

Chimpanzees help conspecifics obtain food and non-food items

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Chimpanzees (*Pan troglodytes*) sometimes help both humans and conspecifics in experimental situations in which immediate selfish benefits can be ruled out. However, in several experiments, chimpanzees have not provided food to a conspecific even when it would cost them nothing, leading to the hypothesis that prosociality in the food-provisioning context is a derived trait in humans. Here, we show that chimpanzees help conspecifics obtain both food and non-food items—given that the donor cannot get the food herself. Furthermore, we show that the key factor eliciting chimpanzees' targeted helping is the recipients' attempts to either get the food or get the attention of the potential donor. The current findings add to the accumulating body of evidence that humans and chimpanzees share the motivation and skills necessary to help others in situations in which they cannot selfishly benefit. Humans, however, show prosocial motives more readily and in a wider range of contexts.

Keywords: helping; cooperation; *Pan troglodytes*; prosociality

1. INTRODUCTION

One of the biggest challenges in explaining human cooperation is accounting for the evolution and stability of cooperation between genetically unrelated individuals or individuals who will never encounter each other again [1,2]. This is especially the case when it comes to those forms of cooperation that involve immediate costs for the actor and yield benefits exclusively for the recipient (hereafter helping behaviour). It has been suggested that helping behaviour in humans relies on a derived psychology, specifically humans' unique concern for the welfare of others, also known as other-regarding preferences [3,4].

Many animal species cooperate with conspecifics [5]. Among primates, chimpanzees (*Pan troglodytes*) regularly exhibit a wide range of cooperative behaviours, such as coalitions and alliances, territory border patrols, and hunting [6,7]. However, these behaviours may be based on selfish motivations, since the actors can benefit directly and immediately from the cooperative interaction. Other behaviours such as meat-sharing and grooming benefit the recipient of the action at a cost to the actor at the time they are performed, suggesting that these are the result of prosocial motivations. However, it is difficult to conclude from these observations whether the behaviours are, indeed, motivated prosocially by their effect on the recipient. For instance, meat-sharing might be the result of harassment [8,9] and not the result of a true motivation to share with the recipient. Several experimental studies

seem to support this hypothesis (e.g. [10,11]). In these studies, chimpanzees had a choice, at no cost to themselves, between pulling a tray with food for themselves and a partner (1/1) or a tray with food only for themselves (1/0). Chimpanzees did not preferentially deliver food to their partners in these contexts, choosing indifferently. This led to the conclusion that chimpanzees are not motivated to produce outcomes that benefit others and that other-regarding preferences are probably a derived trait in humans. However, the results of these studies contrast with the results from other studies in which chimpanzees helped (i) a familiar and unfamiliar human to obtain out-of-reach objects, (ii) a conspecific to enter a room, and (iii) a conspecific to obtain a tool [12–15]. Although helping in these studies was not necessarily costly (the only exception maybe being [13], experiment 2, in which chimpanzees were required to climb several metres to get the out-of-reach object), even low-cost or no cost behaviour, which does not provide immediate benefits for the actor and only benefits a recipient, can provide insights into social motivations.

There are at least two hypotheses that might explain this discrepancy in results. First, it is possible that helping behaviour in chimpanzees is restricted to certain contexts and does not generalize as far as the context of active food-sharing. Chimpanzees are highly competitive over food [16–18], and although in the wild meat-sharing after hunting is common, there is evidence which suggests that sharing is the result of harassment—the 'sharing-under-pressure' hypothesis ([8,9]; but see [6]). That is, harassment, which is aggressive pressure or intimidation, such as begging gestures which restrict the possessor's movements (i.e. the beggar has physical contact to the carcass or possessor of it [9]), imposes costs on the selfish

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individual, making it easier for him to share under duress than to withhold food. But even in those populations in which harassment does not seem to play a role in meat-sharing behaviour, 'active' sharing is observed only in around 7 per cent of the meat transfer occurrences [19]. Also among mother–offspring dyads, food-sharing is mostly 'passive': mothers tolerate infants taking food from them and, in general, very few instances of active sharing are observed [20]. Thus, chimpanzees might have displayed helping behaviours in some previous experiments either because there was no food involved [12] or food only played an indirect role [13,15]. In contrast, in the experimental paradigms involving the active provision of food [10,11,21], chimpanzees might not have shown prosocial tendencies because they are in general indifferent to others' desires to obtain food as a consequence of the strong intra-group competition over resources typical of the species. We refer to this as the *food hypothesis*.

In addition, it has been suggested that paradigms in which subjects are engaged in obtaining food for themselves hinder (or interfere with) the subjects' ability to notice the effect of their choices on their partners [12,22]. However, studies with chimpanzees which included experimental conditions in which actors were not preoccupied obtaining food for themselves because payoffs to the actor were eliminated [11], or actors could first obtain food for themselves and then later help [21], still found no clear evidence for helping. Furthermore, de Waal *et al.* [23] and Lakshminarayanan & Santos [24] have both obtained positive results with capuchins using a paradigm in which actors are also engaged in obtaining food for themselves.

