

Chimpanzees (*Pan troglodytes*) Instrumentally Help But Do Not Communicate in a Mutualistic Cooperative Task

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Chimpanzees cooperate in a variety of contexts, but communicating to influence and regulate cooperative activities is rare. It is unclear whether this reflects chimpanzees' general inability or whether they have found other means to coordinate cooperative activities. In the present study chimpanzees could help a partner play her role in a mutually beneficial food-retrieval task either by transferring a needed tool (transfer condition) or by visually or acoustically communicating the hiding-location of the needed tool (communication condition). Overall, chimpanzees readily helped their partner by delivering the needed tool, but none of them communicated the hiding location of the tool to their partner reliably across trials. These results demonstrate that although chimpanzees can coordinate their cooperative activities by instrumentally helping their partner in her role, they do not readily use communication with their partner for this same end.

Keywords: chimpanzee, mutualism, helping, communication, *Pan troglodytes*

Chimpanzees engage in a number of cooperative activities such as reciprocal grooming, joint mate guarding, boundary patrolling, group hunting, and forming alliances and coalitions (Muller & Mitani, 2005), which all provide mutual benefits to all participants. From a cognitive perspective, experimental data has shown that chimpanzees can quickly learn to coordinate actions with a partner, and identify, remember, and recruit the best collaborators, and even help their partner perform her role (Bullinger, Wyman, Melis,

& Tomasello, 2011b; Melis, Hare, & Tomasello, 2006; Melis & Tomasello, 2013). This is possible because they understand others as intentional agents who behave predictably and they know how the partner's actions relate to their own goals (Call, Hare, Carpenter, & Tomasello, 2004; Schmelz, Call, & Tomasello, 2011). In many instrumental tasks in which the potential helper herself has no access to that food and the recipient signals her needs/goals, chimpanzees behave prosocially toward the partner helping her to access food (Greenberg, Hamann, Warneken, & Tomasello, 2010; Melis et al., 2011; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Yamamoto, Humle, & Tanaka, 2009, 2012).

Communication, in which individuals explicitly inform one another of what they know, can be a very useful tool to coordinate mutualistic activities and is a key component of human cooperation (Tomasello, 2009). Even brief periods of communication in humans are known to increase cooperation (Balliet, 2010), promote a positive relationship, and improve coordination (Bochet, Page, & Putterman, 2006; King et al., 2011). Communication in such situations suggests that individuals (1) can detect what information is relevant for the partner and (2) are motivated to help the partner by providing relevant information. Chimpanzees communicate intentionally on a regular basis in their social environment such as by soliciting grooming, inviting others to play, recruiting support, or informing ignorant group members of danger (Crockford, Wittig, Mundry, & Zuberbühler, 2012; Hobaiter & Byrne, 2011; Liebal & Call, 2012). They gesture flexibly to one another, take into account the partner's attention and attract it if necessary (Call & Tomasello, 2007). However, in the context of collaborative problem-solving, many studies have found that communication among chimpanzee partners is rare or nonexistent, even though it would help them both (Hirata & Fuwa, 2007; Povinelli &

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O'Neill, 2000; but see Crawford, 1937 for a possible exception and Savage-Rumbaugh, Rumbaugh, & Boysen, 1978 for findings with chimpanzees after specific training). Even when chimpanzees have conflicting preferences and must coordinate and agree on one out of two possible tasks, they mainly solve problems without intentional communication (Melis, Hare, & Tomasello, 2009). Bullinger et al. (2011b) found some evidence for intentional communication among pairs of chimpanzees in a stag-hunt scenario, but in the form of attention-getters to attract the partner after one of the individuals had taken the "leader" role and decided to go for the "stag." However, there was no evidence for any kind of communication before leaving the "hare" to facilitate coordination. Similar requesting behavior has sometimes also been observed when chimpanzees interact with human partners in comparable situations (Hirata & Fuwa, 2007; but see Warneken, Chen, & Tomasello, 2006 for the opposite finding). These findings suggest the hypothesis that chimpanzees may not use communication with conspecifics as an effective means to influence and regulate a collaborative activity (Hirata & Fuwa, 2007; Tomasello, 2008).

The aim of the current study was to investigate, in a single experimental paradigm, whether chimpanzees would provide not only physical help but also informational help (via communication) to their partner in a mutually beneficial cooperative task. Specifically, in the first experiment we investigated whether chimpanzees would help a partner (to their mutual benefit) by transferring a needed tool, in one condition, and by communicating the hiding-location of the needed tool in another condition. In the second experiment we increased the salience and potential for communication by shifting the target of communication to the more interesting target, that is, the food itself, to investigate whether this shift would better motivate chimpanzees to communicate.

Experiment 1

Method

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 m³) consisting of six rooms with interconnecting raceways. The group is additionally fed four times a day with fruits, vegetables, posho (maize flour dish), and porridge; water is available ad libitum. The subjects were tested in pairs in familiar rooms of the holding facility (each 69 m²) 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. EC635).

