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What's in it for me? Self-regard precludes altruism and spite in chimpanzees

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Sensitivity to fairness may influence whether individuals choose to engage in acts that are mutually beneficial, selfish, altruistic, or spiteful. In a series of three experiments, chimpanzees (*Pan troglodytes*) could pull a rope to access out-of-reach food while concomitantly pulling another piece of food further away. In the first study, they could make a choice that solely benefited themselves (selfishness), or both themselves and another chimpanzee (mutualism). In the next two experiments, they could choose between providing food solely for another chimpanzee (altruism), or for neither while preventing the other chimpanzee from receiving a benefit (spite). The main result across all studies was that chimpanzees made their choices based solely on personal gain, with no regard for the outcomes of a conspecific. These results raise questions about the origins of human cooperative behaviour.

Keywords: behavioural biology; evolutionary psychology; game theory; inequity; *Pan troglodytes*

1. INTRODUCTION

There are four ways that one individual can interact with another based on fitness gains and losses for both individuals: altruism, mutualism, selfishness, and spite (Hamilton 1964)—see table 1. Of these, altruism and spite are the most puzzling because of their costs to the actor. Darwin (1871) recognized that for altruism to evolve there must be benefits to the altruist, and Hamilton (1964) and Trivers (1971) suggested how inclusive fitness and reciprocity, respectively, can provide these benefits. Even so, the existence of altruism in animals remains controversial (e.g. Hammerstein 2003). Spite has received far less attention than altruism, and though theoretically plausible (Hamilton 1970; Wilson 1975), its existence in animals is also debated (e.g. Foster *et al.* 2001).

Despite its benefits for cooperative group-living, altruism as exhibited by humans has been claimed to be unique in the animal kingdom (Fehr & Fischbacher 2003). It is possible that spite may be just as beneficial—and as uniquely human—as altruism (Nesse 2000). For instance, punishment is a form of spite with potential return-benefits (Trivers 1985; Gardner & West 2004), and it can maintain cooperative behaviour in humans (Henrich & Boyd 2001) and animals (Clutton-Brock & Parker 1995) by imposing costs on cheaters and defectors. Human spite may be unique in that the benefits of an act of punishment can extend to others in the group, and that this 'altruistic punishment' (Boyd *et al.* 2003; Fehr & Fischbacher 2003; Johnstone & Bshary 2004), when paired with altruism, forms the basis of what has been called 'strong reciprocity' (Fehr & Gächter 2002; Gintis *et al.* 2003). Concern for the outcomes of others and a sense of fairness (Loewenstein *et al.* 1989; Fehr & Schmidt 1999; Bolton & Ockenfels 2000) are strong underlying motivations for human altruism and spite. According to Loewenstein *et al.* (1989) and Fehr & Schmidt (1999), the perception of unfairness leads individuals to correct inequitable gains, namely when another individual's gains are greater than one's own (disadvantageous inequity aversion), and when one's own gains are larger (advantageous inequity aversion).

It has been suggested by Brosnan *et al.* (2005) that one of humans' closest living relatives, the chimpanzee (*Pan troglodytes*), has a sense of fairness in that they are sensitive and averse to disadvantageous inequity. In their study, captive chimpanzees exchanged PVC tubes with a human experimenter for food. If another chimpanzee received a higher quality piece of food for equal effort, the focal subject would be more likely to reject the human experimenter's offer. These results require some qualification, however, as chimpanzees living in long-term groups almost never rejected food, and overall, chimpanzees did not show sensitivity to unfair offers based on differences in effort, whereas brown capuchins (*Cebus apella*) did (Brosnan & de Waal 2003). More critically, the application of the results of these studies to inequity aversion is confounded by the fact that the individuals could not directly correct inequitable outcomes; in fact, by rejecting 'unfair' offers, they were actually increasing disadvantageous inequity.

Silk *et al.* (2005) did allow chimpanzees to control outcomes for conspecifics and found that they did not take others' outcomes into consideration (i.e. they were not other regarding). Chimpanzees from two research centres were given two different apparatuses that allowed them to pull food towards themselves. When paired with conspecifics, the chimpanzees could choose between mutualism (1/1 payoff) and selfishness (1/0 payoff). Chimpanzees in this study were found to be not averse to inequity—they were just as likely to make a mutually beneficial choice as a selfish one. While this is a valuable contribution to the study of the evolution of fairness, Silk *et al.* tested for other-regarding behaviour in only one context (mutualism versus selfishness), and there was no

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Table 1. Payoff matrix for costs and benefits to two individuals (actor and recipient) as a result of the actor's actions (after Hamilton 1964).

		recipient	
		gains (+)	loses (−)
actor	gains (+)	mutualism (+,+)	selfishness (+, −)
	loses (−)	altruism (−,+)	spite (−, −)

direct demonstration that the chimpanzees understood or attended to the distal consequences of their choices.

We gave captive chimpanzees the opportunity to control outcomes for both themselves and conspecifics in three food-acquisition tasks designed to probe both advantageous and disadvantageous inequity aversion using the Hamilton payoff matrix, and we examined their understanding of the tasks. We used a modified version of a food-pulling procedure that Hauser *et al.* (2003) used on cotton-top tamarins (*Saguinus oedipus*). To make out-of-reach food accessible by pulling on a rope, the chimpanzees also made another piece of food move further away; they could, therefore, pull food towards *or* away from another individual. In the first study, chimpanzees could choose between mutualism and selfishness. If averse to advantageous inequity, chimpanzees should choose mutualism over selfishness; if averse to disadvantageous inequity, they should choose selfishly to prevent free-rider benefits to the other; if not averse to inequity, or if not other-regarding, then chimpanzees should show no preference. In the second study, chimpanzees were given a choice between altruism and weak spite (doing nothing led to the same outcome). If chimpanzees are not averse to disadvantageous inequity, they should make altruistic choices; if averse to disadvantageous inequity, they should be as likely to do nothing because to be spiteful as both would have the same outcomes; an absence of a preference would again suggest a lack of awareness—or indifference—towards the outcomes of another. In the final study, the competing choices were between altruism and true spite (here, unlike experiment 2, inaction would lead to a positive outcome for the other). If not averse to disadvantageous inequity, chimpanzees should either do nothing or make altruistic choices; if averse to disadvantageous inequity, they would choose spitefully; again, the absence of any preference would suggest that chimpanzees are not other-regarding or are not averse to perceived inequities.

