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Early emergence of metacognition in rhesus monkeys

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Research highlights

- Studies of nonhuman primate cognitive development can provide insights into the evolutionary roots of human metacognition
- We examined whether rhesus monkeys are sensitive to opportunities for information-seeking, and how this skill develops across the life course
- Young monkeys already show skills for metacognitive information-seeking comparable to adults
- These results provide support for the 'core metacognition' hypothesis, which argues that foundational metacognitive skills emerge early and are phylogenetically shared

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Abstract

Metacognition, or monitoring and controlling one's knowledge, is a key feature of human cognition. Accumulating evidence shows that foundational forms of metacognition are already present in young infants and then scaffold later-emerging skills. While many animals exhibit cognitive processes relevant to metacognition, it is unclear if other species share the developmental trajectories found in human development. Here, we examine the emergence of metacognitive information-seeking in rhesus monkeys (*Macaca mulatta*). We presented a large sample of semi-free-ranging monkeys, ranging from juvenility to adulthood, with a one-shot task where they could seek information about a food reward by bending down to peer into a center vantage point in an array of tubes. In the *hidden* condition, information-seeking was necessary as no food was visible on the apparatus, whereas in the *visible* control condition information-seeking was not necessary to detect the location of the reward. Monkeys sought information at the center vantage point more often when it was necessary than in the control condition, and younger monkeys already showed competency similar to adults. We also tracked additional monkeys who voluntarily chose not to approach to assess monkeys' ability to actively infer opportunities for information-seeking, and similarly found similar performance in juveniles and adults. Finally, we found that monkeys were overall slower to make metacognitive inferences than to approach known rewards, and that younger monkeys were specifically slower to detect opportunities for information-seeking compared to adults. These results indicate that many features of mature metacognition are already detectable in young monkeys, paralleling evidence for 'core metacognition' in infant humans.

Key words: metacognition, information-seeking, uncertainty, comparative development

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1. Introduction

Metacognition is a suite of cognitive processes that allows individuals to monitor their own knowledge states and then act to acquire new knowledge when needed (Ackerman & Thompson, 2017; Flavell, 1979; Smith, 2009). Several views suggest that metacognition emerges fairly late in development (Flavell, 1999; Flavell, 2000), and may depend on other cognitive processes such as language, executive function, or theory of mind (e.g. Kuhn, 2000; Roebers, 2017; Schneider, 2008; Veenman, Van Hout-Wolters, & Afflerbach, 2006; Veenman, Wilhelm, & Beishuizen, 2004; Weil et al., 2013). However, recent studies have developed simpler paradigms to investigate foundational metacognitive capacities, and found that young children and non-verbal infants can engage in some forms of uncertainty monitoring and information-seeking (Balcomb & Gerken, 2008; Ghetti, Hembacher, & Coughlin, 2013; Goupil & Kouider, 2016, 2019; Goupil, Romand-Monnier, & Kouider, 2016; Vo, Li , Kornell, Pouget, & Cantlon, 2014). This evidence is the basis of the 'core metacognition' hypothesis (Goupil & Kouider, 2019), which proposes that young infants already possess foundational metacognitive capacitities that scaffold later-emerging skills.

'Core metacognition' is specifically proposed to comprise basic metacognitive skills that allow infants and toddlers to monitor uncertainty and act accordingly when they lack information (Goupil & Kouider, 2019). 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), and toddlers will further request help from an adult when they are unsure of a toy's location but make a direct choice when they are sure (Goupil et al., 2016). These abilities are further proposed to rely on phylogenetically-conserved mechanisms shared with other animals (Goupil & Kouider, 2019). In fact, there is an emerging consensus that several nonhuman species possess some

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metacognitive abilities. For example, a variety of species will choose to 'opt-out' of difficult memory and perceptual judgements, suggesting that they are sensitive to their own lack of knowledge (see Kepecs & Mainen, 2012; Smith, 2009 for reviews; Smith, Beran, Cosuchman, & Coutinho, 2008). While those paradigms generally require extensive training to participate in computer-based tasks, other work has examined patterns of information-seeking that harness animals' natural behavioral repertoires, more similar to work with young children (Call & Carpenter, 2001). Here, animals are typically faced with a choice between containers that may or may not contain a reward, and the question is whether they preferentially seek out missing information by changing their physical position to view the containers before making a choice (for example, by bending down to peer into tubes before choosing one; Call & Carpenter, 2001). In fact, a variety of primate species show these information-seeking behaviors (see Crystal & Foote, 2011; Marsh, 2019; Roberts, McMillan, Musoline, & Cole, 2012 for reviews), highlighting that at least some nonhuman species display several relevant metacognitive processes.

However, little is known about the development of metacognition in other primates, in part because many studies are limited by small sample sizes and typically involve samples of mixed-age animals. Studies of comparative cognitive development of nonhuman cognition are important to assess whether a given set of skills reflect shared cognitive mechanisms with humans, as adult animals may show behaviors that seem to parallel those in human children but recruit different cognitive processes (Gomez, 2005; Matsuzawa, 2007; Matsuzawa, Tomonaga, & Tanaka, 2006; Rosati, Wobber, Hughes, & Santos, 2014). For example, some monkey species show patterns of gaze-following that mirror those seen in human infants, but they only acquire these skills in adulthood after an extended period—suggesting that some forms of social

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experience or learning shapes the animals' responses in a manner that is different than for the forms of early-emerging gaze following in infants (Ferrari, Coude, Gallese, & Fogassi, 2008; Ferrari, Kohler, Fogassi, & Gallese, 2000). Similarly, recent work on decision-making and executive function shows that animals exhibit a variety of developmental trajectories that sometimes parallel and sometimes diverge from humans (Cantwell, Buckholtz, Atencia, & Rosati, 2022; Haux, Engelmann, Arslan, Hertwug, & Herrmann, 2022; Huang, Chang, Santos, & Rosati, 2024; Rosati, Emery Thompson, Atencia, & Buckholtz, 2023). This indicates that developmental continuity between humans and other primates cannot be assumed based on similar outcomes at maturity. As such, comparisons of development in nonhumans can provide an important test of the core metacognition hypothesis, specifically assessing whether skills that emerge early in human infancy and skills seen in (adult) animals in fact represent similar cognitive processes.

