Predictions about reward outcomes in rhesus monkeys

Yiyun Huang[1], Hayoung Chang[3], Laurie R. Santos[4], & Alexandra G. Rosati[1,2]*

[1]Department of Psychology
[2]Department of Anthropology
University of Michigan
Ann Arbor, MI USA

[3]Department of Human Evolutionary Biology
Harvard University
Cambridge, MA USA

[4]Department of Psychology
Yale University
New Haven, CT USA

*Correspondence to: rosati@umich.edu

Abstract

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*

Introduction

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, Erdeniz, & Done, 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 judgements, and even moral reasoning (Cushman, 2013; d'Acremont, Lu, Li, Van der Linden, & Bechara, 2009; Ergo, De Loof, & Verguts, 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, 1986; Hood & Santos, 2009; Onishi & Baillargeon, 2005; Santos & Hauser, 2002; Spelke, 2003, 2022; Spelke & Kinzler, 2007; Vallortigara, 2012; Wynn, 1992; Wynn, Bloom, & Chiang, 2002). Recent work further argues that increased looking responses similarly function as a learning signal to optimize behavior (Berger & Posner, 2022; Köster, Kayhan, Langeloh, & Hoehl, 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, Surian, & Baillargeon, 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, Dayan, & Montague, 1997; Watabe-Uchida, Eshel, & Uchida, 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 (Abler, Walter, Erk, Kammerer, & Spitzer, 2006; Bayer & Glimcher, 2005; D'Ardenne, McClure, Nystrom, & Cohen, 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, Markman, & Otto, 2014; Kuss et al., 2013; Otto, Gershman, Markman, & Daw, 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, Iannaccone, Walitza, Brandeis, & Brem, 2015), but these signals appear to be degraded in old age (Chowdhury et al., 2013; Samanez-Larkin, Worthy, Mata, McClure, & Knutson, 2014). These neural changes mirror broader age-related shifts in decision-making preferences across the lifespan (Casey, Getz, & Galvan, 2008; Eppinger, Nystrom, & Cohen, 2012; Hartley & Somerville, 2015), supporting the claim that prediction error signals are behaviorally relevant for choice behavior.

Work from developmental psychology and comparative animal cognition has similarly harnessed responses to unexpected outcomes to understand cognition 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, Dubuc, & Higham, 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, Breinlinger, Macomber, & Jacobson, 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, 2015; Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011; Martin & Santos, 2016; Martin & Santos, 2014; 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 spatio-temporal 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 subsequently are 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, Tzur, & Posner, 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 earning 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 spatio-temporal 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, Stumph, & Santos, 2021; Arre, Clark, & Santos, 2020; Bettle & Rosati, 2021; De Petrillo & Rosati, 2019; Drayton & Santos, 2015; Higham et al., 2011; Hughes & Santos, 2012; Marticorena et al., 2011; Martin & Santos, 2014; Rosati, Arre, Platt, & Santos, 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 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, Arre, Platt, & Santos, 2016; Rosati et al., 2018; Rosati & Santos, 2017; Rosati, Wobber, Hughes, & Santos, 2014). While rhesus macaques are an important neurobiological model species for studies of reward processing, including in studies of reward prediction error (Bayer & Glimcher, 2005; Enomoto et al., 2011; Lak, Stauffer, & Schultz, 2014; Schultz et al., 1997), prior work using neurobiological techniques have 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, Baldwin, de Biasi, & Montague, 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., 2021; Arre et al., 2020; Bettle & Rosati, 2021; De Petrillo & Rosati, 2019; Drayton & Santos, 2015; Marticorena et al., 2011; Martin & Santos, 2014), and actively attempt 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, Sulkowski, Spaepen, & Hauser, 2002; Santos, Nissen, & Ferrugia, 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 lifespan from infancy to old age, here focusing on the positive reward prediction error condition validated in Study 1. If monkey 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 lifespan 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 & Green, 1992; Bjorklund & Bering, 2003; Gomez, 2005; Matsuzawa, 2007; Matsuzawa, Tomonaga, & Tanaka, 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 lifespan (Rosati et al., 2016). However, they show different patterns of responses than human to socioemotional 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 versus expected outcomes), and was randomly assigned to one of three conditions in a between-subject manipulation: (1) 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*; (2) 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 (3) 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.

