



Flexible information-seeking in chimpanzees

Alexandra G. Rosati^{a,b,*}, Elisa Felsche^{a,c}, Megan F. Cole^{a,d}, Rebeca Atencia^e, Joshua Rukundo^f

^a Department of Psychology, University of Michigan, Ann Arbor, MI, USA

^b Department of Anthropology, University of Michigan, Ann Arbor, MI, USA

^c Department of Comparative Cultural Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

^d Department of Anthropology, University of New Mexico, Albuquerque, NM, USA

^e Jane Goodall Institute – Congo, Pointe Noire, Congo

^f Ngamba Island Chimpanzee Sanctuary / Chimpanzee Trust, Entebbe, Uganda

ARTICLE INFO

Keywords:

Comparative cognition

Metacognition

Decision-making

Comparative development

ABSTRACT

Humans can flexibly use metacognition to monitor their own knowledge and strategically acquire new information when needed. While humans can deploy these skills across a variety of contexts, most evidence for metacognition in animals has focused on simple situations, such as seeking out information about the location of food. Here, we examine the flexibility, breadth, and limits of this skill in chimpanzees. We tested semi-free-ranging chimpanzees on a novel task where they could seek information by standing up to peer into different containers. In Study 1, we tested $n = 47$ chimpanzees to assess if chimpanzees would spontaneously engage in information-seeking without prior experience, as well as to characterize individual variation in this propensity. We found that many chimpanzees engaged in information-seeking with minimal experience, and that younger chimpanzees and females were more likely to do so. In two subsequent studies, we then further tested chimpanzees who initially showed robust information-seeking on new variations of this task, to disentangle the cognitive processing shaping their behaviors. In Study 2, we examined how a subset of $n = 12$ chimpanzees applied these skills to seek information about the location versus the identity of rewards, and found that chimpanzees were equally adept at seeking out location and identity information. In Study 3, we examined whether a subset of $n = 6$ chimpanzees could apply these skills to make more efficacious decisions when faced with uncertainty about reward payoffs. Chimpanzees were able to use information-seeking to resolve risk and choose more optimally when faced with uncertain payoffs, although they often also engaged in information-seeking when it was not strictly necessary. These results identify core features of flexible metacognition that chimpanzees share with humans, as well as constraints that may represent key evolutionary shifts in human cognition.

1. Introduction

Humans can monitor their own knowledge states and then strategically act to acquire new knowledge to reach their goals, a set of abilities for thinking about thinking termed metacognition. Metacognition is crucial in many domains of human life, including in social interactions (Frith, 2012; Heyes, Bang, Shea, Frith, & Fleming, 2020), formal schooling (Isaacson & Fujita, 2006; Ohtani & Hisasaka, 2018), medical decision-making (Huang & Yang, 2020), and political belief formation (Fischer & Said, 2021; Rollwage, Dolan, & Fleming, 2018). Across these contexts, human metacognitive skills are deployed flexibly to deal with diverse problems ranging from school performance to cultural learning,

and typically involve a rich integration of metacognitive awareness with multiple other skills, including language.

Yet there is also an emerging consensus that both human infants and other animals possess some foundational metacognitive abilities that allow them to monitor their own knowledge states and act appropriately (Goupil & Kouider, 2019). Specifically, a variety of non-verbal paradigms have been developed to assess if animals or young children distinguish between situations where they do or do not know something, serving as evidence for metacognitive capacities in these populations. For example, many species of animals have been tested on *uncertainty paradigms* where they have experience making a perceptual or memory judgement, and then sometimes are faced with a more difficult choice

* Corresponding author at: Department of Psychology, University of Michigan, Ann Arbor, MI, USA.

E-mail address: rosati@umich.edu (A.G. Rosati).

<https://doi.org/10.1016/j.cognition.2024.105898>

Received 5 January 2024; Received in revised form 11 July 2024; Accepted 17 July 2024

Available online 25 July 2024

0010-0277/© 2024 Elsevier B.V. All rights reserved, including those for text and data mining, AI training, and similar technologies.

(for example, once animals can consistently assess if dots on a screen are densely versus sparsely distributed, they are then presented with an intermediate density that is difficult to discriminate). On those trials, they can either make the judgement, or choose an ‘opt-out’ option to avoid making the hard choice (Fujita, 2009; Iwasaki, Kuroshima, & Fujita, 2019; Perry & Barron, 2013; Smith, 2009; Smith, Beran, Cosuchman, & Coutinho, 2008; Smith, Redford, Beran, & Washburn, 2010). In related paradigms, they can pay greater costs to complete trials when they are more confident (Beran et al., 2015; Kepecs & Mainen, 2012; Kepecs, Uchida, Zariwala, & Mainen, 2008; Shields, Smith, Guttmanova, & Washburn, 2005). In *information-seeking paradigms*, another commonly used method, animals are faced with a choice between tubes or containers that may contain a reward. In some cases, they see which was baited, whereas in other cases they do not. In fact, some species will seek out missing information needed to solve this problem by changing their physical position to view the problem from a new perspective when they are ignorant (for example, bending down to peer into the tubes before making a choice response; Beran, Smith, & Perdue, 2013; Call, 2010; Call & Carpenter, 2001; Marsh & MacDonald, 2012b; Perdue, Evans, & Beran, 2018; Roberts, McMillan, Musoline, & Cole, 2012; Santos & Rosati, 2015). Similarly, young infants have been tested in parallel paradigms to assess their metacognitive inferences. For example, infants will persist longer in searching for a toy hidden in a box when they are confident it was previously placed there (Goupil & Kouider, 2016). In a parallel version of the information-seeking paradigm, they will request help from an adult when they are unsure of a toy’s location but make a direct choice when they are sure (Goupil, Romand-Monnier, & Kouider, 2016). Overall, this set of results suggests that both animals and babies have some underlying abilities to monitor uncertainty and act accordingly when they lack information.

This work with infants and animals shows that different components of metacognition do not necessarily require language or other human-specific traits that are associated with metacognitive abilities in adult humans. Comparative evidence from animals specifically can inform our understanding of human metacognition in several ways. First, animals not only lack language, formal schooling, and the kinds of cultural learning seen in humans—they likely lack the cognitive foundations for these skills in the first place. As such, studies of animals can provide a crucial line of evidence for assessing the roots of metacognition, and generally for understanding the structure of different metacognitive processes and therefore differentiating between core processes that are more widely shared across species and those processes in humans that build on those foundations (Carruthers & Williams, 2019; Goupil & Kouider, 2019; Hampton, 2019; Heyes et al., 2020; Proust, 2019). For example, current work suggests that some forms of uncertainty monitoring—detecting when one has little information—may be widely shared across taxa ranging from primates to rodents and even insects (Castro & Wasserman, 2013; Foote & Crystal, 2012; Hampton, 2001; Kornell, Son, & Terrace, 2007; Perry & Barron, 2013; Shields, Smith, & Washburn, 1997; Smith, 2009; Smith et al., 1995; Smith, Shields, Allendoerfer, & Washburn, 1998; Smith, Shields, Schull, & Washburn, 1997; Terrace & Son, 2009). In contrast, information-seeking behaviors that allow an individual to acquire information when needed may be seen in only some species, specifically some primates (Basile, Hampton, Suomi, & Murray, 2009; Beran et al., 2013; Bräuer, Call, & Tomasello, 2004; Call, 2010; Call & Carpenter, 2001; Hampton, Zivin, & Murray, 2004; Marsh & MacDonald, 2012b; McMahon, Macpherson, & Roberts, 2010; Paukner, Anderson, & Fujita, 2006; Roberts et al., 2012; Rosati & Santos, 2016).

Comparative studies can also help distinguish between potential mechanisms supporting metacognition. For example, one emergent quality of human metacognition is that people can apply these skills across a wide range of different behavioral situations. As such, a key question is not only whether other animals have some capacity for metacognition at all, but also how animals apply and extend their skills across contexts (Marsh, 2019). Some work has addressed this by testing

whether animals make patterns of metacognitive *errors* similar to humans. For example, much like humans, rhesus monkeys’ uncertainty judgements are affected by a concurrent working memory task, and their post-decision confidence is impacted by the clarity of the stimuli in a memory task (Ferrigno, Kornell, & Cantlon, 2017; Smith, Coutinho, Church, & Beran, 2013). Other studies have used information-seeking tasks to test how animals apply their abilities to different novel contexts, suggesting that reward value, the effort needed to engage in information-seeking, the time delay before making a decision, and the riskiness of making a wrong choice (Beran et al., 2015; Call, 2010; Call & Carpenter, 2001; Hampton et al., 2004; Marsh & MacDonald, 2012b; Mulcahy, 2016) can all influence the responses of other primates in a logical way paralleling humans. Finally, although much work on animal metacognition has focused on the presence or location of a reward, chimpanzees also will engage in information-seeking to acquire information about the properties of tools needed to solve a problem (Bohn, Allritz, Call, & Voelter, 2017; Mulcahy, 2016), and language-trained chimpanzees will seek out information about a reward’s *identity* in a task using lexigram responses (Beran et al., 2013). In contrast, apes seem limited compared to humans in using social feedback to reflect on their knowledge (O’Madagain et al., 2022). Overall, this suggests that at least some species may be able to exhibit more flexible metacognition across some different contexts.

A final potential contribution of comparative work is to integrate both evolutionary and ontogenetic approaches to disentangle how different experiences and biological predispositions shape mature metacognition. For example, while human infants show some core capacities for metacognition (Ghetti, Hembacher, & Coughlin, 2013; Goupil & Kouider, 2019), this complex skillset continues to be refined into adulthood. Studies in children and adolescents show an increase in metacognitive abilities over time, with interdependence over development on emerging executive functions, language and mindreading abilities (e.g. Kuhn, 2000; Roebers, 2017; Schneider, 2008; Veenman, Wilhelm, & Beishuizen, 2004). Furthermore, social interactions with caregivers and peers (e.g. Brinck & Liljenfors, 2013; Whitebread & O’Sullivan, 2012) as well as formal schooling experience (Lee & Schmitt, 2014; Michalsky, Mevarech, & Haibi, 2009; Veenman, Van Hout-Wolters, & Afflerbach, 2006) can shape patterns of metacognitive performance. Thus, several facets of potentially human-unique social and cultural experiences seem to promote the development of metacognitive abilities (Dunstone & Caldwell, 2018; Goupil & Kouider, 2019; Heyes et al., 2020; Shea et al., 2014). Yet humans also exhibit an extended period of brain development which could further contribute to these developmental shifts (e.g. Clark & Dumas, 2016; Weil et al., 2013). Studies of other species with different life history characteristics can therefore help to distinguish these processes. For example, other great apes also possess an extended life history with a long period of juvenile brain development (Bianchi et al., 2013; Charvet, 2021; Leigh, 2012; Sakai et al., 2011; Teffler et al., 2013). Thus, studies of ape cognitive development can help parse the contributions of these slow life history characteristics to ontogenetic changes in human metacognition, and thus the mechanisms underlying these changes.

In the present set of studies, we aimed to address these questions by developing a novel paradigm to examine the development and breadth of chimpanzee information-seeking. In particular, we presented apes with choices between two containers whose contents could be accessed by pulling a string so that the containers came within reach. Crucially, the inside of the containers could not be viewed from the chimpanzees’ normal sitting position, but could be seen if chimpanzees stood or climbed up to peer into the containers from above. Across three studies, we then tested chimpanzees’ willingness to engage in this information-seeking response when they were ignorant and lacked some information about the rewards placed in the containers that was needed to most effectively solve the problem, versus when they were already knowledgeable of the container’s contents.

We tested chimpanzees from two semi-free-ranging populations on

different versions of this task to understand the psychological processes underpinning chimpanzee metacognition. In a first study, we examined a larger sample of $n = 47$ chimpanzees ranging from juvenility to adulthood to assess which individuals would spontaneously adopt an information-seeking strategy, without prior experience, to locate hidden food. In the second study, we examined a subset of $n = 12$ chimpanzees, who showed high rates of spontaneous information-seeking in the first study. Specifically, we assessed how they applied these skills to identify the *location* of a reward versus the *identity* of the reward, in order to test whether this was a flexible skill they could apply across contexts. If information-seeking represents a general searching response that is activated when the location of food is not known (Carruthers, 2008; Crystal & Foote, 2011; Hampton, 2009; Marsh & MacDonald, 2012b), then chimpanzees should be more likely to seek information specifically in the location condition. In contrast, if chimpanzees can flexibly information-look when they are ignorant more generally, then chimpanzee should be equally skilled in both contexts. In the final study, we examined whether a subset of $n = 6$ chimpanzees could apply these information-seeking skills to make more efficacious decisions when faced with uncertainty about reward payoffs. Here, chimpanzees could reduce the risks associated with their decisions by viewing the actualized payoffs of different probabilistic options. While chimpanzees have well-demonstrated understanding of probability and responses decisions under uncertainty (De Petrillo & Rosati, 2021), it is unclear if they can integrate metacognitive skills with risky decision-making to strategically look for information to reduce their uncertainty and maximize their rewards. Across these three studies, we therefore assessed the emergence and flexibility of chimpanzees' information-seeking response

2. Study 1: Spontaneous information-seeking

This study examined a larger sample of chimpanzees on an information-seeking paradigm in which individuals could stand up to look inside containers and see their contents when they initially lacked information about the location of a hidden reward. We had two main goals. First, we aimed to assess whether individuals spontaneously produced these information-seeking responses, in order to characterize patterns of individual variation and developmental change in information-seeking. Second, we used their responses to identify individuals who showed consistent information-seeking responses, who were then tested in one of the subsequent studies examining how these skills are used in different contexts.

2.1. Ethics statement

This research was conducted at two African chimpanzee sanctuaries that are both accredited members of the Pan African Sanctuary Alliance (PASA): Ngamba Island Chimpanzee Sanctuary in Uganda, and Tchimpounga Chimpanzee Sanctuary in Republic of Congo. All behavioral studies at Ngamba Island Chimpanzee Sanctuary were approved by Ngamba Island Chimpanzee Sanctuary / Chimpanzee Trust, the Uganda Wildlife Authority, and the Uganda National Council for Science and Technology. Behavioral studies at Tchimpounga Chimpanzee Sanctuary were approved by the Jane Goodall Institute and the Ministry of Scientific Research and Technological Innovation in Republic of Congo. Research had Institutional Animal Care and Use Committee ethics approval from Harvard University and the University of Michigan.

2.2. Participants

We tested a total of 47 semi-free-ranging chimpanzees (23 females and 24 males; mean age 17.7 years, range: 10–33 years) from two African sanctuary sites. Both sanctuaries are accredited member of the Pan-African Sanctuary Alliance, and animal care complied with PASA standards. Apes in African sanctuaries are typically wild-born and arrive at the sanctuary between 1 and 3 years of age. Age estimates were based

on estimated age on arrival, in some cases adjusted based on data from weight and dental emergence, following prior work (Rosati, 2019; Rosati, Emery Thompson, Atencia, & Buckholz, 2023; Wobber, Wrangham, & Hare, 2010).

Chimpanzees at both sites spend most of their time in large forest enclosures in species-appropriate social groups. Prior work shows typical cognition, behavior, and physiology in these populations (Cole et al., 2020; Dunay et al., 2023; Rosati et al., 2013; Rosati et al., 2023; Wobber & Hare, 2011). Chimpanzees had ad libitum access to water, were never food deprived for testing, and were tested in familiar night dormitories. All tasks were voluntary; if the subject stopped participating for more than three trials, the session was halted. All chimpanzees were naïve to the basic information-seeking paradigm.

