PAPER



Face detection in 2- to 6-month-old infants is influenced by gaze direction and species

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Abstract

Humans detect faces efficiently from a young age. Face detection is critical for infants to identify and learn from relevant social stimuli in their environments. Faces with eye contact are an especially salient stimulus, and attention to the eyes in infancy is linked to the emergence of later sociality. Despite the importance of both of these early social skills-attending to faces and attending to the eyes-surprisingly little is known about how they interact. We used eye tracking to explore whether eye contact influences infants' face detection. Longitudinally, we examined 2-, 4-, and 6-month-olds' (N = 65) visual scanning of complex image arrays with human and animal faces varying in eye contact and head orientation. Across all ages, infants displayed superior detection of faces with eye contact; however, this effect varied as a function of species and head orientation. Infants were more attentive to human than animal faces and were more sensitive to eye and head orientation for human faces compared to animal faces. Unexpectedly, human faces with both averted heads and eyes received the most attention. This pattern may reflect the early emergence of gaze following—the ability to look where another individual looks—which begins to develop around this age. Infants may be especially interested in averted gaze faces, providing early scaffolding for joint attention. This study represents the first investigation to document infants' attention patterns to faces systematically varying in their attentional states. Together, these findings suggest that infants develop early, specialized functional conspecific face detection.

KEYWORDS

attention capture, attention holding, mutual gaze, own-species bias, social behavior, visual attention

1 | INTRODUCTION

Faces are more likely than non-faces to be rapidly and automatically detected, recognized, and remembered (Bruce, Doyle, Dench, & Burton, 1991; Hoehl & Peykarjou, 2012; Palermo & Rhodes, 2007). Faces are also one of the earliest domains of expertise to develop (Le Grand, Mondloch, Maurer, & Brent, 2003; Reid et al., 2017; Slater et al., 2010). Infants efficiently detect faces, even in complex contexts with other items competing for attention (Amso, Haas, & Markant, 2014; Frank, Amso, & Johnson, 2014; Frank, Vul, & Johnson, 2009; Frank, Vul, & Saxe, 2012; Kelly, Duarte, Méary, Bindemann, & Pascalis, 2019). For example, by 6 months, infants are faster to orient to faces and attend longer to faces than non-faces in multi-image arrays (Di Giorgio, Turati, Altoè, & Simion, 2012; Elsabbagh et al.,

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2012; Gliga, Elsabbagh, Andravizou, & Johnson, 2009; Gluckman & Johnson, 2013; Jakobsen, Umstead, & Simpson, 2016; Kwon, Setoodehnia, Baek, Luck, & Oakes, 2016).

2 | IS EYE CONTACT NECESSARY FOR PRIVILEGED FACE PROCESSING?

How do infants accomplish this impressive feat of detecting faces in their environment? In adults and older children (6 to 14 years old), the eyes seem to play a central role in face processing abilities, including privileged attention to faces (Emery, 2000; Gliga & Csibra, 2007). For example, adults orient more rapidly toward a face in their periphery when the face has direct eye gaze than when it has averted gaze, whereas orienting is equally slow to averted gaze faces and non-face images (Mares, Smith, Johnson, & Senju, 2016). Faces with direct eye gaze, compared to averted gaze, hold adults' attention longer and reduce attention to peripheral information (Senju & Hasegawa, 2005a). In adults, direct gaze faces are processed automatically, outside of conscious awareness (Stein, Senju, Peelen, & Sterzer, 2011), recruiting cognitive resources even when task-irrelevant (Conty, Gimmig, Belletier, George, & Huguet, 2010). In visual search tasks, children and adults more quickly and accurately detect faces with direct eye gaze compared to those looking away, a phenomenon termed the stare-in-the-crowd effect (Böckler, van der Wel, & Welsh, 2014; Conty, Tijus, Huguville, Coelho, & George, 2006; von Grünau & Anston, 1995; Senju, Hasegawa, & Tojo, 2005b; Senju, Kikuchi, Hasegawa, Tojo, & Osanai, 2008a). Children and adults are better at remembering and recognizing faces with eye contact compared to faces with eyes averted or closed (Hood, Macrae, Cole-Davies, & Dias, 2003). In sum, there are several ways in which faces appear privileged in their processing compared to other stimuli, but eye contact may be necessary for these effects (Gliga & Csibra, 2007; Itier, Alain, Sedore, & McIntosh, 2007).

Despite the importance of eye contact for face processing in adults, we know little about the interactions of these processes in infants. In humans, prolonged bouts of eye contact are observed from the first moments after birth (Klaus, Kennell, Plumb, & Zuehlke, 1970; Rödholm & Larsson, 1979), and mutual gaze plays an important role in caregiver-infant bonding and communication (Leeb & Rejskind, 2004; Robson, 1967). Newborns shown pairs of faces look longer and more frequently at direct eye gaze faces compared to faces looking away (Farroni, Csibra, Simion, & Johnson, 2002; Farroni, Menon, & Johnson, 2006), attend more to faces if the eyes are open compared to closed (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000), and display enhanced neural processing of faces with direct compared to averted eye gaze (Farroni et al., 2002). This early sensitivity to eye contact may drive infants to attend to faces and develop advanced face processing skills (Gliga & Csibra, 2007). However, the role of eye contact in infants' detection, recognition, and memory of faces has not been explored.

Research Highlights

- Efficient face detection emerges early, in the first few months after birth; however, the role of eye contact in infants' face detection is unexplored.
- Longitudinally, we examined whether 2-, 4-, and 6-month-olds' detection of human and animal faces is influenced by eye and head orientation in complex displays.
- Across ages, infants better detected and looked longer to faces with eye contact, and were more sensitive to gaze orientation in human than animal faces.
- An early developing face specialization system appears to be tuned to the attentional state of socially relevant (own-species) faces.

3 | EXPERIENCE DRIVES INFANTS' FACE SPECIALIZATION: OWN-SPECIES BIAS

The broader context of the face may also influence sensitivity to eye contact. Infant might, for example, attend more to gaze cues in the context of human faces compared to animal faces, the former of which are arguably more socially and biologically relevant. However, given that sensitivity to own-species faces changes over the first year of life (Scott & Fava, 2013), the influence of species on gaze sensitivity may likewise change with development. In their first year, infants display an experience-driven pattern known as perceptual attunement, in which they show greater improvements in processing the types of stimuli to which they are more commonly exposed. For example, 4- to 6-month-old infants can discriminate facial identities for human and animal faces, but by approximately 9 to 12 months of age, infants are more specialized and display superior discrimination for human faces relative to animal faces (Pascalis, de Haan, & Nelson, 2002; Simpson, Varga, Frick, & Fragaszy, 2011). This facilitated processing of human faces is known as an own-species bias (Scott & Fava, 2013). Already by 6 months, infants, like adults, are more likely to detect, more quickly detect, and look longer at human than animal faces in in complex arrays (Gluckman & Johnson, 2013; Jakobsen et al., 2016; Simpson, Buchin, Werner, Worrell, & Jakobsen, 2014a), suggesting an own-species bias for face detection may emerge early in development. In fact, newborns may even display an early bias for human compared to animal faces (Heron-Delaney, Wirth, & Pascalis, 2011). However, all previous studies of own-species bias in face detection used direct gaze faces, so it remains unclear whether preferential attention to conspecific faces is driven by eye contact.

