

Face Detection and the Development of Own-Species Bias in Infant Macaques

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In visually complex environments, numerous items compete for attention. Infants may exhibit attentional efficiency—privileged detection, attention capture, and holding—for face-like stimuli. However, it remains unknown when these biases develop and what role, if any, experience plays in this emerging skill. Here, nursery-reared infant macaques' (*Macaca mulatta*; $n = 10$) attention to faces in 10-item arrays of nonfaces was measured using eye tracking. With limited face experience, 3-week-old monkeys were more likely to detect faces and looked longer at faces compared to nonfaces, suggesting a robust face detection system. By 3 months, after peer exposure, infants looked faster to conspecific faces but not heterospecific faces, suggesting an own-species bias in face attention capture, consistent with perceptual attunement.

Despite the visual system's immaturity at birth, newborns exhibit remarkable face preferences (Johnson, Senju, & Tomalski, 2015; Salva, Farroni, Regolin, Vallortigara, & Johnson, 2011). Early biases to attend to face-like stimuli compared to nonfaces are reported in face-naïve infants, including newly hatched chicks (Salva et al., 2011), face-deprived infant monkeys (Sugita, 2008), and human neonates (e.g., Goren, Sarty, & Wu, 1975; Valenza, Simion, Cassia, & Umiltà, 1996). Neonatal face orienting appears to occur through an ancestral, subcortical route, suggesting a specialized system operating from birth (Johnson, 2005; Klein, Shepherd, & Platt, 2009; Morton & Johnson, 1991). This apparently inborn predisposition likely reflects interactions

among evolutionary pressures (Burke & Sulikowski, 2013; Parr, 2011; Pascalis & Kelly, 2009), general (as opposed to face-specific) biases of the visual system (de Heering et al., 2008; Johnson, 2005; Simion & Di Giorgio, 2015), and rapid early learning (Sai, 2005; Slater & Kirby, 1998). Face detection appears foundational for the development of higher level social skills, and predispositions to attend to faces ensures exposure during sensitive periods (Dalrymple & Duchaine, 2015; Johnson, 2005; Mondloch et al., 2013; Morton & Johnson, 1991; Schultz, 2005).

Although there may be broad initial biases to detect and prefer face-like stimuli, infants also appear to become better tuned to process frequently seen face types (Slater et al., 2010), a mechanism reported for face age (Macchi Cassia, Bulf, Quadrelli, & Proietti, 2014), race (Kelly et al., 2007), and species (Pascalis, de Haan, & Nelson, 2002). Specifically, own-species bias (OSB) is a phenomenon in which individuals better recognize conspecific relative to heterospecific faces (Scott & Fava, 2013). This

We thank Scott P. Johnson for constructive feedback on an earlier draft. Supported by the Division of Intramural Research, NICHD, the Alvin V., Jr. and Nancy C. Baird Professorship (KVJ), and NICHD P01HD064653 (PFF). Elizabeth A. Simpson, Krisztina V. Jakobsen, and Annika Paukner developed the study concept and design. Elizabeth A. Simpson, Fabrice Damon, and Annika Paukner collected the data. Elizabeth A. Simpson analyzed and interpreted the data and drafted the manuscript. All authors provided critical revisions and approved the final version of the manuscript for submission.

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DOI: 10.1111/cdev.12565

and other early face biases may emerge through an experience-driven process, involving an enhancement in processing frequently encountered faces.

Studies thus far have relied upon a variety of methods to document face biases in human newborns, including *tracking*, in which a single stimulus is presented directly in front of the infant and slowly moved to one side, measuring infant's head or eye following (e.g., Goren et al., 1975), *paired comparison*, which measures relative interest in two concurrent stimuli (Valenza et al., 1996), sometimes tested following a *habituation* to one of the stimuli (Field, Cohen, Garcia, & Greenberg, 1984). These and other paradigms have been useful for addressing a variety of questions (e.g., attention holding, facial identity discrimination) and continue to be important tools (Fagan, 1990). However, additional tools may compliment our understanding, allowing us to address other questions.

Here, we ask whether and how attention is prioritized among numerous *competing* items, as in more complex natural visual environments (Schmuckler, 2001). In natural visual environments, all stimuli cannot be processed equally due to limited attentional resources; instead, stimuli must be prioritized (Treisman, 1969). In adults, face-like stimuli may be more likely to pass an initial perceptual filter, receiving more in-depth subsequent processing relative to other stimuli (Hershler & Hochstein, 2006; Palermo & Rhodes, 2007). Eye tracking allows more precise spatial and temporal resolution than other methods, providing insights into infants' perceptual and cognitive processing (Aslin, 2012; Gredebäck, Johnson, & von Hofsten, 2009; LoBue, 2015).

