

# Experience-dependent changes in the development of face preferences in infant rhesus monkeys

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## Abstract

It is well known that early experience shapes the development of visual perception for faces in humans. However, the effect of experience on the development of social attention in non-human primates is unknown. In two studies, we examined the effect of cumulative social experience on developmental changes in attention to the faces of unfamiliar conspecifics or heterospecifics, and mom versus an unfamiliar female. From birth, infant rhesus monkeys preferred to look at conspecific compared to heterospecific faces, but this pattern reversed over time. In contrast, no consistent differences were found for attention to mom's face compared to an unfamiliar female. These results suggest differential roles of social experience in shaping the development of face preferences in infant monkeys. Results have important implications for establishing normative trajectories for the development of face preferences in an animal model of human social behavior.

## KEYWORDS

attention, experience, eye-tracking, face, infant development, macaque, preferential looking

## 1 | INTRODUCTION

Numerous studies have documented the important role that experience plays in the development of visual and auditory social perception and its underlying neural circuitry (Casey, Tottenham, Liston, & Durston, 2005; Johnson, 2005). From birth, humans and other animals are strongly attracted to biologically relevant stimuli (Johnson, Dziurawiec, Ellis, & Morton, 1991; Sowards & Sowards, 2002), and these early visual preferences provide essential perceptual information to the developing brain during periods of heightened plasticity. For example, early attraction to faces and face-like patterns have been reported in a variety of vertebrate species in the absence of visual experience with faces (Sugita, 2008; Rosa Salva, Farroni, Regolin, Vallortigara, & Johnson, 2011), and in humans shortly after birth (Goren, Sarty, & Wu, 1975; Rosa Salva et al., 2011; Simion, Leo, Turati, Valenza, & Dalla Barba, 2007; Valenza, Simion, Macchi Cassia, & Umiltà, 1996). It is believed that our early attraction to faces may be driven by a subcortical system, including the superior colliculus, pulvinar, and amygdala that is activated by the visual/sensory properties present in faces (known as CONSPEC, Johnson, 2005; Morton & Johnson, 1991). The system is

experience-expectant, meaning it is selectively activated by information that is common to all members of a species, like faces (Greenough, Black & Wallace, 1987; however, for an alternative perspective see Simion & Di Giorgio, 2015). In the second month of life, this system appears to give way to a more cortically mediated system (known as CONLEARN, Johnson, 2005; Morton & Johnson, 1991) that becomes strengthened with experience due to both progressive (synaptogenesis/myelination) and regressive (synaptic pruning) events that increase the efficiency with which we process relevant and frequently encountered information (de Haan, Humphreys, & Johnson, 2002; Lourenco & Casey, 2013; Morton & Johnson, 1991; Scott, Pascalis, & Nelson, 2007). Together, these two systems function to direct attention to faces which, in turn, provides the information necessary to drive the maturation of cortical circuits that become specialized in adults for processing social information, like faces (de Haan et al., 2002; Johnson, 2005, 2011). The timing of this latter mechanism is more tenuous because human infants show experience-dependent learning before two months of age, for example, infants have a bias to look towards faces of primary caregivers compared to unfamiliar individuals (Bushnell, 2001; Slater & Quinn, 2001).

Studies in both macaques and human infants have shown the importance of early visual experience for the development of typical face processing. Human infants born with congenital cataracts, for example, lack visual input from birth and provide a rare opportunity to study the effects of early visual perception on the development of social cognition and its underlying neural mechanisms. These cataracts can be surgically removed, typically between 3 and 8 months of age, after which the individuals acquire extensive post-surgical visual experience before they are tested between 9 and 30 years of age. These studies have identified numerous, long-lasting effects of early visual deprivation on the development of adult-like face processing, including sensitivity to holistic information (Le Grand, Mondloch, Maurer & Brent, 2004), use of second-order configural features (Grady, Mondloch, Lewis & Maurer, 2014; Le Grand, Mondloch, Maurer & Brent, 2001; Robbins, Nishimura, Mondloch, Lewis, & Maurer, 2010), and face memory (de Heering & Maurer, 2014). Additionally, these patients show reduced selectivity in the activation of cortical circuitry involved in processing faces compared to controls (Grady et al., 2014), although they were unaffected on tasks requiring the basic detection of faces, discrimination of specific features, or the discrimination of non-face visual patterns (Grady et al., 2014; Le Grand et al., 2001; Mondloch, Segalowitz, Lewis, Dywan, LeGrand, & Maurer, 2013; Robbins et al., 2010). Thus, the maturation of adult-like, conspecific face processing mechanisms, for example, holistic and second-order configural processing, face memory, and their underlying cortical circuitry appears to require both early visual experience, and early exposure to the visual/sensory information present in faces.

One study directly addressed the role of visual experience in shaping preference for faces. A group of Japanese macaques were raised from birth in face isolation for 6 to 24 months; they were raised in a visually enriched nursery by human caretakers who wore face shrouds (Sugita, 2008). After this, the monkeys' preference for conspecific versus human faces was tested using a preferential looking task. The results showed that with no prior face experience, the monkeys preferred to look at faces (monkey and human) over non-face objects, suggesting an innate face preference. However, after a month of exposure to either human or monkey faces, the monkeys switched their preference to favor the exposed face category. Surprisingly, these experience-dependent preferences were relatively stable when tested a year later, after the subjects had been moved to an environment that contained other monkeys (Sugita, 2008). Therefore, the monkeys preferred to look at faces from birth, but a brief exposure to faces resulted in long-lasting preferences for the exposed category, despite additional visual experience.

The domain general phenomenon of perceptual narrowing has often been used to emphasize the importance of early experience-dependent learning. Perceptual narrowing is a developmental phenomenon whereby the ability to discriminate between unfamiliar stimuli, for example, those for which we lack experience, declines while preserving the ability to discriminate among familiar stimuli, for example, those for which we have acquired experience. For example, before 6 months of age, human infants are able to discriminate broadly the faces of many different species or races, but this narrows after 9 months of age such that only the ability to discriminate among

commonly encountered faces is retained (Kelly et al., 2007; Pascalis et al., 2002; Scott et al., 2007; Simpson, Varga, Frick, & Frigaszy, 2011; for perceptual narrowing of human phonemes, see Kuhl, Williams, Lacerda, Stevens, & Lindholm, 1992, and multi-sensory stimuli, see Lewkowicz & Ghazanfar, 2009). Additionally, several studies have demonstrated experience-dependent plasticity in both the timing of perceptual narrowing, and the ability to shape face discrimination skills throughout the lifespan. For example, 6-month-old human infants who are exposed to pictures of monkey faces retain their ability to discriminate monkey faces when tested at 9 months of age (Pascalis et al., 2005; Scott & Monesson, 2009), and Fair, Flom, Jones, and Martin (2012) were able to elicit accurate discrimination of novel faces in 12-month-old infants after only 40s of familiarization prior to testing. Moreover, numerous studies have shown experience-dependent changes in the discrimination of other-race faces, and non-face visual stimuli well into adulthood (Diamond & Carey, 1986; Gauthier, Skudlarski, Gore, & Anderson, 2000). Thus, although the timing of perceptual narrowing may reflect the experience-dependent maturation of cortical circuits important for adult-like face processing, evidence suggests that the system retains at least some of its plasticity well into adulthood.

Collectively, these findings are important for understanding neurodevelopmental disorders, like autism. For example, it has been demonstrated that early risk factors for the development of autism can be detected within the first few months of life and include lack of appropriate attention to faces (Chawarska, Macari, & Shic, 2013; Jones & Klin, 2013). Although the specific cause of this phenomenon is unknown, the lack of social input early in life may adversely affect experience-dependent learning for social categories, and the subsequent development and specialization of cortical brain networks resulting in long-lasting social impairments (but see Elsabbagh et al., 2013). Because experience is important not only from birth, but throughout development, and lack of appropriate perceptual experience is associated with a variety of visual processing impairments as well as neurodevelopmental disorders, it is extremely important to understand the role of experience in shaping the normative developmental trajectory of early emerging social and attentional processes. How does attention to social stimuli change over time? What is the role of experience in shaping this trajectory? Is there evidence for critical periods in the development of social attention, defined by distinct shifts in viewing patterns and, if so, what are the possible underlying social and/or biological mechanisms?

Monkeys represent an ideal model for investigating such questions longitudinally. Numerous studies in adult monkeys suggest that experience plays an important role in shaping attention to social stimuli, like faces, including studies of face categorization (Martin-Malivel & Okada, 2007), configural face processing (Neiworth, Hassett, & Sylvester, 2007; Parr, Dove, & Hopkins, 1998; Parr, 2011a), and visual preference for other species' faces (Dahl, Rasch, Tomonaga, & Adachi, 2013; Dufour, Pascalis, & Petit, 2006; Fujita, 1987; Humphrey, 1974; Pascalis & Bachevalier, 1998). However, very little is known about social behavioral development in monkeys or the importance of experience in shaping the normative developmental trajectory of these social preferences (Brown & Dixon, 2000;

Machado & Bachevalier, 2003; Suomi, 2005). Here, we report the results of two longitudinal, eye-tracking studies from birth through 23 weeks of age that examined infant monkeys' preference to attend to faces that varied in terms of their experience and familiarity. Experience was manipulated by showing the faces of unfamiliar conspecifics versus heterospecifics (Experiment 1), and familiarity was varied by showing each subjects' mom's face versus an unfamiliar female (Experiment 2). Preference was measured as the proportion of total looking and the mean duration of each fixation. Each experiment reports the results from three cohorts of monkeys ( $N = 32$ ) born in 2012, 2013, and 2014. The subjects all lived in large social groups during the course of the study and thus their experience with conspecific faces and their familiarity with their mom's face increased steadily over time while they had no experience with the heterospecific faces, or familiarity with the unfamiliar conspecific faces. Similar to human infants, we initially expected that the infants would prefer to look at the more salient category of stimuli, for example, conspecific faces and mom faces (Bushnell, 2001; Sugita, 2008). However, if experience changes attention to faces over time, Experiment 1 would predict that subjects' interest in the unfamiliar heterospecific faces would increase over time, while attention to conspecific faces would decrease. Similarly, Experiment 2 would predict that the subjects would show an initial preference for their own mom's face but with increased social experience this would shift toward a greater preference for the novel, unfamiliar female faces (Bartrip, Morton, & de Schonen, 2001). Overall, fixation duration was expected to be longer for the preferred category.