Subjects. Thirteen unrelated chimpanzees, seven males and six females 9–26 years of age, participated in this study. One individual refused to participate in the second condition (because of sexual swelling) and was replaced by another individual. Two

groups of six individuals participated, one group for each condition-order (see details below). Within each group individuals were paired with two different partners, each in each role in the task one time, resulting in a total of 24 pairs (see Table 1). Based on previous studies conducted with the same group of chimpanzees (Bullinger, Melis, & Tomasello, 2011a; Melis et al., 2006, 2009), tolerant dyads were paired, that is, neither individual reached for the other's food or took it away. Subject-partner order was assigned randomly.

Materials and Design

The study was conducted in two opposing rooms, separated by a corridor (195 cm) with the subject on one side (subject's room) and the partner on the other side (partner's room). At the end of the corridor was a food-apparatus stretched between the two rooms. Depending on the respective condition either a transfer-apparatus or a communication-apparatus was placed at the beginning of the corridor (see Figure 1).

Food-apparatus. Only one individual (the partner) could manipulate the food releasing apparatus, but both individuals simultaneously benefitted from the rewards released. The apparatus consisted of a slat stretched between the two rooms with two food dishes on top of it. Each individual's reward, that is, a 6 cm piece of banana, was tied to a rope and placed in the food dish. To release the mechanism, the partner had to push a tool, that is, a stick, inside a tube so that the slat fell down and the rewards could be pulled within reach. The tool was lost once it was inserted into the tube.

Transfer-apparatus. The transfer-apparatus consisted of a half pipe attached from the top of the subject's room to the bottom of the partner's room, so that the subject could place the tool at the top of the half pipe and the tool slid down.

Communication-apparatus. The communication-apparatus had two potential hiding locations for the tool and could only be reached by the partner. It was built like a swing-bridge (270 cm) placed out of primates' reach with a covered platform at either end. A rope was attached on each platform and both rope ends were extended into the partner's room through the bars of the rooms (ropes extended 20 cm into the room). To move one of the platforms within reach, the partner had to pull the rope attached to that platform. Once one platform was pulled the other rope and platform moved out of reach. On top of each platform was a cover with a hole toward the subject, so that the subject but not the partner could see the contents underneath. The tool could be hidden underneath one of the covers. The position of the hidden tool was counterbalanced across trials and within subjects, with the only constraint that the tool was never placed in the same location for more than two consecutive trials.

The 24 dyads participated in two different conditions. In the *transfer condition*, the subject could help the partner obtain the tool by transferring the tool. In the *communication condition*, the subject could help the partner obtain the tool by communicating its hiding-location. One group (12 dyads) started with the transfer condition and the other group with the communication condition, in a within-subjects design (see Table 1). Subjects were randomly assigned to the groups and the order of partners.

Table 1
The Sex, Estimated Age, Testing Order, and the % of Helping in Both Experiments for Each Subject Tested in the Present Study

Subject	Sex	Est. age	Group	S-P-order	Partner	Exp. 1 [helping]				Exp. 2 [helping]	
						Baseline communication	Communication condition	Baseline transfer	Transfer condition	Baseline	Test
Becky	Female	19	CT	1	Natasha	0	0	25		0	
					Okech				50		0
					Sally				50		0
Robbie	Male	24	CT	1	Kidogo	0	16.67	0	0	0	16.67
					Sally		0		16.67		0
Tumbo	Male	21	CT	1	Natasha	8.33	0	8.33		0	
					Okech				16.67		0
Kidogo	Female	26	CT	2	Kidogo		0		16.67		0
					Tumbo	0	0	16.67	50	0	0
					Robbie		50		100		16.67
Natasha ^a	Female	20	CT	2	Becky	0	0				
Okech ^b	Male	9			Tumbo		0	25	50	25	33.33
					Robbie	0	0	16.67	83.33	0	33.33
Sally	Female	19	CT	2	Becky		0		1		16.67
Asega	Male	12	TC	1	Baluku	0	0	50	1	33.33	16.67
					Yoyo		0		83.33		0
Indi	Male	11	TC	1	Yoyo	0	0	8.33	83.33	0	0
					Umugenzi		0		66.67		0
Namukisa	Female	11	TC	1	Umugenzi	0	0	16.67	50	0	0
					Baluku		0		50		0
Baluku	Male	12	TC	2	Namukisa	0	83.33	41.67	50	75	16.67
					Asega		33.33		83.33		50
Umugenzi	Male	13	TC	2	Namukisa	0	0	0	0	0	0
					Indi		0		0		33.33
Yoyo	Female	11	TC	2	Indi	0	0	25	50	0	33.33
					Asega		0		66.67		50

^a This individual participated only in the communication condition. ^b This individual participated only in the transfer condition and in experiment 2.

Procedure

Familiarization. Before entering the test phase, subjects received pretest and exposure phases to ensure that they understood the different apparatuses and the basic principles of the test. In the pretests, individuals were always tested alone with the connecting raceway between the subject's and the partner's room open. In the exposure-phases, subject and partner were in their respective room with the connecting raceway between them closed.

Pretest 1. This pretest ensured subjects' knowledge how to retrieve food from the food-apparatus. Subjects were confronted with the baited food-apparatus and the tool. They had to use the tool and obtain the reward in the partner's and the subject's room within 1 min on three consecutive trials. A maximum of eight trials per day was conducted; if multiple sessions were needed, they were done on consecutive days. On average, subjects needed eight trials to pass the pretest 1 (mean \pm SE = 8.00 \pm 0.41; range 6–12 trials).