The second hypothesis is that helping behaviour in chimpanzees might be restricted to situations in which actors can make use of very salient cues to infer the other's goals and needs (for a classification of helping behaviours in relation to recipient's behaviours see Warneken & Tomasello [25]). In the experiments by Warneken *et al.* [12,13], the recipients always engaged in behaviours which allowed the subjects to infer the recipients' goals, such as an outstretched arm oriented towards a visible object or an active attempt to open a door. Also in Yamamoto *et al.* [15], recipients signalled their goal or requested help from their conspecific partner by poking an arm through the hole between the two booths, beating the panel between the two booths and using other attention-getters (and indeed results showed that subjects helped more after such communicative signals than without them). This signalling is important because chimpanzees might have limitations in their ability to infer recipients' goals and needs in the absence of overt actions or requests [26]. We call this the *signalling hypothesis*.

We tested these two hypotheses using a paradigm in which one chimpanzee had the opportunity to help another obtain a food reward or an object that was inaccessible to the helper, both in the presence and absence of signals of need. The paradigm allowed us to jointly test both variables and their possible interaction in eliciting or hindering helping. Subject and recipient were positioned in different rooms opposite to each other and an apparatus was located in the middle (figure 1). The reward was placed in the apparatus between the subject's and the recipient's room but out of reach of both

individuals. Subjects could choose to release the reward by removing a hook, so that the reward slid down the apparatus and within reach of the recipient, but they could never obtain the reward for themselves. In order to investigate the two hypotheses, we varied the type of reward, an edible (banana piece) versus a non-edible reward (token). In addition, we used two slightly different variations of an apparatus in an attempt to control whether or not the recipient would reach towards the out-of-reach reward, potentially signalling his desire to get the reward. Specifically, in the *reaching* condition, the recipient could stretch his arm out of the room and pull and/or shake a chain attached to the reward, while in the *no-reaching* condition, he was only able to extend his fingers through the mesh and touch the apparatus. Under the *food hypothesis*, we predicted that subjects would release the reward less often in the food than in the token trials. Under the signalling hypothesis, we expected more reward releases with active behaviour or requests than without. We also ran a recipient-absent control condition (with both types of reward), in which the recipient's room was empty but the recipient was in a room adjacent to the subject's room. All subjects participated in all six conditions: the four conditions with the recipient present (reaching/food, reaching/token, no-reaching/food, no-reaching/token), and in two conditions without the recipient (with food and token as rewards). Recipients did not always signal their interest in the reward (e.g. outstretching their arm towards it) or act instrumentally on it (pulling the chain) in the reaching conditions. In addition, they sometimes expressed an interest in the reward (using attention-getters such as banging against bars, clapping, etc.) or acted on the apparatus (i.e. manipulating it with their fingers) in the no-reaching conditions. To accommodate these naturally exhibited instrumental and communicative behaviours, we coded recipients' behaviour and analysed the results based on whether they were active or passive at signalling their need for help.

2. MATERIAL AND METHODS

(a) *Subjects*

Fourteen semi-free ranging chimpanzees living at the Ngamba Island Chimpanzee Sanctuary in Uganda (seven females and seven males aged 7–13 years, mean = 9.7 years) participated in this study. They were all tested with two unrelated males as recipients (see electronic supplementary material, table S1). Both males were 10 years old and, from observations, seem to be dominant to nine of the subjects and subordinate to the other five subjects. The sanctuary was established in 1998 to care for confiscated orphan chimpanzees as a result of the illegal trade in chimpanzee bushmeat. All subjects had participated in several studies investigating their cooperative problem-solving abilities and/or prosocial tendencies [13,14,27–30].

(b) *Experimental set-up and apparatus*

Chimpanzees were tested in two rooms facing each other and separated by a 2 m-wide corridor. The two rooms were connected by an overhead-raceway with one door at each end. All rooms were made of metal bars, so that chimpanzees were always able to see and hear each other. The testing apparatus was placed in the keepers' corridor between the

