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Animal behaviour

Chimpanzees' (*Pan troglodytes*) strategic helping in a collaborative task

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Many animal species cooperate, but the underlying proximate mechanisms are often unclear. We presented chimpanzees with a mutualistic collaborative food-retrieval task requiring complementary roles, and tested subjects' ability to help their partner perform her role. For each role, subjects required a different tool, and the tools were not interchangeable. We gave one individual in each dyad both tools, and measured subjects' willingness to transfer a tool to their partner as well as which tool (correct versus incorrect) they transferred. Most subjects helped their partner and transferred the tool the partner needed. Thus, chimpanzees not only coordinate different roles, but they also know which particular action the partner needs to perform. These results add to previous findings suggesting that many of chimpanzees' limitations in collaboration are, perhaps, more motivational than cognitive.

1. Introduction

In the Tai forest, chimpanzees' group hunts have been described as coordinated actions between hunters performing different and complementary roles, whereas, in other populations, their behaviour has been described as rather uncoordinated, and success as the by-product of simultaneous individual rather than group efforts [1]. From natural observations alone, it is difficult to conclude how much they understand the role of the partner.

Experimental studies presenting chimpanzees with collaborative tasks involving identical roles, such as pulling a baited board within reach, have found that chimpanzees coordinate actions, waiting for their partner to act so that they can succeed together ([2–4]; see [5] for similar studies with other primates). Furthermore, chimpanzees recruit a skilful partner, by opening a door and allowing her to join them, when they cannot solve the problem individually [3]. This suggests some knowledge about the role that the partner plays in the collaborative interaction or at the very least how the partner's presence relates to their own goal.

In tasks with complementary and different roles, they also spontaneously succeed in performing either role [6,7]. However, in these tasks, they have also exhibited some limitations. For example, when a conspecific partner was present, but doing something else, they did not wait for her to begin acting. Second, chimpanzees did not profit from watching the partner perform her role when they later were required to reverse roles [6]. Third, chimpanzees did not attempt to re-engage or communicatively reactivate a human partner when she unexpectedly stopped performing her role. Instead, chimpanzees tried to solve the task alone or disengaged completely from the task ([7], although see [4]). These results raise the question to what extent chimpanzees understand how each other's actions are interrelated and necessary to achieve the common goal. It is possible that chimpanzees know that the partner's presence is necessary for their own success, but not that the partner needs to perform a particular role or action.

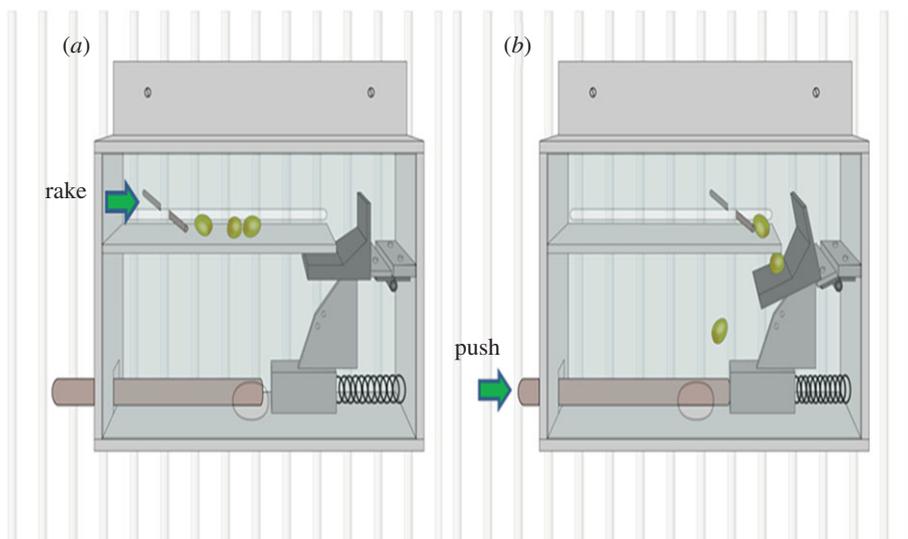


Figure 1. Frontal view of the collaboration apparatus, (a) the individual facing the back side of the box was required to insert a thin stick and rake the grapes from the left to the right side of the box, (b) the individual facing the front side was required to insert a thick long stick and push to tilt the platform. The rewards fell down to the front and back side of the box, so that both individuals obtained something. Individuals were able to see the contents of the box from both angles. (Online version in colour.)

In this study, we familiarized dyads of chimpanzees with a collaborative task that required two different actions. Each action required a different tool and the two tools were non-interchangeable. We measured subjects' willingness and ability to help their partner by providing the partner with the tool she needed. If chimpanzees understand how the different roles are interrelated with each other, and how their own success is dependent on the partner's actions, it is in their own selfish interest to support the partner performing her role.

