# Chimpanzee helping in collaborative and noncollaborative contexts

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Chimpanzees, *Pan troglodytes*, help others in a variety of contexts. Some researchers have claimed that this only occurs when food is not involved and the recipient actively solicits help. In the current study, however, we found that chimpanzees often helped conspecifics obtain food in a pulling task with no solicitation whatsoever, in a situation in which, based on past experience, the conspecific's desire for the food was apparent. We also assessed whether the collaborative context of the situation impacted helping rates. Specifically, we compared how often both partners obtained rewards when one partner needed the help of the other, who had already received a reward for free (helping without collaboration), and when one partner needed the other's help after they had already begun collaborating (helping during collaboration). Partners provided assistance significantly more often in both of these helping conditions than in a control condition in which partners could provide unneeded help. However, unlike human children who have been tested in a similar task, chimpanzees did not help their partner more during (than without) collaboration. These results suggest that chimpanzees' helping behaviour is more robust than previously believed, but at the same time may have different evolutionary roots from the helping behaviour of humans.

Clear and extreme forms of altruism, such as self-sacrifice, are rare in the animal kingdom. However, many organisms cooperate with and help group members in certain contexts including food sharing (e.g. jackdaws, *Corvus monedula*: de Kort et al. 2006), group hunting (e.g. lions, *Panthera leo*: Stander 1992), coalitionary support (e.g. spotted hyaenas, *Crocuta crocuta*: Smith et al. 2010), allogrooming (e.g. vervet monkeys, *Chlorocebus aethiops*: Seyfarth & Cheney 1984), cooperative care of offspring (e.g. cichlids, *Lamprologus brichardi*: Taborsky 1984) and territorial defence (e.g. meerkats, *Suricatta suricatta*: Graw & Manser 2007). Proximate mechanisms supporting such behaviours can evolve if the actor gains compensatory benefits, such as greater inclusive fitness, increased likelihood of future reciprocation or enhancement of some aspect of social reputation or sexual attractiveness (Dugatkin 1997, 2006). Therefore, we are concerned with helping behaviours in which one individual performs an act enabling another recipient individual to reach a goal that the recipient cannot achieve alone (also called 'instrumental helping' by Warneken & Tomasello 2009 or 'targeted helping' by de Waal 2008). We focus on the proximate mechanisms (the cognitive and motivational processes) that enable these helping behaviours, rather than the contentious issue of whether these (or any) behaviours are altruistic in terms of evolutionary fitness.

Recently, researchers have reported a set of conflicting findings about helping in chimpanzees, *Pan troglodytes*. First, two well-known studies reported that when given a choice between an act that delivered food to both themselves and a conspecific and that same act (on a different apparatus) that delivered food only to themselves, chimpanzees chose indifferently (Silk et al. 2005; Jensen et al. 2006). Even when there was zero cost to themselves in terms of either resources or effort, chimpanzees focused only on their own reward and did not help their groupmate at all (and in the Jensen et al. 2006 study there was a control condition ensuring that subjects understood that the two different acts led to different outcomes for the partner). However, other studies have reported that chimpanzees will sometimes help others obtain concrete goals. For example, human-raised chimpanzees readily helped a familiar human fetch an out-of-reach object (Warneken & Tomasello 2006). In a more controlled set of studies it was further found that mother-reared chimpanzees helped humans fetch out-of-reach objects (1) even if the human was unfamiliar; (2) even if the energetic costs were raised (i.e. they had to climb some distance to retrieve the sought-for object); and (3) irrespective of whether they could anticipate a food reward or not (Warneken et al. 2007, Studies 1 and 2).

Two hypotheses to explain the discrepant findings in these two sets of studies might be that: (1) chimpanzees are more likely to

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help a human than another chimpanzee, and (2) chimpanzees are more likely to help others obtain nonfood goals. Warneken et al. (2007, Study 3) therefore gave chimpanzees the opportunity to help a conspecific obtain food. The situation was that one chimpanzee could obtain food in an adjacent room only if the subject unlocked a door (from a third room) by removing a chain. Subjects removed the chain significantly more often when doing so would allow the partner to enter and get the food than in a control condition in which the food was in another room that neither could access. The negative findings of Silk et al. (2005) and Jensen et al. (2006) thus do not result solely from chimpanzees' reluctance to help conspecifics obtain food, although it is possible that the degree to which subjects in the different studies thought they might be able to obtain food in the situation (activating their competitive tendencies) might have played an important role (see Discussion).

A third factor that might be at work in the studies is the degree to which recipients solicited help from the subject. In the Silk et al. (2005) and Jensen et al. (2006) studies, there was little solicitation from the recipient. In contrast, Warneken et al. (2007) found that chimpanzees were more likely to help a human obtain an out-of-reach object when the human communicated his goal (reaching for the object, alternating gaze between the object and the subject, and sometimes saying the chimpanzee's name) than when he did not make any outward attempt. Similarly, Yamamoto et al. (2009) and Melis et al. (unpublished data) both found that subjects were more likely to help a conspecific obtain a needed tool or item of food, respectively, if the conspecific solicited help by doing such things as vocalizing, clapping hands or banging on the cage. (Using a task similar to that of Silk et al. (2005) and Jensen et al. (2006), Vonk et al. (2008) found that subjects did not help recipients whether they reached towards the food or not, but since chimpanzees do not help at all in this paradigm, this paradigm does not appear to be ideal for assessing the role of solicitations.) A general issue here is that one individual can help another only if it knows that the recipient needs help and what kind of help is needed. So 'solicitation' (or 'requesting') may be serving either an informational role (enabling subjects to determine what is needed) or a coercive role (communicating to subjects that the recipient expects or demands help).