In the current study, we therefore examined patterns of information-seeking across the rhesus monkey life-course by testing individuals from a large population of semi-free-ranging monkeys. Prior work in this population validated a one-shot information-seeking task (Rosati & Santos, 2016), showing that rhesus monkeys engage in metacognitive information-seeking in the absence of prior experience. Here, we adapted those methods to specifically contrast younger juveniles with adults to examine developmental change versus stability in these responses. Monkeys completed a single trial in which they could search an array of tubes to find food in the absence of any training or experience. Whereas some monkeys directly observed the location of the food, others did not. This allowed us to assess whether monkeys who were ignorant would preferentially engage in information-seeking by searching at a center vantage location where they could peer into the whole apparatus from one spot. We further tracked monkeys' initial

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decision to search the apparatus (as opposed to choosing to not search at all), as an additional index of metacognitive monitoring of opportunities to acquire needed information as well as to account for any potential age-related shifts in neophobic versus exploratory behavior.

We had several predictions related to the development of information-seeking in monkeys. First, if monkeys do exhibit metacognitive information-seeking, then when monkeys search they should preferentially search in the center when they lack knowledge as in prior work with this paradigm (Rosati & Santos, 2016). Second, if metacognition in monkeys is a skill that matures slowly or requires learning experience, then adults should be more adept at selectively engaging in it when appropriate. Accordingly, we predicted that younger monkeys might engage in information-seeking at overall lower rates when they searched, or be less selective (that is, engage in more 'unnecessary' searches) compared to adults. Third, our measure of whether monkeys searched at all further let us assess any developmental changes in monkeys' abilities to *detect* opportunities for information-seeking. In particular, younger monkeys may not be as skilled at inferring how information-seeking can lead to knowledge as adults, so juveniles may engage in less searching than adults specifically when information-seeking is necessary. This measure further let us assess if neophobia constrained younger monkeys' responses, accounting for the possibility that younger monkeys might be less willing to search a novel apparatus overall (regardless of condition) compared to higher-status adults. Conversely, if these nonhuman information-seeking skills parallel 'core metacognition' in human infants, then young monkeys should already exhibit adult-like competencies in both initially detecting opportunities for information-seeking and effectively searching, mirroring the emergent metacognitive awareness shown by human infants.

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2. Methods

In this preregistered study (https://aspredicted.org/1YB_642), monkeys were tested on a modified version of a previously validated information-seeking task (Rosati & Santos, 2016). Monkeys were randomly assigned to one of two possible conditions: the *hidden* condition where information-seeking was necessary, or the *visible* control where it was not.

2.1 Research site and study population

We assessed a total of *n* = 141 monkeys from the Cayo Santiago Biological Field Station. All non-invasive behavioral tests were approved by the Institutional Animal Care and Use Committee for the University of Puerto Rico Medical Sciences Campus and adhered to site guidelines for animal research.

The Cayo Santiago population consists of more than 1700 individually identifiable monkeys living in natural social groups on a 38-acre island (Rawlins & Kessler, 1987). Animals are well-habituated to human observers and experimental studies (Drayton & Santos, 2015; Winters, Dubuc, & Higham, 2015). This sample consisted of two subgroups: 80 monkeys that searched the apparatus (35 females, 45 males; mean age 7.4 years, range 1.8-20.6 years) and an additional 61 monkeys who observed the demonstration but then chose not to search (26 females, 35 males; mean age 6.9 years, range 1.9-23.5 years). A total of n = 9 monkeys had participated in the prior study by Rosati and Santos (2016) seven years previously (five monkeys who searched, and four who did not search). All of these monkeys were adults in the current study; all other monkeys, including all juveniles, were naive to the apparatus and setup.

Following our pre-registered analysis plan, we tested equal numbers of juveniles (under 5 years) and adults (over 5 years) in the subset of 80 individuals who searched (counterbalanced

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across the two conditions, with 40 total per condition); these age cohorts are based on life history transitions in this species (Rawlins & Kessler, 1986). We selected this sample size as it was similar to or larger than sample sizes on prior studies similarly measuring approach choices in this population (Flombaum & Santos, 2005; Phillips & Santos, 2007; Rosati & Santos, 2016; Santos, Nissen, & Ferrugia, 2006; Santos, Sulkowski, Spaepen, & Hauser, 2002), such that we could test sufficient monkeys to compare across age cohorts and pragmatically complete the planned sample.

During testing, we further tracked the additional 61 monkeys who successfully viewed the demonstration but then did not search the apparatus. That is, these individuals did not approach within our time cutoff of one minute, or they chose to walk away from the testing area after viewing the demonstration. We used this data to assess whether monkeys showed developmental changes in detecting opportunities for information-seeking or general exploratory behavior. Finally, additional monkeys were approached for testing but did not produce a scorable response in this free-ranging context (typically due to social interference from other monkeys), as detailed below.