Pretest 2. This pretest ensured subjects' knowledge how to retrieve the tool from the communication-apparatus and that after pulling one platform within reach, the other platform was inaccessible. Subjects observed how the experimenter baited the food-apparatus and hid the tool underneath one of the covers of the communication-apparatus. Subjects had to retrieve the tool, use it and obtain the reward in the partner's and the subject's room within 1 min on three consecutive trials. A maximum of eight trials

per day was conducted; if multiple sessions were needed, they were done on consecutive days. On average, subjects needed five trials to pass the pretest 2 (mean \pm SE = 5.23 \pm 0.71; range 4–12 trials).

Exposure 1. Partner and subject learned that they were each assigned to a specific room, that is, that the partner always used the tool to release food for both. For that purpose, partners observed under which of the covers of the communication-apparatus the experimenter hid the tool and could then retrieve it, use it and release food for both. Subject and partner of each dyad had to obtain the reward on their respective side within 1 min in four consecutive trials.

Exposure 2. Partner and subject experienced that they failed to get the reward if they did not watch the hiding process. This exposure phase aimed to motivate partners to look for help if they did not know the solution to the problem. For that purpose, partners could not observe where the experimenter hid the tool (they were outside of the room). Subject and partner of each dyad experienced failure in two consecutive trials (none of the apparatuses was actually baited; baiting process only pretended). After each trial, the experimenter showed both individuals where the tool was hidden.

Exposure 3. Partner and subject observed that the tool could slide down the transfer-apparatus and that the partner could take the tool out of it. For that purpose, both individuals observed how the experimenter placed the tool on top of the slide. Subject and

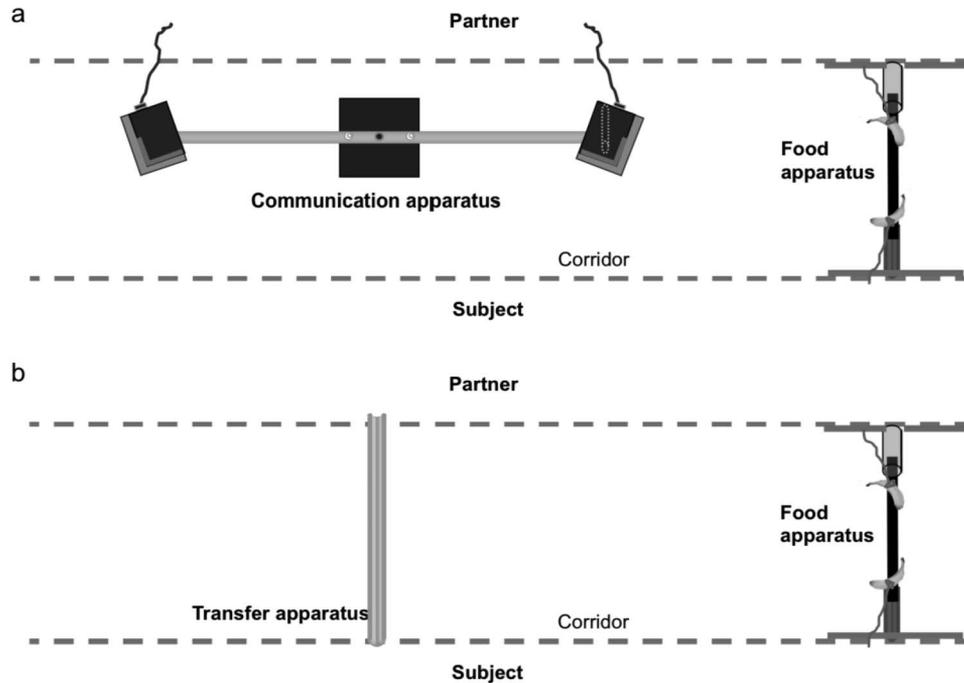


Figure 1. Room layout and set-up in Experiment 1. (a) Communication condition; (b) transfer condition.

partner of each dyad had to obtain the reward on their respective side within 1 min in four consecutive trials.

Baseline. All subjects participated in two sessions of six non-social trials each, conducted once before and once after the actual test phase to measure subjects' general tendency to transfer a tool/indicate its hiding location. A trial ended after 1 min. Individuals were always tested alone with the connecting raceway between the subject's and the partner's room closed and no potential partner in any of the adjacent rooms.

Test. In the *transfer condition*, the food- and the transfer-apparatus were set up, each individual was in her respective room and the tool was given to the subject. A trial ended after 1 min. Within this minute, the subject could either transfer the tool to the partner, or do nothing. The partner could (1) use the tool, and/or (2) request the tool, or (3) do nothing. In the *communication condition*, the food- and the communication-apparatus were set up. Only the subject could observe the hiding of the tool. Partners could see subjects watching the baiting process while they themselves could not see it. The partner entered immediately after the hiding process. A trial ended after 1 min. Within this minute, the subject could either indicate to the partner where the tool was hidden, or do nothing. The partner could (1) react to the subject, and/or (2) pull a platform regardless of the subject's behavior, or (3) do nothing.

