Chimpanzees (Pan troglodytes) develop a successful communicative strategy to collaborate

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Abstract

Successful collaboration often relies on individuals' capacity to communicate with each other. Despite extensive research on chimpanzee communication, there is little evidence that chimpanzees are capable, without extensive human training, of regulating collaborative activities via communication. This study investigated whether pairs of chimpanzees were capable of communicating to ensure coordination during collaborative problem-solving. The chimpanzee pairs needed two tools to extract fruits from an apparatus. The communicator in each pair could see the location of the tools (hidden in one of two boxes), whereas only the recipient could open the boxes. The subjects were first successfully tested for their capacity to understand the pointing gestures of a human who indicated the location of the tools. In a subsequent conspecifics test, the communicator increasingly communicated the tools' location, by approaching the baited box and giving the key needed to open it to the recipients. The recipient used these signals and obtained the tools, transferring one of the tools to the communicator so that the pair could collaborate in obtaining the fruits. The study suggests that chimpanzees have the necessary socio-cognitive skills to naturally develop a simple communicative strategy to ensure coordination in a collaborative task.

Keywords: collaboration, chimpanzees, coordination, communication

Human communication often involves individuals informing recipients of things that they believe will be useful or relevant to them (1). It has been hypothesized that such skills and motivations may have evolved in the context of mutualistic collaboration, in which one partner helping another by providing relevant information ends up benefiting both of them (2-4).

Despite extensive research on chimpanzee communication (5-7), we know very little about their naturally occurring communicative strategies to support collaborative activities, such as group hunting and boundary patrols. Of particular interest are instances of communication intended to facilitate coordination and success when individuals pursue a common goal. There is evidence of communication to coordinate travel to desired locations. In a classic study by Menzel (8-9), chimpanzees followed a knowledgeable leader to a location where food had been hidden. Leaders occasionally encouraged their partners to follow them and naïve individuals learned to read the leader's behavior. There is also evidence of a vocalization to coordinate travel, the "travel hoo", given prior to departure to recruit other group partners, especially allies (10). In these previous studies, attempts to communicate were made mainly to encourage partners to follow (for selfish or prosocial reasons), but not to inform them about anything in particular, nor to influence a collaborative activity coordinating different roles, since leaders can ultimately also start moving alone.

We refer to *collaborative* activities as mutually beneficial activities in which two or more individuals coordinate their actions to obtain a common resource or produce an effect that one individual would not be able to produce on her or his own. Chimpanzees are capable of intentionally coordinating their actions with a partner in collaborative tasks (11-13). They wait for their partner before initiating the collaborative activity and they even recruit the most skillful partner (11,12). They also help their partners instrumentally, by giving them the tools they need to perform their role (13). The focus of this study was on investigating whether chimpanzees are able to coordinate through communication in a mutualistic collaborative task.

A few instances of communication during collaboration have been observed in experiments in which one chimpanzee tried to encourage a human partner to act in some way in order to obtain an out-of-reach reward. In these studies chimpanzees approached the human, seized him by the arm and brought him closer to the problem they were trying to solve in an effort to get the human to obtain the reward for them or get help from them (14-15) (see also 16, but see 17 for negative findings). Evidence for communication between collaborating chimpanzees is scarcer. In a study by Crawford (18), pairs of chimpanzees were trained to pull together to bring a heavy baited box within reach. Occasionally, a chimpanzee lost motivation and stopped pulling and the partner employed various soliciting gestures to encourage the partner to continue pulling. Bullinger et al. (19, see also 20) also found some instances of intentional communication in a stag-hunt game scenario. In this coordination game individuals can choose between hunting alone the lower-quality "hare" or cooperating with the partner to obtain the higher quality "stag. In this study, chimpanzees used 'attention-getters' to get the partner to follow them, once they were already at the stag (19).

In all these previous studies, attempts to communicate were made to reactivate partners, encouraging them to 'do something' or 'follow me', but not to inform them about anything in particular, nor to coordinate roles. Only two previous paradigms, one with language-trained chimpanzees (21-22) and one of our own (23), have investigated whether chimpanzees support collaboration partners by providing the information they need to perform their role.

Savage-Rumbaugh et al. (21) trained two chimpanzees to use a lexigram keyboard that simulated human linguistic symbols. In the collaborative task one individual had to identify a specific tool to open a reward box and use the lexigram to request the tool, whereas the partner had to retrieve the specified tool and give it to the requester, who was then able to obtain the food. The two individuals underwent several training phases that required between 500 and 600 trials. First, they were introduced to the functionality of the different tools and had to learn to request the tools in order to obtain food for themselves. Afterwards, they were trained to name the tools: either they had to name the tool displayed by the human experimenter (E), or select the tool requested by E. Once they had mastered both roles of the task (encoding and decoding) with the human partner, the two chimpanzees were paired together. Initially the chimpanzees requested the tool from the experimenter, and the partner just played with it or dropped it. However, the experimenter facilitated collaboration between the two chimpanzees by communicating she had no tools and encouraging subjects to look and pay attention to each other (by pointing) so that after several trials, they started to realize they could request tools from each other.

This study showed that with artificial means, i.e. a trained symbolic system, and human training chimpanzees can learn to request tools from each other and comply with these requests in the context of a collaborative interaction. However, we do not know whether they can solve similar problems in the absence of training and an artificial communicative system. Furthermore, in the previous paradigm they were first trained to perform both roles (communicator and recipient) with a human partner, and nevertheless the experimenter had to intervene during the conspecifics test to facilitate collaboration and communication between them. Therefore, it is questionable to what extent they grasp the interdependency of their roles and could naturally, and without human training, solve a similar collaboration problem dependent on coordination and communication between partners.

In a previous study(23), we attempted to investigate this question and created a context in which chimpanzees could help partners play their roles either by transferring the needed tool or by communicating the hiding place of the needed tool. Although the chimpanzees readily helped each other by transferring the tool (as in 13), they did not reliably communicate the location of the hidden tool, nor comprehend their partner's communicative behaviors. Communicators sometimes positioned themselves in front of the hiding location, and occasionally combined this behavior with overt communication (e.g. stomping, jumping, mesh-banging). However, the recipients did not follow these signals, so that communicators stopped communicating. If the recipients had paid attention and followed the occasional communicator's signals, the communicator's behavior might have been positively reinforced, leading to a spiraling of successful production and comprehension of communicative signals.