2.3. General setup

The experimenter and the ape sat across from each other at a table (approximately 68 cm wide, 52 cm deep, 37 cm tall) with a sliding top, separated by wire mesh or bars. In the basic setup, there were two upright bowls placed on the table on the far side from the chimpanzees, with short strings attached that chimpanzees could access if the table was pushed forward (see Fig. 1 and Video S1). Across trials, the experimenter placed food into these bowls either visibly (such that the ape knew what was inside each) or behind an occluder (so the ape did not know where various rewards had been hidden). Crucially, chimpanzees could not see into these bowls from their typical sitting position in front of the table in the task, but could see into the bowls if they stood up or climbed up. After a period in which the chimpanzee could move to peek into the containers, the experimenter would push the table forward so the chimpanzee could choose a container by pulling one of the strings.

2.4. Session overview

All chimpanzees completed a single primary session where they first completed a series of introductory trials to familiarize them with the

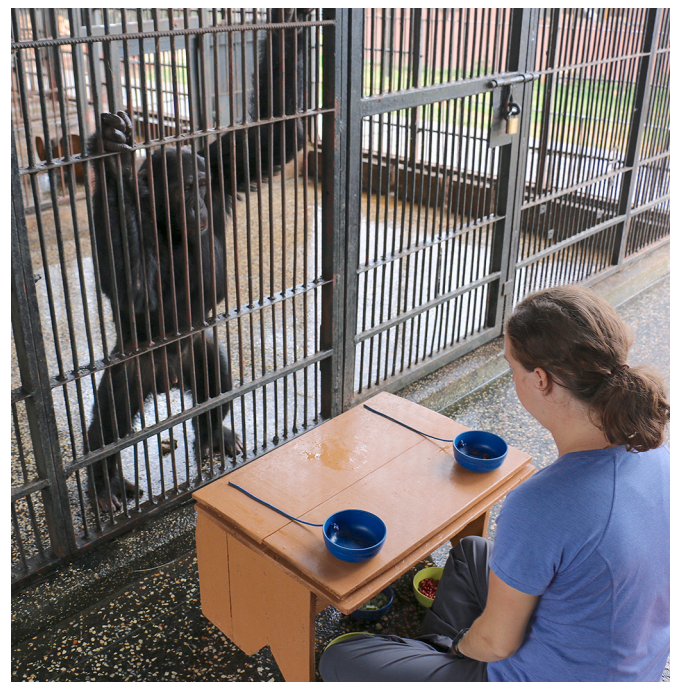


Fig. 1. Basic setup for studies. A chimpanzee stands up and looks inside containers in the task. Chimpanzees could not see into the containers from their typical position (seated in front of the table), but they could see if they stood up or climbed up. When the tabletop was pushed forward, the ends of the strings were within reach so they could choose a container by pulling its attached string.

basic setup, and then completed four *long look test trials* in which they could locate hidden food if they stood or climbed up. These trials were designed to assess the degree to which individuals independently discovered this behavioral response without any prior demonstration of this looking responses. Animals who showed at least one looking response in those trials went on to additionally complete 10 *short look test trials* (which were similar to the long trials but involved a shorter time cutoff for looking). Some individuals did not initially meet criterion in the first session, so they completed an additional repeat session with a similar structure and had to meet this criterion to progress to a later study, as detailed below (see Fig. 2 for a diagram of how animals progressed through the different trial types and subsequent studies).

2.5. Trial types and procedures

In the introductory phase, chimpanzees first completed six *warmup* trials in which they could choose between an empty container and one with a piece of food, to make sure they were comfortable with the string-pulling responses. On each trial, the experimenter first picked up the two bowls to show that they were empty, and then placed them on the left and right sides of the table. She then held up a piece of food and visibly placed it in one container on one side of the table, and then immediately pushed the table forward to allow the chimpanzee to choose by pulling a

string. Chimpanzees experienced trials with three food types (two total per type, side counterbalanced): a highly preferred food (a grape at Ngamba, and a banana slice at Tchimpounga); and intermediately preferred food (a peanut at both sites); or non-preferred food (a cucumber slice at both sites; note that cucumbers are a non-preferred food type, but are a normal component of the chimpanzee diets that they routinely eat in other contexts). Next chimpanzees completed six *food preference* trials. These had an identical procedure to the warmups, except that both bowls were baited with different foods (left side always first, as mentioned above). Apes made pairwise choices between the preferred, intermediate, and non-preferred food (two trials per possible pairing). This was because these three different food types were used in the subsequent studies that contrasted food values (for example, in Study 3 we directly contrasted low-, intermediate-, and highly-preferred foods in the risky choice task). Finally, apes completed four *show food* versus *no-food* trials where they chose between a visibly baited versus empty container. Here, the experimenter always placed five peanuts into one of the bowls, and then subsequently held both containers close to the wire mesh, so that the chimpanzee could look inside and compare the contents of both bowls without standing up. The experimenter then pulled back the bowls to their normal position so that the chimpanzees could only access the string, and immediately pushed the table forward, enabling the subject to choose by pulling one of the strings. This phase

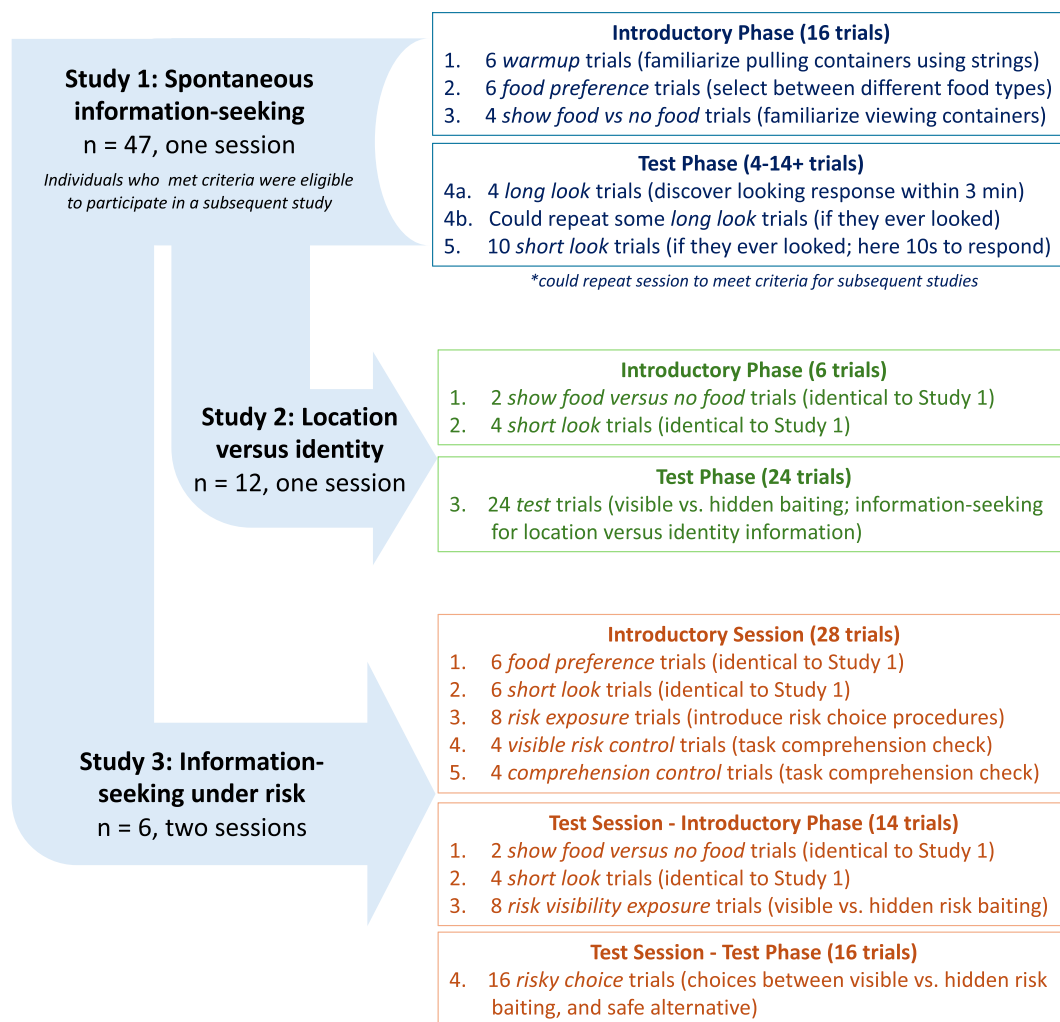


Fig. 2. Overview of studies and trial types. All individuals first completed Study 1; individuals who met criteria in this study were eligible to proceed to subsequent studies (they completed either Study 2 or Study 3). Sessions typically comprised an initial introductory phase that introduced key aspects of the task or confirmed basic comprehension of the setup (such as pulling the container using strings, or preferences for different kinds of foods), and then presented the key trials for the study in a subsequent test phase.

aimed to show that chimpanzees could identify baited locations after seeing the contents of the bowls. Across trials, the side assignment for the baited locations was counterbalanced and quasi-randomized, with no more than three trials in a row with the same baited location, and the left container was always baited first when both containers were baited.

The next phase comprised four *long look* trials, the key trials of focus for this study (see Video S1). The goal of this phase was to assess if chimpanzees spontaneously discovered the information-seeking response when now faced with a new situation where they did not see which container was baited. If they did not discover this on their own, the experimenter prompted this insight by holding up the bowls to encourage them to change their body position in response. In these trials, the experimenter again baited one of the bowls with 5 peanuts, but here did so behind an occluder (61 wide, 42 cm tall) so that the chimpanzee did not know which container had been baited. In trials, she first showed the chimpanzee that the bowls were empty, and then moved the two bowls to the center of the table before putting up the occluder and baiting to further obscure which held the food. After the experimenter then removed the occluder, she moved the bowls to the sides of the table, and then waited to assess if the chimpanzees would spontaneously stand up to look into the containers of their own accord. For the first minute (timed with a stopwatch), the experimenter remained seated at the table while looking downwards. If the chimpanzee did not look in this period, the experimenter left the testing arena and monitored it from about 2 m away for another 2 min, in case the absence of the experimenter prompted the chimpanzees to try different kinds of responses to obtain the food. Chimpanzees who stood or climbed up within this initial three-minute period were scored as having spontaneously looked into the bowls. If the chimpanzee still did not look in this period, the experimenter returned and lifted the bowls above the chimpanzees' head, thereby encouraging them to climb the wire mesh to see inside the bowls (while these chimpanzees thus did see into the bowls, they were not scored as producing a look on these trials). Once the chimpanzee stood up (either spontaneously or by experimenter prompting), the experimenter pushed the table forward with the bowls to enable a choice. In our analyses, we only counted looks independently generated by the chimpanzees in these four trials, not those prompted by the experimenter holding up the bowls.

A second goal of this study was to identify individuals who consistently showed information-seeking to participate in the subsequent studies, where we probed aspects of their understanding further. Thus, individuals who looked at least once across the four initial *long look* trials could be tested in these further phases, whereas those who never produced a looking response were not tested further. First, chimpanzees who looked at least one time in their first four *long look* trials could receive repeated (identical) *long look* trials, to give them more opportunities to engage in this behavior with the longer 3 min time cut-off. Then, individuals who looked at least once on the *long look* trials could further complete 10 *short look* trials (see Video S1). These were quite similar to the *long look* trials, except that here the experimenter waited only 10 s after baiting, and then pushed the table forward regardless of whether the chimpanzee looked or not. Here, we set a criterion that chimpanzees should produce a looking response on at least five of these *short look* trials to be eligible for a subsequent study, that is, showing a rate of looking at least half the time when doing so was necessary to solve the problem. This phase also allowed us to test whether chimpanzees made more correct choices after looking compared to when they did not look (since all chimpanzees saw inside the bowl in the initial *long look* trials because the experimenters held up the bowls if the chimpanzee did not generate the response themselves, we could not analyze this in the *long look* trials). Chimpanzees who never initially looked in the *long look* trials, or did not meet the criteria of looking on at least half of the trials on the *short look* trials, could be later retested in this session to meet criteria and proceed to subsequent studies; two individuals successfully passed on a second session and later participated in Study 3. However, note that we analyzed their

performance from their first session for Study 1 for results reported here. Individuals who participated in later studies needed to both meet criteria from Study 1 and still be available for testing (some individuals did meet criteria, but could not be tested in later studies for reasons unrelated to the present research).

2.6. Coding

All sessions were video recorded and coded from video; a primary coder scored all trials, and a second coder who was blind to study goals and hypotheses coded 20% of sessions for reliability. Our primary dependent measure concerned whether the chimpanzee produced a *looking response* by standing or climbing up, and our second dependent measure was their subsequent choice. We coded looking responses that occurred when a chimpanzee stood up or climbed up and looked down into the bowls *before* they made a choice by pulling a string on one of the containers. In the *long look* trials, we only counted looks that happened spontaneously before the 3 min transition (e.g., before the experimenter intervened by lifting the containers to prompt the chimpanzee to stand up, if they had not already done so in the time limits of these trials). In the *short look* trials, we also coded instances where they did so after the table was pushed forward so that the strings were within their reach, as long as they did so before they had actually made a choice by pulling a string. We also measured the *latency to look*, using the moment the baiting ended (when the last reward was placed) as the trial start reference, and calculated latency to the moment the chimpanzee stood up. In some cases, the chimpanzees stood up and looked while the baiting procedure was still in progress, in which case we treated this as a latency of 0 s. If a chimpanzee looked after making their choice, we did not count this as a look on that trial. For coding, we used the program *MPEG Streamclip*, advancing through each video frame-by-frame and subsequently converted the frames back into seconds. Interrater agreement was excellent for all three dependent variables (looks: Cohen's $\kappa = 0.99$; latency to look: $r_p = 0.99$; choice: Cohen's $\kappa = 0.97$).

2.7. Statistical analyses

Our primary analyses used mixed models to examine chimpanzees' trial-by-trial responses in the *long look* and *short look* trials, respectively. For looking responses and choices (both binary measures), we implemented general linear mixed models (GLMMs) with a binomial structure in R ([R Development Core Team, 2022](#)) using the *glmer* function of the *lme4* package ([Bates, 2010](#)). All models included a random intercept for *subject identity* to account for repeated trials, and *trial number* for that phase of the study (e.g., the models examining looks in the first four *long look* trials included trial numbers 1 through 4). Then, we successively added the factors of *age* (in years), *sex*, and their interaction to test their importance. Models used age in years as a continuous predictor, but some figures and additional checks used *age cohorts* in which we contrasted juveniles (<15 years; $n = 14$) with adults (15 years and up; $n = 33$) using a common age cut-off for adulthood in the wild ([Emery Thompson & Sabbi, 2024](#)). We then compared model fit using likelihood ratio tests ([Bolker et al., 2009](#)), and used the *emmeans* package for post-hoc comparisons of predictors ([Lenth, 2018](#)). Latencies were analyzed with linear mixed models using the *lmer* function in a similar fashion. As some trials had 0 s latencies as noted above (e.g., trials in which chimpanzee started looking into the bowls before the experimenter completed the entire baiting procedure), we also checked for the robustness of the latency results by also running these models after removing these trials. Finally, to assess if performance on pretest trials, as well as choice responses in the main trials following looks or no looks, we one-sample *t*-tests to examine chimpanzees' choice patterns with respect to chance.

2.8. Results and discussion

We first confirmed that chimpanzees showed appropriate responses in the pretest phases of the session. In the initial *warmup* trials, where chimpanzees simply had to pick the container they had previously seen baited (with varying food types across trials), they chose correctly on mean = $95.4 \pm SE = 1.3\%$ of trials where they made a choice [$t_{46} = 35.72, p < 0.0001$]. Chimpanzees refused to make a choice on a small subset of trials, all of which involved the non-preferred food (i.e., on 21 trials where the only option available was a cucumber slice, they refused to pull any container). They also showed expected performance on the *food preference* trials: they chose the preferred food over the non-preferred on $95.7 \pm 3.0\%$ of trials [$t_{46} = 15.37, p < 0.0001$]; the intermediate food over the non-preferred food on $93.6 \pm 2.5\%$ of trials [$t_{46} = 17.73, p < 0.0001$] and the preferred food over the intermediate food on $66.0 \pm 5.7\%$ of trials [$t_{46} = 2.79, p < 0.01$], indicating that these were overall appropriate food options to contrast in the subsequent studies. Finally, they choose the baited bowl on $94.7 \pm 2.0\%$ of trials in

the *show food vs. no food* trials, which were similar to the initial *warmup* trials but where the experimenter showed them the inside of the bowls before choosing [$t_{46} = 22.31, p < 0.0001$]. Overall, this indicates that chimpanzees could appropriately track and choose baited bowls in this setup, and also showed the expected food preferences over the different items used in subsequent studies.

