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Chimpanzees, *Pan troglodytes*, prefer individual over collaborative strategies towards goals

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Chimpanzees engage in a number of group activities, but it is still unclear to what extent they prefer mutualistic collaborative strategies over individual strategies to achieve their goals. In one experiment, we gave chimpanzees the choice between pulling a platform to within reach either individually or collaboratively with a tolerant partner, both strategies having equivalent payoffs. Overall, chimpanzees preferred the individual option, and this preference was independent of the type of reward for which they were working (food or tool). In a second experiment, chimpanzees switched to the collaboration option as soon as the payoff was increased for this option. These results suggest that chimpanzees prefer to work alone in foraging-like situations and choose collaboration only if it maximizes their reward. These results thus make a strong case for the hypothesis that differences between humans' and chimpanzees' collaboration are to a great extent due to motivational differences.

Chimpanzees engage in a number of group activities such as forming alliances and coalitions, boundary patrolling, meat sharing and group hunting (Muller & Mitani 2005). Group hunting behaviour has received much attention and it is particularly interesting given the likely transition from individual to collaborative foraging in human evolution (Sterelny 2007). However, despite many years of observations in the wild (Goodall 1986; Boesch 2002; Watts & Mitani 2002; Gilby et al. 2008), it is still a matter of debate to what extent chimpanzees collaborate (hereafter defined as behaviours in which two or more individuals coordinate their actions to produce outcomes from which both individuals benefit immediately, Warneken & Melis, in press) during group hunts. Differences across field sites have been reported in both hunting frequency and in relation to whether group hunts are collaborative or the result of simultaneous solitary hunts (Boesch 2002; Watts & Mitani 2002; Gilby et al. 2008). Thus, whereas the majority of group hunts (77%) at Tai have been described as collaborative in which individuals perform different and complementary roles and coordinate their actions in time and space (Boesch & Boesch 1989), at Gombe most hunts have been described as simultaneous individual hunts (Stanford 1998). Observations from other field sites are inconclusive regarding the level of coordination between hunters since most observers have argued that it is extremely difficult to follow and document hunters' actions during hunts (Mahale: Hosaka et al. 2001; Ngogo: Watts & Mitani 2002).

Recent experimental studies have helped to specify both the motivational and the cognitive bases of chimpanzee collaboration. From a motivational perspective, chimpanzee collaboration in food retrieval tasks is constrained by their low tolerance levels over food, that is, dominant individuals monopolize all the food (Melis et al. 2006a; Hare et al. 2007). Only pairs who were able to feed together and share food succeeded in pulling a tray containing food towards them. In addition, when food was clumped in the middle of the tray, even among tolerant pairs, dominants tended to monopolize the food and collaboration broke down. This shows that chimpanzees' motivation to coordinate activities is strongly influenced by the likelihood of obtaining some reward.

From a cognitive perspective, experimental data have shown that chimpanzees can quickly learn to coordinate actions with a partner and know when that partner is needed (Melis et al. 2006b). In this study chimpanzees could maximize their payoff, by either recruiting a partner or choosing not to. Chimpanzees recruited a partner, allowing her to enter the test room, only when the task required collaboration but not when the task could be solved individually. This seems totally rational when collaboration entails sharing the spoils at the end, and solving the problem alone allows individuals to keep all of the rewards for themselves. These findings suggest that chimpanzees understand the requirements of collaboration. However, it also suggests that they probably view their partner as

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a social tool to reach their own individual goals, which could point to a major difference in the psychology underlying collaboration in chimpanzees compared to humans. In humans, children prefer to engage in games together with a partner even if the game does not depend on the partner's participation. This is particularly the case if the game has been introduced as a social game, which suggests that they do not view the other person as a social tool to reach their own individual goal, but that instead they view the joint activity as a goal and rewarding in itself (Tomasello et al. 2005; Gräfenhain et al. 2009; Warneken et al., in press).

