



Do chimpanzees reciprocate received favours?

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(Received 15 August 2007; initial acceptance 27 October 2007;
final acceptance 9 May 2008; published online 24 June 2008; MS. number: 9489R)

Reciprocal interactions observed in animals may persist because individuals keep careful account of services exchanged with each group member. To test whether chimpanzees, *Pan troglodytes*, possess the cognitive skills required for this type of contingency-based reciprocity, we gave chimpanzees the choice of cooperating with a conspecific who had helped them previously or one who had not helped them in two different experimental tasks. In the first experiment, one of the partners preferentially recruited the subjects to cooperate in a mutualistic task, while the other potential partner never chose to cooperate with the subject, but rather chose a different partner. In the second experiment, one of the partners altruistically helped the subjects to reach food, while the other partner never helped the subject, but rather took the food himself. In both experiments there was some evidence that the chimpanzees increased the amount they cooperated with or helped the partner who had been more helpful towards them compared to their baseline behaviour towards the same individual (or in a control condition). However, in both experiments this effect was relatively weak and subjects did not preferentially favour the individual who had favoured them over the one who had not in either experiment. Although taken together, these experiments provide some support for the hypothesis that chimpanzees are capable of contingent reciprocity, they also suggest that models of immediate reciprocation and detailed accounts of recent exchanges (e.g. Tit for Tat) may not play a large role in guiding the social decisions of chimpanzees.

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Keywords: chimpanzee; cognitive constraint; *Pan troglodytes*; reciprocal altruism; reciprocity; recruitment

Although compelling theoretically, there is scarce experimental evidence for reciprocal altruism in nonhuman species (Hammerstein 2003; Stevens & Hauser 2004). Reciprocal altruism occurs when individuals alternate their roles as donor and recipient of altruistic acts, such that any costs incurred in a single interaction are recouped after repeated interactions. Therefore, reciprocal altruism assumes a contingent relationship between altruistic acts given and received: if an individual stops receiving from a cooperative partner, it should in turn stop giving to that partner (Trivers 1971; Axelrod & Hamilton 1981).

Noting the lack of solid experimental demonstrations of reciprocal altruism, Stevens & Hauser (2004) and Stevens

et al. (2005) suggested that initial papers on the subject may have underestimated the basic cognitive abilities that are necessary for reciprocal altruism: mechanisms that may be lacking in most nonhumans. They proposed that numerical discrimination, memory, inhibitory control, low temporal discounting rates, and detection and punishment of cheaters are essential for contingency-based reciprocity. This set of cognitive skills may collectively constrain the ability of many species to establish and maintain reciprocity, which could explain why finding evidence for contingent reciprocity in nonhuman animals has been difficult (Hammerstein 2003; Stevens & Hauser 2004; Silk 2007).

Initial reported cases of reciprocal altruism among baboons, *Papio anubis*, vampire bats, *Desmodus rotundus*, and sticklebacks, *Gasterosteus aculeatus* (Packer 1977; Wilkinson 1984; Milinski 1987) have been repeatedly questioned, since these studies have not been replicated, and alternative explanations such as kin selection and mutualism probably cannot be ruled out (Berkovitch 1988; Noë

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1990; Hammerstein 2003; Stevens & Hauser 2004). Furthermore, many of the studies that suggest reciprocal exchanges are based on correlations between services given and received that cannot completely rule out an intervening variable (such as association levels) mediating between the two exchanged services (e.g. Hunte & Horrocks 1986; Silk 1992; Watts 1997). Therefore, studies that look at the temporal sequence of behavioural exchanges and experimental studies that can rule out intervening variables are necessary to test the contingency of behavioural exchanges (i.e. Seyfarth & Cheney 1984; Hemelrijk 1994; de Waal 1997).

Chimpanzees, *Pan troglodytes*, are arguably one of the best candidate species to look for evidence of reciprocal altruism. First, chimpanzees cooperate in many different contexts in which they potentially exchange goods and services. Male chimpanzees cooperate during hunting episodes, sharing meat, defending territories against other communities and during intragroup coalitionary aggression (Muller & Mitani 2005). Furthermore, Langergraber et al. (2007) showed that kinship probably plays a minor role in explaining cooperative interactions between male chimpanzees, with the majority of affiliative and cooperative interactions taking place between distant relatives. These results suggest that the cooperative behaviours observed in chimpanzees are maintained through mutualism, reciprocal altruism or some combination of both. Moreover, a number of studies provide strong evidence that reciprocity may be important in chimpanzees' cooperative interactions. For example, de Waal (1997) found that captive chimpanzees were more likely to share food with a partner who had previously groomed them than with one who had not. Koyama et al. (2006) investigated the temporal relationship between grooming and agonistic support in chimpanzees, and observed interactions that were consistent with calculated interchange. Finally, observational studies of wild chimpanzees have reported that males reciprocally exchange grooming, coalitionary support and meat sharing even after association frequencies were controlled for (Mitani 2006). Furthermore, these males also trade different services; they interchange grooming for coalitionary support, grooming for meat and meat for support, with these correlations persisting even after for variables such as kinship, age, dominance rank and association frequency have been controlled for (Watts 2000, 2002; Mitani 2006; although see Gilby 2006).

In addition to these observational studies that show that reciprocal exchanges probably occur within the natural interactions of chimpanzees, there is experimental evidence that suggests that chimpanzees probably possess many of the sociocognitive skills necessary to keep track of interactions with others, and to detect and punish cheaters. First, chimpanzees are sensitive to the intentions of others in that they can discriminate between intentional and accidental actions (Call et al. 2004). Second, when a chimpanzee has food stolen by another chimpanzee it is likely to punish that individual actively by preventing it having access to the food (Jensen et al. 2007). Finally, chimpanzees readily discriminate between a skilled and unskilled collaborator after only a few trials and remember their identity for several days, punishing those

who were unskilled by shunning them as cooperative partners, and choosing instead skilled individuals (Melis et al. 2006a). Therefore, previous experimental work suggests that chimpanzees should be able to account for favours they have previously received and then potentially return favours to those who previously helped them. However, chimpanzees have never been experimentally tested for the ability or tendency to reciprocate towards individuals who have previously shown a preference for them or have helped them in a novel cooperative interaction (see de Waal 2000; Hauser et al. 2003; Hattori et al. 2005 for relevant experiments with monkeys). If in addition to having a preference for reciprocity in social interactions, they can wait for payoffs that are delayed in time (i.e. low temporal discounting rates as demonstrated by Rosati et al. 2007), and they have numerical abilities (e.g. Beran & Beran 2004; Hanus & Call 2007) and altruistic tendencies (Warneken & Tomasello 2006; Warneken et al. 2007; but see also Silk et al. 2005; Jensen et al. 2006), then the main psychological requirements for reciprocal altruism might be met. The present study was designed to test whether chimpanzees track, remember, discriminate and reciprocate towards individuals who previously showed a preference for cooperating with them, or who provided them with some kind of service.

