



Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members

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We conducted experiments on two populations of chimpanzees, *Pan troglodytes*, to determine whether they would take advantage of opportunities to provide food rewards to familiar group members at little cost to themselves. In both of the experiments described here, chimpanzees were able to deliver identical rewards to themselves and to other members of their social groups. We compared the chimpanzees' behaviour when they were paired with another chimpanzee and when they were alone. If chimpanzees are motivated to provide benefits to others, they are expected to consistently deliver rewards to others and to distinguish between the partner-present and partner-absent conditions. Results from both experiments indicate that our subjects were largely indifferent to the benefits they could provide to others. They were less likely to provide rewards to potential recipients as the experiment progressed, and all but one of the 18 subjects were as likely to deliver rewards to an empty enclosure as to an enclosure housing another chimpanzee. These results, in conjunction with similar results obtained in previous experiments, suggest that chimpanzees are not motivated by prosocial sentiments to provide food rewards to other group members.

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Humans participate in a range of activities that benefit others. These behaviours range from simple acts of courtesy (holding the door for shoppers laden with packages) to modest forms of charity (sending money to victims of hurricane Katrina) and extraordinary feats of heroism (firefighters taking great risks to rescue victims of the 9/11 bombings). These activities are all prosocial because they benefit others, and some are altruistic because donors incur costs and receive no direct benefit themselves when they provide benefits to others. In many

cases, the actors are unknown to the beneficiaries, thus eliminating the possibility of future reciprocity. In this paper, we consider whether chimpanzees take advantage of very low cost opportunities to behave prosocially towards conspecifics.

In an effort to gain insight about the origin and evolution of other-regarding preferences in humans, we conducted a series of experiments on chimpanzees. We focus on chimpanzees for a number of reasons. First, chimpanzees are our closest living relatives (Glazko & Nei 2003). The absence of other-regarding preferences in chimpanzees would suggest that these preferences (and possibly reputational concerns) are derived properties of humans that evolved after *Homo* and *Pan* diverged. Conversely, the presence of other-regarding preferences in

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chimpanzees would indicate that the foundation for prosocial behaviour existed before the human and ape lineages diverged and was elaborated within the human lineage.

Second, chimpanzees may share some of the cognitive capacities and moral sentiments that underlie prosocial behaviour in humans. Chimpanzees sometimes console victims of aggression (de Waal & van Roosmalen 1979), which may be evidence of compassion (de Waal & Aureli 1996). There are also anecdotal accounts of solicitous treatment of injured group members, human caretakers and other species that have been interpreted as evidence that chimpanzees feel empathy (Flack & de Waal 2000; Preston & de Waal 2002). However, conclusions about chimpanzees' capacity for empathy and other-regarding sentiments rest on subjective interpretations of behaviour and have not been subjected to systematic analysis (Silk 2007).

Third, chimpanzees participate in a wider range of cooperative activities than most other nonhuman primates. In the wild, adult males frequently groom one another, form coalitions, share food, jointly defend access to mates, hunt cooperatively and collectively defend the borders of their community ranges (Nishida & Hosaka 1996; Watts 1998; Mitani et al. 2000; Boesch & Boesch-Achermann 2002). Male chimpanzees cooperate mainly with males with whom they maintain close social bonds, but these relationships are not limited to pairs of close maternal kin (Mitani et al. 2000, 2002).

Chimpanzees' performance in cooperative tasks in the laboratory (Povinelli & O'Neill 2000; Melis et al. 2006a, b; Warneken & Tomasello 2006; Hirata & Fuwa 2007) has not consistently demonstrated their ability to take the perspective of others into account. Chimpanzees may not have succeeded in some collaborative tasks in the laboratory because they lack an understanding of the perspectives of others (see Visalberghi et al. 2000). However, recent experiments conducted on chimpanzees suggest that they readily master joint tasks when paired with tolerant partners (Melis et al. 2006a) and consistently differentiate between effective and ineffective collaborators (Melis et al. 2006b).

Prosocial behaviour may also depend on the ability to appreciate the goals, desires and intentions of others, as well as the motivation to confer benefits on others. Chimpanzees display considerable knowledge of the consequences of their own behaviour and the behaviour of others, but there is continuing disagreement about how much they know of others' thoughts and intentions (Povinelli & Vonk 2003, 2004; Tomasello et al. 2003a, b). Recent evidence that young chimpanzees provide appropriate forms of instrumental assistance to familiar human caretakers suggests that they can appreciate the perspectives of others and are motivated to provide aid (Warneken & Tomasello 2006). On the other hand, chimpanzees' behaviour in other experimental exchange tests suggests that they are strongly influenced by selfish motives. Chimpanzees sometimes reject exchanges in which they receive less valuable rewards than others (Brosnan et al. 2005). But unlike humans in many societies, whose social norms are based on a broad principle of fairness

(Fehr & Schmidt 1999; Henrich et al. 2005), chimpanzees do not appear to have aversions to inequities in situations in which they receive more valuable rewards than their partners (Brosnan et al. 2005). Thus, chimpanzees seem to be adept at calculating the value of resources, but their concerns are focused on the benefits that they receive themselves, not the benefits they can provide to others (Henrich 2003; Brosnan et al. 2005; Brosnan 2006).

These observations raise important questions about the factors that underlie cooperation in chimpanzees. It is possible that chimpanzees possess other-regarding sentiments, even though cooperative behaviour may not be deployed in the same way or in the same contexts as it is in humans. Alternatively, it is possible that chimpanzees do not possess other-regarding sentiments, and that cooperative behaviour is motivated mainly by self-interest. Importantly, the latter interpretation does not assume that chimpanzees never help each other. Rather, this behaviour might be consistent with the logic of self-interest, arising from evolutionary models such as direct and indirect reciprocity (including reputation-based models).

In a previous set of experiments, we evaluated whether chimpanzees would take advantage of opportunities to provide benefits to others at no cost to themselves (Silk et al. 2005). We devised a protocol in which actors faced a choice between two options: Option 1 provided a food reward only to the actor and Option 2 delivered an identical food reward simultaneously to both the actor and another member of the subject's group. We included a condition in which actors were presented with the same two choices, but no other chimpanzee was present. If these chimpanzees' actions were based on other-regarding sentiments, they were expected to choose Option 2 significantly more often when another chimpanzee was present than when they were alone. We studied two chimpanzee populations using two different apparatuses. The presence of another chimpanzee had no significant effect on actors' choices at either site. Jensen et al. (2006) independently replicated these findings in another group of socially housed chimpanzees using a similar paradigm. The results of these sets of experiments are consistent with the hypothesis that chimpanzees are indifferent to the welfare of other group members.

However, this conclusion has recently been challenged by findings derived from another set of experiments. As noted above, Warneken & Tomasello (2006) showed that young human-reared chimpanzees retrieved objects and returned them to their trainers, who were trying to reach them. In a second set of experiments, conducted with a different group of chimpanzees, help was also extended to unfamiliar humans who were unable to reach an object. In additional experiments, help was offered to familiar conspecifics who were trying to open a door and enter an adjacent enclosure (Warneken et al. 2007).

The apparently discrepant findings from these various studies provide an opportunity to gain insight about the factors that shape prosocial preferences in chimpanzees. For example, Warneken et al. (2007) suggested that prosocial responses might not have been observed in experiments conducted by Silk et al. (2005) and Jensen et al. (2006) because the actors 'were preoccupied with

retrieving food for themselves, and the recipient did nothing to indicate any need for help'. In addition, it is possible that, in earlier experiments, the chimpanzees had difficulty understanding the impact of their own actions with the apparatus for others (see also Jensen et al. 2006).