We investigated chimpanzees' preference to work individually or together with a partner to gain access to a reward. In the first experiment we investigated chimpanzees' preference to perform the same problem-solving task either alone (solo option) or together with a tolerant partner (collaboration option) in a situation in which both options resulted in the same payoff. Because chimpanzees are very competitive over food, we tested them in two conditions, one with food as a reward and another with a tool that allowed them to obtain food later from the experimenter. We hypothesized that using a tool as reward would decrease the potential for competition between partners, increasing the chances that individuals would choose the collaborative option. In the second experiment we increased the payoff of the collaboration option to investigate whether a slight difference in payoffs would motivate chimpanzees to prefer the collaboration option.

Based on previous studies and observations we had two different hypotheses each with different predictions.

Hypothesis 1: chimpanzees are not intrinsically motivated to work together with others and base their decisions to collaborate on expected material payoffs (Melis et al. 2006a, b; Jensen et al. 2007). This hypothesis leads to the following two predictions.

(1) Chimpanzees will always choose the solo option as long as the solo option leads to the same payoff.

(2) Chimpanzees will prefer to collaborate if this option is associated with a higher payoff.

Hypothesis 2: chimpanzees are intrinsically motivated to work together with others and base their decisions to collaborate not only on expected material payoffs, but also on the rewarding aspect of the joint activity (Perelberg & Schuster 2009).

(1) Chimpanzees will choose the collaborative option in both conditions (food and tool) since both options lead to equitable payoffs (in contrast to Melis et al. 2006b where recruiting the partner yielded half the reward), and in addition subjects can benefit from interacting with the partner.

(2) Chimpanzees will choose the collaborative option only in the tool condition, since the food condition creates the potential for competition between partners (a limiting social factor constraining chimpanzees' tendency to work together with others).

EXPERIMENT 1

Methods

Ethical note

Subjects came from a group of semifree-ranging chimpanzees from Ngamba Island Chimpanzee Sanctuary in Uganda. The sanctuary houses a social group of 42 orphaned, confiscated chimpanzees on Ngamba Island in Lake Victoria, Uganda. Throughout the day the entire group has access to the 40 ha forest on the island to forage and roam freely. At night all chimpanzees sleep in a large holding facility (542 m^3) consisting of six rooms with interconnecting raceways. The group is additionally fed four times a day with fruits, vegetables, posho and porridge and water is available ad libitum. The subjects were tested in pairs in familiar rooms of the holding facility (69 m^2) and were separated at all times from the experimenter by caging. The chimpanzees were never food deprived in any way for this study and could stop participating at any time. The research was approved and reviewed by the local ethics committee of CSWCT (Chimpanzee Sanctuary and Wildlife Conservation Trust) as well as the Uganda Wildlife Authority and the Uganda National Council for Science and Technology (File no. EC 635).

Subjects

Thirteen unrelated chimpanzees, eight males and five females 9–19 years of age, participated in this study. For the purpose of the study we needed to make sure that subjects were able and willing to collaborate with each other (Melis et al. 2006a) and therefore needed pairs of highly tolerant individuals. Based on previous studies conducted with the same group of chimpanzees, which investigated their collaborative problem-solving abilities with the same apparatus (Melis et al. 2006a, b, 2008, 2009), tolerant pairs were easy to identify. In the end we tested seven pairs in which both individuals played the role of the subject as well as the partner (see details about roles below), with the exception of two individuals who only participated as subjects and one individual who only participated as partner (Table 1). In addition, another female took part but was excluded from further testing because she was intolerant of all partners with whom we paired her. In the

Table 1
The sex, estimated age, experimental history and the % of solo choices in both experiments for each subject tested in the present study

