

Chimpanzees are indifferent to the welfare of unrelated group members

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Humans are an unusually prosocial species—we vote, give blood, recycle, give tithes and punish violators of social norms. Experimental evidence indicates that people willingly incur costs to help strangers in anonymous one-shot interactions^{1,2}, and that altruistic behaviour is motivated, at least in part, by empathy and concern for the welfare of others (hereafter referred to as other-regarding preferences)^{1–3}. In contrast, cooperative behaviour in non-human primates is mainly limited to kin and reciprocating partners, and is virtually never extended to unfamiliar individuals⁴. Here we present experimental tests of the existence of other-regarding preferences in non-human primates, and show that chimpanzees (*Pan troglodytes*) do not take advantage of opportunities to deliver benefits to familiar individuals at no material cost to themselves, suggesting that chimpanzee behaviour is not motivated by other-regarding preferences. Chimpanzees are among the primates most likely to demonstrate prosocial behaviours. They participate in a variety of collective activities, including territorial patrols, coalitionary aggression, cooperative hunting, food sharing and joint mate guarding^{5–12}. Consolation of victims of aggression¹³ and anecdotal accounts of solicitous treatment of injured individuals suggest that chimpanzees may feel empathy^{14,15}. Chimpanzees sometimes reject exchanges in which they receive less valuable rewards than others, which may be one element of a ‘sense of fairness’, but there is no evidence that they are averse to interactions in which they benefit more than others^{16–18}.

We conducted two experiments to assess the existence of other-regarding preferences in two different populations of chimpanzees. In both experiments, subjects were able to deliver benefits to others at no cost to themselves. Subjects were presented with an apparatus that gave them a choice between two alternatives. If the subject (hereafter referred to as the actor) chose option 1, the actor obtained a food reward and another chimpanzee simultaneously received an identical reward (hereafter referred to as the ‘1/1 option’). If the actor chose option 2, the actor obtained the same size and type of food reward, but no food reward was delivered to the other chimpanzee (the ‘1/0 option’). As a control, actors were presented with exactly the same reward options when there was no other chimpanzee present.

If chimpanzees have other-regarding preferences, they will choose the 1/1 option more often when another chimpanzee is present to receive the reward than when they are alone. If chimpanzees are indifferent to the welfare of others, the presence of a potential recipient will have no impact on their choices. (Alternatively, chimpanzees might have ‘antisocial’ preferences. If so, they would choose the 1/1 option less often when another chimpanzee is present than when they are alone.)

This experimental setup maximizes the likelihood of observing other-regarding behaviour in two ways. First, actors can provide benefits to others at no cost to themselves, so other-regarding sentiments do not compete with selfish motives to obtain rewards. Second, actors interact with familiar group members. Prosocial responses in this experiment might occur because chimpanzees favour those that they cooperate with outside the context of this experiment, even if they lack other-regarding sentiments. However, the absence of prosocial behaviour in this experimental situation would provide strong evidence for the lack of other-regarding sentiments.

Our experiments were conducted at two different study sites. In Louisiana, our subjects were seven unrelated adults that have been living together for at least 15 yr, and have participated regularly in cognitive and behavioural tests since they were 3–4 yr old¹⁹. In Texas, our subjects were drawn from six stable social groups originally formed in 1978. We tested 11 same-sex pairs of adults drawn from the same social groups. These animals were well socialized, but had no experience in cognitive or behavioural testing before the present study began.

The physical layout of the testing areas differed, so we designed different apparatuses for each site (see Supplementary Information). At both sites, subjects were clearly able to view each other, the testing apparatus, the baiting process, the distribution of food rewards, and the consumption of food rewards. After the actor selected one option (by pulling a rope or hose), both were able to obtain food rewards (if present) from the trays closest to them. All trials were videotaped and coded by independent observers. For all measures, high levels of inter-observer reliability were obtained (Cohen’s kappa ≥ 0.98).

At both sites, the subjects were familiarized individually with the apparatus before testing. Pre-testing established that the chimpanzees understood how to operate the apparatus to obtain food rewards for themselves and that they were highly motivated to do so. Pre-testing also demonstrated that the chimpanzees understood that they would obtain food only from the near tray (Louisiana) or their own side (Texas).

In Louisiana, actors chose the 1/1 option on average 56% (s.d. = 8.2) of the time when they were alone, and 58% (s.d. = 6.3) of the time when another chimpanzee was present. None of the seven chimpanzees chose the 1/1 option significantly more often when another chimpanzee was present than when they were alone (Fig. 1). A power analysis indicates that sample sizes were large enough to detect even modest differences between the two conditions. If actors were 15% more likely to choose the 1/1 option when another chimpanzee was present than when they were alone, the chance of

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failing to detect a difference of this magnitude in any of the subjects is just 3.5%.