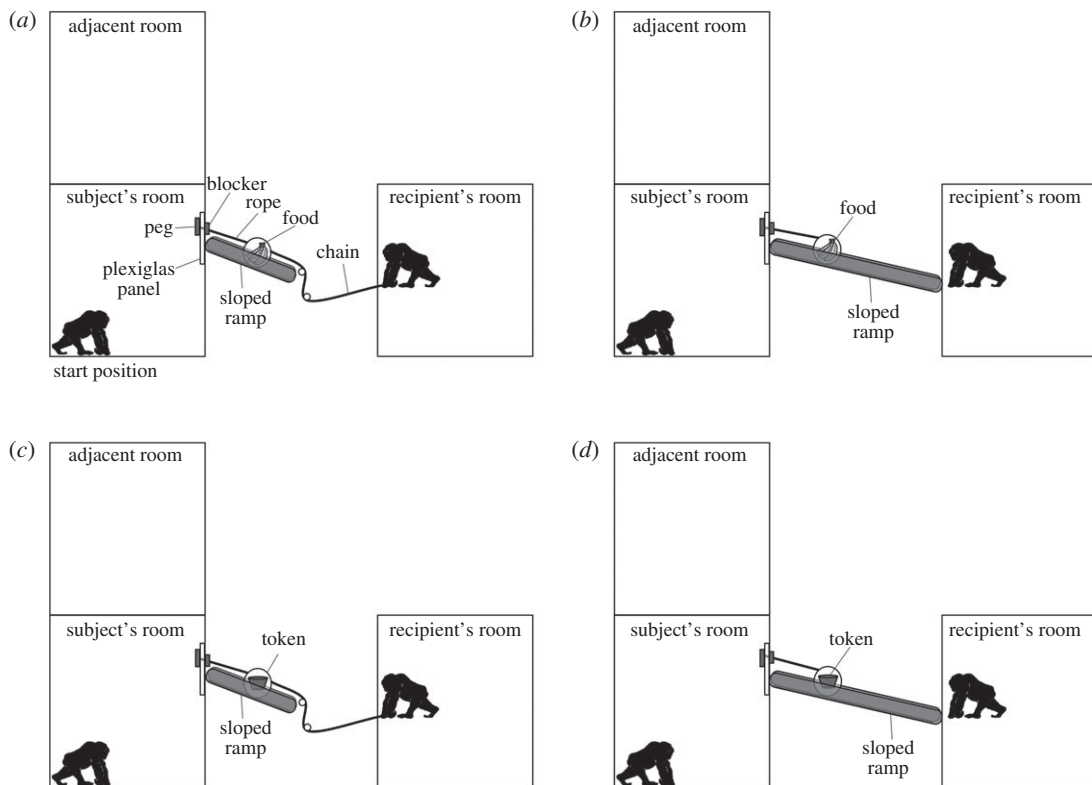


Figure 1. (a) Reaching/food condition, (b) no-reaching/food, (c) reaching/token, (d) no-reaching/token. In the reaching conditions, recipients could reach their arm outside the room and shake and/or pull the chain. In the no-reaching conditions, since they could not reach their arm outside the testing room, they could only use attention-getters as described in §2. In the recipient-absent control conditions, the recipient was positioned in the adjacent room.

subject's and the recipient's room and underneath the overhead-raceway. The apparatus consisted of a plastic ramp (15 cm diameter) fixed at the subjects' side at 1 m height. The ramp functioned as a support for the transparent plastic bag containing the reward. The reward bag was placed at 1 m distance from the subject's side and was fixed with a rope at the subject's side. At the subjects' end of the rope there was a wooden peg (8 × 2 cm) that was placed horizontally across the vertical bars of the subjects' room (bars were separated by 3.2 cm). The peg was attached to the rope and stopped the reward bag from sliding down the ramp. When the peg was turned vertically, it fell between the bars, and together with the rope and the bag, fell down the ramp to the recipients' side. To stop the subject from trying to pull the rope with the reward inside her room, we attached a Plexiglas blocker (9 cm diameter) right behind the peg. Furthermore, the area surrounding the peg and the gutter at the subject's side was blocked with a Plexiglas sheet (63 × 50 cm) and additional metal bars, making it impossible for the subject to pull in the reward.

The length of the ramp and rope was varied depending on the condition. In the *reaching*-condition, the ramp was 1.2 m long and ended at 44 cm height and 0.9 m from the recipients' room. To the rope and attached reward bag, we connected a 2 m long chain that reached the recipient's room, which the recipient could pull. Recipients could extend their arm outside their room through a gap between the metal bars (7.5 × 23 cm) and shake and pull the chain. In the *no-reaching* condition, an additional piece of ramp was added, extending the total length to 2.07 m, so that it reached the mesh of the recipients' room. In this condition, the rope with the attached reward bag did not have the chain connected to it.