2. EXPERIMENT 1: MUTUALISM AND SELFISHNESS

The purpose of experiment 1 was to determine if chimpanzees prefer to allow a recipient to receive an equivalent amount of food as the result of her actions (mutualism), or to choose to eat alone while denying the recipient any food (selfishness). Unlike Brosnan *et al.* (2005), but like Silk *et al.* (2005), chimpanzees were physically separated to reduce harassment-induced food-sharing (Wrangham 1975; Stevens & Stephens 2002; Stevens 2004), and they controlled inequitable outcomes directly.

Table 2. Test subjects and their kin relationships with recipients (degree of genetic relatedness, *r*).

		Brent		*Robert*	
actor	experiments	kinship	*r*	kinship	*r*
Corry	dropped	none	0	none	0
Dorien	1, 2, 3	none	0	none	0
Fifi	1, 2, 3	none	0	familial	0.5
Fraukje	2	none	0	none	0
Frodo	2	full-sib	0.5	familial	0.5
Gertruida	1, 2, 3	half-sib	0.25	familial	0.5
Jahaga	2, 3	half-sib	0.25	familial	0.5
Natascha	2	maternal	0.5	none	0
Patrick	1, 2, 3	half-sib	0.25	familial	0.5
Riet	2	none	0	none	0
Sandra	2	half-sib	0.25	familial	0.5
Ulla	1, 2, 3	none	0	none	0

(a) *Methods*

The experimental design was loosely based on Hauser *et al.* (2003) in that individuals could either 'share' food by pulling it towards themselves and/or another individual or do nothing. Our design was exceptional because in addition to the option of doing nothing, in each trial an individual could choose between two actions that had opposing (positive or negative) consequences for another individual. The strengths of this design are that it provides individuals with more options and allows a direct assessment of mutually incompatible behavioural strategies. Silk *et al.* (2005) used a similar design, but presented a different amount of food on the two choices, resulting in a prepotent bias towards the side with the larger amount of food in six out of seven chimpanzees during pre-testing.

(i) *Subjects*

Subjects were socially housed chimpanzees at the Wolfgang Koehler Primate Research Centre. All subjects had taken part in a variety of tests of physical and social cognition, including a cooperative task involving rope pulling (Melis *et al.* in press), but the testing paradigm for this study was novel to the subjects. Subjects had *ad libitum* access to water and were not food deprived. They were divided into two groups: actors and recipients. A member from each of the extremes of the social hierarchy—the alpha male and a 5-year-old male—were selected as recipients to draw out the widest possible range of behaviours from the actors. The actors, who were the focal individuals of the study, were three adult females, two adolescent females and one adolescent male (for details, see table 2). (One adult female was later excluded from the analysis because she failed to demonstrate an understanding of the apparatus.) Actors were tested with each recipient.

(ii) *Apparatus and setup*

The test apparatus consisted of two tables on wheels (figure 1) standing outside the chimpanzees' rooms in the human corridor. The tables were 2 m apart and were connected by a single rope, which ran through pulleys behind them. Pulling one of the rope ends pulled that table closer while at the same time pulling the other table away and causing the other rope end to fall out of reach. One table, the accessible table, overlapped with the actor's room and the recipient's room to the actor's right. The other