That recipients did not follow the communicator's signals is maybe not surprising given that there is mixed evidence about chimpanzees and other great apes' capacity to understand informative social cues. In some studies, some chimpanzees have been found to be capable of using pointing to make an informed choice about which container to select (24-27, see 28 for review). However, in other studies chimpanzees have failed to make use of such cues (e.g. 29-33). Enculturated apes typically perform better than non-enculturated apes (34- 36) (although see 37), although the level of enculturation of many of the successful subjects goes well beyond a rich socio-communicative environment, since many of these subjects were language trained apes that underwent extensive training designed to foster human-chimpanzee communication. Therefore, one may question to which extent their use of social cues is based on simple associative processes that only emerge after extensive training (29). Alternatively, apes' difficulty to use social cues could be due to attentional constraints, since the salience of the signals also seems to play a role and adding vocalizations to bodily gestures seems to facilitate subjects' understanding, even among non-enculturated apes (24,25,38). There is also some evidence that distal set-ups, in which subjects must choose between containers that are further apart (>100cm) or approach the container to choose from a distance, also improve subjects' comprehension of communicative signals, the reason potentially being that the proximal set-up prevents subjects from paying attention to the experimenter's signals (27,39). In summary, there is evidence for chimpanzees' pointing comprehension but also many studies in which they perform rather poorly, and the exact factors that contribute to pointing comprehension are not well understood.

In the current study we tested whether pairs of chimpanzees would find a way of communicating the location of tools that the pair needed to obtain food. The chimpanzees had previously participated in the collaborative task (13, see Fig. 1a). However, we added a new level of complexity by hiding in one of two possible locations the tools they needed to collaborate. We were interested in both the production and the comprehension side of the interaction. The communicator in each pair could see the location of the tools, whereas only the recipient could open one of the boxes (see Fig. 1c,d). After obtaining the tools, the recipient needed to transfer one of the tools to the communicator so that each individual could perform her role in extracting the grapes.

The subjects participated in three experiments. In experiment 1, we investigated chimpanzees' ability to understand the communicative signals of a human partner. All ten subjects played the recipient role, and a human partner pointed distally to the location of the tools. In experiment 2, we focused on chimpanzees' tendency to communicate the location of the tools intentionally. The five pairs of chimpanzees (n = 10) played both roles (communicator and recipient). In the test condition, the communicators could communicate the location of the tools to the recipients, and in the control condition the recipients were absent to test the intentionality of the communicators' behavior. Since the chimpanzees increased their communication as experiment 2 progressed, we conducted experiment 3 to investigate recipients' comprehension as the communicators communicated more reliably. In experiment 3, subjects received additional trials of the test condition of experiment 2. A new group of chimpanzees (n = 6) participated in a follow-up control condition to test whether the recipients' behavior could be explained with a local enhancement mechanism.

Methods

Subjects

Ten chimpanzees (six females, four males) living at Sweetwaters Chimpanzee Sanctuary, Kenya participated in this study. All ten subjects had previously participated in (13) and were familiar with the collaborative task employed in this study. In addition, six other chimpanzees participated in the control condition of experiment 3 (SI Materials and Methods).

Apparatus

The collaboration apparatus consisted of a transparent box placed between two testing rooms (13). The individual facing the back of the box was required to insert a thin stick and rake the grapes, whereas the individual facing the front of the box was required to insert a long stick through a hole on the left side of the box and push to tilt the platform (Fig. 1a). Two identical opaque boxes, attached between two testing rooms, served as hiding locations for the tools (see Fig. 1b,c,d). Each box had a small transparent window on the back and a guillotine door on the front, which could only be opened by inserting a key below the door. The door only opened once the key was completely pushed inside to prevent subjects from pulling the key out to re-use it to open the second box.

Procedure and Design

Pre-tests

The subjects were individually introduced to the different contingencies of the hiding boxes (pre-tests 1 to 4,see SI Materials and Methods). In the last individual metacognition pretest (pretest 4), subjects had to look through the windows on the backs of the boxes to determine the location of the rewards before choosing which box to open (see Fig. 1b and Video 1). We were less interested in their metacognitive skills per se than in using this pre-test as a necessary prerequisite for participation in the communication test. If chimpanzees searched for the required information before opening one of the boxes, they might also be more likely to use the information provided by the communicator. There were considerable individual differences in how quickly subjects started to check the contents of the boxes before opening one of them (see supplementary materials for further details). This fits with the results of previous studies of primates' metacognitive capacities (40-41). Dyads also received a couple of reminder collaboration sessions, in which they had to transfer one of the tools to their partner in order to collaborate obtaining the grapes (pre-tests 5 and 6, see SI Materials and Methods).

Experiment 1: The set-up was as in the conspecifics test (Fig. 1c,d), except that the human (E1) positioned herself in Room 1, equidistant from the two hiding boxes. The tools were hidden in one of the hiding boxes and the key to open the hiding boxes was placed equidistantly between the two hiding boxes in Room 2. The moment the subject started to enter Room 2, E1 called the subject's name and food-grunted while being slightly bodily oriented, looking at and pointing (cross-pointing) to the baited box. Each subject participated in two sessions of six test trials each.

Experiment 2: Cooperative communication between chimpanzees – focus on production

Each test session consisted of four different kinds of trial, beginning with two introduction trials, followed by two trios of trials. Each trio comprised one trial of each type (i.e. test, control and motivation) in a randomized order (SI Materials and Methods). In the test trials (Fig. 1c,d), the collaboration box was baited with eight grapes. The two hiding boxes were closed, and one contained the tools. The communicator in Room 1 was able to see the content of the hiding boxes. If the recipients opened the correct box and obtained the tools, they had to transfer the raking tool to the communicator so that they could collaborate in obtaining the grapes. The control trials were as the test trials, except that the recipient never entered Room 2. The motivation trials were similar to the test trials, except that the two hiding boxes were open and one contained the tools (i.e. the recipients were able to obtain the tools straight away). In half of the test and control sessions, the key to the hiding boxes was placed in Room 2 (mid-way between the two hiding boxes), whereas in the other half of the sessions, the communicators had the key. All dyads participated in six sessions (two trials of each type per session), after which the subjects exchanged roles (i.e. communicators became recipients and vice versa) and participated in another six sessions.

