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Original Article

Chimpanzees coordinate in a negotiation game

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Abstract

A crucially important aspect of human cooperation is the ability to negotiate to cooperative outcomes when interests over resources conflict. Although chimpanzees and other social species may negotiate conflicting interests regarding travel direction or activity timing, very little is known about their ability to negotiate conflicting preferences over food. In the current study, we presented pairs of chimpanzees with a choice between two cooperative tasks—one with equal payoffs (e.g., 5-5) and one with unequal payoffs (higher and lower than in the equal option, e.g., 10-1). This created a conflict of interests between partners with failure to work together on the same cooperative task resulting in no payoff for either partner. The chimpanzee pairs cooperated successfully in as many as 78–94% of the trials across experiments. Even though dominant chimpanzees preferred the unequal option (as they would obtain the largest payoff), subordinate chimpanzees were able to get their way (the equal option) in 22–56% of trials across conditions. Various analyses showed that subjects were both strategic and also cognizant of the strategies used by their partners. These results demonstrate that one of our two closest primate relatives, the chimpanzee, can settle conflicts of interest over resources in mutually satisfying ways—even without the social norms of equity, planned strategies of reciprocity, and the complex communication characteristic of human negotiation.

Keywords: Chimpanzees; Cooperation; Negotiation; Food; Coordination

Within all social species individuals must negotiate over such things as travel direction and activity timing if they are to avoid the costs of group fissions (see Conradt & Roper, 2005 for a review). However, little is known about how individuals of social species negotiate conflicting interests over resources, since situations involving food and other resources generally do not require individuals to choose between mutually exclusive cooperative options. Meanwhile, when human beings bargain over resources, they typically operate within the context of mutually recognized norms of fairness and equity—the breaking of which leads to negative or punitive reactions from both participants and bystanders (Fehr & Fischbacher, 2004; Fehr & Schmidt, 1999; Rabin, 1993). In addition, when humans interact face-to-face, reciprocity and reputation effects play a very important role (thus, to control for such effects the majority of economic experiments are done anonymously). Thus, in the few existing face-to-face bargaining experiments in which two individuals must agree on a monetary split, humans almost always agree on a 50:50 split (Bohnet & Frey, 1999a, 1999b; Hoffman, McCabe, & Smith, 1996; Hoffman & Spitzer, 1982, 1985; Nydegger & Owen, 1975). In addition, humans can solve conflicts of interest in which an immediate fair distribution of rewards is not possible often by using reciprocally altruistic strategies, essentially taking turns and benefiting over time from cooperation (Andreoni & Miller, 1993; Gaechter & Falk, 2002; Trivers, 1971). In all of these situations, humans' sophisticated skills of communication allow bargainers to coordinate their behavior so that cooperative outcomes can be more easily achieved (Sally, 1995).

One of humans' two closest primate relatives, chimpanzees (*Pan troglodytes*), engage in a wide variety of cooperative activities such as mutual grooming, group hunting, and intra- and intergroup coalitionary behavior (Boesch & Boesch-Achermann, 2000; de Waal, 1982; Muller & Mitani, 2005). Experimental studies have shown that in collaborating to obtain equal food payoffs chimpanzees

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recognize both when they need the services of a partner and which partners are more skillful at cooperation (Melis, Hare, & Tomasello, 2006a). However, although chimpanzees might recognize the benefits of working together with others, it is unclear what mechanisms they have for solving conflicts of interest over unequal resource distributions when collaborating. For example, there is conflicting evidence that chimpanzees are averse to inequity or possess something like a sense of fairness (Boesch & Boesch-Achermann, 2000; Bräuer, Call, & Tomasello, 2006; Brosnan, Schiff, & de Waal, 2005; Jensen et al., 2007a). Furthermore, although chimpanzees engage in reciprocal interactions in different contexts (e.g. Mitani, 2006 although see Gilby, 2006), possibly even involving some kind of mental scorekeeping (so-called calculated reciprocity, de Waal, 1997; de Waal & Brosnan, 2006; see Koyama, Caws, & Aureli, 2006; Melis, Hare, & Tomasello, 2008), there is no evidence that they understand the long-term benefits of taking turns and can use reciprocal strategies in a prospective way to solve conflicts of interest over resource distribution. Indeed, there is experimental evidence that when the division of spoils is made more problematic—for example, when there is a clumped resource that dominants can potentially monopolize—success at collaboration begins to break down (Hare, Melis, Woods, Hastings, & Wrangham, 2007; Melis, Hare, & Tomasello, 2006b).

In the current study, we presented a group of proficient chimpanzee cooperators with a new coordination task they had never before experienced. Unlike other tasks that these same subjects have previously solved skillfully, this new task creates a potential conflict of interest between partners in choosing how to cooperate to obtain food for both. Specifically, we presented pairs of chimpanzees with a choice between two potential food trays, on which two dishes of food were attached (one on each end). One of the trays always had an equal split of food, whereas the other tray always had an unequal split—such that the larger amount was more than the amount on the equal tray whereas the smaller amount was less (e.g., 5-5 vs. 10-1). Subjects had to work together (pulling simultaneously on a rope) in order to bring one (and only one) of the trays within their reach. Failure to agree on a cooperative option within a fixed amount of time ended the trial with neither subject receiving any food.

Based on our own studies and those of others examining chimpanzees' cooperation, it is unclear whether or how chimpanzees might solve such a coordination/negotiation problem. One could easily imagine that cooperation would break down since both partners want the largest reward possible—resulting in disagreement over which tray to retrieve together. One could also imagine that subordinates immediately accept whatever dominants want including the unequal (and for them disadvantageous) tray, since any reward is better than none (as in Jensen et al., 2007a). Finally, one could also imagine that despite an initial conflict of interest, chimpanzees might be able to cooperate and come to a mutually satisfactory solution, perhaps even on a different split than initially made available by the dominant's first choice. To our knowledge, no experimental task with this structure has ever been presented to chimpanzees or any other nonhuman primate (i.e., cooperation is required but a choice of cooperative problems must be negotiated).

