Chimpanzees prepare for alternative possible outcomes

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Abstract

When facing uncertainty, humans often build mental models of alternative outcomes. Considering diverging scenarios allows agents to respond adaptively to different actual worlds by developing contingency plans ("covering one's bases"). In a preregistered experiment, we tested whether chimpanzees (*Pan troglodytes*) prepare for two mutually exclusive possibilities. Chimpanzees could access two pieces of food, but only if they successfully protected them from a human competitor. In one condition, chimpanzees could be certain about which piece of food the human experimenter would attempt to steal. In a second condition, either one of the food rewards was a potential target of the competitor. We found that chimpanzees were significantly more likely to protect both pieces of food in the second relative to the first condition, raising the possibility that chimpanzees represent and prepare effectively for different possible worlds.

A key feature of human cognition is the ability to represent not only what is the case (actual events), but also what could be the case (non-actual events). The ability to consider alternative possibilities lies at the core of some of the greatest scientific, artistic, technological, and societal innovations. This type of imagining is also prevalent in everyday reasoning, such as when we think about what could have been or what may happen in the future (Beck & Riggs, 2014; Redshaw & Ganea, 2022). Modal reasoning (reasoning about possibilities) underpins many forms of human thought, from future planning and causal reasoning, to moral judgment and logical inference (Leahy & Carey, 2020; Phillips & Cushman, 2017; Phillips & Knobe, 2018). One central application of modal reasoning is in the domain of action planning (Maier, 2015): Individuals facing uncertainty in the environment can generate contingency plans and thereby simultaneously prepare for alternative possibilities.

Acting effectively in light of uncertainty is a key adaptive pressure faced by many animals, so, from an evolutionary perspective, it seems reasonable to believe that nonhuman animals have at least some capacity to engage in modal reasoning (Godfrey-Smith, 1996; Sterelny, 2001; Tomasello, 2022). However, according to influential accounts, modal reasoning marks uniquely human thought and emerges relatively late in human ontogeny, potentially on the basis of acquiring the corresponding natural language capacities (Beck et al., 2011; Leahy & Carey, 2020; Redshaw & Suddendorf, 2020; Shtulman & Carey, 2007; Suddendorf & Corballis, 1997, 2007). Support for this view comes from experimental results which suggest that young human children and chimpanzees fail to appreciate multiple, mutually exclusive possible events in situations of uncertainty (reviewed in Leahy & Carey, 2020).

An alternative account holds that some forms of thinking about possibilities are present in young human children and nonhuman animals. Evidence comes from studies showing that 18-30 month old toddlers flexibly identify multiple possible causes for an effect (Goddu et al., 2021) and 36 month old children reliably differentiate an option that must produce a desired reward from one that only might do so (Alderete & Xu, under review). In addition, observational studies of wild animals demonstrate patterns of decision-making (for example in the context of foraging decisions) that are plausibly based on the consideration of alternative possibilities (Janmaat et al., 2013, 2016; Janson, 2007; Thouless, 1995). Finally, there is also experimental evidence that chimpanzees might consider and respond appropriately to alternative possibilities under conditions of "epistemic uncertainty" (Engelmann et al., 2021; but see Engelmann, Haux, et al., 2022) – when one's uncertainty results from a lack of epistemic access to a world that has already been determined (e.g., prey has already chosen one possible escape route but the predator lacks visual access).

The extent to which chimpanzees prepare for "physical uncertainty" – when one's uncertainty stems from an undetermined future (e.g., prey has not yet chosen a particular escape route) – is not known (note that for human adults, representation of possibilities under conditions of physical uncertainty seems to be more difficult than under conditions of epistemic uncertainty; human children possibly show the opposite tendency, see Robinson et al., 2006). Most relevant to the current investigation, two earlier studies indicate that chimpanzees have difficulty taking effective action when preparing for mutually exclusive possibilities under physical uncertainty. When an experimenter drops a reward into an inverted y-shaped tube, chimpanzees cover only one exit (Redshaw &

Suddendorf, 2016); likewise, when an experimenter releases a reward into one of two vertical tubes, chimpanzees again cover only one of the tubes (Suddendorf et al., 2017). However, these results have been criticized on methodological grounds. The behavior required to demonstrate competence – covering the openings of both tubes with the palms of one's hands – does not come naturally to chimpanzees (Lambert & Osvath, 2018). Here, we aim to give chimpanzees another opportunity to demonstrate competence, using a more appropriate experimental paradigm.