Here we present the results of two additional experiments that address these concerns. In these experiments, the delivery of food rewards to actors and potential recipients required independent but identical actions. One option delivered a reward only to the actor and another option delivered a food reward only to the recipient. Actors were able to select either of these two options, or to choose them both. The chimpanzees had the opportunity to make prosocial choices before or after consuming their own rewards, avoiding the possibility that obtaining food for themselves distracted them from obtaining food for their partner. In addition, the recipients were able to communicate their desires to the actor by using begging gestures. In these experiments there is some cost associated with prosocial behaviour, but the amount of effort required to deliver rewards to others is very small. As before, we compared the chimpanzees' performance when another chimpanzee was present to receive the reward with their performance when no other chimpanzee was present. Chimpanzees are expected to take advantage of opportunities to provide benefits to themselves in all conditions. If chimpanzees have prosocial preferences, they should provide rewards for other chimpanzees over the course of the experiment as well, even though such acts involve some cost, but only when the other chimpanzee is present. Moreover, they should respond to explicit requests from potential recipients. Alternatively, if chimpanzees are indifferent to providing benefits for others, they should minimize the costs to themselves and not provide rewards for others. Moreover, as they learn that they are unable to obtain the reward from the other enclosure, they are expected to choose the other reward with decreasing frequency in both conditions. By including repeated interactions and building the opportunity for learning explicitly into the design, we open the possibility of observing change in individuals' willingness to deliver food to another chimpanzee and thereby gain additional insight into the potential underlying motivations.

EXPERIMENT 1

Subjects were given the opportunity to use a stick-like tool to dislodge two identical food rewards (Fig. 1). When dislodged, one food reward rolled down a ramp towards the actor and the other food reward rolled down a ramp into another enclosure that the actor could not enter. In the 'recipient-present' (RP) condition, the other enclosure was visibly occupied by another member of the actor's social group. In the 'recipient-absent' (RA) condition, the other enclosure was visibly empty. If the chimpanzees are motivated to obtain rewards for themselves, they might be expected to dislodge both rewards initially. As they gained more experience with the apparatus, they were expected to learn that they could obtain only the



Figure 1. Experimental apparatus used in experiment 1. This figure does not show the black mesh barriers that divided the top of each ramp and that were used in all phases of the experiment. The mesh barriers replaced the clear Lexan barriers that are depicted here before testing began. When the capsule placed on the actor's side of the mesh barrier was dislodged, it rolled down the ramp towards the actor. When the reward on the recipient's side of the mesh barrier was dislodged through the mesh, it rolled down the ramp towards the opposite enclosure. The actor and recipient were 2.74 m apart and could see each other and the distribution of rewards.

reward that rolled into their own enclosure ('own reward' hereafter). If chimpanzees have other-regarding preferences, they are expected to continue to dislodge rewards that roll into the other enclosure and that can be collected by another group member ('other reward' hereafter) more often when the other enclosure is occupied by another chimpanzee than when it is empty. However, if chimpanzees do not have other-regarding preferences, their behaviour is not expected to be influenced by the presence or absence of a chimpanzee in the other enclosure.

Methods

Subjects

The experiment was conducted in the laboratory of the Cognitive Evolution Group, at the University of Louisiana. Seven unrelated chimpanzees, one male and six females, who had been raised together in a stable social group for at least 12 years, participated in this experiment. Five of the chimpanzees were nursery reared in a group of their peers. The other two chimpanzees were mother-reared for less than a year before joining the same social group around the age of 2 years. The chimpanzees have free access to five indoor and five outdoor enclosures, which contain various enrichment items, and are separated briefly only for testing twice daily 5 days a week. These chimpanzees have participated in a wide range of cognitive and behavioural tasks throughout their lifetimes, including the experiments described in Silk et al. (2005). At the beginning of testing they ranged in age from 15 years 9 months to 16 years 8 months. The experiment took approximately 3 months to complete. (For more details about the history of this study group, see Povinelli 2003.)

Experimental set-up

The experiment was conducted in three adjacent outdoor enclosures that were arranged in a row (for additional details concerning the enclosures see Povinelli 2003). One enclosure housed the actor, the middle enclosure housed the testing apparatus and the far enclosure either housed another group member (the potential recipient), or was empty. Lexan windows, which allowed the actor and recipient to see each other, separated the testing apparatus in the middle enclosure from the other two enclosures. The testing apparatus was composed of two double-sided ramps, centred on the long axis of a table (Fig. 1); a single ramp on each side of the table sloped downwards, one towards each of the adjacent enclosures. At the apex of each ramp was a flat platform, divided by a mesh barrier. The actor and recipient were 2.74 m apart.

Food rewards consisted of a quarter piece of fruit, such as apple, orange or banana, or three grapes, and were identical in size. Food rewards encased in transparent, round, plastic capsules (a food delivery method that was familiar to the chimpanzees) were placed on the platform that was bisected by the mesh barrier. The actor had access to a lightweight, 123 cm long PVC tool, which could be used to dislodge the food rewards. The actor could not reach or dislodge either reward without the tool. Both rewards were dislodged with equally minimal contact with the tool. The reward placed on the actor's side of the mesh barrier rolled down the ramp towards the actor when it was contacted with the tool. To dislodge the reward placed on the other side of the mesh barrier, the actor contacted the capsule through the mesh, and the capsule rolled down the ramp towards the other enclosure. Neither reward could be pushed over the barrier to roll down the opposite side of the ramp (e.g. the actor could neither obtain both pieces of food, nor deliver both pieces to the recipient). Rewards rolled into shallow troughs at the bottom of the ramps so the chimpanzees could easily reach them.

Procedure

Training. The first phase of training was designed to ensure that the chimpanzees were able to use the tool to dislodge the food rewards and to teach them that they had the option of dislodging either reward or both rewards on every trial. In these training sessions, a chimpanzee (the actor) was brought into the actor's enclosure. At the start of each trial, a transparent barrier was lowered into position, blocking the actor's access to the apparatus. Then, an experimenter baited the apparatus with two food rewards while the actor watched through the Lexan window. The experimenter placed one reward on the actor's side of the barrier at the top of each ramp, always beginning with the ramp on the actor's left. Once the apparatus was baited, the experimenter placed the tool at a 90-degree angle to the Lexan door, equidistant between the two ramps, and then left the middle enclosure. This experimenter, with the help of a second experimenter, then pulled the apparatus into position and raised the barrier so that the actor could respond. The actor was given 2 min to dislodge one or both rewards. The barrier

was lowered as soon as both rewards were dislodged, or at the end of 2 min. There was no recipient present in the opposing enclosure during these training sessions.

Training sessions consisted of two of these trials and continued until actors (1) retrieved a reward on both trials within a session and (2) dislodged both rewards during at least one trial. All actors reached criterion rapidly (range 1–3 sessions), and none required prompting from experimenters to use the tool to dislodge the food rewards.

The second step in training ('demonstration') was designed to ensure that actors had the opportunity to see a chimpanzee in the opposite enclosure receive a food reward. To accomplish this goal, one subject was brought into the actor's enclosure and another chimpanzee was brought into the opposite enclosure. The experimenter placed a single food reward on the recipient's side of the mesh barrier (on the actor's right). A small 'plug' inserted on the apex of the ramp caused the food reward to rest precariously, although this plug was not visible to the chimpanzees. The apparatus was then pulled into position by two experimenters, and the barrier was lifted. As the apparatus was shifted, the reward was 'accidentally' dislodged and rolled towards the recipient. The experimenters ensured that the actor had observed this process and had witnessed the recipient retrieve the reward.

Each subject participated in one demonstration trial as an actor and one demonstration trial as a recipient. One demonstration trial was rerun because the actor did not watch the recipient retrieve the reward on the first attempt.