Methods

Ethics statement

All non-invasive behavioral tests reported in this paper were approved by the Institutional Animal Care and Use Committee (IACUC) for the University of Puerto Rico Medical Sciences Campus (protocols #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 2m 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 monkeys face in order to later code their looking times from video. As the current 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 dataset. 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 dataset, 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 1500 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 versus three) represented an expected versus unexpected outcome depended on the particular condition, as described below. Monkeys that did not watch and provide scoreable responses to both trials (for example, because they walked away or were displaced by other monkeys before completing the session) were not included in the final dataset, as described in more detail below.

In a given session, experimenter 1 (E1) the presenter, knelt approximately 2m away from the monkey and placed the apparatus in from 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 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 towards 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 Video S1 for example 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 8s) 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 towards 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" while 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 judgement that they were looking was confirmed by checking the video. E2 timed this period using the camera timer, and then said "stop" when 10s had passed. Each trial therefore took about 20s when considering the initial demonstration phase when the experimenter manipulated the boxes, setting up the test trial, and the subsequent 10s 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 towards 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.

(a) General testing setup

(b) Apparatus overview

(c) Conditions and test trial outcomes

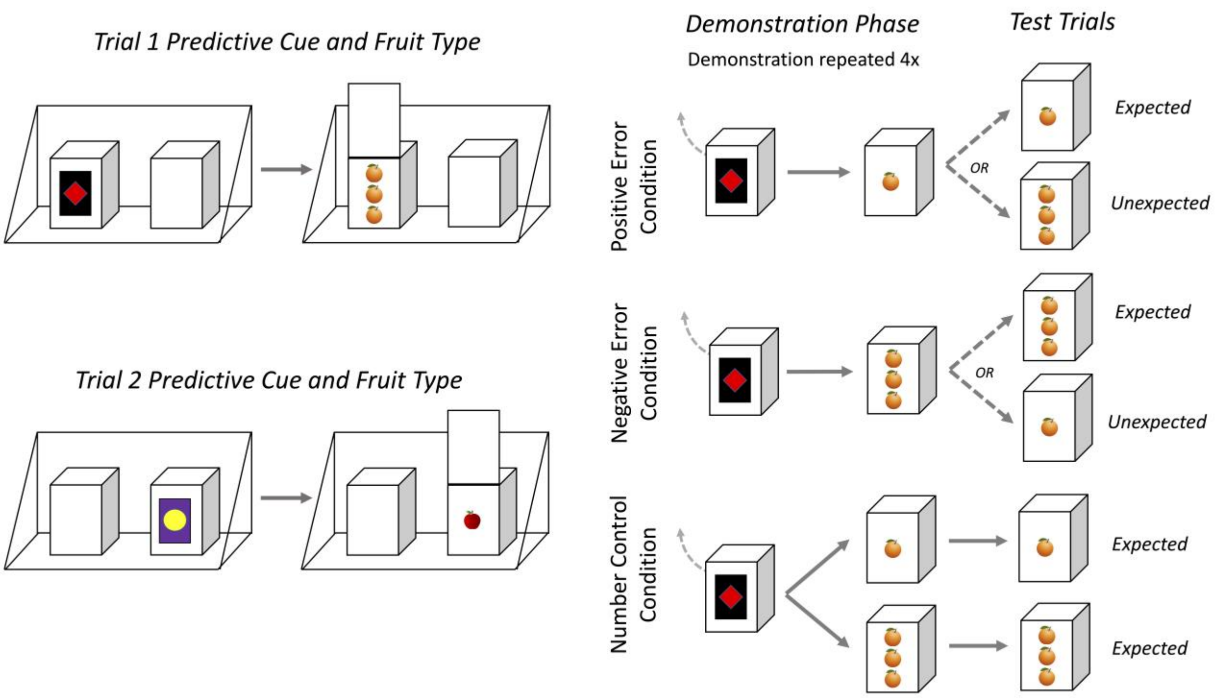

Fig. 1: **Study 1 procedure and conditions.** (a) The primary experimenter knelt approximately 2m away from the monkey and manipulated the apparatus while the monkey observed. (b) The apparatus consisted of a stage with two boxes; each box was white on two sides but had a unique visual cue on front and 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 towards 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 towards different amounts of fruit without violated expectations.

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 was 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) was 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 scoreable 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 apparatus) would make the judgement to stop the session because the monkey had ben interfered with or walked away; note that this is typically clear to assess as the monkey typical 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 dataset.

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 dataset). A given trial clip started 1-2 seconds 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 Video S1 for example 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 10s, following typical methods used in prior looking time studies in this population (Arre et al., 2021; Arre et al., 2020; Bettle & Rosati, 2021; De Petrillo & Rosati, 2019; Drayton & Santos, 2018; Martin & Santos, 2014; Rosati et al., 2018). Specifically, clips were always coded for exactly 10s 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 towards the apparatus for the subsequent 10s. 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 dataset (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, 2010; Bates, Mächler, Bolker, & Walker, 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 report 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, 2021).