1. Methods

1.1. Subjects

Twelve semi-free ranging chimpanzees (five females and seven males, age 4–14 years, M=7.8 years) living in a social group of 39 individuals at Ngamba Island Chimpanzee Sanctuary in Uganda (www.ngambaisland.org) participated in this study. All of the chimpanzees were born in the wild, are unrelated, and are orphans of the illegal trade in chimpanzee bushmeat, having been confiscated from poachers. During the day, the chimpanzees are released to range freely in the 39 hectares of primary tropical forest on the island. In the evening, the chimpanzees return to eat food provided by caregivers and sleep in a large holding facility (4 m high and approximately 140 m^2) consisting of seven rooms (3×5 m) with interconnecting raceways. Therefore, subjects could be tested in their indoor enclosure before being released into the forest each day. To supplement the food they find in the forest, the chimpanzees are also fed four times a day with fruits, vegetables, posho (maize flour cake), and millet porridge. The subjects are not food deprived, and water was available at all times throughout the tests. Subjects could choose to stop participating at any time (e.g., by sitting in front of the exit to the testing room and refusing to participate in the cooperation task) and would be released into the forest for the day.

See Table 1 for the sex, estimated age, and previous experience of each subject, as well as the dominant individual in each cooperative pair. Individuals in each pair were chosen because they were highly tolerant of one another which allowed them to successfully cooperate (Melis et al., 2006a, b). All subjects were skilled at working in pairs in the cooperative pulling task used in the present study as shown by their ability to (1) coordinate and synchronize their behavior to that of their partner (2) actively recruit a partner for cooperation when necessary and (3) distinguishing between a skilled and unskilled partner. This means all subjects understood the role of the partner in their success when they were cooperating. Ten of the subjects demonstrated these skills when tested by Melis et al., 2006a. Meanwhile, two adult females did not participate in Melis et al., 2006a and, thus, were given similar experience as the rest of the subjects before starting the present experiment. They quickly showed that they understood the need for their cooperative partner in this experimental context since they coordinated their behavior to that of the partner, waiting up to 30 s for the partner before pulling.

Table 1
The sex, estimated age, and experimental history of each subject in each pair tested in the present study

Pair	Subject	Sex	Est. Age	Dominance test Exp. 1	Dominance test Exp. 2	Exp. History
1	**Asega**	Male	7	**6***	**6***	1, 2
	Indi	Male	6	0	0	1, 2, 3
2	**Umugenzi**	Male	8	**5**	**6***	1, 2, 3
	Baluku	Male	7	1	0	1, 2, 3
3	**Bwambale**	Male	4	**6***	**6***	1,2
	Okech	Male	6	0	0	1, 2, 3
4	**Bili**	Female	7	**6***	**6***	1, 2, 3
	Namukisa	Female	6	0	0	1, 2, 3
5	**Yoyo**	Female	6	**6***	**6***	1, 2, 3
	Kalema	Male	9	0	0	1, 2, 3
6	**Becky**	Female	14	**6***	3	2
	Sally	Female	14	0	3	2

Although all pairs were highly tolerant of one another, individuals in bold were dominant in a food competition test (see procedure). The number of trials out of six in which each subject in a pair monopolized the food in the competition test is presented. Significant differences between individuals ability to monopolize the food is indicated by an asterisk (binomial probability, $p<.05$). (1) Melis et al., 2006a, (2) Melis et al., 2006b, (3) Warneken et al., 2007.

1.2. Apparatus and setup

The cooperation apparatus and set up was highly similar to previous experiments (Hare et al., 2007; Melis et al., 2006a, 2006b, 2008) with the exception that we used two cooperation trays instead of just one. The two feeding trays were placed out of the subjects' reach (0.9 m) outside two adjacent testing rooms (each 3×5×4 m), separated by a sliding door (80×80 cm) (Fig. 1). The partition between the two rooms was opaque so that subjects could not see each other unless they went to the door. The two trays were 1.5 m apart from each other. Each feeding tray (17 cm×3.4 m) had a feeding plate (17×27 cm) at each end. A rope (5.8 m long) could be threaded through loops fixed on top and across the length of each of the trays so that both rope ends extended from the tray through the metal bars into the testing room. However, the rope's ends in each of the trays were too far apart (3 m) for one individual to pull simultaneously. Therefore, in order to retrieve one of the trays, two individuals were required to pull both ends of the rope simultaneously. If a single individual attempted to retrieve a tray by pulling one end of the rope, the rope came unthreaded from the loops on the tray making the rope ineffectual (based on Hirata & Fuwa, 2007).

1.3. Procedure

1.3.1. Dominance tests

The dominant individual within each pair was identified using a food competition test. A Plexiglas tube (25 cm length) with a piece of banana inside was attached to the metal bars of a testing room. The two subjects were then allowed to enter the room simultaneously to see who obtained the food by monopolizing the apparatus. All pairs participated in two sessions of three trials each before each Experiment (1 and 2) because there was 6 months between the first and second experiment. Dominance was assigned based on who obtained the food in the majority of trials (see Table 1 above for results).

1.3.2. General procedure

All pairs participated in the two experiments. Each pair was tested separately, and each pair was always tested with the same partner throughout all the testing. The two food trays were positioned outside the testing room, the door between the two adjacent rooms was opened, and each of the food plates was baited in full view of the subjects by an experimenter (E). As described below, different amounts of food were placed in each plate depending on the condition. The dominant individual of each pair was allowed to enter the testing room first. Thus, the dominant could double