4 | INFANT SOCIAL ATTENTION PREDICTS HEALTHY DEVELOPMENT

It is of critical importance to better understand the interaction of infants' developing social skills—attention to faces and attention to the

eyes—which lay the groundwork for more complex social skill development (Capozzi & Ristic, 2018; Gillespie-Smith et al., 2016). Indeed, attention to faces in early infancy predicts later emerging social skills. For example, infants who attend more to faces at 7 months of age exhibit more prosocial behaviors at 2 to 4 years of age, including spontaneous helping, emotion understanding, and mentalizing (Peltola, Yrttiaho, & Leppänen, 2018). In contrast, lower rates of looking at a parent's face at 1 to 6 months of age predict higher callous-unemotional traits (e.g., lack of empathy) at 2 to 3 years of age (Bedford, Pickles, Sharp, Wright, & Hill, 2015; Wagner et al., 2016).

Attention to the eyes (mutual gaze) in early infancy is similarly positively associated with later social skills, including rates of neonatal imitation (Heimann, 1989; Paukner, Simpson, Ferrari, Mrozek, & Suomi, 2014), facial mimicry (de Klerk, Hamilton, & Southgate, 2018), attentional control (Niedźwiecka, Ramotowska, & Tomalski, 2018), emotion regulation (MacLean et al., 2014), and infant-adult neural synchrony (Leong et al., 2017). Mutual gazing behavior between 2 to 8 months of age is positively associated with children's communication skills and positive social behaviors at 2 years of age (Cohen & Beckwith, 1979; Young, Merin, Rogers, & Ozonoff, 2009). In contrast, gaze aversion (avoiding eye contact) during interactions at 2 to 4 months of age is associated with developmental delays and behavioral problems (e.g., aggressive behaviors, separation problems, compulsive behaviors) at 6 years of age (Keller & Gauda, 1987). Furthermore, declining attention to the eye region of faces between 2 and 6 months seems to distinguish infants who go on to develop autism spectrum disorder (ASD) from those who do not (Jones & Klin, 2013), and differences in infants' brain activity (eventrelated potentials) in response to direct and averted gaze faces at 6 to 10 months are associated with later emerging ASD at 3 years of age (Elsabbagh et al., 2012). Despite growing evidence demonstrating the importance of attention to faces and eye contact for healthy development, it remains unexplored whether infants' face detection is influenced by eye contact.

5 | DOES EYE CONTACT INFLUENCE INFANTS' FACE DETECTION?

This study represents the first investigation, to our knowledge, of young infants' attention to faces systematically varying in their attentional states. In a longitudinal design, we examined 2-, 4-, and 6-month-old infants' attention to human and animal faces that systematically varied in their head and eye gaze orientation (direct or averted).

We hypothesized that faces' attentional states (eye and head direction) would influence infants' face detection. We predicted: (1a) Faces with direct head and eye orientations—gazing directly at the viewer, the most "prototypical" faces—would receive the greatest attention. (1b) Faces with averted eyes and heads would receive the least attention. (1c) Eye gaze direction would influence attention more than head direction, overall. That is, when the eye and head direction are inconsistent (one is direct and one is averted), infants

would be more sensitive to the orientation of the eyes as a cue of attention, relative to the head orientation, and would, therefore, attend more to faces with eye contact compared to faces with averted eyes, regardless of head direction. (2) Sensitivity to eye contact would grow stronger with age.

We also hypothesized that the species (human or animal) would influence infants' face detection efficiency. We predicted: (3a) Infants' attention would be more strongly influenced by gaze cues displayed by human faces compared to gaze cues displayed by animal faces, given that human faces are more familiar and socially relevant. That is, infants would exhibit stronger differential attention to gaze cues conveyed in the context of human faces, but less strong or not at all in the context of animal faces. (3b) This own-species bias will be reflected in human faces holding infants' attention longer than animal faces. (4) These own-species biases would grow stronger with age, reflecting increases in face specialization, driven by infants' early experience with human faces.

Finally, we tested the effects of (and controlled for) infant sex, birth weight, and number of people in the home. Previous studies reported sex differences in infant face detection, for example, female infants looking longer to faces at 6 and 12 months (Gluckman & Johnson, 2013; Lutchmaya & Baron-Cohen, 2002). In addition, as infants grow and mature, there are improvements to eye-tracking precision (Paukner, Johnson, & Simpson, in preparation), and we wanted to control for the possibility that infants with larger body size might be more likely to attend to faces because the eye-tracker may better capture their gaze. Finally, infants' early social experiences may influence their face processing skills (Gredebäck, Eriksson, Schmitow, Laeng, & Stenberg, 2012; Rennels & Davis, 2008). We hypothesized that infants who have more people living in their home, and are therefore, exposed to more people, might display stronger face preferences.

6 | METHODS

6.1 | Participants

We recruited typically developing infants (N = 65) at 2 months (7-9 weeks; n = 55), 4 months (14-18 weeks; n = 58), and 6 monthsof age (30–34 weeks; n = 51) through community events (e.g., pregnancy classes, baby fairs) in Miami, Florida. Approximately half of the sample (n = 35) completed all three visits, and 30 infants completed two visits (14 completed visits at 2 and 4 months, 6 completed visits at 2 and 6 months, and 9 completed visits at 4 and 6 months). One or both parents spoke English. Infants' ethnicity (40% Hispanic, 19% Black, 37% Non-Hispanic Caucasian, 4% Not specified) reflected the demographics of the broader community (broader metro area: 70% Hispanic or Latino, 19% Black or African American, 12% Non-Hispanic White or Caucasian; US Bureau of the Census, 2010). Infants were healthy, born full-term (>37 weeks gestation for singletons; >35 weeks gestation for multiples), and had normal or corrected-to-normal vision. We excluded an additional 14 infants who only participated at one time point (n = 9), could not be calibrated (n = 3), or whose data were lost due to technical issues (n = 2). Families were paid \$50 for each visit. We obtained caregivers' informed consent for infants' participation. The Institutional Review Board for Human Subject Research at the University of Miami approved this study.