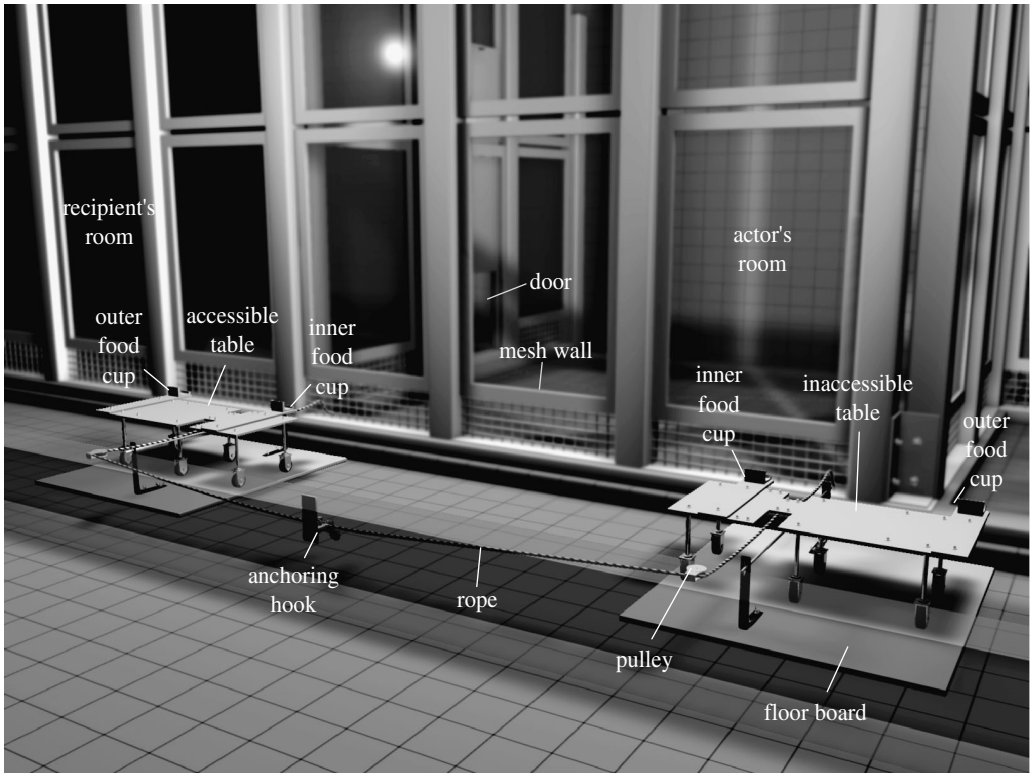

Figure 1. Diagram of the apparatus and testing rooms. The control room (not shown) is to the right of the image.

table—the inaccessible table—overlapped with the actor's room and an empty space to the actor's left. There were two plastic cups on each of the two tables and food (quartered bananas) could be visibly placed in these cups. The inner cups of both tables were the only ones that were directly accessible from the actor's room when the tables were pulled closer. The outer cup on the accessible table was accessible from the recipient's room, and the outer cup on the inaccessible table (to the left) was never accessible.

(iii) *Procedure*

All chimpanzees were first familiarized with the test apparatus with two unconnected ropes, allowing both tables to be pulled towards the mesh wall. For all other trials, a single rope connected the tables, allowing only one table to be pulled within reach. For each trial, the experimenter baited the cups then centred the actor between the two ropes using small food incentives. Once outside the sleeping room, the experimenter signalled that the trial would begin and released the rope from an anchoring hook. Trials ended when the actor pulled one table completely to the mesh wall, or after 60 s if he or she made no choice.

Actors were tested separately with each recipient (order counterbalanced across subjects). For each recipient, they were given a session consisting of both knowledge probe and control trials both before and after the test session proper. See table 3 for details.

Preference probe. All sessions began with six preference probe trials, the purpose of which was to measure side preferences independently of the position of another individual (the second chimpanzee was in the recipient's room during test sessions and in the control room in knowledge probe and control trials). The inner cups of both tables were baited, therefore, the actor received the same payoff for either choice (figure 2*a*).

Knowledge probe. The purpose of the knowledge probe was to determine whether chimpanzees understood the consequences of their choices (figure 2*b*). All four cups were baited and the door between the actor's and vacant recipient's room was open. By choosing the accessible table, the actor could reach the food in both the outer and inner cups, whereas by choosing the inaccessible table, the actor could only reach the food in that inner cup. Assuming that chimpanzees were motivated to maximize the amount of food they received, they were expected to choose the accessible table for a return of two banana pieces as opposed to one piece for choosing the inaccessible table. Six knowledge probes were given randomly with control trials (with the stipulation of no more than four consecutive trials of each condition) on separate days both before and after the test proper.

Control. The control provided a direct comparison to the test (figure 2*c*). All four cups were baited and the door to the vacant recipient's room was closed, therefore, regardless of choice the actor could only receive one banana piece. Since the recipient was in the control room and was, therefore, not in a position to reach the food, the actor's choice was not influenced by payoffs to the recipient. Choices were, therefore, expected to be random. There were six control trials randomly interspersed with knowledge probe trials on separate days both before and after the test session.

Test. In the test (figure 2*d*), the second chimpanzee was in the recipient's room and could reach the outer cup of the accessible table if this were chosen by the actor. The actor could only reach the inner cups of either table. All four cups were baited. Pulling the accessible table gave both actor and recipient one banana piece each (mutualism); pulling the inaccessible table resulted in only the actor getting food (selfishness). There were twelve test trials. At the end of the session, the door separating

Table 3. Conditions for all three experiments. The numbers of trials per condition are given; for experiment 3, these are the mean numbers of trials to reach criterion. Preference probes were given in experiments 1 and 2 and warm-up trials were used in experiment 3. Payoff/trial shows the maximum number of banana pieces the actor could access in a trial.

		experiment 1		experiment 2		experiment 3	
session	conditions	number of trials	payoff/trial	number of trials	payoff/trial	number of trials	payoff/trial
familiarization		4	3	—	—	—	—
pre-test (1st recipient)	preference probe/warm-up	6	1	6	1	3	1
	knowledge probe	6	2	6	1	6	1
	control	6	1	6	0	6	0
test (1st recipient)	preference probe/warm-up	6	1	6	1	2	1
	test	12	1	12	0	12	0
post-test (1st recipient)	preference probe/warm-up	6	1	6	1	2	1
	knowledge probe	6	2	6	1	6	1
	control	6	1	6	0	6	0
test (2nd recipient)	preference probe/warm-up	6	1	6	1	2	1
	test	12	1	12	0	12	0
post-test (2nd recipient)	preference probe/warm-up	6	1	6	1	2	1
	knowledge probe	6	2	6	1	6	1
	control	6	1	6	0	6	0