(c) Procedure and design

(i) Apparatus familiarization

All subjects were individually introduced to the apparatus to ensure that they became familiar with the function of the peg. The subject's start-position was the recipients' room; the two doors of the overhead-raceway were open so that subjects could move freely between the two rooms. Subjects had to go through the overhead-raceway, release the peg and come back to the recipient's room to obtain the reward. They were all introduced first to the apparatus of the reaching condition and in a second session to the apparatus of the no-reaching condition. In both cases, experimenter 1 (E1) put a banana piece in the transparent bag in full view of the subject. Experimenter 2 (E2) then distracted the subject, while E1 positioned the rope with the reward in the ramp and fixed the peg across the bars of the room (and in the reaching condition extended the chain to the recipient's side). A trial started when E2 stopped distracting the subject and the subject positioned herself in front of the ramp. The criterion to consider the subjects ready to initiate experimental phases (see following) was that they had to start releasing the peg within 30 s from trial's start and do this in three consecutive trials. Subjects experienced a maximum of 10 trials per session. Subjects reached criterion on average after 4.7 trials (range: 3–13) in the reaching condition and after 3.6 trials (range: 3–7) in the no-reaching condition.

(ii) Inhibition phase

After having learned to manipulate the apparatus to obtain food for themselves, we speculated that subjects could potentially carry over a high tendency to release the peg even when they did not have access to the reward (because the doors

connecting both rooms were closed). This could be the case especially if subjects were in the room without any other alternative activity to engage in. Therefore, we introduced several alternative enrichment activities or distracters to ensure that subjects did not start the testing phase with a high tendency to release the peg for no apparent reason. Subjects were positioned in the room with access to the peg (subject's room). The doors of the overhead-raceway were closed so that subjects could not access the recipients' room (and thereby obtain the reward after releasing the peg). In full view of the subject, E1 placed the bag containing a banana piece in the ramp, then, while E2 distracted the subject in the left-front corner of the room, E1 fixed the peg (attached to the food reward) horizontally across the bars. A trial started when E2 stopped distracting the subject and both experimenters left the testing area. Subjects participated in inhibition trials until they did not release the peg for 60 s in three consecutive trials. The following distracters were introduced:

- *Rope*: we attached a non-functional 6 m long rope to the bars close to the subject's start-position (left corner of the room). At the end of the rope, we attached a wooden peg like the one from the testing apparatus. However, most of the subjects did not show much interest in the rope and did not reach the criterion within 10 trials (three pilot subjects not even after two sessions of 10 trials each; see electronic supplementary material, table S2). Therefore, we added the following distracters.
- *Juice-soaked towel*: at the beginning of each trial, subjects received a piece of towel (9 × 14 cm) that was soaked in fruit juice. Subjects could chew the towel but were still able to move freely through the room and release the peg. All subjects quickly reached the criterion after introducing the juice-soaked towel (see electronic supplementary material, table S2).
- *Toothbrush*: three subjects (one of whom ignored the juice-soaked towel) still released the peg in three out of four baseline trials of the pre-tests described below. These three subjects were given the juice-soaked towel plus a toothbrush to chew on and play with.

(iii) *Experimental phase*

The general procedure for all different conditions described below was as follows. The subject was positioned in the subject's room. The non-functional distracter rope remained attached to the bars of the subject's room in all different conditions. E1 baited the plastic bag with a reward in full view of the subject. While E1 positioned the bag with the reward in the ramp and fixed the peg in the subject's room, E2 distracted the subject in the left-front corner of her room showing her the enrichment objects she was going to receive. A trial started immediately after E2 gave the subject the juice-soaked towel (and additional toothbrush to three of the subjects) and both experimenters left the testing area. The dependent measure was whether subjects released the peg within 60 s from the trial's start. Regardless of whether or not and when subjects released the peg, the experimenters never returned to the testing area before the 1 min trial concluded. In addition, the inter-trial duration (from the end of one trial until the start of the next one) was always at least 1 min.

(iv) *Pre-tests and post-tests: knowledge and baseline trials*

All subjects participated in two sessions of four knowledge and four non-social baseline trials each, administered once

before, and once after the actual test phase. In these controls, subjects were in the testing rooms by themselves, with no other partner located in any of the adjacent rooms. In the knowledge condition subjects had access to both rooms, which meant that subjects could release the peg, move across the raceway through the open door and retrieve the food in the recipient's room. In the baseline condition, the doors connecting the two rooms were closed, so that releasing the peg had no function. The two conditions (knowledge and baseline) were administered in a blocked design, and the order of the conditions was counterbalanced across subjects and sessions. Since three subjects showed a high tendency to release the peg in the baseline trials before the test, they were given a new distracter and tested in another round of eight pre-test trials.

(v) *Test: helping test and control*

All subjects participated in the following six test conditions. In four experimental conditions, we manipulated whether (i) the recipient signalled his need for help (i.e. whether he was able to extend his arm towards the reward or not), and (ii) the type of reward that the recipient could obtain (food versus object). In two control conditions, we assessed whether subjects would release the peg even though the conspecific was in an adjacent room instead of the recipient room. In all test conditions, the doors connecting the subject's and the recipient's room were always closed.