In the present study, we assessed attention prioritization to faces in displays with multiple distractors with three discrete aspects of visual attention, extracted from eye tracking data: (a) *detection*, or the likelihood of fixating on a stimulus (e.g., Adler & Oprecio, 2006; Amso, Haas, & Markant, 2014; Franklin, Pilling, & Davies, 2005; Jakobsen, Umstead, & Simpson, 2015; Sasson, Turner-Brown, Holtzclaw, Lam, & Bodfish, 2008; Simpson, Mertins, Yee, Fullerton, & Jakobsen, 2014), also referred to as *face foraging* (Elsabbagh et al., 2013) or *accuracy* (Hershler & Hochstein, 2006; Tomonaga & Imura, 2015); (b) *attention capture*, or the extent to which a stimulus spontaneously elicits attention, measured as the speed or response time (RT) to fixate on a target (e.g., Adler & Gallego, 2014; Adler & Oprecio, 2006; Franklin et al., 2005; Jakobsen et al., 2015; Simpson, Buchin, Werner, Worrell, & Jakobsen, 2014); and (c) *attention holding*, the duration of

looking at images, also called *dwell time* or *perseveration*, which reflects attention maintenance, a proxy of interest (Chevallier et al., 2015; Di Giorgio, Méary, Pascalis, & Simion, 2013; Di Giorgio, Turati, Altoè, & Simion, 2012; Elsabbagh et al., 2013; Gluckman & Johnson, 2013; Jakobsen et al., 2015; Sasson et al., 2008). Although related, these attentional mechanisms—detection, attention capture, and attention holding—make up attentional efficiency and reflect fundamental aspects of visual processing (Cohen, 1972); therefore, together these measures provide a more complete picture of attention allocation.

These measures of attentional efficiency can be concurrently assessed with visual search tasks in which participants view arrays of images. In these tasks, adults exhibit OSB in face attention capture (humans: Simpson, Buchin, et al., 2014; Simpson, Mertins, et al., 2014; chimpanzees: Tomonaga & Imura, 2015). In visual search tasks adapted for infants (i.e., free-viewing), 6-month-olds exhibit superior attention capture and holding for conspecific faces relative to nonfaces (Di Giorgio et al., 2012; Elsabbagh et al., 2013; Gliga, Elsabbagh, Andravizou, & Johnson, 2009) and heterospecifics (Gillespie-Smith et al., 2015; Gluckman & Johnson, 2013; Jakobsen et al., 2015), suggesting privileged attentional mechanisms for own-species faces. However, 6-month-olds have had significant experience with conspecifics; therefore, from these studies, the relative contributions of inborn biases and experience to OSB are unclear. To complicate matters further, OSB is theorized to operate in a different way than other early face biases due to its evolutionary relevance (Scherf & Scott, 2012), possibly appearing earlier (e.g., Simpson, Suomi, & Paukner, 2015).

Although testing human newborns prior to substantial face exposure would be ideal, accurate eye tracking technology (essential to measure attention in visual search tasks) is currently unavailable for this population. Macaque monkeys are an excellent model species in this regard. Like humans, macaques are highly gregarious and infants engage in complex face-to-face interactions (Ferrari, Paukner, Ionica, & Suomi, 2009). Macaques and humans share a number of similarities in social attention (Parr, 2011). When viewing faces, both humans and monkeys exhibit a left side bias (Guo, Meints, Hall, Hall, & Mills, 2009) and spend longer viewing the inner than outer features (Dahl, Wallraven, Bülthoff, & Logothetis, 2009), especially the eyes (Gothard, Brooks, & Peterson, 2009). Importantly, macaques' looking behavior can be assessed with remote eye tracking in the first weeks of life (e.g., Paukner,

Simpson, Ferrari, Mrozek, & Suomi, 2014), and monkey infants' exposure to faces can be controlled (e.g., Sugita, 2008). In addition, animal studies allow greater precision in addressing questions about the brain, such as at the single cell level (Zhang, Smith, & Chino, 2008). However, we must first understand each species' behavioral and cognitive capacities before we can understand their translational value for models of the human brain (Hall-Haro, Johnson, Price, Vance, & Kiorpes, 2008). Previous studies exploring attentional mechanisms in nonhuman primates have used different measures than those used in humans, making comparisons across species difficult. Here, we use a behavioral measure in infant monkeys that has been used in humans (adults: Simpson, Buchin, et al., 2014; Simpson, Mertins, et al., 2014; infants as young as 6 months: Jakobsen et al., 2015), allowing a direct comparison across species. This approach, therefore, allows us to establish normative trajectories of visual attention mechanisms in an animal model.