Experiment 3: Cooperative communication among chimpanzees – focus on comprehension
Each test session started with four introduction trials, in which the communicator was absent, and the hiding boxes were empty, followed by six test trials like in Exp. 2, except that now the communicator always had the key. The subjects received a total of 18 test trials. The follow-up control experiment was conducted with a new group of six subjects. They also received sessions of four introduction trials, followed by six test trials (total of 18 test trials) in which there was no communicator and subjects encountered the key positioned close to the baited box (see SI Material and methods).

Coding and Analysis

All trials were videotaped and a second observer independently scored 30% of the trials for reliability purposes. We coded which of the hiding boxes subjects opened and all instances of behavior directed to indicate one of the boxes. We coded as communicative behaviour all instances of behaviour in which the communicators positioned themselves close to (or behind) one of the boxes, and touched, looked at the box or gave to the recipient the key close to it before the recipients started to open one of the boxes (see SI Materials and Methods for further details on coding methods and inter-observer reliability). We used non-parametric tests to compare subjects' performance with chance outcomes. Furthermore, given that we had individuals in each dyad playing both roles (communicator and recipient) and all dyads received multiple trials, we also analyzed the data using Generalized Linear Mixed Models (GLMM) (42), and included the identities of the dyad, the communicator and the recipient as random factors to control for the non-independence of the data. Since our responses were always binary, the models were fitted with binomial error structure and logit link using the function glmer of the R-package lme4 (43-45). Each full model was compared to a null model that included the control predictors and random effects by using a likelihood ratio test (46). As random effects we included random intercepts for the dyad and the communicator (since normally each communicator only had one recipient). Furthermore, to keep type I error rates at the nominal level of 0.05 we included various random slopes (47-49). Please refer to the electronic supplementary material for more details on each of the models. The datasets supporting this article have been uploaded as part of the supplementary material.

Results

In experiment 1 the human partner indicated the location of the tools by calling the subject's name and food-grunting to get the chimpanzees' attention and using cross-pointing and gaze alternation between the subject and the baited box (see Video 2). As a group the chimpanzees performed above chance and followed the human pointing in 81% of trials ($P = 0.02$, exact Wilcoxon signed-ranked test, $n = 10$, $T+ = 55$,). Five out of the ten subjects performed individually above chance. After obtaining the tools, the chimpanzees transferred the raking tool to the human experimenter, who then collaborated with the subject to obtain the grapes.

In Experiment 2, pairs of chimpanzees were required to communicate with each other. We did not observe any gestures (i.e. pointing) or attempts to signal the boxes from a distance, but we observed a clear and effective strategy to signal one of the boxes and influence the partner's choices. Subjects' communicative behavior consisted of approaching and positioning themselves behind or very close to one of the boxes just before recipients could make a choice, sometimes touching, looking at the box or giving the key to the recipient close to the box (see also the supplementary material and Videos 3 and 4). We observed this behavior in 50% of trials of the test condition, and in only 20% of control trials when recipients were absent (P = 0.006, exact Wilcoxon signed-ranked test, n = 10, T += 53, see Figure 3a). We also fitted a GLMM to test the effect of condition and trial on individuals' likelihood of communicating. We included communication as the dependent variable and as fixed factors the interaction between trial number and condition and the fixed factors: communicators' possession of key, role order and baited box (left/right). The full model was significantly different from a more parsimonious model without the interaction between trial number and condition, but all the fixed factors and the random intercepts and slopes (Likelihood ratio test: $\chi^2(1) = 15.419$, $p < .001$).The subjects were more likely to communicate in the test condition but less likely in the control condition with increasing trial numbers (estimate = 1.262, SE = 0.330, Z = 3.819, P < 0.001; Figure 3b), whereas the other factors had no effect (see SI for full model outputs). Throughout this experiment, the subjects seemed to learn the necessity of signalling the location of the tools when the recipients were present.

In experiment 2, the recipients opened the indicated box in 52% of trials with communication, which is not significantly different from a chance outcome (P = 0.54, exact Wilcoxon signed-ranked test, n = 10, T+ = 23). However, comparison between success levels in the absence or presence of communication shows that the subjects tended to be more successful when their partners communicated than when they did not (M = 52.79% vs. M = 28.45%; exact Wilcoxon signed-ranked test: n = 10, T+ = 38, P = 0.07, see graph in SI for individual data). We fitted a GLMM to test the effect of "communication" on the recipients' likelihood of opening the box with tools. The full model included "Success finding the tools (yes/no)" as the dependent variable, and communication (yes/no), trial number, role order, communicator's possession of the key and baited box as fixed factors. The full model was significantly different from a more parsimonious model that included all control predictors (trial, role order, communicator's possession of the key and baited box) and the random intercepts and slopes (Likelihood ratio test: $\chi^2(2) = 5.327$, $p = .021$). The recipients were more likely to find the tools when their partners communicated whereas none of the other factors had any effect (estimate = 1.295, SE = 0.476, Z = 2.724, P = 0.021; see SI for full model output and additional model details). Given that communicators only communicated reliably as the experiment progressed, overall the dyads were not that successful.

In experiment 3, the communicators signalled one of the boxes, by positioning themselves and transferring the key almost into contact with the baited box, in 81.11% of trials (range = 28 100%) and they indicated the correct box (the one containing the tools) in 86% of trials with communication (range = 63–100%, see Fig. 4a), significantly more often than expected by chance (Wilcoxon exact test: N = 10, T+ = 55, p = 0.002). We ran a GLMM to test whether individuals' likelihood of communicating the location of the tools increased with trial number (see SI Material and Methods). We included "correct communication" (yes/no) as the dependent variable (no communication or signalling the empty box were considered incorrect responses) and as fixed factors trial number, role order, and baited box. The full model was not significantly different from a more parsimonious model that included only role order and baited box as control predictors and the random intercepts and slopes. There was no evidence that subjects improved their communication with increasing numbers of trials (likelihood ratio test: $\chi2(1) = 0.066$, $p = 0.798$). The subjects seem to have learned the need for communication in the previous experiment and started this new set of trials performing at high levels. Only two subjects (Amahirwe and Jojo) communicated very little, and their performance did not change throughout the experiment.