EXPERIMENT 1

In this experiment we used a paradigm based on partner choice (Melis et al. 2006a), which allows chimpanzees to choose with whom they want to collaborate, based on how the potential collaborators behaved towards them in the recent past. In contrast to other experiments on reciprocity, our dependent measure was not the differential propensity of the subjects to cooperate or reciprocate across conditions, but instead, which partner subjects choose to cooperate with, which more closely resembles the type of decisions individuals must make in their daily interactions with others (Noë 2001, 2006). Therefore, subjects in the current experiment were required to recruit a partner to cooperate in pulling a food tray within reach so that both individuals could obtain food. The dependent measure was the subjects' tendency to recruit one of two potential partners before and after an exposure phase in which we manipulated their two potential partners' behaviour. One of the partners was a 'nice' stooge, who always chose the subjects (and never chose a second individual), whereas the second partner was a 'mean' stooge who never chose the subjects (and instead always chose a second individual). Our task did not directly involve an altruistic action since recruiting a partner was a prerequisite for self-benefit (otherwise subjects could not pull the tray within reach). However, by choosing or not choosing a partner with which to collaborate individuals allowed or prevented that partner having access to food, and therefore affected his payoffs. We predicted that if chimpanzees are able to keep track of received 'favours' they should preferentially choose to recruit the individual that chose them in the past or show a positive shift in their tendency to recruit him.

Methods

Subjects

Ten chimpanzees, seven males and three females, ranging between 4 and 9 years of age participated in this study (Table 1). They lived in a social group of 39 individuals in Ngamba Island Chimpanzee Sanctuary in Lake Victoria, Uganda. The sanctuary was established in 1998 to care for confiscated orphan chimpanzees in Uganda. All subjects were unrelated. At the time of the present study they had all been in the sanctuary for at least 4 years.

All subjects had participated in several studies investigating their cooperative problem-solving abilities (Melis et al. 2006a, b, unpublished data; Hare et al. 2007; Warneken et al. 2007). They had all shown that they understood the necessity to synchronize and coordinate their behaviour with that of their partner, to succeed in the cooperation task used in the present study. They had also shown that they could successfully recruit a collaborator (by allowing him/her to enter the test room) when collaboration was necessary to solve the cooperative problem, and were familiar with the choice paradigm, in which they could choose between two potential partners (Melis et al. 2006a).

Apparatus

The cooperation apparatus consisted of a flat platform (17 cm × 3.4 m) with a food dish (17 × 27 cm) attached to each end of the platform (Melis et al. 2006a, b; Hirata & Fuwa 2007). The apparatus was placed 1 m away from the metal bars of the test room (15 m²), out of reach of the subjects. A rope (6 m) was threaded through loops on top of 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. Since the distance between the two ends of the rope was too wide (3 m) for a single individual to reach them simultaneously, subjects could pull the platform within their reach only if two individuals each simultaneously pulled one end of the rope towards the room. Once the platform was pulled closer to the test room, subjects could reach through the metal bars and obtain the reward placed in its dishes (i.e. a tool that allowed them to obtain food).

Experimental procedure

The general procedure was to allow subjects to enter the test room and let them choose between recruiting one of the two potential stooges locked in the two adjacent rooms (rooms 1 and 2, Fig. 1), to pull the cooperation platform within reach. We measured the subjects' tendency to recruit the stooges before and after an exposure phase, in which one of the stooges behaved as a 'nice' partner, who always chose the subjects, and the other behaved as a 'mean' partner, who always refrained from choosing the subjects. To avoid tolerance constraints between the subjects and the two potential stooges (as in Melis et al. 2006b), instead of food rewards, we placed on the platform two empty bowls (one for each subject) that subjects needed to obtain the food. Before starting the test phase, subjects and stooges participated in an introductory phase designed to make sure that: (1) individuals would cooperate and recruit a partner when the platform contained empty bowls instead of food rewards; (2) subjects were equally successful at obtaining the bowls (and consequently the food rewards) with both stooges; (3) stooges would behave in the exposure phase in a programmed and predictable way.

Individual introduction to the tool to obtain food. All subjects were individually introduced to the pulling tray which now contained an empty drinking bowl. The rope in the tray was positioned with its two ends close enough

Table 1. Sex and estimated age of the subjects that participated in experiments 1 and 2

	Sex	Estimated age	Experiment		Previous experience
			1	2	
Subjects					
Kalema	Male	9	✓	✓	1, 2, 3, 4
Umugenzi	Male	8	✓	✓	1, 2, 3, 4, 5
Bili	Female	7	✓	✓	1, 2, 3, 4, 5
Yoyo	Female	6	✓	✓	1, 2, 3, 4, 5
Namukisa	Female	6	✓	✓	1, 2, 3, 4, 5
Okech	Male	6	✓		1, 2, 3, 4, 5
Indi	Male	6	✓		1, 2, 3, 4, 5
Bwambale	Male	4	✓		1, 2, 3, 4
Umutama	Male	10		✓	1
Nkumwa	Female	10		✓	1, 5
Asega	Male	7		✓	1, 2, 3
Stooges					
Asega	Male	7	✓		1, 2, 3
Baluku	Male	7	✓		1, 2, 3, 4, 5
Indi	Male	6		✓	1, 2, 3, 4, 5

Estimated age is age in experiment 1 (experiment 2 was conducted 1 year later). Previous studies on cooperation in which subjects had participated were: (1) Melis et al. 2006a; (2) Melis et al. 2006b; (3) A.P. Melis, B. Hare & M. Tomasello, unpublished data; (4) Hare et al. 2007; (5) Warneken et al. 2007.

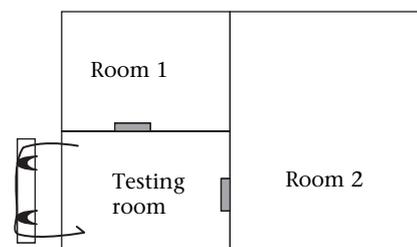


Figure 1. Room set-up in experiment 1. Subject in the test room had the option to open the door leading to room 1 or the door leading to room 2 to recruit a partner. After recruiting a partner, subjects could cooperate and pull the tray within reach. The tray contained two empty food bowls that the experimenter would then fill with food. In the exposure phase a 'mean' or a 'nice' stooge was in the test room and subjects were locked in rooms 1 and 2. The 'mean' stooge never recruited the subject, whereas the 'nice' stooge always recruited the subject. We measured the subjects' tendency to recruit these two stooges before and after the exposure phase.

for a single individual to pull them simultaneously. Individuals were required to pull the tray within reach to obtain the bowl, and then bring the bowl to the experimenter (E), who then filled it with the food reward. All subjects participated in two sessions of six trials each.

