

Predictions About Reward Outcomes in Rhesus Monkeys

Yiyun Huang¹, Hayoung Chang², Laurie R. Santos³, and Alexandra G. Rosati^{1, 4}

¹Department of Psychology, University of Michigan

²Department of Human Evolutionary Biology, Harvard University

³Department of Psychology, Yale University

⁴Department of Anthropology, University of Michigan

Human infants and nonhuman animals respond to surprising events by looking longer at unexpected than expected situations. These looking responses provide core cognitive evidence that nonverbal minds make predictions about possible outcomes and detect when these predictions fail to match reality. We propose that this phenomenon has crucial parallels with the processes of reward prediction error, indexing the difference between expected and actual reward outcomes. Most work on reward prediction errors to date involves neurobiological techniques that cannot be implemented in many relevant populations, so we developed a novel behavioral task to assess monkeys' predictions about reward outcomes using looking time responses. In Study 1, we tested how semi-free-ranging monkeys ($n = 210$) responded to *positive error* (more rewards than expected), *negative error* (less rewards than expected), and a *number control*. We found that monkeys looked longer at a given reward when it was unexpectedly large or small, compared to when the same quantity was expected. In Study 2, we compared responses in the *positive error* condition in monkeys ranging from infancy to old age ($n = 363$), to assess lifespan changes in sensitivity to reward predictions. We found that adolescent monkeys showed heightened responses to unexpected rewards, similar to patterns seen in humans, but showed no changes during aging. These results suggest that monkeys' looking responses can be used to track their predictions about rewards, and that monkeys share some developmental signatures of reward sensitivity with humans, providing a new approach to access cognitive processes underlying reward-based decision making.


Keywords: reward, prediction error, looking time, comparative development, primates

Supplemental materials: <https://doi.org/10.1037/bne0000573.supp>

Adult humans frequently make predictions to guide decisions and then update our predictions when they are wrong. Consider a choice between different take-out restaurants: if a person's preferred restaurant suddenly took an exceptionally long time to deliver food—or did not show up at all—this might affect how preferred it is next time. This kind of updating based on “reward prediction errors”—the discrepancy between our initial predictions and what then actually happens—is thought to be a fundamental process supporting learning (Dayan & Daw, 2008; Garrison et al., 2013; Niv & Schoenbaum, 2008; Schultz, 2016b). Indeed, such reward

prediction errors are proposed to feed into many higher level cognitive processes including decision making, declarative memory, prosocial judgments, and even moral reasoning (Cushman, 2013; d'Acremont et al., 2009; Ergo et al., 2020; Gershman & Goodman, 2014; Kuss et al., 2013; Oya et al., 2005; Sinclair & Barense, 2018). Work from cognitive science similarly shows that nonverbal infants and animals make predictions about the world, detecting when outcomes do not match their predictions—here using looking responses to index when individuals detect unexpected events across many different situations (Baillargeon,

Yiyun Huang  <https://orcid.org/0000-0001-5269-3775>

Alexandra G. Rosati  <https://orcid.org/0000-0002-6906-7807>

The Cayo Santiago Field Station is supported by a National Center for Research Resources CM-5-P40RR003640 award and an Office of Research Infrastructure Programs of the National Institutes of Health through Grant 5P40OD012217 to the Caribbean Primate Research Center and the University of Puerto Rico. This research was supported by the National Institute of Mental Health (Grant No. R01MH096875), the National Science Foundation (Grant No. 1944881), and a Sloan Foundation Fellowship (Grant No. FG-2019-12054).

The authors thank Alyssa Arre, Megan Cole, Francesca De Petrillo, Liz Jones, Laura Lewis, Samantha Monier, Rebecca Spaulding, and Emily Walco for assistance with data collection and coding, and Consulting for Statistics, Computing, and Analytics Research at the University of Michigan for statistical advice. The authors also thank the Cayo Santiago Field Station staff including Angelina Ruiz Lambides, Nahiri Rivera Barreto, Giselle

Caraballo Cruz, and Bianca Giura for their support.

Yiyun Huang played a lead role in writing—original draft, a supporting role in data curation and writing—review and editing and an equal role in formal analysis and visualization. Hayoung Chang played a lead role in data curation, a supporting role in writing—original draft, and writing—review and editing and an equal role in investigation. Laurie R. Santos played a supporting role in methodology, writing—original draft, and writing—review and editing and an equal role in conceptualization, funding acquisition, project administration, resources and supervision. Alexandra G. Rosati played a lead role in data curation, methodology and writing—review and editing, a supporting role in writing—original draft and an equal role in conceptualization, formal analysis, funding acquisition, investigation, project administration, resources, supervision and visualization.

Correspondence concerning this article should be addressed to Alexandra G. Rosati, Department of Psychology, University of Michigan, 530 Church Street, Ann Arbor, MI 48109, United States. Email: rosati@umich.edu

1986; Hood & Santos, 2009; Onishi & Baillargeon, 2005; Santos & Hauser, 2002; Spelke, 2003, 2022; Spelke & Kinzler, 2007; Vallortigara, 2012; Wynn, 1992; Wynn et al., 2002). Recent work further argues that increased looking responses similarly function as a learning signal to optimize behavior (Berger & Posner, 2022; Köster et al., 2020; Stahl & Feigenson, 2015, 2017, 2019). Here, we propose that these two phenomena—reward prediction errors and expectancy violation looking responses—may reflect overlapping cognitive processes. We test this idea by developing a novel violation-of-expectation looking time paradigm (see Margoni et al., 2022; Stahl & Feigenson, 2017 for overviews) to assess if monkeys' expectations about reward outcomes generate longer looking times when their predictions do not match real outcomes, compared to when they do. We finally examine developmental changes in these looking responses in a large sample of monkeys to test whether our task also captures key developmental signatures of reward sensitivity seen in humans.

Reward prediction error signals are a concept from neurobiology and decision science that hinge on the detection of expectation violations. In particular, reward prediction errors reflect a discrepancy between what is *predicted* to happen (the reward one expects to receive) and what *actually* happened (the reward one actually receives). This concept was first proposed in the context of reinforcement learning (Rescorla & Wagner, 1972), and subsequent research using neurobiological techniques in animals has demonstrated that these error signals are encoded at the level of neurons (Dayan & Daw, 2008; Glimcher, 2011; Niv & Schoenbaum, 2008; Schultz, 2016b; Schultz et al., 1997; Watabe-Uchida et al., 2017). This work shows that dopamine neurons do not fire to rewards in general but rather fire specifically in response to such prediction errors. When a reward is unexpectedly delivered or unexpectedly better than predicted, dopamine neuron firing increases; conversely, when expected rewards are withheld or unexpectedly less than expected, dopamine neuron firing is suppressed. These prediction error responses are thought to be a key learning signal for adaptively learning and updating behavior.

Subsequent work using neuroimaging techniques has detected neural correlates of reward prediction errors in humans across several brain regions implicated in a variety of decision-making processes, suggesting that this is fundamental to how humans assess value and evaluate different possible options (Ablner et al., 2006; Bayer & Glimcher, 2005; D'Ardenne et al., 2008; Enomoto et al., 2011; Watabe-Uchida et al., 2017). For example, prediction errors may play a role in cognitive processes including economic decision making, memory, and social decision making (Cushman, 2013; Ergo et al., 2020; Gershman & Daw, 2017; Gershman et al., 2014; Kuss et al., 2013; Otto et al., 2013; Sinclair & Barense, 2018), showing how this fundamental reward learning process may scaffold other diverse cognitive functions. This work with humans further has allowed for developmental studies of sensitivity to prediction errors across the lifespan. In fact, human adolescents show heightened sensitivity to reward prediction errors (Cohen et al., 2010; Hauser et al., 2015), but these signals appear to be degraded in old age (Chowdhury et al., 2013; Samanez-Larkin et al., 2014). These neural changes mirror broader age-related shifts in decision-making preferences across the life span (Casey, Getz, et al., 2008; Eppinger et al., 2012; Hartley & Somerville, 2015), supporting the claim that prediction error signals are behaviorally relevant for choice behavior.

Work from developmental psychology and comparative cognition has similarly harnessed responses to unexpected outcomes to understand cognition in infants and animals using behavioral techniques. This line of work often uses looking time methods to assess if individuals detect unexpected or surprising events by measuring how long they look at different possible outcomes (see reviews of looking time methods in Margoni et al., 2022; Winters et al., 2015). In fact, babies and animals look longer to unexpected compared to expected events across many conceptual domains, spanning knowledge of objects, numerical cognition, and social cognition. For example, human infants and monkeys look longer at scenes where objects violate physical principles, such as by passing through solid walls compared to when an object's pathway is blocked by barriers as would be expected (Hood & Santos, 2009; Santos & Hauser, 2002; Spelke et al., 1992; Spelke & Kinzler, 2007). Similarly, infants and animals look longer when agents perform actions that are inconsistent with their inferred knowledge and goals compared to when the agent's actions align with what they know or want (Drayton & Santos, 2016; Marticorena et al., 2011; Martin & Santos, 2014, 2016; Onishi & Baillargeon, 2005; Woodward, 1998). Thus, violation-of-expectancy looking time methods have become a key method to infer how animals and infants understand their respective worlds (Margoni et al., 2022; Spelke, 2022).

However, while looking time methods are in wide use, the specific cognitive processes that generate these responses are still unclear. One recent proposal argues that longer looking times index a learning signal that motivates children to preferentially engage with aspects of the environment that have unexpected properties in order to learn about them (Stahl & Feigenson, 2015, 2017, 2019). For example, when children see one object that acts "normally" in accordance with spatiotemporal contact principles, whereas another object violates these principles (e.g., appearing to move through a solid wall), children looked longer at the unexpected event compared to the expected event, and then were subsequently more likely to explore the object that violated their expectations compared to the object that did not. Along the same lines, recent proposals have interpreted infant violation-of-expectancy looking responses from the perspective of predictive processing, arguing that longer looking is a predictive signal allowing infants to learn about their environment (Köster et al., 2020). Related proposals point out that these looking responses share a neural basis with adult predictions (Berger & Posner, 2022). For example, infants' inferences about arithmetic (e.g., that one plus one equals two) generate predictable event-related neural responses to incorrect numerical outcomes (Berger et al., 2006) that are similar to those seen in adults (Berger & Posner, 2022).

Together, these theoretical perspectives suggest that longer looking times in response to expectancy violations share some key features with reward prediction errors: both index the difference between one's prediction about an outcome and reality, and both are proposed to be crucial signals for adaptive learning and updating in a predictive learning framework. However, no work to date has specifically linked violation-of-expectation looking responses to reward prediction errors. Here, we propose that such reward prediction errors may scaffold more complex forms of predictions and inferences, and empirically test whether reward prediction errors generate increased looking responses to violations of expectations in monkeys. Crucially, prior infant work considering how looking time responses relate to infant's predictions has focused on other kinds of violations,

such as violations of spatiotemporal object knowledge, social knowledge, or arithmetic knowledge (Berger & Posner, 2022; Köster et al., 2020; Stahl & Feigenson, 2019). Here, we focus on reward predictions, the foundation of prior neurophysiological work with animals. We therefore developed a behavioral task using a looking time violation-of-expectation method to assess monkeys' responses to reward outcomes. In particular, we adapted the basic premise of expectancy violation looking time methods that have been previously used to assess a wide variety of cognitive skills in monkeys, including physical knowledge, social knowledge, and statistical inference (Arre et al., 2020, 2021; Bettle & Rosati, 2021; De Petrillo & Rosati, 2019; Drayton & Santos, 2016; Higham et al., 2011; Hughes & Santos, 2012; Marticorena et al., 2011; Martin & Santos, 2014; Rosati et al., 2018), modeled on parallel work with infants. As studies of reward prediction error in both animals and adult humans typically use neurobiological techniques (Bayer & Glimcher, 2005; Garrison et al., 2013; Schultz, 2016b; Watabe-Uchida et al., 2017), we aimed to validate this novel task for wider use with infant and other animal populations that cannot be assessed with such neurobiological methods.

To do so, we developed a novel looking time task to measure predictions about reward outcomes in semi-free-ranging monkeys at the Cayo Santiago Biological Field Station. While such field experiments are inherently less controlled than experiments conducted in laboratory environments, the benefit of this approach is that we could test responses in a large population of monkeys. Furthermore, as this is a freely breeding naturalistic population, monkeys vary in age from infancy to old age. As such, Cayo has emerged as a crucial site for work examining comparative cognitive development in primates (Arre et al., 2020; Hughes & Santos, 2012; Rosati et al., 2014, 2016, 2018; Rosati & Santos, 2017). While rhesus macaques are an important neurobiological model species for studies of reward processing, including studies of reward prediction error (Bayer & Glimcher, 2005; Enomoto et al., 2011; Lak et al., 2014; Schultz et al., 1997), prior work using neurobiological techniques has been fairly limited in terms of sample size and thus unable to assess such questions about comparative cognitive development in animals.