2.3 Conditions

Each monkey completed a single trial where they were randomly assigned to one of two conditions: the *hidden* condition (where information-seeking was necessary, as it was unclear where the food was) or the *visible* control (where there was visible food on the apparatus; see Figure 1). In both conditions, monkeys saw an identical baiting procedure: the demonstrator showed the monkey a food reward, appeared to bait the apparatus behind an occluder, and then picked up the occluder and moved away from the apparatus so the monkey could search (Figure

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1a). Whereas in the *hidden* condition no food was visible after this demonstration, in the *visible* control condition she left a grape placed on top of the distal end of one tube (see Figure 1b-c). This let us assess if monkeys preferentially approached the center where they could peer into both tubes in the hidden condition (Figure 1d-e; see also Supplemental Video S1 for the experimental demonstration and example monkey responses).

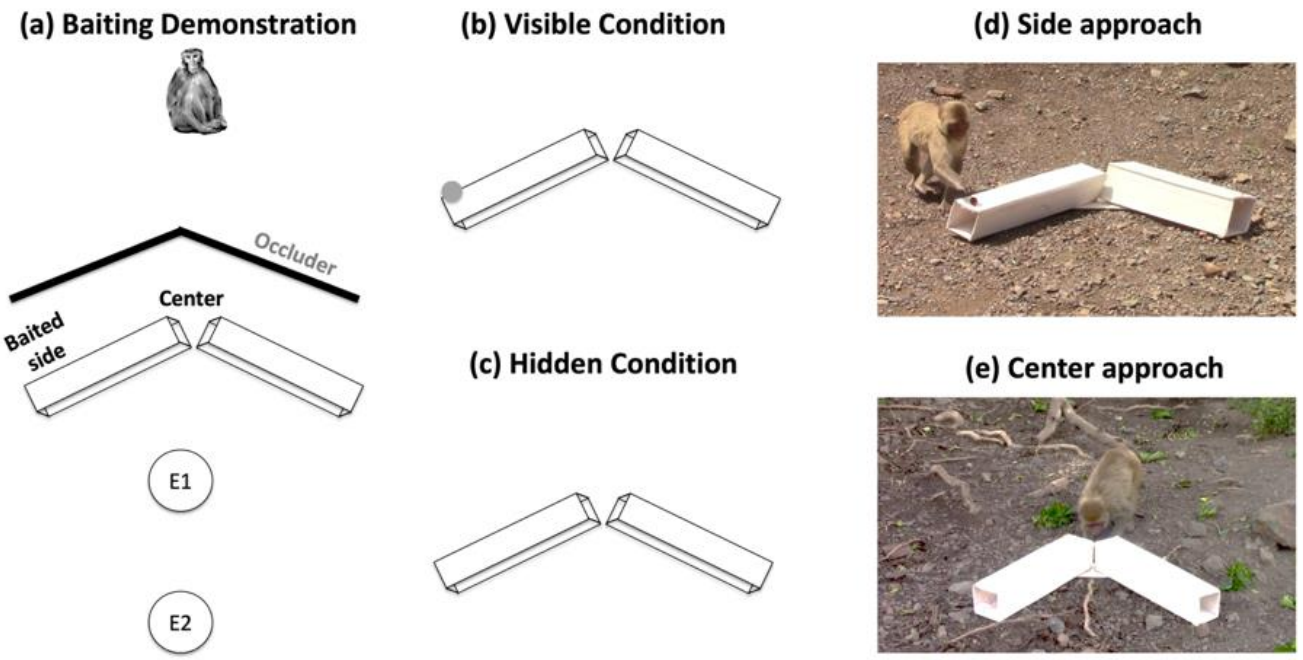


Figure 1. Setup for the study. (a) In both conditions, monkeys observed the same initial demonstration where the demonstrator, experimenter one (E1), showed the two tubes, placed them in a v-formation, and then appeared to bait a food reward behind an occluder. The camera person, experimenter two (E2), filmed the monkey's behavior. (b) In the *visible condition*, E1 removed the occluder to reveal that a food reward (a grape) was placed on one distal end of a tube, and walked back to E2 so the monkey could approach. (c) In the *hidden condition*, E1 performed the same actions, but no visible food was revealed. (d) Screenshot of monkey approaching from the side to take visible food on the tube. (e) Screenshot of a monkey approaching the center vantage point to peer into the tubes.

Importantly, the *hidden* condition in the current study was identical to the primary test condition in the prior study by Rosati & Santos (2016), also involving hidden baiting demonstration (behind the occluder) of the two tubes apparatus. However, the current *visible*

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condition differed from those in the prior paper. Specifically, the prior study included three control conditions: a condition with two tubes involving a visible baiting procedure the experimenter moved her arm to the side location to visibly (fake) baited the tube (e.g., not behind the occluder); and two more conditions where the experimenter performed the same actions as in the hidden and visible conditions in the two-tube setup, but where there was only one tube present (e.g., information seeking was not possible as there was no vantage point to look inside). Here, we implemented a new visible baiting control condition: we again used two tubes, but here the demonstrator performed identical actions as in the hidden condition, and rather left a grape on the apparatus that was only visible after the experimenter stood up and removed the occluder. We implemented this new control for two main reasons. First, we aimed to further validate the premise of the information-seeking paradigm, as the new control allowed for an identical apparatus and experimenter demonstration actions in both conditions unlike in the prior study. Second, as the grape was placed on the apparatus behind the occluder, monkeys could only detect it if they were actively attending to the apparatus from a distance *after* the experimenter stood up and left the area; note that the two conditions were otherwise identical so this would show monkeys were generally attending to the apparatus in both conditions. This provides a stronger contrast for our measure of the monkeys' ability to initially detect opportunities for information-seeking.

