

RESEARCH ARTICLE

Do young rhesus macaques know what others see?: A comparative developmental perspective

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Abstract

Humans undergo robust ontogenetic shifts in the theory of mind capabilities. Are these developmental changes unique to human development or are they shared with other closely related non-human species? To explore this issue, we tested the development of the theory of mind capacities in a population of 236 infant and juvenile rhesus macaques (*Macaca mulatta*). Using a looking-time method, we examined what developing monkeys know about others' perceptions. Specifically, we tested whether younger monkeys predict that a person will reach for an object where she last saw it. Overall, we found a significant interaction between a monkey's age and performance on this task ($p = .014$). Juvenile monkeys (between two and 5 years of age) show a nonsignificant trend towards human infant-like patterns of performance, looking longer during the unexpected condition as compared to the expected condition, though this difference is nonsignificant ($p = .09$). However, contrary to findings in human infants, infant rhesus macaques show a different trend. Infant monkeys on average look slightly longer on average during the expected condition than the unexpected condition, though this pattern was not significant ($p = .06$). Our developmental results in monkeys provide some hints about the development of the theory of mind capacities in non-humans. First, young rhesus macaques appear to show some interest in the perception of other agents. Second, young rhesus seems able to make predictions based on the visual perspective of another agent, though the developmental pattern of this ability is not as clear nor as robust as in humans. As such, though an understanding of others' perceptions is early-emerging in human infants, it may require more experience interacting with other social agents in our non-human relatives.

KEYWORDS

development, macaques, social cognition, theory of mind

1 | INTRODUCTION

As we navigate our social world, we readily ascribe intentions, perceptions, desires, and knowledge to other beings. Unsurprisingly to those of us studying non-human primates (hereafter, primates), humans are not alone in these abilities. Indeed many of our closest relatives share the capacity to reason about others' mental

experiences (for a review see Rosati, Santos, & Hare, 2010). Nevertheless, the degree to which primates represent others' mental experiences is largely a point of contention, as decades of research suggest that primates may not be quite as sophisticated in their mentalizing abilities as humans (Call & Tomasello, 2008; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Martin & Santos, 2016). As such, research into the nuances of

primates' reasoning about other agents is important for improving our understanding of how exactly primates perceive the perceptual and mental states of others.

Although adult humans exhibit fairly stable theory of mind abilities, human infants and children undergo rich developmental transitions in their theory of mind abilities (Wellman & Liu, 2004; Wellman, Fang, & Peterson, 2011). Almost from birth, infants show a proclivity for making eye contact with other agents (Haith, Bergman, & Moore, 1977) that likely provides an important scaffold for later developing a theory of mind abilities. Later on in development, human children begin to show more sophisticated perspective-taking capacities, and these abilities typically emerge in a fairly robust order (Wellman & Liu, 2004), especially when tested using traditional verbal tasks. Young infants begin representing the desires of other agents (Wellman & Woolley, 1990), and then afterwards begin to represent others' beliefs (Luo & Johnson, 2009; Onishi & Baillargeon, 2005; Wellman, Cross, & Watson, 2001; Wimmer & Perner, 1983; but see Powell, Hobbs, Bardis, Carey, & Saxe, 2018), knowledge and ignorance states (Perner, 1995; Perner, 2000), and finally, emotional states (Harris, Johnson, Hutton, Andrews, & Cooke, 1989; Wellman & Liu, 2004). Lastly, and not typically until late adolescence, do we see more sophisticated reasoning about other agents' linguistic intentions, including nuances such as metaphor usage and irony (Happé, 1994).