We next examined responses in the first four *long look* trials, our primary measure of interest in this study. In their first trial, before any subsequent exposure, 72% of the chimpanzees spontaneously produced a look within three minutes (see Fig. 3a for breakdown by age and sex), and chimpanzees looked spontaneously across mean = $64.2\% \pm SE = 6.1\%$ of all trials. This indicates that chimpanzees were able to spontaneously infer that they can solve this novel problem by engaging in information-seeking by moving to change their view of the setup. Yet there was also variation across individuals in their propensity to respond like this: whereas juveniles looked on in $98.2\% \pm 1.8\%$ of their trials, adults did so on only $49.7\% \pm 7.3\%$ of trials. To analyze this individual variation, we constructed a base GLMM accounting for *trial number* and

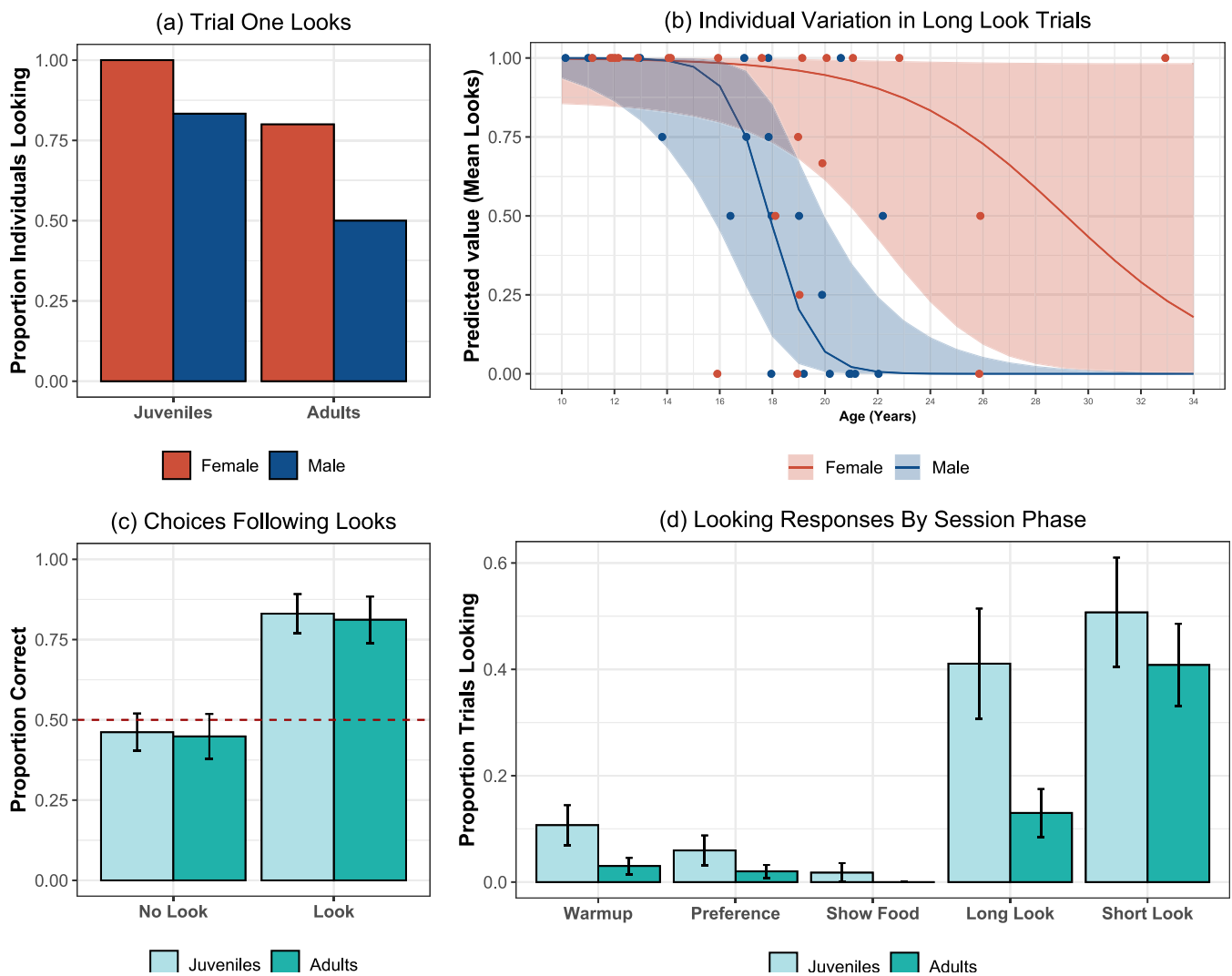


Fig. 3. Spontaneous information-seeking (Study 1). (a) Overall, 72% of individuals looked within three minutes on their first experience with the novel problem on the *long look* trials; panel shows breakdown by sex and age cohort and sex. (b) Individual variation in propensity to engage in information-seeking. Younger chimpanzees and females showed more looking responses across the four *long look* trials each lasting up to 3 min; ribbon indicates 95% CI from GLMM model estimates of trial-by-trial data accounting for *trial number* as well as *age, sex,* and their interaction; scatter plot indicates individuals' mean proportion of looks. (c) Choices in the *short look* trials by looking response and age cohort. Chimpanzees of all ages selected the correct option at high rates after they looked on these trials (in a ~10s interval), but chose at chance if they did not. Dashed line indicates chance; error bars indicate SE. (d) Looking responses that occurred within 10s across all trial phases, broken down by age cohort. Chimpanzees showed low rates of baseline looking responses in the three initial introductory phases where such responses were not necessary, but showed increases in looking responses in the subsequent *long look* and *short look* trials; error bars indicate SE.

subject, which revealed no overall change in looking across trials. We then added age, which improved model fit [$\chi^2 = 13.70$, $df = 1$, $p < 0.0005$]: younger individuals looked more often than older individuals. Inclusion of sex further improved fit [$\chi^2 = 7.46$, $df = 1$, $p < 0.01$]: females looked more than males. Finally, the inclusion of age \times sex interaction also improved fit [$\chi^2 = 7.12$, $df = 1$, $p < 0.01$; see Fig. 3b and Supplemental table S1 for model parameters]. Post-hoc tests showed that there was steeper age-related decline in males than in females [$p < 0.05$], indicating variation in spontaneous information-seeking both with age and by sex.

We also examined latency to look on long look trials (for those trials where chimpanzee did produce a look on their own, without being prompted by the experimenter first raising up the bowls). Overall, chimpanzees took an average of mean = $47.4 \pm SE = 6.4$ s to look on these trials, with individual averages ranging from 3 s to 149 s. We analyzed these data using LMMs taking the same approach as for producing a looking response. The base model with trial number indicated no significant change in latencies over trials, and neither the inclusion of age [$\chi^2 = 1.71$, $df = 1$, $p > 0.19$, n.s.], sex [$\chi^2 = 1.85$, $df = 2$, $p > 0.39$, n.s.], nor their interaction [$\chi^2 = 2.47$, $df = 3$, $p > 0.48$, n.s.; see Supplemental Table S2 for model parameters] improved fit compared to this base model. This indicates that when chimpanzees did produce a look, the speed of their response were fairly similar across different ages and sexes. Additional checks removing four trials with 0 s latencies showed the same results (e.g., trials where the chimpanzee looked before the experimenter completed the entire baiting process; see Supplemental Materials). Finally, we confirmed that chimpanzees chose the baited option in $89.4 \pm 2.2\%$ of these trials, above chance [$t_{46} = 17.51$, $p < 0.0001$]. As noted earlier, chimpanzees had seen into the bowls on all of these trials before choosing (either because they had looked on their own, or because the experimenter held up the bowls to prompt a look), so this was the expected response.

We then examined responses in the 32 individuals who completed the short look phase (using only first session data for subjects who repeated the session). In contrast to the initial long look trials, these trials only provided a short ~10s period when animals could look before the table was pushed forward for their choice, and therefore allowed us to confirm that chimpanzees made more accurate responses when they produced looking responses versus when they did not. Here, chimpanzees looked on an average of mean = $54.5 \pm SE = 6.0\%$ of trials. As only individuals who had already looked spontaneously in the long look phase proceeded to this part of the test, we did not expect major individual differences in production of looking responses in this phase (i.e., this data only existed for individuals who already demonstrated that they would produce some looks spontaneously), and accordingly there was no improvements relative to the base model including trial number by adding age [$\chi^2 = 1.69$, $df = 1$, $p = 0.19$, n.s.], sex [$\chi^2 = 1.99$, $df = 2$, $p = 0.37$, n.s.] or their interaction [$\chi^2 = 2.42$, $df = 3$, $p = 0.49$, n.s.]. That is, individuals that already showed a high propensity to look in the earlier phases of the session did not show major individual variation in their responses in these subsequent trials. As in the analyses of long look trials, there were also not major differences in latencies by sex or age when individuals did look (see Supplemental Materials). Finally, these trials crucially allowed us to compare likelihood of correct responses when the chimpanzees did versus did not produce a look, to confirm that information-seeking in this context did improve subsequent decision-making. Here, we found that chimpanzees chose the baited container above chance on trials where they looked first before choosing [$82.1 \pm 4.7\%$, $t_{27} = 6.82$, $p < 0.0001$], but chose at chance levels when they did not first look and thus remained ignorant about the reward's location [$45.3\% \pm 4.8\%$; $t_{26} = -0.97$; $p = 0.34$, n.s.]. This pattern was true for both juveniles and adults tested in these trials (see Fig. 3c). This indicates that looking responses did provide necessary information to correctly solve the task.

As a final check to confirm that our setup in the long look and short look phases induced more information-seeking responses compared to

baseline rates of these behaviors, we finally examined looking responses across all phases of the session—that is, also examining any such looking behaviors that chimpanzees exhibited in the initial warmup, preference, or food versus no-food trials in the session, all trial phases where such looking behavior was unnecessary given that the animals directly saw the containers baited. Because trial length varied across these different trial types (e.g., the long look trials could last up to three minutes, unlike the other trials), here we examined only looking responses that occurred within 10s after the demonstration was complete, in order to equate the time animals could have produced this looking response across the different trials. We found that in fact looking responses in the three initial pretest phases was generally quite low, averaging from 0.5% of trials in the show food versus no food trials, to 5.3% in the warmup trials (see Fig. 3d for breakdown by cohort). In contrast, chimpanzees looked within 10s on an average of 21.4% of long look trials, and on 45.2% of trials in the short look trials (for those who proceeded to this phase). To analyze this, we constructed a base GLMM of looks accounting for subject, trial number (within trial type), age, and sex, and then added trial type in a second model. Here, we lumped all pretest trials as one category (warmup, preference, and show food vs. no food) given the few trials and overall low rates of looking in this initial phase of the session. In fact, this improved model fit [$\chi^2 = 235.32$, $df = 2$, $p < 0.0001$; See Table S3 for parameters from this model]. Posthoc tests showed that chimpanzees looked more in both the long look trials and short look trials compared to the pretest trials [$p < 0.0001$]. This indicates that chimpanzees rarely engaged in this kind of looking response when it was not necessary to solve the task, but rather started producing it at much higher rates in the phases of the session, where doing so could provide useful information for solving the problem.

Overall, Study 1 first validated the general method by showing that chimpanzees could participate in this novel task (e.g., by easily pulling the containers) and needed to engage in information-seeking by standing up to look into the containers in order to successfully locate rewards. Second, we showed that many chimpanzees can spontaneously engage in such looking behaviors with minimal prior experience: the majority of individuals showed a looking response on their first long look trial (the first trial where such looks provided useful information), whereas few individuals engaged in this sort of behavior at baseline, as assessed in the initial pretest trial phases. Finally, we found individual variation in the propensity to engage in information-seeking: while both males and females showed fairly high levels of spontaneous information-seeking in juvenility, adults are less likely to do so, with a steeper decline in males. Importantly, the results from the short look trials also show that individuals who did produce a look tended to then exhibit more accurate responding when selecting a container, whereas individuals who did not look chose the baited container at chance, indicating that such information was necessarily to make correct choices in this context. Our subsequent studies then built on these initial results to test how chimpanzees flexibly deploy these information-seeking responses across different contexts.

3. Study 2: Location versus identity information

Previous comparative information-seeking tasks have often assessed if animals can use information-seeking to locate a hidden food reward—that is, to solve spatial problems. For example, in the original study by Call and Carpenter (2001), great apes were confronted with two tubes—but only one was baited with a reward—and could bend down to peer into the tubes to see which had the treat. Several additional studies have built on this result to examine patterns of information-seeking for food locations across different species (Basile et al., 2009; Bräuer et al., 2004; Hampton et al., 2004; Marsh & MacDonald, 2012b; McMahon et al., 2010; Paukner et al., 2006; Roberts et al., 2012; Rosati & Santos, 2016). However, some critiques have suggested that this information-seeking behavior is not truly metacognitive, but may rather represent a more general ‘searching response’ that is activated when the

location of food is not known (Carruthers, 2008; Crystal & Foote, 2011; Hampton, 2009; Marsh & MacDonald, 2012b). That is, if animals do not know where to find food then they start looking around, but this does not mean that they specifically infer that they need to seek new information in order to resolve their uncertainty. In this interpretation, information-seeking would be prompted by situations that involve generally not knowing where any food rewards are located. Specifically, when animals know the location of food they might quickly produce a choice response, whereas if they do not know a location then they might experience response conflict and, eventually, develop an alternative looking strategy through trial-and-error (Marsh & MacDonald, 2012a).

One set of studies partially addressed this interpretation by integrating information-seeking paradigms involving locating hidden food, with other contextual cues that might allow animals to infer the location even though they did not directly see the food hidden. For example, in the original study by Call and Carpenter (2001) involving two tubes, apes would sometimes look into only the empty tube and then make a choice without checking the other tube, suggesting they had used inference by exclusion to guess the location of the food in the other tube although they had not directly seen it. Similarly, orangutans look more under a clear table top when there are multiple opaque cups that could be the hiding location of food, compared to situations where only one of the possible cups is opaque and the rest are transparent and thus it can be inferred by exclusion where the food was placed without peering underneath (Marsh & MacDonald, 2012a). This suggests that apes may not be using such a simple generalized search strategy, or at least that they do not need to directly perceive food to inhibit such a strategy but can rather use inferences about location to drive their choices. In contrast, lion-tailed macaques may indeed use such a generalized search strategy, as they show information-seeking responses if there is no food in sight even if the location of the food could be clearly inferred by exclusion (Marsh, 2014).