Multivariate analyses of the Louisiana data set indicate that the likelihood of choosing the 1/1 option was more strongly influenced by the position of the 1/1 option than by the presence of another chimpanzee (Table 1). The odds ratios indicate that actors were 95% more likely to choose the 1/1 option when it was presented on the right side than on the left side of the apparatus ($P < 0.001$). In contrast, the presence of another chimpanzee increased the chance of choosing the 1/1 option by only 11% ($P < 0.580$). The chimpanzees were more likely to choose the 1/1 option as the experiment progressed, but this increase was not influenced by the presence of another chimpanzee, and the interaction between trial block and condition (partner present/absent) was nonsignificant (see Supplementary Table 6).

In Texas, not all subjects responded on every trial and not all subjects completed all sessions. Therefore, we computed the proportion of 1/1 choices by dividing the number of 1/1 choices by the total number of responses. On average, actors chose the 1/1 option 48% of the time (s.d. = 7.2) when they were alone and 48% of the time (s.d. = 16.7) when another chimpanzee was present. None of the actors chose the 1/1 option significantly more often when another chimpanzee was present than when they were alone (Fig. 2). The chance of failing to detect a 15% difference between the partner present and partner absent conditions in any of these subjects is just 0.2%. (When we combine subjects from both sites, the chance that we would fail to detect at least one prosocial chimpanzee is only 0.006%.)

Again, the likelihood of choosing the 1/1 option was more strongly affected by the actors position than by the presence of another chimpanzee in the adjoining enclosure. The probability of choosing the 1/1 option was 56% greater when the 1/1 option was positioned in the upper tray than the lower tray ($P < 0.001$), whereas the presence of a potential recipient increased the probability of choosing the 1/1 option by only 11% ($P < 0.40$). There was no significant change in the likelihood of choosing the 1/1 option across sessions.

In trials in which only one tray was baited on the actor's side (1/0 or 1/1), actors chose the option that provided food to themselves on 92% (105 out of 114; 94 no response) of all trials when they were alone and 94% (106 out of 113; 79 no response) of all trials when another chimpanzee was present. Thus, actors were attending closely

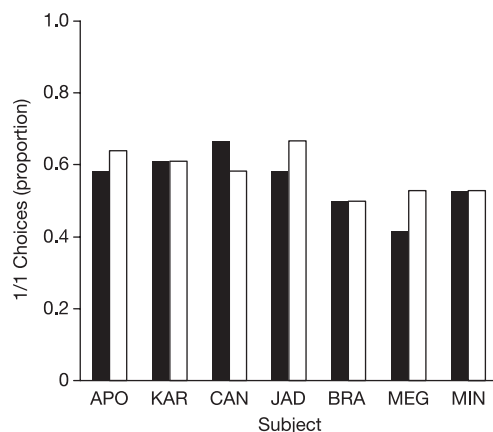


Figure 1 | Proportion of 1/1 choices made by Louisiana subjects. Black bars represent sessions in which the subject was alone. White bars represent sessions in which another chimpanzee was present in the opposite enclosure. All subjects completed 36 single trial sessions for each condition. None of the subjects chose the 1/1 option significantly more often when another chimpanzee was present than when they were alone (Fisher's exact test: APO, $P = 0.809$; KAR, $P = 1.000$; CAN, $P = 0.627$; JAD, $P = 0.479$; BRA, $P = 1.000$; MEG, $P = 0.479$; MIN, $P = 1.000$).

Table 1 | Factors that influence the likelihood of choosing the 1/1 option

Parameter*	Estimate	Standard error	t-ratio	P-value	Odds ratio	95% bounds	
						Upper	Lower
Louisiana							
Condition	0.102	0.185	0.553	0.580	1.107	1.590	0.771
Position	0.666	0.185	3.602	<0.001	1.946	2.796	1.355
Trial block	0.117	0.054	2.162	0.031	1.124	1.251	1.011
Texas							
Condition	0.108	0.128	0.844	0.398	1.114	1.431	0.867
Position	0.445	0.125	3.572	<0.001	1.561	1.993	1.223
Session	-0.006	0.024	-0.250	0.803	0.994	1.041	0.949

* The two logistic regression models include dummy variables for individuals as predictors, in addition to the predictor variables shown (see Supplementary Information for details). Variables are coded so that the odds ratios would exceed 1 for condition if actors were more likely to choose the 1/1 option when a potential recipient was present than when they were alone. Position was coded so that odds ratios >1 indicate that actors were more likely to choose the 1/1 option when it was positioned on the right side (Louisiana) or the top tray (Texas) of the apparatus. Finally, odds ratios for trial block (in Louisiana) and session (Texas) would exceed 1 if actors were more likely to choose the 1/1 option as the experiment progressed.

to the distribution of payoffs for themselves, not picking options at random.

It is possible that the chimpanzees in our experiments understood how to obtain food for themselves but not that they were responsible for delivering rewards to the chimpanzee in the adjoining enclosure. Several factors mitigate against this alternative. Chimpanzees are adept at manipulating push/pull apparatuses like the one used in Louisiana, and understand the necessity of their actions in generating contingent effects²⁰. The bar-pull apparatus used in Texas was similar to apparatuses that have been widely used in studies of contingent cooperation and mutualism in non-human primates^{21–24}. Actors and potential recipients could see and hear each other at both sites, and actors had many opportunities to watch recipients consume food rewards after they chosen the 1/1 option. In Louisiana, all subjects participated in the experiment as both actors and potential recipients. Potential recipients sometimes displayed begging gestures, suggesting that they had some understanding of the actor's role in delivering rewards to them. Finally, results of a second set of experiments using an entirely different apparatus (in Louisiana) and slightly different protocol (in Texas) generated results very similar to the ones reported here.