Some of the most famous evidence for the sophisticated theory of mind like abilities is in human infants at 15 months of age (Onishi & Baillargeon, 2005). In the "true belief" condition, both the infant subject and the presenter watched as an object was hidden in one of two locations. Critically, during the test trial, the subjects then watched as the presenter reached into the location where both she and the participant watched the object hidden or the opposite empty location. If infants are able to take the visual perspective of the presenter and use this perspective to form expectations for how other agents should act, then they should look longer when the presenter does the unexpected thing and reaches into the empty box. Indeed, Onishi and Baillargeon found that infants do look longer when another agent does the unexpected thing and acts inconsistently with her visual perspective. This is in contrast to the condition where the presenter acts consistently with her visual perspective (the expected condition). This task has been adapted and replicated in a number of different subjects, and in subjects as young as 10 months of age (Luo, 2011; Luo & Baillargeon, 2007; Sodian, Thoermer, & Metz, 2007). These more recent results and the original findings from Onishi and Baillargeon imply that visual perspective-taking is an emerging ability in humans that requires relatively little input and experience.

Here, we use a nearly identical task to examine the developmental origins of a similar visual perspective-taking ability in one primate species: the rhesus macaque (*Macaca mulatta*). Rhesus macaques are one of the most well-studied primate species in the domain of social cognition (Call & Tomasello, 2008; Chang et al.,

2013; Drayton & Santos, 2016; Platt, Seyfarth, & Cheney, 2016; Rosati et al., 2010). The rhesus macaque is a species of old-world monkey that makes a good candidate for studying the origins of visual perspective-taking for a couple of reasons. First, because of this species' complicated social structure, we can test what aspects of complex sociality is enough to scaffold the emergence of some of these sociocognitive abilities. Rhesus macaques exhibit a linear dominance hierarchy, whereby individuals must compete for resources including water and food, but also social activity such as grooming and mating opportunities (Maestriperi & Hoffman, 2012). One might expect that a prerequisite to succeeding in such a despotic social environment would be sophisticated social cognition. For nearly two decades, scientists have been studying exactly this question, specifically, what theory of mind abilities adult rhesus macaques possess (for a review, see Drayton & Santos, 2016; Ghazanfar & Santos, 2004). To date, available evidence suggests that adults of this species are able to take the visual perspective of other agents and to use this information when deciding whom to steal from (Flombaum & Santos, 2005). More recent work from the same population has demonstrated that adult rhesus monkeys can flexibly use the visual perspective of another agent, habituating across repeated uninformative gaze cues (Bettle & Rosati, 2019; Rosati, Arre, Platt, & Santos, 2016), forming expectations about how other agents should act based on these perspectives (Martcorena, Ruiz, Mukerji, Goddu, & Santos, 2011), and representing visual perspectives to make inferences about behavior when the other agent is knowledgeable or ignorant (Drayton & Santos, 2017, 2018; Horschler, Santos, & MacLean, 2019). There is less evidence, however, that this species can represent others' false beliefs (Martcorena et al., 2011; Martin & Santos, 2014).

Despite the abundance of work testing theory of mind abilities in adult rhesus monkeys, we actually know very little about social cognition changes in younger individuals of this species. However, these types of comparative developmental studies are important for informing critical theories in human development, specifically, those theories outlining what kinds of experiences are necessary for the emergence of certain sociocognitive abilities (Rosati, Wobber, Hughes, & Santos, 2014; Tomasello, 2019). Though adult primates share with humans a complex social structure, and frequent engagement and observance of social interactions, they lack some social behaviors implicated in early human social development such as false belief representational abilities (Martcorena et al., 2011; but see Krupenye, Kano, Hirata, Call, & Tomasello, 2016).

To fill this gap, here we studied the development of visual perspective-taking in young rhesus macaques. Specifically, we tested 236 infant and juvenile rhesus macaques on a task assessing visual perspective-taking that had previously been validated both with human infants (Onishi & Baillargeon, 2005) and adult macaques of this exact population (Martcorena et al., 2011).