We conducted two looking time studies in this population. In Study 1, we tested 210 monkeys to validate our novel behavioral task. Monkeys first experienced that a distinct cue predicted a certain number of fruits. Then in test trials, they saw that same cue proceeded either more fruits than expected (*positive reward prediction error*), less fruits than expected (*negative reward prediction error*), or the number of fruits expected (*no discrepancy*). We compared monkeys' looking responses to expected and unexpected outcomes across these situations. Our key prediction was that monkeys would look longer when the outcome fruit number did not match their expectations compared to when it did. While our task does not directly provide food rewards that the animals could consume (given the nature of looking time studies), our goal was to create an analog of reward prediction error tasks using an expectancy violation methodology. In fact, while some studies of reward prediction errors in humans have used consumable rewards like typical animals studies (e.g., D'Ardenne et al., 2008; Salas et al., 2010), other studies have used hypothetical rewards, monetary rewards (which are physically realized after the fact), or even pleasant visual stimuli like attractive faces (Bray & O'Doherty, 2007; Cohen et al., 2010; Jauhar et al., 2021; Knutson & Cooper,

2005). This work with humans shows that comparable prediction error signals can be invoked in the brain by other kinds of rewarding experiences beyond consumption of food rewards, including anticipation of rewards and rewarding visual stimuli—more similar to our approach here. Along these lines, extensive prior work with this monkey population using comparable fruit stimuli has shown that monkeys find it rewarding to look at food stimuli and appear to perceive these fruits as real rewards. For example, the monkeys have shown keen interest in such fruit stimuli in a variety of other looking time studies (Arre et al., 2020, 2021; Bettle & Rosati, 2021; De Petrillo & Rosati, 2019; Drayton & Santos, 2016; Marticorena et al., 2011; Martin & Santos, 2014) and actively attempt to approach and attempt to search for these items as in comparable tasks using real food (Flombaum & Santos, 2005; Phillips & Santos, 2007; Rosati & Santos, 2016; Santos et al., 2002, 2006).

Study 2 then examined individual variation in the responses 363 monkeys to examine lifespan changes in responses. This study was aimed at using an individual differences approach to test whether sensitivity to positive reward prediction errors changes across the monkey life span from infancy to old age, here focusing on the positive reward prediction error condition validated in Study 1. If monkeys share the developmental signatures of reward prediction error seen in humans, we predicted that adolescent monkeys should show heightened looking responses to reward prediction errors, whereas older monkeys would show reduced sensitivity. Yet it is important to note that rhesus monkeys also show several important differences in life history characteristics compared to humans, including relatively faster growth and brain maturation during the juvenile period, no period of reproductive cessation (menopause), and a shorter absolute life span than humans (Alberts et al., 2013; Bogin & Smith, 1996; Leigh, 2004, 2012). As such, it is possible that rhesus monkeys would show different developmental trajectories than humans, a key focus of the emerging field of comparative cognitive development (Bjorklund & Bering, 2003; Bjorklund & Green, 1992; Gómez, 2005; Matsuzawa, 2007; Matsuzawa et al., 2006; Rosati et al., 2014). Indeed, work to date has revealed a mixed picture concerning shared versus divergent patterns of cognitive development in rhesus monkeys compared to humans. In some domains, such as gaze-following, humans and macaques show similar patterns across the life span (Rosati et al., 2016). However, they show different patterns of responses than human to socio-emotional information during aging (Rosati et al., 2018). As such, rhesus monkeys might also show different cognitive patterns than humans during early development or aging given their different life history traits and developmental trajectories.

Study 1: Looking Responses to Reward Prediction Errors

Study 1 familiarized monkeys to a specific sized reward outcome and then tested whether monkeys would look longer at unexpectedly larger or smaller reward outcomes compared to expected reward outcomes. Rhesus macaques were first shown that a distinct visual cue predicted a specific number of fruits (one or three fruits across conditions). Monkeys then saw a key test trial in which the same cue predicted either the expected number of fruits or a different, unexpected number of fruits as the final outcome. Each monkey completed two trials in a within-subject manipulation (e.g., comparison of responses to unexpected vs. expected outcomes) and was randomly assigned to one of three conditions in a between-

subject manipulation: (a) monkeys in the *positive error condition* were always initially familiarized to one fruit and then saw one fruit (the expected number) in the *expected trial*, but three fruits (more than expected) in the *unexpected trial*; (b) monkeys in the *negative error condition* were initially familiarized to three fruits and then saw the expected number of fruits in the *expected trial*, but only one fruit (less than expected) in the *unexpected trial*; and finally, (c) monkeys in the *number control* condition always saw the expected number of fruit in both trials (one or three across the two trials). The goal of this number control condition was to capture baseline differences in responses to different numbers of fruit (in the absence of any unexpected outcomes), as we expected that monkeys would generally look longer overall at more compared to less fruit. In terms of validating our task as a looking time measure of prediction errors, our key prediction was that the monkey's initial expectations would impact their looking, such that monkeys in the positive and negative error conditions would look longer at unexpected outcomes (that either produced more or less fruit than predicted) compared to expected outcomes that were consistent with their initial experience of the cue-fruit pairing.

Method

Ethics Statement

All noninvasive behavioral tests reported in this article were approved by the Institutional Animal Care and Use Committee for the University of Puerto Rico Medical Sciences Campus (Protocol Nos. A140116 and 8310106) and adhere to site guidelines for animal research.

Overview of Field Experimental Approach

We implemented a novel behavioral task by adapting looking time methods developed in prior work with infants and animals, and specifically by using the looking time methods that have been used extensively in the Cayo Santiago rhesus monkey population. In this approach, monkeys are tested while they free-range in natural groups. Experimenters carry a portable testing apparatus around the island and search for individuals who are in an appropriate position to be tested—that is, sitting calmly on the ground in a location where the experimenters can appropriately place the apparatus approximately 2 m in front of them so they can observe the experimental stimuli with an unobstructed view. One experimenter presents the experimental stimuli by manipulating the apparatus (as described in more detail below), whereas a second experimenter films the monkey's face in order to later code their looking times from the video. As the present study involved within-subjects comparison of responses to two trials, monkeys needed to stay in their location observing the stimuli for both trials in order to be included in the final data set. To assess looking times, individual trials were clipped out of longer session videos and coded blind to condition and trial type by two experienced coders. Both coders assessed all trials in the data set, allowing us to assess reliability across the whole study.

Participants

We tested 210 monkeys from the Cayo Santiago Field Station in Puerto Rico (70 per condition). The final sample included 109 females and 101 males, with a mean age of 8.0 years (range: 1.4–21.8), with a similar sex distribution and average age across

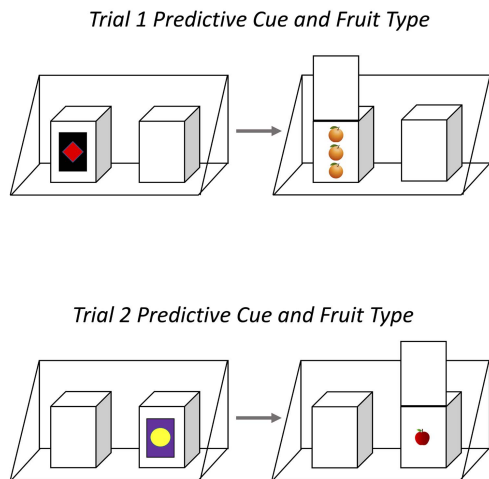
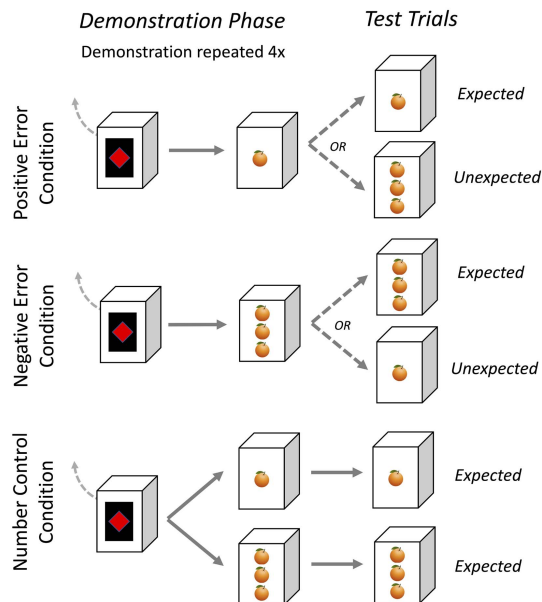
conditions. Splitting by the age cohorts used in Study 2 (see that study for details of these cutoffs based on life history transitions), this included $n = 45$ juveniles; $n = 50$ adolescents; $n = 94$ adults; and $n = 21$ older adults distributed across the six possible condition-trial order combinations. The Cayo Santiago population consists of more than 1,500 individually identifiable monkeys living in natural social groups on a 38-acre island off the coast of Puerto Rico (Rawlins & Kessler, 1986). Animals are well-habituated to human observers, and many monkeys have participated in multiple prior cognitive studies, as mentioned previously, but were naïve to this particular task and apparatus. Additional monkeys were approached for testing but did not complete the task in this free-ranging context, as detailed below.

Apparatus and Procedure

In sessions, two experimenters approached a calmly sitting monkey. Based on their sex and estimated age when identified as a potential subject, monkeys were randomly assigned to one of three possible conditions (*positive error condition*, *negative error condition*, *numerical control*; 70 per condition) in a between-subjects manipulation, with the goal of keeping the age and sex distributions of these conditions similar. As this was a field study where we tested free-ranging individuals opportunistically as they were located on the island (not a laboratory study where we could assign known individuals to conditions in advance), we specifically tracked the distribution of successfully tested subjects at the end of each day so that we could keep the subjects as balanced as possible across testing days. Each monkey then completed one session involving two trials (involving a one-fruit or three-fruit outcome, in counterbalanced order) in a within-subjects manipulation. Whether a given fruit outcome (one vs. three) represented an expected versus unexpected outcome depended on the particular condition, as described below. Monkeys that did not watch and provide scorable responses to both trials (e.g., because they walked away or were displaced by other monkeys before completing the session) were not included in the final data set, as described in more detail below.

In a given session, Experimenter 1 (E1), the presenter, knelt approximately 2 m away from the monkey and placed the apparatus in front of them so that the monkey could observe the apparatus (see Figure 1a). She then manipulated the apparatus to reveal the different reward outcomes across trials. Experimenter 2 (E2) knelt behind the primary demonstrator and filmed the monkey's face with a camera so that their looking times could be coded. Monkeys in appropriate positions to be tested were initially approached for the study blind to condition assignment, but E1 then necessarily knew the monkeys' condition assignment in order to assign them to a condition and manipulate the apparatus appropriately. However, E1 was blind to the monkey's looking responses in trials, as she looked down during those periods. As E2 could not see how E1 manipulated the apparatus from their position, she remained blind to condition; E2 therefore made the assessment to exclude monkeys when they walked away or experienced interference blind to the monkeys' condition assignment.

