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Materials and Methods

Figs. S1 to S7

References

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Chimpanzees Recruit the Best Collaborators

Alicia P. Melis,* Brian Hare,* Michael Tomasello

Humans collaborate with non-kin in special ways, but the evolutionary foundations of these collaborative skills remain unclear. We presented chimpanzees with collaboration problems in which they had to decide when to recruit a partner and which potential partner to recruit. In an initial study, individuals recruited a collaborator only when solving the problem required collaboration. In a second study, individuals recruited the more effective of two partners on the basis of their experience with each of them on a previous day. Therefore, recognizing when collaboration is necessary and determining who is the best collaborative partner are skills shared by both chimpanzees and humans, so such skills may have been present in their common ancestor before humans evolved their own complex forms of collaboration.

Human society depends on people's ability to collaborate with unrelated individuals in a flexible manner (1, 2). From a young age, human children recognize when they need help in solving a problem, actively recruit collaborators, come to agreements about what type of actions to perform jointly, and recognize others' roles while coordinating their efforts to ensure success (3, 4). Adult humans maintain long-term collaborative partnerships with non-kin by actively monitoring the roles of individuals during collective efforts and basing future collaborations on individual contributions (5, 6).

Although it is clear that human collaborative skills are exceptional, if not unique, in their frequency and complexity, the phylogenetic origins of such skills remain unclear. Of special importance in attempting to identify these origins are humans' nearest primate relatives, such as chimpanzees [see (7–14) for studies of cooperation in other mammals]. Observations from

the wild suggest that chimpanzees possess some collaborative skills; specifically, they may know both when they need a collaborator and something about how they should collaborate. For example, chimpanzees hunt monkeys in groups more often when prey are in dense forest canopy, with many escape routes, than in broken canopy, when escape routes are more limited and individual hunting might be successful (15, 16). During group hunts, chimpanzees seem to coordinate their positions within tree(s) so as to surround monkey prey (15, 16). During risky intergroup encounters, chimpanzees approach the area from which a strange male has called only if their party includes enough adult males to outnumber the rivals (17). In addition, chimpanzees may use their social experience to make judgements about the quality of different collaborative partners. Thus, male chimpanzees form long-term alliances with other individuals, jointly defending their territory from other groups and ensuring their access to females within their own group (15, 18). Chimpanzees also tend to reward their favored partners with reciprocal social attention, support, and valuable resources such as meat and mating opportunities. Such preferential

treatment of favored partners may maintain long-term collaborative partnerships, because noncollaborators suffer when they are excluded from potential collaborative interactions (19–21).

However, it is difficult to determine the precise cognitive skills underlying chimpanzees' cooperative activities through natural observations alone. That is, it remains plausible that group hunts may simply consist of the independent yet simultaneous actions of multiple individuals who have little, if any, regard for or understanding of the roles of others in ensuring mutual success (7, 16). Similarly, in most observational studies examining the maintenance of collaborative relations through reciprocal exchange, these interactions can be explained as by-products of symmetrical attraction or aversion between individuals; such symmetry-based reciprocation does not necessarily involve a precise accounting of costs and benefits when choosing to collaborate with different individuals (22). Experimental studies of chimpanzee collaboration are also inconclusive, because the few such studies that have been conducted found very modest collaborative skills when individuals were not explicitly trained [(23–25); see (11–14) for experimental studies with other primate species]. Moreover, no experiments have ever examined whether chimpanzees can recognize when they need a collaborative partner and whether they can identify, remember, and then preferentially recruit the most effective partner available to them.

In contrast to previous studies, a recent experiment found that most captive chimpanzees can spontaneously (without training) solve a collaborative problem, as long as their social relationship is controlled and they are paired with a tolerant partner (26). This new finding raises the possibility of presenting chimpanzees with more complex collaborative situations in order to examine which skills found in humans are derived or inherited. In the current

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study, we investigated whether chimpanzees (i) know when collaboration is necessary and (ii) choose the more effective of two potential collaborators, based on previous experience with each of them.

In the first experiment, eight semi-free-ranging chimpanzees at Ngamba Island Chimpanzee Sanctuary in Uganda were given the opportunity to recruit a collaborative partner when they either (i) needed help in solving a food retrieval problem or (ii) did not need help in solving a food retrieval problem. Subjects were introduced to a “key” (a wooden peg) that could be removed only from inside the testing room (27). The key locked a sliding door between the testing room and an adjacent room. If the key was removed by the subject, the sliding door could easily be opened manually (Fig. 1). Subjects were also introduced to a feeding platform in a separate session (27). The feeding platform was placed next to the testing room but out of the reach of the subject(s), and both feeding dishes were always baited with equal amounts of food. A rope was then threaded through two metal loops anchored to the feeding platform, and both ends of the rope were extended into the testing room. Therefore, in each trial if the subject(s) pulled both ends of the rope simultaneously, the feeding platform could be pulled within reach; however, if only one end of the rope was pulled, the rope became unthreaded and the food was lost (Fig. 1) (27, 28).