Testing. Testing consisted of 48 single-trial sessions per actor. Each actor participated in 24 sessions with a recipient present (four trials with each of the six other subjects serving as recipients) and 24 sessions without a recipient present. Recipient-present and recipient-absent sessions alternated, with four subjects beginning with recipient-absent trials and three subjects beginning with recipient-present trials. On each trial, one ramp was baited with a reward on the actor's side of the mesh barrier and the other ramp was baited with a reward on the other side of the mesh barrier. The placement of these rewards was counterbalanced within blocks of six trials in each condition. In addition, within each pairing, the placement of rewards on recipient-present trials was counterbalanced. On these trials, the order of pairings was randomized with the constraint that each actor was paired with each of the six recipients before any pairings were repeated. Each chimpanzee participated as an actor in one to four trials per day and as a recipient for a maximum of an additional four trials per day, no more than 5 days per week.

In the beginning of test trials, the actor was brought into the designated enclosure with the response barrier in the lowered position. In the recipient-present condition, another chimpanzee was brought into the opposite enclosure. In the recipient-absent condition, the opposite enclosure was empty. The experimenter baited the apparatus in full view of the actor, always baiting the actor's left side of the apparatus first, and then positioned the tool as in training. Next, the experimenter left the middle enclosure, pulled the apparatus into position and raised

the response barrier to allow the actor access to the tool. The actor then had 2 min to dislodge one or both rewards and retrieve the food. For the first 24 sessions, the response barrier was lowered as soon as the time limit expired or when both food rewards had been dislodged, whichever occurred first. Beginning with session 25 for all actors, the response barrier remained in the raised position until 2 min had expired regardless of whether both rewards had already been dislodged. Although not all actors dislodged both rewards on every trial, we implemented this change to avoid the possibility that actors might dislodge the second reward to bring about the end of the trial. Note that this motivation for the behaviour would not result in critical differences between the recipient-present and recipient-absent conditions, but it might artificially inflate the rate of dislodging the other reward across both conditions.

A response was defined as the actor dislodging a food reward. If the actor did not dislodge either reward within the time limit, the trial was rerun at the end of all of the sessions within that testing slot (i.e. morning or afternoon testing session). This event occurred only once in the course of the experiment. On all other trials, the actors dislodged at least their own reward.

Data coding

All responses by the actor were recorded by two experimenters and archived digitally. Two independent raters coded the videos and recorded which reward was dislodged first, which of the rewards were dislodged by the end of the trial and the latencies to dislodge each of the rewards. (One trial was inadvertently not recorded; for this trial we used the experimenters' records for response, but we do not have information about the latency of responses). Rater agreement for the first two measures was perfect, yielding Cohen's kappa values of 1.0. The raters' latency calculations were highly correlated (Pearson $r = 0.99$, $P < 0.001$).

All manual begging gestures by the potential recipient were coded from the videotapes by two independent raters. Raters noted the time at which the gestures occurred from the beginning of the trial as well as the time at which rewards were dislodged. Rater agreement for whether gestures were given was high, yielding a Cohen's kappa value of 0.96. We used the primary rater's data in all analyses.

Statistical analysis

We used a binary logistic regression model to assess the effects of trial, condition (recipient-present/absent), position of the food reward (left or right) and actor identity on the likelihood of dislodging the other reward. Because the data involved repeated measures from the same individuals, we used two standard approaches to deal with the lack of independence. First, we included individual identity as a categorical variable, which should remove the source of nonindependence by controlling for individual differences. Second, we used clustered robust standard errors to calculate the confidence intervals for predictor variables (Williams 2000). This approach removes the

assumption of independent observations within individuals and relies instead only on the independence of different individuals.

In addition, we conducted exact tests for individual subjects, comparing the percentage of trials on which actors dislodged the other reward when another chimpanzee (recipient) was present and when no other chimpanzee was present. We used a corrected alpha value to control for the lack of independence of data points. These tests allowed us to determine whether any prosocial chimpanzees might exist in our sample, despite the potential lack of an overall effect.

Furthermore, to test our subjects' understanding of the task, we used a repeated measures ANOVA to determine whether they dislodged their own and the recipient's rewards at different rates, and whether the time to dislodge rewards varied between experimental conditions (recipient present versus absent). If actors are primarily concerned with their own benefits and if they understand which rewards they can retrieve themselves and which rewards they will not be able to obtain, we might expect a difference in the response times for type of reward but not for condition.

We used a binary logistic regression model to assess the effects of recipient gestures (present or absent), trial and actor identity on the likelihood of dislodging the other reward. We used the methods described above to deal with the problem of nonindependence of data from the same individuals.

Results

As expected, the chimpanzees were highly motivated to obtain rewards for themselves. Six subjects dislodged their own reward on every trial throughout the course of testing, and one subject dislodged her own reward on all but one trial.

Actors dislodged the other reward on a mean \pm SE of $70 \pm 8\%$ of all recipient-absent trials and $64 \pm 8\%$ of all recipient-present trials (Fig. 2). The results of the two binary logistic regressions appear in Table 1. Values for the predictor variable 'condition' indicate that the presence of another chimpanzee in the opposite enclosure had no

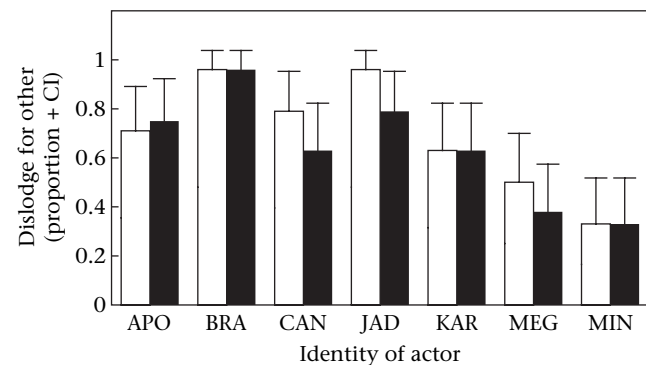


Figure 2. Percentage of trials on which each actor dislodged the other reward in experiment 1 when a recipient was absent (□) or present (■). Error bars indicate 95% confidence intervals.

Table 1. Factors that influenced the likelihood of dislodging the other reward in experiment 1

Parameter	Odds ratio	SE	Z	P	95% bounds	
					Upper	Lower
Model 1*						
Condition	0.69	0.19	-1.32	0.187	0.40	1.19
Trial	0.94	0.01	-5.61	<0.001	0.92	0.96
Position	0.79	0.22	-0.88	0.379	0.45	1.35
Brandy	10.10	8.21	2.85	0.004	2.05	49.64
Candy	0.88	0.43	-0.26	0.796	0.34	2.29
Jadine	2.87	1.65	1.85	0.064	0.94	8.86
Kara	0.57	0.27	-1.17	0.243	0.23	1.46
Megan	0.23	0.11	-3.07	0.002	0.09	0.59
Mindy	0.14	0.07	-4.04	<0.001	0.05	0.36
Model 2†						
Condition	0.75	0.14	-1.51	0.131	0.52	1.09
Trial	0.95	0.02	-2.75	0.006	0.92	0.98
Position	0.84	0.18	-0.80	0.426	0.55	1.29

*The binary logistic regression model included categorical variables for individuals as predictors in addition to the variables shown. Variables were coded so that the odds ratios would exceed 1 for condition if actors were more likely to dislodge the other reward when a recipient was present. For trial, the odds ratio would exceed 1 if chimpanzees were more likely to dislodge the other reward as the experiment progressed. The odds ratio was significantly less than 1, indicating that the chimpanzees were less likely to dislodge the other reward as the experiment progressed. Position was coded so that odds ratio would exceed 1 if the actors were more likely to dislodge the other reward if it was positioned on the right. The odds ratios for individuals indicate whether each of these six subjects was more or less likely to dislodge the other reward than was Apollo.