6.2 | Materials

Infants viewed a series of 16 arrays, presented on a remote 58.4 cm monitor (28 cm tall × 51 cm wide) with integrated eye tracking technology. We measured visual attention via corneal reflection using a Tobii TX300 eye tracker, with a sampling rate of 300 Hz. Each array contained chimpanzee and/or human face(s) among non-face objects. Faces were upright with neutral expressions and visible, open eyes, as well as visible noses and mouths. Human faces were of diverse in their race/ethnicity (12 White or Caucasian, 2 Black or African American, 2 Hispanic or Latino), gender (5 women, 11 men), and age (7 young adults, 5 middle-aged, 4 elderly). Faces of each species systematically varied in their head and eye gaze orientation (direct or averted 45°): Averted head and averted gaze, averted head and direct gaze, direct head and averted gaze, direct head and direct gaze (Figure 1). Two-month-old infants viewed 16 4-item arrays (Figure 2a,b), half with a chimpanzee face and half with a human face, among distractors. Four- and 6-month-old infants viewed 16 arrays, with 6 items (Figure 2c) and 12 items (Figure 2d), respectively, each with both a chimpanzee and a human face (matched on head and eye gaze orientation). We chose to present the 2-month-olds with arrays containing only one face at a time, because we did not want to make the task too challenging for the 2-month-olds. Our goal was not to present identical stimuli across age groups, but to create a task for each age group that was developmentally appropriate (determined by pilot testing, see procedure). The remaining images (distractors) were common man-made objects (e.g., furniture, vehicles) and natural items (e.g., trees, flowers). Faces were equally likely to appear on the left and right, and on the top and bottom of the arrays. Face locations were determined prior to testing and were counter-balanced between participants across conditions by creating two semi-randomized orders for each age group. All factors (face location, distractor objects) were held constant across these orders, such that any differences observed could be attributed to our systematically manipulated independent variables (e.g., species). Each colored image was square and was equally spaced in circular arrays. The 2- and 4-month-old infants' images measured 180 × 180 pixels $(4.76 \times 4.76 \text{ cm}; \text{ visual angle of } 4.54 \times 4.54^{\circ})$, whereas the 6-monthold infants' images measured 110 × 110 pixels (2.91 × 2.91 cm; visual angle of $2.78 \times 2.78^{\circ}$) - to accommodate additional images on the screen. Images were collected through online searches, cropped, and positioned using GNU Image Manipulation Program (GIMP; www. gimp.org) and Microsoft PowerPoint. To ensure novelty, each image appeared only once and the location of each image within the arrays was counter-balanced across the variables of interest (e.g., species, gaze). For all arrays, we chose heterogeneous images instead of matching images on low-level features (Hershler & Hochstein, 2005).

A Saliency toolbox analysis ensured that there were not significant differences in low-level salience, including features such as color or shape (Gluckman & Johnson, 2013; Hershler & Hochstein, 2005; Ho-Phuoc, Guyader, & Guérin-Dugué, 2010; Walther & Koch, 2006).

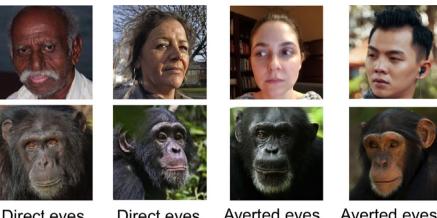
6.3 | Procedure

Testing took place when infants were awake, alert, and calm. Infants who were sleepy or fussy were given a break to nap, feed, or be changed as needed. Infants sat on their caregiver's lap approximately 60 centimeters in front of a Tobii TX300 eve tracker. Parents were instructed to remain quiet and still. Each infant was calibrated using 5-9 calibration points for each eye with Tobii Studio's preset locations. A central cartoon and music attracted the infant's attention to the center of the screen before each array (Figure 3). For 2-montholds, arrays were shown for 10 s each, and for 4- and 6-month-olds, arrays were presented for 8 s each. These times were chosen to account for the increasing attentional adeptness that comes with age; older infants can process information more quickly than younger infants (Rose, Feldman, & Jankowski, 2002). Our goal was to present the images for a duration that would enable infants to look at some but not all of the images, determined by pilot testing and previous studies (Jakobsen et al., 2016; Maylott et al., under review; Simpson, Maylott, Leonard, Lazo, & Jakobsen, 2019). Infants were videotaped with a Sony HDR-PJ540 Full HD Handycam. In total, testing took 3 min.

6.4 | Measures

We created areas of interest (AOIs) around each image. The AOI is a region on the screen in which fixations are recorded by the eye tracker. For 2- and 4-month-olds, AOIs were sized 220 × 220 pixels $(5.82 \times 5.82 \text{ cm}; \text{ visual angle of } 5.55 \times 5.55^{\circ})$, and for 6-month-olds AOIs were sized 140 × 140 pixels (3.70 × 3.70 cm; visual angle of 3.53 × 3.53°). We used Tobii Studio software (Tobii Technology), and the Tobii (default) filter to extract fixations, defined as occurring within a 35 pixel dispersion for at least 100 ms. Our independent variables were Species (human, chimpanzee), Head orientation (direct, averted), and Eye gaze orientation (direct, averted). Our dependent variables were (a) fixation response time (i.e., time from the start of the trial to the first fixation on the face), a measure of attention capture (Adler & Orprecio, 2006; Jakobsen et al., 2016; Maylott et al., under review), (b) look duration (i.e., proportion of time looking: the total time looking at a face, out of the total time looking to all images), a reflection of attention maintenance (Bronson, 1991; Di Giorgio, Leo, Pascalis, & Simion, 2012), and (c) detection (i.e., proportion of faces detected: the number of trials in which there was at least one fixation on the face, out of the total number of trials completed), a reflection of the likelihood of fixating on a stimulus (Amso et al., 2014; Jakobsen et al., 2016; Simpson et al., 2019). Together, these measures capture distinct but related aspects of visual attention, including attention-getting and attention-holding (Cohen, 1972; Gluckman & Johnson, 2013; Jakobsen et al., 2016).