Another way to assess this is to examine if animals can engage in information-seeking outside of the context of locating a specific reward—that is, in a context where the location is already known, but other information is needed to effectively solve the problem. To date, few studies have examined information-seeking for non-spatial information, likely because implementing such setups is more challenging. Two studies of note adapted the basic premise of the study by Call and Carpenter (2001) to examine whether chimpanzees and orangutans would seek information about the functional properties of tools (Bohn et al., 2017; Mulcahy, 2016). Here, the tools had been placed into a similar apparatus such that some aspects of their characteristics were out of view. However, this is a setup that would only be relevant to species (like chimpanzees) that use tools. Another notable study examined whether chimpanzees would seek information about what type of reward was placed in a container, when they needed to report the identity of the food on a lexigram touch pad to receive it (Beran et al., 2013). These results suggest that some animals can extend their metacognitive abilities to seek needed information about the specific characteristics of food, not only their presence or absence in particular spatial locations (see also Perdue et al., 2018 for a follow-up study). However, both of these studies involved three chimpanzees who had prior extensive training with an artificial symbolic language which taught them to communicate with humans using a lexigram keypad, and the setup of the initial study also hinged on this unusual rearing experience as their responses about reward identity were made using the lexigram buttons. Importantly, there is some evidence that such language training experiences, and human enculturation more generally, may re-structure a variety of cognitive skills in apes (Bandini et al., 2021; Beran, Perdue, Bramlett, & Menzel, 2012; Buttelmann, Carpenter, Call, & Tomasello, 2007; Carpenter & Tomasello, 1995). As such, it is unclear if this skill would generalize to chimpanzees more broadly. Finally, no studies have directly compared animals' information-seeking responses when reasoning about the location of a reward versus the identity of a reward in a matched context, which is important because

the 'general search strategy' interpretation predicts that information-seeking will be most common in response to missing location information, but not necessarily when other kinds of information are lacking.

Here, we tested this by adapting the information-seeking task validated in Study 1, allowing for a more general setup that did not require language-training to assess information-seeking for identity information. Specifically, we either baited one of two bowls with a preferred food type (in the *location condition*), or baited both bowls with different items, one which was preferred and one which was non-preferred (in the *identity condition*). We further contrasted whether the chimpanzees observed the baiting or not (*hidden* versus *visible* baiting). The premise of this setup was that while information-seeking was necessary to successfully choose the single baited container in the location condition, both containers were always baited in the identity condition and thus any choice would always result in a food treat. Information-seeking in this context was therefore only necessary to ensure the choice was for the better type of food. We had two main predictions. First, we predicted that chimpanzees would generally engage in more information-seeking when the baiting was hidden compared to when baiting was visible—a basic confirmation that they understood the premise of the setup and modulated their searching responses such that they produced them more when actually necessary to solve the task. We then contrasted two views concerning responses in the hidden location trials versus the hidden identity trials. If chimpanzees rely on general search heuristics to prompt information-seeking—such that they produce a looking response whenever they do not know the location of food—we predicted that they should engage in more information-seeking in the location condition. Conversely, if chimpanzees can flexibly deploy their metacognitive skills across different kinds of information contexts, then they should be similarly proficient at information-seeking in both conditions, as information-seeking in the identity condition allowed them to obtain the more preferred food.

3.1. Participants

We tested 12 chimpanzees from Tchimpounga Chimpanzee Sanctuary (7 females, 5 males; mean age 16 years, range: 10–23 years) in this study. These individuals had all participated in Study 1 between 1 and 14 days earlier, and had passed our criterion of producing a looking response in at least 5 of the 10 *short look* trials in that study to proceed to this second study.

3.2. Session overview

Chimpanzees completed a single session using the same basic setup as in Study 1 (see Fig. 2 for a diagram of the study sequence and trial types). They first completed a series of introductory trials to again familiarize them with the basic setup, and then completed 24 primary *test trials* where we used a 2×2 within-subject design to vary whether (1) whether one reward was baited in only a single location, versus two rewards of differing identity were baited in each of the containers; and (2) whether the baiting process was visible or hidden to the chimpanzees, such that they either knew or did not know what rewards were placed where in advance.

3.3. Trial types and procedures

In the introductory phase, we first presented subjects with two *show food* versus *no food* trials to remind them of the basic setup. These were identical to those in Study 1: the experimenter placed five peanuts into one of the bowls, and then subsequently held both containers close to the wire mesh, so that the chimpanzee could look inside and compare the contents of both bowls before choosing. They then completed 4 *short look* trials which also followed the same procedure as in Study 1, where the experimenter baited one location with 5 peanuts behind an occluder, and then pushed the table forward after 10s.

Chimpanzees then completed 24 *test* trials contrasting *information type* (reward location versus reward identity) and *baiting visibility* (hidden or visible baiting). Chimpanzees experienced the four possible trial types in blocks of six trials (e.g., six trials with hidden baiting of location information in a row), with the order of these trial blocks counterbalanced across individuals. As in the previous *short look* trials, the experimenter baited the bowls and then waited 10 s while looking down before pushing the table forward and allowing the participant to make a choice. As such, when the baiting was hidden chimpanzees had to engage in information-seeking in order to locate the only piece of food in the location trials. While they were ensured to receive some reward regardless of which container they chose in the identity trials, they needed to engage in information-seeking to ensure they would obtain the higher-quality reward but not to determine whether any food was present (see Video S2).

In the *location* condition, the experimenter always baited only one of the two bowls with a preferred reward (banana piece). The general procedure for these trials was similar to the *short look* trials. In the case of the *visible baiting* trials, the experimenter first showed the chimpanzee that the bowls were empty, and then placed both bowls at the center of the table. The experimenter showed the chimpanzee a banana in her open hand, visibly placed it in one of the two bowls, and then moved the bowls to the side locations for the chimpanzee's response. In the *hidden baiting* trials, her actions were identical except the bowls were occluded during the baiting. Here, the experimenter showed the preferred food in her hand above the occluder, but then the chimpanzees could not observe which specific bowl it was placed in behind the occluder.

In the *identity* condition, the chimpanzees experienced that one container was baited with a preferred reward (banana) and the other with a non-preferred reward (cucumber). As the goal in this condition was to ensure that the chimpanzees clearly saw that both containers had been baited and thus contained something, we used a slightly different procedure than in the location trials. Specifically, the experimenter always initially showed the chimpanzee both of the two available food items (e.g., one slice of cucumber and one slice of a banana) in separate 'outcome' bowl, tipping it towards them so they could initially look inside and see these two food items. She then moved the bowl's orientation away from them so the chimpanzee could not see into it, visibly reached into the bowl and removed one item to bait the left bowl, and then did the same for the right. In the *visible baiting* trials, the experimenter used her open hand to bait the bowls, such that the food was visible in her fingers after she pulled it out the outcome bowl. In the *hidden baiting* trials, in contrast, her actions were the same except she used a closed hand to complete this action such that the specific food was not visible. As such, the chimpanzees saw the experimenter place something in both bowls in both situations, but could only directly see what it was in the visible baiting trials.

3.4. Coding and analysis

All sessions were video recorded, and looking behavior, latencies, and choice responses were coded from video in the same way as Study 1. A primary coder scored all trials, and a second coder who was blind to study goals and hypotheses coded 25% of sessions with excellent interrater agreement (looks: Cohen's $\kappa = 0.91$; look latency: $r_p = 0.97$, choices: Cohen's $\kappa = 0.98$). Our analysis approach was similar to that in Study 1. We again examined trial-by-trial binary looking and choice responses in the primary *test* trials by fitting GLMMs with a binomial error structure in R (R Core Team, 2013) using the *glmer* function of the *lme4* package (Bates, 2010). In the base model we accounted for *subject identity* as a random effect, *age* (in years), *sex*, and *trial number* (*within trial type*). To test our main hypotheses about chimpanzees' information-seeking performance across contexts, we then added *baiting visibility* (hidden versus visible), *information type* (identity versus location), and their interaction to test their importance as predictors of propensity to look. We then compared model fit again using likelihood ratio tests. As

in Study 1, latencies to looks were analyzed with linear mixed models using the *lmer* function, and we again examined results by running another set of models removing trials with 0 s latencies (i.e., where the chimpanzee initiated their look before the experimenter had fully completed the baiting process).

3.5. Results and discussion

We first checked that chimpanzees' responses during the introductory trials were appropriate. All individuals chose the correct option on all *show food vs. no food* trials, indicating that they could still correctly select containers they had viewed being baited. Similar to the results from Study 1, the chimpanzees in the four *short look* trials produced an information-seeking response on an average of mean = $62.5\% \pm SE = 9.0\%$ of trials. After looking, participants made a correct choice on $92.4\% \pm 5.2\%$ of trials, above chance [$t_{10} = 8.15$, $p < 0.0001$]. In contrast, their choice tended to be below chance level when they did not first produce a looking response [$31.5\% \pm 8.1\%$; $t_8 = -2.29$; $p = 0.051$, n.s.]. This again validates the premise of the task, as it shows that the chimpanzees need to engage in information-seeking to correctly respond in this setup.

We then examined chimpanzees' performance in the main *test* trials, to assess if chimpanzees engage in more information-seeking when the baiting was hidden, as expected; as well as to compare patterns of information-seeking for location information compared to identity information. Overall, apes looked more often when the baiting was hidden and thus they were ignorant about the reward's location or identity (mean = $58.3\% \pm SE = 8.5\%$) compared to when the baiting was visible ($19.4\% \pm 6.1\%$; see Fig. 4a). We then analyzed patterns of looking across these conditions using GLMMs. The base model included *age*, *sex*, and *trial number*, and revealed that males in this sample looked more than females overall, and there was a decline in looking over trials. To address our main questions, we then added *baiting visibility* to a second model, which improved model fit [$\chi^2 = 57.31$, $df = 1$, $p < 0.0001$]: chimpanzees looked more often when they had not seen the baiting and therefore were ignorant about the location or identity of the food treat, compared to when they had seen the baiting. However, subsequent inclusion of *information type* [$\chi^2 = 2.35$, $df = 1$, $p = 0.13$, n.s.; see Supplemental Table S4 for parameters] as well as the interaction of *baiting visibility* and *information type* [$\chi^2 = 3.42$, $df = 2$, $p = 0.18$, n.s.] did not further improve model fit. Thus, chimpanzees looked more when they lacked information overall, and were similarly proficient at engaging in information-seeking when they lacked information about the location of a single reward versus the identity of the best reward.

We also examined the *latency* of looking responses on those trials where chimpanzees did produce a look (both when baiting was visible and hidden). Overall, chimpanzees were quicker to look on trials with hidden baiting where they needed to produce a look to make an optimal choice (mean = $2.6\text{ s} \pm SE = 0.7\text{ s}$) compared to trials with visible baiting where this was not strictly necessary ($3.5\text{ s} \pm 0.9\text{ s}$). To model this, we used LMMs with a base model that again included *age*, *sex*, and *trial number*, and revealed faster latencies over trials. Inclusion of *baiting visibility* in a second model significantly improved model fit [$\chi^2 = 4.09$, $df = 1$, $p = 0.04$], indicating that chimpanzees were quicker to look on trials with hidden versus visible baiting. However, there was no further improvement by adding *information type* [$\chi^2 = 0.98$, $df = 1$, $p = 0.32$; see Supplemental Table S5 for parameters], nor the interaction between *information type* and *baiting visibility* [$\chi^2 = 1.48$, $df = 2$, $p = 0.48$, n.s.]. Overall, these latencies patterns then match the general pattern in production of looks. We also checked results when removing all 0 s latencies where the chimpanzees initiated their looking response while the baiting process was still ongoing. Here, there were no differences between baiting conditions (see Supplement for details). However, in this study there were many such looks initiated before the baiting process was complete (39%; 44 out of 112 trials with a look; 37 of these instances occurred in the hidden condition specifically), so this may be a

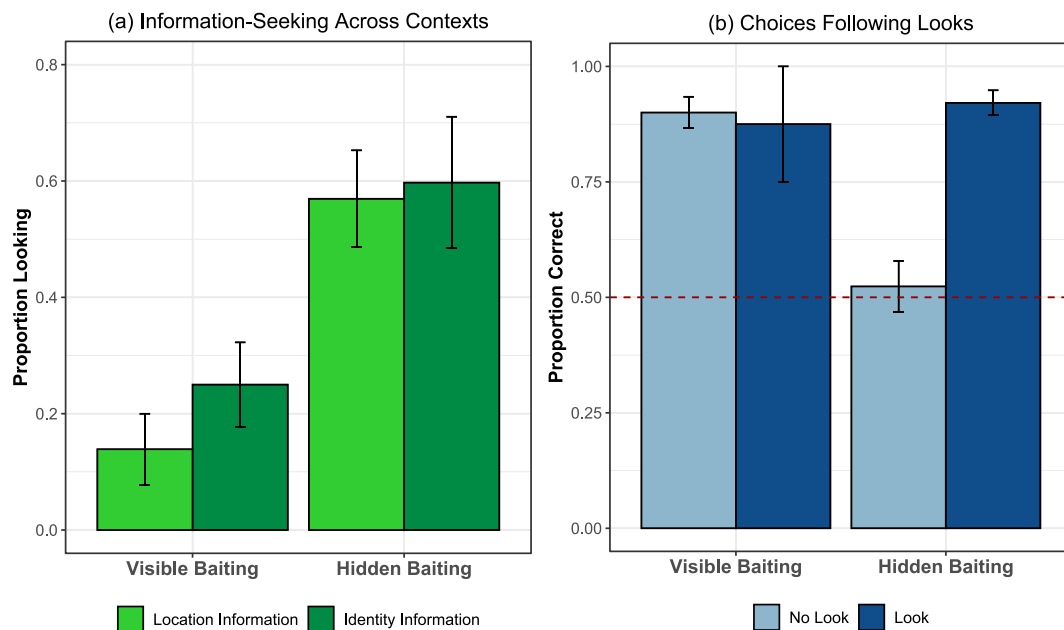


Fig. 4. Information-seeking about reward location versus identity (Study 2). (a) Chimpanzees looked more often after hidden baiting compared to visible baiting, and did so at similar rates for information about the location of a reward and information about the identity of available rewards. (b) Across both conditions, chimpanzees selected the correct option at high rates when baiting was visible regardless of whether they looked. After hidden baiting, they also chose at high rates after looking, but chose at chance if they did not look. Error bars indicate SE, and dashed line indicates chance.

sample size issue. Interestingly, this also suggests that chimpanzees were generally looking more rapidly than they were in the first study, perhaps due to their increased experience with the problem.

Finally, we examined the chimpanzees' choice patterns across the test trials (see Fig. 4b). As expected, chimpanzees chose correctly when baiting was visible regardless of subsequent looking behavior: they did so on mean = $87.5\% \pm SE = 12.5\%$ of trials where they produced a look [$t_7 = 3.00, p = 0.02$], and on $90.01\% \pm 3.4\%$ of trials where they did not look [$t_{11} = 11.74, p < 0.0001$]. This is not surprising, since on these trials looking was not necessary to solve the problem because of the visible baiting procedure. Conversely, in the hidden baiting trials looking was necessary to make a correct choice. Here, chimpanzees chose at chance if they did not engage in information-seeking [$52.4\% \pm 5.5\%$; $t_9 = 0.43, p = 0.68, n.s.$] indicating that they could not otherwise detect where the reward or higher-value reward was, but chose correctly above chance after a hidden baiting when they stood up to look [$92.1\% \pm 2.7\%$; $t_{11} = 15.50, p < 0.0001$]. Overall, this shows that chimpanzees generally selected the correct option if they had initially seen the baiting procedure, but needed to engage in information-seeking to choose correctly in the hidden baiting condition.

The results from Study 2 provide evidence for two main conclusions. First, the direct comparison of responses in the hidden versus visible baiting conditions showed that chimpanzees need to engage in information-seeking to solve this basic problem, aligning with conclusions from Study 1 based on performance in the *short look* trials. More importantly, the results show that chimpanzees are similarly adept at engaging in information-seeking both to locate a single hidden piece of food, but also to differentiate the identity of different possible rewards when they have seen both locations baited with food of unknown type. Unlike the predictions of the generalized searching hypothesis, chimpanzees here showed similar facility with information seeking for both location and identity information and seem to be able to apply their metacognition skills in a more flexible fashion to solve different kinds of problems. Study 3 then builds on this result by testing whether chimpanzees can not only engage in information-seeking for different types of information, but also integrate metacognition with assessments of reward probability to produce optimal responses.