†The binary logistic regression model used clustered robust standard errors to calculate the confidence intervals for predictor variables.

significant effect on the likelihood that the actor would dislodge the other reward. The odds ratios in both regression models were below one (0.69, 0.75), indicating that the presence of a recipient tended to decrease the probability of dislodging the other reward. Values for the predictor variable 'Trial' indicate that actors initially dislodged both rewards in both conditions on most trials, but as the experiment progressed, the likelihood of dislodging the other reward declined in both conditions. Specifically, the odds ratio of dislodging the other reward decreased by a factor of approximately 1.67 for every 10 trials (based on the estimate in Table 1). Note that odds ratios and confidence intervals for individual variables indicate only whether the likelihood of each individual dislodging the other reward significantly differed from the likelihood that a randomly selected subject (Apollo) dislodged the other reward, not that these subjects dislodged the other reward more often than predicted by chance. Thus, of the six subjects compared to Apollo, only one, Brandy, was significantly more likely to dislodge the other reward, and only two, Megan and Mindy, were significantly less likely to dislodge the other reward, collapsed across conditions.

Analyses based on the behaviour of individual chimpanzees were consistent with the aggregate data. Fisher's exact tests revealed that none of the seven chimpanzees dislodged the other reward more often when another recipient was present than when absent (Apollo: $P = 0.50$;

Kara: $P = 0.62$; Candy: $P = 0.20$; Brandy: $P = 0.76$; Megan: $P = 0.28$; Mindy: $P = 0.62$; Jadine $P = 0.09$).

Six of the seven subjects continued to dislodge the other reward on at least half the trials in both conditions through the last block of testing (Fig. 3). This result might suggest that the chimpanzees did not understand that they were unable to obtain the reward that was positioned on the other side of the mesh barrier. However, the order and latency of the actors' responses suggest that this was not the case. There was a significant decline in the likelihood of dislodging the other reward first over the course of the experiment, and this decline was not affected by the presence or absence of another chimpanzee in the other enclosure. When both rewards were dislodged during the first block of 12 trials, actors dislodged their own reward before they dislodged the other reward in 78% of recipient-absent trials ($N = 36$) and 80% of recipient-present trials ($N = 40$). During the remaining trials, actors dislodged their own reward first in all but one of the trials in which both rewards were dislodged (recipient-absent: $80/80 = 100\%$; recipient-present: $66/67 = 99\%$). In addition, there was a considerable delay before actors dislodged the reward that rolled into the other enclosure. Actors dislodged their own reward a mean \pm SE of 4.5 ± 0.38 s after the barrier was lifted and they dislodged the other reward after 61.1 ± 2.52 s (Fig. 4). A repeated measures ANOVA on the latency to dislodge both rewards indicated that the presence of a chimpanzee in the other enclosure did not affect the latency to dislodge either reward ($F_{1,12} = 0.945$, $P = 0.350$) and confirmed that the actor dislodged his/her own reward more quickly than he/she dislodged a reward for the other chimpanzee ($F_{1,12} = 155.514$, $P < 0.001$). The interaction between condition (recipient-present or recipient-absent) and reward (own, other) was not significant, so the actor did not dislodge the other reward more quickly in the presence of the recipient.

In 55% of all trials, potential recipients gestured before the actor had dislodged the food reward on the recipient's

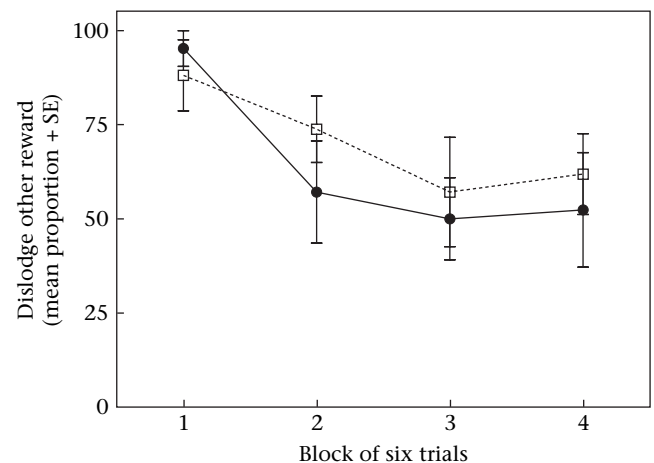


Figure 3. Mean \pm SE percentage of trials on which actors dislodged the other reward across blocks of six trials in experiment 1 when a recipient was present (●) or absent (□).

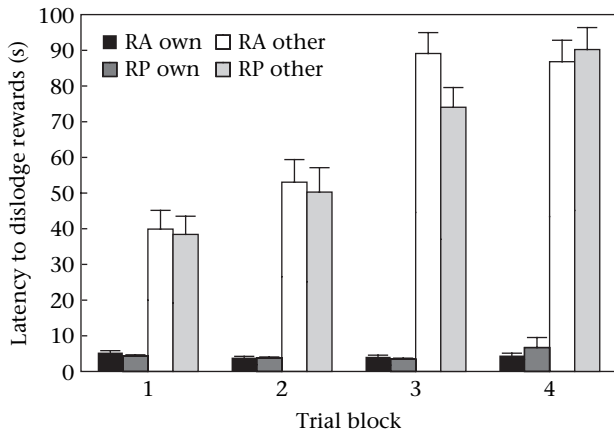


Figure 4. Mean ± SE latency to dislodge own and other rewards by condition (recipient-present, RP; recipient-absent, RA) and block of six trials in experiment 1.

side. There was considerable variability in how often the seven chimpanzees made begging gestures when they were participating as potential recipients (range 0.13–0.92; 24 trials per individual), but there was much less variability in how often each chimpanzee was the target of begging gestures (range 0.42–0.66). We examined the effect of gestures on the likelihood that actors would deliver food to recipients. Overall, begging gestures had no significant effect on the likelihood of dislodging the other reward (Table 2). The odds ratio was below 1, indicating that the recipients’ begging tended to decrease the likelihood of actors dislodging the other reward. Three individuals were slightly more likely to dislodge the reward on the recipient’s side when begging gestures were made, while four were slightly less likely to do so (Fig. 5).

Table 2. The effect of begging gestures on actor’s responses

Parameter	Odds ratio	SE	Z	P	95% bounds	
					Upper	Lower
Model 1*						
Gesture	1.04	0.42	0.09	0.925	0.47	2.32
Trial	0.91	0.02	-5.25	<0.001	0.88	0.95
Position	1.56	0.63	1.10	0.271	0.71	3.42
Brandy	4.57	4.32	1.61	0.108	0.72	29.12
Candy	0.48	0.35	-1.02	0.308	0.12	1.97
Jadine	1.32	1.02	0.36	0.718	0.29	5.97
Kara	0.20	0.14	-2.25	0.025	.05	0.81
Megan	0.12	0.09	-2.81	0.005	0.29	0.53
Mindy	0.09	0.07	-3.15	0.002	0.02	0.41
Model 2†						
Gesture	0.82	0.20	-0.79	0.427	0.51	1.32
Trial	0.93	0.02	-3.48	<0.001	0.90	0.97
Position	1.41	0.32	1.53	-0.127	0.91	2.19

*The binary logistic regression model included categorical variables for individuals as predictors in addition to the variables shown. The variable gesture was coded so that the odds ratios would exceed 1 if actors were more likely to dislodge the other reward when a recipient gestured.