1. *Reaching-food* recipients could reach their arm outside their testing room and shake and/or pull on the chain connected to the bag with a banana piece (one-third banana). If subjects released the peg, recipients could pull the chain with the reward attached to it.
2. *No-reaching-food* a metal mesh (gaps size: 5.5 × 6 cm) was fixed to the recipients' side (160 × 102 cm). Therefore, recipients could not reach or pull on the rope attached to the reward.
3. *Reaching-token* the apparatus set-up was as in 1. The only difference was that in this condition the bag contained a plastic token (3 × 1.5 cm), the value of which was only known to the recipients. Recipients were previously trained to exchange the token for a food reward. If subjects released the peg, recipients could take the token in the bag and exchange it for food with E3, who was positioned in a hidden part of the testing room. Subjects never saw the exchange between recipients and E3. In addition, subjects were given a similar object but which had no reinforcement value in each token session.
4. *No-reaching-token* the apparatus set-up was identical to that of 2 and the content of the bag was a token as in 3.
5. *Recipient absent-token control* the recipient was positioned in the room adjacent to the subject's room. The recipient's room was empty. The content of the bag was a token.
6. *Recipient absent-food control* the recipient was positioned in the room adjacent to the subject's room. The recipient's room was empty. The content of the bag was one-third of a banana.

In the recipient-absent control conditions, we used the reaching apparatus (demi-ramp) for half of the subjects and the no-reaching apparatus (long ramp) for the other half. Subjects received only one type of condition per session, and

four trials per condition–session (24 trials in total). The variable recipient (reaching, no-reaching, absent) was administered in a blocked design, whereas the type of reward alternated every session. In addition, the identity of the recipient (Baluku and Asega) changed every two trials.

(d) Coding and analyses

A.M. and A.S. live-coded whether or not subjects released the peg within 60 s from the trial's start. A trial started when the two experimenters simultaneously attached the peg and gave the subject the distracter objects in the start position. Twenty-five per cent of trials were randomly selected and independently coded from videotape by a second coder who was blind to the study's hypotheses (Cohen's $\kappa = 0.92$). In addition, another blind-coder also coded the behaviour of the recipients from videotape. We distinguished whether recipients were active or passive on a given trial. A recipient was 'active' if he interacted with the apparatus in a way that created some sound (e.g. shaking the chain, lifting the gutter, moving the chain sideways along the bars) and/or was oriented towards the subject and used attention-getters (e.g. banging against the bars, stomping on the ground, clapping, drumming on objects or floor, or emitting raspberries) for at least five consecutive seconds. Instances in which the recipient did not interact with the apparatus, did not use attention-getters or did so for less than 5 s were designated as passive. Reliability for this category was good: active or passive (Cohen's $\kappa = 0.76$). Non-parametric Friedman's and planned Wilcoxon's exact-signed rank tests were used. All analyses were two-tailed. We also used a multi-level logistic regression model (GLMM, [31]) using the LME4 software package v. 0.999375-31 [32] in the statistics program R (v. 2.9.1) to assess the effects of trial (within a session: 1–4), condition (recipient: active, passive, absent) and reward type (food or token) on the likelihood of releasing the reward.

3. RESULTS

Overall, chimpanzees released the reward more often when the recipient was active than passive or was absent (control condition) (Friedman's test; $\chi^2 = 7.244$; $n = 14$, $p = 0.027$; Wilcoxon matched-pairs exact test, active–passive: $n = 14$ (two ties), $t+ = 67$, $p = 0.025$; active–absent: $n = 14$ (four ties); $t+ = 49$, $p = 0.027$; passive–absent: $n = 14$ (three ties); $t+ = 37$, $p = 0.765$; figure 2 and see electronic supplementary material, videos). Results showed that subjects released the reward more often in the food than in the token trials (Wilcoxon matched-pairs exact test, food–token: $n = 14$ (three ties), $t+ = 63$, $p = 0.005$). An analysis of the effect of the reward per condition produced mixed results. If the recipient was active, there was no difference between the two types of reward (Wilcoxon matched-pairs exact test, active: $n = 14$ (three ties), $t+ = 12$, $p = 0.781$). This was also true in the control condition in which no recipient was present (absent: $n = 14$ (seven ties), $t+ = 4$, $p = 0.11$). However, if the recipient was present but passive, subjects released the food reward more often than the token (passive: $n = 14$ (five ties), $t+ = 5$, $p = 0.04$; figure 2). Contrary to our prediction, subjects were more likely to perform the target action when food was involved. However, since there was a similar trend in the condition in which the recipient was