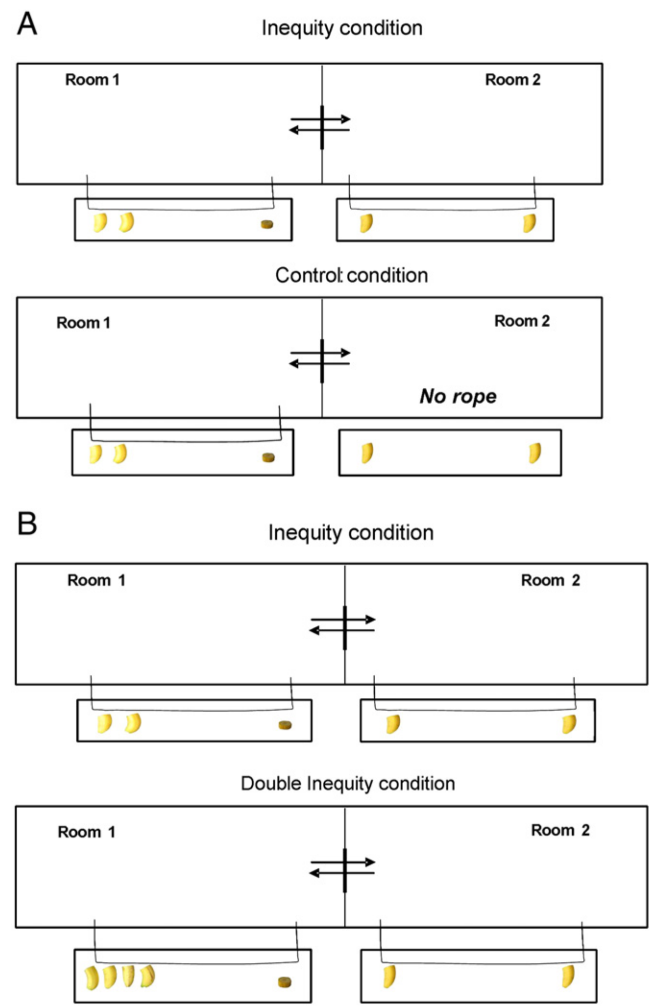

Fig. 1. General setup of the two experiments (1 and 2). In Experiment 1 (A), pairs were presented with the Inequity condition, in which one tray had an unequal split and the second tray had an equal amount of food rewards. In a control condition, subjects could only pull the unequal tray since the tray with equal amounts of food did not have a rope they could pull from. In Experiment 2 (B), pairs were presented with the same inequity condition of the previous experiment, and with a new (double inequity) condition, in which the large amount of food in the unequal tray was doubled.

check the contents of each of the four plates and position herself in front of one of them while potentially holding the associated rope end. Ten seconds after the dominant entered, the subordinate partner was released into the testing room. By allowing one individual to enter first the late comers could see as soon as they entered the testing room what food reward their partners were aiming for (and what they would get for themselves if they accepted). That is, this procedure allowed us more easily to operationalize the behavior of the individual who first entered as an "offer" and the behavior of the individual entering later as a refusal or acceptance. Dominants and subordinates did not switch roles since, based on the dominance tests and a pilot phase, we did not expect subordinates to be able to claim the large reward of the unequal tray. That is, if subordinates would have entered first and positioned themselves in front of the large reward of the unequal tray, dominants would have likely displaced them or subordinates would have abandoned this position when seeing the dominant approach. Since we were interested in subjects' reaction to the offer of a small and unequal reward in the presence of a better alternative, it was important that the "proposer" (individual entering first) was able to unequivocally claim the large reward. Therefore, we always allowed the dominant partner to enter first.

A trial started when the subordinate entered the room and ended when subjects (1) succeeded by working together to pull one of the trays within reach or (2) failed either by having one subject independently pull the rope out of one of the trays (leaving it out of reach) or after 5 min expired with the ropes in place but without a tray being retrieved. In all cases, after a trial ended the door between the two adjacent rooms was closed so subjects understood they could only obtain or attempt to obtain one of the food trays.

In both Experiments 1 and 2, prior to the test, there was an introduction phase in which subjects were familiarized with the rule that they could only obtain one of the trays at the same time that we tested whether subjects could discriminate between the different amounts of food that would be used in the test. Subjects were thus given the choice between two potential trays. The two plates of each tray were baited with the same amount of food, but one of the trays always had a larger amount of food than the other. There was therefore no conflict of interest between individuals. Before the first experiment all pairs participated in the three following conditions: (a) Slice vs. Nothing: one tray had one banana slice per plate while the other tray was left empty; (b) Slice vs. Half: one tray had one banana slice per plate and the second tray a half-banana piece per plate. (c) Half vs. Whole: one tray had one banana half while the other tray had two half-banana pieces (a whole banana) per plate. After each pair finished the introduction trials of Experiment 1, they then participated in the following two test conditions (see Fig. 1):

(a) Inequity Condition: One of the trays was baited with a banana slice in one plate and a whole banana (two-half banana pieces) in the second plate. The plates of the second tray were both baited with a half-banana per plate (note: the total amount of food per tray was nearly identical).

(b) Control condition: the two trays were baited identically as in the inequity condition with the exception that no rope was provided to potentially obtain the tray with a half banana in each plate. Therefore, subjects only had to decide whether and from which rope end they were willing to pull the one tray with unequal rewards.

In Experiment 2, subjects were again given the same introduction from Experiment 1 with the exception that we replaced the Slice vs. Nothing condition with the 2 Whole vs. Whole condition in which one tray was baited with two half-banana pieces (a whole banana) while the other tray was baited with four half-banana pieces (2 whole bananas). As in Experiment 1, after each pair had completed all of their introduction trials they were tested in two test conditions. One of these conditions was the Inequity condition originally used in Experiment 1 while the second condition was new:

(c) Double Inequity condition in which one of the trays had a single banana slice in one plate and four banana halves (2 whole bananas) in the second plate. Meanwhile, the plates of the second tray were both baited with a half-banana per plate. Note that the total amount of food on each tray was not equal. The tray with an unequal distribution had double the amount of food of the other tray.

1.4. Design

In the introduction of both experiments (1 and 2), subjects participated in three sessions of six trials each in which they received two blocks of three trials. In each trial-block, each of the three conditions of the introduction was presented once in a mixed order with the constraint that both the first condition presented and the overall order of conditions were counterbalanced across pairs. Therefore, in each of the two introductions, each pair received a total of six trials, with each of the three conditions for a total of eighteen trials.

In the test phase of both Experiments 1 and 2, all six pairs participated in both conditions, receiving 16 trials per condition or 32 trials total per experiment. In both experiments, the two test conditions were administered in a blocked design. In addition, the first condition presented was counterbalanced across pairs (half of the subjects received one condition first while the other half received the other condition first). In the first experiment, subjects received two sessions per condition (or eight trials per session). The same general alternating block design was used in Experiment 2 except we reduced the number of trials per session so that a single individual would not obtain more than six bananas per session in Experiment 2. This is because the potential food payoff was much larger in Experiment 2. By lowering the trial number, we could maintain food motivation throughout the test session even though it was possible for some individual to acquire large amounts of food in just a few trials of the double inequity condition. All pairs participated first in Experiment 1 and then in Experiment 2.