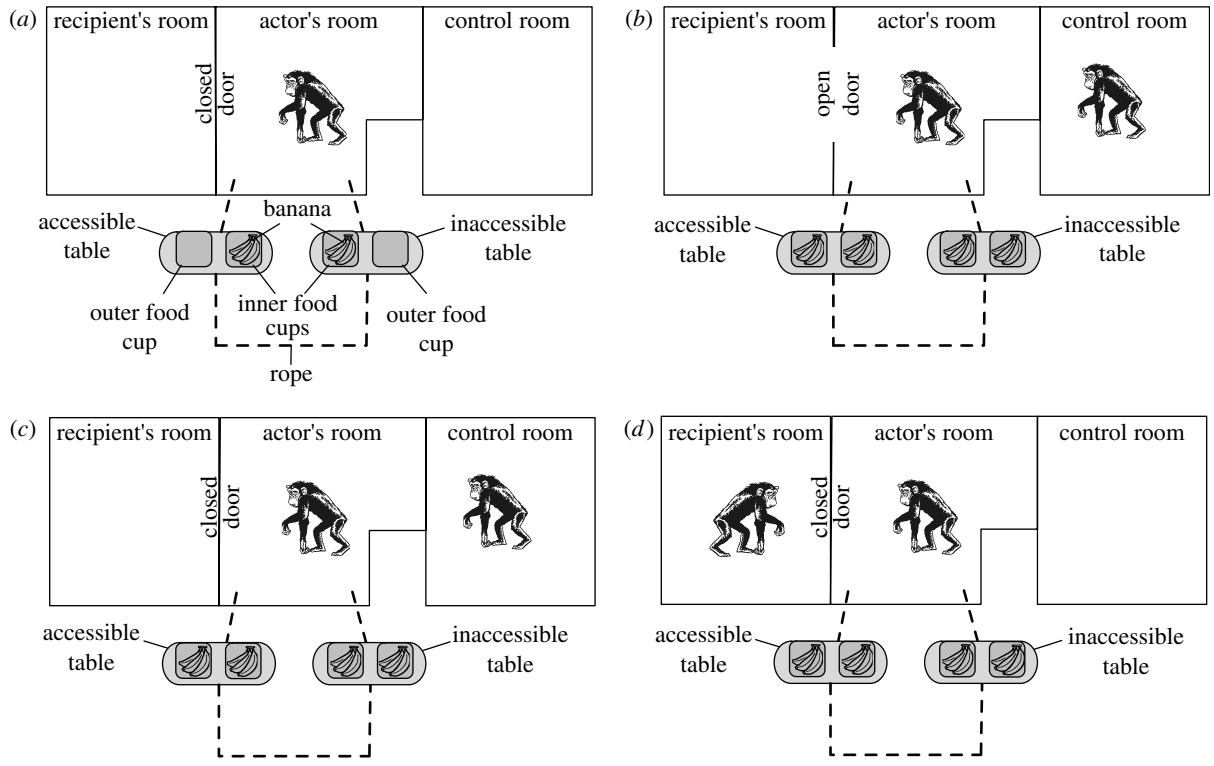

Figure 2. Experiment 1 conditions. (*a*) Preference probe: the door to the recipient's room is closed, the second chimpanzee can be in either the recipient's room or the control room and the two inner cups are baited. (*b*) Knowledge probe: the door to the vacant recipient's room is open and all four cups are baited. (*c*) Control: the door to the vacant recipient's room is closed and all four cups are baited. (*d*) Test: the second chimpanzee is in the recipient's room and all four cups are baited.

the actor and recipient was opened and their interactions were filmed for 5 min.

(iv) *Coding and analysis*

All trials were filmed with four video cameras and recorded on a Sony DV-Walkman outside the sleeping room. Which table, if any, was pulled by the actor was coded *in situ* by the first author. If a pull was not sufficient for the food cups to be reached, or if the force was excessive and caused the banana to fall off, these were coded as non-choices. Interobserver reliability comparisons using Kappa's coefficients were performed on a randomly chosen 20% of the trials, with the second coder blind to hypotheses. Interobserver reliability for side chosen was perfect (Cohen's $\kappa = 1.0$). All values reported are mean $\pm$ s.d.

All analyses were done on SPSS 11.5. Differences across sessions, recipient's identity, order effect and kinship were

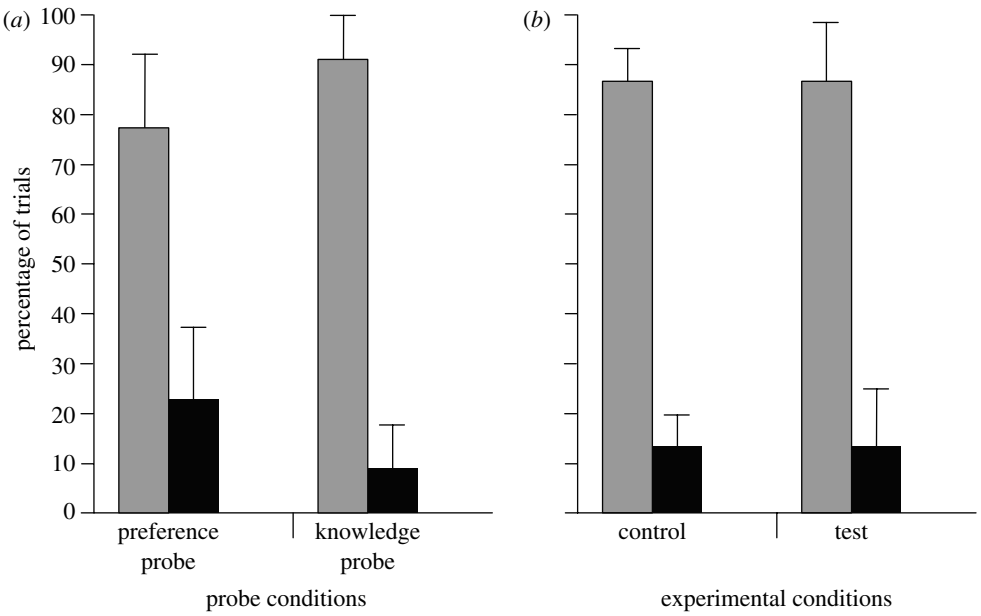

Figure 3. Percentage of trials in experiment 1 (mutualism and selfishness) in which chimpanzees pulled the accessible table (grey bars) and the inaccessible table (black bars).

included as factors in three-way ANOVAs; data were collapsed when results were non-significant. *t*-tests were used for analysing whether the chimpanzees made a choice (dependent measure) in the control and test trials and when comparing choices made within a condition. Factors analysed in the two-way repeated-measures ANOVAs (general linear model) were condition × choice. The Greenhouse and Geisser correction was used if the sphericity assumption was violated (Howell 2002).

