with their partner in the cooperation test, while some of the subjects with a poor understanding of the task succeeded immediately with the partner in the cooperation test. However, even though all but one subject pulled the rope in the familiarization session, we

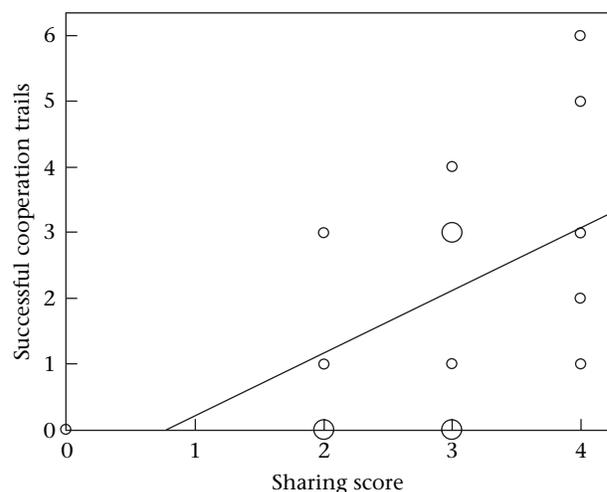


Figure 4. Correlation between the food-sharing score obtained in the food-sharing tests and the number of successful trials in the cooperation tests of experiment 2. Larger circles represent two data points.

could not rule out the hypothesis that certain individuals could be inhibited or disinclined to manipulate the apparatus in the presence of any other conspecific, independently of the relationship to them. That is, some of the unsuccessful subjects could be generally inhibited individuals that are disinclined to feed together with others and less likely to manipulate the apparatus. We designed experiment 3 to investigate this alternative explanation.

EXPERIMENT 3

If the lack of cooperation in experiment 2 was due to the relationship between the individuals in a dyad, then all subjects, if paired with a tolerant partner, should be able to succeed in the cooperation task. Therefore experiment 3 was designed to test whether unsuccessful subjects from experiment 2 would be able to succeed spontaneously in the cooperation test with a more tolerant partner. In addition, we tested whether levels of cooperation would decrease by pairing previously successful subjects with a high-ranking and low-tolerant individual.

Methods

Subjects and apparatus

We tested 12 subjects from experiment 2. We chose as subjects the individuals from those pairs with the lowest level of tolerance and success in no more than one trial in the cooperation test (intolerant pairs were defined as those that obtained a sharing score of ≤ 2). Thus, there were eight unsuccessful subjects. We also chose two of the most tolerant successful pairs (sharing score = 4) from experiment 2. The remaining six subjects had also participated in the previous experiment 2 and were chosen as new partners for some of these subjects. The apparatus was the same as in experiment 2. This experiment was conducted right after experiment 2 within a 6-week period.

Procedure and design

First, we had to find tolerant partners for the eight unsuccessful subjects. The choice of potential tolerant partners was based on observations of their daily interactions and, once the potential partner was chosen, we conducted food-sharing tests to confirm these observations. As in experiment 2, subjects participated in food-sharing tests (six trials) until each of the eight subjects had a new partner with a sharing score of at least 3. We chose 3 as the cut-off sharing score for a tolerant pair, because in experiment 2 only 14% of the dyads with a sharing score of ≤ 2 succeeded in more than one trial, whereas 64% of the dyads with a score of > 2 succeeded in more than one trial. We also had to find intolerant partners for previously successful subjects. Therefore, we tested the four lowest-ranking and successful subjects from experiment 2 with the highest-ranking individual in their group (an adolescent male and adult female).

The 12 subjects participated in one session of six cooperation trials with the new partner. The food platform

was baited exactly as in experiment 2. After that, on a different day, they participated in another session of six cooperation trials with the old partner to control for order effects.