Our goal was to clarify the development of face processing generally from conspecific face processing (Whyte, Behrmann, Minshew, Garcia, & Scherf, 2015). We hypothesized that 3-week-olds, despite little face experience, would prioritize attention to face stimuli, reflected behaviorally in face biases (Frank, Amso, & Johnson, 2014; Macchi Cassia, Simion, & Umiltà, 2001). We predicted that, given their ecological and social importance, infants would exhibit greater attentional efficiency—reflected in detection, attention capture, and attention holding—for faces relative to nonfaces. Consistent with perceptual attunement, we hypothesized that with age, infants' attentional efficiency would improve for conspecifics relative to heterospecifics. Given the evolutionary relevance of conspecifics (Dukas, 2002), we hypothesized OSB would emerge relatively early, before, or by 6 months of age.

Method

Subjects

Ten rhesus macaques (*Macaca mulatta*), six females and four males, were tested at 3 weeks ($M = 19$ days, $SD = 4$), 3 months ($M = 93$ days, $SD = 2$), and 6 months ($M = 156$ days, $SD = 4$). Infants were healthy and were separated from their mothers on the day of birth, after which they were reared in a nursery facility for unrelated studies. Infants could see other infants housed in adjacent cages but lacked species-typical exposure to adult conspecifics' faces. Caregivers wore personal

protective equipment, including goggles, masks covering the nose and mouth, and hats, so only their eyes were visible. Although difficult to estimate precisely, face exposure was limited for infants compared to human newborns. By 3 months, infants had more extensive experience with conspecifics. From 37 days old, half the infants were housed in a small group and half were housed individually but received 2 hr per weekday of playtime together. For rearing details, see Appendix S1. Data were collected from May 2014 to November 2014.

Stimuli

Infants viewed 12 arrays, 910 (width) \times 720 (height) pixels, each with one face and nine nonfaces (Figure 1a). Nonfaces included natural and man-made items. Four arrays contained a macaque face, four contained a chimpanzee face, and four contained an otter face. All faces were forward facing (deviating no more than 45°), direct gaze, and had clearly visible features and neutral expressions. Face locations within the arrays were counterbalanced across species (matched in their locations). A functional salience model suggested that the faces were not the most salient regions of the arrays nor were there differences in saliency across species (Figure 1b; see Appendix S1).

Apparatus

We recorded infants' eye movements via corneal reflection using a Tobii TX300 eye tracker, a remote 58.4-cm monitor with integrated eye tracking technology and a sampling rate of 60 Hz. We used Tobii Studio Software (Tobii Technology, Stockholm, Sweden) to collect and summarize the data.

Procedure

One experimenter held an infant 60 cm from the screen. Three-week-olds were swaddled, and 3- and 6-month-olds were held in a fleece pouch. Each infant was calibrated using a 5-point calibration to Tobii Studio's preset locations. Infants viewed six arrays in each test session and completed two sessions on two separate days, at each age. A central cartoon and music attracted the infant's attention to the center of the screen, at which time a second experimenter pressed a key to start the first trial. An array was shown until the infant accumulated 10 s of cumulative looking, monitored via live-tracking, after which the experimenter pressed a