## 2 | GENERAL METHODS

### 2.1 | Subjects

Data were collected from three cohorts of infant rhesus monkeys during the 2012, 2013, and 2014 birthing seasons (approximately April–September). All infant subjects were estimated full-term (>450 g) offspring of mid-ranking, multiparous females. Both mothers and infants lived in large social groups containing over 100 individuals at the Yerkes Primate Center field station. Mothers were given at least 3 days after birth to bond with their infant before testing began. All of the infant subjects were tested with their mothers and the pair remained socially housed within their original birth group during the duration of the study. All procedures were approved by the Institutional Animal Care and Use Committee of Emory University and followed the standards of the American Psychological Association for the ethical treatment of animals. Table 1 lists the infants' mean age and range in days for each week of testing in both experiments.

Eleven subjects were tested during the 2012 season (four male, seven female). Testing began in the first week of life and continued every week through 12 weeks of age. Ten male subjects were tested in the 2013 season, beginning in the first week of life and continuing through 23 weeks of age. Finally, 11 male subjects were tested in the 2014 season, beginning in the first week of life and continuing through 23 weeks of age. The rationale for testing only male subjects, and differences in the ages of testing after the 2012 season was due to the focus of the Autism Center of Excellence funding.

**TABLE 1** Mean age and range in days for infants tested on PN and mom trials in the 2012 (Experiment 1) and 2013 (Experiment 2) cohorts

Week	2012 cohort				2013 cohort				2014 cohort			
	PN		Mom		PN		Mom		PN		Mom	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
1	6.2	5–7	6.0	5–7	4.0	3–5	4.0	3–5	5.7	5–6	5.5	4–7
2	13.8	12–18	13.8	12–18	10.0	10	10.3	9–12	10.5	9–12	11.3	9–13
3	20.7	19–25	20.0	17–25	24.6	22–28	18.4	16.21	19.6	15–22	20.0	19–21
4	26.4	24–29	26.3	25–27	24.4	22–28	24.7	22–28	25.2	22–28	25.0	22–28
5	33.8	31–39	33.8	31–39	31.5	29.35	31.2	29–35	33.1	29–35	33.4	29–35
6	41.3	38–47	41.3	38–47	–	–	–	–	–	–	–	–
7	48.1	45–54	48.4	45–54	46.6	44–50	47.0	45–50	47.1	43–49	47.1	43–49
8	54.4	52–56	55.0	54–56	–	–	–	–	–	–	–	–
9	61.0	59–63	61.7	61–63	59.8	58.63	59.8	58–63	60.8	57–67	61.7	57–67
10	68.6	66–70	68.6	66–70	–	–	–	–	–	–	–	–
11	74.7	73–76	75.0	73–76	74.2	73–76	74.2	73–76	–	–	75.2	71–78
12	82.2	80–84	81.5	78–84	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	89.0	86–91	–	–	87.8	85–90
15	–	–	–	–	–	–	102.2	101–105	–	–	103.7	101–106
17	–	–	–	–	–	–	116.8	116–119	–	–	117.3	115–120
19	–	–	–	–	–	–	130.1	128–133	–	–	130.8	127–133
21	–	–	–	–	–	–	144.0	141–147	–	–	144.8	141–147
23	–	–	–	–	–	–	157.6	156–158	–	–	158.6	155–161

The dash indicates that subjects were not tested during that week.

## 2.2 | Procedures

For testing, the mother–infant pair was accessed from its social group using established procedures (e.g., Sanchez et al., 2010). Briefly, research staff entered the compound, secured the adult males in an indoor holding area, identified the specific mother–infant pair and moved them into an adjacent indoor holding area. After securing the mother–infant pair, the males were reunited with their social group and the mother–infant pair was taken to the onsite testing facility. These procedures lasted only a few minutes.

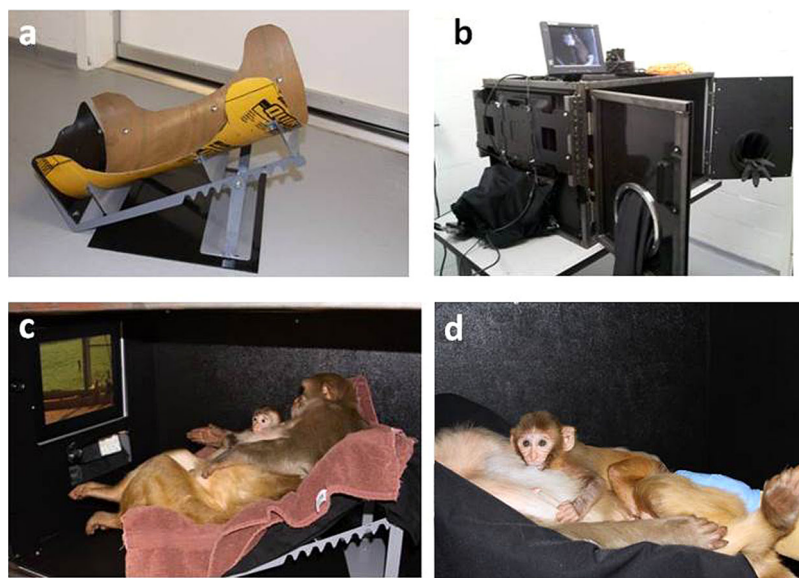
Once inside the testing facility, the mother–infant pair was transferred to a standard primate housing cage where the mother was anesthetized (3–5 mg kg<sup>-1</sup> telazol, i.m.). The pair was then carried to a dedicated testing room containing a custom testing booth and eye-tracking equipment and placed comfortably in a reclining seat (Figure 1a) located inside the testing chamber (Figure 1b, 87 × 57 × 52 cm). Attached to this testing chamber was a 19" (42.6 cm, 45.27° diagonal) computer monitor (1024 × 768 pixels) where the experimental stimuli were presented (Figure 1c). The eye-tracking camera (<http://www.iscaninc.com/> 60 Hz) was mounted on a motorized gimbal located beneath the monitor, which was controlled by an experimenter to track the location of the infant's eye. The experimenters remained concealed from the infant during testing, but the infant's looking behavior could be monitored via the eye-tracking camera and a second camera that provided a wide angle view of the inside of the testing chamber. While seated in this position, the infant remained calm and could voluntarily watch the stimuli presented on the monitor while its eye-movements were recorded (Figure 1d).

Once settled inside the testing chamber, a full-screen video was played to maintain the infant attention towards the monitor. These videos included various cartoons, nature scenes, and colorful animations. While subjects were attending to these videos, individual

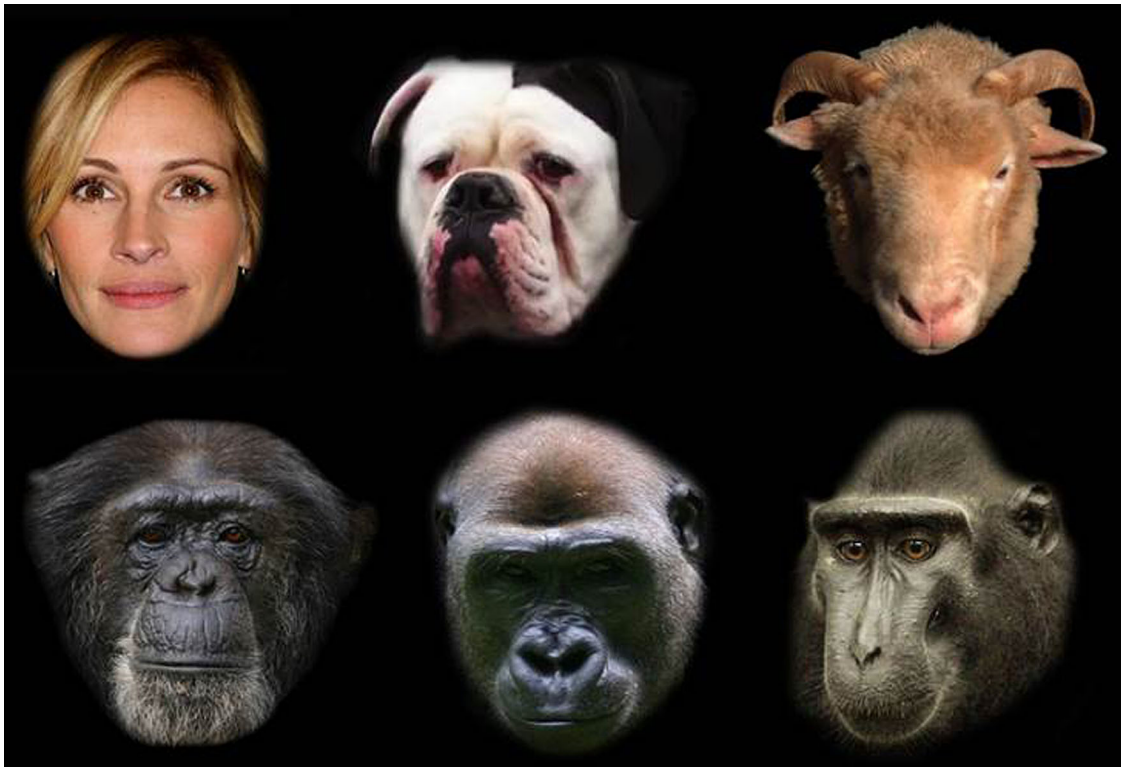
calibration points were presented in five different locations using custom software that paused the video while the calibration point was displayed on a black background. Calibration points were custom, 100 pixel (3.5° diagonal) videos consisting of static pictures, animated cartoons, or spinning/flashing points of light. After all five points had been calibrated, their accuracy was checked by re-presenting a calibration stimulus at each location. Points could then be recalibrated using the same procedure until all five were accurate on visual inspection. The presentation of experimental stimuli (described below) began immediately after the calibration routine and the entire testing time was restricted to 30 min to limit the mother's time under anesthesia. After testing, the mother–infant pair was returned to the adjacent room for recovery. Later in the afternoon, when the mother was fully alert, the pair was returned to their social group. If a testing session was unsuccessful, for example, the infant slept, was fussy, or had poor calibration, it was attempted again within the same week, but only two attempts were made per week for any given subject.