Subjects participated in 12 trials per condition, administered in two sessions of six trials each on two consecutive days. The subject within the pair being tested first had to complete the first condition before the same pair was tested in reverse for the same condition. After both individuals had completed the first condition, they received the second condition.

Coding and Analyses

All trials were recorded with four cameras, one of which focused on the food-apparatus and three of which focused on the transfer/communication-apparatus, two focusing on the subject and one on the partner. A trial started when the subject received the tool (in the transfer-condition) or when the partner entered the room (in the communication-condition) and finished after 1 min. Data came from live coding and coding from videotapes for the following variables: (1) occurrence of helping, that is, tool-transfer or overt communication; (2) timing of helping; and (3) overall success. Additionally, in the transfer condition the requesting behavior of the partner was coded, that is, partner stomping, jumping, mesh-banging, whining, teetering, or vocalizing, that is, grunting and raspberry sound, while sitting in front of the transfer-apparatus. Further, in the communication condition, the subject's behavior and the accuracy of the communication were coded. The subject's behavior was separated into three categories: (a) subject overtly communicating, that is, grunting, stomping, jumping, mesh-banging while sitting in front of one platform (tactile communication was not possible); (b) subject positioning herself in front of one platform without overtly communicating; and (c) subject positioning herself in front of the food-apparatus away from the potential hiding-location of the tool. While categories (a) and (b) were (potentially) informative for the partner, category (c) was clearly noninformative.

To assess interobserver reliability, a second coder, ignorant of the hypotheses and the procedure of the study, coded 25% of the videotapes. There was 97.22% agreement with respect to whether the subject helped, the overall success (100%) and the accuracy of communication (94.23%; all Cohen's $K > 0.88$) and 88.9% agree-

ment with respect to the partner's requesting behavior (Cohen's $K = 0.602$). Agreement on the timing of helping was also high (Spearman's $\rho = 0.861$, $p < .001$, $n = 29$).

Results and Discussion

A repeated-measures ANOVA (condition \times condition-order \times subject-partner-order) found no main effects for condition order or subject-partner order. There was a three-way interaction, however, between condition, condition order, and subject-partner order such that subjects communicated more in the communication condition if they had first had the transfer condition and if they had first been the partner, whereas this interaction was not the case in the transfer condition ($F(1, 8) = 7.422$, $p = .026$, $\eta^2 = .481$). No other interactions were found. Furthermore, subjects' behavior was not influenced by the partner they were paired with: Subjects trans-

ferred the tool and communicated at similar levels with both partners.

The main finding was a main effect of condition, such that subjects helped their partner by transferring the tool more often than they helped her by communicating the tool's location ($F(1, 8) = 30.851$, $p = .001$, $\eta^2 = .794$; Figure 2a). Subjects helped in the transfer condition on average in 51% (range 0–92%) of the trials. There was no effect of sex (*independent-sample t* test: $t(10) = 1.313$, $P = .177$). They transferred the tool significantly more in the test than in the nonsocial baseline (paired-sample *t* test: $t(11) = 4.495$, $p = .001$; Table 1) and did so significantly faster in the test than in the baseline (paired-sample *t* test: $t(60) = 2.221$, $p = .03$). Once a pair discovered that transferring the tool led to success, they almost always continued to do so (69% of the remaining trials; Figure 2b). Partners sometimes begged for the tool (28.3% of