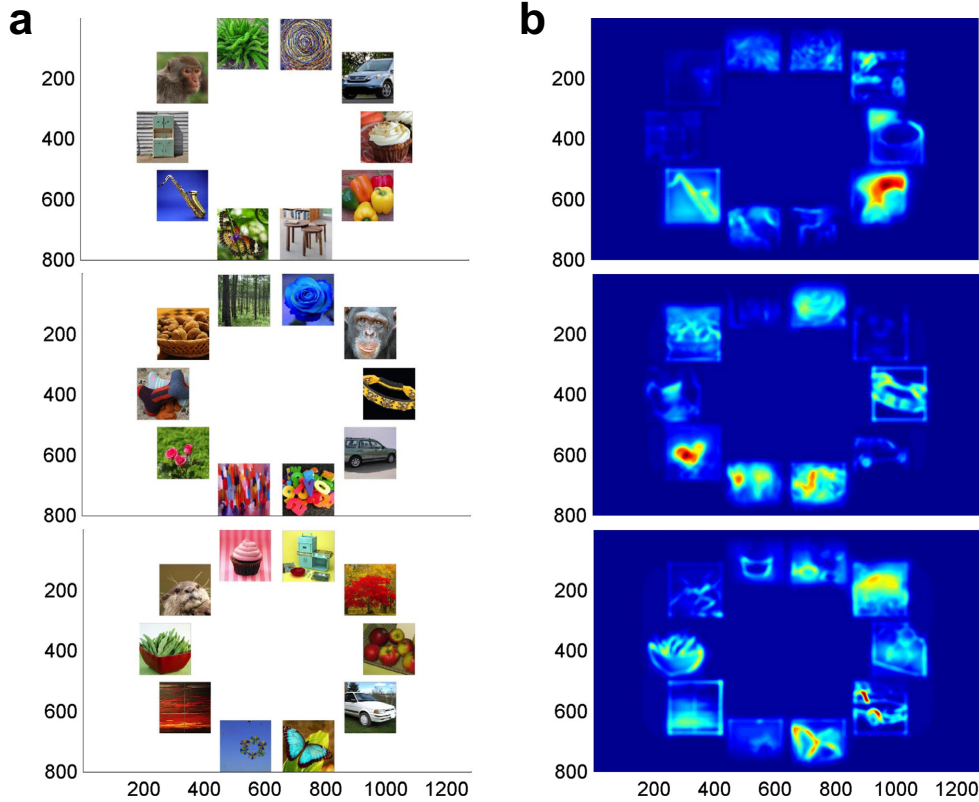


Figure 1. Sample arrays (a) and their saliency maps (b) with the most salient regions in light gray (red in online version) and the least salient in black (blue in online version).

key and the attention-getter appeared again until the infant fixated on the screen, at which point the next trial started (see Video S1).

Data Analysis

Areas of interest surrounded each image: 200 (width) \times 180 (height) pixels. We extracted data using the Tobii filter in Tobii Studio. Our dependent measures were (a) detection (proportion of trials in which the stimulus received at least one fixation out of the total trials; Figure 2a), (b) attention capture, measured with response time (RT; from the start of the stimulus to the first fixation; Figure 2b), and (c) the proportion of time looking at the face out of total time viewing all items. We averaged across all items of the same type (e.g., all nonfaces, all faces) to account for their differing frequencies (one face paired with nine nonfaces).

First, we analyzed visual attention to faces relative to nonfaces with a repeated measures analysis of variance (ANOVA), exploring age (3 weeks, 3 months, and 6 months), species (macaque, chimpanzee, and otter), and for RT and detection, stimulus type (face and nonface). Second, to test more

specifically for an OSB, we carried out planned paired-samples *t* tests for each age group, for RT and detection, comparing each species' face to the nonfaces with which it was paired, and for look duration proportions, we compared looking at each face type. For look duration proportions, we carried out one-sample *t* tests to compare looking to chance (0.10). For each of our main dependent measures (detection, response time, and look duration), we compared the most salient nonface item (determined with Saliency Toolbox; see Appendix S1) to the faces in an Age (3 week, 3 month, 6 month) \times Species (macaque, chimpanzee, otter) \times Stimulus type (face, nonface) repeated measures ANOVA. We additionally analyzed frequencies of fixations and locations of first fixations (see Appendix S1). All tests were two tailed.

Results

Our measures are theorized to reflect distinct but related aspects of visual attention; we therefore conducted intercorrelations for statistical confirmation (Sasson et al., 2008). We found no association