Pair	Subject	Sex	Estimated age (years)	Experimental history	Experiment 1 (solo choices)		Experiment 2 (solo choices)
					Tool condition	Food condition	
1	Baluku	Male	12	a, b, c, d	58.33	100	0
	Indi	Male	11	a, c, d	75	83.33	0
2	Becky	Female	19	b, d	100	91.67	0
	Sally	Female	19	b, d	33.33	66.67	8.33
3	Kalema	Male	14	a, b, c, d	25	25	0
	Okech	Male	9	a, b, c, d	100	91.67	0
4	Nkuumwa	Female	14	a, b, c	91.67	50	8.33
	Umugenzi	Male	13	a, b, c, d	66.67	75	0
5	Bwambale	Male	11	a, b, c, d	100	8.33	0
	Namukisa	Female	11	a, b, c, d	100	83.33	66.77
6	Yoyo	Female	11	a, b, c, d	83.33	75	8.33
	Bwambale*	Male	11	a, b, c, d			
7	Asega	Male	12	a, b, c, d	91.67	41.67	0
	Umutama†	Male	14	b, c			

Subjects participated in 12 trials per condition (tool and food), administered in two sessions of six trials each. Previous studies in which subjects had worked with the same apparatus: a: Melis et al. (2006a); b: Melis et al. (2006b); c: Melis et al. (2008); d: Melis et al. (2009).

* This individual participated as partner for an additional subject.

† This individual was not tested as a subject since he did not pass the pretests.

previous studies most subjects demonstrated knowledge of the different requirements needed to succeed on the platforms: subjects were able to (1) synchronize and coordinate with their partner, (2) open the door to recruit a partner and (3) use bowls as tools to get food. Those subjects who had no or limited experience with either of these tasks (Table 1) were given similar experience to the rest of the subjects before starting the present study.

Apparatus and set-up

The study was conducted in three adjacent rooms, separated by sliding doors (80 × 80 cm). We used two platforms (17 × 340 cm and 2.5 cm high), each with two feeding dishes (17 × 27 cm and 2.5 cm high) at either end (Melis et al. 2006a, b, 2008, 2009; Hirata & Fuwa 2007). These platforms were placed in the keeper's corridor outside the outer rooms (120 cm), one on each side, so that they were beyond the chimpanzees' reach (Fig. 1 and the movie in the Supplementary Material). A separate rope was threaded through loops in each of the two platforms and their ends were extended into the test rooms through the bars of the rooms. To move one of the platforms within reach, both ends of the rope needed to be pulled simultaneously. The ropes on the platforms could be adjusted by the experimenter according to their function: (1) for the solo platform, the rope ends were knotted together to form a single rope end that could be pulled by a single individual (rope extended 230 cm into the test room); (2) for the collaboration platform, the rope ends were kept separately (280 cm apart from each other), so that they were too far apart to be pulled by just one individual (rope ends extended 35 cm into the test room).

Procedure and design

Warm-up/tolerance test. Subjects and partners were given a brief warm-up using the collaboration platform to refresh their knowledge of the different requirements needed to succeed in the task: subjects opening the doors (removing a peg), partners waiting for the subject to join in and pull in synchrony, subjects and partners using the tools. In this warm-up session the collaboration platform was baited with two pieces of banana (3 cm each) per dish or one bowl per dish. Each dyad then participated in three types of trials: (1) both subjects were released into the test room simultaneously; (2) subject 1 was allowed to open the door, enter the room and join the waiting partner; (3) subject 2 was allowed to open the door, enter the room and join the waiting partner. A trial ended when the pair pulled the platform within reach, or if it failed to obtain the food within 1 min. Each pair had to succeed in six trials (two consecutive trials of each type). This warm-up also revealed whether or not the pair was tolerant enough, that is, none of the individuals tried to monopolize the food (reach for the other's food or take it away).