In experiment 3, the recipients opened the box indicated by the partner in 81.11% of trials with communication which is significantly above chance levels (P = 0.002, exact Wilcoxon signed-ranked test, n=10, T+ = 55; see Fig. 4b). Overall, pairs succeeded in obtaining the tools in 69.8% of trials, which is also significantly above chance (P = 0.002, exact Wilcoxon signed-ranked test, n = 10, T+ = 55). We fitted a GLMM to test the effect of "correct communication" on the recipients' likelihood of opening the box with tools. Since the subjects communicated at such high levels, we did not look at simple communication but at ‘correct communication’ (i.e signalling the box containing the tools). We included “Success finding the tools (yes/no)” as the dependent variable, and correct communication, trial number, role order and baited box as fixed factors. The full model was significantly different from a more parsimonious model that included trial number, role order and baited box as control predictors and the random intercepts and slopes (Likelihood ratio test: $\chi^2(1) = 6.267$, p =0.012; see SI for full model outputs).

The recipients were more likely to obtain the tools when their partners communicated correctly (estimate = 1.884, SE = 0.590, Z = 3.194, P = 0.012), whereas all other factors, including trial number had no effect on levels of success, suggesting that recipients chose to open the box indicated by the communicators from the outset of this new set of trials.

A low-level interpretation of the recipients’ behaviour could be that the subjects opened the box to which they were closest to when they got the key, without any understanding of their partners’ communicative intentions. To rule out this explanation, we ran a control experiment with a new group of subjects. The human experimenter hid the fruit rewards in one of the boxes and cued the box by positioning the key close to it. The subjects opened the ‘cued’ box in 66.67% of trials, which is not above chance levels (P= 0.12, exact Wilcoxon signed-ranked test, n = 6, T+ = 14). We also conducted another analysis using these results (67%) as a baseline to which to compare recipients’ tendency to open the box indicated by their partners (81.11%), finding that the communicators’ behavior added something to simply finding a key next to one of the boxes (P = 0.02, exact Wilcoxon signed-ranked test, n= 10, T+ = 50; see SI for additional analysis showing that trial number has no effect).

Discussion

The chimpanzees developed a successful communicative strategy to coordinate their actions in a collaborative task. Individuals in the communicator role approached and gave the key to the recipient close to the box containing the tools, and the recipients correctly inferred from this behavior the location of the tools that they both needed. The same chimpanzees also made use of the informative cues of a human experimenter who pointed to the location of the tools from a distance.

These results support previous findings concluding that chimpanzees comprehend human pointing (28). The findings are particularly interesting because these subjects were not language-trained chimpanzees (as in 25,34), they had never previously participated in a communicative task of this type, and we employed a more challenging distal pointing as opposed to the proximal pointing of other previous studies (25,26). One might argue that these sanctuary-living chimpanzees had experienced a richer socio-communicative environment that had allowed them to learn the meaning of human informative pointing (34,36). However, it has been previously argued that much more intense enculturation, than the one typical of sanctuary-living chimpanzees, is necessary to promote apes’ pointing comprehension (26). In our opinion, one cannot rule out the positive impact that daily positive interactions with humans have on these chimpanzees. However, something else about the way our study was conducted must have had a positive impact since chimpanzees with similar life histories did not perform above chance levels in other studies (33).

Our study methods differed from previous ones in several ways. First, the subjects participated in a metacognition pre-test. It is possible that the experience from this pre-test helped the subjects become more receptive and attentive to the human pointing, perhaps because they understood that they lacked information to succeed in the task, or because they learned to inhibit the prepotent response of opening the box straight away. Second, we used a distal set-up in which subjects had to approach one of the boxes to select it. Mulcahy and Call (27) found that great apes were better at using human pointing in a distal object-choice set-up and argued that a proximal set-up prevents subjects from paying attention to the experimenter’s signals (although see 32,33). Third, we used highly conspicuous signals by combining simulated chimpanzee food-grunts with a pointing gesture and gaze. Other previous studies (24, 25,38) also found that vocalizations and noises in combination with behavioural cues facilitated subjects’ performance (although see 32). Therefore, it is possible that these three factors contributed helping subjects to pay attention to the human. If this is indeed the case, this would suggest that chimpanzees’ difficulty following social cues is related to inhibitory and attentional constraints, rather than an inherent inability to understand communicative intentions.

Further studies will be necessary to identify the exact factors that facilitate and constraint chimpanzees' understanding of human social cues.

In the critical test of this study, pairs of chimpanzees were required to communicate and coordinate with each other. We found that the subjects learnt to communicate over the course of the first experiment with conspecifics. Their communicative behavior consisted of approaching, looking, touching the box and/or giving the key to the recipient close to the baited box, and these behaviors increased in frequency during the first twelve trials. The control condition rules out that communicators were merely attracted to the tools. There are at least two potential explanations for the emergence of this successful communicative strategy. A lean explanation could be that there was something similar to a rapid ritualization process during the study regarding the communicators' behavior and intentionality. Initially, the communicators' approaches to the tools box may have been unintentionally communicative. The communicators may have approached the box anticipating that the recipients would open it. The recipients may have occasionally opened it, fulfilling the communicators' expectations. Soon, the communicators may have intentionally performed this approach behavior over and over to elicit the recipients' opening of the box. Alternatively, a richer, but in our opinion more plausible, interpretation may be that the communicators' behaviour was intentional from the beginning, but only once they made a couple of positive experiences with a responsive partner they started to communicate consistently. Note that in our previous study with a different group of chimpanzees (23), chimpanzees also communicated in a similar task, but recipients ignored them so that communicators stopped communicating. Chimpanzees and other great apes spontaneously indicate to a human partner the location of food and food-extracting tools (34, 51-52; see 53 for a review), but whereas chimpanzees have many opportunities to learn the positive effects of requesting things from humans, requesting things from conspecifics is generally less successful (54-55).