1.5. Coding and data analysis

A number of behavioral measures were coded within every trial, but the main three behaviors coded were the initial offers made by the dominants, the first rope touched by the recipient (subordinates) upon entering the testing rooms, and the final outcome of the negotiation.

We defined the *initial offer* made by the Dominant (proposer) in each trial as the half of the food tray that she was sitting nearest while facing a food plate as the Subordinate (recipient) first entered the testing rooms (proposers typically made conspicuous offers by sitting in front of the plate they wanted to retrieve while holding the associated rope end). Therefore, there were three possible types of initial offers that proposers could make depending on where they were positioned when the recipient entered: (1) Equal offer: the proposer was positioned nearest one of the plates on the equal tray; (2) Selfish offer: the proposer was positioned nearest the food plate with the largest amount of food on the unequal tray and (3) Altruistic offer: the proposer was positioned nearest the food plate with the smallest amount of food on the unequal tray.

We also coded the *initial response* of the subordinate (recipient) to the dominants' initial offer. We did this by scoring which of the four potential ropes' ends the recipient first touched upon entering the testing rooms. The strength of this measure is that it reveals the subjects' immediate response to the initial offer before being influenced by the dominants actual behavior in the ensuing negotiation. Therefore, recipients could either (1) accept the dominant's initial offer by touching the other rope end to the same rope on the same tray that the dominant was near or holding when they first entered; (2) they could refuse an offer by touching a rope end on the opposite tray to the one the dominant was near or holding the rope for (effectively making a counter-offer); or (3) they could refuse to participate and not touch any rope (this rarely happened).

The third main measure was the *final outcome* of the interaction. The final outcome was not only defined as whether the pair was successful at cooperating to obtain one of the trays but also by what amount of reward the proposer and recipient received. A *selfish outcome* was scored when the pair succeeded to cooperate but the proposer received the largest food plate and the recipient the smallest food plate on the unequally baited tray. An *equal outcome* was scored when the pair cooperated and both partners received equal amounts of food from the tray with two equally baited plates. An altruistic outcome was scored when the pair cooperated, but the proposer received the smallest food dish and the recipient the largest food dish on the unequally baited tray. A *failed negotiation* was scored when subjects did not successfully retrieve one of the two trays within the 5-min trial (either no tray was pulled or one subject pulled a rope out without coordinating with their partner).

Occasionally, no clear initial offer was made by the proposer (9% of trials). This happened when a proposer was not sitting in front of either tray closer to one or the other food plate and was instead moving between testing rooms at the moment the subordinate subject was entering the testing rooms. Therefore, since no initial offer could be coded, we only scored the final outcome in these trials and only included them in the analysis of overall levels of cooperation.

We also coded the time it took subjects to solve the cooperative problem presented as well as examining their use of various forms of communication. Latencies to reach agreement were scored for each trial by measuring the amount of time between the moment the subordinate individual entered the testing rooms and the moment in which subjects started pulling together one of the trays within reach. We also coded a number of potentially communicative behaviors. We coded subjects more subtle "watching" behavior or all instances in which subjects had yet to agree on a tray to pull and would visually monitor their partners' behavior. We scored "watches" when subjects were in different rooms and one of the two in the pair went to the door between rooms and watched their partner. This measure includes both quick checks (i.e., subjects running in and out of the partner's room) and longer stares where subjects would normally sit at the door and watch their partner for over 5 s. We further distinguished which proportion of these instances were followed by (1) the partner immediately following the watcher, (2) the watcher joining the partner, or (3) watcher returning to original position. Finally, we also looked for any kind of more overt communicative signals between subjects such as the use of gestures or vocalizations.

All analyses were conducted using percentages of trials in which the different types of offers and outcomes occurred (percentages were used since initial offers did not occur at equal rates across conditions). Only trials in which initial offers were coded (91%) were used in the analysis. Finally, analyses of levels of acceptance or refusal of initial offers by the recipients were also conducted using percentages of trials in which the different types of offers occurred. All values reported are Means and standard errors.

The analyses of preferences in the introduction of both experiments were all done using one-tailed Wilcoxon exact tests because based on studies showing that chimpanzees can discriminate different quantities (Hanus & Call, 2007), it was predicted that pairs would prefer to retrieve the tray with larger amounts of food. For the test phase of both experiments (1 and 2) the overall analysis of offers within condition was done by comparing the percentage of the three types of offers using a nonparametric Friedman's test followed by paired comparisons with Wilcoxon exact tests. We only conducted two paired comparisons of types of offers, since we were interested in the dominants' preference to obtain the largest amount of food: and therefore tested selfish vs. equal offers and selfish vs. altruistic offers. Based on previous work showing that chimpanzees do not actively give food to others (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005) and based on the introduction of the current study in which subjects preferred the tray with the largest amount of food, it was predicted that dominant proposers would prefer to offer the subordinate recipients the selfish option (the small reward on the unequal tray) more often than the altruistic option on the unequal tray or the equal option on the equal tray. Therefore, all within-condition comparisons of offers were one tailed. All other analyses—success, latencies, levels of final acceptance or refusal (responses or final outcomes) and subordinates' first rope touch of the different offers within and across conditions—were two tailed, since we did not have clear predictions. Based on the results from Experiment 1 (see below), we predicted that in Experiment 2 subordinates would accept equal offers more often than unequal-selfish offers, and therefore, these analyses are also one tailed. All coding was done from videotape by the first author. To test reliability, 20% of the trials were coded independently by a second coder who was blind to the hypotheses tested and agreement was good to excellent for all variables (initial offer: κ=0.85; first rope touch: κ=0.92; final outcome: κ=0.98; "door-watching" behavior: κ=0.96, latencies: r (n=168)=0.96, p<.001).