## 2.3 | Stimuli

Stimulus playlists consisted of numerous static and dynamic scenes, including faces, social scenes, and non-face objects that were presented pseudorandomly during a testing session. For this report, we describe the visual fixation data for only two types of static face trials, trials that paired the faces of unfamiliar conspecifics and heterospecifics (Experiment 1), and trials that paired the infants' mother's face with an unfamiliar female's face (Experiment 2). Experiment 1 stimuli were presented through 12 weeks of age while the stimuli for Experiment 2 were presented through 23 weeks of age. All face stimuli were standardized using Photoshop (CS6) by aligning the pupils along the horizontal axis, cropping closely around the face



**FIGURE 1** An illustration of the eye-tracking testing system including the reclining chair that holds the mother and infant (a), an overview of the testing box (b), the mother and baby positioned inside the box with videos playing on the eye-tracking monitor (c), and the infant watching the monitor while nursing on its mother (d)



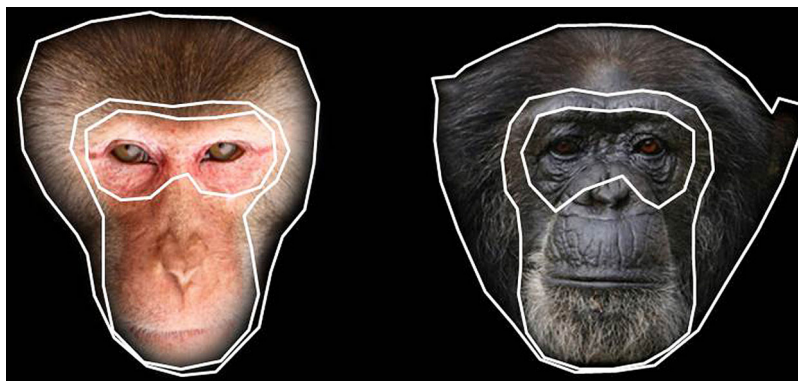
**FIGURE 2** An example of heterospecific face stimuli presented in Experiment 1

(500 vertical pixels,  $24.75^\circ$  diagonal), and removing the background using the black paintbrush tool with a soft outline. Individual trials were then created by placing one example of each image on the left and right sides of a black canvas ( $1024 \times 768$  pixels), where the location of images in each category was counterbalanced across sides. This canvas was then converted into a 10 s .mov file for presentation to subjects. Figure 2 shows an example of the heterospecific faces used in Experiment 1, and Figure 3 shows a screenshot of an individual trial used in Experiment 1. Using Gaze Tracker (<http://www.eyetellect.com/gazetracker/>), specific regions of interest called lookzones were drawn by hand on each face using a polygon tracing tool. These regions included the entire face, the inner facial features, and the eye region.

For illustration, these regions have been overlaid on the faces in Figure 3. Note that the actual lookzones were not visible to subjects during a trial.

## 2.4 | Data analysis

Fixation data were extracted using GazeTracker software and custom MATLAB scripts. GazeTracker computes fixations using three parameters, sample number (acquired at 60 Hz), duration (in ms), and spatial location (diameter in pixels). In this study, fixations were calculated using a minimum of three samples occurring within a radius of 37 pixels ( $1.3^\circ$ ) for at least 50 ms. For each testing session, the data



**FIGURE 3** Example of a trial in Experiment 1 showing a rhesus monkey and a chimpanzee face. Outlined on these faces are the lookzones that were drawn by hand and used as regions of interest in the analyses

from only one trial per stimulus category per subject were included in the analyses. Two dependent variables were calculated, including the percentage of total looking duration, for example, the sum of fixation durations for each stimulus (or lookzone) divided by the overall time spent looking at each trial (maximum of 10 s), and the mean fixation duration.

To determine the developmental trajectories of infant monkey fixation patterns and durations, these data were analyzed using hierarchical linear modeling (mixed model linear regression, SPSS v. 21, IBM, SPSS, Armonk, NY), where stimulus category (conspecific vs. heterospecific or mom vs. other female) was the fixed factor and age (week of testing) was the covariate. Specifically, developmental trajectories representing cubic, quadratic, and linear hierarchical models were tested using an unstructured covariance matrix that predicted a random relationship between stimulus category and age (see Field, 2013). Complete models were performed and the significance of each was evaluated from tests of fixed effects which provide an *F*-test and associated degrees of freedom. In order to identify the model that best fit the relationship between the variables and to test our specific hypotheses, a  $\chi^2$  likelihood ratio test was also performed. For this analysis,  $\chi^2$  values were derived from the change in the log-likelihood ratios generated for each successive model ( $n = 7$ ), for example, simple main effects of age and stimulus category, hierarchical effects of age, and finally hierarchical interactions of age and stimulus categories. The deviance in the log-likelihood ratios is referred to as  $-2LL$ , because of how it is calculated, and has a chi-square distribution (Field, 2013). The largest  $\chi^2$  value for the associated change in the degrees of freedom associated with each model stage was then identified (two-tailed). In this way, we could identify which growth curve most significantly fit the data. A linear trajectory would indicate consistent changes over time, either increasing or decreasing, consistent with our hypotheses. A quadratic trajectory would indicate a single level of change, either increasing then decreasing or vice versa, and a cubic trajectory would indicate two-levels of change, increasing, decreasing, and then increasing again or vice versa. The latter could be the result of a single mechanism that has two developmental periods, or the occurrence of two mechanisms, an early emerging period and then a later one. Both the *F*-test and the  $\chi^2$  values are reported here. Analyses were performed on each cohort separately to provide internal reliability, and then on the combined cohorts. The goal of these analyses was to provide normative developmental trajectories identifying age-related changes in viewing patterns.

### 3 | EXPERIMENT 1, CONSPECIFIC VERSUS HETEROSPECIFIC FACES

#### 3.1 | Subjects

Data were collected from 11 male and female subjects in 2012 (see above) beginning in the first week of life and continuing weekly thereafter until 12 weeks of age, totaling 12 time points. Data were

collected from 10 male subjects in 2013, beginning in the first week of life and continuing weekly through 5 weeks, and thereafter in weeks 7, 9, and 11, totaling eight time points. Data were collected from 11 male subjects in 2014, beginning in the first week of life and continuing weekly through 5 weeks, and thereafter in weeks 7 and 9, totaling seven time points.

#### 3.2 | Stimuli 2012

Infants in the 2012 season were shown four types of trials that paired the faces of conspecifics and heterospecifics. The conspecific faces were all unfamiliar, adult female rhesus monkeys and the heterospecific faces showed humans, chimpanzees, sheep, and dogs. Only one heterospecific face category was shown per week: dog faces in weeks 1, 5, and 9; sheep faces in weeks 2, 6, and 10; chimpanzee faces in weeks 3, 7, and 11; and human faces in weeks 4, 8, and 12. For the purpose of the analyses, heterospecific faces were treated as a single category. Five different examples of these trials were shown each week, each containing novel pairs of faces, totaling 60 unique trials across the 12 weeks of testing.

#### 3.3 | Stimuli 2013 and 2014

Infants in the 2013 and 2014 seasons were also shown four types of trials that paired the faces of conspecifics versus heterospecifics. The conspecific faces were also faces of unfamiliar, adult female rhesus monkeys. Two types of trials were identical to those shown in the 2012 season, the human and chimpanzee faces. However, the remaining two categories were changed to represent primate species. These included gorilla and crested macaque faces. The rationale for changing the heterospecific stimuli to include only primates was to minimize the possibility that subjects were attending to unusual facial features in dogs and sheep that go against the primate pattern, for example, nose shape and length, ear size, and eye displacement. Three novel pairs of images from one heterospecific category were shown each week: chimpanzee faces in weeks 1, 5, and 9; crested macaque faces in week 2; human faces in weeks 3, 7, and 11; and gorilla faces in week 4. This totaled 24 unique trials in 2013 and 21 unique trials in 2014. Note that no data were collected during weeks 6, 8, and 10 during the 2013 and 2014 seasons.

All of the faces presented in Experiment 1 were standardized as described in the General Methods and all of the individuals whose faces were used were unfamiliar to the subjects.

## 4 | RESULTS, EXPERIMENT 1

Trials were excluded from the analyses if the total looking duration per trial was less than 1 s, which resulted in the removal of 21 (of 316) trials in 2012, 9 (of 54) trials in 2013, and 6 (of 67) trials in 2014. Moreover, data were not able to be collected from all subjects at all time points due to problems calibrating the infant, or the infants' fussiness/sleepiness. Therefore, the subsequent analyses contain a different number of subjects at each time point (Table 2).