Once communicators were signalling the baited box reliably, the recipients succeeded obtaining the tools. It might be argued that the recipients simply opened the box to which they were closest when they obtained the key or that they learnt to associate the cued box with the tools. Although we cannot completely rule out this explanation, the control condition provides some evidence to the contrary, since the subjects did not preferentially open the cued box (in the absence of the communicator), nor were there any signs of improvement throughout the experiment. In approaching and remaining at one of the boxes, the communicators' behaviour probably resembled their naturally occurring behaviours when they encounter something interesting (e.g. in a foraging context). Itakura et al. (24) specifically tested this type of cue in an object-choice task and found that chimpanzees successfully selected the container approached or examined by a conspecific (or human). In the current study, the same subjects also performed above chance in the human distal-pointing comprehension task. Therefore, the most likely explanation is that the recipients also interpreted the conspecifics' behavior as intentionally communicative.

There are several possible reasons for the higher performance of our recipients in comparison with Bullinger et al. (23) and Moore et al. (55). First, the recipients had already acquired experience in searching for and attending to relevant information (in the metacognition and human pointing task). Second, recipients were forced to wait and pay attention to the communicators since the communicators were in possession of the key to open the boxes. Third, the communicators in our study provided very evidence-rich expressive behaviors (approaching the baited location and offering the key necessary to open it nearby), what probably facilitated their understanding of the communicators' goals (53).

In summary, this is the first study to show pairs of chimpanzees developing naturally, without artificial communicative means (as in 21,22), a successful communicative strategy to ensure coordination in a collaborative task. Eight out of ten chimpanzees regularly communicated to their partners the location of the tools. The partners used this information and the result was a successful form of complex collaboration that included the successful transfer of information between partners and mutual instrumental support in the form of individuals transferring to each other the necessary tools. Furthermore, the same subjects were able to use the distal pointing gesture of a human partner to find the tools.

In this study subjects did not need to communicate about a specific tool (as in 21) but just the tool's location, an arguably simpler task. However, their successful strategy emerged naturally, without interacting first with a human partner who encouraged them to communicate and fulfilled the recipient's role (as in 21). Subjects in the recipient's role had slightly more experience as they had participated first in the pointing test with the human partner. However, they only received a small number of trials with the human partner and the indicative cues used by the human were different from the ones used by the chimpanzees, so that subjects could not just rely on their previous experience.

These results show that chimpanzees have the capacity to develop new social strategies, including a communicative strategy, to support each other in their respective roles during a mutually beneficial collaborative interaction. At the same time these results suggest that for such communication to emerge and stabilize, subjects need positive experiences with responsive partners. Future studies could investigate if they are still capable of communicating when they cannot approach the tool's location, or a simple approach is not indicative enough.

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References

1. Sperber, D., & Wilson, D. (1985/1996). Relevance: Communication and cognition. Oxford: Basil Blackwell.
2. Tomasello M, Melis AP, Tennie C, Wyman E, & Herrmann E (2012) Two key steps in the evolution of human cooperation: The interdependence Hypothesis. Current Anthropology 53(6):673-692.
3. Sterelny K (2012) Language, gesture, skill: the co-evolutionary foundations of language. Philos Trans R Soc Lond B Biol Sci 367(1599):2141-2151.
4. Smith EA (2010) Communication and collective action: language and the evolution of human cooperation. Evolution and Human Behavior 31(4):231-245.
5. Hobaiter C & Byrne RW (2011) The gestural repertoire of the wild chimpanzee. Anim Cogn 14(5):745-767.
6. Pika S & Mitani J (2006) Referential gestural communication in wild chimpanzees (Pan troglodytes). Curr Biol 16(6):R191-192.
7. De Waal FB & Van Hooff JA (1981) Side-directed communication and agonistic interactions in chimpanzees. Behaviour 77(3):164-198
8. Menzel EW (1975) Purposive behavior as a basis for objective communication between chimpanzees. Science 189(4203):652-654.
9. Menzel EW, Jr. (1971) Communication about the environment in a group of young chimpanzees. Folia Primatol (Basel) 15(3):220-232.
10. Gruber, T. & Zuberbuhler, K. (2013) Vocal recruitment for joint travel in wild chimpanzees. PLoS One 8, e76073, doi:10.1371/journal.pone.0076073
11. Melis AP, Hare B, & Tomasello M (2006) Chimpanzees recruit the best collaborators. Science 311(5765):1297-1300.
12. Melis AP, Hare B, & Tomasello M (2009) Chimpanzees coordinate in a negotiation game. Evolution and Human Behavior 30(6):381-392.
13. Melis AP & Tomasello M (2013) Chimpanzees' (Pan troglodytes) strategic helping in a collaborative task. Biol Lett 9(2):20130009.