2. Results

In the introduction of Experiment 1 and 2—when there was no conflict of interest—pairs were highly successful in agreeing to obtain the tray with more food for them both. In Experiment 1, subjects preferentially pulled the tray with the biggest quantity of food for them both the vast majority of the time (mean pulls±S.E.M.: Slice vs. Nothing=95.8% ±4.2% vs. 4.2%±4.2, n=6, T=21, p=.016; Slice vs. Half=18.2%±7.6% vs. 81.8%±7.6%, n=6, T=15, p=.031; Half vs. Whole: 33%±7.7% vs. 67%±7.7%, n=6, T=10, p=.063, Wilcoxon exact test). Similarly, in Experiment 2, subjects preferentially pulled the tray with the biggest quantity of food for them both (mean pulls±S.E.M.: Slice vs. Half=0% vs. 100%, n=6, T=21, p=.016; Half vs. Whole=22%±8.3% vs. 78%±8.3%, n=6, T=15, p=.031; 2 Whole vs. Whole=86.7%±6.7% vs. 13.3%±6.7%, n=6, T=21, p=.016, Wilcoxon exact test, one-tailed).

2.1. Experiment 1

Table 2 presents the mean percentage of initial offers and the final outcome of the interaction in the two test conditions of Experiment 1. In the Inequity condition, there was a significant difference regarding the initial offers made by the dominant (Friedman test: χ^2=10.174, df=2, p=.002). Dominants tended to offer the selfish more often than the equal option (Wilcoxon exact test: n=6, T=14, p=.06; one-tailed), and offered the selfish significantly more often than the altruistic option (Wilcoxon exact test: n=6, T=21, p=.016; one-tailed). Thus, dominants' initial offers were primarily selfish that is, they positioned themselves in front of the plate with the most food on the unequal tray about 59% (±6.7) of the time, whereas they positioned themselves in front of the equal tray only about 37% (±4.2) of the time (they made altruistic offers with the unequal tray only about 4% of the time). Subordinates' initial response to these initial offers immediately after entering the testing room varied depending on the type of offer made by the dominants (recall, initial response was measured by looking at the first rope touched by the subordinate). Subordinates were more likely to join their partner (touching the rope of the offered tray) if dominants were offering the equal tray than if they were offering the selfish tray (mean first touch±S.E.M.: equal tray=67%±8% vs. selfish tray=19%±11%, Wilcoxon exact test: n=6, T=21, p=.03). This pattern is consistent with the final outcome of the interaction, which also varied depending on the type of initial offer made by the dominant: equal or selfish (ignoring altruistic offers as they were so infrequent) (see Table 2). Subjects ended up pulling the dominants' initial offers more often if the offer was equal than if it was selfish (mean final outcome±S.E.M.: Equal tray=87%±8.5% vs. selfish tray=45%±15%, Wilcoxon exact test: n=6, T=21, p=.03, Fig. 2A). This pattern was also reflected in the latencies to solve the coordination problem, with subjects tending to need less time to "agree" on a tray to pull when the dominant's initial offer was equal than when it was selfish (Mean latency to pull±S.E.M.: equal tray=8.8 s±1.9 vs. selfish tray=23.8 s±8.6, Wilcoxon exact test: n=5, T=15, p=.06). The most interesting situation was when the dominant made an selfish offer and the subordinate did not immediately accept (about 55%±15% of the time). Approximately half of the time in this situation the pair ended up

Table 2
Proportional distribution of initial offers (made by the dominants) and final outcomes for each condition in Experiment 1

Condition	Offer	Final Response/Outcome	
Inequity [83% success]	Altruistic: .04	Accept: .75	
		Refuse: .25	
	Equal: .37	Accept: .87	
		Refuse: .13	
	Selfish: .59	Accept: .45	
		Refuse: .55:	Altruistic: .06
			Equal: .25
			Breakdown: .23
Control [92% success]	Altruistic: .08	Accept: .67	
		Refuse: .33	
	Selfish: .92	Accept: .94	
		Refuse: .06:	Altruistic: .03
			Breakdown: .03

Final responses and outcomes refer to the percentage of offers that were finally accepted or refused. Refusals could end up without agreement (cooperation breakdown), or agreement on a new split.

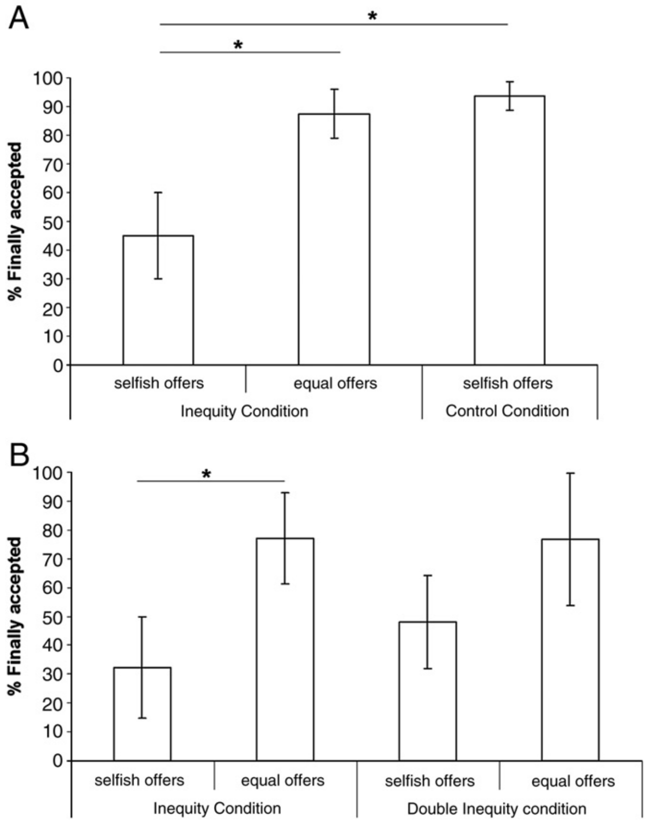

Fig. 2. Mean percentage (±S.E.M.) of initial selfish and equal offers that subjects finally accepted. (A) Experiment 1. (B) Experiment 2. See Results section for further details.

pulling in the equal tray (25.5%±12% of the selfish offers overall). Almost as often (23%±15% overall) they ended up coming to no agreement. The altruistic outcome in which the subordinate obtained the large amount from the unequal tray was infrequent: 6.5%±4% (Table 2).