Very few studies of non-human cognitive development have been conducted on such a large scale, though two (Rosati, Arre, Platt, & Santos, 2018; Rosati et al., 2016) existing studies have

tested social cognitive development in macaques from this same population. In one such study (Rosati et al., 2016), researchers investigated the developmental trajectory of gaze-following, or the ability to co-orient with another individual. They found that despite different early socioecology, rhesus macaque gaze-following abilities followed a human-like, but developmentally delayed trajectory. For young rhesus macaques, this means some gaze following in early infancy (under 1 year of age), with the ability ramping up during the juvenile period (between 2 and 5 years of age). However, it appears that primate subjects do not appropriately use gaze cues until adulthood, as infants are slow to habituate even in the absence of a potential target as compared to adult, and even juvenile subjects. Though other studies have investigated the development of cognitive abilities in macaques as compared with humans (Almeling, Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer, 2016; Ferrari et al., 2006; Ferrari, Kohler, Fogassi, & Gallese, 2000; Ferrari, Paukner, Ionica, & Suomi, 2009; Natale & Spinozzi, 1988; Simpson et al., 2016; Weed, Bryant, & Perry, 2008), these two studies are of particular relevance in part due to their large sample size and coverage across the entire primate lifespan as opposed to focus on a single-age class.

On the basis of this very small body of literature assessing the lifelong development of different cognitive abilities in rhesus macaques, we anticipated that rhesus monkeys would show a similar, but delayed, developmental trajectory as human children. Specifically, we expected we would see limited or no evidence of visual perspective-taking in infant rhesus macaques (<1 year of age), with the ability stabilizing throughout the juvenile period (between 1 and 5 years of age).

2 | METHODS

2.1 | Subjects

We tested infant and juvenile rhesus macaques from the Cayo Santiago Biological Field Station population (Rawlins & Kessler, 1986), a small research site on an island off the east coast of Puerto Rico. The field site has been in operation since 1938, and is home to over 1,500 free-ranging macaques. At 1 year of age, each monkey in this population receives a unique ID, which is tattooed on the monkey's chest and inner right thigh. Additionally, the monkeys on the island are diverse in sex, age, and social rank make-up, making them an ideal population to study comparative development.

All individuals on the island under the age of 5 years (60 months) were eligible for the study. Monkeys younger than 1 year of age were not yet tattooed, and thus were identified by their mother's ID. Infant and juvenile monkeys could be tested alone or clinging ventrally to a calmly sitting mother. In either event, we required a nursing event to properly identify the infant subject. Once a nursing incident was observed between the subject and the mother, the sex of the individual was confirmed by the matriline data provided by our census team. If subjects could not be properly identified, they were excluded (for a more detailed account of exclusions, see the Section

2.4 below). The birthdates of each individual were taken from the matriline database developed by the Cayo Santiago census team and are estimated to have an error window of one to 3 days.

Between January and July 2017, we successfully tested 236 young rhesus macaques, (infant $n = 75$; juvenile $n = 161$). The age cohorts are illustrated in Table 1. Age distribution across the two conditions is illustrated in Figure 1.

2.2 | Apparatus

In the experiment, we presented monkeys a set of stimuli or events taking place on a stage built from foamcore (Figure 2). The box was 30" long and 10" deep. On the front of the stage was a large screen (24" tall), which we used to occlude the entire display from the view of the subject. The back of the stage was 22", approximately chest height of the presenter when she was kneeling. On either side of the stage was a small box (6" × 6" × 6"). The two boxes were different colors (blue and orange) to individuate them, and the inner side of each box was left open but trimmed with fake leaves. This allowed for the moving object (a plastic lemon) to enter and exit the two boxes, but prevented the subject from seeing the content of the box. We cut through the center of the stage to create a track, which allowed the lemon to move between the two boxes. A handle attached to the lemon beneath the stage allowed the experimenter to surreptitiously manipulate the movement of the lemon, out of view of the subject.