14. Kohler W (1925) The Mentality of Apes (Kegan Paul, Trench, Trubner & Co., LTD, London).
15. Hirata S & Fuwa K (2007) Chimpanzees (Pan troglodytes) learn to act with other individuals in a cooperative task. Primates 48(1):13-21.
16. Roberts AI, Vick SJ, Roberts SG, & Menzel CR (2014) Chimpanzees modify intentional gestures to coordinate a search for hidden food. Nat Commun 5:3088.
17. Warneken F, Chen F, & Tomasello M (2006) Cooperative activities in young children and chimpanzees. Child Dev 77(3):640-663.
18. Crawford, M. P. (1937) The cooperative solving of problems by young chimpanzees. Comparative Psychology Monographs 14, 1-88.
19. Bullinger AF, Wyman E, Melis AP, & Tomasello M (2011) Coordination of Chimpanzees (Pan troglodytes) in a Stag Hunt Game. International Journal of Primatology 32(6):1296-1310.
20. Duguid S, Wyman E, Bullinger AF, Herfurth-Majstorovic K, & Tomasello M (2014) Coordination strategies of chimpanzees and human children in a Stag Hunt game. Proceedings of the Royal Society B-Biological Sciences 281(1796).
21. Savage-Rumbaugh ES, Rumbaugh DM, & Boysen S (1978) Linguistically mediated tool use and exchange by chimpanzees (Pan troglodytes). Behavioural and Brain Sciences 1(4):539-554.
22. Savage-Rumbaugh, E. S., Rumbaugh, D. M., & Boysen, S. (1978). Symbolic communication between two chimpanzees (Pan troglodytes). *Science*, *201*(4356), 641-644.
23. Bullinger AF, Melis AP, & Tomasello M (2014) Chimpanzees (Pan troglodytes) instrumentally help but do not communicate in a mutualistic cooperative task. Journal of Comparative Psychology 128(3):251-260.
24. Itakura S & Tanaka M (1998) Use of experimenter-given cues during object-choice tasks by chimpanzees (Pan troglodytes), an orangutan (Pongo pygmaeus), and human infants (Homo sapiens). Journal of Comparative Psychology 112(2):119.
25. Lyn H, Russell JL, & Hopkins WD (2010) The Impact of Environment on the Comprehension of Declarative Communication in Apes. Psychological Science 21(3):360-365.
26. Hopkins WD, Russell J, McIntyre J, & Leavens DA (2013) Are chimpanzees really so poor at understanding imperative pointing? Some new data and an alternative view of canine and ape social cognition. PLoS One 8(11):e79338.
27. Mulcahy NJ & Call J (2009) The Performance of Bonobos (Pan paniscus), Chimpanzees (Pan troglodytes), and Orangutans (Pongo pygmaeus) in Two Versions of an Object-Choice Task. Journal of Comparative Psychology 123(3):304-309.
28. Leavens DA & Bard KA (2011) Environmental influences on joint attention in great apes: implications for human cognition. Journal of Cognitive Education and Psychology 10(1):9.
29. Povinelli DJ, Reaux JE, Bierschwale DT, Allain AD, & Simon BB (1997) Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. Cognitive Development 12(4):423-461.
30. Tomasello M, Call J, & Gluckman A (1997) Comprehension of novel communicative signs by apes and human children. Child Dev 68(6):1067-1080.
31. Hare B, Brown M, Williamson C, & Tomasello M (2002) The domestication of social cognition in dogs. Science 298(5598):1634-1636.
32. Herrmann E & Tomasello M (2006) Apes' and children's understanding of cooperative and competitive motives in a communicative situation. Dev Sci 9(5):518-529.
33. Kirchhofer KC, Zimmermann F, Kaminski J, & Tomasello M (2012) Dogs (Canis familiaris), but not chimpanzees (Pan troglodytes), understand imperative pointing. PLoS One 7(2):e30913.
34. Call J & Tomasello M (1994) Production and comprehension of referential pointing by orangutans (Pongo pygmaeus). J Comp Psychol 108(4):307-317.
35. Tomasello M & Call J (2004) The role of humans in the cognitive development of apes revisited. Anim Cogn 7(4):213-215.

36. Lyn H, Russell JL, & Hopkins WD (2010) The Impact of Environment on the Comprehension of Declarative Communication in Apes. Psychological Science 21(3):360-365.
37. Call J, Hare BA, & Tomasello M (1998) Chimpanzee gaze following in an object-choice task. Anim Cogn 1(2):89-99.
38. Call, J., Agnetta, B. & Tomasello, M. (2000)Cues that chimpanzees do and do not use to find hidden objects. Animal Cognition 3, 23-34.
39. Barth J, Reaux JE, & Povinelli DJ (2005) Chimpanzees' (Pan troglodytes) use of gaze cues in object-choice tasks: different methods yield different results. Anim Cogn 8(2):84-92.
40. Call, J. Do apes know that they could be wrong? (2010) Anim Cogn 13, 689-700, doi:10.1007/s10071-010-0317-x.
41. Hampton, R. R., Zivin, A. & Murray, E. A. (2004) Rhesus monkeys (Macaca mulatta) discriminate between knowing and not knowing and collect information as needed before acting. Anim Cogn 7, 239-246, doi:10.1007/s10071-004-0215-1.
42. Baayen, R.H. (2008). Analyzing Linguistic Data: A Practical Introduction to Statistics Using R, (Cambridge: Cambridge University Press).
43. R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
44. Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.
45. McCullagh, P., and Nelder, J.A. (2008). Generalized linear models, (London: Chapman and Hall).
46. Dobson, A.J. (2002). An Introduction to Generalized Linear Models, 2nd Edition, (Boca Raton, FL: Chapman & Hall/CRC).
47. Barr, D.J., Levy, R., Scheepers, C., and Tily, H.J. (2013). Random effect structure for confirmatory hypothesis testing: Keeping it maximal. J Mem Lang.
48. Schielzeth H & Forstmeier W. (2009). Conclusions beyond support: overconfident estimates in mixed models. Behav Ecol, 20, 416-420.
49. Aarts, E., Dolan, C. V., Verhage, M., & Sluis, S. (2015). Multilevel analysis quantifies variation in the experimental effect while optimizing power and preventing false positives. *BMC neuroscience*, *16*(1), 94.
50. Leavens DA, Hopkins WD, & Bard KA (2005) Understanding the Point of Chimpanzee Pointing: Epigenesis and Ecological Validity. Curr Dir Psychol Sci 14(4):185-189.
51. Zimmermann F, Zemke F, Call J, & Gomez JC (2009) Orangutans (Pongo pygmaeus) and bonobos (Pan paniscus) point to inform a human about the location of a tool. Animal Cognition 12(2):347-358.
52. Leavens DA, Hopkins WD, & Bard KA (1996) Indexical and referential pointing in chimpanzees (Pan troglodytes). J Comp Psychol 110(4):346-353.
53. Moore, R. Evidence and interpretation in great ape gestural communication. Humana Mente, 27-51 (2013).
54. Pele, M., Dufour, V., Thierry, B. & Call, J. Token transfers among great apes (Gorilla gorilla, Pongo pygmaeus, Pan paniscus, and Pan troglodytes): species differences, gestural requests, and reciprocal exchange. J Comp Psychol 123, 375-384, doi:10.1037/a0017253 (2009).
55. Moore R, Call J, & Tomasello M (2015) Production and Comprehension of Gestures between Orang-Utans (Pongo pygmaeus) in a Referential Communication Game. Plos One 10(6).
56. Leavens DA, et al. (2015) Distal Communication by Chimpanzees (Pan troglodytes): Evidence for Common Ground? Child Development 86(5):1623-1638.