2. Material and methods

Twelve chimpanzees (seven females, five males, age 7–28 years, $M = 15$) living at Sweetwaters Chimpanzee Sanctuary, Kenya, participated in this study. Subjects were tested in dyads that were chosen based on tolerance levels. Nine of the subjects had previously participated in a pilot experiment with a different collaborative task in which they were also required to transfer the tool, to the partner to succeed. Three of them transferred the tool, whereas the other six did not (see the electronic supplementary material, for details on the subjects, experimental pre-experiences and living conditions).

All subjects were individually introduced to the apparatus. The apparatus consisted of a Plexiglas box attached to the vertical bars separating two testing rooms. The individual facing the back side of the box was required to insert a thin stick through the long opening in the Plexiglas and rake the grapes, whereas the individual facing the front side 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 (figure 1). They first learned to perform each action separately. Then, they were allowed to move freely between the two testing rooms so that they could approach the box from both sides and perform both actions by themselves. Subjects received sessions of four trials each and participated in 5–10 sessions. Subjects were considered to be skilful when they emptied the box within 5 min during three sessions (for further details, see electronic supplementary material, video S1). Afterwards, subjects participated in a cooperation phase: the two individuals in a dyad sat across from each other in two adjacent rooms with the collaboration box (baited with eight grapes per

trial) between them and the door between the two rooms closed. The experimenter (E) handed the corresponding tool to each individual. Each dyad participated in four sessions of four trials each (two sessions per role). Which role a subject performed (raking versus pushing) alternated across sessions.

In the test, E handed over both tools to the subject and no tool to the partner. All subjects were tested in both roles (role A: subject pushed and should transfer the raking tool to the partner, and role B: subject raked and should transfer the pushing tool to the partner). If a subject failed (no tool transfer) in two consecutive trials, a motivational trial was included in which E handed the correct tool to each individual (subject and partner). Each subject participated in two sessions of four test trials each per role (16 trials total per subject). Half of the subjects were 'subjects' first and the other half participated as 'partners' first. All individuals participated first in role A and then in role B. Individuals who did not transfer any tool in any of the 16 trials participated in another round of 16 trials with a knowledgeable partner. They received one experience session per role type, in which a knowledgeable partner transferred the tool to them in four consecutive trials. Then, they received the two normal consecutive test sessions of four trials each (per role type).

For each trial, we coded (1) success, (2) any tool transfer, (3) first tool transferred (correct or incorrect), (4) number of tool transfers per trial, (5) latencies to transfer the correct tool (for reliability coding, see the electronic supplementary material).

3. Results

Ten out of 12 individuals solved the task by transferring a tool to their partner. However, subjects started handing a tool to their partner at very different stages and levels of experience. Three subjects (Alley, Amahirwe and Alikaka) transferred a tool to their partner from trial 1 onwards. However, these subjects had already started passing tools in the pilot study conducted 6–12 months earlier (in trials 3, 6 and 7, respectively). A second group of subjects (Cheetah, Zee, Jojo and Judi) started transferring tools after additional experience, either after having experienced how a partner transferred the tool to them or after having participated in

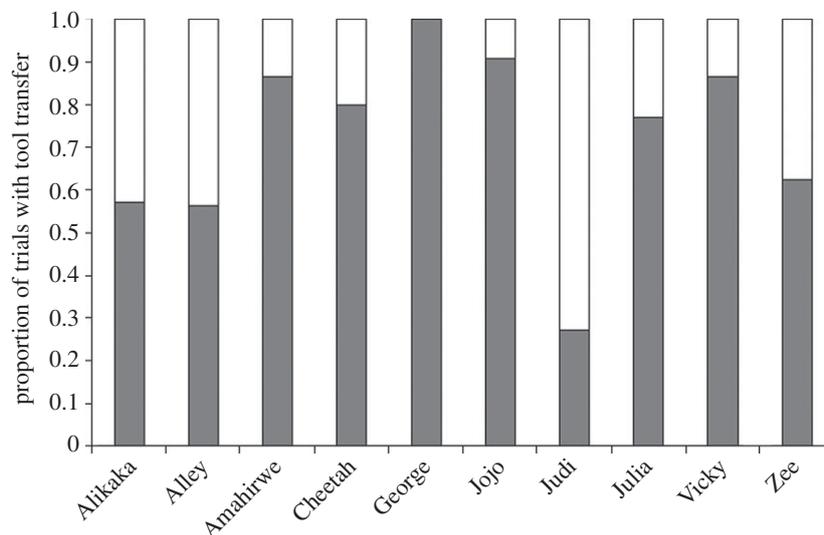


Figure 2. Proportion of trials with tool transfer in which subjects' first choice was the correct (partner's; grey bars) or incorrect tool (white bars).

more trials. The third group of subjects (Julia, Vicky and George) started transferring tools after pairing them with a second and knowledgeable partner and experiencing how this partner gave them the tool (see the electronic supplementary material). Thus, on average, subjects transferred a tool in 57 per cent (s.e. = 10) of the trials (electronic supplementary material). However, after transferring a tool once, they subsequently transferred tools in 97 per cent (s.e. = 3) and succeeded in 86 per cent (s.e. = 7) of the trials (for individual data across all trials and after the first transfer, see electronic supplementary material). The first tool transfer observed in eight out of the 10 subjects was preceded by a request gesture from the recipient (electronic supplementary material, video S2). The other two subjects (Alley and Cheetah) started transferring tools without a request from the partner.