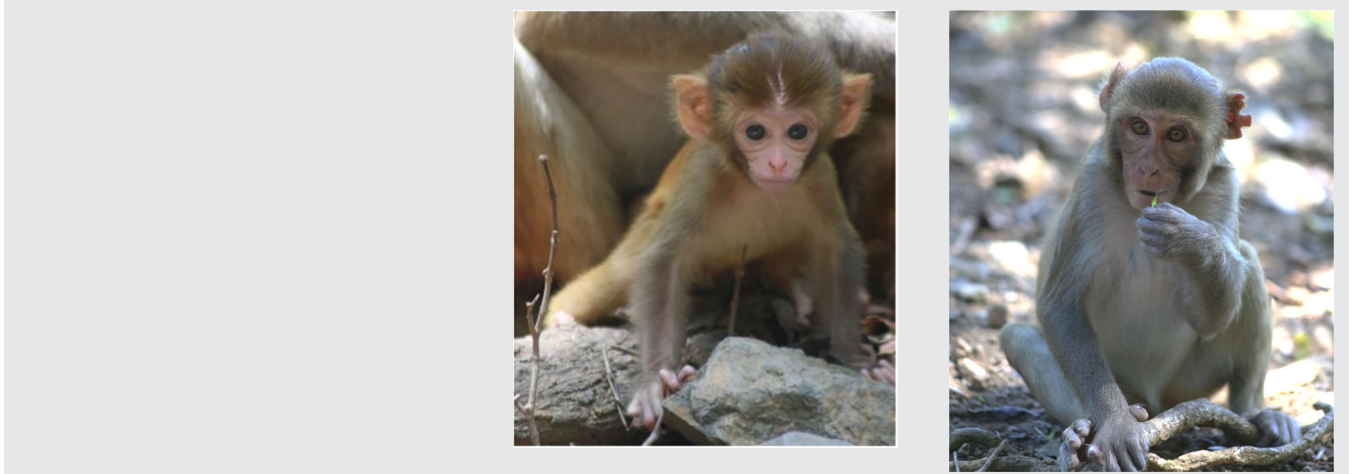
2.3 | Procedure

The experimental procedure was identical to a previous study testing adult macaques from the same population (see Experiment 1 in Marticorena et al., 2011). Two experimenters ran each session. To begin a session, both experimenters approached a calmly sitting monkey. The presenter (E1) would kneel roughly one to three meters away and place the apparatus between herself and the subject monkey. The cameraperson (E2) would then stand over or kneel beside E1 and begin filming the subject. At the start of each trial, E1 would set the apparatus stage and then call "now" as she dropped the occluder. At this cue, E2 would begin timing. After 10 seconds, E2 would call "stop." Each study session consisted of three 10-s trials: two familiarization trials and one test trial (for a detailed illustration, see Figure 2).

In the first familiarization trial (familiarization to the action), monkeys watched as the occluder dropped and the experimenter reached into one of the two boxes, and then held that position for the duration of the trial (10s). In the second familiarization trial (familiarization to the object), the occluder dropped and the experimenter looked down at the object, a lemon, for the duration of the trial. In the final trial, *the test trial*, the occluder dropped and the stage was empty, with the lemon inside in the blue box. Depending on the condition, the lemon either moved out of and into that same blue box, or the lemon crossed the stage and went into the opposite orange box. If subject monkeys tracked the visual

TABLE 1 Subject-age cohort distribution and study results

Age cohort	Infants	Juveniles
Age (months)	0–12	12–60
Lifespan event markers	Birth to weaning age	Weaning age to sexual maturity
Sample size (n)	75	161
Looking-time in expected condition (seconds)	5.00	3.86
Looking-time in unexpected condition (seconds)	3.98	4.49



Note: These cohorts reflect the nomenclature used in the previous cognitive developmental literature on this population (Rosati et al., 2016).

perspective of the presenter and expected her to act consistently with her visual perspective, then they should expect E1 to reach into the box she just watched the lemon go into. To test this, we presented monkeys with either a test trial in which E1 reached into the box holding the lemon (expected test condition) or one in which E1 reached into the box that was empty (unexpected test condition). In both conditions, the experimenter held the reaching position for the duration of the trial. We counterbalanced both the reach in trial one and the box that the lemon was hidden in the test

trial, across subjects, such that in total there were four counter-balanced conditions, two with expected outcomes and two with unexpected outcomes.