Transparency and openness

We report how our sample size, all data exclusions, all manipulations, and all measures in the study. Data and analysis code from these studies will be accessible in Dryad Digital Repository upon publication. Data were analyzed using R v4.1.2. This study's design and analyses were not pre-registered.

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 ± SE = 0.24s) compared to three fruits (the unexpected outcome), a significant difference [3.97 ± 0.30s; $t(69) = 4.88, p < 0.0001$, 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 ± 0.30s at one fruit (the unexpected outcome) and 3.29 ± 0.32s at three fruits (the expected outcome), which did not differ significantly [$t(69) = -0.94, p = 0.35$, 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 ± 0.29s at one fruit and 3.50 ± 0.32s at three fruits, trending to look longer at more fruit [$t(69) = 1.86, p = 0.07$, Cohen's $d = 0.22$]. Overall, this shows that monkey responses in these conditions was not a simple reflection of the number of fruits their 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 versus unexpected trial first). We then added *outcome fruit number* in the second model, which improved fit [$\chi^2 = 11.00$, $df = 1$, $p < 0.001$; 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 [$\chi^2 = 1.58$, $df = 2$, $p = 0.45$; 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 X 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: $\chi^2 = 19.40$, $df = 4$, $p < 0.001$; AIC = 1914.8; see 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 one fruit specifically in the positive error condition [$p < 0.0001$], where three fruits reflected the unexpected outcome, but did not do so in the negative condition where one fruit was unexpected [$p = 0.36$, n.s.] and only trended to do so in the numerical control [$p = 0.07$]. 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 [$p = 0.0001$], and responses to three versus one fruits in the positive error condition trended to be greater compared to the control [$p = 0.052$], indicating that responses to more fruits was 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 (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 [LRT: χ^2 = 18.10, *df* = 2, *p* < 0.001; AIC = 1044.3 compared to 1058.4 in the first model; see 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 [$p < 0.05$] and negative error condition [p = 0.0001]. 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.

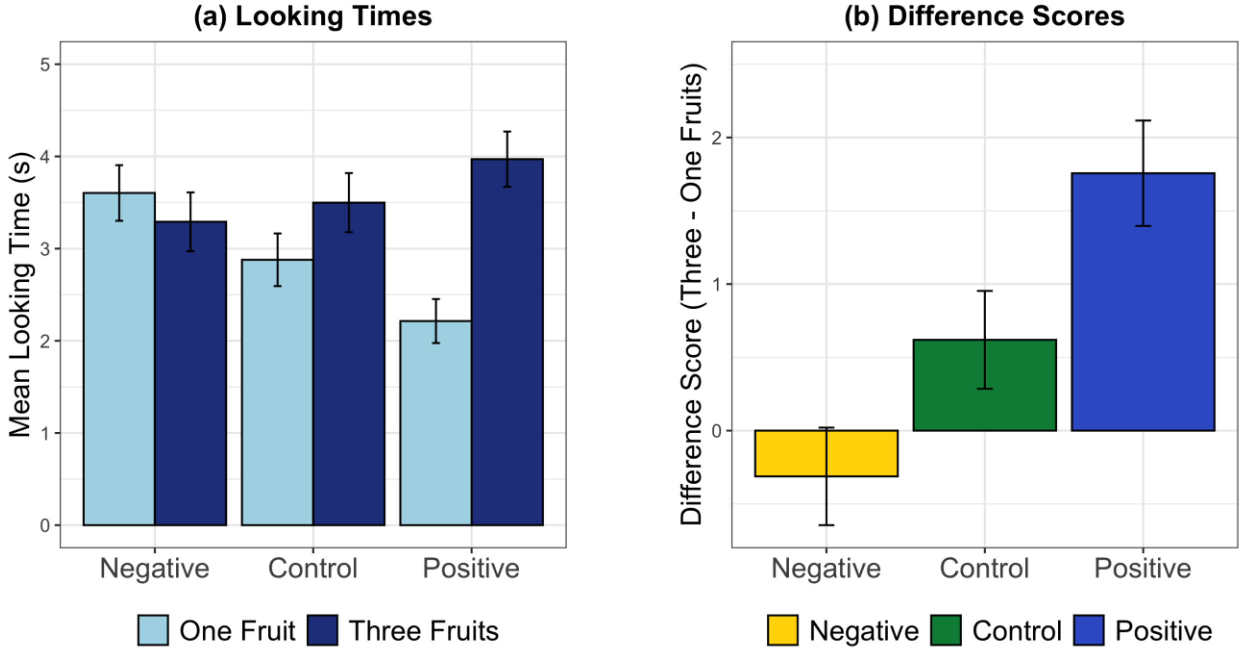

Fig. 2: Responses to reward prediction errors across conditions. (a) Looking times to different reward quantities (one or three fruits) by condition (negative error condition, control, or positive error condition). All monkeys saw a one-fruit and a three-fruit reward outcome (in counterbalanced order 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 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.