†The binary logistic regression model used clustered robust standard errors to calculate the confidence intervals for predictor variables.

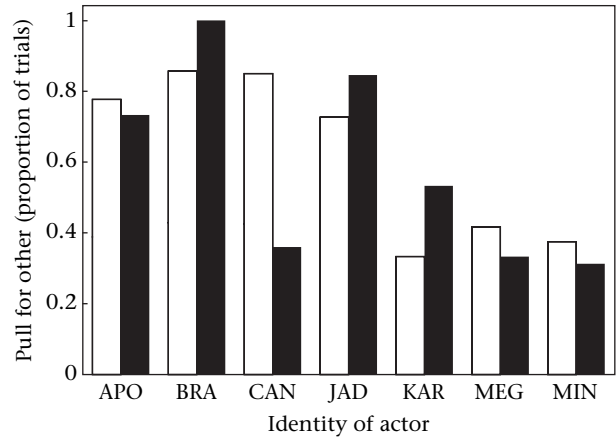


Figure 5. The effect of gestures on response by actor in experiment 1. For each actor, the proportion of trials in which the other reward was dislodged after the recipient performed begging gestures (■) and when no begging gestures were given (□) is shown.

We examined the effect of gesturing on the behaviour of each actor. For six of the seven chimpanzees, begging gestures had no significant effect on the likelihood of dislodging the other reward (Fisher’s exact tests: Apollo: $P = 1.0$; Brandy: $P = 0.49$; Jadine: $P = 0.63$; Kara: $P = 0.42$; Megan: $P = 1.0$; Mindy: $P = 1.0$). The remaining chimpanzee (Candy) was significantly less likely to dislodge the other reward if the potential recipient gestured ($P = 0.03$).

Discussion

Actors were less likely to dislodge the other reward as the experiment progressed, and their likelihood of dislodging the other reward was not influenced by the presence or behaviour of another chimpanzee in the opposite enclosure. Our finding that the chimpanzees continued to dislodge the other reward almost half the time throughout testing suggests that the cost of dislodging the other reward was not sufficiently high to prevent the chimpanzees from behaving prosocially. A strong inclination to dislodge the other reward in both RP and RA conditions can be explained in various ways. For example, the chimpanzees might have been testing their understanding of the apparatus, attempting to make sure that it still worked in the same way as before, or they might simply have taken pleasure in dislodging the other reward. However, no alternative account challenges the critical conclusion that chimpanzees were not influenced by the presence of another chimpanzee, and thus their desire to dislodge the other reward cannot be described as prosocially motivated. While these chimpanzees were highly motivated to obtain rewards for themselves, they seemed indifferent to the opportunity to deliver rewards to others. In further support of this conclusion, no actors were significantly more likely to dislodge a reward for a conspecific when the potential recipient indicated, by gesturing, a desire for the reward. These findings are consistent with those of Silk et al. (2005), which included this group of chimpanzees, and with Jensen et al.’s (2006) findings with another group of chimpanzees.

It is unlikely that chimpanzees failed to understand the relevance of their actions for conferring rewards to others in this experimental setting. Actors consistently dislodged their own reward only a few seconds after the barrier was lifted, but waited much longer (i.e. over a minute) to dislodge the other reward. This result indicates that they clearly differentiated between rewards they could and could not reach themselves. Moreover, in some trials, potential recipients, who were less than 3 m away, directed begging gestures towards actors. Each chimpanzee had multiple opportunities to observe another chimpanzee receive a reward that had been dislodged from the other side of the apparatus and each chimpanzee participated as a recipient 24 times throughout the course of the experiment, giving them the opportunity to appreciate the perspective of the recipient.

EXPERIMENT 2

Experiment 2 was designed to complement experiment 1 and provided a different group of chimpanzees with an analogous set of choices using a different apparatus. Here subjects were given the opportunity to obtain rewards for themselves and to deliver rewards to others by manipulating a two-tiered bar-pull apparatus (Fig. 6; Silk et al. 2005). The apparatus was placed in front of two adjoining enclosures, which were separated by a wire mesh barrier. Only the actor could manipulate the bar-pull apparatus. One tier (hereafter 'tray') of the bar-pull apparatus was baited on the actor's side and the other tray was baited on the other side (out of the actor's reach). In this experiment, none of the chimpanzees changed roles. Actors were paired with the same recipient in all recipient-present trials. In these trials, the actor was brought into the actor's enclosure and the potential recipient was brought into the adjoining enclosure. In the recipient-absent condition, the actor's enclosure was occupied and the other enclosure was empty.

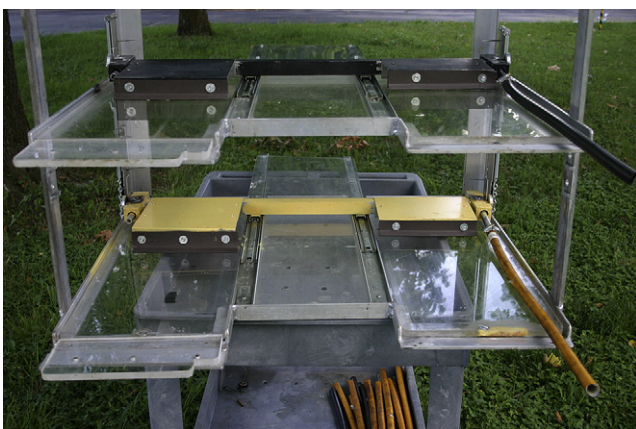


Figure 6. Experimental apparatus used in experiment 2. The two-tiered bar-pull device was designed so that the actor could pull a hose connected to the bar on the upper level and/or pull a hose connected to the bar on the lower level. When the hose was pulled forward, a food reward was swept to within reach of the actor or potential recipient when the other enclosure was occupied.

As in experiment 1, chimpanzees were expected to be motivated to obtain rewards for themselves and to initially try to obtain both rewards. Over time, they were expected to learn that they could obtain the reward on their side of the apparatus but not the reward on the far side of the apparatus. However, if chimpanzees have other-regarding preferences, they should deliver rewards to the adjacent enclosure more often in the recipient-present condition, where they can be collected by another chimpanzee, than in the recipient-absent condition. If chimpanzees do not have other-regarding preferences, they should stop delivering rewards to the other enclosure as they learn how the apparatus works and their behaviour should not be influenced by the presence or absence of another chimpanzee in the adjoining enclosure.

Methods

Participants

Subjects came from six corral-housed groups of chimpanzees at the Michale E. Keeling Center for Comparative Medicine and Research of the U.T.M.D. Anderson Cancer Center Science Park in Bastrop, Texas. These groups have been maintained as stable social units since as early as 1978, and range in size from seven to 15 individuals, all including multiple adult males and multiple adult females. All groups have approximately the same age distribution among adults, although the number of immatures varies by group. We tested 11 unrelated same-sex adult pairs drawn from the same social group (three pairs of males and eight pairs of females). Subjects ranged in age from 10 to 40 years. One member of each pair served as the subject (i.e. actor) and the other pair members served as potential recipients. Six of the subjects were wild-caught and mother-reared until they were brought to Bastrop in the 1970s, after which time they were housed socially. The other five subjects were captive-born and mother-reared. Thus, all of the chimpanzees had been living in social groups since group formation approximately 30 years ago or were born into those social groups a minimum of 10 years ago. They live in large outdoor enclosures with climbing structures and other enrichment (Riddle et al. 1982), with access to an indoor area as well. They have ad libitum access to primate chow and water and receive four enrichment meals a day (fruits, vegetables and treats).

Unlike the subjects in experiment 1, actors did not exchange roles or partners over the course of the experiment. In addition, these chimpanzees had little experience with cognitive or behavioural testing before this study.