**TABLE 2** Number of subjects tested in each week in Experiment 1 across the three cohorts, including the total number of fixations and trials analyzed per year

Week	Cohorts		
	2012	2013	2014
1	5	2	3
2	6	2	2
3	9	8	7
4	9	7	9
5	9	6	9
6	7	-	-
7	9	7	7
8	7	-	-
9	8	6	9
10	5	-	-
11	3	6	-
12	5	-	-
#Fixations	7,213	1,943	1,946
#Trials	295	45	67

#### 4.1 | Analyses by lookzone

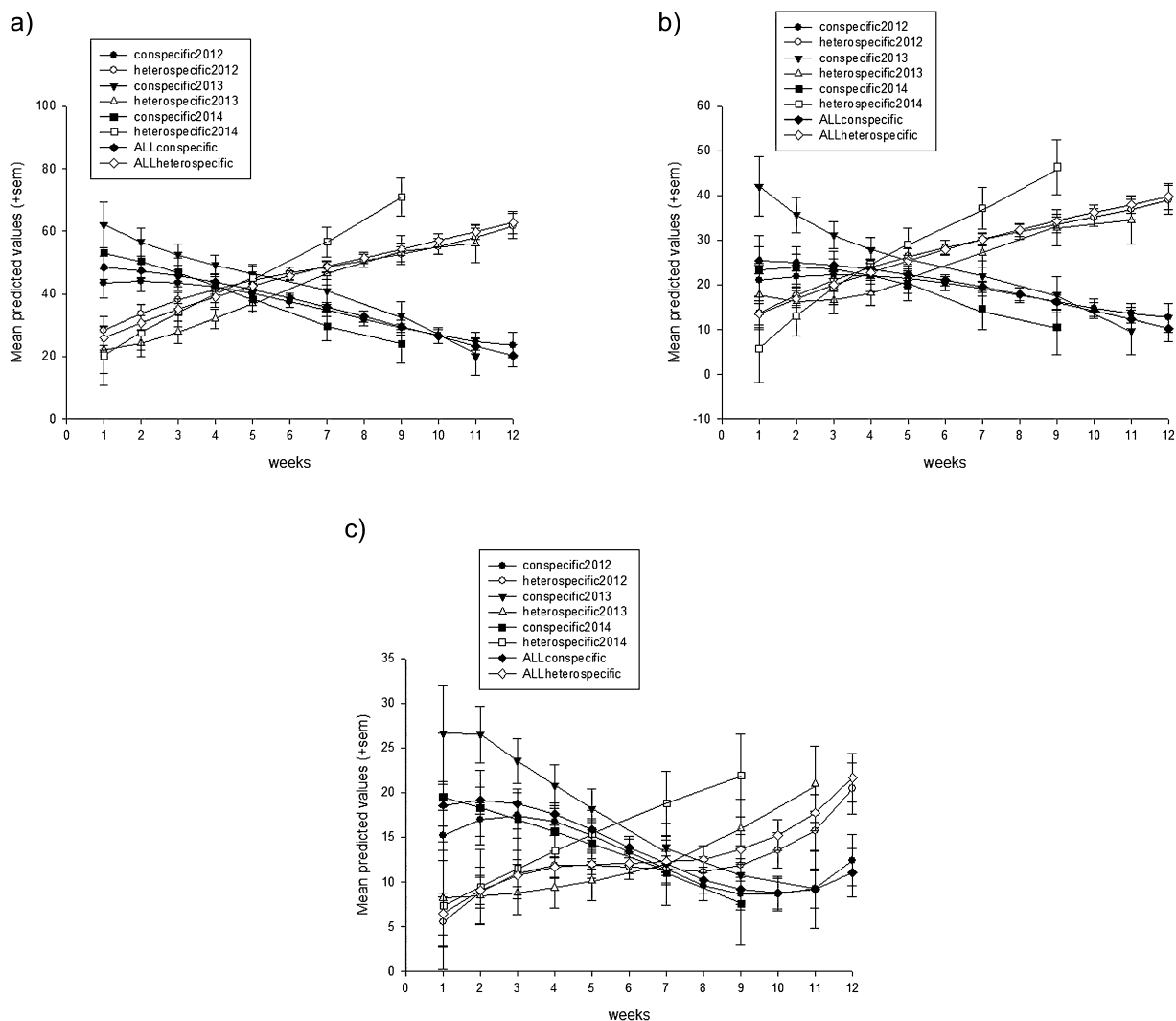
Age-related differences in the percentage of time subjects spent viewing the different lookzones for the conspecific and heterospecific faces was analyzed using hierarchical linear modeling. In the 2012 cohort, age-related changes in total viewing time for all lookzones were best characterized by linear interactions: face,  $F(1,590.0) = 49.43$ ,  $p < .001$ , inner face,  $F(1, 590.0) = 31.55$ ,  $p < .001$ , and eyes,  $F(1, 590.0) = 15.31$ ,  $p < .001$ . In all cases, the percentage of total looking decreased for conspecific faces and increased for heterospecific faces as a function of the infants' age. Changes in the log-likelihood ratio values (-2LL) confirmed that for each of these lookzones, the linear interaction (stimulus category  $\times$  week) was a significantly improved fit over the cubic main effect of age (week<sup>3</sup>): face,  $X^2(2) = 47.47$ ,  $p < .001$ , inner face,  $X^2(2) = 30.74$ ,  $p < .001$ , eyes,  $X^2(2) = 15.11$ ,  $p < .001$ , with no further improvement from the quadratic interaction (stimulus category  $\times$  week<sup>2</sup>) interactions: face,  $X^2(2) = 0.48$ ,  $p = \sim 1.0$ , inner face  $X^2(2) = 0.21$ ,  $p = \sim 1.0$ , and eyes  $X^2(2) = 4.01$ ,  $p > .25$ . For the face and inner face lookzones, there were also significant main effects of stimulus category,  $F(1,590) = 27.15$ ,  $p < .001$  and  $F(1,590) = 30.35$ ,  $p < .001$ , respectively, where the mean percent of total looking at the face and inner face was significantly greater for heterospecific faces than conspecific faces: face ( $C = 35.20\%$ ,  $sem = 1.56$  and  $H = 47.07\%$ ,  $sem = 1.67$ ); and inner face ( $C = 18.76\%$ ,  $sem = 1.26$  and  $H = 28.54\%$ ,  $sem = 1.26$ ).

In the 2013 cohort, age-related changes in total viewing time for all lookzones were best characterized by linear interactions: face,  $F(1,190) = 41.99$ ,  $p < .001$ , inner face,  $F(1,190) = 21.99$ ,  $p < .001$ , and eyes,  $F(1,190) = 15.30$ ,  $p < .001$ . As in 2012, for all of these lookzones the percentage of total looking decreased for conspecific faces and increased for heterospecific faces as a function of infants' age. The change in log-likelihood ratios (-2LL) confirmed that, for each of these

lookzones, the linear interaction model (stimulus category  $\times$  age) was a significantly better fit than the cubic main effect of age (week<sup>3</sup>): face,  $X^2(2) = 37.94$ ,  $p < .001$ , inner face,  $X^2(2) = 20.80$ ,  $p < .001$ , and eyes,  $X^2(2) = 14.71$ ,  $p < .002$ , with no greater fit from the quadratic interaction model (stimulus category  $\times$  week<sup>2</sup>): face,  $X^2(2) = 25.86$ ,  $p < .001$ , inner face,  $X^2(2) = 11.47$ ,  $p < .001$ , and eyes,  $X^2(2) = 3.94$ ,  $p < .05$ . For the eyes lookzone, there was also a significant main effect of stimulus category,  $F(1,190) = 5.62$ ,  $p < .02$ , where the mean percent of total looking at the eyes was significantly greater for conspecific faces (18.04%,  $sem = 2.05$ ) than heterospecific faces (11.89%,  $sem = 1.61$ ).

In the 2014 cohort, age-related changes in total viewing time for all lookzones were best characterized by linear interactions: face:  $F(1,134) = 33.03$ ,  $p < .001$ , inner face:  $F(1,126.28) = 23.01$ ,  $p < .001$ , and eyes:  $F(1,134) = 6.43$ ,  $p < .02$ . The change in log likelihood ratios confirmed that for each lookzone, the linear relationship was a significantly better fit than the cubic main effect of age (week<sup>3</sup>), face:  $X^2(2) = 29.52$ ,  $p < .001$ , inner face:  $X^2(2) = 21.14$ ,  $p < .001$ , and eyes:  $X^2(2) = 6.28$ ,  $p < .03$ , with no further improvement by a quadratic interaction model (stimulus category  $\times$  week<sup>2</sup>), face:  $X^2(2) = 0.18$ , not significant (ns), inner face:  $X^2(2) = 2.1$ , ns, and eyes:  $X^2(2) = 0.48$ , ns. Overall, the proportion of total looking at conspecifics faces declined while interest in the heterospecifics' faces increased with age. For the face and inner face lookzones, there were also significant main effects of stimulus category,  $F(1,134) = 4.67$ ,  $p < .04$  and  $F(1,134) = 9.24$ ,  $p < .003$ , respectively, where the mean percent of total looking at the face and inner face was significantly greater for heterospecific faces than conspecific faces: face ( $C = 37.37\%$ ,  $sem = 3.04$  and  $H = 47.37\%$ ,  $sem = 3.53$ ); and inner face ( $C = 18.51\%$ ,  $sem = 2.36$  and  $H = 29.64\%$ ,  $sem = 2.86$ ).

These findings were repeated for the combined cohorts. Age-related changes in total viewing time for all lookzones were best characterized by linear interactions: face:  $F(1,914) = 112.34$ ,  $p < .001$ , inner face:  $F(1,914) = 69.08$ ,  $p < .001$ , and eyes:  $F(1,901.83) = 33.33$ ,  $p < .001$ . The change in log-likelihood ratios confirmed that for each lookzone, the linear interaction was a significantly better fit than the cubic main effect of age (week<sup>3</sup>), face:  $X^2(2) = 105.95$ ,  $p < .001$ , inner face:  $X^2(2) = 66.60$ ,  $p < .001$ , and eyes:  $X^2(2) = 32.73$ ,  $p < .001$ , with no greater improvement from a quadratic model (stimulus category  $\times$  week<sup>2</sup>), face:  $X^2(2) = 3.42$ , ns, inner face:  $X^2(2) = 1.84$ , ns, and eyes:  $X^2(2) = 0.20$ , ns. Overall, the proportion of total looking at conspecifics faces declined while interest in the heterospecifics' faces increased with age. For the face and inner face lookzones, there were also significant main effects of stimulus category,  $F(1,914) = 19.73$ ,  $p < .001$  and  $F(1,914) = 27.48$ ,  $p < .001$ , respectively, where the mean percent of total looking at the face and inner face was significantly greater for heterospecific faces than conspecific faces: face ( $C = 37.29\%$ ,  $sem = 1.24$ , and  $H = 45.36\%$ ,  $sem = 1.33$ , Cohen's  $d = 0.29$ ); and inner face ( $C = 20.01\%$ ,  $sem = 0.94$ , and  $H = 27.58\%$ ,  $sem = 1.10$ , Cohen's  $d = 0.35$ ). Figure 4 shows the mean predicted values ( $\pm sem$ ) derived from the best fitting model for the percent of total viewing duration on conspecific versus heterospecific faces for each of the three cohorts and the combined cohort (Figure 4a face, b inner face, and c eyes). The raw data for each subjects' proportion of total looking at the total face lookzone can be seen in the Supplementary Material section, Figure S1.