FIGURE 1 Examples of face types used in this study, from humans (top row) and chimpanzees (bottom row), varying in their eye and head directions



Direct eyes, direct head

Direct eyes, averted head

Averted eyes, direct head

Averted eyes, averted head

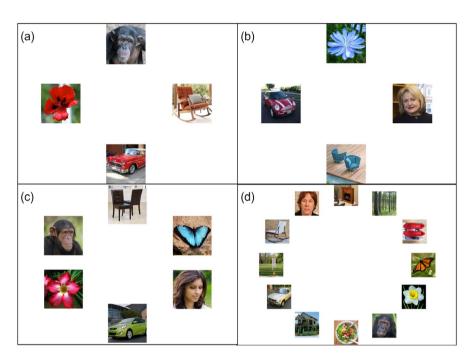


FIGURE 2 Sample stimulus arrays. Faces systematically varied in their head and eye gaze direction (direct or averted 45°): Averted head averted gaze, averted head direct gaze, direct head direct gaze. More complex arrays were shown as infants grew older: Arrays (a) and (b) are examples of 4-item arrays (containing faces with direct head and eye gaze) shown to 2-month-old infants for 10 s. Array (c) is an example of a 6-item array (containing a face with averted head and eye gaze), as shown to 4-month-old infants for 8 s. Array (d) is an example of a 12-item array (containing a face with direct head and averted eye gaze), shown to 6-month-old infants for 8 s. Arrays were shown for different lengths of time at different ages to present infants with more than they could process at a given age, which required them to prioritize their attention and ensure they only looked to some (but not all) of the images

6.5 | Data analysis

We used R version 3.4.4 and R Studio version 1.1.423 (R Core Team, 2019). We ran multilevel models within R, using the ImerTest package (Kuznetsova, Brockhoff, & Christensen, 2017) to account for dependence in our data due to nesting (repeated measures). To prepare the data for analysis, we recoded Age, denoting the youngest Age (2 months) as zero (0). We then looked at the variables of Species (i.e., human, chimpanzee), Head orientation (i.e., direct, averted), and Eye orientation (i.e., direct, averted), controlling for variables of

Sex, Birth weight, and Total number of people in the home. Previous studies reported sex differences in infant face detection (Gluckman & Johnson, 2013; Lutchmaya & Baron-Cohen, 2002), so we wanted to test for this. In addition, there are improvements to eye-tracking precision across these ages that may be related to physical maturity (Paukner et al., in preparation), so we controlled for infant body size. Finally, infants' early social experiences influence their face processing skills (Gredebäck et al., 2012; Rennels & Davis, 2008), so we controlled for the number of people living in the home. Each of the continuous variables was group mean centered. We also

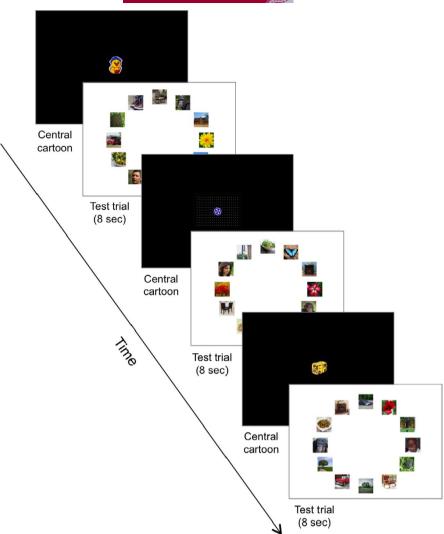


FIGURE 3 Sample stimulus presentation. A dynamic central cartoon and music attracted attention to the center of the screen before each test trial (circular image array). This is an example of what a 6-month-old observed. Each infant completed up to 16 test trials

examined the interactions between Species, Head orientation, and Eye orientation. With this model, we examined the proportion of looking to different face types. We found no effects of Head or Eye Orientation for our fixation response time measure (see Table S1), so we only report the results of proportion of time looking and proportion of faces detected. We found no effects of trial order, so we report averages across all trials.

7 | RESULTS

7.1 | Proportion of time looking

First, we ran an unconditional model with proportion of time looking as an outcome, predicted by a constant, with a random intercept clustered by Infant ID (γ_{00} = 0.11). Furthermore, the intraclass correlation (ICC) for the unconditional model indicated that only 1% of the variance in proportion of time looking was explained by between-infant differences. In other words, there was little to no dependence between infants (i.e., very little between-infant variation). However, given that the design was nested, we maintained a multilevel model (Lininger, Spybrook, & Cheatham, 2015). Next, we assessed the

optimal functional form of change over Age in infants' proportion of time looking. The unconditional growth model, with a random intercept and slope of Age, had a variance of 0.0006, suggesting that there was not a lot of variability in the relationship between Age and proportion of time looking. We included Age as a fixed effect in one model and a random effect in the next model to assess if Age should be included as a random effect in the model. Our model with Age as a random effect did not converge; therefore, we removed Age as a random effect. Boxplots of residuals suggested the data were not homoscedastic, and there was a significant difference in the heteroscedastic and homoscedastic models (p < .001), so we continued with heteroscedastic models. Next, we added level-1 (Species, Head orientation, and Eye gaze orientation) and level-2 (Sex, Birth weight, and Number of people per home) variables to the model and accounted for the proportion of variance explained at each level (see Data S1 for details). None of the covariates—Sex, Birth weight, and Total people in the home-were significant (ps > .05; Table 1). Finally, though our beta (slope) may serve as a measure of effect size, we calculated the partial correlation (r) for each slope to examine the overlap or unique effect that each independent variable had on the proportion of time looking, while we controlled for the other variables in the model.

TABLE 1 Full final model results for proportion of time looking

Labels	Random/Fixed	Greek symbol	Estimate	Standard error	r	p-value
Intercept (b/w group)	Random effect	u _{oj}	0.0006			
Residual (w/in group)	Random effect	e _{ij}	0.0481			
Intercept	Fixed effect	γ_{00}	0.2069	0.0129		<.001***
Age (w/in group)	Fixed effect	γ ₁₀	-0.0244	0.0026	.2974	<.001***
Species	Fixed effect	γ ₂₀	-0.0300	0.0120	.0830	.013*
Head	Fixed effect	γ ₃₀	-0.0121	0.0117		.302
Eyes	Fixed effect	γ ₄₀	-0.0290	0.0117	.0822	.014*
Weight	Fixed effect	γ ₀₁	0.0005	0.0003		.103
Sex	Fixed effect	γ_{02}	0.0053	0.0090		.555
People in home	Fixed effect	γ ₀₃	-0.0006	0.0027		.836
Head*Eyes	Fixed effect	γ_{50}	0.0648	0.0164	.1309	<.001***
Species*Head	Fixed effect	γ ₆₀	-0.0181	0.0168		.281
Species*Eyes	Fixed effect	γ ₇₀	0.0106	0.0167		.526
Species*Head*Eyes	Fixed effect	γ ₈₀	-0.0462	0.0235	.0653	.050*

Note: Labels correspond to the variables in the model. Random and fixed effects are specified. The estimate can serve as the effect size, as well as the partial correlation (r), which explains the unique effect of each fixed effect on proportion of looking.

*ps < .05.

^{***}ps < .001.