Another factor that may influence chimpanzees' helping behaviour is the immediate social context of the potentially helpful act, in particular, the degree to which the subject and recipient are in a cooperative interaction. Thus, human children help peers more when they are in the process of collaborating with them than in more neutral contexts. For example, Hamann et al. (unpublished data) presented pairs of young children with a task that could be solved only by the two of them working together: they had to lift up their end of a stick in synchrony with each other to move a small platform up a series of steps, at which point they could then obtain a reward. In the experimental condition, after only two steps of collaboration one child received her reward first, but the partner still needed help to move the platform up two more steps to obtain her reward. In this condition, 3-year-old subjects, who already had their reward in hand, helped the partner very frequently. In a control condition, the two children encountered the apparatus from the outset with the stick already part-way up the steps so that the first child only needed to reach in and get her reward, without any collaboration, with the second child still needing help moving the platform up. In this condition, in which help was needed outside of an ongoing collaboration, the children sometimes helped, but not nearly as much as in the collaboration/experimental condition. One explanation of these findings is that once children commit themselves to a joint goal, they feel obliged to follow through in the collaborative activity until everyone receives their reward (see Toumela 2007). By this age, children also acknowledge to adult partners when they break an explicit agreement to collaborate and

at even younger ages attempt to reengage adult partners who disengage from a joint activity (Warneken et al. 2006; Gräfenhain et al. 2009). The psychological mechanisms underlying such behaviours are likely to be grounded in strong prosocial motivations as well as the cognitive ability to represent joint goals and share mental states with others.

In both naturalistic and experimental situations, chimpanzees engage in mutualistic collaborative activities relatively readily (see Muller & Mitani 2005; Melis et al. 2009). In these activities, chimpanzees understand when they need help from a partner to succeed, and they actively choose to collaborate with better cooperators (Melis et al. 2006a, b). But there is controversy about whether chimpanzees in these situations are really operating with a joint goal involving a mutual commitment that both receive their share of the spoils (e.g. see Boesch 2005; Tomasello et al. 2005). It is therefore unclear whether a collaborative problem-solving context would facilitate chimpanzees' helping behaviour as it does human children's.

In the current study, we followed the general experimental design that Hamann et al. (unpublished data) used with human children, but with a modified apparatus in which the pair of subjects could collaborate to pull a food platform two 'steps' down a rail (each pulling on one end of a string). As in the child study, in the experimental condition the subject got its reward early but could then potentially follow through and help the partner get one as well, whereas in the control condition the subject had the opportunity to help the partner (by doing exactly the same thing as in the experimental condition) but outside the context of collaboration. This design enabled us, first, to investigate in a new situation whether chimpanzees would help a conspecific obtain food, given that they could not obtain that food for themselves, by collaborating. Second, we could assess whether chimpanzees would help a conspecific without solicitation, however defined, because in this situation partners seldom solicited help (they simply held an end of the string and waited to see what would happen). Finally, we were also able to evaluate the effect of cooperative context on chimpanzee helping. Specifically, we compared how often the two partners obtained rewards when they could cooperate to receive rewards at the same time (mutualism), when one partner needed the help of the partner who had already received its reward for free (helping without collaboration), and when one partner needed the other's help after they had already begun cooperating (helping during collaboration). If chimpanzees cooperate with truly joint goals and commitments, they should behave like the 3-year-old children and help most often in the mutualistic and helping after collaboration conditions, and less often in the helping without collaboration condition.

## METHODS

### Subjects

Subjects were 12 chimpanzees housed at the Wolfgang Köhler Primate Research Center at the Leipzig Zoo, Germany. Eight subjects lived in a social group composed of 17 individuals (three adult males, eight adult females, three adolescents and three youngsters). The other four subjects lived in a social group composed of six individuals (three adult females and three adolescents). Chimpanzees were fed a variety of fruits, vegetables and cereals. Subjects were never food deprived and water was available ad libitum. The groups spend the daytime in an outdoor area (4000 $m^2$ for the large group and 1400 $m^2$ for the small group) and an indoor area (400 $m^2$ for the large group and 175 $m^2$ for the small group) both of which contain climbing structures, natural vegetation, streams and enrichment devices. The groups spend the night in a series of sleeping rooms (about 47 $m^2$ for the large group and 32 $m^2$ for the small group). Subjects were tested in their sleeping rooms with a familiar experimenter.

Each subject was tested separately with two partners from their social group for a total of 12 test pairs (one mother–offspring pair, two father–offspring pairs, and nine pairs that were either half-siblings or unrelated). Because we were not examining how tolerance or dominance impact helping behaviour, we simply tried to pair individuals that we felt confident were tolerant enough of each other to interact with the apparatus at the same time. (Ethical concerns prevented the pairing of individuals if it could cause stress to the subjects or disruption in the group: for example, the two dominant adult males.) In pairing individuals, we relied on data from an ongoing observational study of dominance relations within the large chimpanzee group, the advice of keepers and other researchers, and whether the individuals had cooperated with a conspecific in a previous study (Melis et al. 2006b). Nine of the 12 subjects had previously been tested in a cooperative pulling task that examined effects of tolerance and competition on cooperation although only one pair tested in the current study (Robert and Patrick) had worked together in this previous experiment (Melis et al. 2006b). See Table 1 for more information on the subjects' background, partners and experimental history.