**FIGURE 4** Mean predicted values (+sem) for the percentage of time each cohort and the combined cohort spent viewing the faces (a), inner faces (b), and eyes (c) presented in Experiment 1

Post hoc comparisons between the mean proportion of time spent viewing conspecific versus heterospecific faces at three developmental time points, weeks 1, 5, and 9, were made using *t*-tests, corrected for multiple comparisons ( $\alpha = 0.05/3 = 0.017$ ). This revealed significantly greater viewing for conspecific versus heterospecific faces and innerfaces in week 1,  $t(40) = 3.51$ ,  $p < .001$ , Cohen's  $d = 1.09$  and  $t(40) = 2.54$ ,  $p < .015$ , Cohen's  $d = 0.79$ , respectively. Differences in viewing the eyes lookzone failed to reach significance,  $t(40) = 1.98$ ,  $p = .055$ , Cohen's  $d = 0.61$ . No significant differences in viewing faces were found in week 5. Significantly greater viewing of heterospecific versus conspecific faces and innerfaces were found in week 9; face:  $t(110) = 6.04$ ,  $p < .001$ , Cohen's  $d = 1.14$ , and innerface:  $t(110) = 5.82$ ,  $p < .001$ , Cohen's  $d = 1.10$ , but again the eye lookzone just failed to reach significance:  $t(110) = 2.29$ ,  $p = .024$ , Cohen's  $d = 0.43$ .

## 4.2 | Mean fixation duration

To determine whether the mean fixation duration changed as a function of stimulus category or subjects' age, additional analyses compared the mean fixation duration for each species' face as fixed factors, including

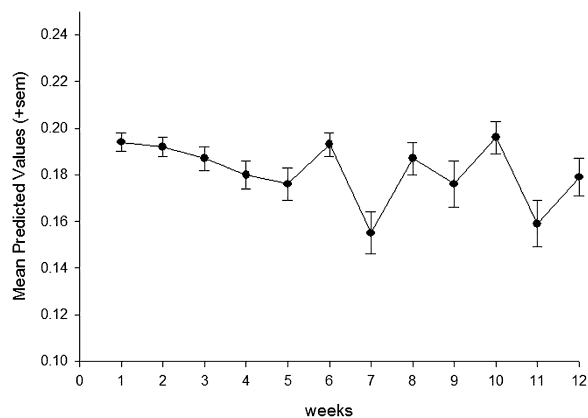
when fixations occurred on the black background, referred to as the screen lookzone. There were 5,652 total fixations included in this analysis in 2012. Hierarchical linear modeling showed a significant quadratic effect of age (week<sup>2</sup>),  $F(1,5280.74) = 16.81$ ,  $p < .001$  and the change in log likelihood ratio confirmed that this was a significantly better fit than the main effect of age,  $X^2(1) = 16.71$ ,  $p < .001$ , and was not further improved by the cubic effect of age (week<sup>3</sup>),  $X^2(1) = 1.89$ , ns. Overall, mean fixation duration decreased with age, but not in a linear manner. Additionally, there was a significant main effect of stimulus category,  $F(1,5647.52) = 31.46$ ,  $p < .001$ . To understand this effect, we compared mean fixation duration for each stimulus category using three independent *t*-tests, adjusted for multiple comparisons ( $\alpha' = p < .017$ ). This revealed significant differences in fixation duration between conspecific and heterospecific faces,  $t(4225) = 2.77$ ,  $p < .01$ ; conspecific versus screen,  $t(3453) = 7.8$ ,  $p < .001$ ; and heterospecific versus screen,  $t(3620) = 6.25$ ,  $p < .001$ . Mean fixation durations (+sem) in seconds for each stimulus category were; conspecific faces = 0.217 (0.005), heterospecific faces = 0.201 (0.004), and screen = 0.167 (0.004). Thus, regardless of age, subjects made significantly longer fixations on conspecifics' faces.



There were 1,943 total fixations included in the analysis of mean fixation duration in 2013. Hierarchical linear modeling revealed a significant linear interaction between stimulus category, for example, conspecific, heterospecific and screen, and age,  $F(1,1935.75) = 5.75$ ,  $p < .01$ . The change in log-likelihood ratio confirmed that this was a better fit than the cubic main effect of age (week<sup>3</sup>),  $X^2(3) = 11.45$ ,  $p < .01$ , and was not significantly improved by a quadratic interaction model (stimulus category  $\times$  week<sup>2</sup>),  $X^2(3) = 0.87$ , ns. Overall, mean fixation duration decreased with age. Additionally, there was a significant main effect of stimulus category,  $F(1, 1919.49) = 8.83$ ,  $p < .001$ . To understand this effect, we compared mean fixation duration for each stimulus category using three independent  $t$ -tests, adjusted for multiple comparisons ( $\alpha' = p < .017$ ). This revealed no significant differences in fixation duration between conspecific and heterospecific faces,  $t(1576) = 1.46$ ,  $p = .15$ , but significantly longer fixations for both conspecific and heterospecific faces versus screen,  $t(1179) = 3.78$ ,  $p < .001$  and  $t(1125) = 3.44$ ,  $p < .001$ , respectively. Mean fixation durations (+sem) in seconds for each stimulus category were; conspecific faces = 0.164 (0.005), heterospecific faces = 0.154 (0.004), and screen = 0.132 (0.005). Thus, regardless of age, subjects made significantly longer fixations on primate faces than the screen background.

There were 1,946 total fixations included in the analysis of mean fixation duration in 2014. Hierarchical linear modeling revealed a significant quadratic interaction between stimulus category, for example, conspecific, heterospecific and screen, and age,  $F(1,1944.59) = 6.87$ ,  $p < .001$ . The change in log-likelihood ratio confirmed that this was a significantly better fit than the linear interaction (stimulus category  $\times$  week),  $X^2(3) = 13.68$ ,  $p < .005$ , that was not significantly improved by the cubic interaction model (stimulus category  $\times$  week<sup>3</sup>),  $X^2(3) = 1.57$ , ns. Overall, mean fixation duration decreased with age, but not in a linear manner. Additionally, there was a significant main effect of stimulus category,  $F(1, 1919.19) = 4.56$ ,  $p < .02$ . To understand this effect, we compared mean fixation duration for each stimulus category using three independent  $t$ -tests, adjusted for multiple comparisons ( $\alpha' = p < .017$ ). This revealed no significant differences in fixation duration between conspecific and heterospecific faces,  $t(1619) = 0.76$ ,  $p = .45$ , but significantly longer fixations for both conspecific and heterospecific faces versus screen,  $t(1033) = 2.58$ ,  $p < .01$  and  $t(1234) = 3.38$ ,  $p < .001$ , respectively. Mean fixation durations (+sem) in seconds for each stimulus category were; conspecific faces = 0.129 (0.004), heterospecific faces = 0.133 (0.003), and screen = 0.113 (0.004). Thus, regardless of age, subjects made significantly longer fixations on primate faces than the screen background.

The combined dataset included 11,102 fixations and 32 subjects. Hierarchical linear modeling showed a significant cubic main effect of age (week<sup>3</sup>),  $F(1,11097.6) = 4.31$ ,  $p < .05$ . The change in log likelihood scores showed that this just reached significance over the quadratic main effect of age (week<sup>2</sup>),  $X^2(1) = 4.31$ ,  $p < .05$ . The results also showed main effects of week,  $F(1,53.6) = 44.07$ ,  $p < .001$ , in addition to stimulus category,  $F(1,11088.05) = 43.54$ ,  $p < .001$ ,  $p < 0.001$ . The change in log likelihood scores between these two main effects was highly significant,  $X^2(1) = 32.51$ ,  $p < .001$ . The main effect of age was due to a gradual decrease in fixation durations over time (Figure 5). To understand the main effect of stimulus category, we compared mean

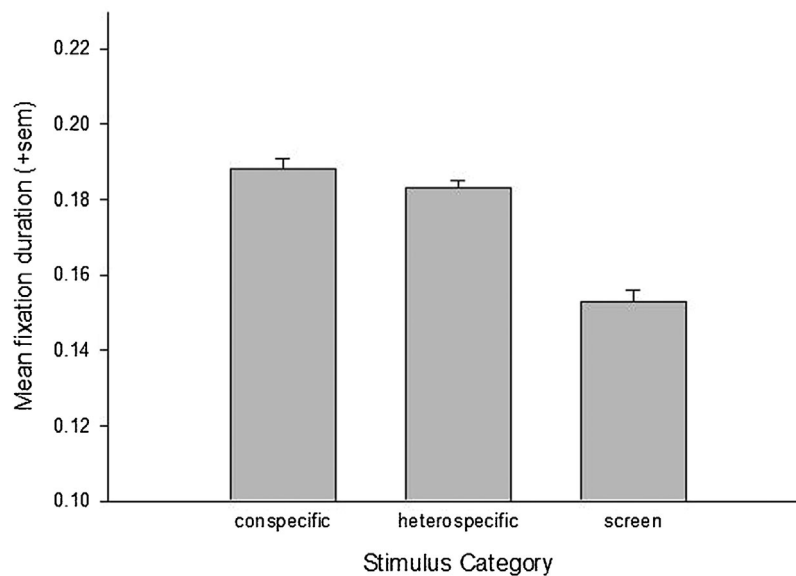


**FIGURE 5** Mean predicted values (+sem) for fixation durations of the combined cohort in Experiment 1

fixation duration for each stimulus category using three independent  $t$ -tests, adjusted for multiple comparisons ( $\alpha' = p < .017$ ). This revealed no significant difference in fixation duration between the faces of conspecifics versus heterospecifics,  $t(8985) = 1.41$ , ns, Cohen's  $d = 0.03$ , but significant differences between mean fixation durations for viewing conspecific face versus the background screen,  $t(6100) = 7.86$ ,  $p < .001$ , Cohen's  $d = 0.22$ , and for viewing the heterospecific faces versus the background screen,  $t(7113) = 8.02$ ,  $p < .001$ , Cohen's  $d = 0.21$ . Mean fixation durations (+sem) in seconds for each stimulus category were; conspecific faces = 0.188 (0.003), heterospecific faces = 0.183 (0.002), and screen = 0.153 (0.003). Thus, regardless of age, subjects made significantly longer fixations to faces versus the screen background (Figure 6).