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2.4 Procedure

In trials, two experimenters approached a calmly-sitting monkey who was positioned alone or some distance away from other individuals in the social group. Experimenter 1 (E1), the demonstrator, knelt approximately 2-3 m away from the monkey while Experimenter 2 (E2), the camera person, stood another 2-3m behind E1 to film the monkey's response. At the start of the trial, E1 placed a black occluder (poster board; each wing 76 cm wide by 50 cm tall) in front of her. This occluder was large enough to block the monkey's view of her arms and shoulders when baiting the apparatus. She then showed the monkeys two large white tubes with square openings (posterboard; 50 cm long, 10 cm wide, 10 cm tall), tapping them together with the open ends pointing to the monkey so they could observe that both were empty; she visually checked that the monkey was attending while she performed this action. She then placed these tubes on the ground in front of the occluder in a V-formation, with the center vantage point oriented toward the monkey; the tubes were aligned with Velcro on a small piece of poster board to ensure that they were positioned in the correct orientation. The distal sides of the tubes were ~75 cm apart, a distance wide enough to pose a small travel cost if the monkey initially approached the wrong location, but where it was still feasible to manipulate the apparatus.

Next, the experimenter then held a food reward (a grape) above the occluder and moved it straight down behind the occluder while the monkey was watching. Because the occluder blocked their view, the monkey could not see where it was specifically placed. In the *visible* condition, the experimenter placed the grape on the distal of one of the tubes (speared on a small toothpick). The side (left or right) was counterbalanced across subjects, and the experimenter used the matched hand to show the grape. She then removed the occluder and walked behind E2. In the *hidden* condition, the experimenter performed the same actions, but no food was left

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visible on the apparatus. Prior work with this monkey population shown that monkeys closely attend to comparable fruit stimuli (Arre, Clark, & Santos, 2020; Arre, Stumph, & Santos, 2021; Bettle & Rosati, 2021; De Petrillo & Rosati, 2019; Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011; Martin & Santos, 2014), and actively attempt to approach and search for such fruit on or inside an apparatus in paradigms measuring active choices as in the current work (Flombaum & Santos, 2005; Phillips & Santos, 2007; Rosati & Santos, 2016; Santos et al., 2006; Santos et al., 2002).

2.5 Social interference and exclusions

In this free-ranging context, some monkeys were approached for testing but did not produce a scorable response, typically due to interference by other monkeys. While we preferentially approached monkeys sitting alone or a distance from other monkeys to reduce the possibility of such interference, and generally set up the apparatus in a given spot for only one monkey at a time, nonetheless additional monkeys could be sitting in the vegetation or move towards the testing area after the session began to displace the subject or approach the apparatus before they could. These monkeys (n = 58) were excluded, a similar exclusion rate as in prior approach studies in this free-ranging population (Flombaum & Santos, 2005; Rosati & Santos, 2016). In addition, in some cases animals were approached for testing more than once (e.g., because their identification was only confirmed after the test; n = 23), in which case we only included their first successful session.

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2.6 Coding and behavioral scoring

We had two phases of coding. One phase assessed if the monkey searched at all (e.g., distinguishing between monkeys who searched, those who voluntarily did not search, and the individuals who were excluded because they experienced social inference before they could respond). Two coders independently scored the monkeys' responses; the reliability coder was blind to the study hypotheses. Each trial was clipped from longer video sessions starting when the demonstrator stood up, and assigned a random ID code to remove additional condition information. Coders examined these video clips using the program Filmora. Monkeys were scored as *searching* if they initiated their movement towards the apparatus within one minute from when the experimenter stood up (e.g., we included individuals who initiated in this timeframe, even if they completed it after this cutoff). Monkeys were considered as engaging in a *voluntary no-search* if they did not move in this period, or if they left the testing area of their own accord before the cutoff. *Social interference* was scored if a monkey was displaced or another individual approached before the subject could. There was high reliability for whether the monkey approached, showed a voluntary no-approach, or experienced interference (97.8% agreement; Cohen's $\kappa = 0.97$).

The second phase of coding scored the characteristics of the monkey's search behavior (for those who did search). Two coders independently again scored the monkeys' responses, with the reliability coder blind to the study hypotheses. We focused on the monkeys' first search, but also coded additional searches as relevant (e.g., sometimes monkeys in the visible condition first looked in the center, so we confirmed that they subsequently moved to the baited location to retrieve the visible grape). Our primary code was the *location* monkeys searched (e.g., center, left, or right), as well as their *latency* to initiate the search. Monkeys who searched either (a)

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visibly *looked* into one or both tubes, either near the apparatus or from a larger distance; (b) *approached* within arm's reach of the apparatus; and/or (c) *touched* the apparatus, including the grape. We coded all of these possible behaviors that occurred at the first location searched. Indeed, many of these behaviors occurred concurrently or in quick succession (e.g., monkeys who touched the apparatus necessarily also came within arm's reach, and monkeys could move towards the apparatus in arm's reach while also peering into a tube). This allowed us to score a comparable metric of searching across both conditions that might prompt different manners of responding (e.g., monkeys more frequently touched the apparatus in the visible condition where there was a grape placed on the tube, versus look into tubes the hidden condition). In some cases, the monkeys then searched at a second location after their initial search, which we also coded as feasible. There was high reliability between the two coders for the first location searched (99% agreement; Cohen's κ = 0.98), latency to search (r_p = 0.99), and specific behaviors while searching (looking in at least one tube: 99% agreement; κ = 0.98; checking both tubes: 100% agreement, κ = 1.0; arm-reach approach: 99% agreement; κ = 0.80; touching apparatus: agreement = 100%, κ = 1.0).