*Apparatus*

The apparatus was mounted in an experimental booth consisting of three mesh panels and one open side (1.2 m wide × 1.0 m long). When tested, two individuals could sit on either side of the booth and were separated by a door. The experimenter, E1, always sat on the open side of the booth. Two identical shelves (26.6 cm wide × 75.6 cm long × 27.5 cm high) were attached to opposite sides of the booth and a sliding platform (85.0 cm wide × 20.0 cm long × 1 cm high) could be attached to and slide along tracks on the two shelves. A rope (330 cm) could be threaded through a metal loop in the middle of the platform such that if both ends were pulled, the platform would slide across the shelves. If only one end of the rope was pulled, it would come free from the mesh and be inaccessible. The apparatus was baited by placing rewards in two holes (diameters 7.1 cm) in the sliding platform. Each shelf had two

openings, one at the 'middle position' and one at the 'end position' (Fig. 1). E1 could close each opening by inserting a red tile. If the baited platform slid across an opening that did not have a red tile inserted, the reward would fall through the opening and into a ramp where the subject could take it. In all trials, two openings were closed and two remained open. Rewards were either grapes, pieces of apple or banana, or banana-flavoured pellets but were always the same for each partner in a pair and for all of a pair's test sessions.

Two stoppers were located on the shelves. The first stopper, operated by E1, was located at the middle position to ensure that subjects could not simply pull the platform all the way to the end position with one quick motion. The stopper consisted of two screws that were inserted vertically into each shelf, preventing the shelf from sliding further. Whenever subjects pulled completely to the middle position, E1 released the stopper by pulling on two strings attached to the underside of the screws, therefore allowing the platform to continue sliding if pulled. Because E1 always released the stopper, it did not alter the subjects' pulling behaviour, but simply prevented the platform from sliding all the way to the second stopper without subjects continuing to pull or pulling a second time. The second stopper was fixed in place after the end position and stopped the sliding platform when it reached the back of the shelves.

*Design*

After a training phase (see below), we conducted eight test sessions per pair over the course of either 7 or 8 days. The main measure was whether subjects continued to pull to the end position. We tested five conditions by manipulating three features of the apparatus. First, we manipulated which openings were closed at the middle and end positions. Second, we manipulated whether the sliding platform started at the middle or end position. Third, we manipulated how the rewards were baited. Either both rewards were baited into the sliding platform requiring subjects to cooperate or one reward was baited into the sliding platform while the other was dropped directly into one partner's ramp where it could be retrieved immediately.

The five conditions resulting from these manipulations are shown in Table 2. In the baseline condition, the pair could pull the sliding platform from the front position and both receive their reward at the middle position with no need to continue pulling to the end position. In the mutualism conditions, the pair could pull the sliding platform from the front position (mutualism 1) or the middle position (mutualism 2) and both receive their reward at the end position. In the helping without collaboration condition, the sliding platform started at the middle position. E1 baited one subject's side of the sliding platform with a reward while dropping the other reward directly into the other subject's ramp at the end position; in other words, one partner got her reward 'for free' (Fig. 1a). In the helping during collaboration condition, the pair could pull the sliding platform from the front position to the middle position where only one partner was rewarded and then continue pulling to the end position where the other partner was rewarded (Fig. 1b).

Half of the pairs had the helping without collaboration trials as their first altruism condition and the other half had helping during collaboration first. Which type of helping trial was given first within a session alternated for the first four sessions. For the second four sessions, each pair started with the type of helping they had not started with in the first four sessions and again alternated across sessions.

*Procedure*

Before entering the test phase, subjects first went through a training phase to ensure that they understood how the apparatus

**Table 1**
Summary of subjects and their previous test experiences

| Subject | Sex | Age (years) | Rearing history | Partners (P1, P2) | Relation to partners | Experimental history |
|---|---|---|---|---|---|---|
| Alex | M | 7 | Nursery/ peers | P1: Fifi P2: Gertruida | P1: none P2: none | 2, 3 |
| Fifi | F | 15 | Mother | P1: Alex P2: Jahaga | P1: none P2: half sister | 1 |
| Gertruida | F | 15 | Mother | P1: Jahaga P2: Alex | P1: half sister P2: none | 1 |
| Jahaga | F | 16 | Mother | P1: Gertruida P2: Fifi | P1: half sister P2: half sister | 1 |
| Pia | F | 9 | Mother | P1: Lome P2: Ulla | P1: half sister P2: none | — |
| Lome | M | 7 | Mother | P1: Pia P2: Corry | P1: half brother P2: son | — |
| Corry | F | 32 | Nursery/ peers | P1: Ulla P2: Lome | P1: half sister P2: mother | 1 |
| Ulla | F | 31 | Nursery/ peers | P1: Corry P2: Pia | P1: half sister P2: none | 1 |
| Sandra | F | 15 | Mother | P1: Robert P2: Frodo | P1: daughter P2: half sister | 1 |
| Robert | M | 33 | Nursery/ peers | P1: Sandra P2: Patrick | P1: father P2: father | 1 |
| Patrick | M | 11 | Mother | P1: Frodo P2: Robert | P1: half brother P2: son | 1 |
| Frodo | M | 15 | Mother | P1: Patrick P2: Sandra | P1: half brother P2: half brother | 1 |