We tested whether chimpanzees (N=15) simultaneously prepare for two mutually exclusive possibilities. Motivated by earlier work showing that chimpanzees demonstrate advanced cognitive skills predominantly in competitive interactions (Hare & Tomasello, 2004), we observed subjects' preparatory responses in a situation where valuable resources were under threat. Subjects were presented with two pieces of food, each placed on a tiltable platform. Crucially, subjects could only access the two pieces of food if they successfully protected them from a human competitor. The human tried to steal food by dropping a stone through a tube, causing one of the platforms to tilt towards the human and away from the chimpanzee (and the reward to roll outside the chimpanzee's reach). In the *single tube condition*, chimpanzees could predict with certainty which food platform the competitor would target because the tube had only one exit (Figure 1B). In the *y-shaped tube condition*, chimpanzees could not predict the target because the tube had two exits and the stone could collapse either platform, i.e., they acted under uncertainty (Figure 1A). We asked whether chimpanzees would be more likely to protect both platforms – by stabilizing them with their hands – in the *y-shaped tube condition* compared to the *single tube condition*.

Methods

Experimental Set-up and Design. Fifteen chimpanzees (seven females), living at Ngamba Island Chimpanzee Sanctuary, Uganda, ranging in age from 15 to 26 years (M = 22 years) participated in this study. Chimpanzees interacted with the experimental apparatus through openings in their enclosure. The apparatus had two main components: platforms and a tube. The two platforms (15cm x 32cm) were attached 12cm from one another to a wooden board such that they could tilt away from the chimpanzee. The tube was installed above the platform. There were two different tubes, a single tube and a y-shaped tube (one for each condition). The two tubes were of the same color (grey), material (plastic), length (110cm) and diameter (8cm). The only difference was that one was a single straight tube with one exit, whereas the other tube was an inverted y-shaped tube and had two exits (see Figure 1A,B).

In a within subjects design, chimpanzees participated in the two conditions – the *y-shaped tube* and *single tube condition* – in counterbalanced order. Each condition consisted of two sessions of eight trials. In both conditions, both platforms were baited.

Procedure. Chimpanzees were first familiarized with the experimental setup through a sequence of three steps (for details on all steps, please refer to the Supplementary Information, SI). Once chimpanzees had passed the familiarization phase, they moved to the test phase, which consisted of two stages (an *observation stage* and an *experimental stage*). Chimpanzees first participated in the observation and experimental stage for one condition and then in the observation and experimental stage for the second condition (in counterbalanced order).

During the *observation stage*, chimpanzees were introduced to the tubes and observed six times how the stone was dropped into the single tube or the y-shaped tube (depending on condition). More specifically, platforms and tubes were placed at 1 meter from the chimpanzees (so that they could not access them). The first experimenter (E1) baited the two platforms and left the testing station. Then the second experimenter (E2; the competitor) appeared, stepped behind the tube, extended their arm above the tube, looked up (so that they could not observe and react to the subject's behavior during the experimental stage), and, after two seconds, dropped the stone in the tube. Finally, E1 reappeared and handed the food that remained on one of the platforms to the chimpanzee. The *observation stage* took place immediately prior to the *experimental stage* on the same day.

The procedure of the *experimental stage* was identical to the procedure of the observation stage, except that the platforms were placed in front of the chimpanzees (where they had been during the familiarization phase). This meant that chimpanzees could stabilize the platforms by placing their fingers, hands, or feet on top of them, thereby preventing them from collapse (when hit by the stone) and the food rolling out of reach to the human competitor. E2 left the testing station once their stone had hit one of the platforms, either empty handed (if the chimpanzee had successfully stabilized both platforms) or with one piece of food (if the chimpanzees had not stabilized the platform that was hit by the stone).