(b) *Results*

Neither session, recipient's identity, nor the order of testing had any effect on choice; data were therefore collapsed. In other words, whether the recipient was a low-ranking male or the alpha male had no bearing on the choices made, nor did choices change across session.

In the knowledge probe, chimpanzees preferred the accessible table to the inaccessible table ($t_4 = 10.91$, $p < 0.001$), demonstrating an understanding that their choice made food available in the recipient's room (figure 3). Actors had a preference for the accessible table over the inaccessible table in the preference probe as well ($t_4 = 4.30$, $p = 0.01$), though less so than in the knowledge probe ($t_4 = 3.07$, $p = 0.04$).

The primary result was that there was no difference between control and test in the choices made (condition × choice $F_{1,4} < 0.001$, $p = 1.0$), and the main effect of choice revealed an overall preference for the accessible table ($F_{1,4} = 270.21$, $p < 0.001$). The presence or absence of a recipient did not influence the actors' choices in any way.

In the five-minute reunions following a test session, there were no obvious differences in social interactions relative to behaviour normally exhibited when the chimpanzees are routinely moved into and out of the different rooms by keepers and scientists.

(c) *Discussion*

The fact the chimpanzee actors primarily chose the accessible table in the knowledge probe trials (and more often than in the preference probe) suggests that they knew how the apparatus worked: specifically, they knew that their actions made food available in the adjacent room. They also predominantly chose the accessible table in the test—which made food available to the recipient—suggesting the possibility that they chose mutualistically. However, this same preference for the accessible table was also apparent in the control (as well as the preference probe)—when the recipient was not in the recipient's room at all—thus raising the possibility of a general side bias towards the recipient's room (unfortunately, for physical reasons we could not counterbalance side in this study). Despite this possible side bias, what can be said with confidence is that the chimpanzees in this study did not pull especially often to keep food away from the recipient (they were not selfish). In other words, they were not averse to disadvantageous inequity. These results agree with those of Silk *et al.* (2005).

3. EXPERIMENT 2: ALTRUISM AND WEAK SPITE

In experiment 2 we eliminated payoffs to the actor. This allowed us to determine whether chimpanzees would show a preference for altruism (no aversion to advantageous inequity) or spite (disadvantageous inequity aversion). Spite in this study was weak in that doing nothing would also result in the recipient not getting any food, and at no cost to the actor (Gadagkar 1993).

(a) *Methods*

Eleven chimpanzees took part in experiment 2. These included the original adult females and adolescent male from experiment 1 in addition to four other adult females, one adolescent female and one adolescent male. The testing procedure was identical to that of experiment 1, with one modification (table 3). Instead of four banana pieces in the four cups, there were only two banana pieces, which were placed in the outer cups (except in the preference probe, which had two banana pieces in the inner cups, as before). Latency to make a choice (number of seconds from the moment the rope was released to

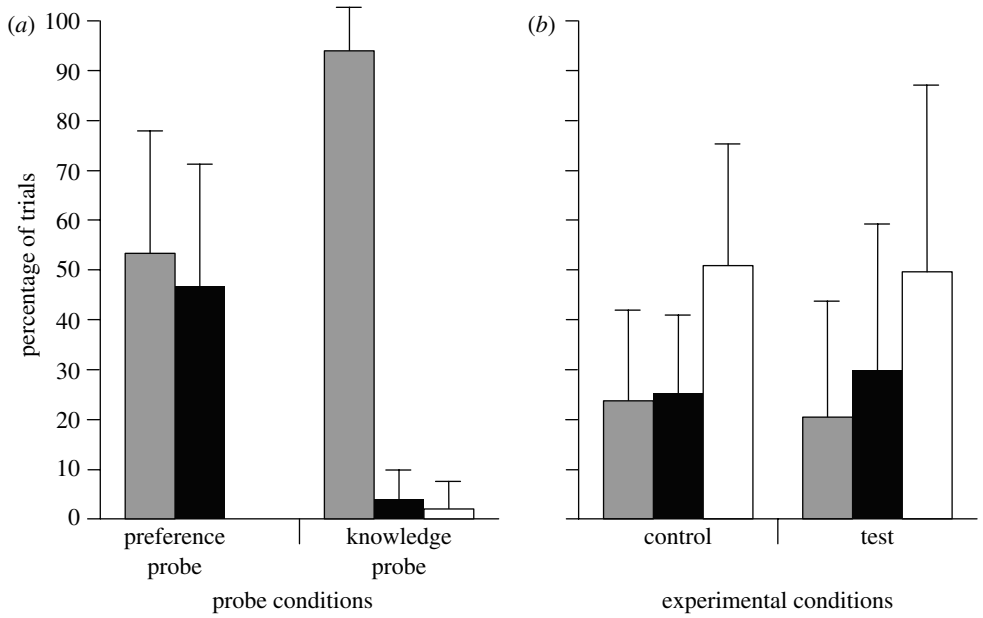

Figure 4. Percentage of trials in experiment 2 (altruism and weak spite) in which chimpanzees pulled the accessible table (grey bars), the inaccessible table (black bars), and made no choice all (white bars).

when the actor first started pulling) was also recorded to measure motivation or certainty. Interobserver reliabilities were very high (Cohen's $\kappa = 0.98$ for choice, Pearson's $r = 0.98$ for latency).