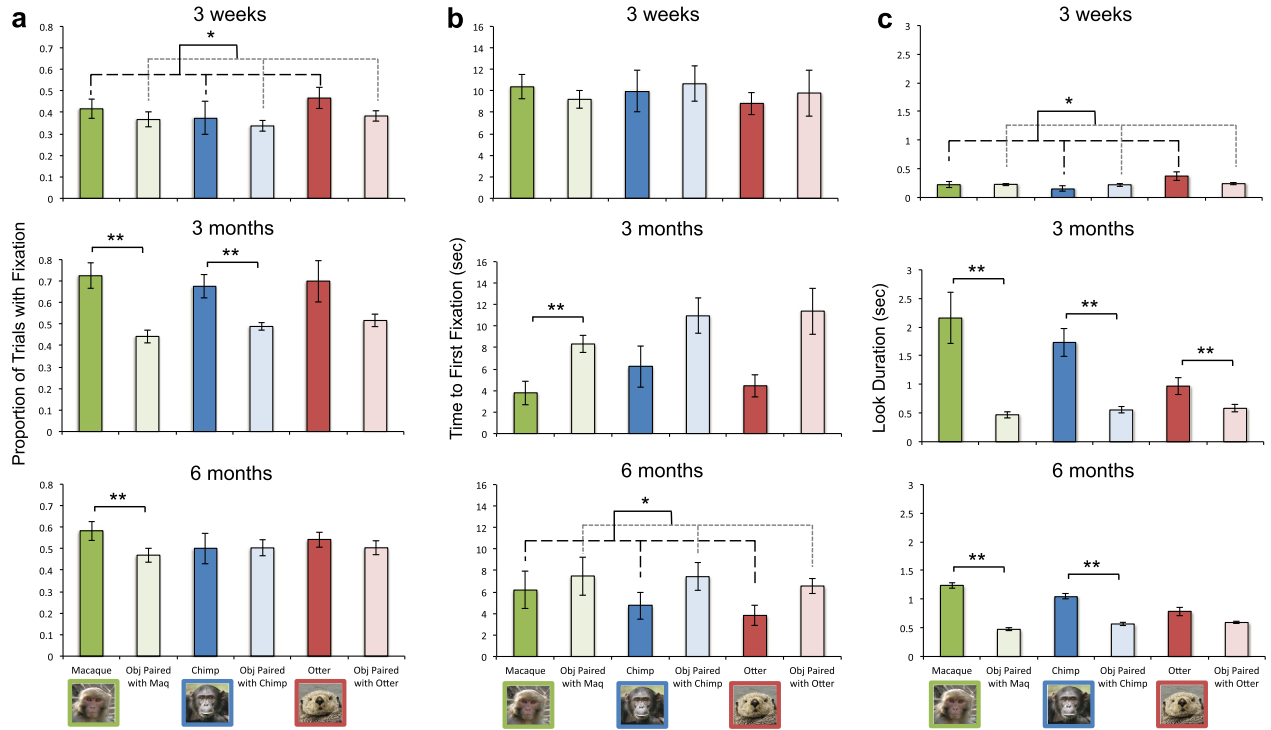


Figure 2. Face detection (a), attention capture (b), and attention holding (c). Dark bars reflect faces and light bars reflect the nonfaces with which they were paired. * $p < .05$. ** $p < .016$.

between RT and detection, $r = .093$, $p = .391$, but duration was correlated with both RT, $r = -.301$, $p = .004$, and detection, $r = .571$, $p < .001$. These results suggest that our measures are not only related but also somewhat independent.

Detection

An ANOVA assessing detection revealed main effects of age, $F(2, 18) = 8.46$, $p = .003$, $\eta_p^2 = .484$, and stimulus type, $F(1, 9) = 76.70$, $p < .001$, $\eta_p^2 = .895$, qualified by an Age \times Stimulus Type interaction, $F(2, 18) = 8.39$, $p = .003$, Figure 2a. Paired t tests revealed an increase in face detection from 3 weeks ($M = 0.42$, $SD = 0.10$) to 3 months ($M = 0.70$, $SD = 0.14$), $t(9) = 4.07$, $p = .003$, $d = 1.29$, which then showed a decline from 3 to 6 months ($M = 0.54$, $SD = 0.14$), $t(9) = 2.37$, $p = .042$, $d = 0.75$, with a parallel improvement for nonfaces from 3 weeks ($M = 0.36$, $SD = 0.08$) to 3 months ($M = 0.48$, $SD = 0.07$), $t(9) = 3.29$, $p = .009$, $d = 1.04$, which did not change further from 3 to 6 months, $p = .804$. More interestingly, infants exhibited greater detection of faces compared to nonfaces at 3 weeks and 3 months, $t(9) = 2.29$, $p = .048$, $d = 0.73$, and $t(9) = 6.85$, $p < .001$, $d = 2.16$, respectively, but no effect in 6-month-olds, $t(9) = 1.59$,

$p = .146$. At each age, a majority of infants exhibited higher detection of faces compared to nonfaces: at 3 weeks, 8/10 infants; at 3 months, 10/10 infants; and at 6 months, 7/10 infants.

Planned t tests revealed that 3-week-olds exhibited no differences in detection across species, $p > .05$. By 3 months, effect sizes were larger for conspecific versus heterospecific: Infants were more likely to detect faces compared to nonfaces for macaques, $t(9) = 4.63$, $p = .001$, $d = 1.46$, chimpanzees, $t(9) = 3.60$, $p = .006$, $d = 1.14$, and otters, $t(9) = 2.26$, $p = .05$, $d = 0.71$. By 6 months, infants were more likely to detect macaque faces compared to nonfaces, $t(9) = 3.47$, $p = .007$, $d = 1.10$ but were not more likely to detect either chimpanzee or otter faces compared to nonfaces, $t(9) = 0.06$, $p = .952$, and $t(9) = 1.04$, $p = .326$, respectively.

Attention Capture

A 2 (stimulus type) \times 3 (age) ANOVA assessing response time (RT) revealed a main effect of stimulus type, $F(1, 7) = 14.20$, $p = .007$, $\eta_p^2 = .67$, qualified by a Stimulus Type \times Age interaction, $F(2, 14) = 3.86$, $p = .046$, Figure 2b. Paired t tests revealed that, for faces, there was an improvement in speed from 3 weeks ($M = 9.94$ s, $SD = 5.04$) to

3 months ($M = 5.04$ s, $SD = 3.04$), $t(9) = 4.52$, $p = .001$, $d = 1.43$, which did not change further at 6 months ($M = 4.91$ s, $SD = 3.05$), $p = .937$; no parallel improvements in speed were observed for RT to nonfaces, $ps > .10$. There was no effect of stimulus type on 3-week-olds' RTs, $t(9) = 0.05$, $p = .961$, but faster RT to faces than nonfaces in 3- and 6-month-olds, $t(9) = 2.89$, $p = .016$, $d = 0.91$, and $t(9) = 2.87$, $p = .018$, $d = 0.91$, respectively. Although only six of the ten 3-week-olds showed faster RT to faces than nonfaces, eight of the ten 3-month-olds and eight of the ten 6-month-olds were faster to look to faces than nonfaces.