2.7 Statistical analyses

We analyzed the data in R v4.2.1 (R Development Core Team, 2022). For our primary analyses of whether the monkeys searched at all, and whether they searched the center location if they did so, we implemented logistic regressions using *glm*. In our analyses of latency to search, we implemented regressions using *glm* with an inverse gaussian distribution, as this data had right skew; this is similar to a log-transformation, but the models directly account for the data structure (Lo & Andrews, 2015). Across models, we accounted for subject's *sex* in a base model, and then added *condition* (hidden versus visible), subject's *age*, and their interaction to test their

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importance. We then compared model fit using likelihood ratio tests, and also report Akaike information criterion (AIC) comparisons, where lower AIC indicates better fit.

2.8 Data availability

Data from this study will be available in Dryad Digital Repository.

3. Results

We first examined monkeys' initial decisions to search the apparatus after watching the demonstration, contrasting choices to search with voluntary choices to not search at all in the overall sample of 141 monkeys. Here we found that mean = 90.1% of monkeys searched in the *visible* condition where there was a grape placed on the apparatus, whereas only 41.2% searched in the *hidden* condition where information-seeking was necessary (see Figure 2a). Using logistic regressions, we found that inclusion of *condition* improved fit [χ^2 = 34.62, df = 1, p < 0.0001; AIC = 164.26 in the second model compared to 196.88 in the base model]: monkeys were more likely to search in the visible condition. However, neither the inclusion of *age* [χ^2 = 0.43, df = 1, p = 0.51, n.s.; AIC = 165.83], nor an *age X condition* interaction [χ^2 = 1.43, df = 2, p = 0.49, n.s; AIC = 166.83], further increased fit compared to the condition-only model. This shows that detecting opportunities for information-seeking in the hidden condition was generally more challenging than approaching food in the visible control, and further reveals that juveniles were similarly skilled as adults at detecting such opportunities. That is, the experimental condition the monkey experienced was the major determinant of their initial decision to search, with no evidence that younger monkeys were more neophobic and reticent to search compared to adults.

We next examined the 80 monkeys who did search the apparatus. Our first question was whether monkeys preferentially engaged in center searches when information-seeking was necessary to locate the food. Indeed, 92.5% of monkeys first approached the center in the *hidden* condition, whereas only 10.0% of monkeys did so in the *visible* control. We also checked that

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monkeys actually searched the correct (baited) side in the visible condition, and indeed 100% of the monkeys who searched a side in the visible condition did so correctly. We then modeled decisions to search the center versus a side location. Inclusion of *condition* improved fit [χ^2 = 63.09, df = 1, p < 0.0001; AIC = 53.00 in the second model versus 114.09 in the first]: monkeys were more likely to search the center in the hidden condition. Inclusion of *age* further improved fit [χ^2 = 5.46, df = 1, p = 0.019; AIC = 49.55]: older monkeys were overall more likely to search the center than younger monkeys. Finally, we added an *age X condition* interaction to test if this age shift was specific to one condition; this did not further improve fit in likelihood ratio tests but was the best model by AIC comparisons [χ^2 = 2.64, df = 1, p = 0.10; AIC = 48.90]. Post-hoc comparisons of age slopes indicated a trend for greater age-related increases in center searching in the visible condition [p = 0.083], suggesting that this age shift was driven primarily by older monkeys engaging in 'unnecessary' center searches in the visible condition where food was present (see Figure 2b). This interpretation is further supported by the fact that while unnecessary searches in the visible condition occurred infrequently, 20% of adults did so whereas no juveniles did. In contrast, both younger and older monkeys had similar rates of erroneous side searches in the hidden condition, where no grape was present (10% of juveniles and 5% of adults approached a side location in this condition).

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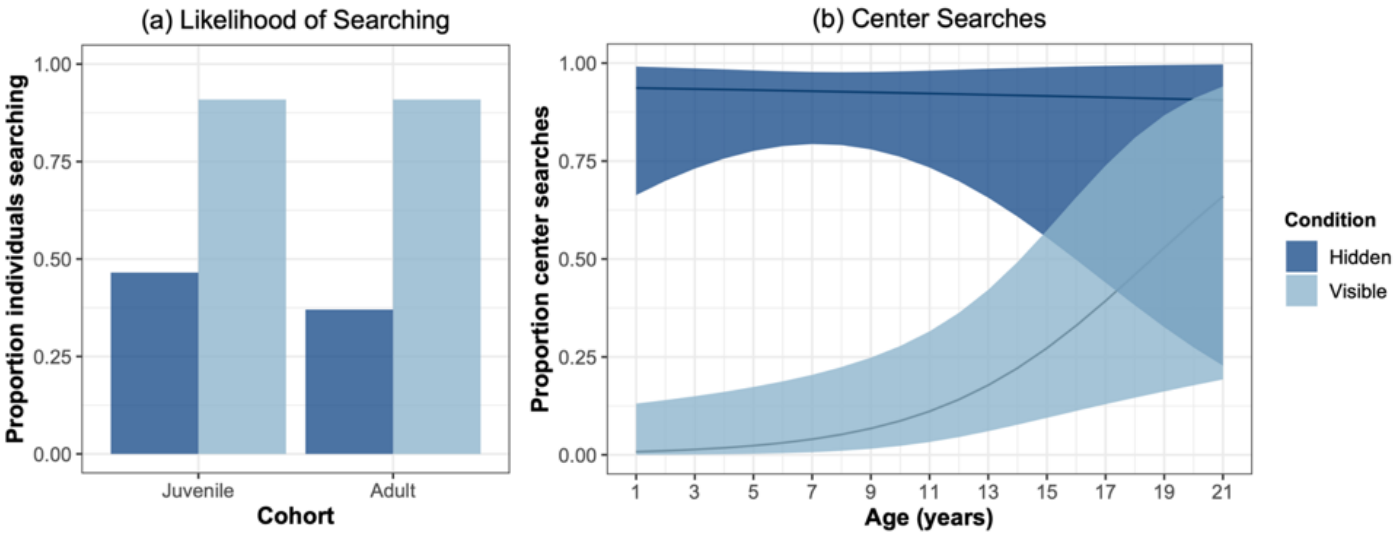