Across the two trials, the monkey observed E1 manipulate two different boxes to present the cue and fruit rewards (see Figure 1b). The boxes (each 15 cm wide, 16.5 cm tall) were presented on a white stage made of poster board (50 cm wide, 20 cm tall). Initially, the two boxes on the stage were both oriented such that only the white sides (without a cue) were visible. In a given trial, a single box was

Figure 1*Study 1 Procedure and Conditions***(a) General testing setup****(b) Apparatus overview****(c) Conditions and test trial outcomes**

Note. (a) The primary experimenter knelt approximately 2 m away from the monkey and manipulated the apparatus while the monkey observed. (b) The apparatus consisted of a stage with two boxes; each box was white on two sides but had a unique visual cue on front and back flaps (left box: a red diamond on a black background; right box: a yellow circle on a purple background). These boxes could be opened to reveal either one or three fruits depending on which flap was oriented toward the monkey. The first trial (left box) always involved oranges, and the second trial (right box) involved apples; whether the first trial involved an expected or unexpected outcome was counterbalanced across monkeys and conditions. (c) Example diagram of procedure for the first trial across conditions. Monkeys had different experiences in the demonstration phase depending on condition: in the *positive error condition*, monkeys always first experienced that the cue predicted one fruit (in both trials); in the *negative error condition*, they experienced that the cue predicted three fruits (in both trials); whereas in the number control, they were familiarized to one fruit on one of the trials and three fruits on the other trial. Then, in the final test trial, monkeys saw either one or three fruits as the outcome (order counterbalanced across the two trials). Because of their different demonstration phase experiences, one fruit was the expected outcome, whereas three fruits were an unexpected outcome (more than expected) in the positive condition. In contrast, three fruits were the expected outcome, whereas one fruit was the unexpected outcome (less than expected) in the negative error condition. In the number control condition, the test outcome always matched the demonstration phase, so this condition indexed baseline looking toward different amounts of fruit without violated expectations. See the online article for the color version of this figure.

manipulated by the experimenter (from the monkey's perspective, the left box was manipulated on trial one, and the right box on trial two). Each box had specific visual cue that appeared on both front and back flaps of the box: one flap opened to reveal one fruit,

whereas the other flap opened to reveal three fruits of the same type. Specifically, the left box manipulated in the first trial had flaps with a red diamond on a black background and contained plastic oranges, whereas the right box manipulated on the second trial had flaps with

a yellow circle on a purple background and contained apples. Thus, by surreptitiously rotating the box such that different sides were oriented toward the monkey, the experimenter could manipulate the number of fruits that was revealed after the cue was presented. We used plastic fruit mounted inside the boxes and under the flaps as the rewards in this study; as described previously, prior work with this population has shown that monkeys are interested in looking at plastic fruit as much as they look at real fruit (Bettle & Rosati, 2021; De Petrillo & Rosati, 2019; Marticorena et al., 2011; Martin & Santos, 2014), and further that they will actively approach and search for plastic fruit as though they were real fruit (Phillips et al., 2010; Rosati & Santos, 2016).

In a given trial, E1 tapped the relevant box and called the monkey (e.g., saying “monkey! monkey!”) to initially attract their attention, and turned it so that the flap with the cue was visible (see Supplemental Video S1, e.g., experimental demonstration). She then began an initial *demonstration phase*, consisting of four repetitions where the monkey viewed the flap with the cue, and then the experimenter opened the flap to reveal a given amount of fruit underneath (counting aloud to keep the timing equivalent across trials). This demonstration event repeated four times (for a total of approximately 8 s) to create the expectation that this particular visual cue was linked to this specific number of fruits. The demonstration phase was followed by a single *test event* where the experimenter lifted a flap to reveal either one or three fruits, which could be either an expected (matched the demonstration) or unexpected outcome depending on the initial demonstration (see Figure 1c). These different outcomes were implemented by first turning the box toward a white side and then completing an additional turn so that the appropriate flap would be facing forward in the final test event; the number of box turns was therefore identical for both outcome types.

To initiate the test event, the experimenter again tapped the box and called to ensure the monkey was looking. When she judged the monkey was looking, E1 initiated the trial by saying “now,” opening the box flap, and simultaneously averting her gaze downward so that she was not making eye contact with the monkey during the 10 subsequent seconds. Monkeys had to be looking at the start of a test trial to be included, and E1’s live judgment that they were looking was confirmed by checking the video. E2 timed this period using the camera timer and then said “stop” when 10 s had passed. Each trial therefore took about 20 s when considering the initial demonstration phase when the experimenter manipulated the boxes, setting up the test trial, and the subsequent 10 s test trial period that we coded for monkey’s looking responses. Once the first trial was complete, E1 then repeated this same procedure for the second test trial using the second box on the right side of the stage, again presenting monkeys with the demonstration phase followed by a test event. When a given box was not being actively manipulated for a trial, the experimenter turned the box’s blank white side toward the monkey so they could not see the cue flaps and so that the box would blend into the white background of the stage. The experimenter initiated the second trial as soon as possible after configuring the boxes in the appropriate location for the second trial and tapping the apparatus to ensure the monkey was again attending.

Conditions and Trial Types

To create different expectations about likely fruit outcomes, monkeys experienced different demonstration phases across the

different conditions. In the *negative error condition*, monkeys were always initially shown that the cue predicted three fruits (in both trials); the expected test trial therefore similarly showed three fruits, but the unexpected trial in this condition showed only one fruit (less than expected). The procedure for the *positive error condition* was identical, except that monkeys were always shown that the cue predicted one fruit in the demonstration phase; here, the one fruit outcome was therefore the expected outcome, whereas three fruits were the unexpected outcome. Finally, the procedure in the *number control condition* was similar, except that the number of fruits revealed in both test events was always expected (matched the outcome during demonstration). In particular, one trial involved four demonstrations that the cue predicted one fruit, whereas the other trial involved demonstrations that the other cue predicted three fruits (order counterbalanced). Then, the test event always matched the demonstrations. This allowed us to index baseline differences in looking time to different amounts of fruit. As trial order was counterbalanced within monkeys, the particular cue and fruit used in the unexpected versus expected trial (e.g., the red diamond on a black background predicting different numbers of oranges and the yellow circle on a purple background predicting different numbers of apples) were also counterbalanced across subjects.

Exclusions

In this free-ranging context, monkeys were necessarily tested when other monkeys were also present. As such, some monkeys were approached for testing but would fail to produce a scorable response, typically because they walked away from the testing area before completing both trials or were displaced by other monkeys while the task was ongoing ($n = 121$). These sessions did not have scorable responses because the monkeys did not complete both trials as was necessary for the study. These exclusions are similar to rates in prior studies in this free-ranging population (Bettle & Rosati, 2021; De Petrillo & Rosati, 2019; Marticorena et al., 2011; Martin & Santos, 2014). As noted above, E2 (who was blind to condition as they could not see the front of the apparatus) would make the judgment to stop the session because the monkey had been interfered with or walked away; note that this is typically clear to assess as the monkey typically left the testing area and therefore could no longer see the apparatus to complete the session. In addition, in some cases, animals were approached for testing more than once (e.g., because their identification was only confirmed after they completed the test, $n = 18$), in which case we only included and analyzed their first successful session in the final data set.

Video Coding

Two coders (AGR and a second coder not otherwise involved in the study) who were blind to trial type and condition independently scored both test trials from the final set of subjects. Both coders had previous experience coding monkey looking time data by coding prior studies. Coders were blind to both condition and trial type because each individual trial was clipped from longer video sessions, randomized across all trials, and renamed with a random number ID (e.g., Clips 1 through 420, the total number of trials in the final data set). A given trial clip started 1–2 s before the experimenter said “now” while E1 initially attracted the monkey’s attention, which allows coders to better judge where the monkey is looking at

the start of the trial as a reference, and ended after E2 said “stop” (see Supplemental Video S1, e.g., monkey looking responses in these clips).

The coders examined these video clips frame-by-frame using MPEG Streamclip to access total looking time at the apparatus per trial out of a total of 10 s, following typical methods used in prior looking time studies in this population (Arre et al., 2020, 2021; Bettel & Rosati, 2021; De Petrillo & Rosati, 2019; Drayton & Santos, 2018; Martin & Santos, 2014; Rosati et al., 2018). Specifically, clips were always coded for exactly 10 s from when E1 initiated the trial to equate total trial duration across monkeys. This coding followed the methods of prior looking time studies in this population noted above, where the monkey’s initial looking direction at the start of the trial (when the experimenter said “now”) as the reference to code their looking toward the apparatus for the subsequent 10 s. Monkeys had to be looking at the apparatus with their eyes. Note that there was no audible or visible condition or trial type information in these clips, nor was such information included in the coding file, so coders did not know what monkey, condition, or trial number they were coding. There was high reliability between the two coders for the full data set (Pearson’s $r = 0.96$).

Statistical Analyses

We analyzed the data in R v4.1.2 (R Core Team, 2022). Our first analyses examined duration of looking to different reward outcomes using linear mixed models (LMMs) implemented with the *lmer* function in the package lme4 (Bates et al., 2015). To index relative patterns of looking for each individual, we also calculated a *difference score* capturing relative change in looking time to larger rewards (looking time to three fruits – looking time to one fruit). To analyze these difference scores, we implemented linear regressions using the *lm* function. Across models, we accounted for *sex* and *age* (as a continuous predictor, in years), as well as *subject identity* (as a random factor to account for repeated measures) or trial order when relevant. We then added *fruit outcome*, *condition*, and any relevant interactions to test their importance as predictors. We compared model fit using likelihood ratio tests and also reported Akaike information criterion (AIC) values where lower AIC means better fit (Bolker et al., 2009). AIC values were extracted using the *AICtab* function in the package bbmle (Bolker, 2022).

Transparency and Openness

We report our sample size, all data exclusions, all manipulations, and all measures in the study. Data and analysis code from these studies are available at Dryad Digital Repository and can be accessed at <https://doi.org/10.5061/dryad.bg79cnp>. Data were analyzed using R v4.1.2. This study’s design and analyses were not preregistered.

Results and Discussion

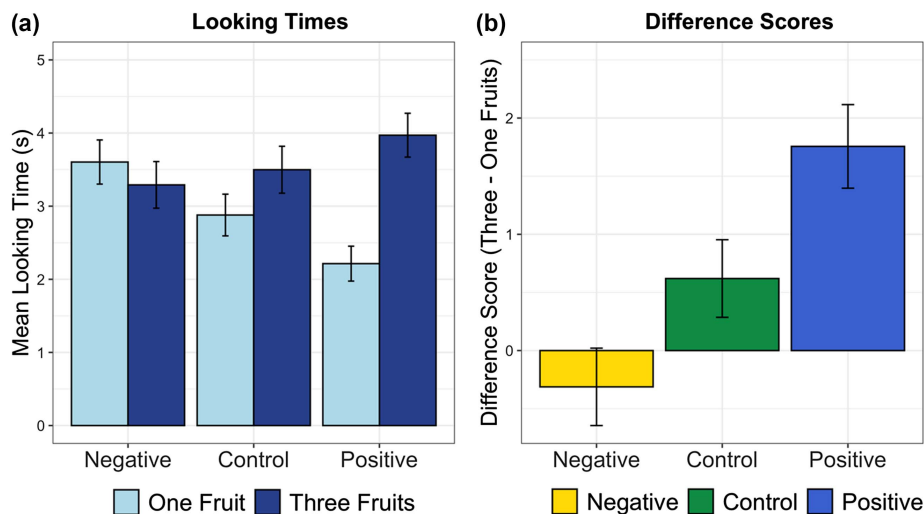
We first examined whether monkeys modulated their looking responses to different quantities of fruit in the test trials, based on the expectations they developed in the demonstration phase (see Figure 2a). In the positive error condition, in which monkeys initially saw that the cue preceded one fruit, monkeys looked less at one fruit (the expected outcome; $2.21 \pm SE = 0.24$ s) compared to

three fruits (the unexpected outcome), a significant difference, 3.97 ± 0.30 s; $t(69) = 4.88$, $p < .0001$, Cohen’s $d = 0.58$. In contrast, in the negative error condition, in which monkeys initially saw that the cue preceded three fruits, monkeys looked for 3.60 ± 0.30 s at one fruit (the unexpected outcome) and 3.29 ± 0.32 s at three fruits (the expected outcome), which did not differ significantly, $t(69) = -0.94$, $p = .35$, Cohen’s $d = 0.11$. Finally, in the number control assessing baseline responses to different numbers of fruits (e.g., where both outcomes matched their respective demonstration phases), monkeys looked for 2.88 ± 0.29 s at one fruit and 3.50 ± 0.32 s at three fruits, trending to look longer at more fruit, $t(69) = 1.86$, $p = .07$, Cohen’s $d = 0.22$. Overall, this shows that monkey responses in these conditions was not a simple reflection of the number of fruits they saw in the trial, but crucially depended on their expectations: monkeys looked more at more fruits in the positive condition where this was the unexpected outcome, but did not do so when this was the expected outcome in the negative condition, and only trended to look more at three fruits in the numerical control.