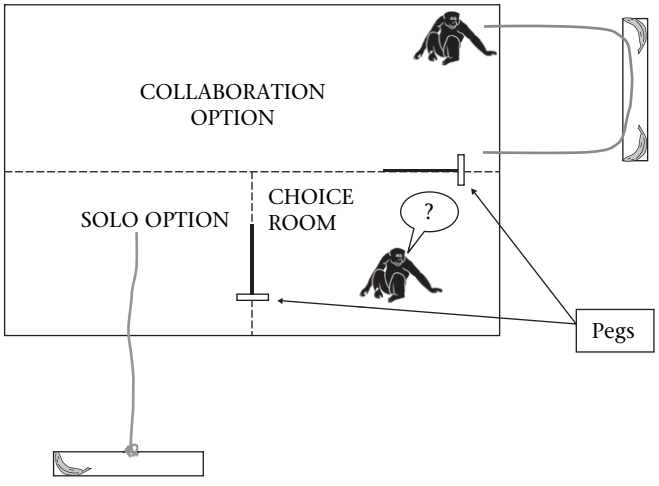

Figure 1. Room layout and set-up in experiments 1 and 2. The platforms were placed in the keeper's corridor beyond the chimpanzees' reach. The position of the different options was counterbalanced across trials and within subjects (see the movie in the Supplementary Material).

Pretests. Subjects entered the choice room through a corridor and had 1 min to choose (by removing a peg and opening a door) to enter one of two rooms where the respective options were presented. After opening one door, the other door was closed so that the other option was no longer accessible. Depending on the type of (pre)test, two of the following options were combined (pretest 1: SO–CI; pretest 2: CO–CI; test: SO–CO).

(1) Solo (SO): the solo platform was positioned beyond the subject's reach. The subject was potentially able to pull the platform within reach without requiring any assistance.

(2) Collaboration (CO): the collaboration platform was positioned beyond the subject's reach and the tolerant partner waited in the room. The subject and partner could potentially pull the platform together to bring it within their reach.

(3) Collaboration impossible (CI): the collaboration platform was positioned beyond the subject's reach but the partner was absent. The subject was therefore unable to pull the platform within reach.

The position of the different options was counterbalanced across trials and within subjects. Three pretests were conducted before starting this test. In pretest 1 the two options were (1) solo (SO) versus (3) collaboration impossible (CI). This served to test the subjects' understanding that without a partner they could only get the reward by pulling the solo platform. In pretest 2 the two options were (2) collaboration (CO) versus (3) collaboration impossible (CI). This tested subjects' understanding that the collaboration platform could only be pulled within reach together with a partner. In both pretests subjects had to choose the correct option and obtain the reward in four consecutive trials. On average, subjects needed 11 trials to pass pretest 1 (mean ± SE = 10.92 ± 0.66) and 15 trials to pass pretest 2 (mean ± SE = 14.83 ± 2.48). To avoid subjects being biased by the pretest they either did first or last, and also to test the subjects' ability to attend and switch reliably between the different options, we gave the subjects sessions of eight more trials (pretest 3), four of which were pretest 1-type trials and four of which were pretest 2-type trials, conducted in a random order. Subjects had to choose the correct option and obtain the reward in three of four trials of each pretest type. On average, subjects needed two sessions (tool condition: mean ± SE = 2.28 ± 0.34; food condition: mean ± SE = 1.75 ± 0.37) to pass pretest 3.

Test. In the test trials the two options were (1) solo (SO) versus (2) collaboration (CO). Both platforms yielded the same payoff for the subject (and partner), that is, two pieces of banana (3 cm each) for each individual. In the food condition the bananas were placed inside the dishes, while in the tool condition one empty bowl was placed inside each dish. Individuals could then approach the experimenter with their bowls, who would then fill them with the bananas, making sure that each individual got its reward. Subjects participated in 12 trials per condition, administered in two sessions of six trials each. The subject within the pair being tested first had to complete an entire set of 12 trials from the first condition, before the same pair was tested in reverse for the same condition. After both individuals had completed the first condition, they switched to the second condition. Subject–partner order was assigned randomly. Which condition subjects received first was counterbalanced across pairs. The position (left/right room) of the different options was counterbalanced across trials and within subjects, with the only constraint that the same option was never placed in the same location for more than two consecutive trials.