Figure 2. Searching responses in the task. (a) Proportion of monkeys who searched the apparatus by condition and cohort. Monkeys were more likely to search the apparatus in the *visible* condition where a piece of food was left on top of one of the tubes, compared to the *hidden* condition where information-seeking was necessary. However, there was no shift in these responses across younger versus older monkeys. (b) If monkeys did search, both younger and older individuals consistently engaged in center searches in the *hidden* condition, and did so more often than in the *visible* condition. There was also a trend for increasing (unnecessary) information-seeking during old age in response to the *visible* condition. Estimated values are derived from logistic regressions also accounting for subject's sex. Ribbons indicate 95% confidence intervals.

We then examined more detailed characteristics of the specific behaviors the monkeys engaged in while searching. As noted above, our overall measure of searching comprised three different possible behaviors that the monkey could perform in some combination at the location they searched at: *looking* into the tubes, *approaching* within arm's reach, and/or *touching* the apparatus. When decomposing the specific behaviors monkeys performed while searching, we found that most monkeys who looked inside the tubes were in the hidden condition and approached the center (see Figure 3a). Of those who first approached the center vantage point, the vast majority visibly looked in at least one tube from that location (97.3% of the 37 'correct' center searches in the hidden condition involved looking, as well as all of the four monkeys who engaged in 'unnecessary' searches in the visible condition; see Figure 3a). This indicates that monkeys were indeed trying to see inside the tubes when they went to the center, even in the

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unnecessary searches by older adults in the visible condition. Moreover, the majority of the monkeys (64.9%) who searched the center in the hidden condition were additionally scored as actively checking both tubes during their search. In contrast, monkeys rarely looked inside a tube when they approached a side in the visible condition with a grape present (only 5.6% of the 36 monkeys who did so in the visible condition) and did so at intermediate levels in the few cases where they erroneously approached a side in the hidden condition (two of the three monkeys who did so). Accordingly, monkeys produced a looking response while searching more often in the hidden condition [χ^2 = 63.59, df = 1, p < 0.0001; AIC = 51.93 versus 113.53 in the base model], as well as whenever they first searched the center location [χ^2 = 14.13, df = 1, p <0.0005; AIC = 39.80]; age or sex were not significant predictors of looking responses. This aligns with the interpretation that monkeys were specifically engaging in metacognitive information-seeking in the hidden condition, whereas they rarely looked into a side tube when food was present in the visible condition.

Second, we found that most monkeys approached within arm's reach across both conditions regardless of age (95.0% of adults, and 100% of juveniles), suggesting no major age differences in overall exploratory behavior or general neophobia towards the apparatus if the monkey did make a response. This aligns with the results from initial choices to search or not, indicating that juveniles and adults showed similar overall willingness to closely approach the novel apparatus. Finally, 100% of monkeys who approached a side in the visible condition touched the apparatus (unsurprising given they had to do so to retrieve the grape), regardless of age. There were more intermediate rates of touching in the hidden condition where touching was not specifically necessary (60.0% of monkeys did so; 70% of juveniles and 50% of adults). Together, this pattern of results supports the interpretation that monkeys approached the center to

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actively look inside the tubes, and that such information-seeking emerges early and remains stable across development, again without any major differences in exploratory behavior or neophobia by age.