In the Control condition in which only one tray was available and it was unequal (the other baited tray was present, but with no rope), we expected that subordinates, knowing that there was no alternative, would accept anything. As expected, dominants made many more selfish than altruistic offers on the one available tray (mean initial offers± S.E.M.: selfish offers=92%±4.6% vs. altruistic offers=8%± 4.6%, Wilcoxon exact test: n=6, T=21, p=.016; one-tailed). Subordinates accepted these selfish offers almost all of the time (94%±05%), and more often than when there was a better alternative available in the inequity condition above (Wilcoxon exact test: n=6, T=21, p=.03, Fig. 2A). Subjects also tended to come to an agreement (i.e., final outcome) twice as fast when dominants offered the selfish split in the control condition than when the dominant made the same offer in the presence of a better alternative in the inequity condition (Mean latency to final outcome±S.E.M.: Control condition=10.4 s±5.3 vs. Inequity condition=23.8 s±8.6, Wilcoxon exact test: n=5, T=15, p=.06).

Overall, subjects were highly successful in both the inequity and the control condition at pulling together to retrieve one of the trays—regardless of the initial offer and the initial response to that offer. There was no difference in success cooperating between the two conditions (mean success retrieving a tray±S.E.M.: Control condition=92% ±4.4%; Inequity condition=83%±5.1%, Wilcoxon test: n=6, T=11, p=.35).

2.2. Experiment 2

Table 3 presents the mean percentage of initial offers and final outcome of the interactions in the two test conditions of Experiment 2. In the inequity condition, essentially all of the results from the first experiment replicate. Again, there was a significant difference regarding the initial offers made by the dominants (Friedman exact test: χ^2=11.565, df=2, p<.001). Dominants again offered the selfish more often than the equal option (Wilcoxon exact test: n=6, T=15, p=.031; one-tailed) or the altruistic option (Wilcoxon exact test: n=6, T=21, p=.016; one-tailed, see Table 3). Subordinates' initial response (first rope touched) was like in the previous experiment: they were more likely to join their partner if the tray being offered had the equal split (mean percent first touch±S.E.M.: equal offer=64%±16% vs. selfish offer=23%±15 Wilcoxon exact test: n=6, T=15, p=.03, one-tailed). Likewise, by looking at the final outcome, subordinates ended up accepting initial equal offers at higher rates than initial selfish offers (Wilcoxon test: n=6, T+=15, p=.03, one-tailed, Table 3, Fig. 2B). Refusals to equal offers only occurred occasionally, in addition this was almost exclusively observed among one pair (the youngest pair of males), whose dominance relationship did not seem as stable or as established as that of the other pairs. That is, the subordinate individual in this pair occasionally refused the

Table 3
Proportional distribution of initial offers (made by the dominants) and outcomes for each condition in Experiment 2 (as explained in Table 2)

Condition	Offer	Final response/ outcome	
Inequity [94% success]	Altruistic: .01	Accept: 0	
		Refuse: 1	
	Equal: .36	Accept: .77	
		Refuse: .23	
	Selfish: .63	Accept: .32	
		Refuse .68:	Altruistic: .09
			Equal: .56
			Breakdown: .03
Double Inequity [78% success]	Altruistic: .02	Accept: .50	
		Refuse: .50	
	Equal: 07	Accept: .77	
		Refuse: .23	
	Selfish: .90	Accept: .48	
		Refuse: .52:	Altruistic: .08
			Equal: .22
			Breakdown: .22

equal offers and attempted to obtain the large reward of the unequal tray, which he was then often able to obtain. With regard to the latencies to come to an agreement we found in both the inequity and double inequity conditions combined that, as in the previous experiment, subjects needed less time to agree on a tray to pull when the dominant's offer was equal than when it was selfish (mean latency to pull: equal offer=15.6 s±6; selfish offer: 30.9 s±8, n=5, T=21, p=.031, Wilcoxon exact test).

In the double inequity condition there were significant differences regarding the offers made (Friedman exact test: χ^2=11.143, df=2, p=.001). Dominants again initially offered the selfish more often than the equal option (Wilcoxon exact test: n=6, T=21, p=.016; one tailed), and the altruistic option (Wilcoxon exact test: n=6, T=21, p=.016; one tailed). Since, in three of the six pairs, dominants did not make a single equal offer in the double inequity condition, we could not make the same within-condition comparisons as in the previous condition (Fig. 2B).

Given the fact that the payoffs were higher in the selfish option of the double inequity condition than the inequity condition, we compared offers and final outcomes between the two conditions. First, dominants made selfish offers more often in the double inequity condition than in the inequity condition (mean percent selfish offers±S.E.M.: double inequity=90%±5%; inequity=63%±6.6%, Wilcoxon exact test: n=6, T=21, p=.031). Second, there was a strong trend regarding the proportion of selfish offers that ended in an equal outcome across conditions. These initial selfish offers ended up in equal outcomes more than twice as often in the normal inequity condition as in the double inequity condition (mean percent of selfish offers ending in equal outcome: inequity condition=56%±18%; double inequity condition=22%±11%,Wilcoxon test: N=6, T+=15, p=.063). Moreover, the proportion of selfish offers that ended up in no resolution (i.e. failure to cooperate) was only 3% (±02) in the inequity condition while it was 22% (±09) in the double inequity condition. However, this difference was not statistically different (Wilcoxon test: n=6, T=18, p=.19).

Overall, subjects were highly successful in both the inequity and the double inequity condition in agreeing to pull one of the trays—regardless of the initial offer and the initial response to that offer. In addition, there was no difference in cooperation success between the two conditions although subjects tended to be less successful in the double inequity condition (mean success retrieving a tray± S.E.M.: Inequity condition=94%±4.4%; Double Inequity condition 78%±5.1%, Wilcoxon test: n=6, T=19, p=.094).

2.3. Adjustments of dominants' offers over time

In both experiments, we looked at whether dominants learned to adjust their behavior and offered more equal splits in the second session of the experiment. We found no difference in the percentage of equal offers between the first half and the second half of the inequity condition of Experiment 1 (Equal offers first half: 35%±7.6%, second half: 33%±7%; Wilcoxon exact test: n=6, T=11, p=1.0), and no difference in the percentage of equal offers between the first half and the second half of the inequity condition of Experiment 2 (equal offers in first half: 31%±4.5%, second half: 40%±8.3%, Wilcoxon test: n=6, T+=12.50, p=.25). We could not perform the same analysis in the double inequity condition of Experiment 2 since 3 subjects never offered the equal tray.