Coding and analyses. All trials were recorded by four cameras, two of which focused on the two doors and two of which focused on the two platforms. A trial started when the subject entered the choice room and finished when the subject (and the partner) received the reward. Data came from live coding and coding from videotapes for the following variables: (1) subject's choice; (2) partner's behaviour during the subject's decision-making process, that is, from when the subject entered the choice room until she made a choice. The observed behaviours were separated into three categories: (1) partner waiting silently at the rope; (2) partner waiting silently at the door; (3) partner trying to get the subject's attention by moving the door, stomping or grunting. For analysis of potential reciprocation, we compared subjects' choices between subject 1 and subject 2 across the two conditions (first and second condition).

To assess interobserver reliability, a second coder, ignorant of the hypotheses and the procedure of the study, coded 25% of the videotapes. There was 100% agreement with respect to subject's choice (Cohen's $K = 1.0$) and 86.11% agreement with respect to partner's behaviour (Cohen's $K = 0.80$).

Results

We conducted a 2×2 repeated measures ANOVA (choice $\times$ condition) to determine subjects' preferences and whether these preferences were different across our two conditions (food versus tool). Overall, subjects preferred the solo option over the collaboration option ($F_{1,11} = 12.975$, $P = 0.004$, $\eta^2 = 0.541$; Table 1, Fig. 2). There was no main effect of condition ($F_{1,8} = 0.919$, $P = 0.366$, $\eta^2 = 0.103$), condition order ($F_{1,8} = 0.063$, $P = 0.808$, $\eta^2 = 0.008$) or subject–partner order ($F_{1,8} = 0.017$, $P = 0.900$, $\eta^2 = 0.002$). There was no interaction between choice and condition ($F_{1,11} = 1.097$, $P = 0.317$, $\eta^2 = 0.091$). Furthermore, subjects' behaviour was independent of the condition and the subject–partner order: no interaction could be found between condition and condition order ($F_{1,8} = 0.578$, $P = 0.469$, $\eta^2 = 0.067$), between condition and subject–partner order ($F_{1,8} = 1.588$, $P = 0.243$, $\eta^2 = 0.166$) or condition and condition order and subject–partner order ($F_{1,8} = 0.002$, $P = 0.969$, $\eta^2 < 0.01$).

Subjects chose the solo option on average in 72% (range 25–96%) of the trials: in the tool condition on average in 77% of the trials (range 25–100%) and in the food condition in 66% of the trials (range 8–100%).

Overall, chimpanzees chose the solo option above chance (one-sample t test: $t_{11} = 3.601$, $P = 0.004$) and did not have a side preference (one-sample t test: $t_{11} = 0.031$, $P = 0.976$). The 12 apes as a group chose the solo option above chance in the tool condition (one-sample t test: $t_{11} = 3.544$, $P = 0.005$) but not in the food condition (one-sample t test: $t_{11} = 1.924$, $P = 0.081$). At an individual level six subjects (Baluku, Becky, Indi, Namukisa, Okech, Yoyo) chose the solo option significantly more often than the collaboration option whereas one subject (Kalema) chose the collaboration option significantly more often than the solo option (Table 1). Sex differences for the solo choices could not be detected (independent-sample t test: $t_{10} = 0.837$, $P = 0.422$).

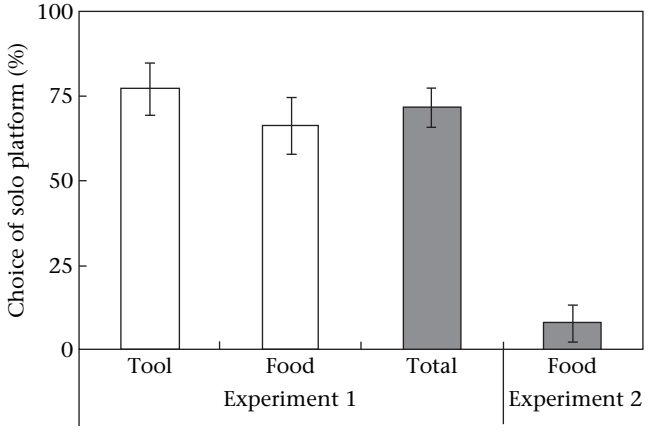

Figure 2. Mean percentage and SE of solo choices for subjects across the two conditions and the totals of experiment 1 and experiment 2 (only food condition).