2.4 | Exclusions

To count as a successful session, we required that subject monkeys complete all three 10-s trials. In total, we successfully tested 236 monkeys. We also approached another 139 monkeys that did not successfully complete the session because the subject monkey approached the box (3), was interfered with or displaced by another monkey, most commonly its mother (10), stopped attending to the stimuli (7), walked away (33), had seen the entire study at an earlier date (41), or were never correctly identified (a). An additional 44 more sessions were excluded immediately after collection due to presenter error. During three sequential days of data collection (June 3–6, 2017) we determined that E1 was presenting the incorrect order of stimuli to the subjects such that the conditions did not match those originally presented during the initial data collection session (January 3–15, 2017). To ensure consistency across data collection trips, we excluded all successful sessions collected during this three-day period (44 sessions). All subject monkeys tested during this time were also ineligible for testing in the subsequent days of data collection. The decision to exclude the sessions from these dates was made the day the error was discovered, June 6, 2017, before data clipping, coding, or analysis. Even with this error, the study had about a 65.5% success rate, which is consistent with other cognitive studies carried out on Cayo Santiago (Drayton & Santos, 2017,

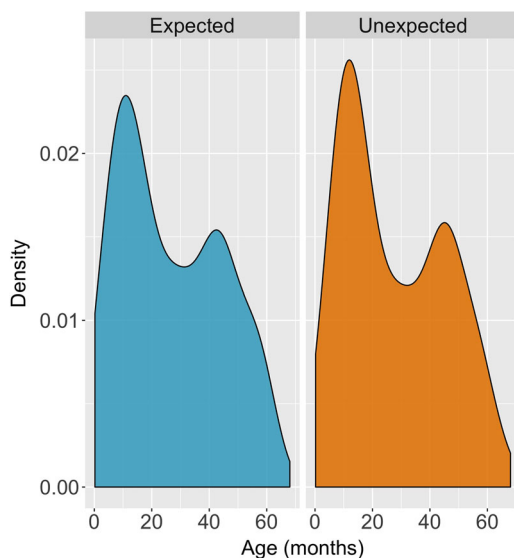


FIGURE 1 Histograms of the subject age distribution (in months) split by session condition. There was no significant difference in overall age variance between the two conditions

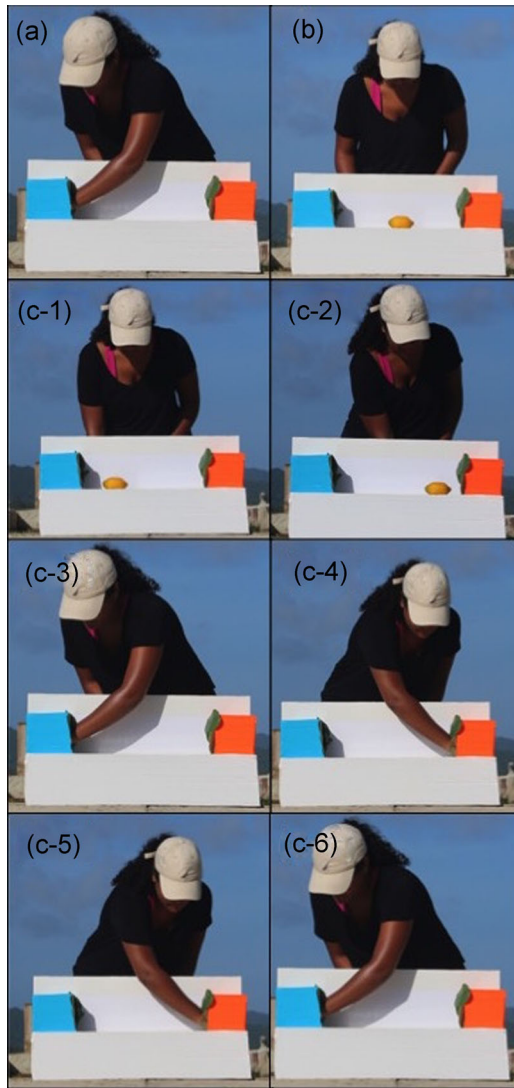


FIGURE 2 Demo photos of each trial type. (a) Trial 1: Familiarization to action; (b) Trial 2: Familiarization to object and (c1–6) Trial 3: Test trial: the subject and presenter watch as the lemon exits the blue box and either (c1) returns to the blue box or (c2) crosses the stage and enters the orange box. The presenter then either acts consistently with her visual perspective, (c3, 4) reaching the box which she and the subject just watched the lemon disappear into (the expected condition) or acts inconsistently with her visual perspective, (c5, 6) reaching into the box opposite of the lemon (the unexpected condition)

2018; Horschler, Santos, & MacLean, 2019; Marticorena et al., 2011; Martin & Santos, 2014).