Analyses and Results

Following the preregistered analysis plan (https://osf.io/en56p/?view_only=1711fe8cc8db43ffb18863978985ce8b), we fitted a generalized linear mixed model (GLMM) with binomial error structure and logit link function to investigate whether the chimpanzees were more likely to stabilize both trays in the *y-shaped tube condition* than in the *single tube condition*. We included as fixed effects condition, trial number (within condition, 1-16), and the order of conditions (y-shaped-tube-first, single-tube-first). Additionally, we included subject ID as random intercept and condition as random slope within subject ID (the random slope of trial number was removed due to convergence issues following our preregistered contingency plans).

Chimpanzees were significantly more likely to stabilize both trays in the *y-shaped tube* (Mean ± SE: 0.73 ± 0.06) than in the *single tube condition* (Mean ± SE: 0.49 ± 0.06; $\chi^2 = 14.97$, df = 1, $p < 0.001$), see Figure 1C. We found no evidence that chimpanzees simply learned the appropriate behavior over time: trial number ($\chi^2 = 0.48$, df = 1, $p = 0.48$) and order of conditions ($\chi^2 = 3.17$, df = 1, $p = 0.08$) had no significant effect on performance.

When chimpanzees stabilized only one platform, they were significantly more likely than expected by chance to obtain both food items in the *single tube condition* (Mean ± SE: 0.86 ± 0.04; z = 4.51, p < 0.001) but not in the *y-shaped tube condition* (Mean ± SE: 0.47 ± 0.09; z = -0.85, p = 0.395), showing that chimpanzees could not predict the trajectory of the food reward in the *y-shaped tube condition*. We also found that chimpanzees were not more likely to stabilize both platforms on a subsequent trial if they had stabilized one platform and obtained only one piece of food on the previous trial (compared to if they had stabilized both platforms and obtained two pieces of food; $\chi^2 = 0.01$, df = 1, $p = 0.940$), suggesting that stabilizing both platforms was not a reaction to a reward loss on the previous trial. For details on the pre-registered experimental protocol and analysis plan, please refer to the SI.

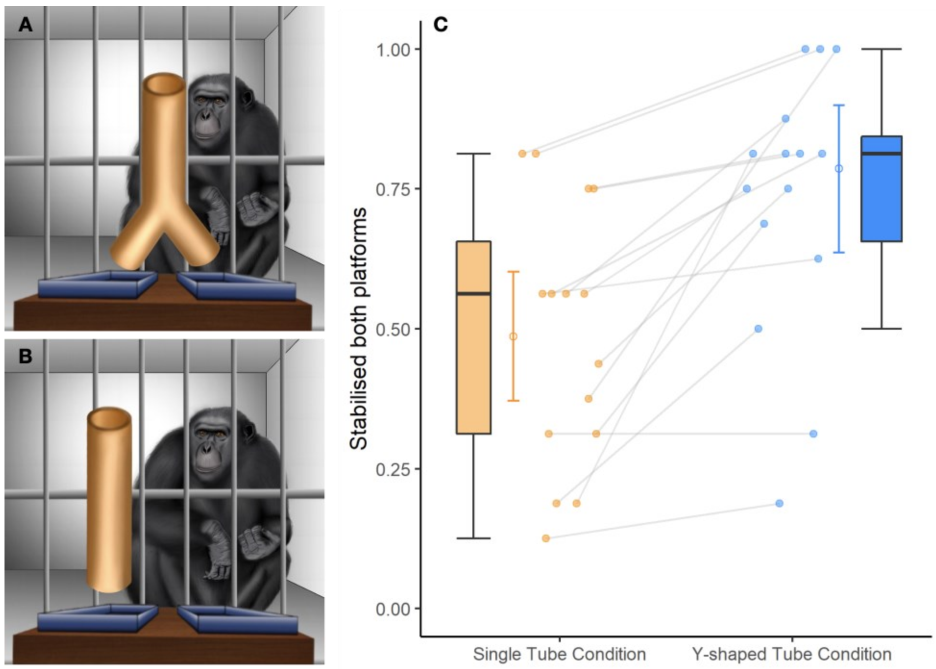

Figure 1. A. Experimental setup in the *y-shaped tube condition*. B. Experimental setup in the *single tube condition*. C. Box and dot plot showing the proportion of trials in which the chimpanzees stabilized both platforms across the two conditions. Dots represent individual mean values and lines connect values of the same individuals. The error bars represent bootstrapped 95% confidence intervals; open circles show the fitted values.