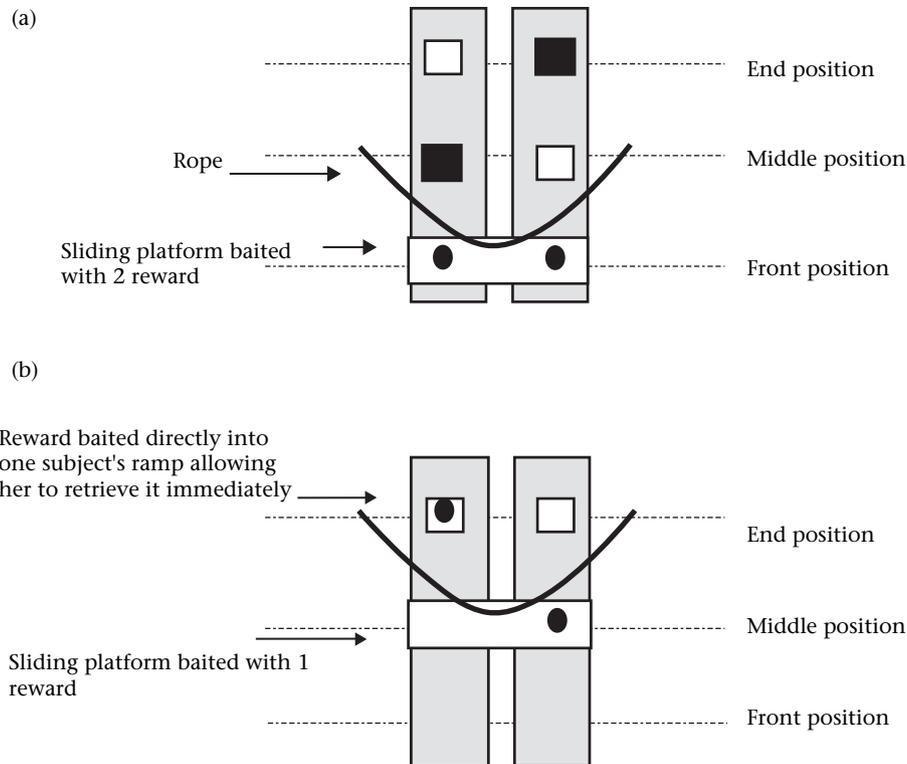(1) Melis et al. 2006b; (2) Warneken et al. 2006; (3) Warneken & Tomasello 2006.

**Figure 1.** Bird's-eye representation of the apparatus. White squares represent open holes in the shelves. Black squares represent holes that the experimenter has closed using tiles. (a) The starting position for the helping during collaboration condition. When both ends of the rope are pulled, the sliding platform will deliver a reward to the subject on the right at the middle position and, if the pair keeps pulling, to the subject on the left at the end position. (b) The starting position for the helping without collaboration condition. One reward is baited in the sliding platform while the other is available to the subject on the left 'for free.'

functioned and how to work with a partner to obtain rewards simultaneously.

*Training*

(1) Demonstration: in this phase, a second experimenter, E2, demonstrated that rewards could be acquired by pulling the rope. The subject sat on one side of the experimental booth and E2 on the other. The door separating the subject and E2 was closed and both ends of the rope were strung through E2's side of the booth. E2 pulled both ends of the rope causing a reward to be delivered to herself and the subject. E2 took his reward, showed the subject that he had also received a reward and pretended to consume it. E1 manipulated the openings at the middle and end positions to create four types of trials that were run in a set order: both openings were open at the middle position and closed at the end position, both openings were closed at the middle position and open at the end

**Table 2**
Description of responses and reward outcomes for each condition

| Condition | Response to middle position | Outcome at middle position (self/other) | Response to end position | Outcome at end position (self/other) |
|---|---|---|---|---|
| Baseline | Collaboration | 1/1 | Collaboration | 0/0 |
| Mutualism 1 | Collaboration | 0/0 | Collaboration | 1/1 |
| Mutualism 2 | None | 0/0 | Collaboration | 1/1 |
| Helping without collaboration | None | 0/1 | Helping | 1/0 |
| Helping during collaboration | Collaboration | 0/1 | Helping | 1/0 |

position, one opening at the middle position and one at the end position were open (and vice versa). This phase consisted of eight trials with the subject and E2 switching sides after four trials. The subject had to retrieve the reward on seven of eight trials to proceed to the next phase.

(2) Individual pulling: in this phase, subjects learned to pull both ends of the rope, that there were always two rewards delivered, and that sometimes it was necessary to continue pulling to the end position to get the second reward. Subjects were tested individually with the door that separated either side of the experimental booth remaining open. Each trial started after E1 showed the subject both rewards, placed them on the shelf, and then strung both ends of the rope through the mesh in one of three positions. In the 'together' position, the ends were through the same mesh hole in the back panel of the booth. In the 'apart' position, the ends were approximately 1 m apart in the back mesh panel of the booth. And in the 'around the corners' position each end was strung through one of the side panels of the booth. The subject had to pull both ends within 30 s and retrieve both rewards within 30 s of pulling for a trial to be considered successful. When the subject succeeded on three consecutive trials or three of four trials, E1 moved the ends of the rope further apart to the next position. If a subject failed to receive at least one reward on four consecutive trials, E1 moved the ends of the rope back to the previous position. E1 alternated through four possible types of trials, as in the previous phase.