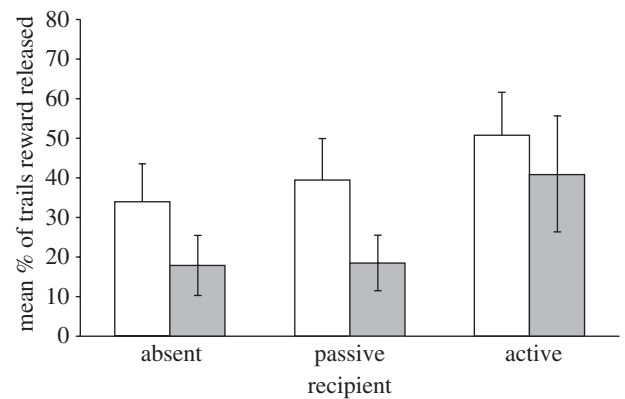


Figure 2. Proportion of trials (mean \pm s.e.m., $n = 14$ individuals), in which subjects released the reward (food (white bars) and token (grey bars)) when the recipient was absent or present in the recipient's room. The recipients' behaviour was classified as active or passive (see §2), Wilcoxon matched-pairs exact test, absent–passive: ns; passive–active: $p < 0.05$; absent–active: $p < 0.05$.

absent—it is possible that subjects were simply more attracted to the apparatus when it contained food than when it contained tokens.

The results of the multi-level logistic regression confirmed these results. Specifically, with releasing the reward as binary response, we fitted a model including subject as random factor, trial within each session (1–4) as a covariate (i.e. continuous predictor) with fixed effect, and reward type (food, token) and recipient behaviour (active, passive, absent) as fixed factors. This analysis confirmed that subjects were more likely to release the reward when the reward was food than when it was a token, and were also more likely to do so when the recipient was active (table 1). Guided by our two hypotheses about the influence of reward type and recipient behaviour, we compared the full model first with a model that did not include reward type as a factor. The fit of this more parsimonious model resulted in a significant reduction of fit (likelihood ratio test comparing both models: $\chi^2 = 19.2$, $p < 0.001$). Secondly, we compared the full model to a model which did not include recipient behaviour, also resulting in a significant reduction of fit which indicates that recipient behaviour explains a significant amount of variance (likelihood ratio test $\chi^2 = 7.9$, $p < 0.02$). In addition, releasing the reward decreased over the four trials of a session (table 1), but since this happened equally across all sessions (recipient present and absent), it does not change the main finding that subjects helped more when recipients were active. Additional analyses showed no interaction effects among these factors (likelihood ratio tests comparing models comprising all three interactions with models comprising only two of them: reward \times recipient behaviour: $\chi^2 = 0.65$, d.f. = 2, $p = 0.72$; trial \times recipient behaviour: $\chi^2 = 0.54$, d.f. = 2, $p = 0.76$; trial \times reward: $\chi^2 = 0.73$, d.f. = 2, $p = 0.39$).

It is very unlikely that subjects released the reward because they were aiming to obtain it for themselves. This is because there were two further conditions—the knowledge and baseline conditions—which demonstrated that subjects knew the experimental set-up and the consequences of their actions (see §2). Specifically, in the

Table 1. Factors that influenced the likelihood of releasing the reward.

factor	estimate	s.e.	<i>z</i>	<i>p</i>
reward	-1.375	0.323	-4.262	0.00002
trial	-0.673	0.183	-3.676	0.000237
recipient behaviour				
active-absent	1.215	0.436	2.785	0.0053
passive-absent	0.290	0.35	0.825	0.409
active-passive	1.019	0.426	2.39	0.016

knowledge condition (in which subjects had access to the recipient's side of the apparatus through an open door), subjects released the peg in the majority of trials, whereas when subjects did not have access to the empty recipient's room because the door was closed (baseline condition) they rarely did (knowledge–baseline, Wilcoxon matched-pairs exact test: $n = 14$ (0 ties), $t^+ = 105$, $p < 0.001$). This difference between conditions was already present prior to the test and also persisted after the test (figure 3).

An alternative explanation is that in the test phase, subjects were more aroused by the mere presence of a partner (the recipient) in an adjacent room and were therefore more likely to perform the target action. This is unlikely since in the recipient-absent control condition, the recipient was in an adjacent room close to the subject, and subjects did not release the reward as often (in addition, a direct comparison between the baseline and control condition revealed no difference in the subjects' tendency to release the reward: Wilcoxon matched-pairs exact test: $n = 14$ (one tie), $t^+ = 47.5$; $p = 0.91$). Moreover, even when a recipient was there in the experimental conditions, subjects did not release the reward unless the recipient drew attention to himself or the apparatus by reaching, rattling the chain or signalling his need for help.

Since Yamamoto *et al.* [15] found that subordinate chimpanzees were more likely to help their dominant partner than vice versa, we compared the helping rates between the group of subjects who were dominant and the group of subjects who were subordinate to the recipients. We found that the group of subjects who were subordinate to the recipients ($n = 9$) helped on average in 57.7–59.35% of the trials (s.e. = 12), whereas the group of subjects who were dominant to the recipients ($n = 5$) helped on average in 23–31% of the trials (s.e. = 10). This difference was, however, not statistically significant (Mann–Whitney test, recipients active: $U = 79.5$, $n_1 = 5$, $n_2 = 9$, $p = 0.11$).