Experimental set-up

Chimpanzees were tested in the familiar indoor dens of their home enclosure. The chimpanzees were positioned in adjacent dens, divided by wire mesh. They were able to see each other, vocalize and groom through this barrier. The two-tiered bar-pull apparatus spanned most of the width of the adjoining enclosures (Fig. 6). The trays were made of clear Lexan and were approximately 45 cm apart. Each tray had a coloured metal sweeper mounted on the tray

with tracks. Each sweeper had a hose, which served as a handle (in the same colour as the bar) attached to it on the actor's side; when a handle was pulled, the sweeper attached to that handle was moved along the tracks towards the chimpanzees. Food rewards were always pieces of banana that were equivalent in size. Food placed on the Lexan tray in front of the sweeper was swept close to the edge of the enclosures when the handle was pulled, allowing the chimpanzees to obtain rewards (when present).

Procedure

Training. Training was designed to ensure that the actors (1) learned to obtain food by pulling the handles attached to the sweeper or bar-pull, (2) had the opportunity to observe the chimpanzee in the other enclosure obtain food and (3) learned that they could make two responses in each trial. During these training sessions, one chimpanzee was placed in the actor's enclosure and another chimpanzee was placed in the adjoining enclosure. In these sessions, both sides of each tray of the bar-pull apparatus were baited with identical rewards. Thus, either choice would deliver rewards to both the actor and the other chimpanzee. The actor could pull one or both of the handles.

Each training session consisted of 20 trials. On each trial, the apparatus was baited by the experimenter, who always baited the top tray first. Following baiting, the experimenter moved the apparatus to within the actor's reach, then left the testing area for 60 s. Thus, the experimenter was not visible to either chimpanzee and could not see what choices were made until after the trial was completed. Following the trial, the experimenter returned, pulled the apparatus away, removed any remaining food, rebaited the apparatus, and moved it back within the actor's reach. If the actor pulled at least one of the handles within five trials, trials continued until the end of the session or until the actor did not pull either handle for five consecutive trials. If the actor failed to pull either handle for five consecutive trials, the next trial was a 'demonstration' trial. In the 'demonstration' trial, the experimenter baited the trays in the same way, moved the apparatus into place, then simultaneously pushed both sweepers all of the way forward towards the actor. After the 'demonstration' trial, there were five additional 'delayed demonstration' trials in which the actor was given 30 s to pull a handle while the experimenter was out of the room; if the actor did not pull either handle, the experimenter came back in and pushed both trays forward simultaneously. If the actor pulled without prompting within five trials, unprompted trials began again. If this did not occur within five trials, the actor was given two 90 s unprompted trials unless this would be the last pull of a session, in which case delayed demonstration trials continued. We resumed the unprompted trials to make sure that the actor did not simply learn to wait for the experimenter to push the sweepers forward on each trial. If the actor pulled on one of these two unprompted trials, these trials were continued. If the actor did not pull, five additional delayed demonstration trials were conducted, using the same criteria outlined above.

Each training session concluded after a total of 20 trials (which included demonstration and prompted trials if given), regardless of the performance of the actor. The training phase was completed when the actor pulled in eight of the last 10 trials in a session without prompting. If the actor did not reach criterion within five sessions, that individual was not included in the experiment. Five actors reached criterion on the first session, five actors reached criterion within two or three sessions, and one actor required five sessions to reach criterion. Eleven more potential actors did not reach criterion within five sessions and were excluded from further testing. None of these potential actors were used as recipients in testing, so no recipient had any experience as an actor, nor did any actor have experience as a recipient.

Training was conducted across a period of 2–3 months. No chimpanzee ever participated in more than one training session per day, and sessions occurred no more than five times per week. All training sessions were digitally archived.

Testing. Testing consisted of 10 20-trial sessions (alternating five recipient-present sessions and five recipient-absent sessions). In all testing trials, one tray was baited on the actor's side and one tray was baited on the other side. Baitings were counterbalanced within a session such that there were 10 trials in each session baited with the actor's reward on the top tray and 10 trials baited with the actor's reward on the bottom tray. These trials were distributed randomly within each session with two exceptions. First, baitings were counterbalanced within each half of a session, such that there were five actor top and five actor bottom trials within the first 10 trials and five actor top and five actor bottom trials within the second block of 10 trials (trials 11–20). Second, the random numbers were restricted such that there were no more than three consecutive trials of any type (actor top or actor bottom). The basic procedure was identical to that of training, but no demonstration trials were included. Trials in which actors made no response were not rerun.

Each pair participated in only one session per day, and no pair was tested more than five times per week. Testing sessions for individual pairs were conducted across a period of 3–4 months. All trials were videotaped.

Data coding

The experimenter coded the data during testing. Two raters who did not participate in the experiment also coded all of the trials independently from videotape. The raters coded which handles the actors pulled and in what order. They also recorded the latency to pull after the experimenter placed the apparatus in front of the enclosures. Both raters coded the actor's choice on 400 randomly chosen test trials. The raters agreed about the order in which the actor pulled the handle(s) on all trials, yielding a Cohen's kappa of 1.0. The raters also showed almost perfect agreement on the latency to pull the handles (Pearson correlation: $r = 0.99$, $P < 0.001$). One session for one subject was inadvertently not captured on tape and was not included in analyses. Poor visibility

of potential recipients inside their enclosures on the videotapes precluded analyses of their gestures.

Statistical analysis

We again used two binary logistic regression models to assess the effects of trial, session, condition (recipient-present/absent), position (top/bottom) and actor identity on the likelihood of dislodging the other reward. Individuals were included as categorical variables to control for dependence and partial out variation based on individual differences, and clustered robust standard errors were used to calculate confidence intervals. Because trials were consecutive, we also examined a lagged variable (actor's choice in previous trial) to control for autocorrelation. In contrast to the previous experiment, actors did not respond by pulling on all trials within sessions (actors failed to pull either tray on 43% of the total number of trials). Following Silk et al. (2005), we first present the results of analyses based on trials in which the actor pulled at least one of the two trays. Then, using a multinomial logistic regression to examine the full complement of trials, we show that dropping the trials in which the actor does not do anything does not influence the results.

In addition, we again conducted exact tests on each subject, comparing the percentage of trials on which individual actors chose to make the other reward accessible to an adjoining enclosure when a recipient chimpanzee was present or absent in that adjacent enclosure. These analyses would reveal whether individuals behaved prosocially, regardless of the group outcome.

Results

In virtually every testing trial in which actors responded, they obtained rewards for themselves (99%, $N = 1253$ trials). However, overall, the presence of another chimpanzee had no significant effect on the likelihood of delivering rewards to the adjoining enclosure. Table 3 presents results for the binary logistic regression with individual effects and with clustered robust standard errors (and confidence intervals). Both regressions showed odds ratios for the effect of a partner presence that were indistinguishable from 1, indicating no significant effect. Note that odds ratios and confidence intervals for individual variables indicate only whether the likelihood of each individual dislodging the other reward differed significantly from the likelihood that a randomly selected subject (Coco) dislodged the other reward, not that these subjects dislodged the other reward more often than predicted by chance. An additional binary logistic, not shown, with individual categorical variables and a lagged predictor variable produced the same pattern of results (i.e. effects of trial and session but not of condition) and is not shown here. Actors pulled the handle that delivered rewards to the adjacent enclosure on a mean \pm SE of $43 \pm 6\%$ of all recipient-absent trials and $48 \pm 5\%$ of all recipient-present trials. Six chimpanzees delivered rewards to the other enclosure more often in the recipient-present condition than in the recipient-absent condition, while five chimpanzees showed the opposite pattern (Fig. 7).