(b) *Results*

As in experiment 1, there was no effect of order or recipient's identity on any of the analyses; data were therefore collapsed.

In the knowledge probe, actors had a preference for the accessible table over the inaccessible table ($t_{10} = 22.69$, $p < 0.001$), again showing an understanding of the consequences of this choice (figure 4). There was no preference for either table in the preference probe ($t_{10} = 0.46$, $p = 0.66$) and the preference for the accessible table was weaker in the preference probe than in the knowledge probe ($t_{10} = 7.16$, $p < 0.001$).

Chimpanzees chose to do nothing equally often in the test and the control ($t_{10} = 0.17$, $p = 0.87$). There was also no difference between test and control in the choices the actors made when they did choose (condition × choice $F_{1,10} = 0.33$, $p = 0.58$). Thus, chimpanzees were as likely to do nothing whether there was a recipient or not, and when they did choose, they did so randomly. Chimpanzees took the same amount of time to choose in the control (12.1 ± 9.7 s) and test (6.9 ± 3.5 s; $t_{10} = 1.69$, $p = 0.12$) and there was no difference in the latency to pull food towards (8.6 ± 3.1 s) or away from (5.1 ± 4.9 s) a recipient during the test ($t_5 = 1.24$, $p = 0.27$).

Interestingly, kinship with the recipient—here defined as full-sib, maternal and filial—influenced whether the actor made a choice or not. Kin made fewer choices in the test than controls ($F_{1,9} = 18.96$, $p = 0.002$ for the juvenile male; $F_{1,9} = 8.11$, $p = 0.02$ for the alpha male), thus not helping kin. Altruistic and spiteful choices were not affected ($F_{1,9} = 0.01$, $p = 0.98$ for the juvenile and $F_{1,9} = 0.04$, $p = 0.84$ for the alpha male). When reunited, the recipient did not engage in any interactions with the actor that could be regarded as 'grateful' or 'punitive'.

(c) *Discussion*

In experiment 2, the presence of a recipient had little effect on the actions of chimpanzees. Chimpanzees were neither altruistic nor spiteful. Chimpanzees made half as many choices when they did not receive food as opposed to when they did, regardless of the effect on a second individual. It is likely that chimpanzees were not other-regarding, though the possibility that they were averse to disadvantageous inequity (passive spite) cannot be ruled out. Unlike experiment 1, there was no side bias: chimpanzees chose randomly when their choices were not rewarded. When a choice was made, it was influenced by personal gain; the presence of—and payoffs to—another individual had no influence on the actor's choices. That the actors almost always chose the accessible table when they themselves could get the food in the knowledge probe trials indicates that they knew that their actions would make food accessible to the recipient when he was there; on the whole, they just chose not to. Contrary to what would be expected from kin selection theory (Hamilton 1964), kinship had no effect on altruism or weak spite, though kin were less likely to make any choice at all than were non-kin.

The opportunity for altruism or spite did not influence the motivation or decision-making latencies of chimpanzees.

4. EXPERIMENT 3: ALTRUISM AND SPITE

The previous experiment did not allow for 'true' spite in that the recipient could do nothing and still deny the recipient food. In experiment 3, we gave the chimpanzees the opportunity to be truly spiteful. If the actor did nothing, the recipient automatically received the banana after a set time interval. Only by pulling the inaccessible table could the actor prevent the recipient from receiving food. Therefore, individuals averse to disadvantageous inequity would be spiteful, individuals with no aversion to disadvantageous inequity would either do nothing or choose altruistically, and individuals lacking other-regard would show no clear preference.

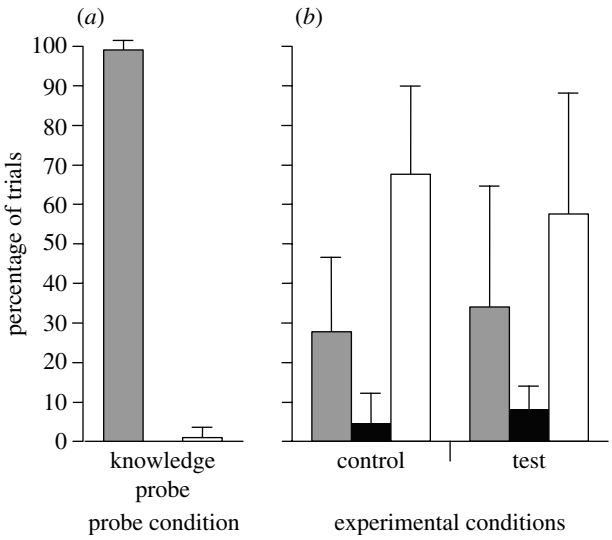

Figure 5. Percentage of trials in experiment 3 (altruism and spite) in which chimpanzees pulled the accessible table (grey bars), the inaccessible table (black bars), and made no choice all (white bars).

(a) *Methods*

Six chimpanzees (two adult females, three adolescent females and one adolescent male) took part in experiment 3. All had taken part in experiment 2, and with the exception of one adolescent female, in experiment 1 as well. It was not possible to maintain recipient order from the previous studies; however, since order had not been a factor, this was not considered problematic. The set-up was similar to experiments 1 and 2, with one primary change. A block-and-tackle system allowed the experimenter, from outside the testing rooms, to draw the accessible table towards the mesh wall if the actor did not make a choice after 15 s. This 'ghost pull' took 10 s and the actor could still choose during this interval. Only one banana piece, which could only be reached from the recipient's room, was used in all conditions to eliminate the possibility of low-probability selfishness.