Cooperation to obtain the tool. In this cooperation phase the tray contained one empty bowl per food dish (i.e. one bowl on each end of the platform). The distance between the two ends of the rope was wide enough (3 m) that a single individual could not reach both ends simultaneously so that subjects were required to cooperate to obtain their bowls. The two subjects were allowed to enter the test room simultaneously from one of the two adjacent rooms. Once subjects successfully pulled the tray and were able to obtain the bowls, they could approach E who would fill their bowls with the food reward. The two stooges were first tested as a pair together (six trials), and then each subject was tested with each of the stooges for a total of 12 trials per subject (six trials per stooge). Subjects participated in two sessions of six trials each, in which the stooges alternated in consecutive trials. Which of the two rooms subjects and stooges entered from was counterbalanced across trials.

Recruitment test. The subject was allowed to enter the test room whereas the partner was locked in an adjacent room. To pull the tray within reach, the subject had to open the door for the partner by removing a wooden key that blocked the door (Melis et al. 2006a). Once the two subjects were together in the test room they could pull the tray and each obtain a bowl. The eight subjects were tested in four pairs, and the two stooges formed an additional pair as well. In this phase, we did not test any of the subjects with any of the stooges. Each subject was given the opportunity to recruit a partner for six trials, and was then the potential partner for another subject for six consecutive trials.

Stooge training. During the exposure phase, stooges would be given the opportunity to recruit one of two potential subjects as a partner in the cooperative task. It was necessary that stooges should open only one of the doors (i.e. the subject's door to which they should be 'nice'). To ensure that subjects perceived the events in the exposure phase as resulting from the stooges' choice to open or not to open doors for certain individuals, we used a removable metal screw that could be used to lock the doors, but could not be removed by the stooges. Consequently, we could remove the padlocks that were typically used to lock both doors so that it appeared that the stooges could open either door during the exposure phase. However, by using the removable wooden key to block one door and the irremovable metal screw to block the other, we could manipulate the stooges' choice of partner without the subjects being aware. The stooges completed a training phase, in which they learned that the door with the wooden key could be opened, whereas the second door with the second screw could not be opened. Although the metal screw blocking one of the doors was potentially visible, it was small and its colour matched the

material of the door. Therefore, stooges could more easily use the presence of the wooden key as a visual cue that indicated which door they were able to open. During the individual familiarization, the stooges first saw the experimenter throw one piece of banana into each of the adjacent rooms. Then they saw the experimenters remove the padlocks that locked the doors between the test room and the two adjacent rooms. Finally, they were allowed to enter the test room, where only the door with the wooden key could be opened, whereas the second door with the metal screw could not be opened. Subjects had to show that they understood they could only open the door with the key by selectively attempting to open this door first on seven out of eight trials for two consecutive days before they were considered ready to perform their role as stooge. The stooges (Asega and Baluku) reached criterion after four and five familiarization sessions of 7–10 trials each. In the last two sessions both individuals met the criterion of first trying to open the door with the wooden key in at least seven out of eight trials. Although subjects still occasionally tried to open the second blocked door, they usually gave up very quickly. This suggests that they had learned that the door without the key could not be opened.

After finishing the introductory phase, we started the test phase. This phase consisted of an initial preference test (baseline), exposure phase (in which the stooges chose the subjects) and reciprocity test.

Baseline. In the baseline we assessed the subjects' preferences to collaborate with one or the other stooge. Subjects were given the choice to recruit one of the two stooges to pull the tray and obtain the empty food bowls. Once the subject had made a choice to let one of the stooges into the test room by removing the wooden peg associated with his door (or tried to open one door for at least 10 s), an animal caretaker locked the second door with a padlock. The position of the stooges (in rooms 1 or 2) was counterbalanced within and across subjects. All eight subjects participated in one session of six trials.

Exposure phase round 1. In the exposure phase we reversed the positions of subjects and stooges. Stooges were in the test room and subjects locked in the adjacent rooms 1 and 2 (see Fig. 1). One stooge always opened the door for a given subject and the second stooge never opened the door for that subject. The role ('nice' versus 'mean') of the stooges was assigned based on subjects' previous preferences to recruit one or the other stooge during the baseline phase. The stooge that was chosen less frequently by that subject, that is, the less-preferred stooge, was assigned to play the role of the 'nice' stooge in the exposure phase. Subjects were exposed to the stooges in dyads. The general procedure was as follows: the two subjects each waited in one of the two (locked) rooms adjacent to the test room (rooms 1 and 2, Fig. 1). The stooge was allowed to enter the test room, and the two padlocks locking the doors to the adjacent rooms were concurrently removed. The stooge could open only one of the doors leading to a particular subject (previously assigned) because that door was blocked with the removable wooden

key, whereas the second subject could watch the interaction but could not be released (because her door was blocked by the metal screw). In between trials the locations of the wooden key and metal screw were switched. Then on the next trial the second stooge was allowed to enter the test room; he could open only the door to the second subject (the one previously blocked by the metal screw). In this way, the two subjects experienced alternating trials in which they were released by one of the stooges, and not released by the other stooge. Subjects participated in two sessions of 12 trials each, during which they were recruited six times by one stooge and ignored six times by the other stooge. The two sessions were administered within a time frame of 2–3 days.

Reciprocity test round 1. The test was conducted the morning after the last exposure session. All eight subjects were given the choice to recruit one of the two stooges to cooperate. Each subject completed six trials in one session identical in format to the baseline session.

We conducted a second round of exposure and test trials to test whether subjects would show a stronger tendency to recruit the 'nice' stooge (and avoid the 'mean' one) after additional exposure trials. In this second round the test was conducted a couple of hours after the last exposure trials to avoid possible reciprocation between subjects in currencies other than the one under study. Furthermore, we tried to make the behaviour of the stooges more relevant or salient to the subjects by conducting the exposure trials in a blocked design.

Exposure phase round 2. The second exposure phase was almost identical to the first exposure phase, except that trials were administered in blocks of three; that is, each stooge chose a given subject for three trials in a row, while the second subject remained locked during those three consecutive trials. Subjects participated in two sessions (conducted on two consecutive days) of 12 trials each. They were recruited for six trials per session and were not chosen for the other six trials per session.

Reciprocity test round 2. This test was conducted 1–2 h after the second session of the second exposure phase. During this 1–2 h time frame subjects and stooges were separated in different rooms to avoid any kind of potential reciprocal exchange, which might influence their later choice. This second round was conducted 1 week after round 1.