After separate introductions to the key and pulling task (27), subjects participated in two types of test conditions. In the collaboration condition, the subject and partner watched from separate rooms adjacent to the testing room as the baited food platform and ropes were positioned so that the two ends of the rope were placed 3 m apart: too far for one individual to pull both simultaneously. The subject was then released into the testing room while the partner remained “locked” in the adjacent room, unless the subject chose to release her by removing the key and unlocking the door so that they could work together to obtain the food. The solo condition differed from the collaboration condition only in that the two ends of the rope were placed 55 cm apart, so that a subject did not need help in obtaining the food because she could potentially pull both rope ends simultaneously by herself [movie S1 (27)]. Subjects were tested in two test sessions in which they received a maximum of 12 trials per condition during each session.

Overall, when both sessions are considered together, subjects unlocked the door to recruit their partner significantly more often in the collaboration condition, when they needed assistance to obtain the food, than in the solo condition, when they did not (Table 1; $t = 7.27$, $df = 7$, $P < 0.001$, paired t test). As individuals, seven of eight subjects recruited significantly more in the collaboration than the solo condition across the two sessions (Table 1; Fisher’s exact test,

$P < 0.05$). A 2×2 repeated-measures analysis of variance (ANOVA) (condition \times session) revealed that the six subjects opened the door significantly more in the collaboration condition [$F(1,5) = 71.42$, $P < 0.001$], whereas there was no effect of session and a significant interaction between condition and session [$F(1,5) = 8.81$, $P < 0.031$], with subjects’ recruitment in the collaboration condition increasing in the second session ($t = 2.39$, $df = 5$, $P < 0.031$, paired sample t test).

Subjects’ preference for recruiting a collaborator when needed appeared relatively spontaneously within the first session, as each

subject began recruiting a partner. In the session in which they started to open the door, five of eight subjects, as individuals, opened it significantly more in the collaboration condition (Table 1). A repeated-measures ANOVA also found that there was little change in subjects’ preference for recruiting in the collaboration condition during the second session (the session in which all subjects recruited), because there was only a main effect of condition [$F(1,7) = 56$, $P < 0.001$] but no effect of trial (comparing the first three trials of a given condition to the last three trials of that condition) or interaction between trial and condition.

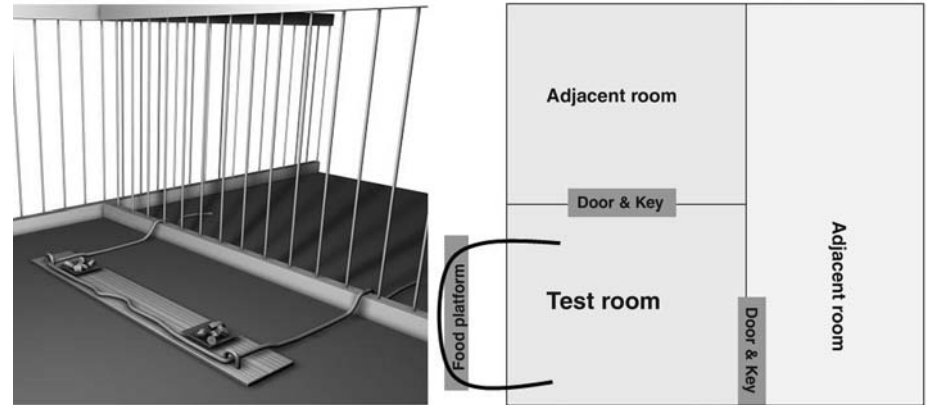


Fig. 1. Experimental setup. The baited food platform, metal loops, threaded rope extended into the test room, room layout used in the two studies, and placement of the food platform. In experiment 1, the subject was released from an adjacent room into the testing room, while the partner was “locked” in another adjacent room that only the subject could open with a key (a wooden peg) from inside the testing room. In experiment 2, the subject was released directly into the test room from a third adjacent room not represented here, while two potential partners were each locked in one of two adjacent rooms that the subject could again open with a key.