Actors and recipients were first familiarized with the new set-up by giving them access to no ropes, and the inaccessible table rope alone. They quickly learned (24 ± 3.5 trials) that by doing nothing, the accessible table would come to the recipient's room and that by pulling the inaccessible table, the food on the accessible table was pulled away. Instead of preference probe trials, warm-up trials, in which only the inaccessible table rope was available, were given at the start of each session (or at the end if that was not possible) to determine if actors remembered what they had learned in the familiarization session. Criterion was set at two consecutive non-pulls. Knowledge probe, control and test trials were the same as in the previous two experiments, with the exception of the use of one banana piece (table 3). Interobserver reliabilities were very high (Cohen's $\kappa = 1.0$ for choice, Pearson's $r = 0.95$ for latency).

(b) *Results*

Order and recipient identity had no effect. Chimpanzees again demonstrated an understanding of the consequences of choosing the accessible table, pulling it more than the inaccessible table in the knowledge probe ($t_5 = 106.14$, $p < 0.001$; figure 5). They also demonstrated some understanding of the consequences of choosing the inaccessible table, needing only 2.6 ± 1.1 warm-up trials to avoid pulling that table in two consecutive trials.

Actors were just as likely to make no choice in both the test and control ($t_5 = 0.87$, $p = 0.43$), resulting in the accessible table being pulled to the recipient's room by the experimenter (figure 5). As in the first two studies, whether a recipient was present or not did not influence the choices made by the actors (condition × choice $F_{1,5} = 0.02$, $p = 0.88$). Chimpanzees were quicker to choose in the test (10.4 ± 5.0 s) than in the control (17.3 ± 3.9 s; $t_4 = 2.71$, $p = 0.05$). However, there was no difference in how quickly chimpanzees chose to be spiteful or altruistic ($t_4 = 0.88$, $p = 0.43$).

Kinship had no effect on whether or not the actors did nothing when paired with the alpha male ($F_{1,4} = 0.03$, $p = 0.96$), or pulled food either towards or away from him ($F_{1,4} = 0.30$, $p = 0.61$). The adolescent recipient was not paired with any kin. During the reunions, recipients and actors did not engage in any interactions that were unique in any way.

Two of the six actors showed some possible signs of altruism. One was an adolescent female who preferentially chose the accessible table for both the adolescent recipient ($\chi^2_2 = 6.35$, $p = 0.04$) and the adult recipient ($\chi^2_2 = 15.00$, $p < 0.001$), and an adult female who did the same, but only for the adolescent recipient ($\chi^2_2 = 11.25$, $p = 0.002$). However, it is notable that these individuals were also the only two individuals who begged from, or harassed, the recipients after pulling the table towards them—suggesting the possibility that they assessed the probability of getting food for themselves to be higher if they pulled the food towards the recipient than when the recipient received the food passively.

Collectively, there were more first trial choices of the accessible table in the test than in the control ($t_5 = 4.55$, $p = 0.006$), but there was no significant decline in altruism within test sessions ($F_{1,10} = 1.16$, $p = 0.307$).

(c) *Discussion*

In experiment 3, there was little evidence for inequity aversion; chimpanzees could have eliminated disadvantageous inequity by making a spiteful choice, and they failed to do so. These results by themselves cannot distinguish between lack of other-regard and tolerance of disadvantageous inequity aversion through inaction. The recipient had little effect on the choices of the actor. When chimpanzees did not get food for their efforts, they most frequently did nothing. When they did choose, they chose equally in the control and test.

Two individuals appeared to have been altruistic, one towards both recipients and one towards the lower ranking recipient only, but since they begged from or harassed these recipients immediately afterwards, the motivations were probably misguidedly selfish (across the three studies, recipients never once passed food through the mesh to the actor in the 272 trials in which they received food).

(d) *Comparison of the three experiments*

Figure 6 presents the overall results from the three experiments. Chimpanzees were influenced by personal payoffs: they were less likely to do nothing when they directly benefited (experiment 1) as opposed to when they

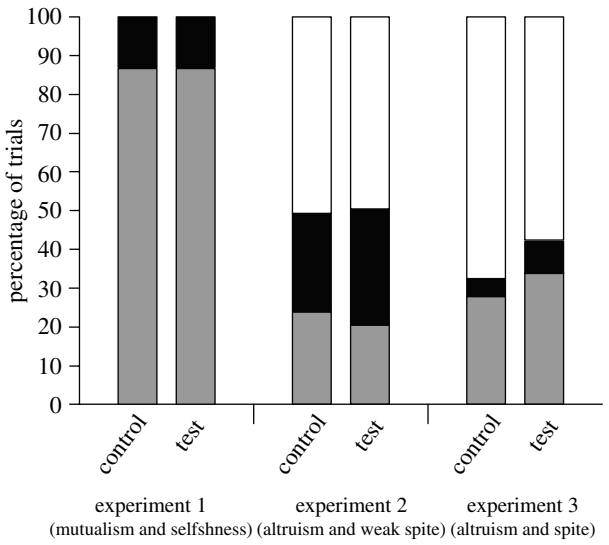

Figure 6. Percentage of trials in all three experiments in which chimpanzees pulled the accessible table (grey bars), the inaccessible table (black bars), and made no choice all (white bars) when alone (control) and when with a recipient (test).