## 5 | DISCUSSION, EXPERIMENT 1

The results of Experiment 1 revealed several developmental changes in the viewing behavior of infant monkeys from birth through 12 weeks of life. First, the results of Experiment 1 supported our initial hypotheses. We found clear and consistent effects of experience on the development of infants' viewing patterns to conspecific and heterospecific faces. In each of the three cohorts, infants showed strong early preferences to look at unfamiliar rhesus monkey faces. These viewing preferences showed a significant decrease over time, while attention to novel heterospecific faces showed a significant increase over time. Both categories of stimuli consisted of novel exemplars each week, so the reduction in preference for conspecific faces cannot be explained by habituation to specific stimuli. Rather, the gradual and consistent reduction in preference for conspecific faces, in favor of increased attention to heterospecific faces, was most likely due to the infants' increasing familiarity with conspecific faces, both experimentally and experientially, in combination with the categorical novelty of the heterospecific faces. Moreover, the heterospecific face consisted of both novel photographs and different species' faces each week which ensured that this category remained experimentally novel. A clear critical period marking the shift in infants' preference for viewing these two



**FIGURE 6** Mean fixation duration (+sem) for each stimulus category presented in Experiment 1, conspecific faces, heterospecific faces, and background screen

face categories was identified around 5–6 weeks of age, and this was consistent across all three cohorts and for all face lookzones. Therefore, using a preferential looking paradigm, infant rhesus monkeys showed a clear preference to attend to conspecific faces from birth, but this preference gave way to novel, heterospecific faces over time based on their infants' increasing experience with conspecific faces over the first few months of life.

Second, the analyses of fixation duration also revealed significant developmental changes. Overall, fixation duration decreased over the first 5 weeks of life (Figure 5), after which the pattern became sporadic. Developmental studies of infant monkey vision report that the infant's visual abilities come to match the adult state around 5 weeks of age, making this a key time point for the maturation of oculomotor functions (Boothe, Dobson, & Teller, 1985). This suggests that infants may have greater control of their own scanning behavior after 5 weeks of age, resulting in stimulus-driven patterns that may vary due to the content of the specific stimuli shown during each testing session, although more work would be needed to directly test this hypothesis.

Finally, for both the proportion of looking and fixation duration, significant main effects of stimulus category were found. Infants spent a greater proportion of time viewing the heterospecific compared to conspecific faces. With the exception of the 2012 cohort, where infants' had longer fixations to conspecific faces compared to heterospecific faces, the overall pattern in the remaining and combined cohorts was for fixation duration to be longest for faces compared to the background screen. So, despite a greater overall preference to look at the heterospecific faces, there were no significant differences between the overall fixation duration for the two categories of faces but fixations falling on faces were significantly longer than those falling on the background screen. Similar findings have been reported in human infants (Hunnus & Geuze, 2004). Therefore, the differences in overall viewing behavior reported above could not be explained simply by differences in the duration of individual fixations to each face category.

## 6 | EXPERIMENT 2, MOM VERSUS UNFAMILIAR FEMALE FACE

### 6.1 | Subjects

The same subjects used in Experiment 1 were tested in Experiment 2.

### 6.2 | Stimuli

In Experiment 2, subjects were shown trials containing their mom's face paired with an unfamiliar female. Photographs of the mom were taken each week starting after the birth of the infant. Unfamiliar females were individuals living in other social groups at the Yerkes Primate Center that were not in direct visual contact of the subjects' group. Three novel examples of these trials were shown each week, which included new photos of the mom paired with three photographs of a new unfamiliar female. Mom and unfamiliar females were matched within three years of age when the photographs were taken and general head orientation was matched within each trial. All images were processed as described in the General Methods.

Data were collected from these trials in all weeks tested, weeks 1–12 in 2012, totaling 12 time points, weeks 1–5 and then every other week through week 23, totaling 14 time points, in the 2013 and 2014 seasons.

## 7 | RESULTS, EXPERIMENT 2

Trials were excluded from the analyses if the total looking duration per trial was less than 1 s, which resulted in the removal of 10 (of 189) trials in 2012, 15 (of 137) trials in 2013, and 8 (of 174) trials in 2014. Moreover, data were not able to be collected from all subjects at all time points due to problems calibrating the infant, or the infants' fussiness/sleepiness. Therefore, the subsequent

**TABLE 3** Number of subjects tested in each week across the three cohorts in Experiment 2, including the total number of fixations and trials analyzed per year

Week	Cohorts		
	2012	2013	2014
1	4	2	4
2	6	3	3
3	10	8	4
4	6	5	8
5	9	5	9
6	7	-	-
7	5	6	8
8	3	-	-
9	4	4	7
10	5	-	-
11	4	6	5
12	6	-	-
13	-	3	9
15	-	3	6
17	-	4	3
19	-	6	9
21	-	4	11
23	-	5	7
#Fixations	4,088	2,524	3,952
#Trials	179	122	166

analyses contain a different number of subjects at each time point (Table 3).

## 7.1 | Analyses by lookzone

Age-related differences in the percentage of time subjects spent viewing the different lookzones for the mom versus unfamiliar female faces was analyzed using hierarchical linear modeling. In the 2012 cohort, age-related changes in proportion of total viewing reached significance for the face and inner face lookzones. For the face lookzone, this relationship was best characterized by a cubic interaction,  $F(1,358) = 3.82, p = .051$ , and for the inner face lookzone, this was best characterized by a quadratic interaction,  $F(1, 358) = 4.07, p < .05$ . However, for both of these lookzones, the significance was marginal and the change in log-likelihood ratios between different stages of the model failed to reach significance. No model describing age-related changes in total viewing time reached significance for the eye lookzone. There were also no significant main effects. Overall there was a trend for an increase in the proportion of looking at mom's face, for example, 26.35% in week 1 and 43.31% in week 12, whereas the proportion of time spent viewing the unfamiliar female faces remained fairly stable, for example, 46.31% in week 1 versus 40.41% in week 12.

In the 2013 cohort, age-related changes in total viewing time for both the face and inner face lookzones were best characterized by

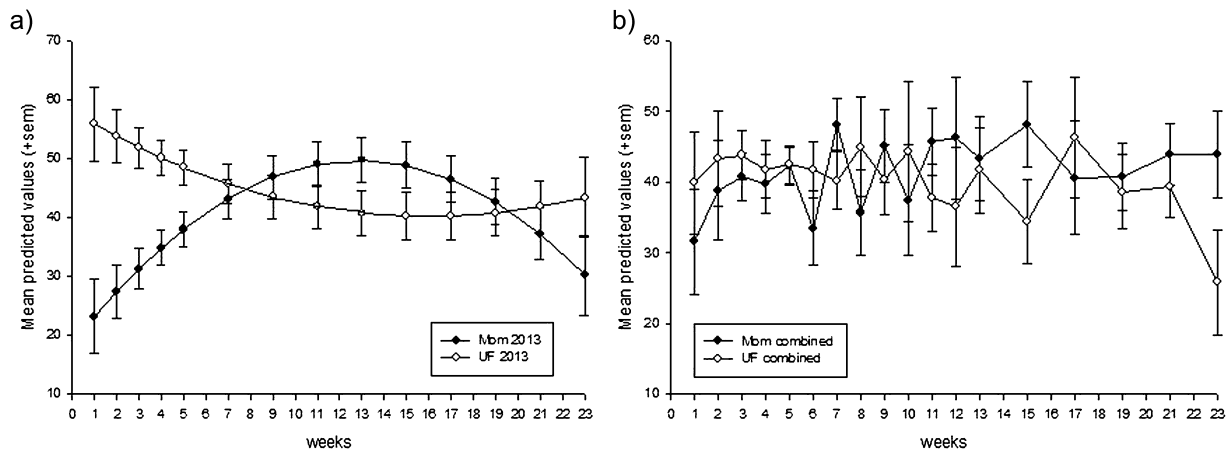
significant quadratic interactions: face,  $F(1,244) = 9.82, p < .01$  and inner face,  $F(1,244) = 6.78, p < .01$ . The change in log-likelihood ratios ( $-2LL$ ) confirmed that for both of these lookzones, the quadratic interaction was a significantly better fit than the linear interaction (stimulus category  $\times$  week): face,  $X^2(2) = 10.53, p < .01$ , and the inner face,  $X^2(2) = 6.69, p < .05$ , and no further improvement was found for the cubic interaction (stimulus category  $\times$  week<sup>3</sup>) for either lookzone: face,  $X^2(2) = 0.57, ns$ , and the inner face,  $X^2(2) = 0.77, ns$ . No significant model was found for proportion of time infant's spent looking at the eyes. For the face lookzone, there was also a significant main effect of stimulus category,  $F(1,244) = 4.90, p < .05$ , where the proportion of total looking at the unfamiliar female's face (42.45%,  $sem = 2.38$ ) was significantly greater than for mom's face (38.97%,  $sem = 2.07$ ).