Table 1. Percentage of trials in session 1, session 2, and both sessions combined in which subjects opened the door for the potential partner in the adjacent room in experiment 1 ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$, Fisher’s exact test). Scores are in bold if during the first session in which a subject began recruiting the subject also had an immediate preference for recruiting in the collaboration condition. In the first session, two of the four subjects who recruited partners did so significantly more often (as individuals) in the collaboration condition. In the second session, four subjects recruited partners for the first time and three of them did so significantly more in the collaboration condition. Of these three subjects, one did not participate in session 1, whereas the other two never recruited in session 1 but discovered the method in a brief warm-up between sessions (27). Moreover, four of these five subjects, in the first testing block (the three-trials-block) in which they started recruiting, did so in the collaboration condition one to three times and never in the first three trials of the solo condition. (Note: if subjects did not discover the possibility of opening the door in session 1, they were given only six trials in each condition of session 1.)

Subject name	Session 1		Session 2		Combined	
	Collaborate	Solo	Collaborate	Solo	Collaborate	Solo
Namukisa	0	0	100***	0	66.7***	0
Kalema	0	0	100***	8.3	66.7***	4.6
Okech	91.7***	8.3	100***	33.3	95.8***	20.8
Baluku	58.3**	0	100***	25	79.2***	12.5
Umugenzi	25	16.7	100***	16.7	62.5***	16.7
Indi	100	100	75***	8.3	83.3**	38.8
Bili	—	—	100*	66.7	100*	66.7
Asega	—	—	100	83.3	100	83.3
Combined	45.8	20.8	96.8	30.2	73.4	30.4

Given the finding that chimpanzees recruit a collaborator only when needed, a second experiment was designed to test whether they can also learn to recruit the more effective of two partners on the basis of a limited number of interactions with each of them. Six chimpanzees, who had previously participated in experiment 1, were first reintroduced to the key mechanism and shown that now both sliding doors connecting to two rooms adjacent to the testing room could be opened by use of the key in each door (Fig. 1) (27). Then subjects were all introduced and tested with the same two potential collaborators. These two potential collaborators had previously demonstrated very different levels of success in pulling the food tray with others (27) and on this basis were designated as the more effective and the less effective partner. Subjects in experiment 2 had not previously collaborated with either of the two potential partners in this context [see (27)]. The testing procedure was identical to that in the collaborative condition from experiment 1, with the exception that in each trial, the more and less effective collabora-

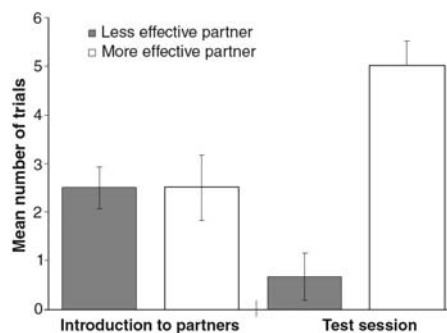


Fig. 2. The mean number of times (\pm SEM) that the subjects chose the less or more effective partner in the introductory and test sessions of experiment 2.

Table 2. The percentage of trials in which subjects responded to a previous success by staying with the same partner (win-stay) and to a failure by shifting partners (lose-shift) versus the percentage of trials in which subjects responded by shifting partners after a success (win-shift) and staying after a failure (lose-stay). Several subjects, as individuals, made win-stay and lose-shift responses significantly more than win-shift and lose-stay responses (Fisher's exact test, $*P < 0.05$).

Subject	Win-stay and lose-shift	Win-shift and lose-stay
Okech	90.9*	9.1
Bili	81.81*	18.19
Umugenzi	80*	20
Asega	83.33	16.67
Namukisa	55.56	44.44
Baluku	54.54	45.46
Overall	74.34	25.64

tors were in the two separate rooms adjacent to the testing room and both doors were locked with a key, so that the subject could open either door from inside the testing room (Fig. 1).

Subjects participated in two sessions. In an introductory session, subjects were introduced to the potential collaborators by being released into the testing room and allowed to recruit either the more or less effective collaborator (by choosing whose door to open) in six consecutive trials. In the test session, occurring on a subsequent day, subjects were again released into the testing room during six trials and allowed to choose which of the two partners to recruit for the job of pulling in the food platform [movie S1 (27)].