2.5 | Data analysis

Experimental trials were then clipped so that they could be coded blind to condition; we removed all identifying information (including subject ID, trial number, condition, and session type) from each clip and gave each a randomized identifying code. Two independent experimenters each coded all of the clips for subject looking-time toward the entire experimental setup during each frame. Interobserver reliability was high

(Pearson's $R = 0.92$), which is consistent with other studies from this field site (Drayton & Santos, 2017, 2018; Horschler, Santos, & MacLean, 2019; Marticorena et al., 2011; Rosati et al., 2018). Data from the first coder was used for the purpose of the data analysis, though the results are the same regardless of the data used. All analyses were done using RStudio statistical software, Version 1.0.153 (R Core Team, 2016).

2.6 | Data availability statement

The data (Arre, Clark, & Santos, 2019) that support the findings of this study are openly available in the Open Science Framework data repository at https://osf.io/76439/?view_only=cf6cef3b7c9e40679c61e8403d4f4c0f.

2.7 | IACUC approval and ethics statement

All research protocols reported in this manuscript were reviewed and approved by the Institutional Animal Care and Use Committee of Yale University (IACUC Protocol #2014-11624) and the University of Puerto Rico (Protocol #8310106). The research presented in this manuscript adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates and the legal requirements of Puerto Rico.

3 | RESULTS

Since we predicted that we might see different looking patterns in the critical test trial as a function of age, we first ran a two-way analysis of variance on the sample ($n = 236$) to examine the effect of

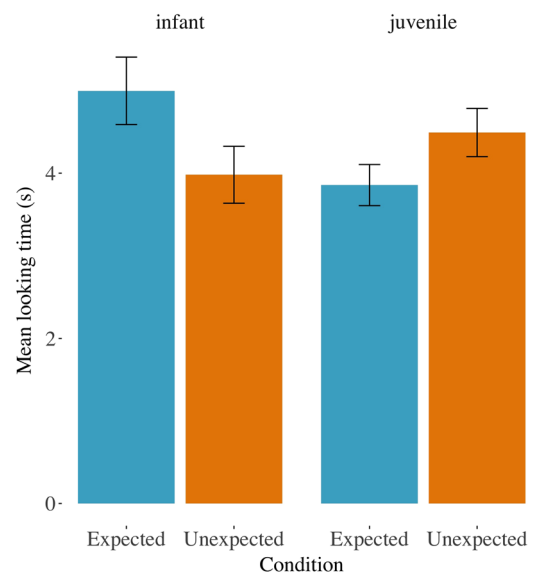


FIGURE 3 Although a two-way analysis of variance revealed a significant interaction between cohort and condition, $F(1, 232) = 6.082$, $p = .014$, $\eta p^2 = 0.05$, the looking-time between conditions within each cohort (infants [$p = .06$] and juveniles [$p = .09$]) did not differ significantly

age cohort and condition on the subject monkeys' looking-time. We found a weak but significant interaction in monkeys' patterns of looking between conditions as a function of their age cohort, $F(1, 232) = 6.08$, $p = .014$, $\eta^2 = 0.05$; Figure 3. We then looked at simple main effects of condition on subjects of each age cohort's looking-time using an independent samples t test. Infants (less than 1 year of age; $n = 75$) looked longer in the expected condition ($M = 5.00$ s, standard deviation [SD] = 2.49 s) as compared to the unexpected ($M = 3.98$ s, $SD = 2.13$ s) condition, though this trend was not statistically significant, $t(73) = 1.91$, $p = .06$, $d = 0.440$). In contrast, juvenile monkeys (between 1 and 5 years of age; $n = 161$) looked longer in the unexpected condition ($M = 4.49$ s, $SD = 2.63$ s) than the expected ($M = 3.86$ s, $SD = 2.23$ s) condition, though again this trend was not significant, $t(159) = -1.66$, $p = .09$, $d = 0.261$. Note that while these two different trends were not significant with each age cohort (infants: $p = .06$; juveniles: $p = .09$), the emerging pattern for the two age categories is significantly different ($p = .014$). Put simply, juvenile monkeys showed a trend toward a more adult-like pattern (Marticorena et al., 2011) in their looking behavior, and looked on average longer when the presenter reached inconsistently with her visual perspective (unexpected condition) than when she acted accordingly with her visual perspective (expected condition). Infant monkeys showed the reverse trend, looking longer when the presenter reached consistently with her visual perspective as compared to when she acted inconsistently with her visual perspective.

