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Chimpanzees consider alternative possibilities

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Humans reason not only about actual events (what is), but also about possible events (what could be). Many key operations of human cognition involve the representation of possibilities, including moral judgment, future planning, and causal understanding[1]. But little is known about the evolutionary roots of this kind of thought. Humans' closest relatives, chimpanzees, possess several cognitive abilities that are closely related to reasoning about alternatives: they plan for the future[2], evaluate other's actions[3], and reason causally[4]. However, in the first direct test of the ability to consider alternatives, Redshaw and Suddendorf[5] claim that chimpanzees are not able to represent alternative possibilities. Here, using a novel method, we challenge this conclusion: our results suggest that, like human cognition, chimpanzee thought is not limited to what is, but also involves reasoning about what could be the case.

The original study by Redshaw and Suddendorf[5] as well as a follow-up study[6] failed to detect evidence of reasoning about alternative possibilities in great apes. These studies share two notable characteristics. Conceptually, they investigate whether great apes can represent possibilities involving external or physical uncertainty (such as not knowing the outcome of a die not yet thrown), as opposed to epistemic uncertainty (the die has been thrown but you do not know the result). However, external uncertainty has consistently been shown to be harder for human adults to reason about than epistemic uncertainty, so this may not be the best place to start (although children seem to show the opposite tendency)[7]. Methodologically, both studies involve variants of a 'tube task', in which a reward has to be caught before it falls out of reach. The key idea is that the reward can come down either one of two vertical tubes, so passing this task requires subjects to cover the openings of both tubes with the palms of their hands, which is a behavior that does not come naturally to great apes — making the task inappropriate for chimpanzees[8]. What is needed, therefore, to probe great apes' understanding of alternative options is a test which zeros in on their understanding of possibilities involving epistemic uncertainty, using a methodology better suited to their behavioral repertoire.

Here we provide such a test. Across two preregistered experiments, chimpanzees were shown a piece of apple, which was subsequently hidden in one of two containers. In Experiment 1, six chimpanzees participated in a *transparent condition* (in which the containers were see-through: Figure 1A and Video S1) and an *opaque condition* (containers were covered: Figure 1B and Video S1). In Experiment 2, nine chimpanzees participated in an *observed condition* (in which they could observe the hiding process) and an *unobserved condition* (in which they could not observe the hiding process).

We ran generalized linear mixed models (GLMM) to examine whether chimpanzees were more likely to pull both ropes in the opaque than in the transparent condition (Experiment 1) and in the unobserved than in the observed condition (Experiment 2). We included as fixed effects condition, trial number, session, and the interaction