(3) Exposure to failure with no partner: this phase was meant to give subjects the experience of failing when only one end of the rope was accessible and there was no partner to pull the other end. The set-up was identical to the final position in the previous phase except that the door separating the sides of the booth was closed. Subjects were tested individually on one side of the booth, where one end of the rope could be pulled. In three consecutive trials, E1

showed the subject both rewards, baited the apparatus and positioned the ends of the rope in the 'around the corners' position. There was no correct or incorrect response for each of the three trials and after 30 s, E1 removed both rewards and the rope regardless of whether the subject had pulled.

(4) Pulling with a human partner: this part of the training was to ensure that subjects were able to wait for their partners to pull their end of the rope. The set-up was identical to the previous phase except that E2 was present on the opposite side of the experimental booth. E2 acted as a programmed partner, pulling his end of the rope after progressively longer delay intervals (0, 5, 10, 15 and 20 s). At the beginning of a trial, he stood on the opposite side of the cage from the booth with his back to the subject and the apparatus. After the delay interval, E2 turned, walked to the apparatus, pulled the rope, and showed the subject when he received his reward. If the subject had already pulled out its end of the rope so that E2's end was no longer accessible, E2 would attempt to reach his end of the rope and pound on his side of the booth as a sign of frustration. If the subject did not try to pull the rope after a few seconds, E2 encouraged the subject to do so. The subject had to wait successfully for the human partner on two consecutive trials to continue to the next delay interval and finally the next phase. Subjects who reached the 20 s delay criterion within the first session had to pass this criterion on the other side as well. Otherwise, subjects alternated sides across sessions. Between trials, the subject was distracted by a keeper and fed low-value grass pellets so that E1 could set up the rope and apparatus without the subject interfering and so that the subject started each trial from the same location. A trial started when the keeper stopped distracting the subject and left the room. If the subject had a dependent offspring that could not be separated, the keeper did not leave the room but instead played with or fed the youngster in a connecting room so that the mother could work on the task without the youngster interfering. E1 manipulated the openings at the middle and end positions to create three types of trials in which both partners were always rewarded at the same time. These three types of trials were identical to the baseline, mutualism 1 and mutualism 2 conditions and were always run in that order. Each session consisted of a maximum of 24 trials. For individuals that showed great trouble in the delay intervals, we ran intermediary trials with less desirable rewards (i.e. carrots) to make it easier for these individuals to inhibit the pulling response and learn the importance of waiting for a partner. All subjects had to reach criteria with the same type of reward that would be used during the test phase.

(5) Pulling with a conspecific partner: this final phase was meant to test whether subjects were able to pull the ropes simultaneously with their partner so that both obtained a reward. Two subjects were positioned in their respective rooms on either side of the experimental booth with the door between rooms closed. As in the previous phase, subjects were distracted while E1 set up for the next trial and trials began when E1 showed subjects the rewards and baited the apparatus. The three types of trials were alternated in the same fashion as in the previous phase, such that both individuals were always rewarded at the same time. So, although in a previous training phase subjects had pulled individually to obtain one reward at the middle position and another at the end position on the other side of the platform, they never experienced this situation when working with a partner. Each pair had to cooperate successfully to obtain a reward each within 1 min on three of four trials or on three consecutive trials from both sides of the booth (a minimum of six trials total).

It took subjects an average of 57.50 trials (range 12–108 trials) to reach the training criteria for the individual pulling phase and an average of 51.50 trials (range 12–155 trials) to reach the training criteria for the pulling with a human partner phase. It took pairs an average of 6.58 trials (range 6–8 trials) to reach the training criteria for the pulling with a conspecific partner phase. Owing to experimenter error, six individuals initially reached criteria using only the baseline and mutualism 1 positions for the pulling with a human partner phase and the pulling with a conspecific phase. They then rereached the criteria using all three reward positions for the pulling with a conspecific phase.

*Test phase*

Test sessions included trials for the five conditions: baseline, mutualism 1, mutualism 2, helping without cooperation and helping during cooperation. Each session began with a pretest in which the pair had to cooperate successfully in one mutualism or baseline trial and was given a maximum of four trials to succeed. Each test session included two trials from each condition for a total of 10 trials. Within a session, a dyad experienced three trials in which they were both rewarded at the same time (two mutualism and one baseline) followed by two helping trials with one individual needing help in the first helping trial and the partner needing help in the following trial. This pattern was then repeated but with the other type of helping condition. Before each set of five trials, E1 dropped a free reward into the apparatus for each individual to maintain the subjects' motivation. The order of the three trials in which both subjects were rewarded at the same time was counterbalanced within pairs. Which side of the booth each individual was located on was alternated across sessions.

Each individual was tested with two partners. Before being tested with a second partner, each individual again reached the criterion for the individual pulling and pulling with a human partner phases and with the new partner reached the criterion for the pulling with a conspecific partner phase. When individuals were tested with the first partner, each trial ended either when each partner had retrieved its reward, when one partner pulled the rope so that it was no longer accessible to the other partner, or if neither of these occurred, after 1 min. Preliminary coding of the subjects' test phase with the first round of partners showed that when partners pulled to the end position they usually did so almost immediately and always within 30 s. Therefore, when individuals were tested with their second partner, we terminated mutualism and helping trials either when both partners had retrieved their reward, when one partner pulled the rope so that it was no longer accessible to the other partner, or if neither of these occurred, after 30 s. We terminated baseline trials when one partner pulled the rope so that it was no longer accessible to the other partner or after 30 s, even if both partners had taken their rewards, to ensure that partners were given sufficient time to pull to the end position.