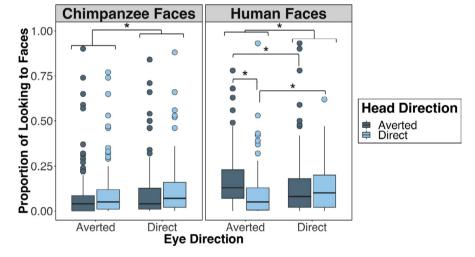


FIGURE 4 Infants spent a greater proportion of time looking to human faces (right) than to chimpanzee faces (left) and attended differently to eye gaze and head orientation cues in the context of socially relevant (human) and animal faces. For chimpanzee faces, infants attended more to faces with direct eye gaze compared to averted eye gaze. For human faces, infants attended more to averted eye gaze than direct eye gaze, but only in the context of faces with averted heads (dark blue). For human faces with direct heads (light blue), infants attended more to faces with direct compared to averted eye gaze. Boxes represent the interquartile range, horizontal lines represent medians, whiskers represent error, which is 1.5 times the interquartile range, and points outside of the boxes represent outliers outside of this range. *ps < .05

Our final model had an effect size of 0.2539 indicating that the variables in our model explained 25% of the variance in proportion of time looking relative to the unexplained variance in proportion of time looking (Lorah, 2018). This is considered a moderate to large effect size (Cohen, 1992). Furthermore, the intercept was significant, so when age was zero (2 months) the mean of proportion of time looking was 0.194 (t = 16.07, p < .001), suggesting that, at 2 months, infants were spending a substantial amount of time (about

19% of the of time) looking at faces. As infants aged, there was a 0.02 decrease in the proportion of time looking to faces ($\gamma_{10} = -0.02$, t = -9.24, r = .29, p < .001), a decline that most likely reflects differences in the tasks presented across ages, because older infants had more images and less time to view them. There was a 0.03 decrease in proportion of time looking to chimpanzee compared to human faces ($\gamma_{20} = -0.03$, t = -2.49, r = .08, p = .013), reflecting infants' greater interest in human compared to animal faces. Infants had a

0.03 decrease in proportion of time looking to faces with averted compared to direct eye gaze (γ_{40} = -0.03, t = -2.47, r = .08, p = .014), indicating more interest in faces with eye contact compared to faces with averted eyes. There was no main effect of Head orientation (γ_{30} = -0.01, t = -1.03, p = .302).

More interestingly, these main effects were qualified by a Species × Head orientation × Eye orientation interaction (Figure 4; $\gamma_{80} = -0.05$, t = -1.96, r = .07, p = .050), which revealed that infants attended differently to eye gaze and head orientation cues in the context of socially relevant (own-species) faces compared to animal faces. Within chimpanzee faces, there was a main effect of Eye orientation, ($\gamma_{10} = -0.04$, t = -2.01, r = .10, p = .046), in which infants looked more to chimpanzee faces with eyes that were direct (M = 0.11, SD = 0.07) compared to averted (M = 0.08, SD = 0.07). This suggests that infants' sensitivity to direct eye contact is not limited to human faces, but also extends to animal faces. There were no other significant effects for the chimpanzee faces, ps > .05.

Within human faces, there was a main effect of Eye orientation, $(\gamma_{10} = -0.03, t = -2.66, r = .13, p = .008)$, in which infants looked longer to faces with averted eyes (M = 0.13, SD = 0.06) than faces with direct eyes (M = 0.12, SD = 0.07). There was also an interaction between Eye and Head orientations, (γ_{30} = 0.07, t = 3.92, r = .19, p < .001). In the human faces with direct eyes, infants looked equally long to the faces with direct heads (M = 0.13, SD = 0.08) and averted heads (M = 0.12, SD = 0.09; γ_{10} = -0.01, t = -0.95, p = .345), but in the human faces with averted eyes, infants looked longer when faces had averted heads (M = 0.17, SD = 0.09) compared to direct heads (M = 0.09, SD = 0.08; γ_{10} = 0.06, t = 4.31, r = .31, p < .001). In other words, when a person is making eye contact, it does not matter which direction their head is oriented, perhaps because the eyes are the more important (relevant) feature. But when the eyes are oriented away, there may be greater interest in what the other individual is focused on, so in that case, faces with averted eyes and heads are the most salient. In human faces with averted heads, infants looked longer to faces with averted eyes compared to direct eyes (γ_{10} = 0.03, t = 2.59, r = .19, p = .010), but in human faces with direct heads, infants looked longer to faces with direct eyes compared to averted eyes ($\gamma_{10} = -0.04$, t = -3.20, r = .23, p = .002). In other words, when an individual has an averted head, their eye direction may provide additional information, resulting in longer looking to faces with averted head and averted eyes—perhaps signaling something of interest in the environment-compared to faces with eye contact. When an individual has a direct head, direct eye contact may provide useful information-potentially signaling interest in a social interaction-compared to averted eye gaze. There were no other significant effects for the human faces, ps > .05.

7.2 | Proportion of faces detected

We carried out the same analysis for detection as we did for look duration. First, we ran an unconditional model with the proportion of faces detected as an outcome, predicted by a constant, with a random intercept clustered by Infant ID (γ_{00} = 0.06). Furthermore, the

intraclass correlation (ICC) for the unconditional model indicated that less than 1% of the variance in detection was explained by betweeninfant differences. However, given that the design was nested, we maintained a multilevel model (Lininger et al., 2015). Next, we assessed the optimal functional form of change over Age in infants' detection. The unconditional growth model, with a random intercept and slope of Age, had a variance of 0.0007, suggesting that there was not a lot of variability in the relationship between Age and proportion of faces detected. We included Age as a fixed effect in one model and a random effect in the next model to assess if Age should be included as a random effect in the model. Our model with Age as a random was not significantly different; therefore, we removed Age as a random effect. Boxplots of residuals suggested the data were not homoscedastic, and there was a significant difference in the heteroscedastic and homoscedastic models (p < .001), so we continued with heteroscedastic models. Next, we added level-1 (Species, Head orientation, and Eye gaze orientation) and level-2 (Sex, Birth weight, and Number of people per home) variables to the model and accounted for the proportion of variance explained at each level (see Data S1 for details). Furthermore, we added a Species × Head orientation × Eye orientation interaction. None of the covariates-Sex, Birth weight, and Total people in the home—were significant (ps > .05; Table 2).