Table 3. Factors that influenced the likelihood of dislodging the other reward in experiment 2

Parameter	Estimate	SE	Z	P	95% bounds	
					Upper	Lower
Model 1*						
Condition	1.25	0.16	1.72	0.085	0.97	1.62
Position	0.90	0.01	-9.11	<0.001	0.88	0.92
Session	0.81	0.02	-9.05	<0.001	0.77	0.85
Trial	1.07	0.14	0.50	0.614	0.83	1.3
Hannah	0.25	0.09	-3.87	<0.001	0.12	0.50
Huey	1.31	0.43	0.82	0.413	0.69	2.4
Jessie	1.11	0.34	0.35	0.724	0.61	2.02
Karin	0.87	0.26	-0.47	0.640	0.48	1.56
Kelly	3.40	1.35	3.08	0.002	1.55	7.40
Martha	1.06	0.45	0.13	0.895	0.46	2.43
Moose	7.99	5.82	2.85	0.004	1.91	33.32
Pepper	2.04	0.62	2.35	0.019	1.12	3.70
Punch	1.49	0.45	1.32	0.188	0.82	2.71
Sandy	1.73	0.57	1.66	0.096	0.91	3.29
Model 2†						
Condition	1.06	0.18	0.34	0.732	0.76	1.47
Position	1.03	0.41	0.09	0.931	0.48	2.24
Session	0.83	0.02	-7.21	<0.001	0.79	0.87
Trial	0.90	0.01	-8.13	<0.001	0.88	0.93

*The binary logistic regression model included categorical variables for individuals as predictors in addition to the variables shown. Variables were coded so that the odds ratios would exceed 1 for condition if actors were more likely to provide the other reward when a recipient was present. Position was coded so that the odds ratio would exceed 1 if the actors were more likely to provide the other reward if it was positioned on the top. For trial and session, the odds ratio would exceed 1 if chimpanzees were more likely to provide the other reward as the experiment progressed within trials or across sessions. An odds ratio of less than 1 for both session and trial indicates learning; the chimpanzees were less likely to provide the other reward across trials within a session and across sessions. The odds ratio for each individual indicates whether these 10 subjects were more or less likely to provide the other reward than was Coco. This analysis was conducted on those trials in which actors chose at least one tray.

†The binary logistic regression model used clustered robust standard errors to calculate the confidence intervals for predictor variables.

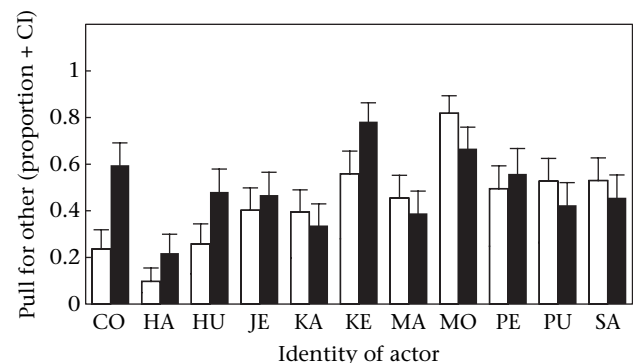


Figure 7. Percentage of trials (out of trials in which actor pulled at least one tray) on which each actor pulled the other reward in experiment 2 when a recipient was absent (□) or present (■). Error bars indicate 95% confidence intervals.

Exact tests comparing the percentage of trials on which actors delivered the other reward in recipient-present and recipient-absent conditions were conducted to test for individual effects. Bonferroni corrections were applied to the analyses owing to the lack of independence from repeated testing, yielding a corrected *P* value of 0.003. The exact tests revealed that differences were significant for only one subject, Coco, who chose the prosocial option more often when another chimpanzee was present than absent (Coco: *P* = 0.002; Hanna: *P* = 0.19; Huey: *P* = 0.052; Jessie: *P* = 0.44; Karin: *P* = 0.46; Kelly: *P* = 0.10; Martha: *P* = 0.755; Moose: *P* = 0.58; Pepper: *P* = 0.45; Punch: *P* = 0.21; Sandy: *P* = 0.56).

The likelihood of delivering rewards to the other enclosure declined significantly as the experiment progressed (Table 3). The odds ratios for both trial and session were significantly less than 1, indicating a decreased likelihood of pulling the other reward as the experiment progressed. The odds ratio for trial, for example, indicates that the likelihood of choosing the other reward declined by a factor of 2.7 for every 10 trials (based on estimates in Table 3). In the first pair of sessions, actors delivered rewards to the other enclosure on 63% of recipient-absent trials and 73% of recipient-present trials. However, by the fifth pair of sessions, these values declined to 33% and 32%, respectively (Fig. 8).

Analyses of the order of actors' responses provide further insights into their understanding of the task and the nature of their preferences. From the outset of the experiment, actors chose their own reward first in the majority of trials. However, this pattern became more pronounced as the experiment progressed (Fig. 9). In the first pair of sessions, actors chose their own reward first on 68% of all trials, but this value rose to 83% by the second pair of sessions and remained at this level for the remainder of the experiment.

In the first session, actors that chose their own reward first also pulled the handle that delivered rewards to the other enclosure 59% of the time. By the final pair of

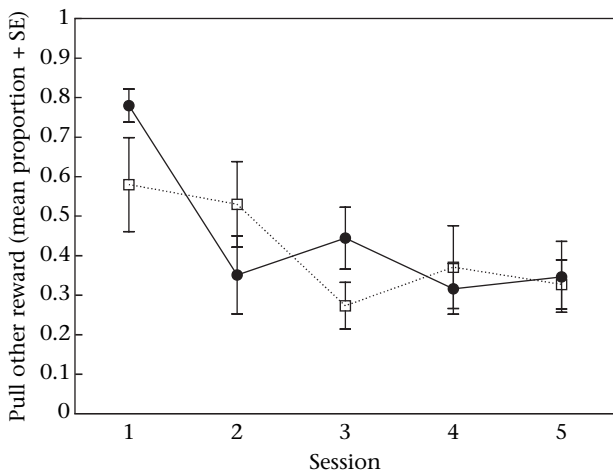


Figure 8. Mean ± SE percentage of trials (out of trials in which actor pulled at least one tray) on which actors pulled the other reward across sessions in experiment 2 when a recipient was present (●) or absent (□).

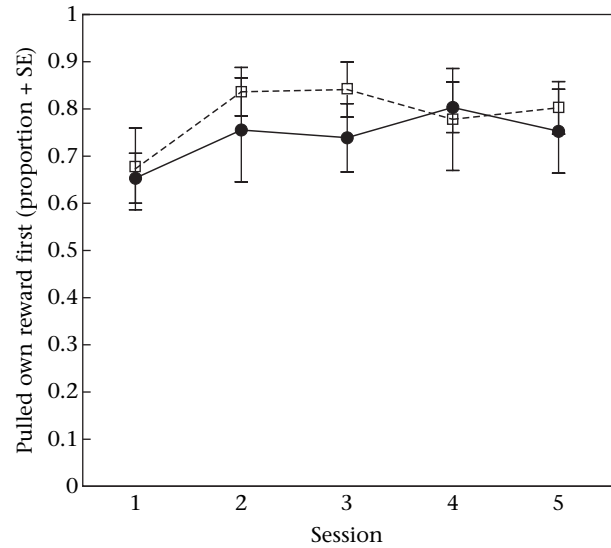


Figure 9. Mean ± SE percentage of trials on which actors chose their own reward first across sessions in experiment 2 when a recipient was present (●) or absent (□).

sessions, actors that chose their own reward first also pulled the other handle only 15% of the time. In contrast, when actors chose the other reward first, they virtually always pulled on the handle that delivered rewards to themselves as well (95%). This pattern remained stable across sessions and suggests that as chimpanzees learned more about how the apparatus worked, they became more likely to choose only the option that delivered rewards to themselves. But if, for some reason, chimpanzees did not obtain rewards from their first choice, they virtually always made a second choice as well.