The test phase for two pairs deviated slightly from this design. We paused testing of Corry and Ulla after they failed the pretest of their second day of testing and were generally unmotivated. They were switched to a more desirable food reward and reached the criteria for pulling with a human partner and pulling with a conspecific partner before again starting the eight-session test. We paused testing of Pia and Lome after the first four test sessions to give Lome two sessions of pulling with a human partner (without any delay interval). This subject, an adolescent, had passed all the training criteria very quickly and showed very forceful, excitable pulling and playing with the rope during the first four test sessions. Our hope was that by giving him more experience pulling the rope, without any explicit training, his excitement would subside and his pulling behaviour would become more deliberate. After these two sessions, he and his partner reached the criterion for the pulling with a conspecific partner phase and proceeded with the remaining four sessions.

*Scoring and Analysis*

All trials were videotaped. E1 coded all pulling responses live and also reviewed the videotape for all helping and baseline trials. In all trials, the dependent measure was whether the pair pulled the platform completely to the back of the shelves. We excluded from analysis 12% of all helping without collaboration trials and 14% of all helping during collaboration trials because the helper did not have an opportunity to help (for example, if the pair did not cooperate to the first stopper in a helping during collaboration trial) or if it was unclear whether the helper had sufficient opportunity to help (for example, if while the helper was still taking the reward, the partner pulled the rope out). A second experimenter blind to the hypothesis being tested randomly selected and coded 20% of trials in each condition. There was 100% agreement between experimenters (Cohen's Kappa = 1.00).

In subsequent analyses, we coded helping requests in all helping trials, regardless of whether help was provided. We defined a 'request' as any communicative signal or outward sign of an individual's desire to get the reward that could indicate to the partner the need for help. Such behaviours could include audible attention-getters (banging on the mesh or clapping), rocking towards the partner or the reward, lifting an arm in the direction of the partner or vocalizing. When help was provided, we coded whether the partner helped immediately after arriving at the apparatus or taking its own reward or after a delay.

When possible, all analyses were done on the level of both the individual and the pair. For individual scores, we calculated the mean percentage of trials in which each subject helped a partner. For pair scores, we calculated the mean percentage of trials in which help was provided within the dyad. Because each subject was tested with two partners, dyad scores could not be considered independent. We therefore report the analyses done on the level of the individual; however, all analyses done on the pair level yielded similar results.

## RESULTS

There was no significant effect for which side of the booth an individual was on, no order effect for the first type of helping trial overall or within a session, and no effect for partner (all $P > 0.2$). Therefore, all subsequent analyses were collapsed across individual location, order and partner. All $P$ values reported are two tailed.

The main dependent measure was whether the pair pulled all the way to the end position. All subjects helped in at least one helping trial, ranging from 6% to 90% of altruism trials. Repeated measures ANOVAs revealed a significant main effect of condition on the dependent measure of pulling together to the end position ($F_{3,33} = 46.38$, $P < 0.001$). Post hoc comparisons using a least significant difference test showed that success was significantly greater in the mutualism condition than in the baseline condition and both helping conditions ($P < 0.001$) and that success in either helping condition was greater than in the baseline condition ($P < 0.001$). Success in the helping during collaboration condition did not differ significantly from success in the helping without collaboration condition ($P = 0.145$). In other words, partners cooperated at the highest rate when both individuals would be rewarded, as opposed to when only one partner or neither partner would be rewarded. Nevertheless, they cooperated more when one partner needed help than when neither partner could benefit, showing that subjects were not pulling indiscriminately but were sensitive to the partner's need for help (Fig. 2).

Because the frequencies of helping upon request or after a delay were so low, we do not report statistical comparisons, but instead use these data to offer a descriptive account of the helping
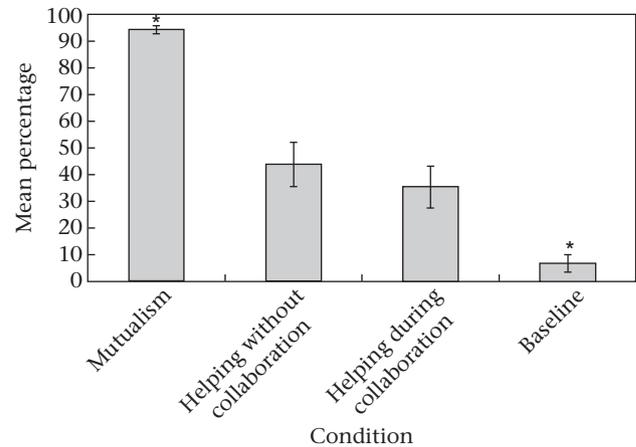


**Figure 2.** Rates of helping (mean ± SE), defined as pulling all the way to the end position with a partner, compared across the five experimental conditions (rates for the mutualism 1 and mutualism 2 conditions are combined). *$P < 0.001$, repeated measures ANOVA.

behaviour observed in this task. Of the 135 trials in which help was provided, only three were preceded by a request. Moreover, in the four other instances of requesting, no helping followed. This suggests that the request of a partner was not an important factor in influencing an individual's choice to help or not. There was perhaps little need or opportunity for requests because if a partner helped, it usually did so almost immediately. In 90% of helping trials in which help was provided, the partner helped immediately. In the remaining 10% of cases, one could argue, the helper needed to reengage in the task to provide help and we should be particularly likely to see requests. However, requests were also given at low rates in these situations. Of the 14 cases in which help was provided after a delay, only two included a potential request. Taken together, these results indicate that if an individual did not help immediately, the partner was not likely to request help. And even if a partner did make a request, it did not seem to enhance the chances that the partner would reengage in the task and help.