Our final model had an effect size of 0.2685 indicating that the variables in our model explained 27% of the variance in proportion of faces detected relative to the unexplained variance in detection (Lorah, 2018). This is considered a moderate to large effect size (Cohen, 1992). Furthermore, the intercept was significant, so when age was zero (2 months) the mean proportion of faces detected was 0.697 (t = 26.79, p < .001), suggesting that infants, at 2 months, were very good at detecting faces (detected them about 70% of the time). As infants aged, there was a 0.04 decrease in the detection of faces ($\gamma_{10} = -0.04$, t = -9.77, r = .31, p < .001), a decline that probably reflects task-related differences across ages (i.e., older infants observed more images and had less time to view them compared to younger infants). There was no main effect of species, p > .05. Infants had a 0.03 decrease in detection of faces with averted compared to direct eye gaze (γ_{40} = -0.08, t = -2.96, r = .10, p = .003), indicating better detection of faces with eye contact compared to faces with averted eyes. There was no main effect of Head orientation, p > .05.

These main effects were qualified by a Species × Head orientation × Eye orientation interaction (Figure 5; γ_{80} = -0.13, t = -2.36, r = .08, p = .019), which revealed that infants' face detection varied as a function of eye gaze and head orientation cues in the context of socially relevant (own-species) faces compared to animal faces. Within chimpanzee faces, there was a (non-significant) trending main effect of Eye orientation, (γ_{10} = -0.02, t = -1.84, r = .09, p = .067), in which infants more often detected chimpanzee faces with eyes that were direct (M = 0.56, SD = 0.24) compared to averted (M = 0.52, SD = 0.26). This suggests that infants' sensitivity to direct eye contact may not be limited to human faces, but may also extend to animal faces (although less strongly). Within chimpanzee faces, there was also a main effect of Head orientation, (γ_{20} = -0.03, t = -2.90,

TABLE 2 Full final model results for the proportion of faces detected

Labels	Random/Fixed	Greek symbol	Estimate	Standard error	r	p-value
Intercept (b/w group)	Random effect	u_{0j}	0.0026			
Residual (w/in group)	Random effect	e_{ij}	0.0714			
Intercept	Fixed effect	γ_{00}	0.6970	0.0260		<.001***
Age (w/in group)	Fixed effect	γ ₁₀	-0.0499	0.0051	.3104	<.001***
Species	Fixed effect	γ_{20}	-0.0031	0.0280		.911
Head	Fixed effect	γ ₃₀	-0.0100	0.0280		.719
Eyes	Fixed effect	γ ₄₀	-0.0829	0.0280	.0983	.003**
Weight	Fixed effect	γ_{01}	0.0000	0.0006		.981
Sex	Fixed effect	γ ₀₂	0.0201	0.0194		.303
People in home	Fixed effect	γ ₀₃	-0.0025	0.0060		.684
Head*Eyes	Fixed effect	γ_{50}	0.1388	0.0391	.1176	<.001***
Species*Head	Fixed effect	γ ₆₀	-0.0691	0.0392		.079
Species*Eyes	Fixed effect	γ ₇₀	0.0325	0.0396		.412
Species*Head*Eyes	Fixed effect	γ ₈₀	-0.1314	0.0558	.0785	.019*

Note: Labels correspond to the variables in the model. Random and fixed effects are specified. The model for detection was built exactly as the model for proportion (see results section for details).

^{***}ps < .001.

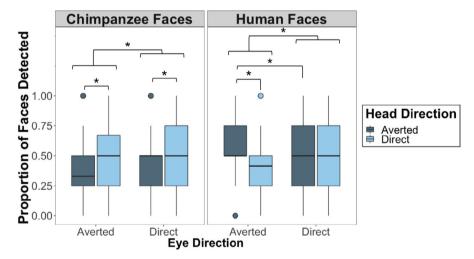


FIGURE 5 For both species, infants were more likely to detect direct compared averted eye gaze. For chimpanzee faces (left), infants were more likely to detect faces with direct compared to averted head orientations. For human faces (right), infants were more likely to detect averted than direct eye gaze, but only in the context of faces with averted heads (dark blue). In human faces, infants attended more to averted (dark blue) compared to direct head orientation (light blue), but only when eyes were averted. Boxes represent the interquartile range, horizontal lines represent medians, whiskers represent error, which is 1.5 times the interquartile range, and points outside of the boxes represent outliers outside of this range. *ps < .05

r = .14, p = .004), in which infants more often detected chimpanzee faces with heads that were direct (M = 0.58, SD = 0.25) compared to averted (M = 0.50, SD = 0.24). Together, these findings suggest that infants may possess a general face detection system, broadly tuned for all faces (including animals), that is sensitive to faces' attentional states. There were no other significant effects for the chimpanzee faces, ps > .05.

Within human faces, there was a main effect of Eye orientation, $(\gamma_{10} = -0.10, t = -3.39, r = .16, p = .008)$, in which infants more often

detected human faces with direct eyes (M=0.60, SD=0.24) compared to human faces with averted eyes (M=0.58, SD=0.26). Within human faces, there was no main effect of Head orientation (p>.05). There was also an interaction between Eye and Head orientations in the human faces, ($\gamma_{30}=0.16$, t=3.90, r=.19, p<.001). In the human faces with direct eyes, infants did not display significant differences in detecting faces with direct and averted heads ($\gamma_{10}=-0.02$, t=-0.63, p=.531), but in the human faces with averted eyes, infants more often detected faces that had averted heads (M=0.64,

^{*}ps < .05.

^{**}ps < .01.

SD = 0.23) compared to direct heads (M = 0.51, SD = 0.24; $\gamma_{10} = 0.14$, t = 4.72, r = .33, p < .001). In other words, head orientation does not seem to matter when a person is making eye contact, possibly reflecting the eye contact superiority effect. In contrast, when the eyes are oriented away, infants appear to have superior face detection, perhaps reflecting infants' increased interest in what the other individual is focused on. Thus, faces with averted eyes and heads appear to be detected the most. In human faces with averted heads. infants more often detected faces with averted eyes compared to direct eyes (γ_{10} = 0.06, t = 2.14, r = .1546, p = .034), but in human faces with direct heads, infants more often detected faces with direct eyes compared to averted eyes (γ_{10} = -0.09, t = -2.76, r = .21, p = .006). In other words, when a person's head is oriented away, their eye direction may provide additional information, resulting in better detection of faces with averted head and averted eyes-perhaps indicating something worth attending to in the environment compared to faces with eye contact. When an individual's head is directed at you, direct eye contact signals interest in a social interaction, compared to averted eye gaze, so these features together offer useful information. Interestingly, these attention patterns for face detection were remarkably similar to those for look duration, suggesting that the types of faces that capture attention are also the most likely to hold attention. There were no other significant effects for the human faces, ps > .05.

8 | DISCUSSION

We examined the development of face detection longitudinally in 2-, 4-, and 6-month-old infants who observed human and animal faces and non-faces in complex visual arrays. We found that eye gaze direction, head orientation, and species influenced infants' face detection.