A 3 (species) \times 3 (age) ANOVA assessing RT revealed only a main effect of age, $F(2, 14) = 5.33$, $p = .019$, $\eta_p^2 = .432$, with RT growing faster from 3 weeks to 3 months, $t(9) = 4.52$, $p = .001$, $d = 1.43$, but no difference between 3 and 6 months, $t(9) = 0.08$, $p = .937$. Planned t tests revealed that OSBs were only evident in RTs at 3 months. By 3 months, infants were faster to look to faces compared to nonfaces, with the largest effect size for macaques, $t(9) = 3.85$, $p = .004$, $d = 1.22$, a smaller effect for otters, $t(8) = 2.50$, $p = .037$, $d = 0.83$, and no difference for chimpanzees, $t(9) = 0.96$, $p = .364$. Moreover, at 3 months, all infants were faster to look to macaque faces compared to nonfaces, whereas only seven infants exhibited faster RT for chimpanzee and otter faces versus nonfaces.

Attention Holding

A 2 (stimulus type) \times 3 (age) ANOVA assessing looking durations revealed a main effect of stimulus type, $F(1, 9) = 42.74$, $p < .001$, $\eta_p^2 = .826$. Overall across age, faces received greater looking than nonfaces. Planned one-sample t tests revealed that the proportion of time looking to the face of each species at all ages was significantly greater than chance (0.10), $t(9) > 2.97$, $ps < .016$, $ds > 0.94$. A majority of infants at each age looked longer to the faces than nonfaces: 7/10 at 3 weeks, 10/10 at 3 months, and 9/10 at 6 months.

An ANOVA assessing look duration proportions revealed a main effect of age, $F(2, 18) = 11.29$, $p = .001$, $\eta_p^2 = .557$, and an Age \times Species interaction, $F(4, 36) = 4.34$, $p = .006$. Paired t tests revealed an increase in the proportion of time looking at macaque faces from 3 weeks ($M = 0.56$, $SD = 0.20$) to 3 months ($M = 0.25$, $SD = 0.18$), $t(9) = 3.41$, $p = .008$, $d = 1.08$, which remained high at 6 months ($M = 0.69$, $SD = 0.12$), not changing further, $p = .42$. Similarly there was an increase in looking at chimpanzee faces from 3 weeks

($M = 0.35$, $SD = 0.26$) to 3 months ($M = 0.74$, $SD = 0.08$), $t(9) = 4.99$, $p = .001$, $d = 1.58$, but interestingly, this dropped at 6 months ($M = 0.61$, $SD = 0.11$), $t(9) = 4.47$, $p = .002$, $d = 1.41$. There were no changes across age in the proportion of time looking to the otter faces, $ps > .10$. In addition, 3-week-olds looked equally long to macaque chimpanzee, and otter faces, $t(9) < 1.59$, $ps > .05$, but 3-month-olds looked longer to macaque and chimpanzee faces compared to otter faces, $t(9) = 9.39$, $p < .001$, $d = 2.97$, and $t(9) = 2.29$, $p = .047$, $d = 0.73$, but looked equally long to faces of macaques and chimpanzees, $t(9) = 0.19$, $p = .855$. By 6 months, infants looked longer at macaque faces compared to either chimpanzee or otter faces, $t(9) = 2.38$, $p = .041$, $d = 0.75$, and $t(9) = 3.70$, $p = .005$, $d = 1.17$, but looked equally long at chimpanzee and otter faces, $t(9) = 1.59$, $p = .147$.

Faces Versus Most Detectable Nonfaces

Detection

For face detection there was a main effect of stimulus type, $F(1, 8) = 19.57$, $p = .002$, $\eta_p^2 = .71$, in which faces were more likely to be detected ($M = 0.51$, $SD = 0.07$) than the most salient nonface ($M = 0.40$, $SD = 0.05$). There was also a main effect of age, $F(2, 16) = 5.92$, $p = .012$, $\eta_p^2 = .43$, in which detection increased from 3 weeks ($M = 0.41$, $SD = 0.12$) to 3 months ($M = 0.54$, $SD = 0.12$), $t(8) = 2.48$, $p = .038$, $d = 0.83$, but did not increase further from 3 to 6 months ($M = 0.58$, $SD = 0.08$), $p = .54$. There were no other effects, $ps > .05$. The majority of infants exhibited higher detection for faces relative to the most salient nonfaces, for macaques (7/10), chimpanzees (7/10), and otters (8/10).