Initially, in the introduction phase, many subjects showed a high tendency to release the food even when they had no access to it, which suggests that the target action was non-costly for them and probably even attractive in the absence of an alternative activity in the room. For this reason, we introduced several distracters to provide subjects with an alternative activity (as in studies with children [33]). This apparently raised the cost, as subjects manipulated the distracters relatively often, and so, perhaps because of this, helped at a lower overall rate (50–55%) than in previous studies (Warneken *et al.* [13], 75%; Yamamoto *et al.* [15], 80%).

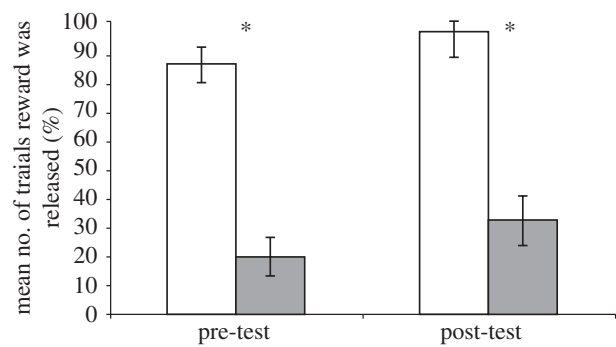


Figure 3. Proportion of trials (mean \pm s.e.m., $n = 14$ individuals), in which subjects released the reward with door opened (knowledge (white bars) and door closed (baseline (grey bars)) ($p < 0.001$ for both comparisons before and after the test). No other partner was in any of the adjacent rooms.

4. DISCUSSION

The current results show that the presence of food does not constrain chimpanzees' tendency to help others, whereas the recipient's active behaviour is a key factor mediating their helping. These results do not support the food hypothesis as a possible explanation for the conflicting findings in the literature, since in the present experiment chimpanzees helped the recipients to obtain the edible and non-edible reward equally often. Therefore, we can conclude that chimpanzees' competitive relationships over resources do not necessarily hinder their tendency to help others access food in situations in which there is not actual, immediate competition. The critical factor eliciting helping behaviour was the recipients' active behaviour. The mere presence of the partner was not enough to elicit helping, and subjects helped only when the recipients were active in trying to obtain the reward or signal the helper (i.e. shaking the chain attached to the reward, lifting the ramp, beating the mesh or stomping on the ground), supporting the signalling hypothesis.

These results might help to explain the negative findings of some previous studies. For example, in Jensen *et al.* [11], recipients did not actively request or signal their need, possibly because of their side-by-side arrangement. In Silk *et al.* [10] and Vonk *et al.* [21], recipients were occasionally observed to signal their interest in the food, and Vonk *et al.* [21] examined the effect that begging gestures had on actors' propensity to help but still found no evidence for helping. It is unclear why the begging gestures in Vonk *et al.* [21] were not as effective as in the present study; maybe recipients could not beg in an effective way (e.g. owing to the experimental set-up), or even population differences could have contributed to these results. In addition, we cannot rule out the possibility that in situations in which chimpanzees are engaged in obtaining food for themselves, especially as in Jensen *et al.* [11] (experiment 1); and Silk *et al.* [10] they do not attend to the effect of their choices on their partners.

The finding that chimpanzees helped only when the recipient was active or signalled the helper raises two further issues regarding the interpretation of their behaviour. First, it is possible that the recipients' signals have a harassing function, and therefore it is not that donors are

behaving prosocially but instead are acting selfishly to stop the beggars. However, it should be noted that the recipients did not have physical access to the donors and although they could beg from the subjects they could not engage in harassment as defined in the literature (e.g. [9], see §1). If anything, it could only be that the auditory cues produced by the recipients had an aversive effect on the subjects. Although this possibility cannot be ruled out, this seems an unlikely explanation since the sounds produced by the recipients were the result of manipulating a chain, stomping on the ground or hitting the mesh panel; they did not scream, have any temper tantrums or produce any distress vocalizations, signals which have evolved to influence others emotionally and more likely have an aversive effect. Furthermore, we never observed any signs of distress in the helpers. Another interpretation is that recipients' active behaviour acted as a form of stimulus or local enhancement attracting subjects' attention to the apparatus and then manipulating it. Although this is something that we cannot rule out in the present experiment—and it would be very interesting to see a future study address the stimulus/local enhancement question directly—prior work suggests that this is not the case. Warneken *et al.* [13] found that the level of helping was not correlated with the movements of the door that needed to be opened, and chimpanzees have helped in several previous experiments in which the target objects were not manipulated at all (see the out-of-reach tasks in Warneken & Tomasello [12] and Warneken *et al.* [13]). Moreover, this explanation does not hold in a recent study where the recipients could not manipulate the wanted tool, but could only point in its direction or signal the recipient in other ways not involving the tool [15]. That is, despite cueing subjects still had to infer what exactly recipients wanted and do the right thing with it (i.e. bring it to the recipient instead of just manipulating it). In the present study, chimpanzees release the peg, but in previous ones they bring the object or tool to the recipient, which involves several different steps and thus degrees of freedom (picking up the object, moving to a location near the recipient, handing it over, releasing it, ...). Thus, it would be worrisome in these studies if the dependent measure was their tendency to pick up an object, but since they engage in a clearly intentional action afterwards, stimulus enhancement cannot easily explain all the subsequent steps involved in the helping behaviour. In addition, subjects in this and previous studies have shown they understand the consequences of their actions, so it is unlikely that they were just blindly manipulating the apparatus [13–15]. The current study was not designed to demonstrate intention-reading and goal-understanding, though we suggest based on evidence presented here and in prior studies that these interpretations are plausible ([26]; see also [34]). Future studies could attempt to tease apart intention-reading from responsiveness to cueing and other behaviour-reading interpretations by having controls for accidental versus intentional cueing.