To be sure that monkeys assigned to the inconsistent reach condition were not looking longer across the entire study session, we also confirmed that the looking during the familiarization trials was functionally the same between conditions within each cohort. Using Welch's t tests, overall we found no significant differences between conditions in the familiarization trials. In the first familiarization trial, we found no significant difference on average looking-time between condition for the infants, $t(72.09) = 1.34$, $p = .185$, who watched equally in the expected ($M = 5.07$ s, $SD = 2.64$ s) versus the unexpected ($M = 4.29$ s, $SD = 2.42$ s) conditions, nor in the juveniles, $t(155.89) = 0.21$, $p = .834$, who also watched equally in the expected ($M = 5.05$ s, $SD = 2.37$ s) and unexpected ($M = 4.97$ s, $SD = 2.08$ s) conditions. The same was true in the second familiarization trial for juveniles, $t(156.33) = -0.42$, $p = .672$; expected condition ($M = 4.83$, $SD = 2.31$ s), unexpected condition ($M = 4.97$ s, $SD = 2.63$ s), and though the infants show a trend to look slightly longer in the expected condition ($M = 5.79$ s, $SD = 2.63$ s), as compared to the unexpected condition ($M = 4.70$ s, $SD = 2.52$), the difference is nonsignificant, $t(72.65) = 1.83$, $p = .070$. Given that the looking-time did not differ significantly between the two conditions in either of the first two familiarization trials, we concluded that any differences observed in the test trial reflect actual differences in attention between conditions and not artifacts of more general age-based differences in subject attention.

Finally, to exclude the possibility that differences we observed in the test trial were the result of subject population differences between conditions, we conducted an F test to check for equal age variance between the two populations. There was no significant

difference in age variance between condition, $F(1, 116) = 0.99784$, $p = .9911$, so a differential age distribution across the two conditions is not likely driving the looking-time differences between conditions.

4 | DISCUSSION

Do young monkeys know what others can see? Here, we present preliminary evidence that younger juvenile rhesus macaques may be able to represent the visual perspective of other agents and form expectations based on these perspective representations. We saw a nonsignificant trend in which juvenile rhesus macaques looked slightly longer when the experimenter acts inconsistently with her visual perspective (unexpected condition), reaching into the empty box, instead of reaching towards the box where she just watched the lemon disappear (expected condition). Note that this trend is similar to the pattern that adult rhesus macaques (Marticorena et al., 2011) and human infants (Onishi & Baillargeon, 2005) show more robustly. If the trend we observed in juvenile macaques holds up when larger samples are tested, then it is possible that those rhesus juveniles can indeed track the visual perspective of another agent and form expectations about how an agent will act based on that perspective-taking.

Does this adult-like pattern of performance extend to rhesus infants? Interestingly, the answer here seems to be no. We found that a monkeys' pattern of looking depends largely on its age; indeed, we found significantly different looking patterns in the critical test trial across our two age cohorts. In contrast to the pattern we observed in juveniles, infant rhesus macaques trend towards looking longer when the agent acted in a *consistent* way (expected condition), reaching towards the location of a hidden object, as compared to the inconsistent behavior (or unexpected condition), when she reached towards the box that both she and the subject knew was empty. This pattern, though nonsignificant ($p = .06$) is the opposite of what is observed in human infants and adult rhesus macaques, both of whom look longer in the unexpected condition when the presenter acts inconsistently with her visual perspective. Our data, therefore, hint that infant rhesus macaques (under 1 year of age) may be unable to form accurate expectations based on the visual perspective of another agent. That said, it's worth noting that though we found a significant difference between our two age cohorts, the pattern we observed within each age cohort was not statistically significant. For this reason, the trends we observed within each group should be considered with caution.