Figure Legends

Figure 1. Experimental set-up of the study, (a) Collaboration Box from Melis & Tomasello (2013). One first needs to rake the grapes towards the right side of the box, and then insert the pushing tool to tilt the platform so that the rakes drop down to both sides of the box. (b) Metacognition individual Pretest. Individuals entered into room 2 from an adjacent room (room 3). The collaboration box

contained grapes inside, and the tools necessary to obtain the grapes were hidden in one of the two opaque boxes. Individuals needed to first check the content of the hiding boxes (looking through the back of the hiding boxes) and then open with the key the box with tools. Once they obtained the tools, they could go back and forth between rooms 1 & 2 to perform both roles and obtain the grapes, (c) and (d): Test condition from the recipient's perspective (c) and communicator's perspective (d). The communicator can see the location of the tools, but only the recipient can open the hiding boxes. After obtaining the tools, the recipient needed to transfer the raking tool to the communicator so that they could collaborate emptying the grapes in the collaboration box.

Figure 2. Number of correct responses (max. 12 trials) per subject when the human experimenter pointed to the location of the tools (* $p<0.05$, two-tailed binomial probability).

Figure 3. (a) Mean proportion of trials (+/-SEM) in the test (i.e. recipients present) and control (i.e. recipients absent) conditions of Experiment 2 in which the communicators (N=10) signalled the position of the tools. (b) Probability of communication in Experiment 2 as a function of trial number and condition (Test vs. Control).

Figure 4. (a) Absolute number of trials in Experiment 3 in which subjects in the communicator's role signalled one of the boxes (empty or with tools). On the X-axis the subjects in the communicator's role with their recipient partners in parenthesis (in the order in which they participated in the communicator's role). (b) Absolute number of trials in Experiment 3 in which recipients followed vs. did not follow, the communicators' signals. On the X-axis the subjects in the recipient's role with their communicator partners in parenthesis (in the order in which they participated in the recipient's role).