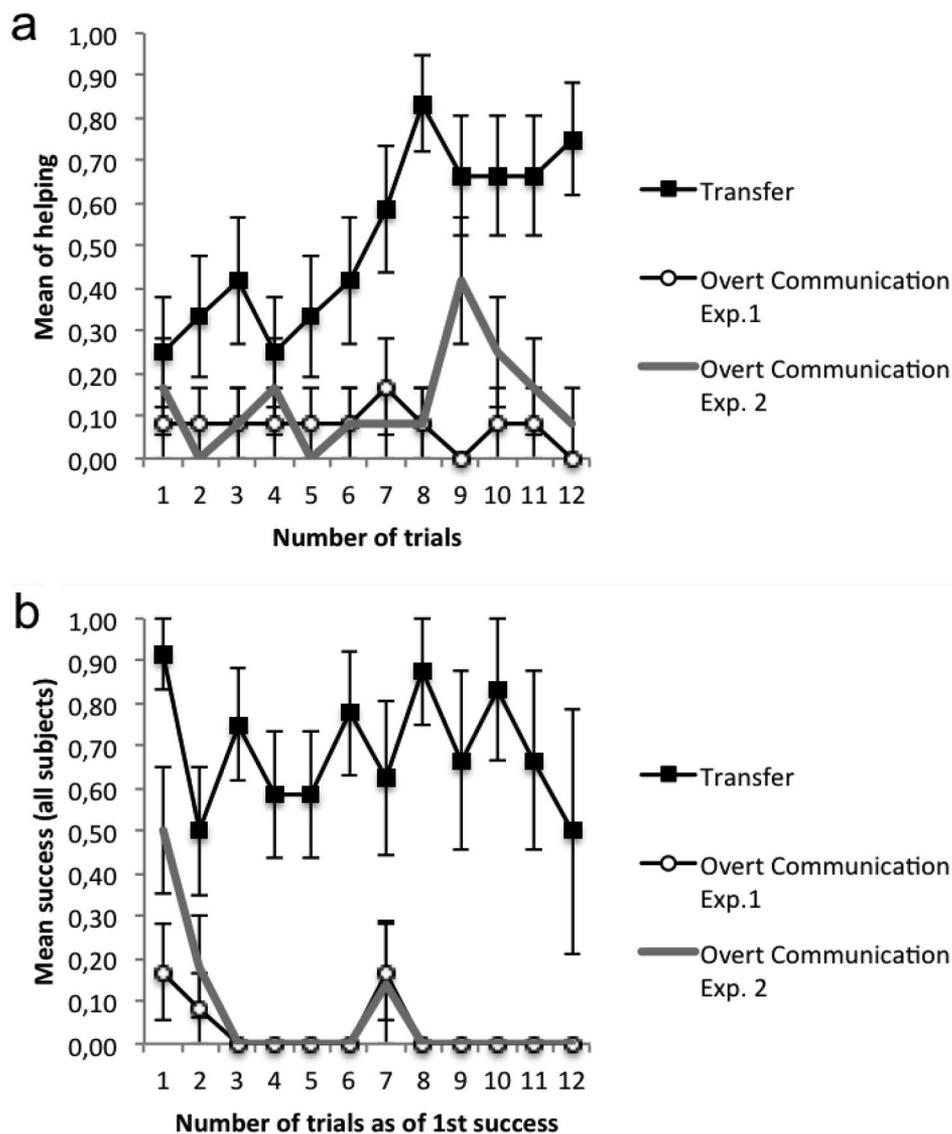


Figure 2. (a) Mean of helping across trials; (b) mean of success of all subjects across trials, starting with the first successful trial for each subject.

the trials), but this behavior had no effect on the subject's amount of helping (paired-samples t test: $t(9) = 1.599, p = .144$). While such overt signaling of their needs and goals had a positive effect on chimpanzees' behavior in instrumental helping tasks (Melis et al., 2011; Yamamoto et al., 2012), our study showed no effect on subject's willingness to transfer the tool. Similar results were obtained in studies focusing on other-regarding preferences showing that begging and reaching attempts either had no or a negative effect on pro-social behavior (Cronin, 2012; Horner, Carter, Suchak, & de Waal, 2011; but see Takimoto, Kuroshima, & Fujita, 2010).

In the communication condition subjects helped by overtly communicating with attention-getters on average in only 8% of the trials (11/144 trials; range 0–58%), performed by only three subjects (Robbie: 8%, Kidogo: 25%, and Baluku: 58%; Table 1). There was no effect of sex (*independent-sample* t test: $t(9) = 1.048, P = .105$). When subjects communicated overtly, they always indicated the correct hiding-location (11/11 trials). Perhaps because of this overall low frequency, the amount of overt communication and the time delay were not significantly different between test and nonsocial baseline (paired-sample t tests: amount: $t(11) = 1.335, p = .209$; Table 1; delay: $t(60) = 1.862, p = .067$), though it is important to keep in mind that on the individual level the three subjects who communicated in the test did not communicate in the baseline, and the one who communicated in the baseline did not do so in the test. Instead of communicating overtly with attention-getters, what subjects were doing most often was either (1) positioning themselves in front of one platform that could potentially have a communicative function (intentional or not) (35% of the trials in the test vs. 23% of the trials in the baseline, paired-sample t tests: amount: $t(11) = 1.666, p = .075$; Table 2), or (2) positioning themselves in front of the food apparatus noninformatively (27% of time). In the remaining 30% of the trials subjects were off camera and could not be classified into any of the categories above. The subjects who positioned themselves in front of the correct platform did not do so consistently across trials, except for one individual (Indi), who positioned himself in front of the correct hiding location throughout all trials.

Table 2
The % of Overt Communication and Positioning in Both Experiments and the Baseline for Each Subject Tested in the Present Study

Subject	Test		Baseline	
	Overt communication	Positioning	Overt communication	Positioning
Asega	0	66,67	0	66,67
Baluku	58,33	25	0	25
Becky	0	16,67	0	16,67
Indi	0	50	0	50
Kidogo	25	8,33	0	8,33
Namukisa	0	50	0	50
Natasha/ Okech	0	8,33	0	8,33
Robbie	8,33	50	0	50
Sally	0	33,33	0	33,33
Tumbo	0	8,33	8,33	8,33
Umugenzi	0	25	0	25
Yoyo	0	83,33	0	83,33

Partners in the communication condition did not use the communicative information potentially available to them. Partners pulled the platform where the subject overtly communicated equally often as they pulled the opposite platform (mean \pm SE = 0.45 ± 0.20 ; one-sample t test: $t(2) = .680, p = .566$), and the same was true when the subject was positioned at one platform without necessarily overtly trying to communicate (mean \pm SE = 0.51 ± 0.11 ; one-sample t test: $t(11) = .368, p = .720$). Because subjects did not always indicate the correct location when they positioned themselves in front of a platform (74% correct location; 37/50), partners were successful on only 75% of these trials in which they potentially followed the subject's spatial cue. Because subjects always indicated the correct location when they communicated overtly with attention-getters (11 trials), partners were successful on all five trials in which they followed the subject's overt communication. Nevertheless, not even in these cases (and also not in any others) did success cause subjects to stabilize their strategy (Figure 2b). This suggests that—unlike in the transfer condition—when subjects were successful this did not then stabilize their strategy, perhaps because they did not understand what led to their success.