Assuming these results hold when larger within-age samples are tested, there are a number of possible explanations for significant developmental change we seem to have observed. One possibility is that monkeys' development of visual perspective-taking shows a human-like pattern, but young monkeys are delayed in their ability to make inferences about how another agent will act based on this visual perspective representation. This parallel, but delayed, the developmental pattern of visual perspective-taking in macaques relative to humans would be consistent with what has been observed in other sociocognitive domains. Specifically, this pattern mirrors the

developmental pattern of gaze following (Rosati et al., 2016), an ability often implicated as a foundational ability required for scaffolding more sophisticated mentalizing skills (Shepherd, 2010; Wellman, 2011).

Though gaze-following and perspective-taking in human infants are present from an extremely young age, the emergence of these abilities in primates appears delayed. Taken together, the trending results presented here, and those from prior work (Rosati et al., 2016), suggest that young rhesus macaques may require more experience in order for their sociocognitive abilities to come online. What types of experiences specifically might help scaffold these early-emerging perspective-taking abilities? Tomasello and colleagues have argued that early human infant engagement in joint attentional activities with other social agents is one activity that may help young infants develop their perspective-taking abilities (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Tomasello, 1995). However, we know that most non-human primates do not engage in joint attention in the same way as humans (Tomasello, Carpenter, Call, Behne, & Moll, 2005). Another possibility, then, is that more input of other types of social experiences, like watching other agents act on their visual perspectives, might be necessary in order for infants to make these predictions themselves. Future work will need to investigate the precise early experiences required for young macaque social cognition.

A different alternative, though, is that the flipped trend of looking we see in infant rhesus macaques is indicative not of a developmental delay, but instead of a neophobic response. A condition in which the presenter acts consistently with her visual perspective may be a more familiar behavior to infants, and thus may be a more preferable gaze target for infant rhesus macaques. Indeed, this pattern of looking longer at the consistent condition is reminiscent of some of the developmental results in human infants (for a review see Houston-Price & Nakai, 2004; Hunter & Ames, 1988). Specifically, human infants sometimes show preferential looking to the familiar or *expected* condition rather than the novel or unexpected condition in a variety of domains. Several researchers have posited that this preferential looking towards the expected condition in looking-time studies may be an artifact of a more domain-general aversion to novel events and stimuli, or neophobia, which human infants show around this age (e.g., Hunter & Ames, 1988). However, it's again worth noting that the difference we observed in infant macaque looking across conditions was non-significant ($p = .06$), and thus we should be cautious in interpreting this pattern of performance too strongly.

Taken together, this first test of non-human primate visual perspective-taking development shows that infant and juvenile rhesus macaques seem to undergo a developmental transition. This transition takes place sometime around their first and second year of age as infants are weaning and gaining independence from their mothers. We found a significant interaction in looking-time patterns between the two cohorts, where juvenile rhesus monkeys showed a trend toward a more adult-like pattern of looking longer at the unexpected condition, whereas infant rhesus showed the opposite trend. To further understand this pattern, future work should test larger within-age cohorts to gain the statistical power needed to determine whether these trends reflect the real

patterns shown by these age groups. Moreover, future work should also attempt to tease apart the types of experiences required for these sociocognitive abilities to emerge, investigating behavioral differences around the weaning transition (1 year of age), to see how infant macaques around that age are changing in their independence, social interactions, and observations of other social agents.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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DATA AVAILABILITY STATEMENT

The data (Arre, Clark, & Santos, 2019) that support the findings of this study are openly available in the Open Science Framework data repository at https://osf.io/76439/?view_only=cf6cef3b7c9e40679c61e8403d4f4c0f, reference DOI: 10.17605/OSF.IO/76439.

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