Study 2: Development of expectations about reward across the lifespan

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 current 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 human-like 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.

Methods

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 4-6 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 lifespan of the monkeys in this population is 15 years, and they rarely exceed 25 years (Hoffman, Higham, Mas-Rivera, Ayala, & Maestripieri, 2010). 58 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. 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 dataset 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 dataset (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 non-linear 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 ± 0.13s) than the expected trial (3.16 ± 0.13s), a significant difference [$t(362) = 10.21$, $p < 0.0001$, 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*: $t(172) = 5.85$, $p < 0.0001$, Cohen's $d = 0.44$; *adolescents*: $t(44) = 7.19$, $p < 0.0001$, Cohen's $d = 1.07$; *adults*: $t(108) = 5.05$, $p < 0.0001$, Cohen's $d = 0.48$; *older adults*: $t(35) = 4.76$, $p < 0.0001$, 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, versus unexpected outcome on trial 2). We then added *age cohort* in the second model, which improved fit [$\chi^2 = 118.29$, $df = 3$, $p < 0.0001$; AIC = 3214.6 compared to 3322.7 in the first model]. In particular, there were significant linear ($p < 0.0001$) and quadratic effects ($p < 0.05$) 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 [$\chi^2 = 9.55$, $df = 3$, $p < 0.05$; AIC = 3212.7; see Table S3 for model parameters]. Post-hoc comparisons showed that while all age cohorts looked longer at the unexpected compared to the expected trial [$p < 0.0001$ for all comparisons], adolescents showed a larger trial type effect (e.g., more relative looking to the unexpected outcome) compared to adults [$p < 0.05$], and trended to do so compared to juveniles [$p = 0.08$]. In contrast, there was no difference in the patterns of response of adults and older adults [$p = 0.55$]. In addition, groups varied in their overall durations of looking in general, irrespective of trial type: juveniles looked longer overall than all other groups [$p <0.0001$] and adolescents looked longer than adults and older adults [$p < 0.05$]. Finally, the inclusion of a three-way interaction between sex, cohort and trial did not further improve fit [$\chi^2 = 2.75$, $df = 7$, $p = 0.91$; AIC = 3221.5], indicating similar patterns of responding in males and females. Comparisons of AIC comparisons further supported model 3 (including the *cohort X 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 a as a predictor (see SOM 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 [$\chi^2 = 9.12$, $df = 3$, $p < 0.05$; AIC = 1712.9 compared to 1716.0 in the first model; see Table S4 for model parameters]. Post-hoc tests showed adolescents had a larger difference score than adults [$p < 0.05$], indicating they showed greater relative looking to the unexpected reward. They trended to show a larger score than juveniles [$p = 0.099$], but there was no difference between adults and older adults [$p = 0.56$, n.s.]. Inclusion of the interaction between *age cohort* and *sex* did not further improve fit [$\chi^2 = 0.26$, $df = 3$, $p = 0.97$; 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 that there was no shift in sensitivity in old age (see SOM).