## DISCUSSION

The current study adds to a growing body of research documenting the surprising robustness and flexibility of chimpanzee helping behaviour. In just the last few years, experiments with various types of control conditions have established that chimpanzees reliably help either humans or conspecifics by: fetching out-of-reach objects for them (Warneken & Tomasello 2006); opening doors for them (Warneken et al. 2007; Melis et al. 2008); unhooking hooks to release food for them (Melis et al. 2008, unpublished data); bringing a needed tool to them (Yamamoto et al. 2009); and now, in the current study, collaborating with them to pull in a reward even though the subject has already been rewarded.

In the last four of these paradigms, chimpanzees helped a conspecific obtain food. This would seem to be contrary to the findings of Silk et al. (2005) and Jensen et al. (2006), in which chimpanzees seemed indifferent to the food acquisition of a conspecific partner. However, in these two earlier studies the subject was most often working to get food for itself, either on the key trials or on surrounding trials, and so this was clearly in a situation in which the subject had ideas about obtaining food for itself. The overall situation may thus have activated in subjects a food competition mode of operation. In the more recent helping studies, in contrast, helping the other obtain food occurred in situations in which it was absolutely clear that the subject had no

chance of obtaining any food, putting the individual, perhaps, in a less competitive mode of operation.

Another novel finding of the current study was that chimpanzees helped without any kind of 'requesting' or 'soliciting' by the recipient. In all of the previous helping studies, some kind of soliciting behaviour was either always involved or else was shown to facilitate helping. In the current study, at the moment when the recipient needed help obtaining food, after the subject had already obtained its own, there was almost no solicitation, as the recipient was simply standing by with the end of the string in its hand. Given the warm-up procedures and pretests, subjects clearly understood the collaborative nature of the task and that the recipient needed help to obtain any food. We thus think that in previous studies, chimpanzees who helped more after solicitation were not responding to any kind of demand from the recipient, but rather were simply gaining information about the recipient's need for help. Solicitation does not seem important in recruiting support during fights when chimpanzees are interacting naturally within their social groups, a situation where it may be clear that one individual needs help (Hemelrijk et al. 1991).

We should also note that helping a conspecific to obtain food (in noncompetitive contexts), and doing so in the absence of solicitation, suggests that chimpanzees' altruism in these kinds of contexts may not be so different from that of cooperatively breeding nonhuman primates. Thus, marmosets, *Callithrix jacchus*, have behaved in a more altruistic manner than chimpanzees in the paradigm of Silk et al. (2005) and Jensen et al. (2006), leading Burkart et al. (2007, 2009) to suggest that the active food-sharing characteristic of cooperative breeders may lead them to more food-related altruism in experiments and other situations. Results from the current study and others in the helping paradigm, however, suggest that there are not such strong species differences in helping others to obtain food. One plausible hypothesis to explain the pattern of results across studies is that for some reason the Silk–Jensen paradigm activates food competition attitudes in chimpanzees that it does not activate in marmosets. It is noteworthy as well in this connection that cottontop tamarins, *Saguinus oedipus*, also cooperative breeders, are not particularly altruistic in the Silk–Jensen paradigm either (Cronin et al. 2009; Stevens 2010).

A final important result of the current study was that chimpanzees helped others obtain their reward equally often whether the opportunity occurred straightaway or only as a continuation of a collaborative activity. This could be considered further evidence of the robustness of chimpanzee helping behaviour, but it is also different from the behaviour of human children (Hamann et al., unpublished data). One hypothesis is that human tendencies towards altruism and helping evolved initially inside mutualistic collaborative activities, in which helping the partner also helps the subject (i.e. towards their joint goal). The proximate mechanism, as it is manifest in children today, comprises normative pressure (subject to sanctioning via social norms) to follow through in a joint activity until all participants have received their share of the spoils (Tomasello 2008, 2009). It is possible that chimpanzee tendencies towards altruism and helping initially evolved in some other context, perhaps with kin. This hypothesis is lent some plausibility by the fact that there are not so many reports of altruism among nonkin for chimpanzees in the wild, and in all of the experimental studies helper and recipient grew up in the same captive group.

As in any experimental study with individuals who live in long-term social groups, it is possible that helping rates were influenced by the nature of specific social relationships and social interactions that occurred outside of the experiment. Interindividual tolerance and dominance asymmetry can impact success in cooperative tasks in primates and other species (Werdenich & Huber 2002; de Waal & Davis 2003; Melis et al. 2006b; Seed et al. 2008) and could

influence helping tendencies as well. As all of our subjects had near-perfect success in the mutualism condition and helped a partner at least once, we do not believe that any extreme tolerance or dominance issues prevented individuals from acting helpfully. For ethical reasons, we were not able to test all pair combinations and compare helping rates between subjects with different types of social relationships. We believe such systematic comparisons could shed light on social factors that mediate helping tendencies in chimpanzees. It would also be interesting to integrate observational data to explore whether helping rates in such experimental tasks are associated with long-term patterns of association or specific types of interactions that immediately precede testing.

Moreover, these results possibly highlight cognitive differences between humans and chimpanzees. Helping requires an understanding of individual goals, and not necessarily the formation of shared intentions in which both agents perform their actions in pursuit of a joint goal. Perhaps chimpanzees are able to represent the former, but not the latter, evidenced by the fact that the mutualistic context did not increase chimpanzees' tendency to help the other individual because they treated both situations as basically the same. Human children, by contrast, differentiate between these situations, and have a stronger commitment to support each other in collaborative activities with a joint goal. Thus, this finding can be regarded as providing further evidence for the claim that one major differences lies in the ability to represent joint intentions (Tomasello et al. 2005), corroborating the finding that chimpanzees do not form joint goals with others in collaborative activities (Warneken et al. 2006).