4. Study 3: Information-seeking under risk

At its core, information-seeking aims to reduce uncertainty, or lack of knowledge about possible outcomes. Individuals may lack some information they need to solve a problem and therefore are unsure of the best course of action, such that seeking more information can resolve this uncertainty. While most animal metacognitive tasks to date have involved reward contingencies that are essentially fixed—one location provides a treat whereas another does not—converging evidence suggests that animals may be sensitive to their degrees of knowledge about different courses of action, and some forms of information-seeking may be engaged when faced with decisions under uncertainty. For example, studies of ambiguity aversion, or preferences for known over unknown risks, show that both macaques and apes prefer options where the possible set of probabilistic outcomes is known compared to options where probabilities are ambiguous, even if the expected value is the same (Hayden, Heilbronner, & Platt, 2010; Rosati & Hare, 2011). Second, macaques prefer options that provide some information about future rewards (such as about the amount of an upcoming reward), over options that result in the exact same outcome but do not provide this information upfront, suggesting that animals place intrinsic value on obtaining information (Blanchard, Hayden, & Bromberg-Martin, 2015; Bromberg-Martin & Hikosaka, 2009, 2011; Kidd & Hayden, 2015). Finally, some work on animals' understanding of counterfactual events—events that did not occur but could have if one chose differently—shows that macaques are willing to give up potential rewards to obtain information about counterfactual outcomes (Wang & Hayden, 2019). Overall this aligns with an emerging view from evolution and ecology that information used by animals may represent a core aspect of adaptive decision making (Bergman & Beehner, 2023; Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005).

An open question, however, is whether animals can actively infer available opportunities to engage in information-seeking responses to resolve uncertainty, as these prior tasks involved choosing between options that either did or did not provide additional information. Indeed, a core aspect of prior work examining animal information-seeking (e.g., Beran et al., 2013; Call & Carpenter, 2001) is that the

information-seeking response is a new form of behavior that animals can choose to adopt of their own accord—that is, changing their position before making a choice to see more information—distinct from the presented choice between available options. As noted by Wang and Hayden (2019), many studies mentioned above where monkeys might gain information also involve extensive training that could have reinforced this pattern of behavior, a point that echoes more general critiques of metacognitive uncertainty paradigms involving an ‘opt-out’ choice option (Carruthers, 2008; Jozefowicz, Staddon, & Cerutti, 2009; Le Pelley, 2012). To date, one study has explicitly tested how assessments of risk (or probabilistic variation in reward outcomes) impacts ape information-seeking in this way. In particular, three orangutans were presented with a task where they could seek out information about which of several possible containers covered a reward, by looking underneath a see-through table to see which container had the reward (Marsh & MacDonald, 2012b). In fact, the orangutans were more likely to look underneath when there were four possible containers that could contain the food item, compared to when there were only two, suggesting some sensitivity to risk or the overall likelihood that a particular container might hold the food treat.

As such, our goal in this study was to present chimpanzees with a risky choice task where they could independently decide to engage in the information-seeking response. Importantly, chimpanzees’ patterns of decision-making under risk have been well characterised in a variety of tasks (De Pettillo & Rosati, 2021). In many of these tasks, chimpanzees face a choice between a risky option that provides some probability of a good payoff versus a bad payoff, or can choose a safe option that provides a certain reward (Haun, Nawroth, & Call, 2011; Haux, Engelmann, Arslan, Hertweg, & Herrmann, 2022; Heilbronner, Rosati, Hare, & Hauser, 2008; Rosati & Hare, 2012, 2013; Rosati & Hare, 2016; Sánchez-Amaro, Tan, Kaufhold, Fernández-Navarro, & Rossano, 2021). That is, they can gamble on the possibility of receiving the good payoff, or play it safe by choosing a certain but less-preferred alternative. Here, we adapted that basic setup to examine if chimpanzees integrate their assessments of reward likelihood in a risky decision-making context with information-seeking behaviors to generate optimal responses.

In particular, we presented chimpanzees with a choice between a risky option (providing a preferred food 50% of the time but non-preferred food the other 50%) and a safe option (that always provided an intermediately preferred food). While in a typical risky choice task decision-makers do not know which reward outcome will be provided by the risky choice (by definition), here we additionally manipulated whether chimpanzees had seen the resolution of the risk outcome before making their choice by varying whether the risky option was baited using a visible versus hidden procedure similar to that used in Study 2’s identity trials. We then examined whether chimpanzees were more likely to engage in information-seeking specifically when they faced unresolved risk, in effect ‘cheating’ the risk paradigm by looking to see what reward it would provide before making their choice. We finally examined chimpanzees’ choice patterns to assess if they could use this information to behave optimally, by choosing either the risky or safe option on a trial-by-trial basis, depending on which option provided the best reward on that particular trial.

4.1. Participants

We tested six chimpanzees from Ngamba Island Chimpanzee Sanctuary (5 females, 1 male; mean age 15 years, age range: 12–19 years). These individuals all participated in Study 1 between 1 and 4 days earlier, and had passed our criterion of producing a looking response in at least 5 of the 10 *short look* trials in Study 1; note that these chimpanzees were a different sub-sample of chimpanzees than those who participated in Study 2. Two additional males also met the criteria in Study 1 and completed the initial introductory session in Study 3, but did not complete the subsequent test session (this was due to the social dynamics of the group, unrelated to the study). These individuals’ data

were not included in the final sample, including in the analyses of the introductory session.

4.2. Session overview

This study consisted of two sessions completed on two consecutive days (see Fig. 2 for a diagram of how animals progressed through the different trial types and studies). The initial introductory session started with trials to re-familiarize the chimpanzees to the basic information-seeking task (similar to those in Study 1 and 2), and then presented an introduction to the risky choice procedure as well as several risk comprehension controls to ensure chimpanzees understood the risk paradigm. The second session was the primary test session that we focused on in most analyses. This included additional introductory phases, and then was followed by the key trial types we focus on: (1) *risk visibility exposure trials* (where only the risky option was available, but which manipulated hidden versus visible baiting as in the choice trials), and (2) *risky choice trials*, in which animals choose between the risky and safe options and we varied whether the animals had seen the baiting of the risky option or not. As such, chimpanzees could engage in information-seeking on hidden baiting trials to ‘resolve’ the risk and discover the particular reward provided by the risky option on that trial, in order to make the most efficacious choice.

4.3. Procedures for introductory session

The initial session started with 6 additional *food preference* trials (two for each possible food combination). These were identical to those implemented in Study 1, except that two chimpanzees were tested with banana slices rather than grapes as the high value food (as they showed a weak preference for grapes in their original Study 1 session). This was followed by 6 *short look* trials that were identical to the procedure in Study 1, aimed at confirming these individuals continued to make information-seeking responses.

In the second half of the session, chimpanzees were then introduced to the basic risk paradigm, which emulated several prior studies (Rosati & Hare, 2011, 2012, 2013; Rosati & Hare, 2016). Here, apes chose between a safe option that always provided the intermediately preferred food, and a risky option that provided the highly preferred or the non-preferred food with 50% probability. In 8 initial *risk exposure* trials, only one container was available to choose on the table, in order to introduce the contingences of the risky option. The experimenter first showed the chimpanzee two potential outcomes in a risk outcome container: the preferred food (banana slice or grape, depending on the individual) and the non-preferred food (a cucumber slice). Then the experimenter reached into the risk outcome container, picked up one of the possible items in closed hand (so that the chimpanzee could not see which item she had picked up), and placed it in the container that the chimpanzee could choose (again by pulling the attached string, as in the prior studies). Chimpanzees experienced half of these trials with a good risk outcome (i.e., they received the preferred reward) and half with a bad risk outcome, with the order pseudo-randomized.

Chimpanzees next completed several control trials to ensure they understood the basic risk paradigm that would be implemented in the main test session. In 4 *visible risk control* trials they could choose between two containers, one which was the risky option (as described above for the risk exposure trials) and the other the safe option (a peanut). Here, the key factor was that both options were baited in view of the participant because the experimenter visibly held the food when placing it in the relevant choice container. The experimenter would show the chimpanzee both possible risky outcomes in the risk outcome container, but then would pick one up with an open hand (rather than a closed fist) so the chimpanzee could see which risk outcome was being baited on that trial. As such, chimpanzees should here choose the risky option if it provided the good risk outcome, but choose safe if the risk option provided the bad risk outcome on that trial, as a check that they were

tracking the baiting process and comparing available options.

Chimpanzees finally completed 4 *comprehension control* trials that manipulated which items were available from the risky and safe options, again to confirm that chimpanzees understood the logic of the procedure and made optimal responses when they could do so. Here chimpanzees always saw two identical pieces of the highly preferred food in the risk outcome container, and the experimenter placed one of them in the risky choice container using a closed fist. This was contrasted against a known alternative, which was either a single piece of the non-preferred food, or two pieces of the highly preferred food. If chimpanzees tracked this complicated baiting procedure, and understood that they would only receive one item from the risk outcome container despite seeing two items in it originally, they should choose the risky option when the alternative was nonpreferred, but chose the safe alternative when it provided two pieces of the preferred food.

4.4. Procedure for test session

The second session started with additional warm-ups: 2 *show food* versus *no food* trials (as in Study 1), 4 *short look* trials (as in Study 1), and then 8 *risk visibility exposure* trials. This final trial type was similar to the *risk exposure* trials in the introductory session, except that we also varied whether the baiting of the choice bowl was visible (where the risky outcome was transferred in an open hand, as in those original exposure trials) versus hidden (item transferred in a closed hand). This aimed to introduce this element of the procedure—the fact that the baiting of the risky option could be hidden or visible—for the primary risky choice trials that came after.

Finally, we presented the participants with 16 key *risky choice* trials. Here, participants chose between a risky option (that provided the highly preferred versus non-preferred outcomes with equal probability) and a safe option that always provided the intermediately preferred food. Here, we pseudo-randomly varied the *visibility* (visible or hidden) of the baiting from the risk outcome container; the safe option was always baited visibly as this is designed as a known outcome. Our key question was whether chimpanzees would selectively engage in information-seeking when the risky baiting was hidden (because they needed information to make the optimal choice), as well as whether they could flexibly shift between choosing the risky versus safe options depending on which provided the highest value option on that trial.

4.5. Coding and analyses

All sessions were video recorded, and looks, latencies, and choices were coded as in the prior studies. A second coder blind to study questions and hypotheses coded 20% of all sessions with high reliability (looks: Cohen's $\kappa = 0.98$; look latency: $r_p = 0.97$; choices: Cohen's $\kappa = 1.0$). As in the prior studies, we analyzed the test trial-by-trial binary looking and choice behavior with GLMMs. To account for repeated measures, base models included a random intercept for *subject identity* as well as the effects of *age*, *sex* and test *trial number* (1–16). To investigate whether participants looked more often when the baiting was hidden versus visible, we then added the *baiting visibility* of the risk outcome as a factor. We used LMMs to analyze latencies using a similar procedure, as in the prior studies. To assess participants' choices, we again compared performance to chance, assessing whether animals made optimal choices on that trial as described in more detail below.

4.6. Results and discussion

We first examined performance in the first introductory and control trials to ensure chimpanzees understood the various components of the task. In the *food preference* test, the chimpanzees chose the highly preferred food over the non-preferred food 100% of the time, chose the highly preferred food over the intermediate food on mean = $83.3 \pm SE = 10.5\%$ of trials, and chose the intermediate food over non-preferred food

100% of the time. This indicates that animals had appropriate food preferences for the subsequent risk task. In the *short look* trials, the subjects produced a look on an average of $86.1\% \pm 5.1\%$ of trials in the introductory session, and on $91.7 \pm 8.3\%$ of these trials in the test session. After looking, participants always made a correct choice, but they performed at chance when they did not look before choosing in both sessions. This aligns with the patterns from Studies 1 and 2. We then checked performance on the control trials to confirm that the chimpanzees understood the risky choice procedure. Chimpanzees chose the correct (value-maximizing) option across $83.3 \pm 5.3\%$ of the *visible risk control* trials [$t_5 = 6.32$, $p < 0.005$], and on $95.8 \pm 4.2\%$ of the *comprehension control* trials [$t_5 = 11.00$, $p < 0.0005$], indicating that chimpanzees understood the risk task setup, and could make optimal choices in these contexts.

We then examined performance in the primary test session. The key question for this session was performance on the *risky choice* trials, where chimpanzees had to choose between the risky and safe option, and we varied across trials whether the risky baiting was visible. We first examined propensity to look on these test trials. Chimpanzees looked on mean = $64.6\% \pm SE = 15.6\%$ of trials when baiting was hidden, compared to $54.2\% \pm 13.6\%$ when it was visible (see Fig. 5a). In the base GLMM model accounting for *age*, *sex*, and *trial number*, we found a decline in overall looking with increasing age. However, including *baiting visibility* in a second model did not significantly improve model fit [$\chi^2 = 1.72$, $df = 1$, $p = 0.19$, n.s.; see Table S6 for model parameters], indicating there was no difference in overall propensity to look. Rather, chimpanzees seemed to show fairly high rates of looking across both the hidden and visible baiting contexts. However, there was a difference in latency to produce these looks across conditions. In fact, chimpanzees looked after an average of 4.9 ± 1.9 s when the baiting had been hidden, but after 8.2 ± 1.9 s when it was visible (see Fig. 5b). LMM analyses of latencies took a similar approach as for choices. The base model included *age*, *sex*, and *trial number*, and the inclusion of *baiting visibility* in a second model improved fit [$\chi^2 = 8.71$, $df = 1$, $p = 0.003$; see Table S7 for model parameters]: individuals looked more quickly when the baiting procedure was hidden compared to when it was visible. This result also held when excluding the 7 trials in this study with a latency of 0 s [$\chi^2 = 6.77$, $df = 1$, $p = 0.009$]. This shows that while chimpanzees had a generally high propensity to look on these (fairly complicated) risk trials, they did so more quickly on those trials where they actually needed the information to make an optimal choice, compared to trials with visible baiting.

As a further check of whether chimpanzees distinguished between the hidden and visible baiting in the risk task, we then examined their looking responses on the *risk visibility exposure trials* that immediately preceded the primary choice trials. These involved the same basic procedure as the risky choice trials, except that only the risky option was available (e.g., there was no safe alternative). As such, while looking was not necessary to make a 'correct' choice, it could allow the chimpanzee to discern if the container had been baited with the high versus low value food prior to pulling the container. In fact, chimpanzees produced a looking response on mean = $62.5\% \pm SE = 15.5\%$ of hidden baiting trials, but only $37.5\% \pm 15.5\%$ of visibly baited trials (see Fig. 5c). We analyzed this using the same approach as for the risky choice trials and found that inclusion of *baiting visibility* in a second model improved fit [$\chi^2 = 5.37$, $df = 1$, $p = 0.02$; see Table S8 for model parameters]: individuals looked more on these trials when the baiting procedure was hidden compared to when it was visible. Overall, this provides converging evidence that the chimpanzees did discriminate the hidden and visible baiting contexts concerning the risky option.