In the 2014 cohort, there were no significant models describing age-related changes in total viewing time for any lookzone. However, for the face and inner face lookzones, there were significant main effects of stimulus category,  $F(1,332) = 21.52, p < .001$  and  $F(1,332) = 6.55, p < .02$ , respectively, where the proportion of total looking at the face and inner face was significantly greater for mom's face: face (48.14%,  $sem = 2.06$ ) and inner face (23.62%,  $sem = 1.49$ ) compared to the unfamiliar female's face: face (34.80%,  $sem = 2.02$ ) and inner face (18.24%,  $sem = 1.50$ ), a pattern that was opposite to that found in the 2013 cohort.

In the combined datasets, age-related changes in total viewing time reached significance for the face lookzone, which was best characterized by a linear interaction,  $F(1,934) = 5.24, p < .05$ . However, the change in log-likelihood ratios between different stages of the model failed to reach significance. No model describing age-related changes in total viewing time reached significance for the inner face or eye lookzones. There were also no significant main effects. Figure 7 shows the mean predicted values ( $+sem$ ) derived from the best fitting model for the percent of total viewing duration on the face lookzone for the 2013 (Figure 7a) and combined cohorts (Figure 7b).

## 7.2 | Mean fixation duration

To determine whether the mean fixation duration changed as a function of stimulus category or subjects' age, additional analyses compared the mean fixation duration for each species' face as fixed factors, including when fixations occurred on the black background, referred to as the screen lookzone. In the 2012 cohort, there were 3,512 fixations included in this analysis. Hierarchical linear modeling showed that a linear model best fit the main effect of age (week),  $F(1,24.12) = 9.21, p < .01$ , and the change in log likelihood ratios confirmed that there was no further improvement from the quadratic main effect (week<sup>2</sup>),  $X^2(1) = 7.19, p < .01$ . Overall, fixations became shorter with age. Additionally, there was a significant main effect of stimulus category,  $F(1,3508.30) = 21.88, p < .001$ . To understand this effect, we compared mean fixation duration for each stimulus category using three independent  $t$ -tests, adjusted for multiple comparisons ( $\alpha' = p < .017$ ). This revealed no significant differences in fixation duration between mom's face and an unfamiliar female's face,  $t(2625) = 1.32, ns$ , but significant differences between mom's face versus screen,  $t(2125) = 6.93, p < .001$ ; and unfamiliar female faces



**FIGURE 7** Mean predicted values (+sem) for the percentage of time spent by the 2013 (a) and the combined cohort (b) viewing the faces in Experiment 2

versus screen,  $t(2268) = 6.18, p < .001$ . Mean fixation durations (+sem) in seconds for each stimulus category were; mom faces = 0.209 (0.005), unfamiliar female faces = 0.201 (0.004), and screen = 0.16 (0.005). Thus, regardless of age, subjects made significantly longer fixations on the faces than on the black background of the testing screen.

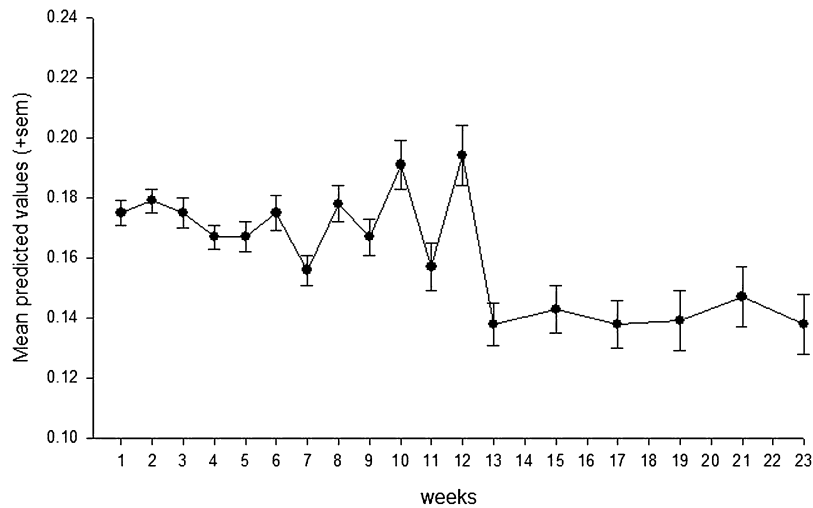
In the 2013 cohort, there were 2,524 total fixations included in this analysis. Hierarchical linear modeling showed that a quadratic model best predicted a main effect of age (week<sup>2</sup>),  $F(1,1646.50) = 6.11, p < .05$ , and the change in log likelihood ratio confirmed that this was a better fit than a linear effect of age (week),  $X^2(1) = 6.01, p < .05$  and was not significantly improved by a cubic effect of age (week<sup>3</sup>),  $X^2(1) = 0.13, ns$ . Additionally, there was a significant main effect of stimulus category,  $F(1, 2512.91) = 14.40, p < .001$ . To understand this effect, we compared mean fixation duration for each stimulus category using three independent *t*-tests, adjusted for multiple comparisons ( $\alpha' = p < .017$ ). This revealed significant differences in fixation duration between the faces of mom versus an unfamiliar female,  $t(2082) = 3.59, p < .001$ , between mom's face and the background screen,  $t(1422) = 3.26, p < .001$ , and the unfamiliar female's face and the background screen,  $t(1538) = 5.41, p < .001$ . Mean fixation durations (+sem) in seconds for each stimulus category were; mom's face = 0.145 (0.003), unfamiliar female faces = 0.162 (0.004), and screen = 0.128 (0.004). Thus, regardless of age, subjects made significantly longer fixations to the unfamiliar female faces versus mom's face or the background screen, and all fixations to faces were longer than to the screen background.

In the 2014 cohort, there were 3,952 total fixations included in this analysis. Hierarchical linear modeling showed that a quadratic model best predicted a main effect of age (week<sup>2</sup>),  $F(1,3759) = 4.71, p < .05$ , and the change in log-likelihood ratio confirmed that this was a better fit than a linear effect of age (week),  $X^2(1) = 4.69, p < .05$ , and was not significantly improved by a cubic effect of age (week<sup>3</sup>),  $X^2(1) = 0.4, ns$ . Additionally, there was a significant main effect of stimulus category,  $F(1,3950.45) = 19.22, p < .001$ . To understand this effect, we compared mean fixation duration for each stimulus category using three independent *t*-tests, adjusted for multiple comparisons ( $\alpha' = p < .017$ ).

This revealed significant differences in fixation duration between the faces of mom versus an unfamiliar female,  $t(3232) = 5.01, p < .001$ , between mom faces and the background screen,  $t(2452) = 4.41, p < 0.001$ , but no significant difference between the unfamiliar females faces and the background screen,  $t(2214) = 0.36, ns$ . Mean fixation durations (+sem) in seconds for each stimulus category were; mom's face = 0.154 (0.003), unfamiliar female faces = 0.135 (0.003), and screen = 0.133 (0.004). Thus, regardless of age, subjects made significantly longer fixations to mom's face versus unfamiliar female faces or the screen background.

The combined dataset included 9,988 fixations and 32 subjects. Hierarchical linear modeling showed a significant quadratic interaction (stimulus category  $\times$  week<sup>2</sup>),  $F(1,9973.72) = 3.62, p < .03$ . However, the change in log likelihood scores failed to show that this model was a better fit than the linear interaction (stimulus category  $\times$  week),  $X^2(3) = 7.23$ , where the cutoff for  $p < .05$  with three degrees of freedom is 7.81. There was also a significant quadratic main effect of age (week<sup>2</sup>),  $F(1,9057.79) = 31.88, p < .001$ , and the change in log likelihood scores showed that this was a significantly better model than a linear main effect of age (week),  $X^2(1) = 31.68, p < .001$ , and was not significantly improved by a cubic effect of age (week<sup>3</sup>),  $X^2(1) = 3.01, ns$ . Overall, mean fixation duration decreased with age, but in a nonlinear manner. Figure 8 shows the mean fixation duration for the combined cohort. Overall, fixation duration showed a small decline through the first 5 weeks of life and then a more considerable decline after 3 months of age.

Additionally, there was a significant main effect of stimulus category,  $F(1,9983.86) = 32.13, p < .001$ . To understand this effect, we compared mean fixation duration for each stimulus category using three independent *t*-tests, adjusted for multiple comparisons ( $\alpha' = p < .017$ ). This revealed no significant difference in fixation duration between the faces of mom versus an unfamiliar female,  $t(7943) = 1.30, ns$ , Cohen's  $d = 0.03$ , but significant differences between mean fixation durations for viewing mom face versus the background screen,  $t(6003) = 7.30, p < .001$ , Cohen's  $d = 0.19$ , and for viewing the unfamiliar females faces and the background screen,  $t(6024) = 6.20, p < .001$ , Cohen's  $d = 0.16$ . Mean fixation durations (+sem) in seconds for each



**FIGURE 8** Mean predicted values (+sem) for fixation durations of the combined cohort in Experiment 2

stimulus category were; mom's face = 0.169 (0.002), unfamiliar female faces = 0.165 (0.002), and screen = 0.143 (0.003). Thus, regardless of age, subjects made significantly longer fixations to faces versus the screen background, although the effect sizes were small.

## 8 | DISCUSSION, EXPERIMENT 2

Unlike the results of Experiment 1, the results of Experiment 2 failed to support our hypothesis that familiarity would alter the development of viewing preferences for conspecific faces. In 2012, there was a non-significant trend for infants to increase their proportion of time spent viewing mom's face, whereas the proportion of time spent viewing an unfamiliar female's face was fairly consistent across the 12 weeks of testing. In 2013, however, infants showed an early preference for the unfamiliar female's face that decreased over time while the preference for mom's face increased. In the 2014 and combined cohort, no developmental model reached significance. Thus, within the category of female conspecific faces, familiarity did not bias viewing patterns.