Scoring and analysis

The sharing behaviour of the subjects and their performance in the cooperation tests were scored as in experiment 2. Furthermore, we coded the behaviour of the subjects in the unsuccessful trials (combining the sessions of experiments 2 and 3) and distinguished the following categories: (1) subordinate pulls rope and dominant is not in the room; (2) subordinate pulls rope and dominant is in the room; (3) dominant pulls rope and subordinate is not in the room; (4) dominant pulls rope and subordinate is within reach of the rope but does not manipulate it; (5) dominant pulls rope after being aggressive towards the subordinate; (6) others. The following three types of aggressive behaviour were observed: display, displacing partner from her side of the rope and vocally threatening the partner. We randomly selected 20% of all trials and a second coder who was blind to the conditions and hypotheses being tested coded them for reliability. There was 100% agreement between the two coders (Cohen's Kappa = 1.00). To test the level of success with the tolerant partner versus the intolerant partner we calculated mean scores per dyad ($N = 6$). We used this more conservative criterion because the 12 subjects were tested in dyads, so that subjects were at the same time partners for other subjects. We calculated the level of success with the original partner from the mean number of successful cooperation trials of the two sessions (from experiments 2 and 3, respectively). We calculated the level of success with the new partner from the mean number of successful cooperation trials that each subject of a dyad had with her new partner.

Results

The number of successful cooperation trials for all 12 subjects depended on the subjects' relationship with the partner (Table 2). Seven of the eight subjects that had been unable to solve the pulling task in experiment 2 succeeded immediately with the more tolerant partner. The same subjects stopped cooperating 1 or 2 days later when paired with the original partner with whom they had a less tolerant relationship. The four previously successful subjects stopped cooperating when paired with the new intolerant partner but they cooperated in all six trials when paired with their tolerant partner from experiment 2. As a group, dyads cooperated significantly more when paired with a tolerant than with an intolerant partner (Wilcoxon signed-ranks test: $T = 21$, $N = 6$, $P = 0.03$).

During the unsuccessful trials with the intolerant partners ($N = 69$ trials) subordinate subjects pulled the rope in only 23% ($N = 16$) of the trials and in 14 of the 16 trials the dominant partner was not in the room. In the 71% ($N = 49$) of the unsuccessful trials in which the dominant individual pulled the rope, however, the situation differed. In 43% ($N = 21$) of these trials the

Table 2. Absolute number of successful cooperation trials in relation to the tolerance level with the partners

Dyad	Subject	Partner in experiment 2	Experiment 3		
			New partner	Old partner from experiment 2	New partner (sharing score)*
1	Cindy	0	5	0	Asega (4)
	Kidogo		3		Megan (4)
	Tolerance level	Intolerant	Tolerant	Intolerant	
2	Nagoti	0	5	0	Bahati (4)
	Megan		3		Kidogo (4)
	Tolerance level	Intolerant	Tolerant	Intolerant	
3	Mawa	1	5	0	Bwambale (3)
	Nkumwa		6		Umugenzi (4)
	Tolerance level	Intolerant	Tolerant	Intolerant	
4	Katie	0	0	0	Tumbo (4)
	Sophie		6		Baluku (3)
	Tolerance level	Intolerant	Tolerant	Intolerant	
5	Sally	3	1	6	Kidogo (1)
	Becky		0		Kidogo (0)
	Tolerance level	Tolerant	Intolerant	Tolerant	
6	Bili	6	0	6	Mawa (1)
	Namukisa		1		Mawa (1)
	Tolerance level	Tolerant	Intolerant	Tolerant	

The number of successful trials is shown for subjects with their partners in experiment 2 and for subjects with new partners and with their previous partners in experiment 3. The maximum number of successful trials was six.

*The food-sharing score of each subject with the new partner is given in parentheses.

subordinate was in the room, within reach of her 'end' of the rope, but did not pull and in 47% ($N = 23$) of these trials, the subordinate did not enter the room. In the remaining 10% ($N = 5$) of these trials, the dominant individual directed some kind of aggressive behaviour towards the partner before pulling the rope.