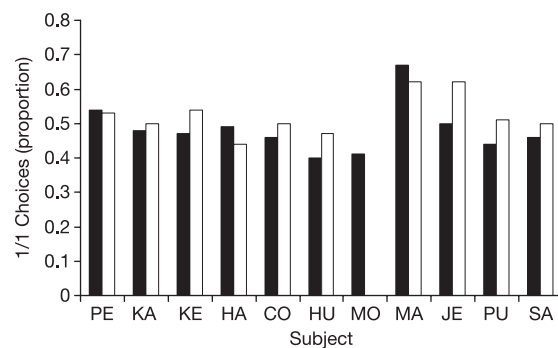


Figure 2 | Proportion of 1/1 choices made by Texas subjects. Values were obtained by dividing the number of 1/1 choices by the total number of 1/1 and 1/0 responses. Conventions as in Fig. 1. The first five subjects completed all sessions and responded on 69–99% of all trials. The next three subjects completed all sessions, but responded on only 18–27% of trials. MO never chose the 1/1 option when a potential recipient was present. The last three subjects did not complete all sessions, but responded on 71–88% of all trials that they began. None of the subjects chose the 1/1 option significantly more often when another chimpanzee was present than when they were alone (Fisher's exact test: PE, $P = 1.000$; KA, $P = 0.868$; KE, $P = 0.491$; HA, $P = 0.596$; CO, $P = 0.704$; HU, $P = 1.000$; MO, $P = 0.271$; MA, $P = 1.000$; JE, $P = 0.237$; PU, $P = 0.539$; SA, $P = 0.823$).

In these experiments, chimpanzees were clearly motivated to obtain rewards for themselves but not to provide rewards for other group members. None of the 18 chimpanzees that we tested was more likely to choose the 1/1 option when another chimpanzee was present than when they were alone. Our findings are strengthened by the fact that chimpanzees from both populations behaved in very similar ways, despite having different life histories and experimental experience.

These results complement observational and experimental studies that indicate that chimpanzees cooperate mainly with kin and reciprocating partners^{9–16} and show no aversion to inequitable exchanges that benefit themselves^{21,22}. The absence of other-regarding preferences in chimpanzees may indicate that such preferences are a derived property of the human species^{25,26} tied to sophisticated capacities for cultural learning, theory of mind, perspective taking and moral judgement^{27,28}. Alternatively, other-regarding preferences might be found in other species that rely more heavily on cooperative strategies than chimpanzees do, such as cooperatively breeding mammals²⁹. Further work on other species will help to clarify the socioecological conditions and cognitive requirements associated with the evolution of other-regarding preferences.

METHODS

Experimental procedure in Louisiana. The two chimpanzees faced each other in opposing enclosures. The testing apparatus spanned the width of an enclosure that adjoined two other enclosures (Supplementary Fig. 1). The apparatus consisted of two expandable arms, each connected to two horizontally aligned food trays. Each trial began with all four food trays collapsed towards the centre of the apparatus. When a handle was pulled, the closest tray on that arm moved to within the actor's reach and the other tray on the same arm extended in the opposite direction to within reach of the potential recipient (when present).

During testing each subject was paired with each of the other group members six times in random order in single trial sessions. Trials were alternated between partner-present and partner-absent sessions. The left/right position of the 1/1 option was counterbalanced within blocks of six trials on the partner-absent trials, and counterbalanced within pairings on the partner-present trials.

Experimental procedure in Texas. The chimpanzees were tested in the indoor runs of their home enclosure. The chimpanzees were put in adjoining cages separated by a wire mesh divider, and the testing apparatus was placed in front of them. The apparatus was placed between the two enclosures and consisted of two clear Lexan trays arrayed vertically (Supplementary Fig. 2). Each tray had a metal bar attached to the tray. A hose was attached to the bar on each tray; when the hose was pulled in, the bar swept forward across the tray and brought the food reward (if present) within the actor's reach. The actor and the recipient were able to reach the tray and remove rewards on their own side when the bar was pulled forward. When one bar was pulled forward, the other tray locked into position and the hose attached to it was retracted.

We conducted 10 sessions per pair, alternating between partner-present and partner-absent sessions. Within each session, 16 trials of the test configuration (1/1 versus 1/0) were conducted. The top/bottom position of the 1/1 option was counterbalanced across trials within sessions. Actors did not exchange roles or partners over the course of the experiment.

To reduce the likelihood that actors would stop attending to the distribution of rewards across trials within sessions, four additional 'attention trials' were randomly interspersed with the test configuration. In these trials, one option was baited only on the actor's side (1/0) and the other was baited only on the other side (0/1). If subjects are attending to the payoffs in these interspersed trials, they will choose the 1/0 option.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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