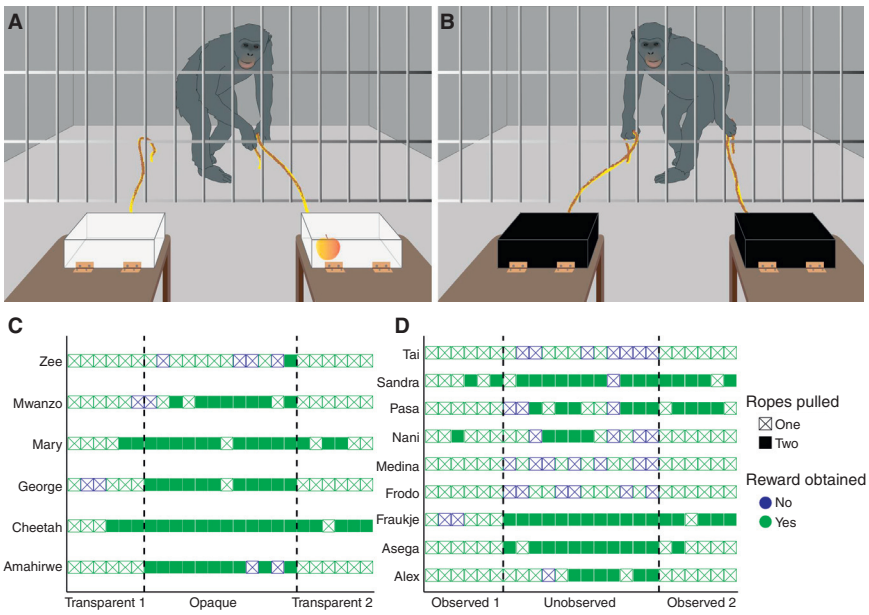

Figure 1. Experimental setup and results for Experiments 1 and 2.
(A) Setup in the transparent condition of Experiment 1. (B) Setup in the opaque condition of Experiment 1 and both conditions of Experiment 2 (observed condition and unobserved condition). Chimpanzees participated in two sessions of each condition in an ABBA design (that is, in Experiment 1, they started with one session of the transparent condition, followed by two sessions of the opaque condition, and one session of the transparent condition; in Experiment 2, chimpanzees started with one session of the observed condition, then had two sessions of the unobserved condition, and, finally, another session of the observed condition). Each session took place on a separate day and comprised six trials. As can be seen in the figure, each container was mounted on a separate platform, and a single rope was threaded through a metal loop on each platform. Both ends of the rope were then extended into the testing room. If subjects pulled the two ends of the rope simultaneously, both platforms could be pulled within reach; if only one end of the rope was pulled, chimpanzees only gained access to the platform attached to that end of the rope, while the other end of the rope moved out of the room and could not be accessed anymore. Before chimpanzees participated in the test phase, they were introduced to the experimental setup in two familiarization phases (see Supplemental information). (C) Behavior (one or two ropes pulled) and success (reward obtained or not) for each subject on every trial of Experiment 1. (D) Behavior (one or two ropes pulled) and success (reward obtained or not) for each subject on every trial of Experiment 2.

between condition and session in the model. The interaction term is important because it allows us to draw inferences regarding potential order effects. In Experiment 1, the interaction was not significant (χ^2 = 0.65, df = 1, p = 0.42). The results of a reduced model without the interaction term revealed a significant effect of condition (χ^2 = 8.63, df = 1, p = 0.003), showing that chimpanzees pulled both ropes more often when they did not know the location of the food (*opaque condition*) compared with when they did (*transparent condition*).

In Experiment 2, the interaction term between condition and session was not significant (χ^2 = 1.63, df = 1, p = 0.202). The results of a reduced model without the interaction term confirmed that the chimpanzees pulled both ropes significantly more often when they did not know the location of the food (*unobserved condition*) compared with when they did (*observed condition*) (χ^2 = 4.06, df = 1, p = 0.044).

These results suggest that chimpanzees consider alternative possibilities. Using response behavior that comes naturally to chimpanzees, and a procedure that involves possibilities under epistemic rather than external uncertainty, we found that chimpanzees flexibly modify their behavior depending on whether or not they know where a reward has been hidden. To solve the current task, on our interpretation, chimpanzees have to represent the fact that the food could be in either of the two potential locations, realize that they need to pull both ropes in order to obtain the food with certainty, and, finally, draw in both platforms.

One possible interpretation of these results is that chimpanzees simply started pulling both ropes over the course of the experiment as this represented a way to maximize their chances of obtaining food. But this cannot explain why most chimpanzees stopped pulling the rope in the second session of the transparent condition (and the non-significant interaction between condition and session in both studies). A second alternative is that chimpanzees expected two pieces of food and thus represented a conjunction (A and B) and not a disjunction (A or B). The results of Experiment 2 rule this out: chimpanzees were significantly less likely to open the second container when they had found food in the first container compared with when the first container was empty (see Supplemental information). A final alternative is that chimpanzees do not represent both possibilities, but are simply ignorant of the contents of the containers, and are tempted to search them because they are habituated to finding food inside opaque containers. However, while this could explain the difference in rope-pulling in the first study, where the containers were transparent in the first condition and opaque in the second, it is ruled out by the second study, in which the containers are opaque in both conditions, and a difference in rope-pulling between conditions is still evident.

The finding that some chimpanzees act in such a way as to accommodate multiple possibilities supports and extends recent work on chimpanzee metacognition[9,10]. When chimpanzees know that a reward has been hidden in one of multiple opaque tubes, they engage in information seeking and inhibit action until they know where the reward is[9]. This result may show that chimpanzees represent multiple possible locations for the reward, but it may also show merely that they represent options in succession — thinking of just one at a time, and searching at each new location that occurs to them until they find the reward. Because our study shows that chimpanzees take action in such a way as to accommodate multiple possibilities at once, it reveals a pattern of action that can only be explained by attributing to them the simultaneous representation of alternative possibilities.

SUPPLEMENTAL INFORMATION

Supplemental information includes experimental procedures and one video and can be found with this article online at https://doi.org/10.1016/j.cub.2021.09.012.

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