did not benefit (experiments 2 and 3; $F_{2,8}=22.18$, $p=0.001$). However, they were not influenced by payoffs to another individual: although they chose the accessible table more often in experiment 1 (mutualism) than in the other two experiments (altruism) ($F_{1,5}=33.89$, $p<0.001$), they were as likely to do so in the control as in the test ($F_{2,8}=1.20$, $p=0.35$). Furthermore, chimpanzees did not show any preference for either the accessible or inaccessible table in experiments 2 and 3 ($F_{1,4}=0.60$, $p=0.48$), and spite (inaccessible table) did not increase between experiments 2 and 3 as a result of making it the only means for preventing another chimpanzee from getting food ($F_{1,4}=1.02$, $p=0.37$). (The effect size (partial eta square, η_p^2) was small for experiments 2 and 3 ($\eta_p^2=0.032$ and 0.005, respectively), indicating that the results of the two studies are directly comparable despite the different sample sizes, and that larger sample sizes would not have produced significant results.) It is clear that neither the presence (test) nor absence (control) of the recipient had any overall effect on subjects' choices across the three experiments.

The declines in actors' overall participation across the three experiments, as well as the decline of altruistic choices in the absence of personal gain, show that making a choice was influenced by personal outcomes irrespective of gains or losses to other chimpanzees. Since not choosing could be interpreted as passively spiteful (disadvantageous inequity aversion) in experiment 2 and as passively altruistic (absence of disadvantageous inequity aversion) in experiment 3, the common denominator was mere passivity (inequity indifference). In the absence of any possibility—no matter how small—of getting food, chimpanzees preferred to do nothing, regardless of how this affected another chimpanzee.

5. GENERAL DISCUSSION

The results of these three experiments suggest that, in a food-acquisition context, chimpanzees are essentially indifferent to differential payoffs for a conspecific. In the first experiment, actors who could choose between mutualistic (not averse to disadvantageous inequity) and selfish (disadvantageous inequity aversion) payoffs did not preferentially choose selfishly and thereby prevent the recipient from receiving free-rider benefits. In the second experiment, when actors did not receive any payoff for their efforts, pulling food towards the recipient dropped from over 85% to 20%. (Kin were less likely to make any choice at all than non-kin.) When they did make a choice, chimpanzees were as likely to pull food towards the recipient as away—regardless of whether the recipient was the alpha male or a low-ranking juvenile male—and the presence or absence of a recipient did not cause any differences in behaviour; they were either averse to disadvantageous inequity and chose to do nothing as a means of preventing it (passively spiteful), or they were indifferent to the outcome to the other individual. In the third experiment, when given an opportunity to actively prevent the recipient from acquiring food, actors mostly did nothing—and, again, when they did act, they did so similarly in the test and control; the chimpanzees were either not averse to disadvantageous inequity and chose to do nothing to allow it (passively altruistic), or they were indifferent. There was some evidence for altruism in the first trials of tests but not controls, but the decline in altruism did not persist across the whole session. The only clear cases of altruism were in two individuals who appeared to be begging or harassing in the unfulfilled hope that the recipient would share the food.

Given the absence of opportunities for reciprocity, it is perhaps not surprising to find no clear evidence of altruism in these studies; it remains to be seen whether chimpanzees would be altruistic in a reciprocal exchange like that of Hauser *et al.* (2003). It is perhaps surprising, however, that spite was also completely absent; if chimpanzees are averse to disadvantageous inequity, as suggested by Brosnan *et al.* (2005), it seems likely that they should have acted to eliminate unfair outcomes.

Considering all three experiments together leads us to conclude that chimpanzees are not other-regarding and are indifferent to inequity in a food-acquisition context. These results thus contrast with those of Brosnan *et al.* (2005), who suggest that some of the chimpanzees in their study (those from an unstable social group) were averse to inequity. However, their conclusion is based on one experiment in which chimpanzees paired with a group member in the same cage could either refuse to exchange a piece of PVC tubing with a human experimenter for food, or refuse food outright when the partner received a higher quality reward. Fourteen out of twenty chimpanzees in their study refused food less than 2% of the time, suggesting either high tolerance for inequity, as the authors suggest, or indifference to it. The design of our study—like that of Silk *et al.* (2005)—allowed chimpanzees to directly control unfair outcomes and is, therefore, more appropriate to the question of inequity aversion as framed by Fehr & Schmidt (1999) than the market-like exchange with a human intermediary used by Brosnan *et al.* (2005). Our results—like those of Silk *et al.* (2005) using two different apparatuses on two groups of chimpanzees—suggest that in food-acquisition situations in which they control outcomes in relation to conspecifics, chimpanzees are almost totally self regarding. Whether this is a general characteristic or is restricted to specific situations is still to be determined. For instance, humans

report being angry when receiving unfair offers, and that this anger motivates spite (Pillutla & Murnighan 1996). There was no evidence of anger in the chimpanzees; it is possible that this test did not tap into their motivational psychology, or perhaps they did not fully understand the nature of the apparatus. Future tests will be needed to rule out these potential difficulties.

One possible explanation for the absence of inequity aversion in the current study is that chimpanzees may be self-regarding utility maximizers. Rather than compare relative gains and losses, chimpanzees may focus simply on their own gains and losses; when there is no material benefit or cost to themselves, they have no interest in payoffs to others. Being self-regarding is, of course, the natural case in evolution, and humans are self-regarding in many situations as well. However, humans frequently compare themselves to others, sometimes to their detriment, for instance incurring losses to make someone else suffer a greater loss in an ultimatum game. However, regard for others—either positively or negatively—would seem to be an important component of the types of cooperation, and competition, seen in human societies (Fehr & Schmidt 1999). The implication is thus that many features of cooperation, sense of fairness, morality and so forth that typify human social interactions have arisen no sooner than the last 6 million years of human evolution.

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