We then directly compared looking responses across conditions using LMMs. The base model accounted for *subject identity* (as a random effect), *sex*, *age* (continuous in years), and *trial order* (expected vs. unexpected trial first). We then added *outcome fruit number* in the second model, which improved fit (likelihood ratio tests: $\chi^2 = 11.00$, $df = 1$, $p < .001$; AIC = 1925.4 compared to 1933.0 in the first model): overall, monkeys looked longer at three fruits compared to one fruit, as expected. We then added a main effect of *condition* (positive error, negative error, or number control) which did not improve fit as a main effect ($\chi^2 = 1.58$, $df = 2$, $p = .45$; AIC = 1929.0), showing that monkeys showed no overall differences in average looking duration across the three conditions. This is important as it indicates that these three conditions were similarly engaging. Finally, we added the interaction between *outcome fruit number* and *condition*, the key test of our prediction that monkeys’ looking responses to the fruit outcomes were modulated by their expectations about the likely fruit outcomes. That is, we tested whether looking responses to one versus three fruits depended on monkeys’ expectations about the likely reward outcomes, as established in the different demonstration phases for each condition. This further improved fit (comparison with Model 2: $\chi^2 = 19.40$, $df = 4$, $p < .001$; AIC = 1914.8; see Supplemental Table S1 for model parameters), indicating that monkeys’ expectations did shape their responses in the test trials; this was also the best-fit model in terms of AIC values. Post hoc comparisons showed that monkeys looked longer at three compared to one fruit specifically in the positive error condition ($p < .0001$), where three fruits reflected the unexpected outcome, but did not do so in the negative condition where one fruit was unexpected ($p = .36$, n.s.) and only trended to do so in the numerical control ($p = .07$). In addition, the difference in looking to three versus one fruit was greater in the positive condition compared to the negative error condition, where one fruit was instead the unexpected outcome ($p = .0001$), and responses to three versus one fruits in the positive error condition trended to be greater compared to the control ($p = .052$), indicating that responses to more fruits were also exacerbated when they were unexpected in this situation. These results show that while monkeys overall in the study looked longer at more than less fruit, this was modulated by their predictions about reward outcomes across the different conditions as predicted.

Finally, we calculated a looking time difference score for each individual, indexing their relative looking at the fruit outcomes

Figure 2
Responses to Reward Prediction Errors Across Conditions



Note. (a) Looking times to different reward quantities (one or three fruits) by condition (negative error condition, control, or positive error condition). All monkeys saw a one-fruit and a three-fruit reward outcome (in counterbalanced order across subjects), but whether these two outcomes were expected versus unexpected depended on condition (assigned between-subjects). For example, while three fruits were the expected outcome in the negative error condition, three fruits were the unexpected outcome (more than expected) in the positive error condition. In the number control, both reward amounts were expected on their respective test trial. (b) Difference scores (looking time to three fruits – looking time to one fruit) across conditions. More positive difference scores reflect relatively greater looking to three fruits, whereas negative scores indicate relatively longer looking to the one fruit outcomes. Error bars in both panels indicate *SE*. *SE* = standard error. See the online article for the color version of this figure.

(looking to three fruits minus looking to one fruit; see Figure 2b) as a parallel test of how their expectations shaped their responses. Here, a more positive difference score indicated the monkeys looked relatively longer at three fruits, where negative scores indicated relatively longer looking at one fruit. We used linear models accounting for *sex*, *age*, and *trial order* (expected vs. unexpected trial first to account for any order effects). We then added *condition* and found that this improved model fit compared to the base model ($\chi^2 = 18.10$, $df = 2$, $p < .001$; AIC = 1044.3 compared to 1058.4 in the first model; see Supplemental Table S2 for model parameters). Post hoc comparisons indicated that difference scores in the positive error condition were greater than those in both the control ($p < .05$) and negative error condition ($p = .0001$). That is, monkeys showed relatively increased looking to the three-fruit outcome specifically when it was unexpected (in the positive condition). Thus, analyses of the difference scores align with results from the overall looking times and show that monkeys modulate their looking to different rewards based on their expectations.

Study 2: Development of Expectations About Reward Across the Life Span

In Study 2, we examined whether monkeys' sensitivity to reward prediction error tracked key developmental changes seen in humans. Specifically, we tested whether monkeys show increased sensitivity to prediction errors in adolescence (Cohen et al., 2010; Hauser et al., 2015), and declining sensitivity in aging (Chowdhury et al., 2013;

Samanez-Larkin et al., 2014). To do so, we tested a large sample of monkeys ranging from juvenility to old age on the positive error condition. Study 1's results showed that monkeys' looking responses in the task at the group level depended on their expectations (e.g., they did not simply look more at larger quantities of fruit, but rather this depended on the amounts they saw in initial demonstrations). In the present study, our focus was on characterizing individual variation in a larger sample of age-varying monkeys, so we decided to implement the positive error condition given that it garnered strong overall responses in Study 1. Monkeys again completed two test trials, here mirroring the positive reward prediction error condition from Study 1, but with a fixed trial order (expected followed by unexpected) in order to reduce variation due to trial order assignment. We predicted that if monkeys share humanlike developmental signatures of reward processing, then adolescent monkeys would show relatively increased looking to unexpected outcomes compared to expected outcomes, whereas older monkeys would show less discrimination between conditions.

Method

Participants

We tested 363 monkeys, for a final sample of 184 females and 179 males, with a mean age of 6.9 years (range: 1.6–26.4 years). We split monkeys into age cohorts based on life history transitions in this species: *juveniles* under 4 years ($n = 173$); *adolescents* between 4 and 6 years ($n = 45$) based on timing of puberty, first sexual

reproduction, first birth, and completion of body growth (Bercovitch & Clarke, 1995; Rawlins & Kessler, 1986); *adults* between 6 and 15 years ($n = 109$); and *older adults* over 15 years ($n = 36$), as the median life span of the monkeys in this population is 15 years, and they rarely exceed 25 years (Hoffman et al., 2010). Fifty-eight of these monkeys had previously participated in Study 1, a year or more prior to their participation in Study 2.

Procedure

The procedure was largely identical to the positive error condition in Study 1 (see Figure 1), except that the trial order was fixed with the expected trial always first across all monkeys, rather than being counterbalanced. We chose a single testing order here because our goal was to detect individual variation in responses to the trials, and thus, we aimed to remove any order effects on the individual differences analysis (such as potential declines in looking over trials), following the same approach used in prior work in this population examining lifespan age-related shifts in looking time responses (Rosati et al., 2018). As in Study 1's positive error condition, monkeys always saw one fruit in the demonstration phase. Then, in the first test trial, they saw one fruit (the expected outcome), and in the second, they saw three fruits (the unexpected outcome). While this study was completed more than a year after Study 1, we also used different visual cues on the test boxes to further avoid any potential carryover effects. The first box now showed a red circle overlaid on a blue rectangle, and the second box showed a purple diamond on a green rectangle.

Exclusions

An additional 168 subjects were approached by the experimenters but excluded from analyses because they did not complete the test session due to interference or leaving the testing area, as in Study 1. In addition, in some cases, animals were approached for testing more than once (e.g., because their identification was only confirmed after they completed the test, $n = 52$), in which case we only included their first successful test session in the final data set as in Study 1.

Coding and Statistical Analyses

Two experienced coders (HC and a second coder not otherwise involved in the study) blind to trial type independently scored all test trials from the entire monkey sample, using the same coding procedures as in Study 1. Both coders had previous experience coding monkey looking time data, both by coding a reference set of videos to calibrate their codes. There was again high reliability between the two coders across all trials in the data set ($r = 0.95$). Our basic analyses followed the same procedures as in Study 1, but here, we specifically compared responses across age cohorts. In analyses, cohort was specified as an ordinal factor to test for the predicted nonlinear age effects on reward sensitivity (e.g., exacerbated sensitivity in adolescents and then reduced in old age).

Results and Discussion

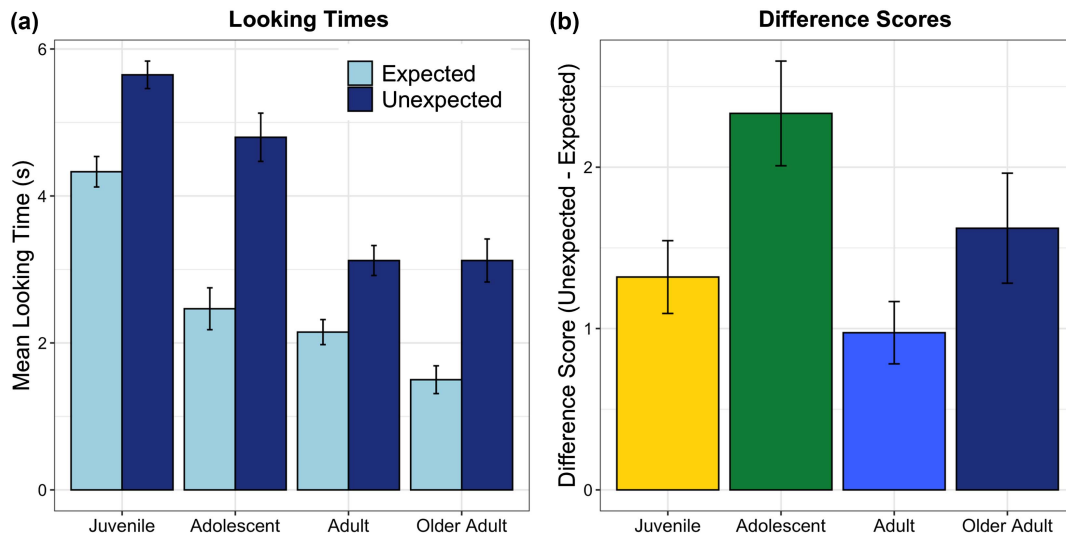
We first examined overall looking responses at the expected outcome (one fruit) versus the unexpected outcome (three fruits; see

Figure 3a). Overall, monkeys looked longer at the unexpected trial (4.53 ± 0.13 s) than the expected trial (3.16 ± 0.13 s), a significant difference, $t(362) = 10.21$, $p < .0001$, Cohen's $d = 0.54$, mirroring the group-level patterns from Study 1. All cohorts showed this same pattern, with an especially strong effect in adolescents, *juveniles*: $t(172) = 5.85$, $p < .0001$, Cohen's $d = 0.44$; *adolescents*: $t(44) = 7.19$, $p < .0001$, Cohen's $d = 1.07$; *adults*: $t(108) = 5.05$, $p < .0001$, Cohen's $d = 0.48$; *older adults*: $t(35) = 4.76$, $p < .0001$, Cohen's $d = 0.79$.

We then compared performance across cohorts using LMMs. The base model accounted for *subject identity* (as a random effect), *sex*, and *trial type* (expected outcome on Trial 1, vs. unexpected outcome on Trial 2). We then added *age cohort* in the second model, which improved fit ($\chi^2 = 118.29$, $df = 3$, $p < .0001$; AIC = 3214.6 compared to 3322.7 in the first model). In particular, there were significant linear ($p < .0001$) and quadratic effects ($p < .05$) of age cohort on overall looking durations. We then added the interaction between *age cohort* and *trial type* to test our key prediction that monkeys' looking to expected versus unexpected outcomes was modulated by their age. That is, we tested whether responses to the unexpected outcome (relative to how much they looked at the expected outcome) were exaggerated in adolescence or attenuated in old age. This interaction further improved fit ($\chi^2 = 9.55$, $df = 3$, $p < .05$; AIC = 3212.7; see Supplemental Table S3 for model parameters). Post hoc comparisons showed that while all age cohorts looked longer at the unexpected compared to the expected trial ($p < .0001$ for all comparisons), adolescents showed a larger trial type effect (e.g., more relative looking to the unexpected outcome) compared to adults ($p < .05$), and trended to do so compared to juveniles ($p = .08$). In contrast, there was no difference in the patterns of response of adults and older adults ($p = .55$). In addition, groups varied in their overall durations of looking in general, irrespective of trial type: juveniles looked longer overall than all other groups ($p < .0001$) and adolescents looked longer than adults and older adults ($p < .05$). Finally, the inclusion of a three-way interaction between *sex*, *cohort*, and *trial* did not further improve fit ($\chi^2 = 2.75$, $df = 7$, $p = .91$; AIC = 3221.5), indicating similar patterns of responding in males and females. Comparisons of AIC comparisons further supported Model 3 (including the Cohort \times Trial Type interaction) as the best-fit model. In order to fully assess any possible shifts in responses during aging, we further examined in the full adult sample using continuous age as the predictor, in case there was more subtle aging effects we did not detect in our main analyses using age cohort as a predictor (see online Supplemental Material for all details). However, we again did not find any shifts between adults and older adults using this approach, concordant with the results reported here indicating that there was no decline in reward sensitivity in older age.