The results derived from analyses based on the full complement of trials (that is, including trials in which the donor made no response) are consistent with the results described above. Here, pulling for self, other, neither or both were treated as separate dependent variables in a multinomial logistic regression. In Table 3, pulling for self was used as the reference variable, so the coefficients on the predictor variables measure the effect of each variable relative to pulling for self. This analysis revealed that chimpanzees were more likely to pull for both themselves and for the other if another chimpanzee was present, indicating a social facilitation effect on willingness to pull. However, the effect of the presence of the recipient on the tendency to pull for self was stronger than the effect of the presence of the recipient on the tendency to pull for other. Said another way, the presence of a potential recipient tended to motivate the subjects to pull for a reward, as opposed to not pulling at all, but they were more inclined to obtain their own reward than to provide a reward for the potential recipient.

Discussion

The results of this experiment, like those of experiment 1, suggest that chimpanzees are strongly motivated to

obtain rewards for themselves, but they are largely indifferent about the opportunity to deliver rewards to others. Only one of the 11 chimpanzees that we tested in this experiment was significantly more likely to pull the handle that was attached to the tray that delivered rewards to the other enclosure when it was occupied by another chimpanzee than when it was empty. However, when that individual (Coco) was later tested with the same partner in the experiments described in Silk et al. (2005), she did not differentiate between the partner-present and partner-absent conditions.

All of the chimpanzees were progressively less likely to deliver rewards to the other enclosure as the experiment progressed. This decline may indicate that the chimpanzees initially did not fully understand that they could obtain rewards from only their own side. As they learned this, they gradually stopped pulling the other option. Learning may have played an important role in this experiment because the first test session was the chimpanzees' first exposure to a situation in which only one of their choices brought them food (in training, both options brought rewards to both donor and recipient). As in experiment 1, the chimpanzees might have continued to pull the other option at low levels in order to monitor the consistency of the experimental parameters. Although actors did not switch roles or exchange partners during this experiment, they did have multiple opportunities to observe their partner, who was often less than 1 m away, and to receive and consume rewards during both training and testing.

The greater variance in responses evident in this population compared to the subjects in experiment 1 might be expected because of their more limited exposure to experimental procedures, and might also be partially explained by differences in motivation to obtain food. The chimpanzees in experiment 2, who received enrichment feedings several times a day outside the context of testing, were much more likely to refuse the opportunity to retrieve rewards for themselves than the chimpanzees in experiment 1.

GENERAL DISCUSSION

The results of these experiments indicate that chimpanzees do not consistently take advantage of low cost opportunities to provide food rewards to other group members. The presence of other chimpanzees did not influence the likelihood of delivering food rewards, and the actors in experiment 1 did not respond to the begging gestures of potential recipients. These results are consistent with those obtained in a similar set of experiments conducted with the same chimpanzees (Silk et al. 2005), and with results obtained independently by Jensen et al. (2006) in a third chimpanzee population. In all of these studies, chimpanzees, as a group, revealed no preferences for outcomes that benefited other group members. The uniformity of results in all of these experiments suggests the chimpanzees' behaviour cannot be explained as an artefact of their failure to understand the affordances of the testing apparatuses or their failure to appreciate the consequences of their own actions on the rewards obtained by others.

Actors continued to deliver food rewards to the opposite/adjacent enclosures over the course of both experiments in both conditions, although the rate at which they did so declined significantly over time. The failure to extinguish this response entirely might suggest that the chimpanzees did not understand how the apparatuses worked: they may have thought that they would be able to retrieve the food on the other side. However, we think that this is unlikely because (1) actors nearly always chose their own reward first, (2) only the rate of choosing the other reward declined over time, not the rate of choosing one's own reward, (3) actors in experiment 1 also experienced the experiment as recipients, and (4) actors were never given the opportunity to obtain food from the other side of the apparatus in training or testing. We think it is more likely that the chimpanzees continued to choose the other reward on some trials either because they were testing the parameters of the experiment or because they were unable to fully inhibit the response to manipulate the apparatus or tool.

These findings raise the possibility that chimpanzees are prone to behave selfishly when food is present (Warneken & Tomasello 2006). Although chimpanzees sometimes share food with other adults in the wild (and the chimpanzees in both of our study populations also share food with one another), some researchers have argued that food exchanges may be better described as 'tolerated theft' (Blurton Jones 1987) than voluntary sharing (Stevens & Gilby 2004; Gilby 2006). Others have emphasized the role that meat plays in political manoeuvring among adult males (Boesch & Boesch-Achermann 2002), or demonstrated that males are most likely to share meat with those who are more likely to share with them or provide them with other types of benefits (Mitani 2005). In these cases, males' motivation to share food can be explained by calculated self-interest and does not necessarily rely on other-regarding preferences.

It is possible that there are sex differences in the propensity to engage in prosocial behaviours. In the wild, male chimpanzees are more sociable than females and are more active participants in cooperative activities, such as hunting, coalitionary aggression and mate guarding (Boesch & Boesch-Achermann 2002; Mitani 2005). In both of our experiments, the majority of actors were female (6/7 in experiment 1 and 8/11 in experiment 2). More experimental work is needed to determine whether males and females differ in their propensity for prosocial behaviour.

Our findings might be interpreted as contradictory to claims that chimpanzees show compassion and empathy for those in distress (O'Connell 1995; Flack & de Waal 2000; Preston & de Waal 2002; but see Silk 2007) and inconsistent with recent evidence that chimpanzees provide instrumental help to humans and group members (Warneken & Tomasello 2006; Warneken et al. 2007). However, it is possible that other-regarding sentiments are not activated when food is present because food is the object of intense competition in chimpanzees' natural environment (Warneken & Tomasello 2006). Alternatively, it is possible that behaviour that is thought to be the product of prosocial motivations may actually be motivated by more selfish concerns.

The absence of other-regarding sentiments in chimpanzees would not necessarily limit their ability to participate in different types of cooperative enterprises. For instance, their motivation to participate in joint tasks (mutualism) may be based on the rewards that they receive themselves, not on the benefits that they provide to others. Similarly, when chimpanzees engage in tasks that require turn-taking (contingent reciprocity), they may be motivated mainly by their expectation of obtaining rewards in the future. Success in these kinds of tasks in the laboratory or in the wild may be based on selfish motivations, the ability to grasp the requirements of the task (Visalberghi et al. 2000) and the ability to collaborate effectively with particular partners (Melis et al. 2006a, 2006b).

The current experiments contribute to a growing body of evidence that suggests that chimpanzees do not take advantage of opportunities to provide food rewards to other members of their groups, even when they are able to do so at virtually no cost to themselves. In contrast, food sharing plays a fundamental role in all human societies, and often extends beyond kin and strict tit-for-tat reciprocity, even in foraging societies (Gurven 2006). This pattern of findings indicates that while chimpanzees' behaviour is consistent with standard evolutionary models based on kinship and reciprocity, human cooperation and prosociality may require an emerging class of evolutionary models, rooted in the coevolutionary interaction of genes and culture (Boyd et al. 2003; Henrich 2004). Further work is needed to determine whether chimpanzees consistently express prosocial preferences in other contexts and to identify the factors that influence chimpanzees' motivation to provide benefits to others. Present evidence suggests, however, that the motivation to provide food rewards to other individuals and prosocial preferences for equitable distributions of food are derived features of the human species.

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