We conducted a 2×2 repeated-measures ANOVA (partner \times session) to determine subjects' recruitment preferences and whether these preferences changed from the introduction to the test session. Overall, subjects preferred to recruit the more effective partner over the less effective partner [$F(1,5) = 13, P = 0.015$]. But this preference must be interpreted in the context of a significant interaction between partner and session [$F(1,5) = 9, P = 0.027$]: subjects' preference for the more effective partner in the test session only. Indeed, as Fig. 2 shows, subjects had no preference in the introductory session, whereas in the test session they chose the more effective partner over the less effective partner almost exclusively (in 30 out of 34 trials in which a partner was recruited). Subjects' choices on the first trial of each of their two sessions corroborate this change in preference: Five of six subjects first recruited the less effective partner in the introduction session, whereas five of six subjects first recruited the more effective collaborator in the test session [$P = 0.039$, exact bivariate binomial test, two-tailed (27)]. The relative difference in the effectiveness of the two potential partners who were designated more and less effective on the basis of a pretest (27) was again observed in the experiment: Subjects were significantly more successful at retrieving the food with the more effective partner than with

the less effective partner ($t = 4.36, df = 5, P < 0.004$, paired t test).

The change in subjects' preferences between the less and more effective partners across testing sessions suggests the possibility that subjects were tracking their relative level of success with each of the partners and subsequently based their recruitment decisions on previous outcomes. Support for this interpretation comes from the finding that the number of times that a given subject recruited the more effective partner relative to the less effective partner correlates with the level of success that the subject had in retrieving the food with the more effective partner relative to the less effective partner ($r_s = 0.838, n = 6, P = 0.019$, Spearman's rho). This means that subjects who had the highest level of success with the more effective partner also chose him relatively more. In addition, a trial-by-trial analysis reveals that subjects were basing recruitment choices in a given trial on the outcome of the preceding trial. For this analysis, each subject's choice on each trial (after the first) was classified as either staying with the choice of partner from the previous trial or shifting to the other partner. Overall, subjects responded to the outcome of the previous trial by staying after success and shifting after failure significantly more than they responded by staying after failure and shifting after success ($t = 3.87, df = 5, P = 0.006$; Table 2). In addition, a 2×2 repeated-measures ANOVA (previous trial: success or fail \times next choice: stay or shift) revealed that when subjects succeeded in a trial, they stayed with the same partner on the next trial more often than they shifted, whereas when they failed in a trial, they more often shifted than stayed [a significant interaction between the previous trial and the next choice: both sessions, $F(1,5) = 12.25, P = 0.017$; introductory session, $F(1,5) = 15.16, P = 0.011$; Fig. 3]. The correlation and trial-by-trial analysis suggest that subjects' change in partner preference was caused by subjects basing future recruitment choices on the outcome of previous collaboration attempts with each partner.

Finally, it is important to note that failures to obtain the food (with both partners) in the

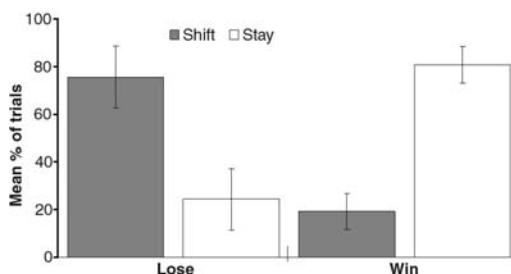


Fig. 3. The mean percentage of trials (\pm SEM) in both sessions of experiment 2 in which subjects responded to a failure (lose) or success (win) on a previous trial by staying with the same partner again or shifting to the other partner on the next trial. In addition to the significant interaction found between previous outcomes and partner choice on the next trial, pairwise comparisons between choices after successful trials reveal that subjects

stayed with the same partner after success more than they shifted (both sessions: $t = 1.972, df = 5, P = 0.006$; intro session: $t = 1.67, df = 5, P = 0.08$, paired t test). Likewise, comparisons between choices after failed trials reveal that subjects shifted to the other partner after a failure more than they stayed (both sessions: $t = 1.97, df = 5, P = 0.053$; intro session: $t = 2.93, df = 5, P = 0.017$, paired t test).

introductory session were due not to the subject's actions but to the partner, because he either pulled the rope prematurely or did not enter the test room (with the less effective partner causing significantly more errors: $t = 2.076$, $df = 5$, $P = 0.047$, paired t test). This raises the additional possibility that subjects may have attributed collaboration failures to the behavior of the partner, and in part developed their preference for the more effective partner because he caused the least errors.