Finally, we again calculated a difference score for each individual (looking responses to three fruits minus responses to one fruit), as another test of whether adolescents showed a peak in reward sensitivity (see Figure 3b). Here, larger difference scores always indexed greater relative looking to the unexpected outcome (three fruits) and thus great sensitivity to reward prediction error. As in Study 1, we used linear models here accounting for *sex* in our base model. We then added *age cohort* to the second model, which improved model fit ($\chi^2 = 9.12$, $df = 3$, $p < .05$; AIC = 1712.9 compared to 1716.0 in the first model; see Supplemental Table S4 for model parameters). Post hoc tests showed adolescents had a

Figure 3
Predictions About Reward Across the Lifespan



Note. (a) Looking responses across age cohorts according to the trial types (expected vs. unexpected). Here, the expected outcome on Trial 1 was one fruit (matched the demonstration phase), whereas the unexpected outcome on Trial 2 was three fruits (more than expected based on the demonstration phase). (b) Difference scores (responses to unexpected – expected outcomes) by age cohort. Error bars in both panels indicate *SE*. *SE* = standard error. See the online article for the color version of this figure.

larger difference score than adults ($p < .05$), indicating they showed greater relative looking to the unexpected reward. They tended to show a larger score than juveniles ($p = .099$), but there was no difference between adults and older adults ($p = .56$, n.s.). Inclusion of the interaction between *age cohort* and *sex* did not further improve fit ($\chi^2 = 0.26$, $df = 3$, $p = .97$; AIC = 1718.6). Comparisons of AIC values also indicated Model 2 was the best-fit model. As with the analyses of overall looking time, further examinations of the full adult sample using continuous age confirmed that there was no shift in sensitivity in old age (see online Supplemental Material).

Overall, these results reveal several key points. First, younger animals generally looked longer at the stimuli, aligning with past work in this population showing that younger monkeys generally look longer at variety of different stimuli in looking time tasks, including those involving rewards but also other kinds of tasks involving social stimuli (De Petrillo & Rosati, 2019; Rosati et al., 2018). However, our questions primarily concerned *relative* looking to the unexpected reward versus expected reward across the lifespan. The key test of this prediction was the interaction effect between *age cohort* and *trial type* (and accordingly the comparison of difference scores), which captures relative looking to the unexpected reward compared to the expected reward as opposed to overall looking durations. These analyses specifically show that adolescents exhibit the largest difference in their looking time to the unexpected reward compared to the expected reward. That is, compared to the other age cohorts, adolescents look relatively longer at the unexpected outcome, when accounting for the different group's general patterns of looking as indexed by responses to the expected outcome. Finally, older adults looked less overall at the stimuli, but continued to differentiate between the expected and unexpected outcome to the same degree as younger adults. This is consistent with the possibility that adolescences are the most sensitive to the

discrepancy between predicted and actual reward outcome, whereas monkeys did not appear to show major changes in relative responses across adulthood.

General Discussion

We developed a novel behavioral task aimed at indexing reward prediction error in a large sample of semi-free-ranging rhesus monkeys using a violation-of-expectation looking time paradigm. In Study 1, we compared responses to positive errors, negative errors, and baseline responses to different numerical quantities, and found that monkeys look longer to reward outcomes that are unexpected because they did not align with their predictions based on their initial experiences. That is, monkeys look longer at an unexpected outcome than they did to an expected outcome that provided a numerically identical amount of fruit. In Study 2, we then examined whether monkeys would share key developmental signatures in sensitivity to reward prediction error with humans. We specifically adapted the positive reward error condition to test a larger sample of monkeys and compare performance across the lifespan. We found that relative looking time to the unexpected larger reward peaked in adolescents, consistent with human results showing that adolescents have greater sensitivity to reward prediction errors. However, we did not find any changes in monkeys' responses in old age, unlike results from humans. Together, this work demonstrates that prediction errors can be tracked using behavioral looking time methods and provides initial evidence that monkeys may share some developmental shifts in reward sensitivity with humans.

Our looking time method allowed us to test the responses of a large population of semi-free-ranging monkeys, who would otherwise be inaccessible to typical neurobiological techniques used to measure reward prediction errors in animals. To do so, our

study was purposefully designed to involve no training, but rather assess reactions to cue and reward presentations after minimal experience. We adapted a violation-of-expectation looking time paradigm to implement this procedure, a method that has been widely used in studies of physical and social cognition with infants and monkeys (Arre et al., 2020, 2021; Baillargeon, 1986; Drayton & Santos, 2016; Hood & Santos, 2009; Hughes & Santos, 2012; Margoni et al., 2022; Martin & Santos, 2014; Needham & Baillargeon, 1993; Onishi & Baillargeon, 2005; Phillips et al., 2010; Phillips & Santos, 2007; Santos & Hauser, 2002; Spelke, 1990, 2022; Spelke et al., 1992, 2010; Spelke & Kinzler, 2007; Stahl & Feigenson, 2015, 2017, 2019). As such, our study aimed to capture the key element of reward prediction errors—whether animals detect the difference between expected and unexpected reward outcomes—using this new approach. Our looking time task necessarily had some key methodological differences from standard reward prediction error tasks used in animals, given the nature of looking time studies. For example, the task hinged on the fact that monkeys from this population like to view fruit stimuli (Arre et al., 2020, 2021; Bettel & Rosati, 2021; De Petrillo & Rosati, 2019; Drayton & Santos, 2016; Marticorena et al., 2011; Martin & Santos, 2014). It is also important to note that many neuroimaging studies with humans use rewards that are not immediately consumed, such as monetary rewards, hypothetical rewards, or even attractive visual stimuli (Bray & O'Doherty, 2007; Cohen et al., 2010; Jauhar et al., 2021; Knutson & Cooper, 2005). In that sense, our animal task parallels this prior human work on reward prediction errors.

Another key aspect of our results is that, since we detected increased looking to unexpected rewards—either positive or negative errors—the looking time responses in our task are consistent with “unsigned” reward prediction errors. This is a key difference from foundational neurobiological work focused on midbrain dopaminergic neurons that show a “signed” or valenced response such that delivery of unexpected rewards increases dopaminergic firing, whereas withholding of expected rewards induces suppression of firing (D'Ardenne et al., 2008; Schultz, 2016a, 2017; Schultz et al., 1997). Other brain regions also show signed responses to positive versus negative prediction errors, although the direction of these responses may differ from dopaminergic neurons. For example, neurons in the habenula are excited by withholding expected reward (or unexpected punishments) but inhibited by cues predicting reward, and neuroimaging studies of humans show a similar reversal of the direction of activation (Matsumoto & Hikosaka, 2007, 2009; Salas et al., 2010). Importantly, other brain regions appear to show unsigned responses to prediction errors—similar changes in response to both expected positive and unexpected negative rewards—a pattern sometimes characterized as a “surprise” response. For example, neurophysiological recordings from monkeys show that anterior cingulate neurons show such surprise signals, firing to both positively and negative-valenced errors (Hayden et al., 2011). Neuroimaging studies of humans invoke similar response in anterior cingulate (Alexander & Brown, 2019; Fouragnan et al., 2019). Along these lines, some works suggest that it is this kind of surprise signal that drives motor outputs and control of actions (Jamous et al., 2023), which could apply to the looking behavior focused on here. Similarly, some evidence from developmental psychology suggests that “surprise” as measured by looking time tasks can also engage the anterior cingulate cortex (Berger & Posner, 2022).

Our looking results here are more consistent with this kind of unsigned prediction error. In particular, monkeys in Study 1 showed increased looking behaviors to unexpected rewards in both the positive and negative error conditions. However, it is also important to note that animals also showed more looking to larger rewards and that the effect of reward amount had opposing effects on the positive and negative error conditions (e.g., the larger rewards were expected in the negative error condition but unexpected in the positive condition). Conversely, it would be in principle possible for animals or infants to show a “signed” looking response, as they could look away from stimuli invoking negative errors. Other related responses that can be measured noninvasively, such as pupillometry (Zhang & Emberson, 2020), could similarly display a signed prediction error response. Future studies using identical reward amounts across both the positive and negative error conditions would therefore be important to assess whether looking or related responses best align with signed versus unsigned prediction error responses when equating reward amount in this way.

Prior work in this population of monkeys has examined a variety of skills related to numerical competency and object individuation abilities (Flombaum et al., 2005; Phillips & Santos, 2007; Santos et al., 2002), building off large body of work in human infants examining how infants track numbers and objects (McCrink & Wynn, 2004; Wynn, 1992, 1998; Wynn et al., 2002; Xu, 2002; Xu & Carey, 1996; Xu et al., 2004). These prior studies have focused on whether monkeys and babies can discriminate different quantities, compute mathematical functions like addition, or track when object identities change. Our work necessarily overlaps with those tasks, in part because the phenomenon of reward prediction errors overlaps with these concepts. For example, in order to be “surprised” that their predictions about rewards do not match real reward outcomes, a decision maker needs to be able to discriminate different quantities or volumes of rewards and to detect whether the rewards they received align with the rewards they predicted. Along these lines, we found that monkeys show different patterns of looking at identical numbers of fruits (one or three) in Study 1 depending on whether that outcome was expected or unexpected based on the initial familiarization they experienced. That is, monkeys did not respond to reward quantities alone but were instead detecting the discrepancy between initially shown rewards and ultimate reward outcomes.

One open question from our setup concerns the extent to which the predictive visual cues in the task actually impacted the monkeys' responses. The premise of prediction error tasks is that decision makers form expectations about likely reward outcomes and then detect when these expectations are fulfilled or not. In many animals' tasks, this is often established by training animals that a particular visual cue predicts subsequent rewards and then assessing neural responses when unexpected rewards (without the initial cue) are delivered or predicted rewards are withheld after the cue is presented (Schultz, 2016a, 2017; Schultz et al., 1997). Following this line of work, we designed our task so that distinctive visual cues would predict a specific number of fruits in the apparatus. However, it is unclear whether monkeys actually used this cue information in our task. Specifically, our results do show that monkeys form expectations about the amounts of rewards that would be presented based on their initial experience, as their looking responses were strongly dictated by the number of fruits they saw following the cue in the demonstration phase, but it is not clear what specific role the visual cue itself played in these responses. Future studies should

therefore investigate the importance of the cue-reward contingency on their responses.

We also examined monkey's reward predictions using a comparative developmental approach to examine lifespan changes in these processes. Our novel behavioral task allowed us to test a larger and more age-diverse sample of more than 360 monkeys in Study 2, ranging in age from infancy to old age, which would not be possible using current neurobiological techniques aimed at measuring prediction errors. We found that adolescent monkeys looked relatively longer at unexpectedly larger rewards in the positive error condition compared to younger and adult monkeys. This aligns with prior work on adolescent changes in reward sensitivity in humans (Cohen et al., 2010; Hauser et al., 2015). While there have been few studies of comparative development of reward-based decision making in nonhuman primates (De Petrillo & Rosati, 2021), this finding also adds to emerging evidence that adolescent primates may respond differently to rewards and decision-making contexts than do adults, such as by showing more risk-seeking preferences (Haux et al., 2022; Rosati et al., 2023). Conversely, we did not find evidence here that older monkeys showed any declines in their reward sensitivity as younger and older monkeys showed similar looking patterns, unlike in older human adults. This is in line with an emerging pattern from rhesus monkeys: though older monkeys in this population show clear shifts compared to younger adults in responses in tasks assessing social cognition (Rosati et al., 2016, 2018), in line with their changing social behavior (Machanda & Rosati, 2020; Siracusa et al., 2022), they nonetheless appear to retain some core capacities for reward-based decision making similar to younger adults (De Petrillo & Rosati, 2019, 2021). Overall, our findings show how a comparative developmental framework can provide a new perspective on testing hypotheses about cognition across species, as well as provide insights into what aspects of these mechanisms are shared versus divergent across species.

Given that we implemented only the positive error condition in the larger sample tested in Study 2, it is important to emphasize that this study alone cannot fully disentangle the specific mechanisms underlying the observed age patterns. While we have interpreted these findings as consistent with human results showing that adolescents are more sensitive to prediction errors, the exacerbated responses of adolescent monkeys to the unexpected positive outcome could also be due to changes in other related psychological processes. For example, given that unexpected outcomes in the positive error condition were always larger than expected, adolescents could be better at detecting visual differences in displays, or at making numerical judgments discriminating between one and three fruits, rather than more sensitive to unexpected reward outcomes specifically. However, the results from Study 1 show that monkeys' responses (at the group level comprising a range of differently aged individuals) did not simply reflect numerical quantities, as monkeys looked differently at the same amount depending on whether it was the expected versus unexpected outcome. Furthermore, prior evidence looking at the development of number discrimination and visual acuity skills suggests that these capacities are mature fully within the first year of life in both humans (McCrink & Wynn, 2004; Wynn, 1992, 1998; Wynn et al., 2002) and other primates (Espinosa & Stryker, 2012; Ferrigno et al., 2016; Hall-Haro et al., 2008; Rodman, 1994). As such, it is unclear why adolescent monkeys specifically would show this exacerbated response to number or

visual displays from a theoretical perspective. Nonetheless, it would be necessary to characterize age-related changes in monkeys' looking responses to expected and unexpected outcomes in other contexts, such as in the negative error condition where unexpected outcomes were smaller-than-expected amounts to address this possibility.