Therefore, the main finding of the present study is that recipients' signalling is necessary to elicit helping behaviour. This interpretation is consistent with previous helping studies in chimpanzees [12–15]. The helping behaviours in these studies varied, suggesting that

chimpanzees are not simply acting on objects, but doing so in a way that benefits the signaller. The cues provided by the recipient could be signalling 'do something', and the helpers are generally compliant when the recipient's goals are clear. A cognitively low-level interpretation is that chimpanzees do not recognize the intentions of others, but 'do something' until the signalling stops. Still, it is plausible that chimpanzees need to be prompted by recipients' active behaviour owing to limitations in their ability to infer others' needs in the absence of overt cues [13,15,25]. In all these situations helping occurred spontaneously in the sense that subjects were neither trained to do so, nor had they any expectation of obtaining any immediate reward for their helping response. Furthermore, subjects' behaviour was voluntary in the sense that they were not being physically harassed.

Some authors have argued that for helping to be prosocially motivated, it should occur in the absence of signals for help. Burkart *et al.* [35] found that cooperatively breeding common marmosets display helping behaviour, providing food, in the absence of solicitation. However, another cooperative breeder species, cotton-top tamarins (*Saguinus oedipus*), do not behave prosocially in a similar context with a social control condition that is more comparable to the chimpanzee studies [36,37]. Additionally, non-cooperatively breeding capuchin monkeys (*Cebus apella*) choose prosocial outcomes over selfish ones [23,24]. Importantly, although both marmosets and capuchins have demonstrated prosocial behaviour in a food donating context, the proximate mechanisms underlying this behaviour are still unclear since helping in humans is adapted to the signalled needs of the recipients, something common marmosets did not do [35]. It would be important to investigate further whether marmosets' and capuchins' prosocial behaviour is confined to the food-provisioning context, or as in the case of chimpanzees, generalizes to other contexts such as instrumental helping that is targeted at the expressed needs of another individual. A first step in this direction has been undertaken by Barnes *et al.* [38], who adapted the out-of-reach-object paradigm of Warneken *et al.* [13] for capuchin monkeys. Contrary to chimpanzees however, whether or not the experimenter reached towards the target-object had only a marginal effect on the capuchins' inclination to help (whereas the main factor to elicit helping was the presence of a potential reward). Further studies will be necessary to pinpoint the factors underlying the differences among these species.

Although these results might appear to validate observational reports of chimpanzees showing empathy for others [39], further studies will be necessary to elucidate whether helping behaviour in chimpanzees is driven by empathy with the emotional states of the others, as in the case of human infants and adults [40,41]. It is important to emphasize that we cannot conclude whether or not chimpanzees have a concern for the long-term welfare of others such as humans are capable of. However, what the data can rule out is that chimpanzees were motivated by the prospect of an immediate selfish benefit or did not know the consequences of their actions.

Although in the current study subjects and recipients were not genetically related and could not have any expectation of immediate reciprocation, it is possible that the type of low-cost or no-cost helping behaviour that chimpanzees exhibit in these experimental situations evolved

via kinship and/or reciprocity. Humans have enormously amplified both these helping tendencies and the readiness to show them, evolving not only much more sophisticated cognitive skills to understand others' needs and desires, but probably also undergoing major changes in their emotional and motivational systems to the extent of showing concern for others and helping in a wider range of contexts [42,43].

The research was approved and reviewed by the local ethics committee of CSWCT (Chimpanzee Sanctuary and Wildlife Conservation Trust), the organization running the Chimpanzee Sanctuary in Uganda, as well as UWA (Ugandan Wildlife Authorities) and UNCST (Ugandan National Council for Science and Technology).

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