Coding and analysis

In the baseline and test sessions the subjects' choice of door (and therefore stooge) was coded live. In addition, we coded whether the door that subjects opened was also the one they approached first. We also coded whether or not subjects succeeded in obtaining the bowls. In the exposure phase all trials were coded from the videotapes for whether the door that stooges opened was also the one they approached and touched first, and whether subjects succeeded or not. A second person, blind to the test condition, coded 20% of all trials from the videotapes to

assess interobserver reliability. All analyses were conducted with Wilcoxon exact signed-ranks tests. Based on previous theory and studies of reciprocity (see Introduction) we predicted that subjects would prefer the 'nice' stooge over the 'mean' stooge, and if subjects shifted their preference to collaborate with one or the other stooge, then they would shift towards choosing the 'nice' stooge more frequently. We had no reason to believe that subjects would prefer the individual who had never chosen them before. Therefore, these two analyses were calculated using one-tailed tests. We used Cohen's Kappa to test for the degree of agreement between coders. Reliability between both coders was excellent (choice made: $\kappa = 1$, $N = 30$; success: $\kappa = 1$, $N = 69$; first door approached: $\kappa = 1$, $N = 69$).

Results

Introductory phase

In the pretest in which subjects and stooges were allowed to enter the room simultaneously to cooperate in obtaining the bowls, subjects were equally successful with both stooges. There was no significant difference between stooges in the mean number of trials \pm SD in which subjects were successful (Baluku: 5.63 ± 0.52 ; Asega: 5.25 ± 0.71 ; Wilcoxon exact signed-ranks test: $T = 8$, $N = 8$, ties = 4, $P = 0.5$).

Test phase

Baseline. Four subjects chose Baluku in every trial and never opened the door for Asega, whereas the other four subjects showed no preference and opened the door for Asega and Baluku equally often (Table 2). All subjects were highly successful whenever they chose Baluku (mean = 96%, range 83–100% successful trials) whereas there was more variation among the four subjects that chose Asega. Two subjects (Yoyo and Kalema) succeeded on every trial with him, whereas Okech succeeded on

Table 2. Subjects' recruitment of the 'nice' stooge in experiment 1

Subject	Baseline	Test: first round	Test: second round	Identity of 'nice' stooge
Bwambale	3	6 (+50)	6 (+50)	Baluku
Bili	0	2 (+33)	3 (+50)	Asega
Namukisa	0	0 (0)	2 (+33)	Asega
Okech	3	3 (0)	4 (+16.6)	Baluku
Yoyo	3	2 (-16.6)	4 (+16.6)	Baluku
Kalema	3	3 (0)	3 (0)	Baluku
Umugenzi	0	0 (0)	0 (0)	Asega
Indi	0	0 (0)	0 (0)	Asega
Mean	1.5	2 (+8.3)	2.75 (+20.8)	

The numbers indicate absolute number of trials (maximum was 6) in which subjects recruited the 'nice' stooge in the baseline, the first round of the test (+ or - change in % of total number of trials) and the second round of the test (+ or - change in % of total number of trials) of experiment 1. Since subjects always recruited a partner, the difference from 6 corresponds to the trials in which they chose the 'mean' stooge.

only one trial and Bwambale in none of the three trials (mean = 58%, range 0–100% successful trials).

Exposure phase. Asega was chosen as the ‘nice’ stooge for those subjects who had never recruited him, and Baluku was chosen as the ‘nice’ stooge for those who had shown no preference (Table 2). Both stooges opened the door and recruited their assigned partners on every trial. All subjects were successful on every trial.

Test. A comparison between the number of times subjects chose the ‘nice’ stooge and the number of times they chose the ‘mean’ stooge did not reveal any significant difference (Wilcoxon exact signed-ranks test: $T = 12$, $N = 8$, ties = 2, $P = 0.45$). However, a shift in their recruitment preferences (in comparison to baseline preferences) also sheds light on the subjects’ perception of their past experiences with the two stooges. There was no significant change in the subjects’ preferences to choose one or the other stooge after the first round of exposure trials ($T = 5$, $N = 8$, ties = 5, $P = 0.25$; Table 2). However, after the second round of exposure trials, subjects showed a 20% increase in preference for the ‘nice’ stooge compared to baseline levels ($T = 15$, $N = 8$, ties = 3, $P = 0.03$; see Table 2 and Fig. 2). Three subjects (Umugenzi, Indi and Kalema) showed no change in preference. Bili changed from avoiding the ‘nice’ stooge to being indifferent and choosing the ‘nice’ stooge in half of the trials. Namukisa, Yoyo and Okech chose the ‘nice’ stooge slightly more than in the baseline, and Bwambale changed from being indifferent to choosing only the ‘nice’ stooge (this preference switch was already apparent in the first round of exposure trials). See the [Supplementary Material](#) for a video example of a subject choosing a stooge as a cooperative partner (Video 1).

Discussion

Subjects did not choose the partner who had chosen them previously as a cooperative partner (the ‘nice’

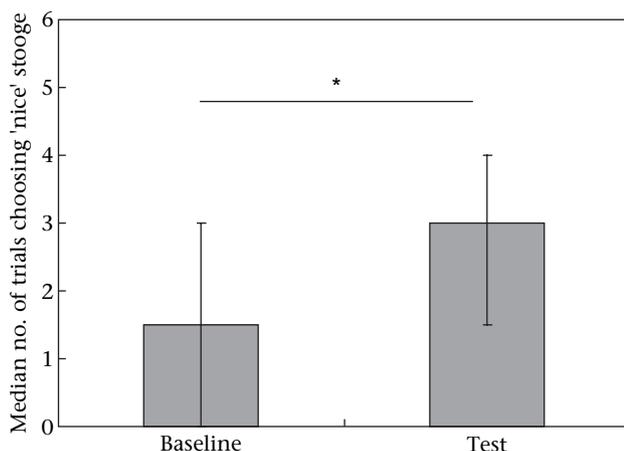


Figure 2. Median \pm quartiles number of trials subjects chose the ‘nice’ stooge before (baseline) and after the two exposure phases (test: second round) to the stooges in experiment 1. Maximum number of trials was 6. * $P < 0.05$.