Discussion

The results of experiment 3 support the hypothesis that tolerance is the main factor constraining cooperation. Previously unsuccessful subjects were immediately successful when paired with a partner with whom they had a more tolerant relationship, but even when subjects knew how to solve the pulling task they stopped working when paired with a less tolerant individual. It was often the subordinate individual in the dyad who did not approach the apparatus or did not pull the rope. Subordinates were observed to pull the rope almost exclusively when they were alone in the room; similarly, when the dominant individual was pulling the rope, subordinates either did not pull the rope or did not approach the apparatus. These results are even more striking since the platform was baited with two dishes of sliced fruit placed almost 3 m apart, a set-up originally designed to reduce competition between partners and facilitate cooperation. Nevertheless, subjects chose not to manipulate the apparatus in the presence of certain partners. With the exception of Katie, all individuals succeeded in the cooperation tests with at least one subject. This result indicates that it was the relationship between the subjects, and not specific individuals, that hindered cooperation.

GENERAL DISCUSSION

Taken together, the results of these experiments support the hypothesis that tolerance constrains the ability of chimpanzees to solve cooperative tasks. The level of tolerance (i.e. the tendency to share food) between the dyads predicted spontaneous success or failure in the cooperation task. In fact, in experiment 2, social tolerance was a better predictor of success than was subjects' understanding of the physical properties of the task. In addition, in experiment 3, subjects who had previously succeeded in cooperating (and probably had some understanding of the physical properties of the task) did not cooperate when paired with a less tolerant partner. Therefore, the lack of tolerance (which is probably related to dominance asymmetries) impeded cooperation. This was the case even when the food platform had been baited with dispersed and shareable food, and the working space between the partners had been maximized, with the two ropes (or the ends of the ropes) far apart.

Primates have repeatedly been found to have strong inhibitions towards approaching or holding objects or food items that are in the possession of another individual, especially when this individual is dominant to them (Sigg & Falett 1985; Kummer 1995; Tomasello & Call 1997). In the current study, unsuccessful dyads in the cooperation test seemed to be inhibited towards the baited apparatus in the presence of certain partners. Subjects often approached and looked at their end of the rope, but seemed to avoid touching it if the partner was already manipulating it. On two occasions we observed two dominant females (one in Leipzig's group and one in Ngamba's group) vocally and gesturally threaten their lower-ranking female partner, when she was attempting

to pull the rope, preventing the partner from continuing. Aggressive interactions were rare, though, which suggests that, in general, subjects were sensitive to their social milieu and probably refrained from manipulating the apparatus in the presence of certain partners to avoid serious conflicts with them. Therefore, in this study the term 'nontolerant' does not necessarily imply overt aggression (as in typical dominance struggles). Instead, nontolerant refers to a difference in status, which translates into low potential for mutual benefit between the cooperative partners and a high level of inhibition towards the baited apparatus on the part of the subordinates. Overall, these results help to interpret the failure of chimpanzees spontaneously to solve cooperative problems in experimental studies in which there was no assessment of social tolerance between dyads and in which dyads were together in a small working space (i.e. the two ropes were positioned close to each other) with an easily monopolizable food reward (Crawford 1937; Povinelli & O'Neill 2000).

Food distribution in our first experiment was related to the chimpanzees' tendency to cooperate. This was shown by the fact that the related pairs from experiment 1 succeeded less often and lost synchronization when confronted with clumped food rewards (two large fruit pieces), which the dominant partner would not share. The dominant parents also did not encourage their offspring to continue cooperating in future trials by sharing some of the reward, regardless of whether it was monopolizable (see Ueno & Matsuzawa 2004 for similar findings). This result is consistent with the idea that most, if not all, forms of cooperation in chimpanzees are explained by mutualism (Mitani et al. 2000; Stevens 2004; Stevens & Gilby 2004). Our results contrast, however, with those obtained with capuchin monkeys and show a clear difference in levels of tolerance between the two species. de Waal & Davis (2003), who studied capuchins' tendencies to cooperate in a similar pulling task, also found that capuchins' tendencies to cooperate dropped when subjects were confronted with clumped food rewards. However, in their study, there was a greater drop in cooperation among non-kin dyads than kin dyads. Related subordinate capuchin monkeys still obtained nearly 50% of the food pieces in the clumped tests (de Waal & Davis 2003), whereas in our study related subordinates almost never obtained any of the reward (only in 4% of the clumped tests). Furthermore, de Waal & Berger (2000) showed that capuchins spontaneously shared rewards with a partner who helped to obtain them, even when they could have avoided sharing because a mesh wall separated the two subjects.