We finally examined the chimpanzees' choice patterns in the risk task. Given our question about whether chimpanzees could use information-seeking to 'resolve' risk, we examined correct choices in terms of the likelihood that the chimpanzee chose the option providing the best available outcome on that trial. The correct option was therefore defined as the risky option on those trials where it provided the

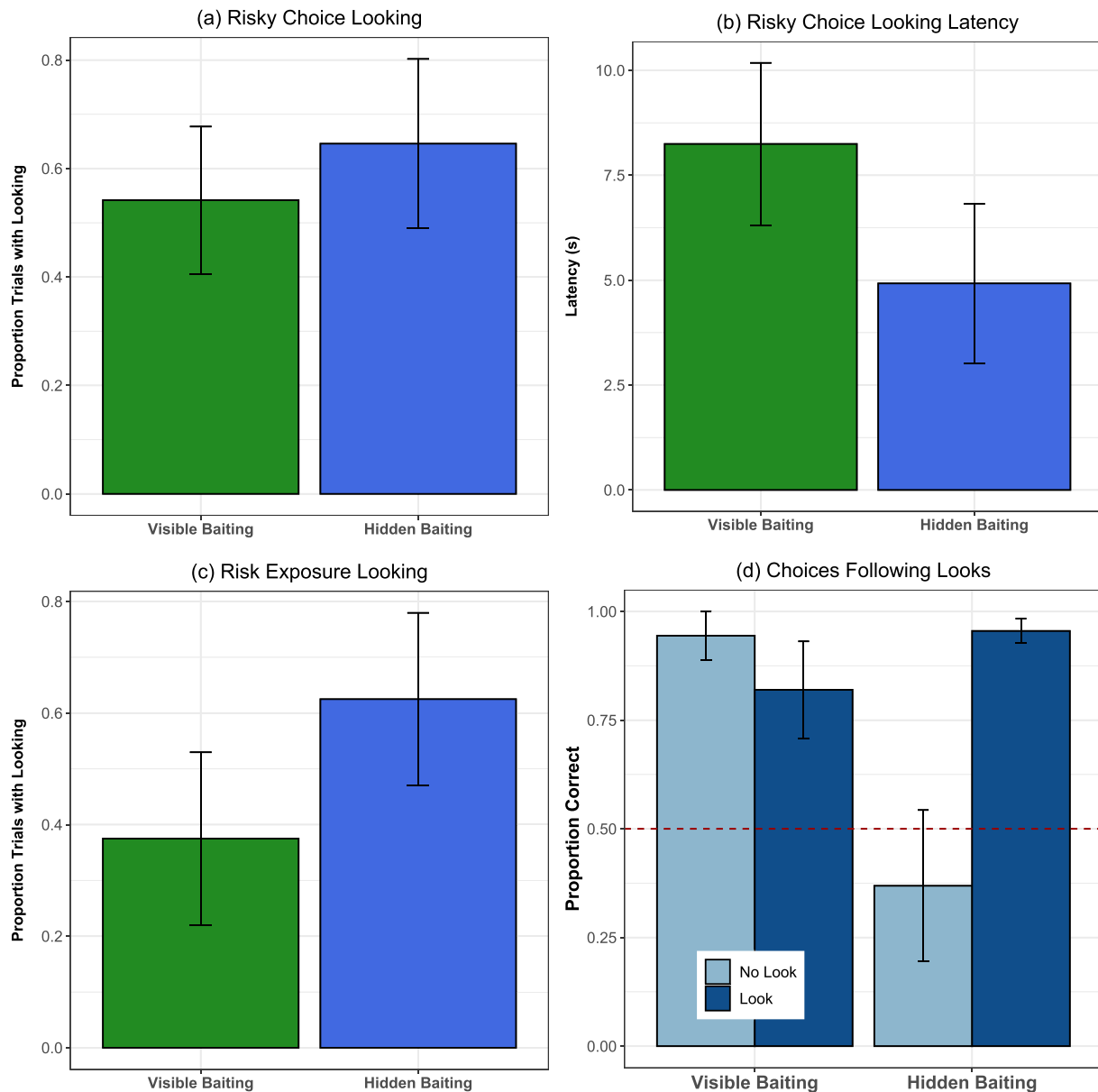


Fig. 5. Looking and choice patterns in response to risky outcomes in Study 3. On *risky choice* trials, chimpanzees showed (a) a similar propensity to look across baiting conditions, but (b) they were faster to look after hidden compared to visible baiting of risky outcomes. (c) On *risk visibility exposure* trials, which were identical to risky choice trials except that only the risky option was available, chimpanzees produced more looks following hidden baiting. (d) Chimpanzees selected the correct option on *risky choice* trials (that is, the option that provided the optimal reward on that trial, which depended on the risky outcome) at high rates when baiting was visible regardless of whether they looked, and when they looked after hidden baiting, but chose at chance if they did not see the baiting and did not produce a look. Error bars indicate SE, and dashed line indicates chance.

good food outcome, but the safe option when the risky alternative provided the bad food outcome. As expected, chimpanzees chose above chance in trials with visible baiting, regardless of whether they looked or not [overall correct choice: $89.6 \pm 6.8\%$; $t_5 = 5.83$, $p < 0.005$]. They also selected the correct option on hidden baiting trials when they looked [$95.5 \pm 2.8\%$ correct; $t_5 = 16.07$, $p < 0.0001$], but they were at chance on hidden trials when they did not look [$36.9 \pm 1.7\%$ correct; $t_3 = -0.75$, $p = 0.51$, n.s.; see Fig. 5d]. That is, chimpanzees produced optimal responses when they either saw the baiting, or produced a look when they did not see the baiting, and thus knew whether the risky versus safe option provided the best outcome. Conversely, if the baiting was hidden and they did not look, they chose similarly between the risky and safe options.

The results from Study 3 provide evidence for two main conclusions. First, patterns of looking show that chimpanzees look more quickly on

trials where the outcome of the risky option was not known in advance. In the main *risky choice* trials, they showed high rates of looking regardless of whether the risky baiting was visible (that is, they also produced unnecessary looks), but they were faster to produce this response on the hidden trials where it was necessary to make an optimal response. Performance on the test session's *risk visibility exposure* trials (which were less complex as there was only one option) also shows that chimpanzees distinguished these situations, as they produced more looking responses after hidden baiting. This also aligns with the results from Study 2 showing that animals will engage in information-seeking to ascertain the identity of a reward. In this case, such looking was not necessary to select an option (as only one was ever available), but could reveal the contents of the container before the chimpanzee chose to pull it. Finally, these results show that chimpanzees can flexibly integrate these various sources of information to resolve risk and act optimally.

Here, chimpanzees had to integrate assessments of reward probability to decide whether to look, and then produce an optimal response—either choosing the risky versus the safe alternative on a trial-by-trial basis depending on which outcome the risky option provided.

5. General discussion

Across three studies, we examined patterns of flexible information-seeking and metacognitive inference in chimpanzees. First, in Study 1 we adapted the basic premise of prior work where animals could bend down to peer into tubes or under cups (Call, 2010; Call & Carpenter, 2001; Marsh & MacDonald, 2012b; Rosati & Santos, 2016), here with a modified setup where animals could stand up to look into containers from the top and access those containers by pulling a string. We used this setup to examine spontaneous information-seeking responses, and tested a large sample of chimpanzees spanning the late juvenile and adult periods. We found that a majority of chimpanzees would spontaneously change their position to look into containers on their first experience with this problem, showing that chimpanzees can discover metacognitive solutions to problems in the absence of training or experience. However, there were also clear individual differences: younger chimpanzees and females were more likely to engage in information-seeking. In subsequent studies we further tested individuals who showed these information-seeking responses in order to disentangle how they used these skills. In Study 2, we found that chimpanzees were similarly proficient at engaging in information-seeking both to obtain new information about the location of a reward and about the identity of rewards, suggesting that these skills can generalize to some degree across different contexts. Finally, in Study 3, we examined whether a smaller subset of chimpanzees could use information-seeking to resolve risk in a dynamic trial-by-trial fashion. We found that while chimpanzees produced looks at similar rates for both hidden versus visible baiting conditions in this complex context, they were faster to do so when this information was needed, and they could also use this information to make optimal choices. Performance on the simpler risk exposure trials further showed that they did distinguish between hidden and visible baiting of the risky option. Across all three studies, additional checks showed that chimpanzees needed to engage in information-seeking to effectively solve these problems when baiting events were hidden, as they choose randomly when they did not information-seek. Taken together, these results show that several core features of flexible information-seeking in humans are shared with chimpanzees.

Our findings build on and extend evidence that some aspects of human-like metacognition are shared with other animals. One previous line of work on animal metacognition has focused on uncertainty monitoring where animals can choose to ‘opt-out’ of a perceptual or memory judgement when it is too difficult. This work has found that several species will make opt-out responses (Castro & Wasserman, 2013; Foote & Crystal, 2012; Hampton, 2001; Kornell et al., 2007; Shields et al., 1997; Smith et al., 1995; Smith et al., 1997; Smith et al., 1998). However, this approach has also been critiqued as these tasks often involve extensive training and responses may reflect reinforcement of the opt-out response rather than inference about one’s own knowledge or ignorance (Carruthers, 2008; Jozefowicz et al., 2009; Le Pelley, 2012). Other work has used information-seeking paradigms that generally do not involve such extensive training and found that at least some species will change their visual perspective on a problem to locate hidden food (Basile et al., 2009; Beran et al., 2013; Bräuer et al., 2004; Call, 2010; Call & Carpenter, 2001; Hampton et al., 2004; Marsh & MacDonald, 2012b; McMahon et al., 2010; Paukner et al., 2006; Roberts et al., 2012; Rosati & Santos, 2016). However, this work has also been critiqued as possibly reflecting a more general pattern of exploratory searching behavior whenever animals do not know the location of food, rather than reflecting metacognitive inferences per se (as described by Carruthers, 2008; Marsh, 2014; Marsh & MacDonald, 2012a). Our work addresses these points by (1) examining information-seeking in the

absence of training or prior experience in Study 1; and (2) assessing how these skills generalize to contexts where the specific location of rewards is known, but rather their identity (or the likelihood of a given outcome) is not known in Studies 2 and 3. Regarding point one, we found that a majority of the chimpanzees in Study 1 (72%) could intuit how to solve a novel problem by changing their position on their first trial, without any prior experience with doing so. Regarding point two, we found that chimpanzees consistently engaged in information-seeking for the identity of rewards in Study 2, at a rate similar to information-seeking for location information. They also engaged in information-seeking to resolve risk about the quality of the provided reward when the location was already known in Study 3—including when this was not necessary to select the correct option but only to know its contents in advance, as in the risk visibility exposure trials. Together, the results from these three studies provide converging evidence from past work (Beran et al., 2013; Call & Carpenter, 2001; Marsh & MacDonald, 2012a; Perdue et al., 2018) that animals are not simply engaging in simple generalized search heuristics when they do not know where food is located, and further shows that many individuals can discover such an information-seeking strategy without prior experience.

Along these lines, another key aspect of our work examined how information-seeking could be applied to decision-making under uncertainty. In the real world, decision-makers often face situations with incomplete knowledge, such as where the specific outcome of a decision is probabilistic or ambiguous (Dall et al., 2005; Schmidt, Dall, & Van Gils, 2010). Understanding how animals respond to such situations is thus important both from a psychological perspective—what cognitive mechanisms do different species use when faced with uncertainty?—but also an evolutionary perspective—what functional role do different cognitive skills play in important behavioral contexts? It is clear that many animals can detect uncertainty, and apes in particular show sensitivity to both probabilistic variation and ambiguity in payoffs in experiments (De Petrillo & Rosati, 2021; Haun et al., 2011; Haux et al., 2022; Rosati & Hare, 2011; Rosati & Hare, 2016; Santos & Rosati, 2015). They also engage in a variety of risk-sensitive behaviors in the wild that involve uncertain outcomes, including decisions about when to hunt moneys or go on territorial boundary patrols (Gilby & Wrangham, 2007; Mitani & Watts, 2005)—suggesting that an ability to assess risk is crucial for particular behaviors this species naturally exhibits. While one way to deal with uncertainty is to avoid it, another way is to seek out new information to reduce it. That is, if individuals can both make metacognitive distinctions about when they lack knowledge, and figure out how to act to increase their knowledge, they can act more effectively when faced with uncertainty. For example some observational evidence suggests chimpanzees use hills as elevated viewpoints to assess the number of chimpanzees present in neighboring territories before deciding to engage in a boundary patrol (Lemoine, Samuni, Crockford, & Wittig, 2023). Study 3 provides experimental evidence that chimpanzees can use information-seeking to resolve economic uncertainty in a similar way, building on prior work in orangutans using a different approach (Marsh & MacDonald, 2012b). In our study, we implemented a risky choice task where individuals could choose directly between a risky and safe option and manipulated whether chimpanzees could see the outcome of the risky option before choosing (such that it no longer presented a true risk on that trial), or did not see this as in prior studies of risky choice in chimpanzees (De Petrillo and Rosati, 2021). In contrast to those prior studies, however, here animals could decide to engage in information-seeking before making a choice in order to resolve the risk.

We found that our risky choice task presented a challenging problem for the chimpanzees, as they also used an information-seeking strategy when it was not strictly necessary on visible baiting trials, rather than selectively deploying it only when the baiting outcome had been hidden. This difficulty might have also been related to the fact that the baiting procedure changed trial-by-trial, thus requiring chimpanzees to attend to this in a dynamic fashion. Aligning with this interpretation, chimpanzees were faster to look when the baiting was hidden, showing that

they did distinguish between situations where they were knowledgeable versus ignorant of the risky option's outcome. Our analysis of risk visibility exposure trials further indicates that animals engaged in more information-seeking when the outcome of the risky option was unknown. While information-seeking was not necessary to make a correct choice on these trials (as only the risky option was available to choose), this again shows that chimpanzees distinguished these situations, and aligns with the idea that they engaged in more seemingly unnecessary information-seeking in the choice trials because of their greater procedural complexity. One possibility is that the unnecessary looks on trials with visible baiting reflect a 'passport effect' (Call, 2010; Call & Carpenter, 2001): checking that you have your passport before travel, even though you know you have already packed it. The logic of this is that while such double-checking may seem unnecessary or even illogical, the cost of forgetting your passport is high whereas the cost of checking again is low. As a consequence, chimpanzees may have defaulted to engage in more information-seeking than was strictly necessary because doing so was less costly than accidentally making an incorrect choice; this may have further been easier to implement as a simple rule that held across the dynamically varying risky choice trials. One way to test this further would be to directly manipulate the costs of looking, such as by requiring a more energetically costly body movement than standing up, to see if this reduced such 'unnecessary' looking responses. In addition, there is evidence that the imposition of longer delays may increase engagement of metacognitive processes because individuals may forget (or be concerned they forgot) what they previously observed (Call & Carpenter, 2001; Fujita, 2009; Goupil, Romand-Monnier, & Kouider, 2016; Hampton, 2001). Thus, another relevant test would be to manipulate the delays before the chimpanzees can choose, in which case longer delays should increase looking responses compared to shorter delays.

Another consideration for these results relates to an emerging set of findings on the evolution of curiosity—that is, valuing information for its own sake (Gottlieb, Oudeye, Lopes, & Baranes, 2013; Loewenstein, 1994). Across our three studies, we consistently found that chimpanzees were more likely to engage in information-seeking when it was necessary to solve a problem (that is, obtaining the information had a functional consequence) compared to when it was not needed—for example, chimpanzees looked more on the test trials in Study 1 compared to the initial introductory trials, and generally looked more (or more quickly) on trials with hidden baiting in Studies 2 and 3 where the chimpanzees lacked some important information to make a correct choice. Yet in Study 3, we also found that chimpanzees were sometimes willing to pay some small energetic cost to look into the containers even when they did not strictly need to do so to make an efficacious choice, such as in the risk visibility exposure trials (where there was only one option available to choose). One possibility is that the chimpanzees were intrinsically motivated to find out the outcome of the risky gamble, even though it had no direct consequence for their subsequent choice behavior. In fact, there is accumulating evidence that animals and young children may value information for its own sake, at least in some contexts, and further that such curiosity may underpin metacognitive information-seeking (Forss et al., 2024; Goupil & Proust, 2023; Kidd & Hayden, 2015). Thus, an important question for future work is whether the chimpanzees' responses here reflect 'errors' of action selection, versus actual valuation of information for its own sake.