stooge) significantly more often than the ‘mean’ stooge. However, subjects showed an increase in their tendency to recruit the ‘nice’ stooge. Five of eight subjects chose the stooge who had previously chosen them more often than in the baseline. Among these five subjects there were both subjects with a clear preference in the baseline for only one of the stooges, and subjects without any clear preference (or equal preference) for one or the other stooge. Although the effect was relatively weak, with only one subject showing an individual preference, all subjects’ preferences for one or the other stooge either did not change at all or changed in the direction predicted if chimpanzees engage in reciprocal interactions. No individual’s preference changed in the opposite direction. These significant results appeared after the second round of exposure trials. This could be because in the second round the test was conducted just 1–2 h after the exposure phase. In this short time interval subjects and stooges were separated so that they could not reciprocate with other currencies. Furthermore, the exposure trials were conducted in blocks of three so that both factors might have contributed to make the experimental manipulation more salient and easy to remember for the subjects. Alternatively, just additional exposure trials might account for the significant results of the second round. It is also possible that, at least partly, the increase in preference for the ‘nice’ stooge can be explained through the regression to the mean effect. Since two of the subjects had extreme scores in the baseline preference test. The regression to the mean effect refers to the fact that any measure with extreme scores at one point in time will, for purely statistical reasons, probably have less extreme scores the next time it is measured. Since these subjects never chose the ‘nice’ stooge in the baseline, any change at a later time could be in only one direction, for example, an increase in the number of times the ‘nice’ stooge was chosen. However, in our opinion these extreme scores are not unrepresentative measures in time, but clear measures of stable attitudes towards the stooges, so that we find it unlikely that subjects in such a short period of time just randomly changed their preferences. In fact an equal proportion of subjects, who in the baseline also had extreme scores, never changed their preferences after the exposure.

During the exposure phase, subjects were always successful with both stooges, and after obtaining the bowl they were always able to get the food reward, so that it seems plausible that the changes in their recruitment preferences are best attributed to the fact that subjects remembered who chose them in the recent past. However, one individual did not succeed with one stooge in the baseline trials, so we cannot rule out the possibility that this subject’s preference for the ‘nice’ stooge after the exposure phase was due to his differential success with two stooges (as in Melis et al. 2006a). Since the measure of the present study was which partner subjects chose to cooperate with, and not the differential propensity of the subjects to cooperate, it is unlikely that alternative mechanisms such as instrumental conditioning or social facilitation explain subjects’ preferences (as in Hauser et al. 2003). Critically, subjects did not gain more by choosing the ‘nice’ stooge and similarly they did not incur higher

costs by choosing the 'mean' stooge. This is because stooges and subjects did not alternate their roles as donors of the cooperative act, and choosing the 'mean' stooge did not bear any additional costs. Therefore, the fact that we found a shift in subjects' preferences at all is particularly interesting, since it suggests that this cannot be the result of a learning process during the test phase. Instead, the most plausible explanation for this shift in the subject's choice of partners is an ability to remember the stooges who had chosen them previously during the exposure phase.

Although subjects did shift their preferences, it is equally striking that they did not completely shift them towards the partner who had preferred them. There are a number of potential explanations for this finding. First, subjects may have interacted outside of the experiment, between the exposure and test phase, a time in which they had the opportunity to reciprocate with other currencies. While this could explain the null results of the first round, it cannot explain the subjects' behaviour towards the stooges in the second round, since in the second round of the experiment subjects were prevented from interacting with the stooges between the exposure and test phases. Another possible explanation is that individuals might have interpreted the stooges' behaviour as unintentional. In this case the subjects may have perceived that the stooges were unable, instead of unwilling, to open one of the doors during the exposure phase. This seems unlikely in this context since: (1) subjects had experienced only the situation in which both doors could be opened and their choices of partner were not constrained; (2) subjects often started screaming in frustration, after they were not chosen (by the stooge) and the experimenter locked their door, which suggests that they believed the door was potentially openable until that moment; and (3) stooges behaved as planned and almost always went directly to the correct door. However, given that chimpanzees can discriminate intentions in actions (Call et al. 2004), the attribution problem, that is, establishing whether subjects attribute to others intentional cooperative or uncooperative behaviour, seems an important variable, which deserves further study. Finally, another plausible explanation is that our manipulation during the exposure phase simply was not enough fully to change individuals' established attitudes towards their partners (including attitudes of indifference), especially since the cooperative currency under study (i.e. recruiting a partner) was not altruistically motivated. To explore this last possibility we conducted a second experiment, in which the 'nice' stooge was trained to provide a clearly altruistic service, whereas the 'mean' stooge stole the food from the subject.

EXPERIMENT 2

In this experiment we used a paradigm based on Warneken et al. (2007), in which a recipient tries to open a door to gain access to a room (in which food has been hidden) but the door is locked with a chain that only the actor can remove. Removing the chain allows the recipient, and only the recipient, to enter the room

and get the food. Therefore, the currency here is clearly altruistic, since actors do not obtain any immediate benefits from opening the door for their partner. The dependent measure in this experiment was the subjects' differential tendency to open the door (i.e. release the chain) for two potential partners after an exposure phase in which we manipulated their two partners' behaviour. One of the partners was a 'nice' stooge who always opened the door for the subjects, whereas the second partner was a 'mean' stooge who never opened the door for the subjects and instead always opened a door for himself that allowed him to obtain the food that the subjects could otherwise get.

Methods

Subjects

Ten chimpanzees, six males and four females, ranging between 6 and 10 years of age participated in this experiment (Table 1). Two of them acted as stooges (Baluku and Indi) and eight were subjects. Five of the subjects had also participated in experiment 1, whereas the other three had not. Table 1 indicates which subjects had participated in Warneken et al. (2007) as well as in other cooperation studies.

Experimental procedure

Individual introduction to the releasing chain. To make sure that all subjects understood (or had not forgotten) the releasing mechanism, each subject was confronted with the problem that he/she could not gain access to a room containing food because a chain was blocking the sliding door leading to that room. To enter the room the subject had first to release the chain and then slide the door sideways. The chain was attached to the sliding door between rooms 1 and 2 (room 2 being the subjects' starting position) and was hooked up on the other end with a peg positioned horizontally between the bars of the separating wall between rooms 1 and 3. The peg had to be twisted from its horizontal to a vertical position, so that it would fit through the space between the bars. Subjects were required to go from room 2 to room 3 to reach and then release the blocking peg, then to go back to room 2 to slide the door sideways and enter room 1 (Fig. 3). We used the same criterion as in Warneken et al. (2007): subjects had to release the chain within 60 s and enter through the door within 20 s of its removal, and they had to do so in two consecutive trials.