The current results demonstrate that chimpanzees understand when it is necessary to recruit a collaborator and can identify and choose the better of two potential collaborators after only a small number of interactions with each. In the first study, chimpanzees almost always unlocked the door for a potential partner when they needed help in retrieving a food tray, whereas these same individuals almost never unlocked the partner's door when they could retrieve the food on their own. Even though these subjects never had the opportunity to open a door for another individual in a collaborative situation before the test, the majority of them did so on their very first trial when collaboration was necessary. This indicates that chimpanzees can quickly adapt a recently learned skill (removing the key) for a novel purpose (initiating a collaborative activity). In the second experiment, chimpanzees used a win-stay/lose-shift strategy while interacting with two partners that differed in their collaborative skills. Although subjects had not collaborated with either potential partner previously, they learned to choose the more effective partner as a collaborator: In an initial introductory session, subjects did not prefer the more effective partner, whereas in a subsequent session, subjects almost exclusively chose to recruit the more effective partner (showing this change of preference in their very first trial of the test). Therefore, subjects may have remembered the two partners' collaborative performance in the introduction and then developed their preference for the more effective partner because of their higher success rate with him [as opposed to making choices based on other behaviors or on intrinsic differences between the potential partners (29, 30)]. It is even possible that subjects developed their preferences for the more effective partner after attributing more failures to the less effective partner in the introduction. Regardless, subjects' ability to quickly develop and remember a preference for the most effective partner resulted in fewer opportunities for the less effective partner to collaborate, as well as higher rates of food intake for subjects. This mechanism probably facilitates the maintenance of some cooperative strategies, such as reciprocal relationships between dyads.

Overall, the current findings, in conjunction with previous natural observations, challenge the hypothesis that cooperative behaviors in

chimpanzees do not represent active collaboration in which individuals intentionally choose with whom and when to work together (7, 20). The implication is that human forms of collaboration are built on a foundation of evolutionary precursors that are present in chimpanzees and a variety of other primate species (10–14). Further study of chimpanzee, and perhaps bonobo, collaboration is necessary to more precisely identify the derived forms of human collaboration that have arisen since our species split from our last common ancestor with nonhuman apes (3, 6).

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29. Before each subject's choice in experiment 2, the behavior of the two potential partners was coded in order to examine whether subjects might have preferentially chosen the more effective partner more in the second session solely on the basis of a change in behavior in one or both partners while waiting for a choice to be made (27). A 2×2 repeated-measures ANOVA (session \times partner) revealed no effect of session and no interaction between partner and session, but a main effect of the different partners' tendency to sit directly in front of the door during the 5 s before the subject's choice [$F(1,5) = 20.59$, $P < 0.006$]. In addition, the same analysis again revealed no effect of session and no interaction between partner and session, but a main effect of the different partners' tendency to shake the door before a subject's choice [$F(1,5) = 9.31$, $P < 0.028$]. Therefore, although the more effective partner was more often directly in front of the door and shaking it before being chosen, the behavior of the two potential partners did not change across the two sessions. This makes it difficult to explain the subject's change in preferences between sessions as being based on a change in the behavior of the potential partners in the different sessions. In addition, in the introduction session, equal numbers of subjects were successful at working with both of the potential partners in at least one trial. Four of six subjects succeeded once with the less effective partner and four of six subjects succeeded at least once with the more effective partner (in one case, the more effective partner was never chosen by the subject). This suggests that subjects' social relations were friendly enough in all potential dyads to allow for cooperation with either potential partner (that is, subjects were not simply too afraid of the less effective partner to choose him).
30. The two potential partners differed from one another in a number of intrinsic characteristics (such as size, age, dominance, etc.), and so it is important to establish that the relative effectiveness of the partner was indeed a critical variable in the subjects' choice of partner and change of preferences between sessions. First, the intrinsic characteristics of group mates with which subjects should be familiar probably did not change between sessions. Therefore, it seems more likely that subjects' change of preference occurred as they learned about the two partners' relative effectiveness as collaborators, because they had not previously interacted with them in this context before the introductory session. Second, it also seems that the partners' behavior that might indicate eagerness to participate, as measured observationally, also did not change across sessions (29). Third, subjects would not be predicted to base their choices of partners on the outcomes of previous trials if their choices were overwhelmingly influenced by intrinsic differences between potential partners, yet subjects appear to have used a win-stay/lose-shift strategy throughout both sessions. It seems that subjects applied this same strategy with both partners. Subjects also responded to previous outcomes by staying after success and shifting after failure significantly more than staying after failure and shifting after success with both of their potential partners (less effective partner: $t = 3.8$, $df = 5$, $P < 0.007$; more effective partner: $t = 2.0$, $df = 5$, $P = 0.051$, paired sample t test; fig. S2), with no difference between how often this strategy was used with either subject ($t = 0.525$, $df = 5$, $P = NS$, paired t test).
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Supporting Online Material

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