Another alternative is that this change in looking responses reflects some other related psychological process that shifts during adolescence besides reward prediction sensitivity *per se*. There is a great deal of converging evidence that adolescents show a suite of different responses to rewards compared to both younger juveniles and adults, spanning work on not only reward prediction error sensitivity but also other aspects of motivation, emotional regulation, and reward-based decision making (Blakemore & Robbins, 2012; Burnett et al., 2010; Casey, Getz, et al., 2008; Casey, Jones, et al., 2008; Crone & Steinbeis, 2017; Defoe et al., 2015; Hartley & Somerville, 2015; Paulsen et al., 2011; Reyna et al., 2011; Reyna & Farley, 2006; Spear, 2000; Steinberg, 2005, 2007; van den Bos & Hertwig, 2017). For example, adolescents show several differences in reward motivation (Braams et al., 2015; Galvan, 2010; Van Leijenhorst et al., 2010) compared to adults. One way to differentiate these processes might be to simultaneously implement our current task along with independent measures of reward motivation, such as persistence in seeking an unobtainable reward (e.g., as in De Petrillo et al., 2022), to assess how these different measures covary across individuals and age groups. This would be an important next step also to assess what aspects of human adolescent development are shared with versus divergent from other primates from an evolutionary perspective.

More generally, our results support a proposed link between detection of reward prediction errors and expectancy violation looking responses. Though looking time paradigms have emerged as an important tool to understand cognition in nonverbal minds, the underlying cognitive processes that support these looking time responses have remained unclear. Recent proposals have taken a predictive processing's perspective on the infant mind and brain and argued that these looking responses reflect predictions about the environment (Berger & Posner, 2022; Köster et al., 2020), or more generally learning signals to drive adaptive behavior (Stahl & Feigenson, 2015, 2017, 2019). Our results build on this framework by explicitly testing if reward predictions errors—generated by mismatches between expected and realized reward outcomes—can be indexed through looking responses in an expectancy violation paradigm. Our results suggest that violation-of-expectation responses may sometimes reflect reward prediction errors, at least in simple contexts that involve tracking reward quantities. Reward prediction errors are thought to be a crucial signal in learning (Niv & Schoenbaum, 2008; Rescorla & Wagner, 1972; Sutton & Barto, 1998) such that individuals can use prediction errors to update responses in order to maximize reward outcome. Future studies could therefore complement our current looking time method with a subsequent choice task, in order to test whether longer looking responses in monkeys actually drive subsequent learning and exploration as predicted by both of these views.

Importantly, prior work looking at children's and animals' expectations in violation-of-expectation looking time tasks has generally involved much more complex scenarios involving judgments about the physical or social world (Drayton & Santos, 2016; Hood & Santos, 2009; Spelke, 2022; Spelke & Kinzler, 2007), whereas the present work involved simpler reward predictions. Theoretical views of reward prediction error sometimes refer to such

reward expectations as “model-free” predictions, capturing situations where individuals’ reward values are based on their direct experience of changes to the environment. Conversely, “model-based” learning involves updating responses based on an internal representation of the environment (Bray & O’Doherty, 2007; Cushman, 2013; Dayan & Berridge, 2014). One possibility is that this kind of model-based framework is an analogue for how infants and animals use concepts about the physical world or social agents to make predictions in looking time tasks focused on physical reasoning or social cognition, providing an important bridge between the more foundational reward prediction processes we focused on here and higher level cognitive inferences (Daw et al., 2011; Decker et al., 2016). To test this, future research could investigate how these two learning systems might interact in monkeys and assess whether animal’s reward prediction error signals support mechanisms for these higher level, complex inferences.

In conclusion, we developed a novel behavioral task utilizing a violation-of-expectation looking paradigm to measure responses to reward discrepancies in free-ranging monkeys. We found that monkeys could detect reward prediction errors and that exhibit exaggerated sensitivity to prediction errors during adolescence similar to patterns seen in humans. As predictions about reward outcomes are a fundamental mechanism allowing individuals to track events in the world and learn from them, prediction error like the ones we have observed may allow individuals to understand possible outcomes, detect expected outcomes, and update behavioral responses accordingly.

References

- Abler, B., Walter, H., Erk, S., Kammerer, H., & Spitzer, M. (2006). Prediction error as a linear function of reward probability is coded in human nucleus accumbens. *NeuroImage*, 31(2), 790–795. <https://doi.org/10.1016/j.neuroimage.2006.01.001>
- Alberts, S. C., Altmann, J., Brockman, D. K., Cords, M., Fedigan, L. M., Pusey, A., Stoinski, T. S., Strier, K. B., Morris, W. F., & Bronikowski, A. M. (2013). Reproductive aging patterns in primates reveal that humans are distinct. *Proceedings of the National Academy of Sciences of the United States of America*, 110(33), 13440–13445. <https://doi.org/10.1073/pnas.1311857110>
- Alexander, W. H., & Brown, J. W. (2019). The role of the anterior cingulate cortex in prediction error and signaling surprise. *Topics in Cognitive Science*, 11(1), 119–135. <https://doi.org/10.1111/tops.12307>
- Arre, A. M., Clark, C. S., & Santos, L. R. (2020). Do young rhesus macaques know what others see? A comparative developmental perspective. *American Journal of Primatology*, 82(11), Article e23054. <https://doi.org/10.1002/ajp.23054>
- Arre, A. M., Stumph, E., & Santos, L. R. (2021). Macaque species with varying social tolerance show no differences in understanding what other agents perceive. *Animal Cognition*, 24(4), 877–888. <https://doi.org/10.1007/s10071-021-01485-5>
- Baillargeon, R. (1986). Representing the existence and the location of hidden objects: Object permanence in 6- and 8-month-old infants. *Cognition*, 23(1), 21–41. [https://doi.org/10.1016/0010-0277\(86\)90052-1](https://doi.org/10.1016/0010-0277(86)90052-1)
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bayer, H. M., & Glimcher, P. W. (2005). Midbrain dopamine neurons encode a quantitative reward prediction error signal. *Neuron*, 47(1), 129–141. <https://doi.org/10.1016/j.neuron.2005.05.020>
- Bercovitch, F. B., & Clarke, A. S. (1995). Dominance rank, cortisol concentrations, and reproductive maturation in male rhesus macaques. *Physiology & Behavior*, 58(2), 215–221. [https://doi.org/10.1016/0031-9384\(95\)00055-N](https://doi.org/10.1016/0031-9384(95)00055-N)
- Berger, A., & Posner, M. I. (2022). *Beyond infant’s looking: The neural basis for infant prediction errors*. Perspectives on Psychological Science.
- Berger, A., Tzur, G., & Posner, M. I. (2006). Infant brains detect arithmetic errors. *Proceedings of the National Academy of Sciences of the United States of America*, 103(33), 12649–12653. <https://doi.org/10.1073/pnas.0605350103>
- Bettle, R., & Rosati, A. G. (2021). The evolutionary origins of natural pedagogy: Rhesus monkeys show sustained attention following nonsocial cues versus social communicative signals. *Developmental Science*, 24(1), Article e12987. <https://doi.org/10.1111/desc.12987>
- Bjorklund, D., & Green, B. (1992). The adaptive nature of cognitive immaturity. *American Psychologist*, 47(1), 46–54. <https://doi.org/10.1037/0003-066X.47.1.46>
- Bjorklund, D. F., & Bering, J. M. (2003). Big brains, slow development and social complexity: The developmental and evolutionary origins of social cognition. In M. Bruene, H. Ribbert, & W. Schiefenhoefel (Eds.), *The social brain: Evolution and pathology* (pp. 111–151). Wiley. <https://doi.org/10.1002/0470867221.ch7>
- Blakemore, S. J., & Robbins, T. W. (2012). Decision-making in the adolescent brain. *Nature Neuroscience*, 15(9), 1184–1191. <https://doi.org/10.1038/nn.3177>
- Bogin, B., & Smith, B. H. (1996). Evolution of the human life cycle. *American Journal of Human Biology*, 8(6), 703–716. [https://doi.org/10.1002/\(SICI\)1520-6300\(1996\)8:6<703::AID-AJHB2>3.0.CO;2-U](https://doi.org/10.1002/(SICI)1520-6300(1996)8:6<703::AID-AJHB2>3.0.CO;2-U)
- Bolker, B. M. (2022). *bbmle: Tools for general maximum likelihood estimation*. [Computer Software] Retrieved from: <https://CRAN.R-project.org/package=bbmle>
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H., & White, J. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Braams, B. R., van Duijvenvoorde, A. C., Peper, J. S., & Crone, E. A. (2015). Longitudinal changes in adolescent risk-taking: A comprehensive study of neural responses to rewards, pubertal development, and risk-taking behavior. *The Journal of Neuroscience*, 35(18), 7226–7238. <https://doi.org/10.1523/JNEUROSCI.4764-14.2015>
- Bray, S., & O’Doherty, J. (2007). Neural coding of reward-prediction error signals during classical conditioning with attractive faces. *Journal of Neurophysiology*, 97(4), 3036–3045. <https://doi.org/10.1152/jn.01211.2006>
- Burnett, S., Bault, N., Coricelli, G., & Blakemore, S. J. (2010). Adolescents’ heightened risk-seeking in a probabilistic gambling task. *Cognitive Development*, 25(2), 183–196. <https://doi.org/10.1016/j.cogdev.2009.11.003>
- Casey, B. J., Getz, S., & Galvan, A. (2008). The adolescent brain. *Developmental Review*, 28(1), 62–77. <https://doi.org/10.1016/j.dr.2007.08.003>
- Casey, B. J., Jones, R. M., & Hare, T. A. (2008). The adolescent brain. *Annals of the New York Academy of Sciences*, 1124(1), 111–126. <https://doi.org/10.1196/annals.1440.010>
- Chowdhury, R., Guitart-Masip, M., Lambert, C., Dayan, P., Huys, Q., Düzel, E., & Dolan, R. J. (2013). Dopamine restores reward prediction errors in old age. *Nature Neuroscience*, 16(5), 648–653. <https://doi.org/10.1038/nn.3364>
- Cohen, J. R., Asarnow, R. F., Sabb, F. W., Bilder, R. M., Bookheimer, S. Y., Knowlton, B. J., & Poldrack, R. A. (2010). A unique adolescent response to reward prediction errors. *Nature Neuroscience*, 13(6), 669–671. <https://doi.org/10.1038/nn.2558>
- Crone, E. A., & Steinbeis, N. (2017). Neural perspective on cognitive control development during childhood and adolescence. *Trends in Cognitive Sciences*, 21(3), 205–215. <https://doi.org/10.1016/j.tics.2017.01.003>
- Cushman, F. (2013). Action, outcome, and value: A dual-system framework for morality. *Personality and Social Psychology Review*, 17(3), 273–292. <https://doi.org/10.1177/1088868313495594>