Stooges training. It was important to make sure that both stooges would reliably behave in the programmed way during the exposure phase. The 'mean' stooge went through a procedure designed to make sure that he would not release the chain to the subject's door and would release only his chain (which allowed only him, and not the subject, to get the food; Fig. 3a). The procedure required the actions of three experimenters (E1, E2 and E3) and was as follows. For the purpose of training the stooges another partner, who was not used in the actual test, was positioned in room 1. Next, while E1 distracted

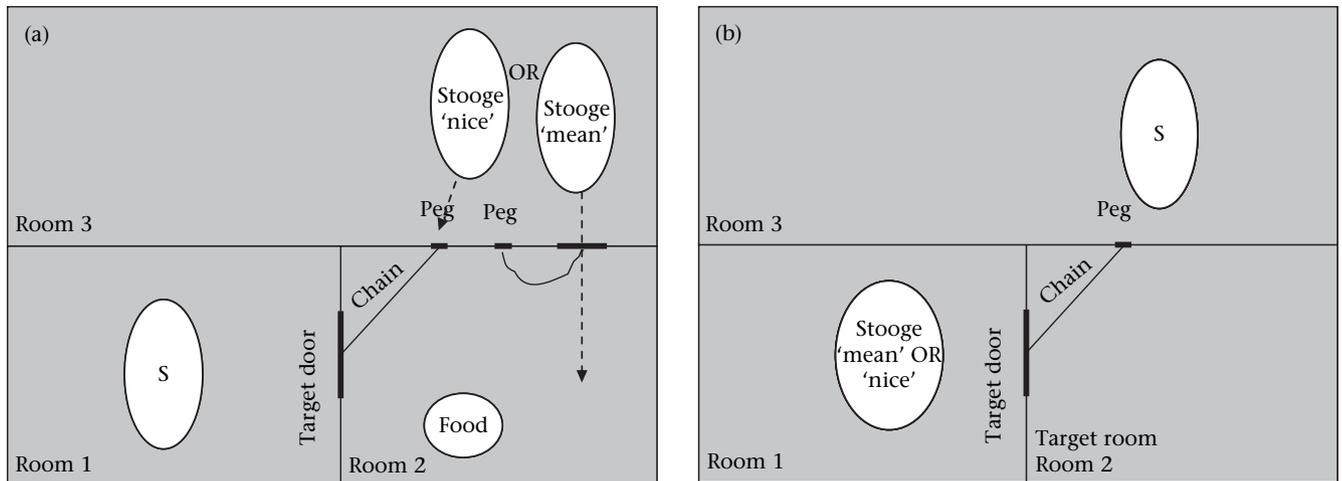


Figure 3. Experimental set-up of experiment 2 (a) Subjects' (S) exposure to the stooges ('nice' or 'mean'). (b) Test, in which the positions of stooges and subjects were reversed and subjects' tendency to open the door for each of the stooges ('nice' and 'mean') was measured.

the stooge in room 3 with food, E2 went into room 2 and positioned the two pegs so that the partner's door and the stooge's door were locked (the pegs were placed between the bars separating rooms 2 and 3). E2 then left room 2 and in full view of both individuals (stooge and partner) threw a banana piece into room 2. Once the banana was in place, E2 and E3 removed the padlocks of the two sliding doors leading to room 2. Once the padlocks were removed, only the pegs and chain systems were holding the doors closed. Therefore, by removing the peg holding either the partner's or stooge's door the stooge could free one of the doors to be opened manually. In the case of the 'mean' stooge he was trained to release only the chain that blocked his door to enter room 2 and obtain the food for himself. If he made the mistake of first releasing the chain that blocked the partner's door, the partner was able to obtain the food that otherwise the stooge could have obtained for himself. The criterion we used to know when the stooge was proficient at opening only his own door to obtain the food for himself was three consecutive trials within 1 min of the padlocks being initially removed. The 'nice' stooge was trained in a similar fashion with the exceptions that (1) he was rewarded for releasing the chain that blocked the door between rooms 1 and 2 (Fig. 3a) and (2) only the peg and chain that potentially opened the partner's door was present. The role that each stooge played was counterbalanced across subjects. Baluku was the 'mean' and Indi the 'nice' stooge for four subjects (Bili, Namukisa, Asega, Kalema), whereas Baluku was the 'nice' and Indi the 'mean' stooge for the other four subjects (Umutama, Yoyo, Nkuumwa, Umugenzi).

Once subjects had shown they understood the releasing mechanism, and the stooges were proficient in their respective roles ('nice' and 'mean') we started the test phase. The test phase consisted of, in the following order (1) an exposure phase in which subjects experienced help or no help from both stooges ('nice' and 'mean'); (2) a baseline phase, designed to measure (and inhibit) the subjects' tendency to release the chain when there was no partner and no reason for them to release the chain; and

(3) the test, in which we measured the subjects' tendency to release the chain for each of the stooges ('mean' and 'nice') on separate trials (note this is different from experiment 1 in which subjects had to choose with whom to work in each trial).

Exposure to 'mean' stooge. The procedure was identical to the training procedure described above. The subject was in room 1 and the stooge in room 3. The stooge released the chain that blocked his door and entered room 2, obtaining the food that the subject could otherwise have obtained (Fig. 3a).

Exposure to 'nice' stooge. The procedure was identical to the training procedure described above. The subject was in room 1 and the stooge in room 3. The stooge released the chain that blocked the door between rooms 1 and 2, allowing the subject to enter room 2 and obtain the piece of food (Fig. 3a).

Subjects participated in four exposure sessions conducted on 4 consecutive days. In each of these exposure sessions each subject received three trials with each of the stooges ('mean' and 'nice'), administered in a blocked design. Therefore, subjects had three consecutive trials with one stooge and then three consecutive trials with the other. Subjects received only one session per day, and the order in which they were presented to the different stooges was counterbalanced across sessions and subjects.

Target behaviour baseline. Before starting the test we ran another pretest to make sure that subjects did not have a strong tendency to release the chain when there was no need to do so. We reasoned that in the absence of an alternative activity, the subjects might release the chain irrespective of any need to do so. Therefore, as in Warneken et al. (2007) we introduced them to an alternative activity by attaching a rope ca. 5.7 m long to the bars of the wall separating rooms 2 and 3. This rope was nonfunctional, but the subjects could pull it inside their room and

play with it. Subjects were in room 3, with no possibility of entering rooms 1 and 2. There was no food accessible and no other individual was present in any of the three rooms. We measured the subjects' tendency to release the chain, and the criterion to start the test phase was that the subjects did not release the chain for 60 s in two consecutive trials. This baseline was conducted the same day, after the last exposure session to the stooges.