Discussion

These results raise the possibility that chimpanzees generate mental models of alternative outcomes. Faced with an uncertain future, chimpanzees "cover their bases" in a way that suggests preparation for diverging possibilities. In contrast to earlier findings, the current results present evidence that chimpanzees engage in modal reasoning and acknowledge multiple, distinct possibilities.

Why did we find evidence for this capacity in chimpanzees, while prior research did not? One possible reason might be that we tested chimpanzees in a competitive and naturalistically relevant experimental paradigm. We adopted a setup that has been used in prior research – comparing a single tube to a y-shaped tube (Beck et al., 2006) – and placed it in the context of a competitive social interaction. Although chimpanzees cooperate in a variety of contexts (Crockford et al., 2012; Melis & Tomasello, 2019; Samuni et al., 2021), there is evidence that competitive experimental settings are more conducive to revealing sophisticated cognition in chimpanzees than cooperative experimental settings (Hare & Tomasello, 2004; Schmelz & Call, 2016). Competing with others for food is a naturalistically relevant context that chimpanzees regularly experience in their daily life (Muller & Mitani, 2005). In addition, the risk of losing a valued resource that is placed directly in front of the chimpanzee on a food platform (as in the current version of the y-shaped tube task) might be a stronger motivator for chimpanzees than the prospect of gaining a valued resource (as in previous versions of the y-shaped tube task); this interpretation is supported by chimpanzees' exhibition of the endowment effect (Brosnan et al., 2007; Kanngiesser et al., 2011). A third potential reason is that, contrary to prior research, we confirmed during familiarization that the target behavior (stabilizing both platforms) is within chimpanzees' behavioral repertoire. To solve the current task, chimpanzees did not have to innovate and express a novel behavior, but rather simply had to demonstrate a previously acquired behavior in a context-sensitive way.

One might argue that subjects' decision to stabilize one or two platforms is a learned response to the presence of one tube exit in the *single tube condition* versus two tube exits in the *y-shaped tube condition*. We believe that this is unlikely to account for the current results considering chimpanzees' relatively high likelihood of stabilizing both platforms in the *single tube condition*, as well. In addition, there was no differential reinforcement between conditions prior to the test phase, and we found no evidence of learning within the test phase (i.e., no significant improvement over trials or based on the outcome of the previous trial). Finally, this alternative explanation would also apply to all previous studies using the y-shaped tube, where the widely accepted interpretation is that covering both exits presents evidence for modal reasoning (Beck et al., 2006; Leahy & Carey, 2020; Redshaw & Suddendorf, 2016, 2020; Robinson et al., 2006).

The current findings provide evidence in support of the possibility that chimpanzees make a cognitive-behavioral distinction between single and multiple alternative physical possibilities via a variation on an experimental paradigm that is commonly employed in investigations of modal thought. Conceptually, this paradigm equates the capacity to represent possibilities with the capacity to represent exclusive-OR relations. However, the ability to consider mutually incompatible possibilities is only one instance of the much broader class of contexts in which agents represent possibilities (Harris, 2022). Future studies on the development of modal reasoning – both on a phylogenetic and ontogenetic timeline – should expand beyond this narrow focus to a broader representation of the diversity of modal thought (see, for example, Engelmann, Herrmann, et al., 2022).

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Compliance with Ethical Standards

Research at Ngamba Island Chimpanzee Sanctuary was performed in accordance with the recommendations of the Weatherall report "The use of non-human primates in research". Groups of apes were housed in semi-natural indoor and outdoor enclosures with regular feedings, daily enrichment and water ad lib. Subjects voluntarily participated in the study and were never food or water deprived. Research was conducted in the sleeping and/or observation rooms. No medical, toxicological or neurobiological research of any kind is conducted at Ngamba Island Chimpanzee Sanctuary. Research was non-invasive and strictly adhered to the legal requirements of Uganda. The full procedure of the study was approved by the local ethics committee at the Sanctuary (the board members and the veterinarian) and by the ethics committee at the University of California, Berkeley (Protocol ID: AUP-2020-03-13134; Protocol Title: Chimpanzee Behavioral Research).

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