8.1 | Attentional state influences infant face detection: importance of eye contact

As we predicted, faces with eye contact received more attention compared to faces with averted eyes (Prediction 1a). These findings demonstrate that 2- to 6-month-old infants have an early emerging of face detection system that is sensitive to mutual gaze. While newborns look longer to faces with eye contact (Batki et al., 2000; Farroni et al., 2002, 2006), our findings reveal that, beyond this age, infants demonstrate more complex attention regulation to socially relevant stimuli in "real world" contexts. Indeed, by 2 to 6 months, infants perform similarly to adults, efficiently detecting faces with eye contact (Conty et al., 2006; Senju & Hasegawa, 2005a). While infants were sensitive to changes in eye gaze in both the human and animal faces-suggesting that the eyes are salient regardless of the species-infants were not more likely to detect faces with forward-oriented heads compared to faces with heads oriented away (Prediction 1b). These results are consistent with studies that place eye and head direction in competition with one another. For example,

4-month-old infants, regardless of head direction, exhibit enhanced processing of faces with direct eye gaze, demonstrating facilitated event-related potentials for mutual gaze (Farroni, Johnson, & Csibra, 2004). Similarly, adults are faster and better at detecting faces with eye contact regardless of head direction, showing that gaze information has precedence over head orientation (Conty et al., 2006).

8.2 | Why were infants so interested in faces looking away?

We hypothesized that faces gazing directly at the viewer would receive the greatest attention compared to faces with averted eyes or heads (Prediction 1c), because these are the most prototypical faces (i.e., symmetrical, average angle; Damon et al., 2017; Slater et al., 2010). However, we found that human faces with averted heads and averted eyes received the most attention. Why were infants so interested in faces looking away? One interpretation is that this pattern may reflect the early emergence of gaze following (i.e., the ability to look where another individual is looking). Gaze following begins to develop as early as 2 to 4 months of age (Astor & Gredebäck, 2018; D'Entremont, 2000; Gredebäck, Fikke, & Melinder, 2010; Perra & Gattis, 2010), and stabilizes by around 6 to 12 months (De Groote, Roeyers, & Striano, 2007; Morales, Mundy, & Rojas, 1998; Triesch, Teuscher, Deák, & Carlson, 2006). At first this effect may seem counter-intuitive. If infants are attracted to the averted gaze faces, and following their gaze direction, you would expect infants to look less at the face and more at the gazed-at objects that are the focus of the face's attention. However, we think it is unlikely that infants engaged in gaze-following in this task because of the complexity of our visual stimuli and the short durations of time that they were presented. By the time the infants detected the faces, they likely did not have sufficient time to process them and carry out gaze following before the trial ended. We propose that infants may be especially interested in averted gaze faces, scaffolding joint attention. Consistent with this proposal, infants show enhanced brain responses to faces with eyes that are gazing towards objects, as opposed to away from them, at 9 months of age (Senju, Csibra, & Johnson, 2008b; Senju, Johnson, & Csibra, 2006). Infants may be searching faces for object-directed cues (Gliga & Csibra, 2007). The reverse also appears true: not only do objects enhance processing of the faces gazing upon them, but the presence of faces oriented towards objects can also enhance attention to objects at 4 to 5 months of age (Hoehl, Wahl, & Pauen, 2014; Parise, Reid, Stets, & Striano, 2008). It remains untested, however, whether there may be something special about faces looking at objects that capture infants' attention. What is clear, however, is that infants possess an early sensitivity to attentional state, and this capacity may prepare infants to learn about objects through joint attention interactions.

To our knowledge, this is the first study to report greater attention to human faces with averted gaze in typically developing infants. It is important to keep in mind that infants of this age are just starting to develop gaze following capacities and have fragile, incomplete, abilities that are easily disrupted. Consequently, there may be contextual

factors that influence infants' attention. For example, the context in which faces were presented—surrounded by other images—may have primed infants for attentional cuing. That is, averted gaze faces may have appeared to be looking at the other images in the arrays, which increased infants' attentiveness to the faces. Exploring face processing in a wider variety of contexts will be necessary to more fully understand whether infants' increased attentiveness to averted gaze faces is a precursor to developing gaze following and joint attention.

8.3 | Age differences in sensitivity to eye contact

We did not find support for our prediction that sensitivity to eye contact would grow stronger with age (Prediction 2); however, at each age, infants observed slightly more complex stimuli (more faces, more distractors) and had less time to observe each array, which may have made it difficult to observe age-related changes. In addition, we only measured infants' attention to faces. We did not explore infants' interpretation of these facial signals. It is not until later in development, beginning at approximately 10 months, that infants begin to have a deeper understanding of eye gaze—what it actually means to look at something and see something (i.e., theory of mind)—and thus follow eye gaze more selectively. For example, by 9 to 12 months, infants do not follow a person's gaze when the person has their eyes closed, is blind-folded, or when there is a barrier between the person and the object (Meltzoff & Brooks, 2007; Tomasello, Hare, Lehmann, & Call, 2007). In sum, infants' attention to and understanding of eye gaze may become more accurate and flexible with age (Grossman, 2017).

8.4 | Sensitivity to gaze cues in human versus animal faces: own-species bias

Infants' interest in faces also varied across human and animal faces. Infants were more sensitive to gaze cues in the context of human compared to animal faces. Consistent with our prediction (Prediction 3a), changes in the attentional state of the chimpanzees did not influence infants' looking as much as the same changes in humans. While infants were sensitive to eye direction in both species, they showed the largest differences in response to varying head direction in human faces. Another study found differences in infants' sensitivity to gaze in human and nonhuman stimuli: 12-month-olds looked longer to, and were better at gaze following, when observing videos of humans compared to apes (Kano & Call, 2014). We also found our infants looked longer to human than animal faces (Prediction 3b), consistent with studies in adults, reporting privileged detection of conspecifics (Simpson, Buchin, et al., 2014a; Simpson, Husband, Yee, Fullerton, & Jakobsen, 2014b; Stein, Sterzer, & Peelen, 2012). Our findings of an early own-species bias suggest that infants have already specialized for processing conspecific faces by 2 to 6 months of age. At these ages, infants are developing expertise for the types of faces they most commonly encounter (Scott, Pascalis, & Nelson, 2007). While previous studies report own-species biases in face detection in human infants as young as 5-6 months (Gluckman & Johnson, 2013; Jakobsen et al., 2016) and monkey infants as young as 3 months (Simpson et al.,

2017), this study represents the youngest ages in humans, tested to date, for own-species specialization for face detection.