Attention Capture

For response time (RT) there was only a main effect of stimulus type, $F(1, 5) = 8.84$, $p = .031$, $\eta_p^2 = .64$, in which there was faster looking to the faces ($M = 5.90$ s, $SD = 3.89$) compared to the most salient nonfaces ($M = 9.62$ s, $SD = 3.20$). There were no other effects, $ps > .05$. The majority of infants were faster to look to faces than nonfaces for macaques (8/10), chimpanzees (7/10), and otters (9/10).

Attention Holding

For look duration there was a main effect of stimulus type, $F(1, 8) = 28.14$, $p = .001$, $\eta_p^2 = .78$, in which there was more looking to the faces

($M = 1.49$ s, $SD = 0.45$) than the most salient non-faces ($M = 0.50$ s, $SD = 0.15$). There was also a main effect of species, $F(2, 16) = 10.22$, $p = .001$, $\eta_p^2 = .56$, in which items in macaque arrays ($M = 1.23$ s, $SD = 0.34$) received greater looking than either chimpanzee ($M = 0.99$ s, $SD = 0.29$), $t(9) = 2.22$, $p = .054$, $d = 0.70$ (a noteworthy trend), or otter arrays ($M = 0.77$ s, $SD = 0.23$), $t(9) = 4.28$, $p = .002$, $d = 1.4$, but looking was equal to items in chimpanzee and otter arrays, $t(9) = 2.05$, $p = .070$, $d = 0.65$. Finally, there was a main effect of age, $F(2, 16) = 13.01$, $p < .001$, $\eta_p^2 = .62$, in which 3-week-olds looked less ($M = 0.65$ s, $SD = 0.49$) than either 3-month-olds ($M = 1.92$ s, $SD = 0.83$), $t(9) = 4.11$, $p = .003$, $d = 1.30$, or 6-month-olds ($M = 1.88$ s, $SD = 0.70$), $t(9) = 5.69$, $p < .001$, $d = 1.80$, but 3- and 6-month-olds looked equally, $p = .881$. These main effects were qualified by a Species \times Stimulus Type interaction, $F(2, 16) = 4.33$, $p = .031$, and an Age \times Stimulus Type interaction, $F(2, 16) = 17.65$, $p < .001$. To explore the first interaction, we compared faces to nonfaces within each species, which revealed greater looking to faces compared to nonfaces within each species (macaque: face, $M = 1.91$ s, $SD = 0.77$, nonface, $M = 0.54$ s, $SD = 0.28$; chimpanzee: face, $M = 1.49$ s, $SD = 0.59$, nonface, $M = 0.50$ s, $SD = 0.20$; otter: face, $M = 1.07$ s, $SD = 0.34$, nonface, $M = 0.46$ s, $SD = 0.23$), $t_s > 4.59$, $p_s \leq .001$, $d_s > 1.45$. To explore the Age \times Type interaction, we compared faces to nonfaces within each age group, which revealed 3-week-olds looked equally long to faces and nonfaces, $p = .158$, but 3-month-olds (face, $M = 1.93$ s, $SD = 0.83$; nonface, $M = 0.48$ s, $SD = 0.19$) and 6-month-olds (face, $M = 1.88$ s, $SD = 0.70$; nonface, $M = 0.65$ s, $SD = 0.28$) looked longer to faces than nonfaces, $t_s > 5.72$, $p_s < .001$, $d_s > 1.81$. There were no other main effects or interactions, $p_s > .05$. All infants (10/10) looked longer to faces than nonfaces for macaques, chimpanzees, and otters.

Discussion

In the present study, macaque infants exhibited greater attentional efficiency for faces than nonfaces, even with a high perceptual load (e.g., relatively large array size), suggesting an early face bias. By 3 weeks, infants had only brief and limited exposure to human faces and little exposure to conspecifics. Infants of this age also had no experience with any of the other species depicted in our stimuli. Nonetheless, 3-week-olds detected faces better

than nonfaces, a capacity that improved with age, including improvements in attention capture. Notably, 3-month-olds exhibited more efficient attentional mechanisms for conspecific compared to heterospecific faces, suggesting an OSB face attunement. Together, these results widen our understanding of infants' early face skills and the role of experience in shaping infants' attention, highlighting a promising paradigm for assessing visual attention in infant primates.

Privileged Attention to Faces

We found support for our hypothesis that 3-week-old macaques detect and look longer at faces compared to nonfaces, an impressive feat for 3-week-olds with relatively limited information-processing capacities (e.g., Bjorklund & Green, 1992; Bronson, 1974). Although 6-month-old human infants exhibit more efficient attention capture and holding for faces compared to nonfaces (Elsabbagh et al., 2013; Gliga et al., 2009; Gluckman & Johnson, 2013), the present study reveals a similar pattern in infant macaques.