In any case, although there are still a number of unanswered questions about both evolutionary origins and proximate mechanisms, the current study, along with others of its type, establishes with growing confidence that outside of food competition situations chimpanzees reliably help others in a variety of ways, even to obtain food and even without active solicitation from the potential recipient. Collaborative activities do not facilitate this behaviour, however, as they do in humans, which may suggest different evolutionary roots for altruistic acts in humans and chimpanzees.

## References

Boesch, C. 2005. Joint cooperative hunting among wild chimpanzees: taking natural observations seriously. *Behavioral and Brain Sciences*, **28**, 692–693.

Burkart, J. M., Fehr, E., Efferson, C. & van Schaik, C. P. 2007. Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 19762–19766.

Burkart, J. M., Hrdy, S. B. & van Schaik, C. P. 2009. Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, **18**, 175–186.

Cronin, K. A., Schroeder, K. K. E., Rothwell, E. S., Silk, J. B. & Snowdon, C. T. 2009. Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. *Journal of Comparative Psychology*, **123**, 231–241.

Dugatkin, L. A. 1997. *Cooperation Among Animals*. Oxford: Oxford University Press.

Dugatkin, L. A. 2006. *The Altruism Equation*. Princeton, New Jersey: Princeton University Press.

Gräfenhain, M., Behne, T., Carpenter, M. & Tomasello, M. 2009. Young children's understanding of joint commitments. *Developmental Psychology*, **45**, 1430–1443.

Graw, B. & Manser, M. B. 2007. The function of mobbing in cooperative meerkats. *Animal Behaviour*, **74**, 507–517.

Hemelrijk, C. K., Klomberg, T. J. M., Nooitgedagt, J. H. & van Hooff, J. A. R. A. M. 1991. Side-directed behaviour and recruitment of support in captive chimpanzees. *Behaviour*, **118**, 89–102.

Jensen, K., Hare, B., Call, J. & Tomasello, M. 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society B*, **273**, 1013–1021.

de Kort, S. R., Emery, N. J. & Clayton, N. S. 2006. Food sharing in jackdaws, *Corvus monedula*: what, why and with whom? *Animal Behaviour*, **72**, 297–304.

Melis, A. P., Hare, B. & Tomasello, M. 2006a. Chimpanzees recruit the best collaborators. *Science*, **311**, 1297–1300.

Melis, A. P., Hare, B. & Tomasello, M. 2006b. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Animal Behaviour*, **72**, 275–286.

Melis, A. P., Hare, B. & Tomasello, M. 2008. Do chimpanzees reciprocate received favours? *Animal Behaviour*, **76**, 951–962.

Melis, A. P., Hare, B. & Tomasello, M. 2009. Chimpanzees coordinate in a negotiation game. *Evolution and Human Behavior*, **30**, 381–392.

Muller, M. N. & Mitani, J. C. 2005. Conflict and cooperation in chimpanzees. *Advances in the Study of Behavior*, **35**, 275–331.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2008. Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society B*, **275**, 1421–1429.

Seyfarth, R. M. & Cheney, D. L. 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, **308**, 541–543.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., Lambeth, S. P., Mascaro, J. & Schapiro, S. J. 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, **437**, 1357–1359.

Smith, J. E., Van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K. & Holekamp, K. E. 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology*, **21**, 284–303.

Stander, P. E. 1992. Cooperative hunting in lions: the role of the individual. *Behavioral Ecology and Sociobiology*, **29**, 445–454.

Stevens, J. R. 2010. Donor payoffs and other-regarding preferences in cotton-top tamarins (*Saguinus oedipus*). *Animal Cognition*, **13**, 663–670.

Tomasello, M. 2008. *Origins of Human Communication*. Cambridge, Massachusetts: MIT Press.

Tomasello, M. 2009. *Why We Cooperate*. Cambridge, Massachusetts: MIT Press.

Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. 2005. Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences*, **28**, 675–691.

Toumela, R. 2007. *The Philosophy of Sociality: the Shared Point of View*. Oxford: Oxford University Press.

Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., Schapiro, S. J. & Povinelli, D. J. 2008. Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour*, **75**, 1757–1770.

de Waal, F. B. M. 2008. Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology*, **59**, 279–300.

de Waal, F. B. M. & Davis, J. M. 2003. Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychologia*, **41**, 221–228.

Warneken, F. & Tomasello, M. 2006. Altruistic helping in human infants and young chimpanzees. *Science*, **311**, 1301–1303.

Warneken, F. & Tomasello, M. 2009. Varieties of altruism in children and chimpanzees. *Trends in Cognitive Sciences*, **13**, 397–482.

Warneken, F., Chen, F. & Tomasello, M. 2006. Cooperative activities in young children and chimpanzees. *Child Development*, **77**, 640–663.

Warneken, F., Hare, B., Melis, A. P., Hanus, D. & Tomasello, M. 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biology*, **5**, e184.

Werdenich, D. & Huber, L. 2002. Social factors determine cooperation in marmosets. *Animal Behaviour*, **64**, 771–781.

Yamamoto, S., Humle, T. & Tanaka 2009. Chimpanzees help each other upon request. *PLoS One*, **4**, e7416.