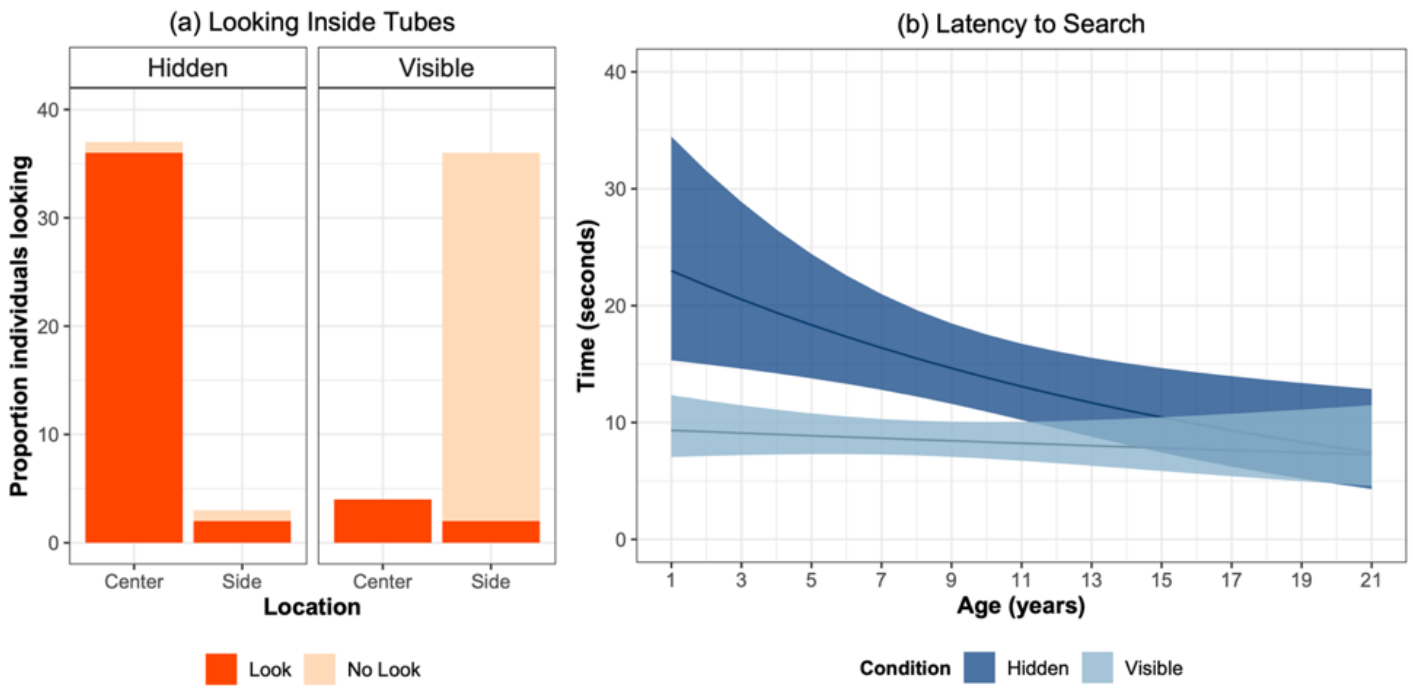


Figure 3. Characteristics of search responses. (a) Proportions of monkeys who looked inside at least one tube during their search; height of stacked bar indicates total number of monkeys who searched at each *location* within a given *condition*. Monkeys in the hidden condition typically searched the center vantage point and overwhelmingly looked inside the tubes, whereas monkeys in the visible condition typically searched a side location without looking inside the tube (and rather only took the food on the apparatus). (b) Latencies to engage in searches by condition. Monkeys of all ages were quick to approach the apparatus in the visible condition, whereas older monkeys were faster than younger monkeys to engage in information-seeking in the hidden condition. Estimated values are derived from logistic regressions also accounting for subject's sex. Ribbons indicate 95% confidence intervals.

We next examined monkeys' latency to engage in their first search, as response time can index the need for more effortful cognitive processes to solve a problem. Whereas monkeys took an average of mean = 8.9 ± SE = 0.9s to initiate their search in the visible condition, they took an average of 17.4 ± 2.6s in the hidden condition. We modeled these latencies using the same general approach as for models of the location of searching. Here, inclusion of *condition*

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improved fit [χ^2 = 0.80, df = 1, p < 0.0001; AIC = 519.38 in the second model versus 536.62 in the first], indicating that monkeys were indeed faster to approach in the visible condition with food on the apparatus. While inclusion of *age* only trended to improve fit as a main effect [χ^2 = 0.13, df = 1, p = 0.058, n.s.; AIC = 517.54], the *age X condition* interaction improved fit compared to the condition-only model [χ2 = 0.26, df = 2, p = 0.02; AIC = 515.96] and was also best by AIC comparisons (see Figure 3b). Post-hoc comparisons of age slopes indicated younger monkeys trended to be slower to search than adults specifically in the hidden condition [p = 0.057]. Overall, this indicates that while juvenile and adult monkeys showed similarly quick approaches in the visible control condition, older monkeys were faster to begin searching in the hidden condition where information-seeking was necessary.

Finally, we examined the monkeys' responses if they searched a second location after their initial choice. We caution that the paradigm was not designed to systematically track this secondary response, and some monkeys may not have been able to continue to search either because the experimenters picked up the apparatus (e.g., to preclude monkeys from moving or damaging it) or due to subsequent social interference following their initial search. In any case, we found that 17 individuals performed a second search. This was proportionally most common in the subset of monkeys who made 'erroneous' initial searches: all four of the individuals who initially searched the center in the visible condition then subsequently retrieved the grape from the side in a second search, and two of the three individuals who initially searched a side in the hidden condition then searched another location. Of the individuals who first (correctly) looked at the center—and thus already could have viewed both sides of the apparatus—only 2 of 37 then searched in another location (both looked into a tube from the side). Conversely, 9 of 36 monkeys who correctly approached a side in the visible condition then engaged in a second

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search where they approached the center: four looked into the *other* tube from that position (e.g., checking side they did not already have information about), four looked into both tubes simultaneously from the center, and one approached the center but did not specifically look in any tube. Overall then, these additional looks seemed primarily oriented towards checking other parts of the apparatus monkeys had not already investigated in their first search.

4. Discussion

Taken together, the current results provide strong evidence that monkeys exhibit metacognitive information-seeking responses when they are ignorant, and further shows that this skill is already mature in young monkeys. In particular, we found that monkeys searched the center more often when they did not know the location of food than when they did. Furthermore, the results examining whether monkeys decided to search at all, as well as their latency to search if they did do so, shows that engaging this metacognitive processing is costly: monkeys were generally slower to search in the hidden condition, and some monkeys did not detect the opportunity for information-seeking at all. Importantly, our study involved a single trial and as such our results cannot be explained by learning over successive trials. Rather, monkeys needed to make a novel inference concerning how to engage in information-seeking in this one-shot situation that did not involve any prior experience. Our results also indicate that young monkeys (all of whom were naïve to the setup) show performance comparable to adults both in terms of deciding whether to search at all, as well as in executing information-seeking responses. Indeed, the main age-related change was that juveniles were slower to engage in information-seeking than adults. Overall, this provides support for the 'core metacognition' proposal that there is phylogenetic continuity in foundational metacognitive skills across species.