- d'Acremont, M., Lu, Z. L., Li, X., Van der Linden, M., & Bechara, A. (2009). Neural correlates of risk prediction error during reinforcement learning in humans. *NeuroImage*, 47(4), 1929–1939. <https://doi.org/10.1016/j.neuroimage.2009.04.096>
- D'Ardenne, K., McClure, S. M., Nystrom, L. E., & Cohen, J. D. (2008). BOLD responses reflecting dopaminergic signals in the human ventral tegmental area. *Science*, 319(5867), 1264–1267. <https://doi.org/10.1126/science.1150605>
- Daw, N. D., Gershman, S. J., Seymour, B., Dayan, P., & Dolan, R. J. (2011). Model-based influences on humans' choices and striatal prediction errors. *Neuron*, 69(6), 1204–1215. <https://doi.org/10.1016/j.neuron.2011.02.027>
- Dayan, P., & Berridge, K. C. (2014). Model-based and model-free Pavlovian reward learning: Revaluation, revision, and revelation. *Cognitive, Affective & Behavioral Neuroscience*, 14(2), 473–492. <https://doi.org/10.3758/s13415-014-0277-8>
- Dayan, P., & Daw, N. D. (2008). Decision theory, reinforcement learning, and the brain. *Cognitive, Affective & Behavioral Neuroscience*, 8(4), 429–453. <https://doi.org/10.3758/CABN.8.4.429>
- De Petrillo, F., Nair, P., Cantwell, A., & Rosati, A. G. (2022). The evolution of cognitive control in lemurs. *Psychological Science*, 33(9), 1408–1422. <https://doi.org/10.1177/09567976221082938>
- De Petrillo, F., & Rosati, A. G. (2019). Rhesus macaques use probabilities to predict future events. *Evolution and Human Behavior*, 40(5), 436–446. <https://doi.org/10.1016/j.evolhumbehav.2019.05.006>
- 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 of London. Series B, Biological Sciences*, 376(1819), Article 20190671. <https://doi.org/10.1098/rstb.2019.0671>
- Decker, J. H., Otto, A. R., Daw, N. D., & Hartley, C. A. (2016). From creatures of habit to goal-directed learners: Tracking the developmental emergence of model-based reinforcement learning. *Psychological Science*, 27(6), 848–858. <https://doi.org/10.1177/0956797616639301>
- Defoe, I. N., Dubas, J. S., Figner, B., & van Aken, M. A. G. (2015). A meta-analysis on age differences in risky decision making: Adolescents versus children and adults. *Psychological Bulletin*, 141(1), 48–84. <https://doi.org/10.1037/a0038088>
- Drayton, L. A., & Santos, L. R. (2016). A decade of theory of mind research on Cayo Santiago: Insights into rhesus macaque social cognition. *American Journal of Primatology*, 78(1), 106–116. <https://doi.org/10.1002/ajp.22362>
- Drayton, L. A., & Santos, L. R. (2018). What do monkeys know about others' knowledge? *Cognition*, 170, 201–208. <https://doi.org/10.1016/j.cognition.2017.10.004>
- Enomoto, K., Matsumoto, N., Nakai, S., Satoh, T., Sato, T. K., Ueda, Y., Inokawa, H., Haruno, M., & Kimura, M. (2011). Dopamine neurons learn to encode the long-term value of multiple future rewards. *Proceedings of the National Academy of Sciences of the United States of America*, 108(37), 15462–15467. <https://doi.org/10.1073/pnas.1014457108>
- Eppinger, B., Nystrom, L. E., & Cohen, J. D. (2012). Reduced sensitivity to immediate reward during decision-making in older than younger adults. *PLOS ONE*, 7(5), Article e36953. <https://doi.org/10.1371/journal.pone.0036953>
- Ergo, K., De Loof, E., & Verguts, T. (2020). Reward prediction error and declarative memory. *Trends in Cognitive Sciences*, 24(5), 388–397. <https://doi.org/10.1016/j.tics.2020.02.009>
- Espinoza, J. S., & Stryker, M. P. (2012). Development and plasticity of the primary visual cortex. *Neuron*, 75(2), 230–249. <https://doi.org/10.1016/j.neuron.2012.06.009>
- Ferrigno, S., Hughes, K. D., & Cantlon, J. F. (2016). Precocious quantitative cognition in monkeys. *Psychonomic Bulletin & Review*, 23(1), 141–147. <https://doi.org/10.3758/s13423-015-0893-5>
- Flombaum, J. I., Junge, J. A., & Hauser, M. D. (2005). Rhesus monkeys (Macaca mulatta) spontaneously compute addition operations over large numbers. *Cognition*, 97(3), 315–325. <https://doi.org/10.1016/j.cognition.2004.09.004>
- Flombaum, J. I., & Santos, L. R. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology*, 15(5), 447–452. <https://doi.org/10.1016/j.cub.2004.12.076>
- Fouragnan, E., Retzler, C., & Phillastides, M. G. (2019). Separate neural representations of prediction error valence and surprise: Evidence from an fMRI meta-analysis. *Human Brain Mapping*, 39(7), 2689–3103. <https://doi.org/10.1002/hbm.24047>
- Galvan, A. (2010). Adolescent development of the reward system. *Frontiers in Human Neuroscience*, 4, Article 6. <https://doi.org/10.3389/neuro.09.006.2010>
- Garrison, J., Erdeniz, B., & Done, J. (2013). Prediction error in reinforcement learning: A meta-analysis of neuroimaging studies. *Neuroscience and Biobehavioral Reviews*, 37(7), 1297–1310. <https://doi.org/10.1016/j.neubiorev.2013.03.023>
- Gershman, S. J., & Daw, N. D. (2017). Reinforcement learning and episodic memory in humans and animals: An integrative framework. *Annual Review of Psychology*, 68(1), 101–128. <https://doi.org/10.1146/annurev-psych-122414-033625>
- Gershman, S. J., & Goodman, N. D. (2014). *Amortized inference in probabilistic reasoning* [Conference session]. Proceedings of the 36th Annual Conference of the Cognitive Science Society.
- Gershman, S. J., Markman, A. B., & Otto, A. R. (2014). Retrospective revaluation in sequential decision making: A tale of two systems. *Journal of Experimental Psychology: General*, 143(1), 182–194. <https://doi.org/10.1037/a0030844>
- Glimcher, P. W. (2011). Understanding dopamine and reinforcement learning: The dopamine reward prediction error hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, 108(Suppl. 3), 15647–15654. <https://doi.org/10.1073/pnas.1014269108>
- Gómez, J. C. (2005). Species comparative studies and cognitive development. *Trends in Cognitive Sciences*, 9(3), 118–125. <https://doi.org/10.1016/j.tics.2005.01.004>
- Hall-Haro, C., Johnson, S. P., Price, T. A., Vance, J. A., & Kiorpes, L. (2008). Development of object concepts in macaque monkeys. *Developmental Psychobiology*, 50(3), 278–287. <https://doi.org/10.1002/dev.20282>
- Hartley, C. A., & Somerville, L. H. (2015). The neuroscience of adolescent decision-making. *Current Opinion in Behavioral Sciences*, 5, 108–115. <https://doi.org/10.1016/j.cobeha.2015.09.004>
- Hauser, T. U., Iannaccone, R., Walitza, S., Brandeis, D., & Brem, S. (2015). Cognitive flexibility in adolescence: Neural and behavioral mechanisms of reward prediction error processing in adaptive decision making during development. *NeuroImage*, 104, 347–354. <https://doi.org/10.1016/j.neuroimage.2014.09.018>
- 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(3), 358–369. <https://doi.org/10.1177/09567976221140326>
- Hayden, B. Y., Heilbronner, S. R., Pearson, J. M., & Platt, M. L. (2011). Surprise signals in anterior cingulate cortex: Neuronal encoding of unsigned reward prediction errors driving adjustment in behavior. *The Journal of Neuroscience*, 31(11), 4178–4187. <https://doi.org/10.1523/JNEUROSCI.4652-10.2011>
- Higham, J. P., Hughes, K. D., Brent, L. J. N., Dubuc, C., Engelhardt, A., Heistermann, M., Maestriperi, D., Santos, L. R., & Stevens, M. (2011). Familiarity affects the assessment of female facial signals of fertility by free-ranging male rhesus macaques. *Proceedings. Biological Sciences*, 278(1723), 3452–3458. <https://doi.org/10.1098/rspb.2011.0052>
- Hoffman, C. L., Higham, J. P., Mas-Rivera, A., Ayala, J. E., & Maestriperi, D. (2010). Terminal investment and senescence in rhesus macaques (Macaca mulatta) on Cayo Santiago. *Behavioral Ecology*, 21(5), 972–978. <https://doi.org/10.1093/beheco/arg098>
- Hood, B. M., & Santos, L. R. (2009). *The origins of object knowledge*. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199216895.001.0001>

- Hughes, K. D., & Santos, L. R. (2012). Rotational displacement skills in rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology*, 126(4), 421–432. <https://doi.org/10.1037/a0028757>
- Jamous, R., Takacs, A., Frings, C., Münchau, A., Mückschel, M., & Beste, C. (2023). Unsigned surprise but not reward magnitude modulates the integration of motor elements during actions. *Scientific Reports*, 13(1), Article 5379. <https://doi.org/10.1038/s41598-023-32508-5>
- Jauhar, S., Fortea, L., Solanes, A., Albajes-Eizaguirre, A., McKenna, P. J., & Radua, J. (2021). Brain activations associated with anticipation and delivery of monetary reward: A systematic review and meta-analysis of fMRI studies. *PLOS ONE*, 16(8), Article e0255292. <https://doi.org/10.1371/journal.pone.0255292>
- Knutson, B., & Cooper, J. C. (2005). Functional magnetic resonance imaging of reward prediction. *Current Opinion in Neurology*, 18(4), 411–417. <https://doi.org/10.1097/01.wco.0000173463.24758.f6>
- Köster, M., Kayhan, E., Langeloh, M., & Hoehl, S. (2020). Making sense of the world: Infant learning from a predictive processing perspective. *Perspectives on Psychological Science*, 15(3), 562–571. <https://doi.org/10.1177/1745691619895071>
- Kuss, K., Falk, A., Trautner, P., Elger, C. E., Weber, B., & Fließbach, K. (2013). A reward prediction error for charitable donations reveals outcome orientation of donors. *Social Cognitive and Affective Neuroscience*, 8(2), 216–223. <https://doi.org/10.1093/scan/nsr088>
- Lak, A., Stauffer, W. R., & Schultz, W. (2014). Dopamine prediction error responses integrate subjective value from different reward dimensions. *Proceedings of the National Academy of Sciences of the United States of America*, 111(6), 2343–2348. <https://doi.org/10.1073/pnas.1321596111>
- Leigh, S. R. (2004). Brain growth, life history, and cognition in primate and human evolution. *American Journal of Primatology*, 62(3), 139–164. <https://doi.org/10.1002/ajp.20012>
- Leigh, S. R. (2012). Brain size growth and life history in human evolution. *Evolutionary Biology*, 39(4), 587–599. <https://doi.org/10.1007/s11692-012-9168-5>
- Machanda, Z. P., & Rosati, A. G. (2020). Shifting sociality during primate ageing. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 375(1811), Article 20190620. <https://doi.org/10.1098/rstb.2019.0620>
- Margoni, F., Surian, L., & Baillargeon, R. (2022). *The violation-of-expectation paradigm: A conceptual overview*. PsyArxiv. <https://doi.org/10.31234/osf.io/5fsxj>
- Martcorena, D. C. W., Ruiz, A. M., Mukerji, C., Goddu, A., & Santos, L. R. (2011). Monkeys represent others' knowledge but not their beliefs. *Developmental Science*, 14(6), 1406–1416. <https://doi.org/10.1111/j.1467-7687.2011.01085.x>
- Martin, A., & Santos, L. R. (2014). The origins of belief representation: Monkeys fail to automatically represent others' beliefs. *Cognition*, 130(3), 300–308. <https://doi.org/10.1016/j.cognition.2013.11.016>
- Martin, A., & Santos, L. R. (2016). What cognitive representations support primate theory of mind? *Trends in Cognitive Sciences*, 20(5), 375–382. <https://doi.org/10.1016/j.tics.2016.03.005>
- Matsumoto, M., & Hikosaka, O. (2007). Lateral habenula as a source of negative reward signals in dopamine neurons. *Nature*, 447(7148), 1111–1115. <https://doi.org/10.1038/nature05860>
- Matsumoto, M., & Hikosaka, O. (2009). Representation of negative motivational value in the primate lateral habenula. *Nature Neuroscience*, 12(1), 77–84. <https://doi.org/10.1038/nn.2233>
- Matsuzawa, T. (2007). Comparative cognitive development. *Developmental Science*, 10(1), 97–103. <https://doi.org/10.1111/j.1467-7687.2007.00570.x>
- Matsuzawa, T., Tomonaga, M., & Tanaka, M. (Eds.). (2006). *Cognitive development in chimpanzees*. Springer-Verlag. <https://doi.org/10.1007/4-431-30248-4>
- McCrink, K., & Wynn, K. (2004). Large-number addition and subtraction by 9-month-old infants. *Psychological Science*, 15(11), 776–781. <https://doi.org/10.1111/j.0956-7976.2004.00755.x>
- Needham, A., & Baillargeon, R. (1993). Intuitions about support in 4.5-month-old infants. *Cognition*, 47(2), 121–148. [https://doi.org/10.1016/0010-0277\(93\)90002-D](https://doi.org/10.1016/0010-0277(93)90002-D)
- Niv, Y., & Schoenbaum, G. (2008). Dialogues on prediction errors. *Trends in Cognitive Sciences*, 12(7), 265–272. <https://doi.org/10.1016/j.tics.2008.03.006>
- Onishi, K. H., & Baillargeon, R. (2005). Do 15-month-old infants understand false beliefs? *Science*, 308(5719), 255–258. <https://doi.org/10.1126/science.1107621>
- Otto, A. R., Gershman, S. J., Markman, A. B., & Daw, N. D. (2013). The curse of planning: Dissecting multiple reinforcement-learning systems by taxing the central executive. *Psychological Science*, 24(5), 751–761. <https://doi.org/10.1177/0956797612463080>
- Oya, H., Adolphs, R., Kawasaki, H., Bechara, A., Damasio, A., & Howard, M. A., III. (2005). Electrophysiological correlates of reward prediction error recorded in the human prefrontal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 102(23), 8351–8356. <https://doi.org/10.1073/pnas.0500899102>
- Paulsen, D. J., Platt, M. L., Huettel, S. A., & Brannon, E. M. (2011). Decision-making under risk in children, adolescents, and young adults. *Frontiers in Psychology*, 2, Article 72. <https://doi.org/10.3389/fpsyg.2011.00072>
- Phillips, W., & Santos, L. R. (2007). Evidence for kind representations in the absence of language: Experiments with rhesus monkeys (*Macaca mulatta*). *Cognition*, 102(3), 455–463. <https://doi.org/10.1016/j.cognition.2006.01.009>
- Phillips, W., Shankar, M., & Santos, L. R. (2010). Essentialism in the absence of language? Evidence from rhesus monkeys (*Macaca mulatta*). *Developmental Science*, 13(4), F1–F7. <https://doi.org/10.1111/j.1467-7687.2010.00982.x>
- Rawlins, R. G., & Kessler, M. J. (1986). *The Cayo Santiago Macaques: History, behavior, and biology*. SUNY Press.
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 64–99). Appleton-Century-Crofts.
- Reyna, V. F., Estrada, S. M., DeMarinis, J. A., Myers, R. M., Stanis, J. M., & Mills, B. A. (2011). Neurobiological and memory models of risky decision making in adolescents versus young adults. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 37(5), 1125–1142. <https://doi.org/10.1037/a0023943>
- Reyna, V. F., & Farley, F. (2006). Risk and rationality in adolescent decision making: Implications for theory, practice, and public policy. *Psychological Science in the Public Interest*, 7(1), 1–44. <https://doi.org/10.1111/j.1529-1006.2006.00026.x>
- Rodman, H. R. (1994). Development of inferior temporal cortex in the monkey. *Cerebral Cortex*, 4(5), 484–498. <https://doi.org/10.1093/cercor/4.5.484>
- Rosati, A. G., Arre, A. M., Platt, M. L., & Santos, L. R. (2016). Rhesus monkeys show human-like changes in gaze following across the lifespan. *Proceedings of the Royal Society B: Biological Sciences*, 283(1830), Article 20160376. <https://doi.org/10.1098/rspb.2016.0376>
- Rosati, A. G., Arre, A. M., Platt, M. L., & Santos, L. R. (2018). Developmental shifts in social cognition: Socio-emotional biases across the lifespan in rhesus monkeys. *Behavioral Ecology and Sociobiology*, 72(10), Article 163. <https://doi.org/10.1007/s00265-018-2573-8>
- Rosati, A. G., Emery Thompson, M., Atencia, R., & Buckholz, J. W. (2023). Distinct developmental trajectories for risky and impulsive decision-making in chimpanzees. *Journal of Experimental Psychology: General*, 152(6), 1551–1564. <https://doi.org/10.1037/xge0001347>
- Rosati, A. G., & Santos, L. R. (2016). Spontaneous metacognition in rhesus monkeys. *Psychological Science*, 27(9), 1181–1191. <https://doi.org/10.1177/0956797616653737>
- Rosati, A. G., & Santos, L. R. (2017). Tolerant Barbary macaques maintain juvenile levels of social attention in old age, but despotic rhesus macaques