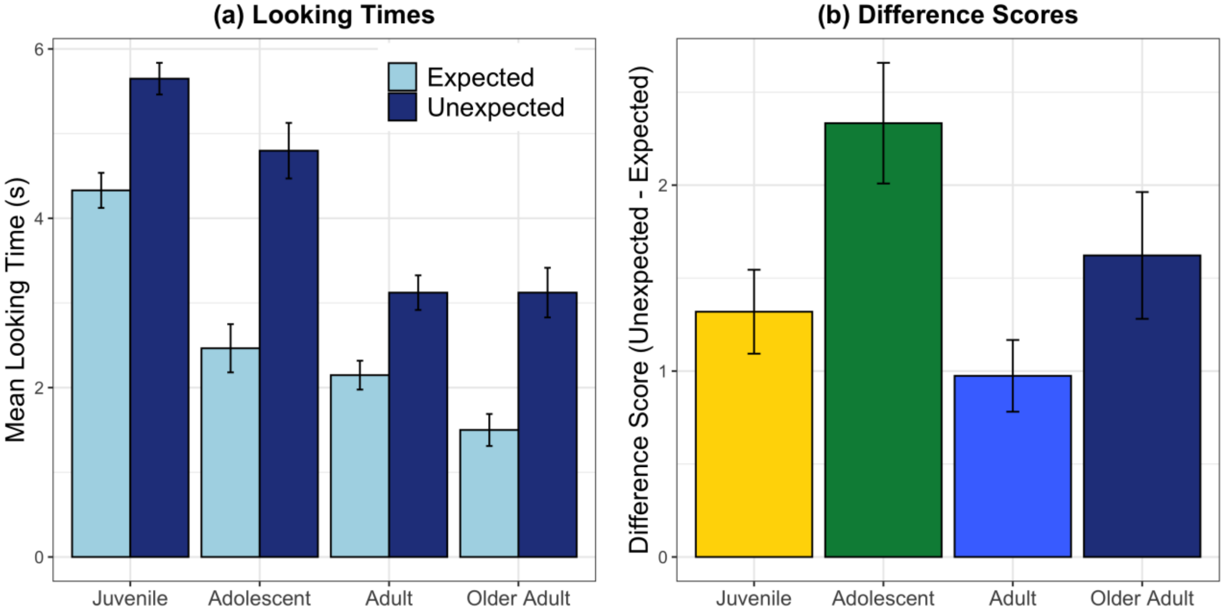

Figure 3: Predictions about reward across the lifespan. (a) Looking responses across age cohorts according to the trial types (expected vs. unexpected). Here, the expected outcome on trial 1 was one fruit (matched the demonstration phase) whereas the unexpected outcome on trial 2 was three fruits (more 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.

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 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., 2021; Arre et al., 2020; Baillargeon, 1986; Drayton & Santos, 2015; Hood & Santos, 2009; Hughes & Santos, 2012; Margoni et al., 2022; Martin & Santos, 2014; Needham & Baillargeon, 1993; Onishi & Baillargeon, 2005; Phillips & Santos, 2007; Phillips, Shankar, & Santos, 2010; Santos & Hauser, 2002; Spelke, Lee, & Izard, 2010; Spelke, 1990, 2022; Spelke et al., 1992; 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., 2021; Arre et al., 2020; Bettle & Rosati, 2021; De Petrillo & Rosati, 2019; Drayton & Santos, 2015; 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-valanced errors (Hayden, Heilbronner, Pearson, & Platt, 2011). Neuroimaging studies of humans invoke similar response in anterior cingulate (Alexander & Brown, 2017; Fouragnan, Retzler, & Philliastides, 2019). Along these lines, some work suggests 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 was 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 non-invasively, 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, Junge, & Hauser, 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, Carey, & Quint, 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, Engelmann, Arslan, Hertwug, & Herrmann, 2022; Rosati, Emery Thompson, Atencia, & Buckholtz, 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 the human results showing adolescents are more sensitive to prediction errors, the exacerbated responses of adolescents 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 in making numerical judgements 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 suggest 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, Hughes, & Cantlon, 2016; Hall-Haro, Johnson, Price, Vance, & Kiorpes, 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 shift 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, Bault, Coricelli, & Blakemore, 2010; Casey, Getz, et al., 2008; Casey, Jones, & Hare, 2008; Crone & Steinbeis, 2017; Defoe, Dubas, Figner, & Van Aken, 2015; Hartley & Somerville, 2015; Paulsen, Platt, Huetell, & Brannon, 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, van Duijvenvoorde, Peper, & Crone, 2015; Galvan, 2010; Leijenhorst et al., 2010) compared to adults. One way to differentiate these process 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, Nair, Cantwell, & Rosati, 2022), to assess how these different measures co-vary 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' 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 judgements about the physical or social world (Drayton & Santos, 2015; Hood & Santos, 2009; Spelke, 2022; Spelke & Kinzler, 2007), whereas the current 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, Gershman, Seymour, Dayan, & Dolan, 2011; Decker, Otto, Daw, & Hartley, 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.

Acknowledgments

We 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 (CSCAR) 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. 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 (ORIP) of the National Institutes of Health (NIH) through Grant Number 5P40OD012217 to the Caribbean Primate Research Center and the University of Puerto Rico. This research was supported by the National Institute of Mental Health (R01MH096875), the National Science Foundation (1944881), and a Sloan Foundation Fellowship (FG-2019-12054).

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