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To test the developmental emergence of metacognition in monkeys, we used a modified version of a paradigm that was previously validated in the same population (Rosati & Santos, 2016). The prior study involved the same basic setup, but we tested a higher proportion of juvenile monkeys in order to examine age-related changes. In addition, we tracked the monkeys' initial decisions to search at all—scoring monkeys that fully observed the demonstration but then voluntarily chose not to approach. This allowed for an additional measure of metacognitive monitoring—monkeys' assessment of when information-seeking was possible—as well as confirmation that juvenile monkeys were not generally more neophobic or otherwise unwilling to approach the apparatus compared to adults. Finally, the prior study included different control conditions validating that center searches represent an information-seeking response, as monkeys rarely searched the center when information seeking was either unnecessary or not possible. Here, we implemented a new visible control condition that allowed monkeys to observe identical experimental demonstrations in both conditions, and rather left a grape on one side of the apparatus in the visible control. We found that monkeys rarely approached the center when information seeking was not necessary as in the prior control conditions. This approach also allowed us to confirm that monkeys attended to the apparatus after the experimenter stood up, given the high rates of approaching when the occluder was raised to reveal a grape in the control condition. Overall, the current results align with the prior findings, while also providing new insights into the development of monkey metacognition.

We found that younger monkeys are similarly adept as adults in assessing whether a given situation requires information-seeking: both juveniles and adults decided to initially search at similar rates, and they also show overall similar patterns of correct search responses when they did search. As such, we did not find any evidence that juveniles were less competent at

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information-seeking or otherwise constrained by neophobic reactions to the apparatus. However, one key difference was that juveniles were slower to engage in the information-seeking response than adults. One possibility is that younger monkeys were slower to respond because they were more vigilant about potential social interference near the apparatus. However, this seems implausible given that such competitive interactions would be more likely when there was contestable food, but younger and older monkeys showed similar fast response times in the visible condition where there was visible food to compete over. An alternative is that younger monkeys required more processing time to recognize opportunities for information-seeking. While there is no directly comparable data from human children, there is an emerging set of work using response latencies to measure implicit forms of metacognition, which shows that response latencies can index cognitive errors and effortful cognitive processing (Ghetti et al., 2013; Leckey et al., 2020; Roderer & Roebers, 2010; Roderer & Roebers, 2014). Finally, it is important to note that our study may not have been able to detect the earliest developmental shifts in monkeys. Our sample comprised a high proportion of juvenile monkeys, but even younger infant monkeys are typically physically clinging to or always very near their mother and cannot be assessed in the same way. However, alternative methods involving looking responses have been successfully implemented with the younger infant monkeys in this population (Huang et al., 2024; Hughes & Santos, 2012; Rosati, Arre, Platt, & Santos, 2016), so looking measures of metacognition could potentially be used to assess the youngest monkeys.

Beyond these (lack of) changes in juvenile monkeys, we detected increases in 'unnecessary' information-seeking in older adult monkeys. While monkeys of all ages showed similar high proficiency at information-seeking in the hidden condition, there was some evidence for increases in unnecessary center looks in the aging monkeys (although as we did not

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specifically target aging adults, their sample size here is relatively small). Importantly, the patterns of second searches indicates that all of these monkeys then subsequently picked up and ate the visible food on the apparatus as a second search response, indicating they were indeed motivated to obtain it. One possibility is that these responses reflect true metacognitive errors, such that these older monkeys incorrectly engaged in these center searches and then subsequently noticed the grape on the apparatus. This interpretation would align with results from humans showing declines in metacognitive flexibility during aging (Hertzog & Dunlosky, 2004; McWilliams, Bibby, David, & Fleming, 2023; Palmer, David, & Fleming, 2014), as well as accumulating evidence that nonhuman primates also show aging deficits in related skills like executive functions (Lacreuse, Raz, Schmidtke, Hopkins, & Herndon, 2020). An alternative possibility is that older monkeys show a shift in curiosity, or valuing information for its own sake (Gottlieb, Oudeye, Lopes, & Baranes, 2013; Loewenstein, 1994). That is, older monkeys may have been more willing to pay some small energetic cost to look into both tubes, even when they did not strictly need to do so. In fact, there is an emerging literature that both humans and some animals may value some kinds of information for its own sake (Forss et al., 2024; Kidd & Hayden, 2015). Thus, an important question for future work is whether these shifts reflect increases in true 'errors' of action selection during aging, versus increased valuation of information for its own sake, which could be tested by more closely examining information-seeking decisions across the adult lifespan.

In sum, we showed that a key form of information-seeking emerges early in rhesus monkey development, with strong continuity from juvenility to adulthood. This pattern of information-seeking development supports the 'core metacognition' hypothesis that these foundational skills emerge early and are phylogenetic conserved across species (Goupil &

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Kouider, 2019). This sets the stage for distinguishing different metacognitive processes in animals using a developmental approach. In humans, metacognitive monitoring and control can be flexibly deployed in a variety of ways, in a variety of decision-making contexts (Fischer & Said, 2021; Frith, 2012; Heyes, Bang, Shea, Frith, & Fleming, 2020; Huang & Yang, 2020; Rollwage, Dolan, & Fleming, 2018). While most studies of information-seeking in animals to date have involved knowledge about the presence or absence of food rewards as in the current study, there is emerging work on information-seeking for reward identity or object properties as well (Beran, Smith, & Perdue, 2013; Bohn, Allritz, Call, & Voelter, 2017; Mulcahy, 2016). Developmental comparisons of other aspects of metacognition monitoring for other kinds of information can help disentangle what aspects of metacognition are biologically foundational versus which may require experience and emerge over a longer time course.

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