2.4. Characterization of chimpanzees strategies

The following patterns were observed among the 6 chimpanzees pairs:

Selfish/despotic: In two of the pairs (33%; 1 male-male; 1 female-male) the subordinate individual tended to accept any type of initial offer relatively quickly (including selfish offers).

Equal pairs: In two of the pairs (33%; 1 male-male; 1 female-female) the dominant almost always initially proposed a selfish split. However, the subordinate partner refused to join her/him, staying at the equal tray, sometimes even without final agreement to cooperate. Overall, these two pairs tended to agree on pulling the equal tray most often.

Tolerant/reciprocal pairs: In two of the pairs (33%; 1 male-male; 1 female-female) there were equal but also unequal outcomes with alternation regarding who obtained the large reward in the unequal tray.

2.5. Communication behavior between partners

Despite the conflict of interest between partners, we did not observe any clear overt communicative or soliciting gestures between pairs. Instead, what often occurred when partners had conflicting interests regarding which tray to pull (evidenced by the fact that each one of them was in a different room at a different tray) was that one individual in the pair (normally the dominant partner) approached the door to watch the partner. Some of these events could be interpreted as if subjects were attempting to recruit their partners, and in fact a small proportion of them (11%) were followed by the partner turning to the subject and following him/her to the other tray. In another proportion of these "monitoring instances" (27%), the subject (the individual watching) decided to join the partner. However, in the majority of the cases (62.5%), nothing happened immediately after the monitoring event, and the subject monitoring the partner returned to the tray (s)he was interested in (without the partner following). Finally, we never saw the use of any visual manual gestures and it was only one pair that we observed vocalizing during the test; the subordinate screamed when she could not retrieve the equal tray and the dominant did not join her.

3. Discussion

The chimpanzees were successful at what can be characterized as a basic form of negotiation in which each pair had to agree in choosing a cooperative task, despite conflicting preferences. Remarkably, even with a conflict of interest, the chimpanzees ended up cooperating, in one way or another, in 78% of trials in the condition with the most unequal distribution of food (double inequity condition) and as many as 94% of trials in the replication of the inequity condition in experiment 2. Against the first two possible predictions, cooperation did not break down altogether, and subordinates did not always (immediately) accept the unequal split offered by dominants. Instead, subordinates often refused the dominants' selfish offers and were often able to outwait their dominant partner so that they ended up retrieving the equal tray.

A conflict of interest arose whenever the dominant offered the selfish split but there was a better alternative available for the subordinate (i.e., the equal tray). On these occasions, subordinates often refused to join them and signaled their preference for the equal tray by sitting in front of it (and gently manipulating the apparatus' rope). Because we know that chimpanzees can read the intentions of others in their actions (see Call & Tomasello, 2008, for a review), it seems safe to assume that while the two chimpanzees were sitting in front of their different trays they understood that the other individual wanted to pull in the tray/reward in front of which she was sitting. Furthermore, the exact same chimpanzees participating in this study had previously shown that they understood the role their partner played in this same cooperation task when only one tray was present; they were not only able to coordinate and synchronize their behavior to that of their partner but were even able to recruit the most skillful of two potential partners and wait for her/him before pulling (Melis et al., 2006a). Therefore, subjects understood the conflicting interests between their partner and themselves, and that one of them had to "give up" for them to obtain any food at all. Although we did not observe any overt communicative gestures or soliciting behavior between partners (and chimpanzees are known to make more overt signals gesturally and vocally in other contexts; see Call & Tomasello, 2007), it is possible that in those situations in which subjects stayed at the door between rooms and monitored the partner (when partners wanted different trays), subjects were attempting to recruit their partners. In any case, intentionally or not, this behavior may have signaled a certain unwillingness or lack of interest to join the partner.

Regarding the subordinates' refusals of selfish offers one could argue that chimpanzees are simply not willing to work for a small payoff such as the smaller one of the unequal tray. However, this cannot be the case since in the control condition of the first experiment; when there was no other available alternative, subordinates were perfectly willing to work for the very small payoff of the unequal tray. Alternatively, one could argue that subordinates were simply egocentrically attracted to the largest reward available (i.e. those not taken by the dominant). However, this hypothesis cannot explain the fact that whenever dominants offered the equal tray subordinates did not attempt to obtain the very largest reward on the other unequal tray. This means subordinates did not just blindly run around looking for the largest unclaimed food reward. Instead, it seems that they understood that obtaining the unequal-selfish split (i.e., the largest food reward) for themselves would not work, since the dominant would not allow them to obtain it. Importantly, note that this pattern of subordinates not attempting to claim the large reward of the unequal tray was apparent prior to any interaction with the dominant as evidenced by subordinates' initial response or very first rope touched (i.e., the subordinates seemed to predict that attempting to obtain the large option of the unequal tray was futile). Chimpanzees thus managed to cooperate even when there was a conflict of interest, and understood at least to a certain degree, their bargaining power and its limits.

Despite the high levels of successful cooperation and the ability of some subordinates to manipulate their dominant partner, there were also some limitations in the chimpanzees' negotiation skills. For example, dominants did not seem to behaviorally adjust to their partners' preferences and continued to make selfish offers regardless of the frequency of previous refusals by the subordinate. Furthermore, subordinates' bargaining power seemed to be less effective when the inequity was doubled. In the double inequity condition, dominants became more selfish in their offers and tended to be more stubborn such that selfish offers were turned into equal outcomes less often and cooperation broke down more often. Another constraint on the chimpanzees' ability to negotiate seems to be their lack of reciprocal strategies in this context. If they had utilized a reciprocal strategy, they could have maximized their own long-term benefits. This is especially the case in the double-inequity condition where alternating who obtains the large reward of the unequal tray would have provided both the dominant and the subordinate the maximum potential payoffs. In two of the six pairs, there was occasionally alternation between the subordinate and dominant obtaining the large reward of the unequal tray. However, it seems that this alternation was a byproduct of relationship factors; one pair had an unstable dominance hierarchy (the two youngest males) while the other pair was an extremely tolerant pair (the two oldest females). The fact that this alternation was mainly seen in the control condition of Experiment 1 and not in the double-inequity condition of Experiment 2—where such a strategy had the highest potential payoff—suggests that it is unlikely that the chimpanzees involved were using a calculated strategy. Neither were they able to learn during the experiment about the higher payoffs of taking turns. Nevertheless, the fact that this type of alternation did appear in an extremely tolerant pair supports the idea that tolerance and more symmetrical relationships may be important for the development of reciprocal exchanges, since tolerant partners might be more willing to tolerate inequities and the alternation of roles within a relationship (Brosnan, Freeman, & de Waal, 2006; Brosnan et al., 2005; Stevens, Vervaecke, Vries, & Van Elsacker, 2005; Trivers, 1971).