One potential reason for these mostly negative results in the communication task is that communicating about a tool was indirect, so it asked individuals for very complex inference. Another potential reason is that partners tended not to pay much attention to subjects. This did not matter in the transfer condition, as the subject simply transferred the tool to the partner whether she was attending or not. However, in the communication condition, partners on average made a choice generally about 6 s after entering the room, so that subjects had only 6 s to communicate. They communicated on average at 4 s. A further indication of this same tendency is that partners preferentially pulled the platform closest to them when they entered the room (one-sample t test: $t(11) = 2.492, p = .030$).

Overall, although many chimpanzee pairs quickly settled on a reliable strategy to solve the mutualistic task in the transfer condition, none of them did the same in the communication task. Although there were some potentially informative communicative acts, the overall frequency was very low, making it unlikely that individuals were intending to inform at all. Even if the three subjects intended to influence the partner's behavior, partners did not take the subjects' behavior into account in any systematic way. Overall, this pattern of results shows that the chimpanzees did not readily use communication as a reliable strategy for coordinating in this cooperative task.

Experiment 2

We were worried that chimpanzees' lack of reliable communicative strategies in the first study was because communicating about a tool was indirect. The goal of the second study, therefore, was to increase the potential for communication among the subjects by shifting the target of communication from the tool to the food. Subjects could help the partner release the food by communicating not the position of the tool but the position of the food that could be hidden in one of two potential food-apparatuses.

Method

Ethical note and subjects. The same subjects and dyads as in Experiment 1 participated in this experiment under the same testing conditions, each individual in each role.

Materials and Design

The basic setup was the same as in Experiment 1, except that instead of the communication-apparatus, there were two food-apparatuses stretched between the two rooms (200 cm apart from each other). The food dishes were covered with an opaque lid, so that from the outside one could not see which apparatus was baited. The tool was made available for the partner by placing it on the mesh between the food-apparatuses with equal distance to each.

Procedure

Familiarization. Before entering the test phase, subjects received three pretest phases and an exposure phase to ensure that they understood the new setup. In the pretests, individuals were always tested alone with the connecting raceway between the subject's and the partner's room open. In the exposure-phase, subject and partner were in their respective room with the connecting raceway between them closed.

Pretest 1. This pretest ensured subjects' knowledge that only one food-apparatus was baited and that the tool could only be used once. Subjects were confronted with the two food-apparatuses and the tool. They had to use the tool on the baited apparatus and obtain the reward in the partner's and the subject's room within 1 min on four consecutive trials. A maximum of eight trials per day was conducted; if multiple sessions were needed, they were done on consecutive days. On average, subjects needed five trials to pass the pretest 1 (mean \pm SE = 4.83 \pm 0.26; range 4–6 trials).

Pretest 2. This pretest ensured subjects' knowledge that the tool could only be used from the partner's room, but not on the subject's room. Subjects were confronted with the two food-apparatuses and the tool, which was placed in the subject's room. They had to transport the tool to the partner's room without trying to use it on the subject's side, use the tool on the baited apparatus and obtain the reward in the partner's and the subject's room within 1 min on four consecutive trials. A maximum of eight trials per day was conducted; if multiple sessions were needed, they were done on consecutive days. On average, subjects needed six trials to pass the pretest 2 (mean \pm SE = 6.42 \pm 0.84; range 4–14 trials).

Pretest 3. Individuals experienced that they failed to get the reward if they did not watch the baiting process. For that purpose, individuals could not observe where the experimenter hid the food. Individuals experienced 100% failure in Trials 1, 2, 4, and 5 (none of the apparatuses was baited; baiting process only pretended), 100% success in Trial 3 (both apparatuses were baited), and on Trial 6 they had a 50% probability of getting the reward (some individuals experienced success and others failure since only one apparatus was baited).

Exposure 1. Partner and subject experienced that they were each assigned to a specific room, that is, that the partner always used the tool to release food for both. For that purpose, dyads

observed where the experimenter hid the food and the partner could then use the tool to release food for both. Subject and partner of each dyad had to obtain the reward on their respective side within 1 min in four consecutive trials.

Baseline. All subjects participated in two sessions of six non-social trials each, conducted once before, and once after the actual test phase to measure subjects' general tendency to indicate the hiding location of the food. A trial ended after 1 min. Individuals were always tested alone with the connecting raceway between the subject's and the partner's room closed and no potential partner in any of the adjacent rooms.

Test. The subject was in her respective room and observed in which food-apparatus the experimenter hid the rewards. Afterward, the tool was placed in between the two apparatuses in the partner's room and the partner entered immediately after. A trial ended after 1 min. Within this minute, the subject could either indicate to the partner where the food was hidden, or do nothing. The partner could (1) react to the subject, (2) use the tool on one apparatus regardless of the subject's behavior, or (3) do nothing.