For 96.5% of the trials, we could determine the partner's behaviour during the subject's decision-making process. Partners mainly waited silently at the door (57.0%, range 9–88%) or at the rope (18.6%, range 0–55%). In 24.4% (range 4–75%) of the trials, partners tried to get the subject's attention by manipulating the door or vocalizing. Neither of these behaviours had any influence on the subject's choice (paired-samples t tests: waiting at rope: $t_{11} = 0.604$, $P = 0.558$; waiting at door: $t_{11} = 0.810$, $P = 0.435$; getting subject's attention: $t_{11} = 0.282$, $P = 0.783$). Overall, subjects' choice did not depend on what the partner had done previously (paired-samples t tests: first condition: choices subject 1 versus choices subject 2: $t_4 = 0.550$, $P = 0.612$; choices subject 2 in first condition versus choices subject 1 in second condition: $t_4 = 0.686$, $P = 0.531$; second condition: choices subject 1 versus choices subject 2: $t_4 = 0.385$, $P = 0.720$).

Discussion

Overall, chimpanzees preferred to act alone rather than with a partner independently of the type of reward (food or tool) for which they were working. Only two male subjects (Kalema and Bwambale), chose the collaborative option (Kalema in both conditions and Bwambale only in the food condition). We cannot easily explain the behaviour of these two males, since from observations outside the test situation they did not seem to be particularly closely bonded with the partners to which they were paired. In fact, in most cases, their partners did not choose to collaborate but instead chose the solo option. However, Kalema, in particular, was going through a period of intense conflict with other males in the group and seemed to be fighting for a higher dominance ranking. Potentially his preference for the collaboration option had to do with recruiting allies.

Overall, we did not find any sex differences regarding the choices made. There was also no evidence for reciprocation between subjects, that is, subjects' choices did not seem to be influenced by their partners' previous choices. Note, however, that the sample size might have been rather small for both analyses (Table 1).

One explanation for the overall preference for avoiding the collaboration option could be that acting together still bears a risk of the partner failing to synchronize and coordinate properly. However, subjects never lost their rewards because of a failure to coordinate effectively. Another explanation could be the threat of competition for food, even if pairs are tolerant. However, when subjects were making a decision or had chosen the collaborative option, we did not observe any intimidation or begging behaviour from the partners that could have led the subject to avoid her/him in future trials. Furthermore, this result was also found in the tool condition, where potential monopolization of food was impossible, as they only received the food from the experimenter subsequently in exchange for the tool. One could argue that the tool does not offer a substantially different reward from the food since the animals had to present the bowl immediately to the experimenter to get the food, rather than at the subject's discretion later on. We cannot completely rule this out. However, we chose to use bowls as tools since the same bowls are used in their daily feeding procedure and individuals are accustomed to them. As long as individuals have their own bowl they are tolerant and respectful of others' bowls. There is never any competition to accumulate bowls, since subjects can get their bowl refilled several times.

Our results show that chimpanzees avoid the collaborative option when there is the alternative of acting alone and obtaining equitable payoffs. This supports the hypothesis that chimpanzees are not intrinsically motivated to collaborate with others (Hypothesis 1). However, it is unclear whether the same subjects would choose to collaborate if that option led to higher payoffs. If this were the case, it would show that subjects are not just generally avoiding their partners, but instead they are choosing to work together with a partner only under certain circumstances.

EXPERIMENT 2

The goal of this experiment was to investigate whether the lack of motivation to work together with a partner in the previous experiment could be overcome by increasing the payoffs in the collaborative option. In this experiment we used only food as rewards.

Methods

Subjects and set-up

The same subjects and dyads as in experiment 1 participated in this experiment and we used the same apparatus and set-up.