Test phase. The subject was now in room 3 and the stooge in room 1. Attached to the bars of the wall separating rooms 2 and 3 was a long distracting rope (as explained above) to give subjects an alternative activity. While E1 distracted the subject in room 3, E2 positioned the chain with its peg between the bars separating rooms 2 and 3. In full view of the stooge, E2 hid a banana piece in a tyre placed in the middle of room 2. Having placed the food, E2 removed the padlock of the sliding door between rooms 1 and 2. When the stooge started manipulating the blocked door, E1 stopped distracting the subject and the trial started (Fig. 3b). A trial ended when the subject released the chain (allowing the stooge to get the food in room 2), or after 1 min. Each subject participated in two sessions of six trials each, in which the identity of the stooges was alternated across trials. In total each subject received six trials per stooge (three trials/stooge/session). Each test session started and ended with a control trial (identical to those of the target behaviour baseline), in which there was no food accessible and no other individual present in any of the three rooms. The first test session was conducted the same day after the last exposure session to the stooges, and after the baseline phase.

Coding and analysis

We coded live whether or not subjects released the chain (i.e. the peg had to drop to the floor) within 1 min of the trial's start in all three conditions: control trials (absence of any partner in the other rooms); presence of 'nice' stooge; and presence of 'mean' stooge. A second person, blind to the test condition, coded 20% of all trials from the videotapes to assess interobserver reliability. We used Cohen's Kappa to test for the degree of agreement between coders. Reliability between both coders was excellent (peg released: $\kappa = 1$, $N = 26$). All analyses were conducted with nonparametric tests. Based on previous studies on reciprocity and our previous experiment we predicted that subjects would help the 'nice' stooge more often than the 'mean' stooge. Based on Warneken et al. (2007) we also predicted that they would perform the target behaviour (releasing the chain) more often in the presence than in the absence of a partner. Therefore, these two analyses were calculated using one-tailed tests. We used Wilcoxon tests as post hoc tests following a significant Friedman test. We used these instead of the standard procedures to keep power at an acceptable level and to prevent type II errors (Cohen & Cohen 1983), which are otherwise likely to occur when dealing with small sample sizes.

Results

Pretests

Individual understanding of the releasing mechanism. All subjects quickly met the criterion of releasing the chain within 60 s in two consecutive trials in to get the food for themselves (mean = 2.7 trials, range 2–5 trials).

Target behaviour baseline. All subjects quickly met the criterion of not releasing the chain for 60 s in two consecutive trials when there was no need to do so, since there was no food accessible and no other partner in any of the rooms (mean = 3.25 trials, range 2–8 trials).

Experimental phase

Overall, as a group, subjects did not open the door for the 'nice' stooge significantly more often than for the 'mean' stooge (Wilcoxon exact signed-ranks test: $T = 6$, $N = 8$, ties = 5, $P = 0.12$). The subjects' target behaviour (i.e. releasing the chain) tended to differ across all three conditions (control trials, 'mean' stooge and 'nice' stooge trials; Friedman exact test: $\chi^2_2 = 5.615$, $P = 0.06$). Closer inspection revealed that, overall, subjects released the chain significantly more often for the 'nice' stooge than in the control (Wilcoxon exact signed-ranks test: $T = 26.5$, $N = 8$, ties = 1, $P = 0.02$), but equally often for the 'mean' stooge and in the control ($T = 26$, $N = 8$, ties = 0, $P = 0.15$; Fig. 4). At an individual level three subjects (Yoyo, Asega and Umugenzi; Table 3) tended to open the door for the 'nice' stooge more often than for the 'mean' stooge, whereas the other five subjects helped both stooges equally often. Since one of the subjects (Yoyo) helped the 'nice' stooge in all six trials, and never the 'mean' stooge (Table 3), we conducted a follow-up in which we reversed the role of the two stooges to test whether this subject would now show a shift in her tendency to help the two individuals. After another exposure phase, in which Baluku (the previously 'nice' stooge) acted as the 'mean' stooge, and Indi (the previously 'mean' stooge) acted as the 'nice' stooge, this subject (Yoyo) continued opening at ceiling levels for Baluku (the 'mean'

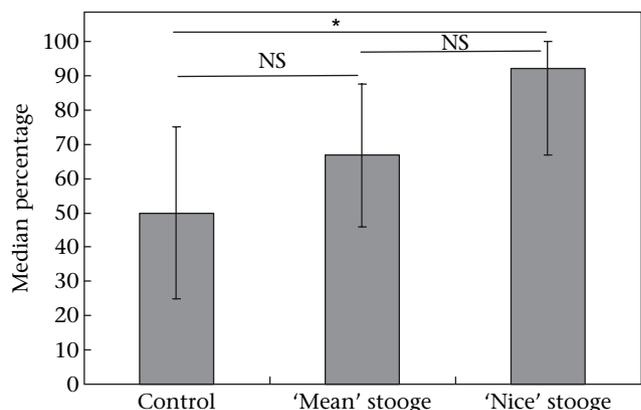


Figure 4. Median percentage \pm quartiles of trials in which subjects performed the target behaviour (releasing the chain) by condition in experiment 2. Each subject participated in all three conditions in a within-subject comparison. * $P < 0.05$.

Table 3. Number (percentage) of trials in which subjects released the chain, in the absence of a partner (control: maximum number of trials was 4) and in the presence of 'mean' and 'nice' stooges (maximum number of trials was 6) in experiment 2

Subject	Control	'Mean' stooge	'Nice' stooge	Identity of 'nice' stooge
Yoyo	4 (100)	0 (0)	6 (100)	Baluku
Umugenzi	1 (25)	3 (50)	5 (83.3)	Baluku
Asega	3 (75)	5 (83.3)	6 (100)	Indi
Umutama	3 (75)	6 (100)	6 (100)	Baluku
Nkumwa	1 (25)	2 (33.3)	2 (33.3)	Baluku
Namukisa	1 (25)	6 (100)	6 (100)	Indi
Bili	1 (25)	4 (66.7)	4 (66.7)	Indi
Kalema	3 (75)	4 (66.7)	4 (66.7)	Indi
Mean	2.13 (53)	3.75 (62.5)	4.9 (81.3)	

stooge), but also opened in four of six trials for Indi (the 'nice' stooge). This represents a 40% increase with regard to the first test (Table 3). See the [Supplementary Material](#) for a video example of a subject helping a stooge (Video 2).

Discussion

In the present experiment subjects as a group did not help the 'nice' stooge significantly more often than the 'mean' stooge. However, we did find that they released the chain significantly more often for the 'nice' stooge (but not for the 'mean' stooge) than in the control condition, in which there was no partner present. At an individual level, two individuals showed a difference in their degree of helpfulness towards the two stooges in the direction predicted by reciprocal altruism, and another individual (Yoyo) exclusively opened the door for the 'nice' stooge. The results from a follow-up test suggest that this female (Yoyo) had a strong preference for one of the stooges (Baluku), and independently of how this individual behaved towards her, she was always willing to open the door for him. However, it is possible that with regard to the second stooge (Indi) our manipulation did have an effect, since after Indi played the 'mean' role, Yoyo never helped him, but after he behaved 'nicely' towards her, she opened for him more often.