Second, unlike the consistent patterns of viewing behavior reported in Experiment 1, the overall proportion of time spent looking at mom versus an unfamiliar female's face was inconsistent across cohorts. Infants in the 2013 cohort spent a greater proportion of time looking at the unfamiliar female's face compared to mom, whereas the reverse was found in 2014, and no significant differences were found in 2012 or the combined cohort. Similar inconsistencies were found for fixation durations. In 2012, fixations were longer when they occurred on faces compared to the background screen. In 2013, however, fixations were longer when they were directed to unfamiliar faces versus mom and this pattern was reversed in 2014, with longer fixations on mom's face compared to the unfamiliar female. Similar to Experiment 1, the combined cohort showed longer fixations to the faces compared to the background screen, with no significant differences based on familiarity. Therefore, because preferences for viewing familiar and unfamiliar female faces did not change over the

first 6 months of life, one might conclude that the experience-dependent changes in viewing behavior found in Experiment 1 were not due to familiarity, but specifically the lack of experience subjects had with heterospecific faces.

## 9 | GENERAL DISCUSSION

These experiments used a simple preferential looking task to evaluate the effects of experience and familiarity on the development of visual preferences in infant rhesus monkeys from birth through 6 months of age. In Experiment 1, infant monkeys in three independent cohorts showed clear and robust preferences to attend to conspecific faces from birth that declined with age. This rapid early preference could be the result an experience-expectant mechanism, although data could not be obtained on day 1 or prior to any exposure to faces. Alternatively, and perhaps more likely is that it is the result of a very fast acting experience-dependent preference, requiring only a few days of exposure to conspecific faces. In contrast to this, the preference to attend to novel and unfamiliar heterospecific faces increased over the first few weeks of life. These preferences switched around 5 weeks of age, a point which marks the maturation of oculomotor visual function in infant macaques (Boothe, Dobson, & Teller, 1985), and the infants' increasing exploration of their social and physical environment (Brown & Dixon, 2000; Machado & Bachevalier, 2003). The infants in these studies were all mother reared in large social groups consisting of over 100 individuals and thus acquired cumulative experience with many individuals of their own species during the course of the 6 month experiment. Additional experience was acquired through the testing procedures themselves, as infants were exposed to numerous faces of conspecifics, both familiar and unfamiliar, during each testing session.

The preferential shift observed for face categories around 5 weeks of age is an interesting developmental finding for several reasons. First, this developmental period may reflect the amount of cumulative experience that infants need with their own species before their

viewing preferences shift to other relevant, novel, or interesting stimuli in the environment. Thus, this shift may be analogous to the critical window between 6 and 9 months of age observed in studies of perceptual narrowing in human infants, although the present study did not employ the same methodological paradigms as those used in studies of perceptual narrowing (e.g., Pascalis et al., 2002). According to some reports, the macaque visual system matures at a rate that is 4 times faster than human infants and thus the 5 week period would correspond to a human infant approximately 5 months of age, making this developmental time point comparable to the beginning of the critical window for perceptual narrowing for faces in human infants (Booth et al., 1985; Machado & Bachevalier, 2003; Pascalis et al., 2002). To further explore this critical window, and the role of experience in shaping the development of social viewing preferences, it would be very interesting to examine these same questions in nursery reared monkeys that have restricted experience with conspecifics in terms of the number of individuals and their frequency of exposure. Thus, nursery-reared monkeys would lack the cumulative experience with conspecifics that is acquired naturally by individuals living in larger social groups and should, therefore, fail to show similar developmental changes in viewing patterns. One might speculate that experimental exposure to faces in these infants could be sufficient to instantiate viewing preferences, as demonstrated by Sugita (2008). Moreover, face-deprived monkeys in the Sugita study (2008) quickly formed a preference for faces they were initially exposed to and this lasted up to year after the initial exposure. Therefore, unlike our subjects, these monkeys continued to prefer the familiar face category. It should be noted that our subjects were mother reared in large social groups and had extensive experience with hundreds of conspecifics faces over the first few months of life, while the face-deprived monkeys had only experienced a few conspecifics and humans after their period of deprivation.

Second, the preferential shift observed for face categories around 5 weeks of age may reflect the transition between subcortical, experience-expectant to cortically mediated, experience-dependent learning for faces. Monkeys are highly attracted to faces from birth (Paukner, Huntsberry, & Suomi, 2010; Sugita, 2008), and as adults show specialized networks for processing faces in infero-temporal regions (Moeller, Freiwald, & Tsao, 2008). As early as 1 week of age, infant rhesus monkeys show connectivity between these ventral temporal regions (TE/TEO) and subcortical structures, for example, superior colliculus and amygdala, that is either absent or greatly refined in adult monkeys (Webster, Bachevalier, & Ungerleider, 1995; Webster, Ungerleider, & Bachevalier, 1991). Moreover, the most exponential rate of growth in overall brain and white matter volume in infant monkeys occurs within the first three months of life (Malkova, Heuer & Saunders, 2006), making this an important transitional time period for ongoing brain maturation. Although there is little direct evidence from human infant studies to substantiate correlations between changes in the maturation of neural networks and developing face preferences, monkeys represent an ideal animal model in which to explore these relationships. Not only are rhesus monkeys closely related to humans, but they have long-lasting social relationships and engage in elaborate social and emotional communication (Hinde &

Rowell, 1962; Maestripieri & Wallen, 1997). The behavioral and visual development of rhesus monkeys follows a similar trajectory as humans, but occurs approximately 4 times faster, making them an efficient model for studying developmental processes (Booth et al., 1985; Machado & Bachevalier, 2003). Finally, compared to human infants, infant monkeys are much more easily accessed for longitudinal, developmental studies involving behavioral testing and repeated functional neuroimaging. Although this discussion raises interesting possible explanations for the critical time period observed in Experiment 1, it remains unclear whether this shift reflects the onset of a new event, such as greater social interest and exploration, or a restriction in an earlier event, such as greater attention to salient faces, such as conspecifics. Further experimentation will be needed to identify the mechanism of change.

Experiment 2 manipulated the infants' experience even further by presenting trials that paired novel photographs of each infant's mom's face with the face of an age-matched unfamiliar female. Unlike the results of Experiment 1, however, this manipulation failed to reveal clear or consistent differences in viewing preferences over time. These findings were unexpected and are inconsistent with the early preferences for mom's face and/or the face of the primary caregiver reported in studies of human infants (Bushnell, 2001). There are several possible explanations for the strong effects of experience-dependent social learning shown in Experiment 1 versus the inconsistent and non-significant effects of familiarity on face preferences in Experiment 2. The first is that infant monkeys may not attend to conspecific faces in a manner that is qualitatively or quantitatively similar to human infants. This would effectively limit the impact that familiarity would have on early emerging face preferences, or extensively delay the amount of time needed to acquire the cumulative experience needed for specific preferences to form. This scenario could explain the lack of discrimination preference for one type of conspecific face over another, given that conspecific faces are themselves highly attractive from birth (e.g., Sugita, 2008). From our own experience, as well as existing reports, infant monkeys are highly attracted to social stimuli from birth and spend considerable time during the first few weeks of life engaged in face-to-face contact with their mom, as well as other conspecifics within the social group (Ferrari, Paukner, Ionica, & Suomi, 2009; Machado & Bachevalier, 2003; Paukner et al., 2010). Thus, by 6 months of age when our testing terminated, infant monkeys would have acquired extensive familiarity with their own mother's face compared to a complete stranger such that preferences for one category over the other should have emerged. Additionally, there is evidence that adult macaques are quite poor at individuating the faces of unfamiliar conspecifics (Parr, Heintz, & Pradhan, 2008; Parr, 2011a, b). Although the preferential looking paradigm used in these experiments did not require discrimination at the individual level, and all trials paired a familiar face with an unfamiliar one, the lack of robust, conspecific face discrimination skills might minimize the formation of early face preferences despite differences in their familiarity. Because studies in adult macaques have not manipulated the familiarity of faces in tests of conspecific recognition, it is unknown whether or how familiarity affects the ability of macaques to individuate between conspecific's faces.

Perhaps the most likely explanation for the lack of face preferences in Experiment 2 is that conspecific faces, regardless of their familiarity, are a highly salient and attractive category of visual stimulus for monkeys from birth. If the infants were attracted to both of these face categories, no specific viewing preferences for one over the other would have emerged. Indeed, Experiment 1 showed clear and robust preferences for attending to the unfamiliar conspecific faces compared to novel heterospecific faces as early as the first week of life. Moreover, the protocol for Experiment 2 not only called for presenting novel examples of the mom's face each week, but these were paired with the faces of different unfamiliar females each week. If the infants are attracted to the novelty of faces, as Experiment 1 would suggest, then any preference for mom's face due to her increasing familiarity would be tempered by showing the faces of equally attractive novel females during every testing session. Perhaps a more sensitive method for testing the specific effects of familiarity on the development of viewing preferences would have been to pair novel photos of the infant's mom each week with novel photos of the same unfamiliar female. In this way, the experimental familiarity of the two individuals would be matched through the testing procedures each week, whereas the experiential familiarity with mom's face would increase cumulatively over developmental time.

Finally, although early experience is important in shaping the perceptual discrimination skills that are required for typical social development, experience-dependent learning is not limited to early critical periods, but can shape social attention in both human and nonhuman primates throughout the lifespan. This can occur through both active training, for example, in the case of bird experts and dog show judges (Diamond & Carey, 1986; Gauthier et al., 2000), or prolonged exposure to unfamiliar categories, such as other race or species faces (de Heering, Liedekerke, Deboni, & Rossion, 2010; Lebrecht, Pierce, Tarr, & Tanaka, 2009; Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005; Sugita, 2008). This flexibility is likely achieved through the ongoing adaptation of the same neural circuitry that becomes specialized by experience during early critical periods. Rather than becoming fixed during early development, these circuits appear to retain some plasticity after the established critical periods, enabling them to become specialized for the discrimination of new classes of perceptual information that become commonly represented in an individuals' environment (Scott & Monesson, 2009). Although the precise mechanisms by which experience shapes the development of social attention and its underlying neural circuitry remain unknown, experience-dependent learning represents one of the most robust developmental processes involved in guiding social learning throughout the lifespan. Understanding its developmental trajectory in primates provides an important initial step in the development of animal models for studying deficits in social attention, social motivation, and social reward in humans.

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## CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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