Procedure and design

Pretest. Since this experiment was conducted immediately after experiment 1, and subjects had just demonstrated an understanding of the different requirements of the task, they did not participate in the warm-up, tolerance test or pretests of the previous experiment again. However, since the manipulation of this new experiment required individuals to discriminate between different quantities of food, we conducted a pretest to be sure that they could make such a distinction.

All subjects participated in a pretest in which they were confronted with the following two options: (1) solo (SO) with two pieces of food versus (2) solo (SO) with three pieces of food. As in the previous experiment the platforms were positioned beyond the subject's reach. The subject was potentially able to pull the platform within reach without requiring any assistance. Subjects had to choose the solo option with three pieces of food in four consecutive trials to start the test. On average, subjects needed six trials to pass this pretest (mean $\pm$ SE $= 6.33 \pm 0.67$).

Test. In the test trials the two options were (1) solo (SO) with two pieces of food versus (2) collaboration (CO) with three pieces of food. Subjects participated in 12 trials administered in two sessions of six trials each. The subject within the pair being tested first had to complete an entire set of 12 trials, before the same pair was tested in reverse. The position (left/right room) of the two options was counterbalanced across trials and within subjects, with the only constraint that the same option was never placed in the same location for more than two consecutive trials.

Coding and analyses. As in experiment 1 we coded two variables: (1) subject's choice; (2) partner's behaviour during the subject's decision-making process. Interobserver reliability was conducted together with data from experiment 1 and is reported above.

Results and Discussion

The 12 apes as a group chose the collaborative option in 92% of the trials (range 33–100%), significantly above chance (one-sample t test: $t_{11} = 7.714$, $P < 0.001$). Subjects did not have a side preference (one-sample t test: $t_{11} = 1.162$, $P = 0.270$). At an individual level all subjects except one female (Namukisa) chose the collaborative option significantly more often (Table 1, Fig. 2). This very low-ranking female also chose the solo option at very high rates in the previous experiment. It is possible that because of her low-ranking status she generally avoided social contexts related to food.

These results show that the subjects were not generally unwilling to work together with their partners. Previous experience with the partners did not hinder the subjects from choosing them as collaborative partners. The results prove that subjects were extremely attentive and good at keeping track of where and how much food was available and that one additional banana piece was enough to shift a subject's preference towards collaboration. The results extend previous findings with the same chimpanzee population (Melis et al. 2006b) by showing that chimpanzees not only choose collaboration when this is the only solution to the problem, but also when collaboration is associated with minimally higher payoffs in comparison to the solo alternative.

GENERAL DISCUSSION

In the first experiment when given the choice between two alternatives leading to equitable payoffs, chimpanzees preferred to act alone rather than with a partner independently of the type of reward (food or tool) towards which they were working. They switched to the collaborative option, however, as soon as its payoff was minimally increased in comparison to that of the solo option. Both experiments together support the hypothesis that chimpanzees are not intrinsically motivated to work collaboratively with others but that they base their decisions to collaborate on expected material payoffs.

The results of the first experiment are surprising considering that we tried to increase the potential for collaboration by doing the following: (1) pairing highly tolerant subjects and ensuring prior to the test phase that they were willing to collaborate with each other, and (2) adding the tool condition, which we hoped would decrease the potential for competition between subjects. The majority of subjects in this study had enormous experience collaborating in the same task (Melis et al. 2006b, 2008, 2009), and during the present study we never observed any aggression or attempts to monopolize the food among the tested pairs.