Subjects participated in 12 trials, administered in two sessions of six trials each on two consecutive days. The subject within the pair being tested first had to complete all 12 trials, before the same pair was tested in reverse. The position of the hidden food was counterbalanced across trials and within subjects and randomized, with the only constraint that the food was never placed in the same location for more than two consecutive trials.

Coding and Analyses

All trials were recorded with four cameras, two of which focused on the subject's room and two of which focused on the partner's room. A trial started when the partner entered the room and finished after 1 min. Data came from live coding and coding from videotapes for the same variables as in Experiment 1, except that subject's behavior was separated into two categories, which were both (potentially) informative for the partner: (a) subject overtly communicating, that is, grunting, stomping, jumping, mesh-banging while sitting in front of one food-apparatus; and (b) subject positioning herself in front of one food-apparatus without overtly communicating. Interobserver reliability was conducted together with data from Experiment 1 and is reported above.

Results and Discussion

There was a subject-partner order effect (independent-sample *t* test: $t(10) = 3.958, p = .003$). Specifically, individuals who started as partners communicated about nine times more frequently than individuals who started as subjects. Furthermore, subjects' behavior was not influenced by the partner they were paired with: Subjects communicated at similar levels with both partners.

Subjects overtly communicated with attention-getters on average in only 13% of the trials (19/144 trials; range 0–42%; Figure 2a). When subjects communicated overtly, they communicated to the correct hiding-location in most of the trials (95%). However, again, the amount of overt communication and the time delay were not significantly different between test and nonsocial baseline (paired-sample *t* tests: amount: $t(11) = .332, p = .746$; Table 1; delay: $t(60) < .001, p = 1.000$). Instead of communicating overtly with attention-getters, what subjects were doing most often was

positioning themselves in front of one food-apparatus, a behavior that could potentially have a communicative function (intentional or not) (69% of the trials). In the remaining 18% of the trials subjects were off camera and could not be classified into any of the categories above.

Again partners did not use the communicative information potentially available to them. Partners inserted the tool where the subject overtly communicated equally often as they inserted it in the opposite apparatus (mean \pm SE = 0.53 ± 0.13 ; one-sample *t* test: $t(7) = .883$, $p = .406$), and the same was true when the subject was positioned at one apparatus (without necessarily overtly communicating) (mean \pm SE = 0.60 ± 0.06 ; one-sample *t* test: $t(11) = .959$, $p = .358$). Because subjects did not always indicate the correct location when they positioned themselves in front of a food-apparatus (77% correct location; 76/99), partners were successful on only 73% of these trials in which they potentially followed the subject's spatial cue. For overt communication the success rate was 90%. Nevertheless, again, success did not lead any pair to be more successful in succeeding trials (Figure 2b). This suggests again that when subjects were successful they did not understand what led to their success.

Again partners tended not to pay much attention to subjects. Partners made a choice generally about 5 s after entering the room, so that subjects had only 5 s to communicate. They communicated on average at 2 s. In this follow-up, however, partners did not preferentially insert the tool into the food-apparatus closest to them when they entered the room (one-sample *t* test: $t(11) = .195$, $p = .849$).

Comparing the two communication conditions of Experiments 1 and 2 revealed that overall chimpanzees did not overtly communicate significantly more in Experiment 2 than in Experiment 1 (paired-sample *t* test: $t(11) = 1.073$, $p = .306$). These results show that even making the communication more direct by shifting the target of communication to the food, chimpanzees did not readily use overt communication as a reliable coordination strategy.

Discussion

Overall, chimpanzees helped more readily by transferring the needed tool rather than by overtly communicating the hiding location of the tool/food in this mutualistic collaborative task. Even though communication would not have cost them anything and both would have immediately benefited, subjects did not consider communication as an effective means to coordinate their actions in this task.

In the transfer condition, success was only possible if subjects transferred the tool. They had 1 min in each trial to find a solution to the problem and were motivated to figure it out. Subjects helped continuously once they understood how they could help, bearing the cost of giving up a tool. This finding is in line with a recent study in which chimpanzees helped their partner by transferring the tool that the partner needed to perform her role in a mutualistic collaborative task (Melis & Tomasello, 2013).

In the communication condition, continuous success was only possible if subjects communicated the hiding location to the partner, so that she could find the tool. Interestingly, playing the role of the partner first had an effect on subject's likelihood to communicate, because they communicated about nine times more frequently than individuals who started as subjects. One could

argue that as partner they experienced how important communication is to succeed, but then one should expect these individuals to also wait longer at the apparatus when playing the role of the partner to give subjects a realistic chance to communicate. This, however, was not the case. Subjects generally communicated very little and spent a lot of time away from the target object when the partner entered the room. Apparently, subjects did not consider communication as an effective means to help the partner play his role in the mutualistic task. However, even if subjects did nearly nothing overtly to help the partners, just positioning themselves in front of the hiding-location could potentially give information to the partner. Partners, however, did not take any of these behaviors into account. They chose the indicated location equally often as the other location.