Our infants were also sensitive to changes in eye gaze in both the human and animal faces, suggesting that the eyes are salient regardless of species. This finding is surprising given that chimpanzee eyes do not have large, white scleras, as human eyes do, making it difficult to identify eye gaze direction (Kobayashi & Kohshima, 2001). Despite lacking large white scleras, direct gaze chimpanzee faces received more attention than averted eye gaze faces. Similar findings were reported in a recent study in adults in which task-irrelevant human and monkey faces with eye contact held attention more strongly than faces with eyes closed (Dalmaso, Castelli, & Galfano, 2017). In sum, it seems that some aspects of face processing are sensitive to gaze direction broadly across species.

8.5 | Age differences in own-species bias and the role of experience

In contrast to our prediction, we did not detect age-related changes in own-species bias (Prediction 4). This consistency with age could be because own-species bias for face detection develops rapidly (Di Giorgio, Leo, et al., 2012), and is already in place in some rudimentary form by 2 months of age. While previous studies reported own-species bias for face detection by 6 months (Jakobsen et al., 2016), our findings suggest that own-species bias in face detection may occur earlier, like face preference (Heron-Delaney et al., 2011). Indeed, by 3 months, infants attend more to nonhuman primate faces when they contain human eyes compared to primate eyes (Damon et al., 2015; Dupierrix et al., 2014).

This specialized processing of own-species faces is likely driven by infants' early experiences with numerous human faces (Fausey, Jayaraman, & Smith, 2016; Jayaraman, Fausey, & Smith, 2017). Face types that are more familiar are more successful at eliciting gaze following. For example, between 5 and 10 months, infants more reliably follow gaze from faces that are of more familiar races and sexes, matching that of infants' primary caretaker, compared to less familiar face types (Pickron, Fava, & Scott, 2017; Xiao et al., 2018). Familiar facial expressions also modulate infants' gaze following, with happy faces eliciting more gaze cuing than other expressions in 9- to 12-month-old infants (Niedźwiecka & Tomalski, 2015). At 4 months of age, infants show enhanced processing of objects when preceded by their mother's face, compared to a stranger's face, looking at the object, either because the mother's face is easier to process, more salient, or both (Hoehl, Wahl, Michel, & Striano, 2012). Regardless of the cause, infants' familiarity with a face appears to increase their sensitivity to eye gaze cues.

Parallel findings documenting the influence of experience are observed in infants' neural discrimination of direct and averted gaze faces. For example, infants born to blind parents, unlike infants born to sighted parents, do not appear to neurally differentiate between direct and averted gaze faces at 6 to 10 months of age (Vernetti et al., 2018). Deaf infants born to deaf parents show superior gaze following abilities compared to hearing infants (Brooks, Singleton, & Meltzoff, 2019). Studies in nonhuman primates offer converging

evidence of the malleability of infants' sensitivity to gaze direction. Infant monkeys reared in richer social environments attend more to direct gaze faces compared to averted gaze faces (Muschinski et al., 2016; Simpson, Paukner, Pedersen, Ferrari, & Parr, 2018).

8.6 | Sensitivity to eye gaze: marker of healthy (or disrupted) development

The capacity to detect direct eye gaze faces, found here, may be advantageous in a number of ways. Infants are better at processing faces-recognizing identity and expressions, and interpreting goaldirected actions-with eye contact (Farroni, Massaccesi, Memon, & Johnson, 2007; Guellai & Streri, 2011; Phillips, Baron-Cohen, & Rutter, 1992; Rigato, Menon, Johnson, Faraguna, & Farroni, 2011; Striano, Kopp, Grossmann, & Reid, 2006). Mutual gaze has a calming effect on 1-month-olds (Zeifman, Delaney, & Blass, 1996), and 3- to 6-month-old infants smile and attend more to social partners making eye contact (Hains & Muir, 1996; Symons, Hains, & Muir, 1998). Mutual gaze between infants and adults enables infants to neurally and behaviorally synchronize with adult partners, facilitating communication and emotion regulation (de Klerk et al., 2018; Leong et al., 2017; MacLean et al., 2014). Rates of mutual gaze across the first 12 weeks of life are positively associated with maternal sensitivity and less infant crying (Lohaus, Keller, & Voelker, 2001). Greater attention to direct eye gaze during parent-infant interactions at 5 months is positively associated with attentional control at 11 months (Niedźwieck et al., 2018). The capacity to align with another's gaze also has important implications for language acquisition (Brooks & Meltzoff, 2005) and children's understanding of others' cognitions, desires, and emotions (Brooks & Meltzoff, 2015). It appears that an early sensitivity to eye gaze may be foundational, laying the groundwork for future higher-level social cognitive development.

Indeed, one of the earliest behavioral signs of ASD is reduced eye contact (Guillon, Hadjikhani, Baduel, & Rogé, 2014). Infants who go on to receive a diagnosis of ASD show an atypical decline in attention to the eyes between 2 and 6 months of age (Jones & Klin, 2013). Around these ages, infants with later ASD also display different patterns of brain activity while observing faces with shifts in eye gaze (Elsabbagh et al., 2012, 2009). These differences in eye contact persist with age. For example, when children search for a face, typically developing 9- to 14-year-olds more rapidly detect faces with eye contact; however, children with ASD do not show this eye contact facilitation effect (Senju et al., 2005b; Senju, Kikuchi, et al., 2008a; Senju, Yaguchi, Tojo, & Hasegawa, 2003). Findings in the present study suggest a developmental perspective may be useful for understanding individual differences in eye gaze sensitivity and processing in both typically developing and high-risk infants.

9 | CONCLUSIONS

Our findings are consistent with the proposal that there may be evolved mechanisms tuned for the detection and processing of direct-gaze (i.e., eye-detection detector; Baron-Cohen, Campbell, Karmiloff-Smith, Grant, & Walker, 1995), which matures rapidly in early development (Taylor, Edmonds, McCarthy, & Allison, 2001). Infants' initial preferences for direct eye gaze faces persist through the first year of life, but also become more sophisticated with age. This study represents the first investigation to document infants' attention patterns to faces systematically varying in their attentional states. Infants appeared more sensitive to eye and head direction in socially relevant (own-species) faces. Together, these findings suggest that infants develop specialized functional conspecific face detection by 2 to 6 months, and display prioritized attention to averted human faces, potentially scaffolding the development of later emerging gaze following and joint attention capacities.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest.

AUTHOR CONTRIBUTIONS

E.A.S. and K.V.J. designed the study. E.A.S. and S.E.M. collected the data. S.E.M., S.G.M., and G.Z. analyzed the data and created the graphs. E.A.S. wrote the manuscript. All authors edited the manuscript.

DATA AVAILABILITY STATEMENT

Data are available from the corresponding author, Elizabeth A. Simpson, upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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