Although our results support the tolerance hypothesis, a remaining question is why subjects in experiment 1 did not cooperate more in the presence of a competitor. One hypothesis is that, in experiment 1, subjects had to continue working to maintain possession of the food platform once they pulled it within reach, because the competitor could pull the food platform away from the subjects at any time. However, some subjects did know how to prevent this (by standing on the rope to keep the platform from moving). Another possible explanation is that subjects were not motivated to compete against a familiar member of their own social group. However,

chimpanzees in other studies have shown skill on tasks when competing for food against familiar groupmates (Hare et al. 2000, 2001; Hare & Tomasello 2004). Therefore, future experiments in which chimpanzees must cooperate to outcompete another individual will be necessary fully to test this 'cooperation for competition' hypothesis. For example, males might be more likely to cooperate to compete against other rival males, perhaps even from another group. The most dynamic coalitionary behaviour seems to occur naturally between male chimpanzees (Wrangham 1999).

Although our study shows that chimpanzees are capable of spontaneous cooperation, further research will be necessary to assess what chimpanzees understand when they are working together. Any experimental study designed to probe the understanding of chimpanzees in cooperative tasks will need to assess and control social constraints on chimpanzee cooperation. Once levels of tolerance are controlled, it will be clearer whether failure or success in tasks requiring more sophisticated forms of cooperation or communication is due to cognitive abilities and not other noncognitive variables. For example, once level of tolerance is taken into account, it should be possible to make powerful comparisons between the social cognitive abilities of humans and chimpanzees while cooperating. Of special interest is whether chimpanzees show some form of human-like shared intentionality, meaning that both partners understand that they share a common goal and have joint intentions (i.e. plans, coordinated roles) to reach that goal (Tomasello et al. 2005). One measure of such an understanding of the joint goal (i.e. joint commitment) might be instances of partner recruitment or communicative attempts to 'reactivate' the partner. Although begging for support in agonistic contexts has frequently been observed among chimpanzees (de Waal & van Hooff 1981), it remains an open question whether chimpanzees are able to make similar communicative attempts spontaneously in novel cooperative situations (e.g. Crawford 1937).

The apparent fragility of chimpanzee cooperation as a result of tolerance constraints does provide direct support for the hypothesis that human-like cooperation and morality evolved following a transition from despotic to egalitarian social systems. Unlike chimpanzees, human hunter-gatherers maintain a relatively egalitarian social system through subordinate coalitions that act to suppress dominants and their potentially selfish, despotic behaviours (Boehm 1999). The evolution of human temperament (i.e. tolerance) may have occurred as individuals within a social group either killed or ostracized those who were overaggressive or despotic, leading to a form of 'self domestication' during human evolution (Boehm 1999; Wrangham & Pilbeam 2001; Leach 2003). In fact, such evolution of temperament may have preceded the evolution of more complex forms of human social cognition (e.g. a more sophisticated theory of others' behaviour or mental states would be of little use when cooperating if individuals are rarely able to share the rewards of joint effort). Only after the human temperament evolved could variation in more complex forms of communicative and cooperative behaviours be shaped by evolution into the

unique forms of cooperative cognition now present in our species (Hare & Tomasello 2005). Thus, the evolution of more egalitarian relationships within social groups may have opened up a new adaptive space, in which human social cognition and higher forms of cooperation could arise in response to other factors such as social complexity (i.e. fission–fusion; Barrett et al. 2003).