Additionally, we did not observe any request for help, but instead the partner immediately chose one potential hiding-location upon entering the room. As a result, even if subjects wanted to help by communication, they had only on average 5.5 s to do so. Even though dyads could have succeeded on average in 95% of the trials, if partners had waited and paid attention to the subjects' overt communication, partners chose to act without having any information about the location of the food/tool. It is possible that the risk of just trying to solve the problem alone was not high enough, because chance level of success was still at 50%. In addition, it is possible that partners did not expect any communicative help from the subjects because (1) they did not know that subjects had information about the location of the tool/food, (2) they did not understand subjects' motivation to help them in this particular context, or (3) they generally did not expect conspecifics to help them obtaining food.

In the present experiment, partners could potentially know that subjects had information about the location of the tool/food, because they could see subjects watching the baiting process while they themselves could not see it and because other studies have shown that chimpanzees often keep track of what others have or have not seen (Hare, Call, Agnetta, & Tomasello, 2000; Kaminski, Call, & Tomasello, 2008). Additionally, half the sample was playing the subject's role before playing the partner's role, thus having experience about the informational level, but these individuals also did not behave differently. The possibility, though, that partners did not pay attention to subjects watching the baiting process is something that we cannot completely rule out. In our opinion, it is more likely that the latter explanations apply. In this particular task, the common goal (or subject's goal) was not as transparent as in other previous collaborative tasks, because the respective actions were not the same and did not occur simultaneously (Melis et al., 2006; Melis & Tomasello, 2013). That way, it was difficult for the partner to infer the subject's motivation to help. Additionally, previous studies have repeatedly shown that chimpanzees do not understand when others try to help them by communicating useful information (e.g., Herrmann & Tomasello, 2006; Kirchofer, Zimmermann, Kaminski, & Tomasello, 2012), so it could equally well be that they generally did not expect conspecifics to communicate to help. However, even if partners would wait for subjects' communicative help, it is unclear whether or not subjects would reliably communicate. From the present results and previous ones it seems that communication to inform others (Bullinger, Zimmermann, Kaminski, & Tomasello, 2011c) or to facilitate coordination in collaborative tasks (Bullinger et al.,

2011b; Hirata & Fuwa, 2007; Melis et al., 2009) is not something that comes up naturally for chimpanzees.

Two limitations of the study are (1) the disparate necessity of coordination needed in the two conditions and (2) the different amount of time in the two conditions the subject had to help. Future studies need to equate the difference in difficulty between the two conditions better. This could be done if the coordination component of the transfer task were increased, for example, by enabling the transfer mechanism only if the partner had opened a door to receive the tool. The second limitation could be solved if efforts were made to ensure that partners pay attention to the subject, for example, by enabling the release mechanism only after a certain time-delay, because this would give subjects more time to potentially communicate, overall increasing potential levels of success and motivating subjects to continue communicating in subsequent trials. This could also be accomplished, if substituting a human experimenter for the conspecific partner, who waits at the communication apparatus until the subject performs a relevant behavior or until the maximum time of the trial has passed. Another possibility would be to give subjects more potential hiding locations to increase the risk of failing (decrease chance level of success) and engender the motivation to search for help. Another possibility would be to present them with collaborative tasks in which the partner can more easily infer the subject's goals and how they relate to her own goal, in the hope that in such a situation they would spontaneously start waiting for subjects' (communicative) help. If a future study would additionally allow subjects to communicate with all modalities, including tactile communication, it might raise the chance to observe increased overall communication rates.

Our results show that chimpanzees are able and motivated to help in a mutualistic situation but only by means of physical help and not by means of communication, even if the potential for communication is increased by shifting the target to the food-apparatuses. Subjects did not consider communication as an effective means to help, nor did partners take any kind of potential information into account. It is unclear, however, whether this reflects chimpanzees' general inability or rather their unwillingness to communicate with certain partners, though we made sure that partners were tolerant with each other, making collaboration more likely to occur. It is important to reiterate that chimpanzees have many of the necessary components for collaborative communication: gesture flexibly to one another, take into account the partner's attention and attract it if necessary, understand others as intentional agents, engage in complex group activities, and having some motives for helping others in certain contexts. It seems that chimpanzees, despite their capacity to act collaboratively and use attention getters in some situations in which they need help (Bullinger et al., 2011a), they do not easily develop communicative strategies to solve problems. Experience with their partners (conspecifics and humans) during their daily interactions may have led to an understanding of how fruitful soliciting behavior is and from whom it is worth asking for help and from whom it is not. This supports the hypothesis that chimpanzees do not consider communication with conspecifics in contrast to communication with humans as an effective means to influence a partner in mutually beneficial interactions (Hirata & Fuwa, 2007; Tomasello, 2008).

It may be, though, that other contexts might facilitate the emergence of collaborative communication in chimpanzees. This could be contexts in which no food is involved or more life-threatening situations in which informing others about an approaching danger does not cost the signaler but saves conspecifics' lives (e.g., Crockford et al., 2012; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012). For whatever reason, it seems that using communication to coordinate mutualistic collaborative activities is not something that comes easily to one of our nearest primate relatives.

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