Our approach also allowed us to test the responses of a large population of semi-free-ranging chimpanzees varying in age and sex. Study 1 was purposefully designed to involve no training, but rather assess spontaneous attempts at information-seeking without prior experience. We then harnessed the large sample size of chimpanzees available in African sanctuaries to test the responses of 47 individuals on this task. We found clear age differences in information-seeking: younger chimpanzees were more likely to engage in this response than older chimpanzees. In terms of developmental change, these age effects were opposite from our predictions as humans tend to show improvements, not

decrements, in metacognition with age (e.g. Kuhn, 2000; Roebbers, 2017; Schneider, 2008; Veenman et al., 2004). One important aspect of our study is that the youngest chimpanzees were already juveniles, so we might find developmental improvements in metacognition if we examined younger infants. Indeed, there are clear aging-related declines in human metacognition, with some larger comparisons suggesting that metacognitive skills show an inverted-U shaped profile (Hertzog & Dunlosky, 2004; McWilliams, Bibby, David, & Fleming, 2023; Palmer, David, & Fleming, 2014). Yet it is important to note that many human studies typically assess how individuals apply a particular metacognitive response to different tasks, whereas we rather assessed if chimpanzees could in some sense 'intuit' a metacognitive solution to a problem. That is, Study 1 assessed individual variation in propensity to invent a novel information-seeking response. One possibility is then that this more 'spontaneous' measure of metacognition, in contrast to many typical human studies, more strongly reflects developmental differences in curiosity. Juvenile primates in general are well known to show high levels of curious and exploratory behaviors, a pattern that also holds specifically in humans (Kidd & Hayden, 2015; Liquin & Gopnik, 2022; Pereira & Fairbanks, 1993). Some forms of exploration even peak in adolescence (Pelz & Kidd, 2020) more like the current patterns with chimpanzees. As such, one important question concerns whether chimpanzees exhibit similar age-related differences when they are already proficient in executing an information-seeking response. For example, we found little individual variation in responses in Studies 2 and 3, where we tested chimpanzees that had already demonstrated proficiency with information-seeking in Study 1 (but note that these studies had smaller sample sizes than Study 1). Conversely, studies of 'spontaneous' information-seeking in humans could address if both humans and other primates show similar shifts in their propensity to intuit metacognitive solutions to novel problems.

We also found clear sex differences in information-seeking: females in Study 1 were more likely to engage in information-seeking than males, and the decline in information-seeking with age was generally less pronounced in females. This was also surprising as there is currently little evidence for sex differences in chimpanzee cognition. For example, when a large sample of chimpanzees were tested on a large battery of different cognitive tasks, males and females differed on only a small minority of the tasks (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007). However, there are some notable exceptions that might be illustrative for the current results. First, some evidence suggests that males may be slightly more risk-seeking but also more ambiguity-averse than females (Haux et al., 2022), which also mirrors patterns of behavior in the wild showing that males are more likely to engage in risky boundary patrol and hunting behaviors (Gilby et al., 2017; Massaro et al., 2022). This might bear on their responses to problems when the location of food is unknown (but note that there is little evidence for sex differences in primate decision-making more generally; De Petrillo & Rosati, 2021). Second, female chimpanzees are more successful than males in a reversal learning task assessing aspects of executive functioning (Cantwell, Buckholtz, Atencia, & Rosati, 2022), a difference that may be linked to sex differences in foraging behaviors whereby wild female chimpanzees engage in more effortful tool use behaviors (Boesch & Boesch, 1981; Lonsdorf, 2005) that require this kind of control. Thus, it might be that implementing information-seeking responses requires some related processes of cognitive control—in Study 1 animals could not respond in the typical fashion (by pulling the container strings) but rather had to conceive of a new solution (standing up). An alternative possibility is that this difference did not reflect individual variation in metacognitive processes, but rather individual variation in the perceived benefits or physical costs of engaging in this action. We note that all chimpanzees in these studies participated in numerous trials where they produced an action (e.g., pulling one of the containers) to receive a food reward, as this was common of all trials, suggesting that all of the tested chimpanzees were interested and motivated to obtain these treats. However, we cannot

exclude the possibility that standing up is more energetically costly for larger chimpanzees (e.g., often those who are male or adults), such that their responses here reflect a physical constraint rather than differences in cognition or problem-solving proclivities. We think this alternative is unlikely given that standing and climbing are routine aspects of chimpanzees' behavioral repertoires. Nonetheless, it is possible that the cost/benefit tradeoff of standing up for rewards in this task were different for some individuals, and so testing a larger sample of chimpanzees on a variety of metacognitive tasks that involve different kinds of (physical) responses could disentangle this possibility.

A final important direction for future work concerns investigating how social contexts and social cognition intersect with metacognition in animals. In some theoretical views, metacognitive capacities for thinking about one's own knowledge states are conceptually inter-related—or even identical to—the ability to think about the knowledge states of other individuals (e.g., Carruthers, 2008; Flavell, 1999; Frith, 2012; Heyes et al., 2020; Kuhn, 2000; Premack & Woodruff, 1978; Shea et al., 2014; Tomasello, 2023). For example, some proposals posit that metacognition depends on cultural learning and that there are distinct metacognitive representations for individualistic versus shared, group-level behaviors (Heyes et al., 2020; Shea et al., 2014). Similarly, some perspectives on animal curiosity and exploration also posit a key role for social context in modulating these behaviors (Forss & Willems, 2022). Yet it is striking how the vast majority of work on animal metacognition does not assess how social information and metacognition interact. Along these lines, all of our tasks here involve forms of non-social problem solving, specifically information-seeking in a foraging context. One notable exception is recent work examining metacognition in apes and human children in two situations: when individual must reconcile conflicting nonsocial information (e.g., the same object looks different from different perspectives) versus conflicting social information (another individual as a different judgement than oneself; O'Madagain et al., 2022). In fact, while human children were similarly able to integrate both kinds of conflicting information and engaged in information-seeking when needed for both social and non-social uncertainty, apes only did so for nonsocial uncertainty, suggesting that this might be a context where animal metacognition is specifically constrained. More generally, given that humans metacognitive skills can be applied to a variety of social interactions and problems (Fischer & Said, 2021; Frith, 2012; Heyes et al., 2020; Huang & Yang, 2020; Isaacson & Fujita, 2006; Ohtani & Hisasaka, 2018; Rollwage et al., 2018), understanding the breadth and limits of animal metacognition requires tests of this domain. Disentangling whether nonhumans do share both social and nonsocial mechanisms for metacognition is a critical next step in illuminating the evolution of human-like cognition.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cognition.2024.105898>.

CRediT authorship contribution statement

Alexandra G. Rosati: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Elisa Felsche:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Megan F. Cole:** Writing – review & editing, Methodology, Investigation, Data curation. **Rebeca Atencia:** Writing – review & editing, Resources. **Joshua Rukundo:** Writing – review & editing, Resources.

Data availability

The data from these studies are publically available in Dryad Data Repository at: <https://doi.org/10.5061/dryad.hqbzkh1rn>

Acknowledgements

We thank Megan Mulhinch for assistance with coding. At Ngamba, we thank Dr. Titus Mukungu, the chimpanzee caretakers, the Ugandan Wildlife Authority, and the Ugandan National Council for Science and Technology for supporting our work. At Tchimpounga, we thank Sofia Fernandez-Navarro, the chimpanzee caretakers, Jane Goodall Institute USA, and the Congolese Ministry of Research for supporting our work. This research was supported by NSF grants 1944881 and 1926653; NIH grants R01AG049395 and R37AG049395; and Sloan Foundation Fellowship FG-2019-12054.

References

- Bandini, E., Motes-Rodrigo, A., Archer, W., Minchin, T., Axelsen, H., Hernandez-Aguilar, R. A., ... Tennie, C. (2021). *Naïve, unenculturated chimpanzees fail to make and use flaked stone tools*. Open Research Europe.
- Basile, B. M., Hampton, R. R., Suomi, S. J., & Murray, E. A. (2009). An assessment of memory awareness in tufted capuchin monkeys (*Cebus paella*). *Animal Cognition*, *12*, 169–180.
- Bates, D. (2010). The LME4 Package: Linear Mixed-effects Models Using S4 Classes. See <http://www.R-project.org>.
- Beran, M. J., Perdue, B. M., Bramlett, J. L., & Menzel, C. R. (2012). Prospective memory in a language-trained chimpanzee (*Pan troglodytes*). *Learning and Motivation*, *43*, 192–199.
- Beran, M. J., Perdue, B. M., Futch, S. E., Smith, J. D., Evans, T. A., & Parrish, A. E. (2015). Go when you know: Chimpanzees' confidence movements reflect their responses in a computerized memory task. *Cognition*, *142*, 236–246.
- Beran, M. J., Smith, J. D., & Perdue, B. M. (2013). Language-trained chimpanzees (*Pan troglodytes*) name what they have seen but look first at what they have not seen. *Psychological Science*, *24*, 660–666.
- Bergman, T. J., & Beehner, J. C. (2023). Information ecology: An integrative framework for studying animal behavior. *Trends in Ecology and Evolution*, *38*, 1041–1050.
- Bianchi, S., Stimpson, C. D., Duka, T., Larsen, M. D., Janssen, W. G. M., Collins, Z., ... Sherwood, C. C. (2013). Synaptogenesis and development of pyramidal neuron dendritic morphology in the chimpanzee neocortex resembles humans. *Proceedings of the National Academy of Sciences*, *110*(Supplement 2), 10395–10401.
- Blanchard, T. C., Hayden, B. Y., & Bromberg-Martin, E. S. (2015). Orbitofrontal cortex uses distinct codes for different choice attributes in decisions motivated by curiosity. *Neuron*, *85*, 602–614.
- Boesch, C., & Boesch, H. (1981). Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report. *Journal of Human Evolution*, *10*, 585–593.
- Bohn, M., Allritz, M., Call, J., & Voelter, C. (2017). Information seeking about tool properties in great apes. *Scientific Reports*, *7*, 10923.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M., ... White, J. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135.
- Bräuer, J., Call, J., & Tomasello, M. (2004). Visual perspective taking in dogs (*Canis familiaris*) in the presence of barriers. *Applied Animal Behaviour Science*, *88*, 299–317.
- Brinck, I., & Liljenfors, R. (2013). The developmental origin of metacognition. *Infant and Child Development*, *22*, 85–101.
- Bromberg-Martin, E. S., & Hikosaka, O. (2009). Midbrain dopamine neurons signal preference for advance information about upcoming rewards. *Neuron*, *63*(119–126).
- Bromberg-Martin, E. S., & Hikosaka, O. (2011). Lateral habenula neurons signal errors in the prediction of reward information. *Nature Neuroscience*, *14*, 1209–1216.
- Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science*, *10*, F31–F38.
- Call, J. (2010). Do apes know that they could be wrong? *Animal Cognition*, *13*, 689–700.
- Call, J., & Carpenter, M. (2001). Do apes and children know what they have seen? *Animal Cognition*, *3*, 207–220.
- Cantwell, A., Buckholtz, J. W., Atencia, R., & Rosati, A. G. (2022). The origins of cognitive flexibility in chimpanzees. *Developmental Science*, *25*, Article e13266.
- Carpenter, M., & Tomasello, M. (1995). Joint attention and imitative learning in children, chimpanzees, and enculturated chimpanzees. *Social Development*, *4*, 217–237.
- Carruthers, P. (2008). Meta-cognition in animals: A skeptical look. *Mind & Language*, *23*, 58–89.
- Carruthers, P., & Williams, D. M. (2019). Comparative metacognition. *Animal Behavior and Cognition*, *6*, 278–288.
- Castro, L., & Wasserman, E. A. (2013). Information-seeking behavior: Exploring metacognitive control in pigeons. *Animal Cognition*, *16*, 241–254.
- Charvet, C. J. (2021). Cutting across structural and transcriptomic scales translates time across the lifespan in humans and chimpanzees. *Proceedings B*, *288*, 20202987.
- Clark, I., & Dumas, G. (2016). He regulation of task performance: A trans-disciplinary review. *Frontiers in Psychology*, *6*, 1862.
- Cole, M. F., Cantwell, A., Rukundo, J., Ajarova, L., Fernandez-Navarro, S., Atencia, R., & Rosati, A. G. (2020). Healthy cardiovascular biomarkers across the lifespan in wild-born chimpanzees (*Pan troglodytes*). *Philosophical Transactions of the Royal Society B*, *375*, 20190609.
- Crystal, J. D., & Foote, A. L. (2011). Evaluating information-seeking approaches to metacognition. *Current Zoology*, *57*, 531–542.

- Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, *20*, P187–P193.
- De Petrillo, F., & Rosati, A. G. (2021). Variation in primate decision-making under uncertainty and the roots of human economic behaviour. *Philosophical Transactions of the Royal Society B*, *376*, 20190671.
- Dunay, E., Owens, L. A., Dunn, C. D., Rukundo, J., Atencia, R., Cole, M. F., ... Goldberg, T. L. (2023). Viruses in sanctuary chimpanzees across Africa. *American Journal of Primatology*, *85*, e23452.
- Dunstone, J., & Caldwell, C. A. (2018). Cumulative culture and explicit metacognition: A review of theories, evidence and key predictions. *Palgrave Communications*, *4*, 1–11.
- Emery Thompson, M., & Sabbi, K. (2024). Evolutionary demography of the great apes. In O. Burger, R. Lee, & R. Sear (Eds.), *Human Evolutionary Demography*.
- Ferrigno, S., Kornell, N., & Cantlon, J. F. (2017). A metacognitive illusion in monkeys. *Proceedings of the Royal Society B*, *284*, 20171541.
- Fischer, H., & Said, N. (2021). Importance of domain-specific metacognition for explaining beliefs about politicized science: The case of climate change. *Cognition*, *208*, Article 104545.
- Flavell, J. H. (1999). Cognitive development: Children's knowledge about the mind. *Annual Review of Psychology*, *50*, 21–45.
- Foote, A. L., & Crystal, J. D. (2012). "Play it again": A new method for testing metacognition in animals. *Animal Cognition*, *15*, 187–199.
- Forss, S., Ciria, A., Clark, F., Galusca, C., Harrison, D., & Lee, S. (2024). A transdisciplinary view on curiosity beyond linguistic humans: Animals, infants, and artificial intelligence. *Biological Reviews*, *99*, 979–998.
- Forss, S., & Willems, E. (2022). The curious case of great ape curiosity and how it is shaped by sociality. *Ethology*, *128*, 552–563.
- Frith, C. D. (2012). The role of metacognition in human social interactions. *Philosophical Transactions of the Royal Society B*, *367*, 2213–2223.
- Fujita, K. (2009). Metamemory in tufted capuchin monkeys (*Cebus apella*). *Animal Cognition*, *12*, 575–585.
- Ghetti, S., Hembacher, E., & Coughlin, C. A. (2013). Feeling uncertain and acting on it during the preschool years: A metacognitive approach. *Child Development Perspectives*, *7*, 160–165.
- Gilby, I. C., Machanda, Z. P., O'Malley, R. C., Murray, C. M., Lonsdorf, E. V., Walker, K., ... Wrangham, R. W. (2017). Predation by female chimpanzees: Toward an understanding of sex differences in meat acquisition in the last common ancestor of Pan and Homo. *Journal of Human Evolution*, *110*, 82–94.
- Gilby, I. C., & Wrangham, R. W. (2007). Risk-prone hunting by chimpanzees (Pan troglodytes schweinfurthii) increases during periods of high diet quality. *Behavioral Ecology and Sociobiology*, *61*, 1771–1779.
- Gottlieb, J., Oudey, P. Y., Lopes, M., & Baranes, A. (2013). Information-seeking, curiosity, and attention: Computational and neural mechanisms. *Trends in Cognitive Sciences*, *17*, 585–593.
- Goupil, L., & Kouider, S. (2016). Behavioral and neural indices of metacognitive sensitivity in preverbal infants. *Current Biology*, *26*, 3028–3045.
- Goupil, L., & Kouider, S. (2019). Developing a reflective mind: From core metacognition to explicit self-reflection. *Current Directions in Psychological Science*, *28*, 403–408.
- Goupil, L., & Proust, J. (2023). Curiosity as metacognitive feeling. *Cognition*, *231*, Article 105235.
- Goupil, L., Romand-Monnier, M., & Kouider, S. (2016). Infants ask for help when they know they don't know. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 3492–3496.
- Hampton, R., Zivin, A., & Murray, E. (2004). Rhesus monkeys (*Macaca mulatta*) discriminate between knowing and not knowing and collect information as needed before acting. *Animal Cognition*, *7*, 239–246.
- Hampton, R. R. (2001). Rhesus monkeys know when they remember. *Proceedings of the National Academy of Sciences*, *98*, 5359–5362.
- Hampton, R. R. (2009). Multiple demonstrations of metacognition in nonhumans: Converging evidence or multiple mechanisms? *Comparative Cognition and Behavior Reviews*, *4*, 17.
- Hampton, R. R. (2019). Monkey metacognition could generate more insight. *Animal Behavior and Cognition*, *6*, 230–235.
- Haun, D. B. M., Nawroth, C., & Call, J. (2011). Great apes' risk-taking strategies in a decision making task. *PLoS One*, *6*, Article e28801.
- Haux, L. M., Engelmann, J. M., Arslan, R. C., Hertwig, R., & Herrmann, E. (2022). Chimpanzees and human risk preferences show key similarities. *Psychological Science*, *34*, 358–369.
- Hayden, B. Y., Heilbronner, S. H., & Platt, M. L. (2010). Ambiguity aversion in rhesus macaques. *Frontiers in Neuroscience*, *4*, 166.
- Heilbronner, S. H., Rosati, A. G., Hare, B., & Hauser, M. D. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters*, *4*, 246–249.
- Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, *317*, 1360–1366.
- Hertzog, C., & Dunlosky, J. (2004). Aging, metacognition, and cognitive control. *The Psychology of Learning and Motivation Advances in Research and Theory*, *45*, 215–251.
- Heyes, C., Bang, D., Shea, N., Frith, C. D., & Fleming, S. M. S. (2020). Knowing ourselves together: The cultural origins of metacognition. *Trends in Cognitive Sciences*, *24*, 349–362.
- Huang, Y., & Yang, C. (2020). A metacognitive approach to reconsidering risk perceptions and uncertainty: Understand information seeking during COVID-19. *Science Communication*, *42*, 616–642.
- Isaacson, R. M., & Fujita, F. (2006). Metacognitive knowledge monitoring and self-regulated learning: Academic success and reflections on learning. *Journal of the Scholarship of Teaching and Learning*, *6*, 39–55.
- Iwasaki, S., Kuroshima, H., & Fujita, K. (2019). Pigeons show metamemory by requesting reduced working memory loads. *Animal Behavior and Cognition*, *6*, 247–253.
- Jozefowicz, J., Staddon, J. E. R., & Cerutti, D. T. (2009). Metacognition in animals: How do we know that they know? *Comparative Cognition and Behavior Reviews*, *4*, 29–39.
- Kepecs, A., & Mainen, Z. F. (2012). A computational framework for the study of confidence in humans and animals. *Philosophical Transactions of the Royal Society B*, *367*, 1322–1337.
- Kepecs, A., Uchida, U., Zariwala, H. A., & Mainen, Z. F. (2008). Neural correlates, computation and behavioural impact of decision confidence. *Nature Neuroscience*, *455*, 227–231.
- Kidd, C., & Hayden, B. Y. (2015). The psychology and neuroscience of curiosity. *Neuron*, *88*, 449–460.
- Kornell, N., Son, L. K., & Terrace, H. S. (2007). Transfer of metacognitive skills and hint seeking in monkeys. *Psychological Science*, *18*, 64–71.
- Kuhn, D. (2000). Metacognitive development. *Current Directions in Psychological Science*, *9*, 178–181.
- Le Pelley, M. E. (2012). Metacognitive monkeys or associative animals? Simple reinforcement learning explains uncertainty in nonhuman animals. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*, 686–708.
- Lee, P. A., & Schmitt, M. C. (2014). Easier language scaffolds the development of independent strategic reading activities and metacognitive awareness in emergent readers. *Reading Psychology*, *35*, 32–57.
- Leigh, S. R. (2012). Brain size growth and life history in human evolution. *Evolutionary Biology*, *39*, 587–599.
- Lemoine, S. R. T., Samuni, L., Crockford, C., & Wittig, R. M. (2023). Chimpanzees make tactical use of high elevation in territorial contexts. *PLoS Biology*, *21*, Article e3002350.
- Lenth, R. (2018). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.2.3. <https://CRAN.R-project.org/package=emmeans>.
- Liquin, E. G., & Gopnik, A. (2022). Children are more exploratory and learn more than adults in an approach-avoid task. *Cognition*, *218*, Article 104940.
- Loewenstein, G. (1994). The psychology of curiosity: A review and reinterpretation. *Psychological Bulletin*, *116*, 75–98.
- Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, Pan troglodytes schweinfurthii, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*, 676–683.
- Marsh, H. (2019). The information-seeking paradigm: Moving beyond 'if and when' to 'what, where, and how'. *Animal Behavior and Cognition*, *6*, 329–334.
- Marsh, H. L. (2014). Metacognitive-like information seeking in lion-tailed macaques: A generalized search response after all? *Animal Cognition*, *17*, 1313–1328.
- Marsh, H. L., & MacDonald, S. E. (2012a). Information seeking by orangutans: A generalized search strategy? *Animal Cognition*, *15*, 293–304.
- Marsh, H. L., & MacDonald, S. E. (2012b). Orangutans (*Pongo abelii*) "play the odds": Information-seeking strategies in relation to cost, risk, and benefit. *Journal of Comparative Psychology*, *126*, 263–278.
- Massaro, A. P., Gilby, I. C., Desai, N., Weiss, A., Feldblum, J. T., Pusey, A. E., & Wilson, M. L. (2022). Correlates of individual participation in boundary patrols by male chimpanzees. *Philosophical Transactions of the Royal Society B*, *377*.
- McMahon, S., Macpherson, K., & Roberts, W. A. (2010). Dogs choose a human informant: Metacognition in canines. *Behavioural Processes*, *85*, 293–298.
- McWilliams, A., Bibby, H., David, A. S., & Fleming, S. M. (2023). Age-related decreases in global metacognition are independent of local metacognition and task performance. *Cognition*, *235*, Article 105389.
- Michalsky, T., Mevarech, Z. R., & Haiji, L. (2009). Elementary school children reading scientific texts: Effects of metacognitive instruction. *The Journal of Educational Research*, *102*, 363–376.
- Mitani, J. C., & Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour*, *70*, 1079–1086.
- Mulcahy, N. J. (2016). Orangutans (*Pongo abelii*) seek information about tool functionality in a metacognition tubes task. *Journal of Comparative Psychology*, *130*, 391.
- Ohtani, K., & Hisasaka, T. (2018). Beyond intelligence: A meta-analytic review of the relationship among metacognition, intelligence, and academic performance. *Metacognition and Learning*, *13*, 179–212.
- O'Madagain, C., Helming, K. A., Schmidt, M. F. H., Shupe, E., Call, J., & Tomasello, M. (2022). Great apes and human children rationally monitor their decisions. *Proceedings B*, *289*.
- Palmer, E. C., David, A. S., & Fleming, S. M. (2014). Effects of age on metacognitive efficiency. *Consciousness and Cognition*, *28*, 151–160.
- Paukner, A., Anderson, J. R., & Fujita, K. (2006). Redundant food searches by capuchin monkeys (*Cebus apella*): A failure of metacognition? *Animal Cognition*, *9*, 110–117.
- Pelz, M., & Kidd, C. (2020). The elaboration of exploratory play. *Philosophical Transactions of the Royal Society B*, *375*.
- Perdue, B. M., Evans, T. A., & Beran, M. J. (2018). Chimpanzees show some evidence of selectively acquiring information by using tools, making inferences, and evaluating possible outcomes. *PLoS One*, *13*, Article e0193229.
- Pereira, M. E., & Fairbanks, L. A. (1993). *Juvenile primates: Life history, development and behavior*. Chicago: University Chicago Press.
- Perry, C. J., & Barron, A. B. (2013). Honey bees selectively avoid difficult choices. *Proceedings of the National Academy of Sciences*, *110*, 19155–19159.
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, *4*, 515–526.

- Proust, J. (2019). From comparative studies to interdisciplinary research on metacognition. *Animal Behavior and Cognition*, 6, 309–328.
- R Development Core Team. (2022). *A language and environment for statistical computing*. Vienna: Austria.
- Roberts, W. A., McMillan, N., Musoline, E., & Cole, M. (2012). Information seeking in animals: Metacognition? *Comparative Cognition and Behavior Reviews*, 7, 85–109.
- Roehrs, C. M. (2017). Executive function and metacognition: Towards a unifying framework of cognitive self-regulation. *Developmental Review*, 45, 31–51.
- Rollwage, M., Dolan, R. J., & Fleming, S. M. (2018). Metacognitive failure as a feature of those holding radical beliefs. *Current Biology*, 28, 4014–4021.
- Rosati, A. G. (2019). Heterochrony in chimpanzee and bonobo spatial memory development. *American Journal of Physical Anthropology*, 169, 302–321.
- Rosati, A. G., Emery Thompson, M., Atencia, R., & Buckholtz, J. W. (2023). Distinct developmental trajectories for risky and impulsive decision-making in chimpanzees. *Journal of Experimental Psychology: General*, 152, 1551–1564.
- Rosati, A. G., & Hare, B. (2011). Chimpanzees and bonobos distinguish between risk and ambiguity. *Biology Letters*, 7, 15–18.
- Rosati, A. G., & Hare, B. (2012). Decision-making across social contexts: Competition increases preferences for risk in chimpanzees and bonobos. *Animal Behaviour*, 84, 869–879.
- Rosati, A. G., & Hare, B. (2013). Chimpanzees and bonobos exhibit emotional responses to decision outcomes. *PLoS One*, 8, Article e63058.
- Rosati, A. G., & Hare, B. (2016). Reward type modulates human risk preferences. *Evolution and Human Behavior*, 37, 159–168.
- Rosati, A. G., Herrmann, E., Kaminski, J., Krupenye, C., Melis, A. P., Schroepfer, K., ... Hare, B. (2013). Assessing the psychological health of captive and wild apes: A response to Ferdowsian et al. (2011). *Journal of Comparative Psychology*, 127, 329–336.
- Rosati, A. G., Sabbi, K., Bryer, M. A. H., Barnes, P., Rukundo, J., Mukungu, T., ... Machanda, Z. P. (2023). Observational approaches to chimpanzee behavior in an African sanctuary: Implications for research, welfare, and capacity-building. *American Journal of Primatology*, 85, e23534.
- Rosati, A. G., & Santos, L. R. (2016). Spontaneous metacognition in rhesus monkeys. *Psychological Science*, 27, 1181–1191.
- Sakai, T., Mikami, A., Tomonaga, M., Matsui, M., Suzuki, J., Hamada, Y., Tanaka, M., Miyabe-Nishiwaki, T., Makishima, H., Nakatsukasa, M., & Matsuzawa, T. (2011). Differential prefrontal white matter development in chimpanzees and humans. *Current Biology*, 1397–1402.
- Sánchez-Amaro, A., Tan, J., Kaufhold, S. P., Fernández-Navarro, S., & Rossano, F. (2021). How environmental unpredictability and harshness affect chimpanzees (Pan troglodytes) in risk-choice and temporal discounting tasks. *Journal of Comparative Psychology*, 135, 232–243.
- Santos, L. R., & Rosati, A. G. (2015). The evolutionary roots of human decision making. *Annual Review of Psychology*, 66, 3221–3347.
- Schmidt, K. A., Dall, S. R. X., & Van Gils, J. A. (2010). The ecology of information: An overview on the ecological significance of making informed decisions. *Oikos*, 119, 304–316.
- Schneider, W. (2008). The development of metacognitive knowledge in children and adolescents: Major trends and implications for education. *Mind, Brain, and Education*, 2, 114–121.
- Shea, N., Boldt, A., Bang, D., Yeung, N., Heyes, C., & Frith, C. D. (2014). Supra-personal cognitive control and metacognition. *Trends in Cognitive Sciences*, 18, 186–193.
- Shields, W., Smith, J., & Washburn, D. (1997). Uncertain responses by humans and rhesus monkeys (*Macaca mulatta*) in a psychophysical same-different task. *Journal of Experimental Psychology: General*, 126, 147–164.
- Shields, W. E., Smith, J. D., Guttmanova, K., & Washburn, D. A. (2005). Confidence judgments by humans and rhesus monkeys. *The Journal of General Psychology*, 132, 165.
- Smith, J. D. (2009). The study of animal metacognition. *Trends in Cognitive Sciences*, 13, 389–396.
- Smith, J. D., Beran, M. J., Cosuchman, J. J., & Coutinho, V. C. (2008). The comparative study of metacognition: Sharper paradigms, safer inferences. *Psychonomic Bulletin & Review*, 15, 679–691.
- Smith, J. D., Coutinho, M. V., Church, B. A., & Beran, M. J. (2013). Executive-attentional uncertainty responses by rhesus macaques (*Macaca mulatta*). *Journal of Experimental Psychology: General*, 142, 458.
- Smith, J. D., Redford, J. S., Beran, M. J., & Washburn, D. A. (2010). Rhesus monkeys (*Macaca mulatta*) adaptively monitor uncertainty while multi-tasking. *Animal Cognition*, 13, 93–101.
- Smith, J. D., Schull, J., Strote, J., McGee, K., Egnor, R., & Erb, L. (1995). The uncertain response in the bottlenosed dolphin (*Tursiops truncatus*). *Journal of Experimental Psychology: General*, 124, 391–408.
- Smith, J. D., Shields, W. E., Allendoerfer, K. R., & Washburn, W. A. (1998). Memory monitoring by animals and humans. *Journal of Experimental Psychology: General*, 127, 227–250.
- Smith, J. D., Shields, W. E., Schull, J., & Washburn, D. A. (1997). The uncertain response in humans and animals. *Cognition*, 62, 75–97.
- Teffler, K., Buxhoeveden, D. P., Stimpson, C. D., Fobbs, A. J., Schapiro, S. J., Baze, W. B., ... Semendeferi, K. (2013). Developmental changes in the spatial organization of neurons in the neocortex of humans and common chimpanzees. *The Journal of Comparative Neurology*, 521, 4249–4259.
- Terrace, H. S., & Son, L. K. (2009). Comparative metacognition. *Current Opinion in Neurobiology*, 19, 76–74.
- Tomasello, M. (2023). Social cognition and metacognition in great apes: A theory. *Animal Cognition*, 26, 25–35.
- Veenman, M. V., Van Hout-Wolters, B. H., & Afflerbach, P. (2006). Metacognition and learning: Conceptual and methodological considerations. *Metacognition and Learning*, 1, 3–14.
- Veenman, M. V., Wilhelm, P., & Beishuizen, J. J. (2004). The relation between intellectual and metacognitive skills from a developmental perspective. *Learning and Instruction*, 14, 89–109.
- Wang, M. Z., & Hayden, B. Y. (2019). Monkeys are curious about counterfactual outcomes. *Cognition*, 189, 1–10.
- Weil, L. G., Fleming, S. M., Dumontheil, I., Kilford, E. J., Weil, R. S., Rees, G., ... Blakemore, S. J. (2013). The development of metacognitive ability in adolescence. *Consciousness and Cognition*, 22, 264–271.
- Whitebread, D., & O'Sullivan, L. (2012). Preschool children's social pretend play: Supporting the development of metacommunication, metacognition and self-regulation. *International Journal of Play*, 1, 197–213.
- Wobber, V., & Hare, B. (2011). Psychological health of orphan bonobos and chimpanzees in African sanctuaries. *PLoS One*, 6, Article e17147.
- Wobber, V., Wrangham, R., & Hare, B. (2010). Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology*, 20, 226–230.