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References

- Barrett, L., Henzi, P. & Dunbar, R. 2003. Primate cognition: from 'what now?' to 'what if?'. *Trends in Cognitive Sciences*, **7**, 494–497.
- Boehm, C. 1999. *Hierarchy in the Forest: the Evolution of Egalitarian Behavior*. Cambridge, Massachusetts: Harvard University Press.
- Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Tai Forest National Park. *American Journal of Physical Anthropology*, **78**, 547–573.
- Boesch, C. & Boesch-Achermann, H. 2000. *The Chimpanzees of the Tai Forest*. Oxford: Oxford University Press.
- Brosnan, S. F., Schiff, H. C. & de Waal, F. B. M. 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society of London, Series B*, **272**, 253–258.
- Chalmeau, R. 1994. Do chimpanzees cooperate in a learning task? *Primates*, **35**, 385–392.
- Chalmeau, R. & Gallo, A. 1993. Social constraints determine what is learned in the chimpanzee. *Behavioural Processes*, **28**, 173–180.
- Chalmeau, R. & Gallo, A. 1996. Cooperation in primates: critical analysis of behavioural criteria. *Behavioural Processes*, **35**, 101–111.
- Chalmeau, R., Visalberghi, E. & Gallo, A. 1997. Capuchin monkeys, *Cebus apella*, fail to understand a cooperative task. *Animal Behaviour*, **54**, 1215–1225.
- Crawford, M. P. 1937. The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs*, **14**, 1–88.
- Crawford, M. P. 1941. The cooperative solving by chimpanzees of problems requiring serial responses to color cues. *Journal of Social Psychology*, **13**, 259–280.
- Goodall, J., Bandora, A., Bergman, E., Busse, C., Matama, H., Mpongo, E., Pierce, A. & Riss, D. 1979. Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: *The Great Apes* (Ed. by D. A. Hamburg & E. R. McCown), pp. 13–53. Menlo Park, California: B. Cummings.
- Hare, B. 2001. Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition*, **4**, 269–280.
- Hare, B. & Tomasello, M. 2004. Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, **68**, 571–581.
- Hare, B. & Tomasello, M. 2005. Human-like social skills in dogs? *Trends in Cognitive Sciences*, **9**, 439–444.
- Hare, B., Call, J., Agnetta, B. & Tomasello, M. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, **59**, 771–785.
- Hare, B., Call, J. & Tomasello, M. 2001. Do chimpanzees know what conspecifics know?. *Animal Behaviour*, **61**, 139–151.
- Hare, B., Call, J. & Tomasello, M. In press. Chimpanzees deceive a competitor by hiding. *Cognition*.
- Hauser, M. D., Chen, M. K., Chen, F. & Chuang, E. 2003. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society of London, Series B*, **270**, 2363–2370.
- Hirata, S. 2003. Cooperation in chimpanzees. *Hattatsu*, **95**, 103–111 [In Japanese].
- Humphrey, N. K. 1976. The social function of intellect. In: *Growing Points in Ethology* (Ed. by P. Bateson & R. A. Hinde), pp. 303–321. Cambridge: Cambridge University Press.
- Kummer, H. 1967. Tripartite relations in hamadryas baboons. In: *Social Communication Among Primates* (Ed. by S. A. Altmann), pp. 63–71. Chicago: University of Chicago Press.
- Kummer, H. 1995. *In Quest of the Sacred Baboon: a Scientist's Journey*. Princeton, New Jersey: Princeton University Press.
- Leach, H. 2003. Human domestication reconsidered. *Current Anthropology*, **44**, 349–368.
- Melis, A. P., Hare, B. & Tomasello, M. 2006. Chimpanzees recruit the best collaborators. *Science*, **311**, 1297–1300.
- Mendres, K. A. & de Waal, F. B. M. 2000. Capuchins do cooperate: the advantage of an intuitive task. *Animal Behaviour*, **60**, 523–529.
- Menzel, E. W. J. 1972. Spontaneous invention of ladders in a group of young chimpanzees. *Folia Primatologica*, **17**, 87–106.
- Mitani, J. C., Merriwether, D. A. & Zhang, C. 2000. Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, **59**, 885–893.
- Petit, O., Desportes, C. & Thierry, B. 1992. Differential probability of coproduction in two species of macaque (*Macaca tonkeana*, *M. mulatta*). *Ethology*, **90**, 107–120.
- Povinelli, D. J. & O'Neill, D. K. 2000. Do chimpanzees use their gestures to instruct each other? In: *Understanding Other Minds. Perspectives from Developmental Cognitive Neuroscience* (Ed. by S. Baron-Cohen, H. Tager-Flusberg & D. J. Cohen), pp. 459–487. Oxford: Oxford University Press.
- Rosenthal, R. 1991. *Meta-analytic Procedures for Social Research*. London: Sage.
- Sigg, H. & Falett, J. 1985. Experiments on respect of possession and property in hamadryas baboons, *Papio hamadryas*. *Animal Behaviour*, **33**, 978–984.
- Stevens, J. R. 2004. The selfish nature of generosity: harassment and food sharing in primates. *Proceedings of the Royal Society of London, Series B*, **21**, 451–456.
- Stevens, J. R. & Gilby, I. C. 2004. A conceptual framework for non-kin food sharing: timing and currency of benefits. *Animal Behaviour*, **67**, 603–614.
- Tomasello, M. & Call, J. 1997. *Primate Cognition*. New York: Oxford University Press.

- Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H.** 2005. Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences*, **28**, 675–735.
- Ueno, A. & Matsuzawa, T.** 2004. Food transfer between chimpanzee mothers and their infants. *Primates*, **45**, 231–239.
- Visalberghi, E., Quarantotti, B. P. & Tranchida, F.** 2000. Solving a cooperation task without taking into account the partner's behavior: the case of capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, **114**, 297–301.
- de Waal, F. B. M.** 1982. *Chimpanzee Politics*. London: Jonathan Cape.
- de Waal, F. B. M.** 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, **18**, 375–386.
- de Waal, F. B. M. & Berger, M. L.** 2000. Payment for labour in monkeys. *Nature*, **404**, 563.
- de Waal, F. B. M. & Davis, J. M.** 2003. Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychologia*, **41**, 221–228.
- de Waal, F. B. M. & van Hooff, J. A. R. A. M.** 1981. Side-directed communication and agonistic interactions in chimpanzees. *Behaviour*, **77**, 164–198.
- Watts, D.** 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, **139**, 343–370.
- Watts, D. & Mitani, J. C.** 2001. Boundary patrols and intergroup encounters among wild chimpanzees. *Behaviour*, **138**, 299–327.
- Watts, D. & Mitani, J.** 2002. Hunting and meat sharing by chimpanzees at Ngogo, Kibale National Park, Uganda. In: *Behavioural Diversity of Chimpanzees and Bonobos* (Ed. by C. Boesch, G. Hohmann & L. Marchant), pp. 244–255. Cambridge: Cambridge University Press.
- Werdenich, D. & Huber, L.** 2002. Social factors determine cooperation in marmosets. *Animal Behaviour*, **64**, 771–781.
- Wilson, M. L., Hauser, M. D. & Wrangham, R. W.** 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour*, **61**, 1203–1216.
- Wrangham, R. W.** 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75**, 262–300.
- Wrangham, R. W.** 1999. The evolution of coalitionary killing. *Yearbook of Physical Anthropology*, **42**, 1–30.
- Wrangham, R. & Pilbeam, D.** 2001. African apes as time machines. In: *All Apes Great and Small* (Ed. by B. F. F. Galdikas, N. Erickson Briggs, L. K. Sheeran, G. L. Shapiro & J. Goodall), pp. 5–17. New York: Kluwer Academic/Plenum.