We did not find any evidence suggesting that the pairs chose one option over the other depending on what their partner had done previously, that is, no reciprocal interaction occurred. Melis et al. (2008, experiment 1) found some positive evidence indicating that subjects were more likely to recruit a partner after the partner had recruited them. However, in that study subjects had to choose between two different partners and not between a solo and a social option. Furthermore, in Melis et al. (2008) reversal of roles took place within a couple of hours and not on different days (as in the present study). In any case, and even though the sample size in Melis et al. (2008) was bigger than that in the present study, the effect found in their study and in other studies (de Waal 1997) was rather weak. Therefore, the present results suggest that if reciprocation of favours plays a role in guiding the social decisions of chimpanzees, it does not occur in a tit-for-tat manner; nevertheless, it may occur over a longer timescale and this may be evidenced after information has been compiled about the collaborative tendencies of conspecifics from several contexts (Melis et al. 2008; Schino & Aureli 2008; Gomes et al. 2009).

The present study was not designed to test subjects' understanding of the role of the partner and requirements for successful collaboration, since this has already been shown in previous studies with the same chimpanzees (e.g. Melis et al. 2006b, 2009). However, subjects' performance in the pretests, in which they (1) chose the solo platform over the collaboration platform without a partner and (2) chose the collaboration platform with a partner over the collaboration platform without a partner, supports previous findings showing that chimpanzees understand the need

of a partner to succeed in certain tasks (Melis et al. 2006b). Whether chimpanzees differ from social carnivores with regard to the level of behavioural coordination between hunters and the cognitive skills needed to solve new collaborative problems is a question that deserves further study, since similar experimental studies are lacking in other species.

These results can be interpreted in the light of positive correlations between the frequency of collaborative hunts and the difficulties of catching prey that chimpanzees face in the wild (Boesch 2002; Watts & Mitani 2002). In the same way as chimpanzees in this study were able to assess correctly in which situation collaboration was profitable, chimpanzees in the wild could be choosing collaboration only when ecological factors make this option more profitable (in terms of hunting success or energetic costs). In the wild, it is typically the males who engage in group activities. In our study, however, we did not find any sex differences in their choice preference.

The motivation underlying these mutually beneficial collaborative interactions, however, can be totally selfish. The goal of the present study was to investigate whether, similarly to human children, chimpanzees find the joint activity in itself somehow rewarding (Tomasello et al. 2005; Gräfenhain et al. 2009; Warneken et al., in press). We did not find any evidence for this. Despite the fact that the collaborative option would have lessened the energetic cost of pulling and would additionally have benefited the partner, chimpanzees chose to collaborate only when this was associated with a higher payoff for themselves. This suggests that chimpanzees concentrate first and foremost on their own potential gain, acting as rational maximizers and ignoring partners' potential benefits when they are occupied obtaining their own material gains. This is true not only for contexts in which they can deliver benefits to others when acting alone (Silk et al. 2005; Jensen et al. 2006, 2007) but also, as the current study establishes, in a collaborative context. Chimpanzees are more likely to help others altruistically in situations in which they are not preoccupied with obtaining selfish goals and recipients signal their needs or goals (e.g. Warneken et al. 2007; Yamamoto et al. 2009; Melis et al. 2011).

We cannot completely rule out that what chimpanzees are avoiding in this study is not 'collaboration' per se but 'feeding together' with a partner. However, this study explicitly aimed to look at a form of collaboration that culminates in feeding, since collaboration for the purposes of acquiring food (as in collaborative hunting and foraging) played a major role in human evolution (Sterelny 2007). Chimpanzees' preference for working alone in a context related to food acquisition could also be related to their natural foraging behaviour and competition between individuals over food (Hare 2001; Williams et al. 2002; Muller & Mitani 2005).

Overall, this study shows that chimpanzees are aware of, and strategic in, their collaborative options, but do not seem to find the collaborative activity rewarding in itself. Whether these findings are restricted to chimpanzees or can be generalized to all primates is a question that deserves further study. If social organization and associated levels of social tolerance and competition over resources have an influence on individuals' motivation to act together with others, comparative studies with more tolerant species, such as the cooperatively breeding callitrichids (Burkart & van Schaik 2010), the bonobo, *Pan paniscus* (Hare et al. 2007; Hare & Kwetuenda 2010) or human children (Warneken et al., in press), promise to reveal important insights into the evolutionary foundations of primate collaboration.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2011.08.008.

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