In the exposure phase the stooges behaved as planned: the 'nice' stooge always opened the door for the subject, whereas the 'mean' one always opened his own door and obtained the food for himself. The manipulation of this experiment, however, did not have a stronger effect on subjects' later helping (or retaliatory) behaviour than the one from the previous cooperation paradigm. In fact, it seems that the cooperation paradigm of the first experiment was possibly even more relevant for the animals, since more subjects changed their recruitment preferences. It is possible that since subjects and stooges were interacting in the same room, and were performing a cooperative activity, the manipulation was more ecologically valid, and had a higher impact than the helping paradigm. The alternative explanation, mentioned previously, that subjects might have interpreted the stooges'

behaviour as unintentional, does not hold in this experiment, since we did not manipulate any of the doors, and the stooges were really behaving intentionally (the 'nice' one because he had been trained to do so, and the 'mean' one because he wanted the food for himself).

GENERAL DISCUSSION

In the first experiment chimpanzees recruited a cooperative partner more often after this partner had already recruited them. In the second experiment chimpanzees altruistically opened a door to help a partner, who had previously helped them, more often than in a control condition without a partner. However, in neither experiment did chimpanzees recruit or help the partner who had previously helped them more than the partner who had not, as the theory of direct reciprocity would predict. Therefore, two very different experimental paradigms have provided similar results which suggest that, although the experimental manipulation had a certain effect on subjects' later behaviour towards the two partners, it was clearly not enough to entirely determine which partner subjects favoured later on.

With the available data, it is not possible to conclude why some subjects tended to reciprocate and others did not. The two stooges were chosen based on several similarities (e.g. sex, age, playfulness, motivation to participate in problem-solving tasks), and we counter-balanced the role that they played across subjects, so that overall the tendency to reciprocate cannot be attributed to any specific characteristic of the stooges. At an anecdotal level, four of the seven subjects who never tended to reciprocate (in both experiments together) were older, and three of them were higher ranking, than the stooges.

One possible explanation for why we did not find a difference in the subjects' level of helpfulness towards the two different partners is simply that chimpanzees lack the capacity to keep track of precise accounts of previous interactions, or may even fail to recognize and remember their interactions with others. However, this seems unlikely since the same individuals tested in the current study used a win-stay lose-shift strategy and then readily recognized and remembered (at least for 24 h) the skillfulness of two different partners when deciding whom to recruit for cooperation in a previous study (Melis et al. 2006a). Moreover, the effect found in the Melis et al.'s (2006a) study was strong and appeared after very few interactions. The difference between these two studies is that in Melis et al.'s (2006a) study, the subjects' particular choice of an unskilful or skilful partner resulted in differential success, and therefore differential payoffs. In the present study, on the other hand, the subjects' choice of a helpful or unhelpful partner (a partner who did or did not recruit or help the subject previously) did not result in differential payoffs for the subject. Keeping track of how the different behavioural exchanges with different individuals affect one's own long-term payoffs might represent an additional level of difficulty. Rutte & Taborsky (2008) reported experimental evidence for direct reciprocity in rats, *Rattus norvegicus*, using an experimental design

almost identical to the one in our second experiment. Subjects first went through an exposure phase, in which they alternately received help from one partner to obtain food and no help from another partner, and then afterwards they were tested in their differential propensity to help the two partners. Overall, subjects helped more frequently the individuals that had helped them before than those that had not. This suggests that they were able to remember the different interactions with the different individuals, and use this information to reciprocate in future encounters with them.

In our opinion, the most plausible explanation for the lack of clear positive results in the present study is that our manipulations during the exposure phase were simply not enough fully to change individuals' established attitudes towards their partners (including attitudes of indifference). The subjects and the stooges knew each other from their daily interactions in a variety of contexts in which they exchanged many different services or goods. It is possible that in species with complex and long-lasting social relationships, reciprocity takes place at a longer time-scale after information is compiled about the cooperative tendencies of others from several encounters and/or contexts. Especially if the cooperative currency under study is not within their natural behavioural repertoire and is not emotionally very salient (as for example partners' support in coalitionary aggression), established attitudes towards different partners might be difficult to overcome. Silk (2003) also discussed how friendships influence reciprocal interactions in humans and that careful count of exchanged favours as well as immediate reciprocation is typical of strangers and casual acquaintances, but not typical among friends. That is, individuals with close and continuous relationships might reciprocate over a longer timescale without keeping an exact record of all favours given and received. In addition, de Waal (1997) found that among chimpanzees close associates were less inclined to reciprocate than individuals having a more distant relationship. Furthermore, it is possible that our sample size was simply not big enough to detect a phenomenon that if present, has a rather weak effect. The effect reported by de Waal (1997) regarding the interchange of grooming and food sharing was also relatively small. Subjects increased their level of food sharing if preceded by grooming by only 5.6% (see also Koyama et al. 2006).

These results raise the question of what is the relevant time frame for determining contingent behaviour in chimpanzees, and whether models of immediate reciprocation and detailed accounts of recent exchanges (e.g. Tit for Tat) are well suited to investigate reciprocity in species with long-term and complex cooperative interactions (McElreath et al. 2003). Therefore, further studies of this type, and if possible with bigger sample sizes, are needed to elucidate the role that contingent reciprocity plays in chimpanzees' and other species' cooperative interactions, as well as the relevant time frame and type of currencies necessary for determining contingent behaviour. Importantly, future studies should also explore the option of introducing differential payoffs or costs to subjects' investments in uncooperative partners (for example, by

alternating the roles of the donor and recipient of the cooperative act), so that subjects can learn about the long-term benefits of reciprocating with cooperative partners, and punishing or avoiding uncooperative ones.

Acknowledgments

We are very grateful to L. Ajarova, D. Cox, the trustees and all the staff of Ngamba Island Chimpanzee Sanctuary (www.ngambaisland.org) for their continuous help and support. In particular, we appreciate the hard work of the animal caregivers: S. Nyandwi, I. Mujaasi, L. Mugisha, G. Musingo, R. Okello, M. Gum, M. Musumba and A. Okello. We also appreciate permission from the Ugandan National Council for Science and Technology and the Uganda Wildlife Authority for allowing us to conduct our research in Uganda. We thank A. Rosati and Nathan Pyne-Carter for editing the manuscript. The research of B.H. and A.P.M. is supported by a Sofja Kovalevskaja award to B.H. from the Alexander von Humboldt Foundation and the German Federal Ministry for Education and Research.

Supplementary Material

Supplementary Material associated with this article can be found, in the online version, at doi: [doi:10.1016/j.anbehav.2008.05.014](https://doi.org/10.1016/j.anbehav.2008.05.014).

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