We conducted a logistic generalized linear mixed model (GLMM) of which tool (correct or incorrect) subjects transferred first, with role (A versus B), and trial number as fixed effects and subject, partner and dyad as random effects. This revealed no effect of trial (estimate \pm s.e. = -0.39 ± 0.42 , $z = -0.93$, $p = 0.35$) and role (estimate \pm s.e. = -0.40 ± 0.88 , $z = 0.46$, $p = 0.65$), but a positive and clearly significant intercept (1.10 ± 0.33 , $z = 3.33$, $p = 0.0008$) meaning a higher probability of transferring the correct tool. Thus, subjects preferentially chose the correct tool (mean = 73%, s.e. = 7; figure 2) independently of which side of the box they were at (see the electronic supplementary material, videos S2 and S3). Nine out of 10 subjects chose the correct tool the very first trial they transferred a tool (binomial test: $p < 0.05$). A GLMM of the latencies (log-transformed) of transferring the correct tool with subject, partner and dyad as random effects and trial number as fixed effect also revealed no changes over time (GLMM: estimate \pm s.e. = -0.10 ± 0.09 , $P_{\text{MCMC}} = 0.24$; see also electronic supplementary material).

Sometimes subject and partner exchanged tools a couple of times before each obtaining the right tool and succeeding in the task. An analysis of the number of tool transfers revealed that in 78 per cent of the successful trials there was a single tool transfer. When subjects were in the raking position, they could rake and once finished pass both tools. Therefore, we compared whether the percentage of trials with more than one tool transfer was higher in the raking role than in the

pushing role, but found no difference ($T^+ = 22$, $n = 7$ (one tie), $p = 0.22$).

4. Discussion

Chimpanzees helped their partner by providing her with the tool she needed. Although there were great individual differences regarding how quickly subjects started transferring tools (and some subjects seemed to rely on experiencing receiving a tool from the partner to start transferring tools themselves), after doing it once, they did it all the time. The fact that subjects transferred a tool at all is surprising, considering that, during the individual training phase, subjects had learned that both tools were valuable and needed to access the rewards.

In addition, subjects transferred the correct tool significantly more often than the incorrect one and this seemed to be the case from the beginning of the experiment. One possible explanation is that subjects discarded the tool they did not need. However, this is an unlikely explanation for several reasons. First, they did not throw the tool out of the room, but transferred it to the partner's room and/or hands. Second, subjects chose the correct tool independently of which role they were performing. When they were in the raking role, they were successful and able to rake the rewards to the correct position in the box, but when they were in the pushing role, they were unsuccessful and the rewards did not move. However, they passed the correct tool equally often in both situations and did not pass their own tool more often when they had just successfully used it (when they were rakers) or it was not working (when they were pushers).

One could still argue that subjects were not reasoning about the partner's needs but maybe just keeping the tool they had just used or would like to use. Although we cannot completely rule out this explanation, it has recently been shown that chimpanzees altruistically help a partner by transferring the tool that the partner needs to access food [8]. In this study, subjects could never use the tools themselves, which suggests that they were choosing the tools based on an understanding of the partner's practical needs.

Being motivated to help the partner in this situation suggests that individuals recognize the relationship between the

different actions necessary to achieve their goal. In this study, chimpanzees were unable to perform both roles alone and spontaneously developed a helping strategy to reach success with a partner (ultimately helping themselves). It is possible that chimpanzees view the partner as a social tool that is needed to produce self-serving outcomes, rather than a collaborative partner with whom they interact based upon a joint plan towards a joint goal. Nevertheless, the social tool interpretation is not at odds with a cognitive process that allows individuals to represent the interrelation between the different actions. The present study provides the first evidence that chimpanzees can pay attention to the partner's actions in a collaborative task, and shows that they are strategic collaborators. Other studies have shown that, when given a choice, they preferentially act alone, choosing collaboration if it is the only way to achieve higher pay-offs [3,9]. The current findings, together with previous ones, provide evidence

that in chimpanzees many of the limitations in collaboration are more motivational than cognitive.

This study was approved by the local ethics committee at the Sanctuary (the board members and the veterinarian) and relevant authorities in Kenya (KWS and UNCST). The subjects were never food deprived and water was available ad libitum. They could choose to stop participating at any time.

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