Finally, perhaps the most apparent constraint on chimpanzees' ability to solve conflict of interests is related to their communicative abilities. We never observed any clear overt communicative signals between partners to help them coordinate their conflicting preferences. This was surprising, since in situations in which the partners were waiting for each other at the different trays (being unable to agree from which tray to pull, and in some extreme occasions waiting for each other up to 3 min), any type of communicative efforts to influence the partner could have facilitated or accelerated the negotiation process (e.g., as the gestures chimpanzees use to recruit coalitionary partners during aggressive interactions, or as in the case of communicative signals reported by Crawford, 1937, between juveniles chimpanzees, and Hirata, Morimura, & Fuwa, in press, when interacting with human partners). Individuals in this study checked and monitored each other, but it is difficult to determine whether or not individuals were attempting to influence the partner during these monitoring events. Future studies will need to investigate which variables constrain chimpanzees' use of intentional communication during cooperative interactions (see Hirata et al., in press and Melis, Warneken, & Hare, in press for discussions on this topic and Tomasello, 2008 for a possible evolutionary account on chimpanzees' communication constraints).

Although it is clear that resource maximization motivated chimpanzees' behavior, it is unclear what role, if any, sensitivity to inequity (or a sense of fairness) played in the current experiment. Certainly, it does not seem to have played a role among the dominants who offered selfish splits at similarly high rates during the whole experiment. However, one could argue that subordinates refused the unequal-selfish offers because they were not pleased that they were getting less food than the dominant for equal effort during cooperation. Alternatively, it is also possible that the chimpanzees' refusals here are due to a pragmatic approach since they were focused on manipulating the dominants' behavior so that they could acquire the larger reward offered on the equal tray. The chimpanzees' behavior in the control condition of the first experiment (where they immediately accepted the disadvantageous unequal split) would in fact support the pragmatic-approach hypothesis, since if they were averse to inequity they should not have pulled in this condition. Related to this, it is important to note that Jensen, Call, and Tomasello (2007b) found that chimpanzees were sensitive to harmful behavior and/or intent but not to simple rewards' disparity over which the partner had no control. This is consistent with intention-based models of fairness (e.g., Rabin, 1993), and therefore, another alternative is that sensitivity towards inequity in chimpanzees and their tendency to punish others appears only in situations in which partners have control over the rewards' distribution, and subjects attribute to them intentional actions. If this is the case, we cannot expect inequity aversion in our control condition. Similarly, this could be an explanation for the negative results of Jensen, Call, and Tomasello (2007a), who found that in a mini-ultimatum game chimpanzees do not punish proposers of unfair offers. It is possible that recipients in Jensen et al. (2007a) did not understand that proposers had a choice in the first place, and that proposers made the choice that harmed them the most. Only future research will be able to disentangle these two possibilities.

The results of this study demonstrate that chimpanzees can settle a conflict of interest over cooperative options toward resources by, in some sense, negotiating. They do this not only on single occasions but also across time: in none of the six pairs—regardless of their overall strategy—did cooperation break down, which means that both members of the pair ended up satisfied to some degree (i.e., enough to keep participating across trials). The results also demonstrate how in a cooperative context, in which dominants are dependent on the subordinates' assistance, subordinates gain leverage and thus gain power to influence the outcome of the interaction (Lewis, 2002). Chimpanzees' high levels of cooperation in this task were very likely due to their solid understanding of the need to coordinate their actions with those of their partner and their capacities for self-control and risk taking. In fact, two new studies have found that chimpanzees have, in comparison to all nonhuman animals tested so far, relatively low temporal discounting rates and are more risk prone than other species tested so far (Heilbronner, Rosati, Stevens, Hare, & Hauser, 2008; Rosati, Stevens, Hare, & Hauser, 2007). These capacities likely enhance one's own bargaining power and allow subordinates to refuse unequal-selfish offers and "counter-offer" (staying bodily oriented) equal ones. This means that with very little (or no) overt communication, and likely without any kind of social norms of equity, one of our two closest living relatives can settle conflicts of interest over resources in mutually satisfying ways. Based on these results, it seems that the basic capacities for negotiating over conflicting interests likely arose before we split from our last common ancestor with chimpanzees and bonobos. Humans, of course, have developed more sophisticated skills of communication, strategies toward reciprocity over time, along with third-party punishment, and norms against noncooperators, which no doubt serve to stabilize and enhance cooperation even further. But these extra skills are not necessary for the basic process of cooperative negotiation over resources.

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Appendix A. Supplementary data

Supplementary data (a videoclip) associated with this article can be found in the online version at doi:10.1016/j.evolhumbehav.2009.05.003.

The two cameras on the top show the room from which the pair can access the unequal tray. The top left camera is placed showing the position from which the subject would obtain the smallest reward (a banana slice), whereas the top right camera shows the position from which the subject would obtain the largest reward (a whole banana). The camera on the bottom left shows the room from which the subjects can access the equal tray (half banana per plate). The trial starts when the dominant female enters the room and positions herself in front of the largest reward of the unequal tray (Top right camera), making thus a 'selfish' offer to subordinate female. The subordinate female, who enters the testing rooms some seconds later, joins the dominant partner briefly and touches the rope of the unequal tray (Top left camera) but refuses to pull and goes to the equal tray (Bottom left camera at time: 9:02:21). The trial ends when the dominant female joins the subordinate and they both pull the equal tray containing half banana per plate (Bottom left camera at time: 9:02:48).

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