- do not. *Animal Behaviour*, 130, 199–207. <https://doi.org/10.1016/j.anbeha.2017.06.019>
- Rosati, A. G., Wobber, V., Hughes, K., & Santos, L. R. (2014). Comparative developmental psychology: How is human cognitive development unique? *Evolutionary Psychology*, 12(2), 448–473. <https://doi.org/10.1177/147470491401200211>
- Salas, R., Baldwin, P., de Biasi, M., & Montague, P. R. (2010). BOLD responses to negative reward prediction errors in human habenula. *Frontiers in Human Neuroscience*, 4, Article 36. <https://doi.org/10.3389/fnhum.2010.00036>
- Samanez-Larkin, G. R., Worthy, D. A., Mata, R., McClure, S. M., & Knutson, B. (2014). Adult age differences in frontostriatal representation of prediction error but not reward outcome. *Cognitive, Affective & Behavioral Neuroscience*, 14(2), 672–682. <https://doi.org/10.3758/s13415-014-0297-4>
- Santos, L. R., & Hauser, M. D. (2002). A non-human primate's understanding of solidity: Dissociations between seeing and acting. *Developmental Science*, 5(2), F1–F7. <https://doi.org/10.1111/1467-7687.t01-1-00216>
- Santos, L. R., Nissen, A. G., & Ferrugia, J. A. (2006). Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Animal Behaviour*, 71(5), 1175–1181. <https://doi.org/10.1016/j.anbehav.2005.10.007>
- Santos, L. R., Sulkowski, G. M., Spaepen, G. M., & Hauser, M. D. (2002). Object individuation using property/kind information in rhesus macaques (*Macaca mulatta*). *Cognition*, 83(3), 241–264. [https://doi.org/10.1016/S0010-0277\(02\)00006-9](https://doi.org/10.1016/S0010-0277(02)00006-9)
- Schultz, W. (2016a). Dopamine reward prediction error coding. *Dialogues in Clinical Neuroscience*, 18(1), 23–32. <https://doi.org/10.31887/DCNS.2016.18.1/wschultz>
- Schultz, W. (2016b). Dopamine reward prediction-error signalling: A two-component response. *Nature Reviews Neuroscience*, 17(3), 183–195. <https://doi.org/10.1038/nrn.2015.26>
- Schultz, W. (2017). Reward prediction error. *Current Biology*, 27(10), R369–R371. <https://doi.org/10.1016/j.cub.2017.02.064>
- Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, 275(5306), 1593–1599. <https://doi.org/10.1126/science.275.5306.1593>
- Sinclair, A. H., & Barense, M. D. (2018). Surprise and destabilize: Prediction error influences episodic memory reconsolidation. *Learning & Memory*, 25(8), 369–381. <https://doi.org/10.1101/lm.046912.117>
- Siracusa, E. R., Negron-Del Valle, J. E., Phillips, D., Platt, M. L., Higham, J. P., Snyder-Mackler, N., & Brent, L. J. N. (2022). Within-individual changes reveal increasing social selectivity with age in rhesus macaques. *Proceedings of the National Academy of Sciences of the United States of America*, 119(49), Article e2209180119. <https://doi.org/10.1073/pnas.2209180119>
- Spear, L. P. (2000). The adolescent brain and age-related behavioral manifestations. *Neuroscience and Biobehavioral Reviews*, 24(4), 417–463. [https://doi.org/10.1016/S0149-7634\(00\)00014-2](https://doi.org/10.1016/S0149-7634(00)00014-2)
- Spelke, E. S. (1990). Principles of object perception. *Cognitive Science*, 14(1), 29–56. https://doi.org/10.1207/s15516709cog1401_3
- Spelke, E. S. (2003). What makes us smart? Core knowledge and natural language. In D. Gentner & S. Goldin-Meadow (Eds.), *Language in mind: Advances in the study of language and thought* (pp. 277–311). MIT Press.
- Spelke, E. S. (2022). *What babies know*. Oxford University Press. <https://doi.org/10.1093/oso/9780190618247.001.0001>
- Spelke, E. S., Breinlinger, K., Macomber, J., & Jacobson, K. (1992). Origins of knowledge. *Psychological Review*, 99(4), 605–632. <https://doi.org/10.1037/0033-295X.99.4.605>
- Spelke, E. S., & Kinzler, K. D. (2007). Core knowledge. *Developmental Science*, 10(1), 89–96. <https://doi.org/10.1111/j.1467-7687.2007.00569.x>
- Spelke, E. S., Lee, S. A., & Izard, V. (2010). Beyond core knowledge: Natural geometry. *Cognitive Science*, 34(5), 863–884. <https://doi.org/10.1111/j.1551-6709.2010.01110.x>
- Stahl, A. E., & Feigenson, L. (2015). Observing the unexpected enhances infants' learning and exploration. *Science*, 348(6230), 91–94. <https://doi.org/10.1126/science.aaa3799>
- Stahl, A. E., & Feigenson, L. (2017). Expectancy violations promote learning in young children. *Cognition*, 163, 1–14. <https://doi.org/10.1016/j.cognition.2017.02.008>
- Stahl, A. E., & Feigenson, L. (2019). Violations of core knowledge shape early learning. *Topics in Cognitive Science*, 11(1), 136–153. <https://doi.org/10.1111/tops.12389>
- Steinberg, L. (2005). Cognitive and affective development in adolescence. *Trends in Cognitive Sciences*, 9(2), 69–74. <https://doi.org/10.1016/j.tics.2004.12.005>
- Steinberg, L. (2007). Risk-taking in adolescence: New perspectives from brain and behavioral science. *Current Directions in Psychological Science*, 16(2), 55–59. <https://doi.org/10.1111/j.1467-8721.2007.00475.x>
- Sutton, R. S., & Barto, A. G. (1998). *Reinforcement learning: An introduction*. MIT Press.
- Vallortigara, G. (2012). Core knowledge of object, number, and geometry: A comparative and neural approach. *Cognitive Neuropsychology*, 29(1–2), 213–236. <https://doi.org/10.1080/02643294.2012.654772>
- van den Bos, W., & Hertwig, R. (2017). Adolescents display distinctive tolerance to ambiguity and to uncertainty during risky decision making. *Scientific Reports*, 7(1), Article 40962. <https://doi.org/10.1038/srep40962>
- Van Leijenhorst, L., Zanolie, K., Van Meel, C. S., Westenberg, P. M., Rombouts, S. A., & Crone, E. A. (2010). What motivates the adolescent? Brain regions mediating reward sensitivity across adolescence. *Cerebral Cortex*, 20(1), 61–69. <https://doi.org/10.1093/cercor/bhp078>
- Watabe-Uchida, M., Eshel, N., & Uchida, N. (2017). Neural circuitry of reward prediction error. *Annual Review of Neuroscience*, 40(1), 373–394. <https://doi.org/10.1146/annurev-neuro-072116-031109>
- Winters, S., Dubuc, C., & Higham, J. P. (2015). Perspectives: The looking time experimental paradigm in studies of animal visual perception and cognition. *Ethology*, 121(7), 625–640. <https://doi.org/10.1111/eth.12378>
- Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition*, 69(1), 1–34. [https://doi.org/10.1016/S0010-0277\(98\)00058-4](https://doi.org/10.1016/S0010-0277(98)00058-4)
- Wynn, K. (1992). Addition and subtraction by human infants. *Nature*, 358(6389), 749–750. <https://doi.org/10.1038/358749a0>
- Wynn, K. (1998). Psychological foundations of number: Numerical competence in human infants. *Trends in Cognitive Sciences*, 2(8), 296–303. [https://doi.org/10.1016/S1364-6613\(98\)01203-0](https://doi.org/10.1016/S1364-6613(98)01203-0)
- Wynn, K., Bloom, P., & Chiang, W.-C. (2002). Enumeration of collective entities by 5-month-old infants. *Cognition*, 83(3), B55–B62. [https://doi.org/10.1016/S0010-0277\(02\)00008-2](https://doi.org/10.1016/S0010-0277(02)00008-2)
- Xu, F. (2002). The role of language in acquiring object kind concepts in infancy. *Cognition*, 85(3), 223–250. [https://doi.org/10.1016/S0010-0277\(02\)00109-9](https://doi.org/10.1016/S0010-0277(02)00109-9)
- Xu, F., & Carey, S. (1996). Infants' metaphysics: The case of numerical identity. *Cognitive Psychology*, 30(2), 111–153. <https://doi.org/10.1006/cogp.1996.0005>
- Xu, F., Carey, S., & Quint, N. (2004). The emergence of kind-based object individuation in infancy. *Cognitive Psychology*, 49(2), 155–190. <https://doi.org/10.1016/j.cogpsych.2004.01.001>
- Zhang, F., & Emberson, L. L. (2020). Using pupillometry to investigate predictive processes in infancy. *Infancy*, 25(6), 758–780. <https://doi.org/10.1111/inf.12358>

Received January 12, 2023

Revision received August 24, 2023

Accepted September 5, 2023 ■