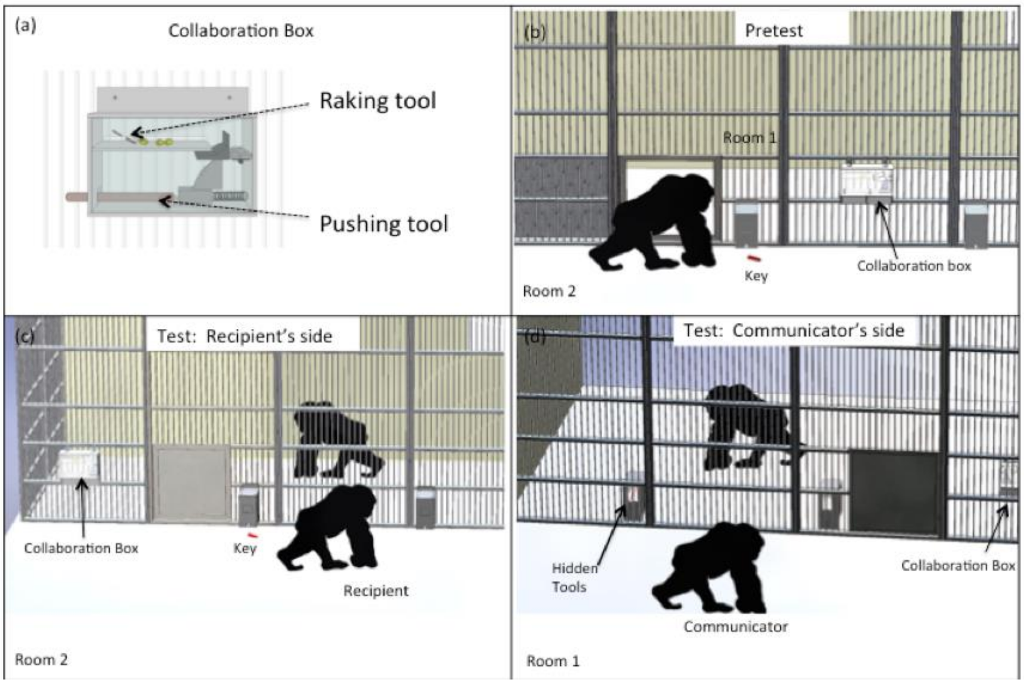

Figure 1

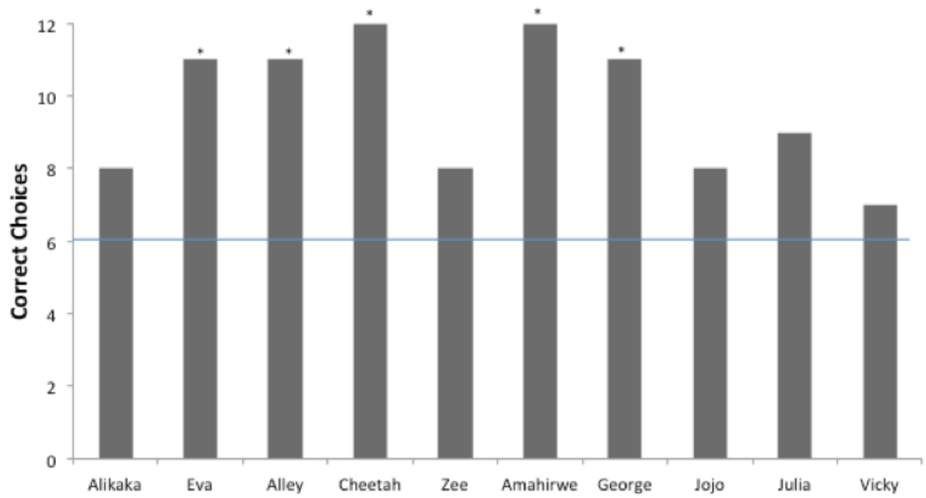

Figure 2

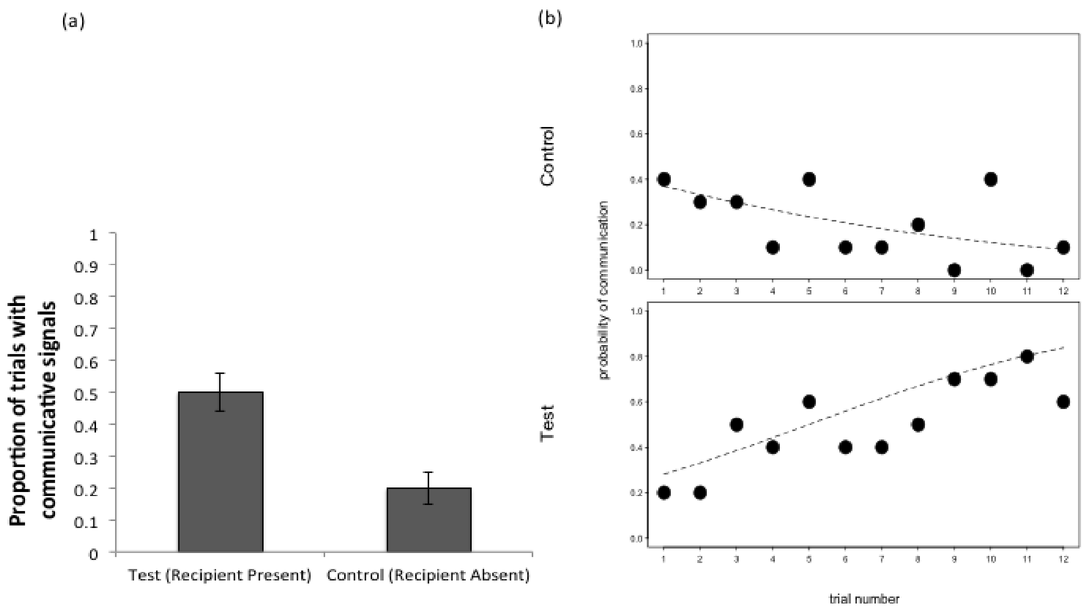

Figure 3

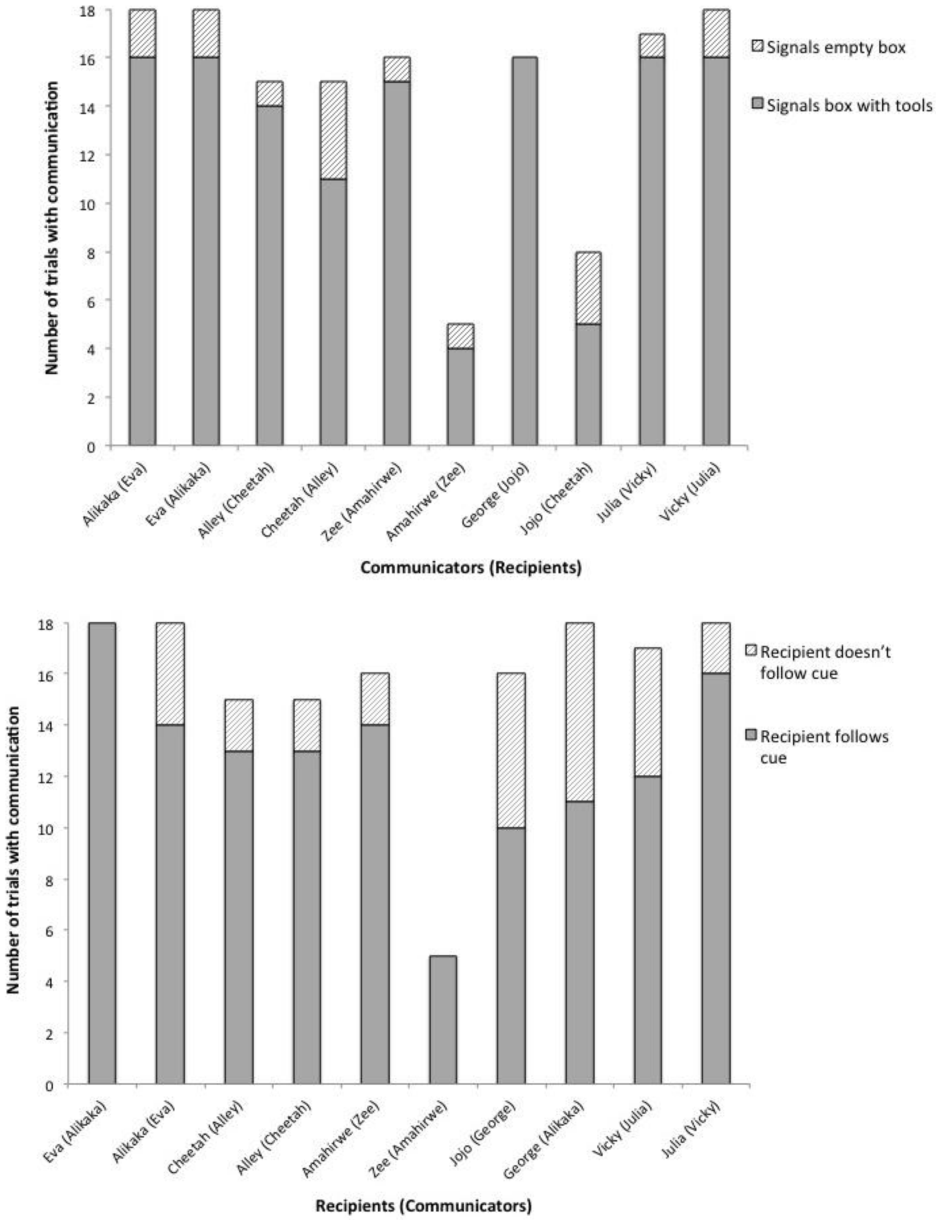
Number of trials with communication
0
2
4
6
8
10
12
14
16
18
Signals empty box
Signals box with tools
Alikaka (Eva)
Eva (Alikaka)
Alley (Cheetah)
Cheetah (Alley)
Zee (Amahirwe)
Amahirwe (Zee)
George (Jojo)
Jojo (Cheetah)
Julia (Vicky)
Vicky (Julia)
Communicators (Recipients)
Number of trials with communication
Recipient doesn't follow cue
Recipient follows cue
Eva (Alikaka)
Alikaka (Eva)
Cheetah (Alley)
Alley (Cheetah)
Amahirwe (Zee)
Zee (Amahirwe)
Jojo (George)
George (Alikaka)
Vicky (Julia)
Julia (Vicky)
Recipients (Communicators)

Figure 4