An early attraction to faces ensures infants learn about faces, which can help them to navigate their social worlds. In newborn humans, face learning can occur quite rapidly (Slater & Kirby, 1998), even after only one trial for the mother's face (Sai, 2005). Moreover, given infants' strong attraction to eyes (e.g., Farroni, Csibra, Simion, & Johnson, 2002), it is possible that, in the present study, daily exposure to caregivers' eyes may have been sufficient for infants to form a rudimentary face template.

For macaques, like humans, faces are an important social stimulus in the days following birth (e.g., Ferrari et al., 2009). Furthermore, faces may generally indicate threats to infants, either through infanticide or predation; therefore, in more than one realm, vigilance to faces may increase survival (e.g., LoBue & DeLoache, 2010; New, Cosmides, & Tooby, 2007; Pauen & Hoehl, 2015). Attentional sensitivities to faces are likely evolutionarily rooted (New et al., 2007) and shared with other vertebrate taxa (Leopold & Rhodes, 2010).

Privileged Attention to Conspecifics

The newborn period is a sensitive period in development for face processing (Farroni et al., 2013; Simpson, Murray, Paukner, & Ferrari, 2014; Vanderwert et al., 2015). We tested competing predictions regarding experience and OSB. Indeed, infants' interactions with peers may shape their

attention to faces, consistent with perceptual attunement (Scott & Fava, 2013). We found that, by 3 months, infants exhibited superior detection and attention holding for primate faces compared to nonfaces, and heightened attention capture to conspecific faces. There was an increase from 3 weeks to 3 months in attention holding of primate faces. By 6 months, infants exhibited OSB: They looked longer to faces only for conspecifics and were better at detecting faces only for conspecifics, similar to adults (Simpson, Buchin, et al., 2014; Simpson, Mertins, et al., 2014; Tomonaga & Imura, 2015).

We found a pattern of general improvement in processing own-species faces, coupled with a pattern of general decline in processing hetero-specific faces, with age, consistent with reports of perceptual narrowing in human infants (Nelson, 2001; Pascalis et al., 2002). Notably, whereas nursery-reared infants' social interactions were limited compared to those of mother-reared infants, such early experiences nonetheless may have had an effect on infants' face processing, suggesting a robust experience-expectant mechanism.

On a second front, these results are notable because they suggest that the process of OSB face specialization, at least for macaques, may begin in the first months of life, whereas in humans, OSB is more often reported around 9–12 months of age (Pascalis et al., 2002; Pascalis et al., 2005; Scott & Monesson, 2009; although for 3-month-old face preference OSB, see Di Giorgio et al., 2013). OSB may appear at different points in development for different capacities or skills. Detecting and focusing on relevant information—and faces in particular—are prerequisite skills upon which later higher order social cognition may be based, requiring an early emergence.

Species differences between macaques and humans, including macaques' precocious development (developing roughly four times faster than humans by some estimates) may also account for an earlier face specialization. That is, a 3-month-old monkey may be, in some ways, maturationally comparable to a 12-month-old human; therefore, in this sense, perceptual attunement windows are actually quite similar across species, considering their relative developmental rates. On the other hand, considering their experiential equivalence, a 3-month-old monkey in the present study is comparable in face experience to a human infant *less than* 3 months old (see Appendix S1, for details). This suggests that own-species face specialization for face detection occurs rapidly during infants' first experiences with conspecifics. The contributions of

maturational processes, independent of, or interacting with, experience is a topic that should be further addressed in future work.

Conclusions and Future Directions

Infant macaque face detection is advanced at 3 weeks, reflecting the importance of faces in the first days of life. The present study is the first to explore how faces relative to nonfaces are attentionally privileged in a primate in the first months of life. Although such studies have yet to be carried out with humans, macaque infants are an excellent model species, offering (a) experimental control of early environments and (b) precision of visual attention measurement through eye tracking in the first weeks of life. These measures of infants' attentional efficiency—face detection, attention capture, and holding—hold promise for identifying infants at heightened risk for neurodevelopmental disorders (Elsabbagh et al., 2013; Gliga, Bedford, Charman, & Johnson; BASIS Team, 2015; Machado, Whitaker, Smith, Patterson, & Bauman, 2015). Animal studies have a critical role in this endeavor, highlighting the phylogenetic roots and neural underpinnings of healthy and atypical social development (Gómez, 2005; Michel, 2013).

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Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's website:

Video S1. Six-Month-Old Completing the Task; Red Dot Indicates Where Infant Is Looking

Appendix S1. Methodological Details and Additional Analyses (Frequency of Fixations and Location of First Look)