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RESEARCH ARTICLE

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Visual preferences for direct-gaze faces in infant macaques (*Macaca mulatta*) with limited face exposure

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Abstract

From birth, human and nonhuman primates attend more to faces with direct gaze compared with averted gaze, and previous studies report that attention to the eyes is linked to the emergence of later social skills. Here, we explored whether early experiences influence attraction to eye contact in infant macaques by examining their attention to face pairs varying in their gaze direction across the first 13 weeks of life. Infants raised by human caretakers had limited conspecific interactions (nursery-reared; *N* = 16) and were compared to infants raised in rich social environments (mother-reared; *N* = 20). Both groups looked longer to faces and the eyes of direct compared to averted-gaze faces. Looking to all faces and eyes also increased with age. Nursery-reared infants did not display age-associated increases in attention to direct-gaze faces specifically, suggesting that, while there may be an initial preference for direct-gaze faces from birth, social experiences may support its early development.

KEYWORDS

attention, infant development, mutual gaze, primate, social attention, vision

1 | INTRODUCTION

Eye contact is a powerful way of establishing a social connection, signaling readiness for social interaction. In human adults, faces with eye contact are located more rapidly and processed preferentially compared to those with averted gaze (Conty, Tijus, Hugueville, Coelho, & George, 2006; Crehan & Althoff, 2015; Doi & Shinohara, 2013; Framorando, George, Kerzel, & Burra, 2017; Senju & Johnson, 2009; Yokoyama, Sakai, Noguchi, & Kita, 2014). This preferential attraction to direct-gaze faces is evident early in development, prior to substantial postnatal experience. For example, human newborns look longer to faces with open compared with closed eyes (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000) and direct compared with averted gaze (Farroni, Csibra, Simion, & Johnson, 2002) and may even show a rudimentary form of gaze following (i.e. looking in the same direction as someone else: Farroni, Massaccesi, Pividori, Simion, & Johnson, 2004). While the neural mechanisms remain to be fully understood, eye gaze is processed quickly and automatically and undoubtedly plays a central role in early communicative development (Hoehl et al., 2009).

Other species also share this preference for direct-gaze faces. Nonhuman primates (NHP), like humans, exhibit faster and longer looking to faces with eye contact (e.g. adult macaques: Leonard, Blumenthal, Gothard, & Hoffman, 2012). Infant NHP also show these preferences. For example, 2- to 8-month-old chimpanzees look longer to faces with their eyes open compared with closed and look longer to faces with direct as opposed to averted eye gaze (Hirata, Fuwa, Sugama, Kusunoki, & Fujita, 2010; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2003). Similarly, infant macaques show a rapid increase in preference for direct compared with averted-gaze faces soon after birth, peaking around 2 months of age (Muschinski et al., 2016). Thus, sensitivity to mutual gaze appears to have early roots in both ontogeny and phylogeny.

According to the two-process theory of face processing, infants are equipped with an initial inborn bias to detect and orient toward faces, termed *conspec* (Johnson, Senju, & Tomalski, 2015; Morton & Johnson, 1991). Studies in humans suggest that preferences for certain low-level properties (e.g. high-contrast elements in the locations of the eyes and mouth) likely guide newborns' initial attention to faces through a primitive face-configuration detection system (Farroni, Menon, & Johnson, 2006). Faces with eye contact are more prototypical—compared with faces with eyes closed or averted—and therefore are the best at capturing infants' attention, likely through a subcortical route operating from birth (Johnson, 2005). Faces with direct gaze have high-contrast eye regions, which may attract infants' attention, a pattern which is disrupted when faces are inverted, suggesting both gaze perception and the configuration of the face (e.g. top-heavy, symmetrical) drive early preferences (Farroni et al., 2005).

This initial interest in faces is further refined by infants' early experiences, in a second more cortically driven process termed *conlearn* (Morton & Johnson, 1991). Faces are one of the most common visual stimuli infants encounter, enabling them to rapidly develop expertise (Gliga & Csibra, 2007). Differences in infants' early experiences with faces can have lasting impacts. For example, human infants who have blind parents, and therefore have reduced experience of parental eye contact and gaze behavior, develop seemingly normal social skills; however, they attend less to eye gaze cues (Senju et al., 2015), particularly in their blind parents (Ganea et al., 2018). These findings may indicate that a lack of experience with direct gaze interactions results in infants paying less attention to the eyes. Further, at 6–10 months of age, infants of blind parents do not neurally discriminate—measured with event-related potentials (ERPs)—between direct and averted-gaze faces, as do infants of sighted parents (Vernetti et al., 2018). This finding may indicate that selective brain responses to perceived gaze shifts may depend on parent–infant communicative experiences. Together, these studies suggest that while newborns exhibit a basic preference for faces and especially the eyes in the context of the face, infants' responses to faces and eyes become more sophisticated as they get older, influenced by their early environments. Early eye detection serves an important communicative function. Indeed, by 3–4 months of age, infants attend longer and smile more in social interactions with partners making eye contact compared to looking away, and, in the presence of someone looking away, try to engage partners in eye contact (Blass & Camp, 2001; Hains & Muir, 1996; Symons, Hains, & Muir, 1998). The early development of face expertise may in fact be driven by attention to the eyes (Gliga & Csibra, 2007).

To better uncover the influence of experience in shaping early attention, more experimental studies are necessary. Attempts to experimentally manipulate infants' early experiences have largely been done in animals (for a review: Davidson & Clayton, 2016). For example, in the first month of life (between 7 and 30 days of age), infant monkeys exhibit considerable individual differences in the extent to which they attend to the eye region of faces: In mother-reared infants, males look longer to the eye region than females (Paukner, Slonecker, Murphy, Wooddell, & Dettmer, 2018), but in nursery-reared infants (who have more limited social experience with conspecifics and are raised by human caretakers), females look more to the eye region than males (Simpson, Nicolini, et al., 2016). Maternal rank was positively associated with attention to the eyes, although this was only the case for infants reared by their mothers, suggesting this attentional preference may be transmitted through social interactions, rather than inherited through some biological mechanism (Paukner et al., 2018). In sum, it appears that there are individual differences in attention to faces and the eye region, shaped by infants' early social experiences in just the first month of life. However, it remains unknown whether earlier social experience—in the first weeks of life—likewise influences attention to faces as a function of their gaze direction (i.e. eye contact or averted-gaze). Further, we currently lack longitudinal studies of eye gaze processing.

In the present study, we were interested in the extent to which infants are initially biased to attend to direct-gaze faces, and how these biases are further refined in the first few months of life as a function of their social experience. We hypothesized that faces with direct gaze are special from birth and take on additional meaning with development. That is, we predicted that with age, infants would exhibit increasing relative interest in faces with eye contact compared with faces looking away.

We chose to study NHP because, unlike humans, we can carefully control infants' early environment, including social experiences and exposure to faces (e.g. Sugita, 2008). In addition, like humans, macaques are highly gregarious and infants engage in complex face-to-face interactions (Ferrari, Paukner, Ionica, & Suomi, 2009) and show considerable individual differences in social behavior, making them a promising model for the study of disorders such as autism (Feczko, Bliss-Moreau, Walum, Pruett, & Parr, 2016). Macaques and humans share a number of similarities in social attention (Parr, 2011). For example, when viewing faces, both humans and monkeys spend longer viewing the inner than outer facial features (Dahl, Wallraven, Bülthoff, & Logothetis, 2009), especially the eyes (Gothard, Brooks, & Peterson, 2009). Importantly, infant macaques' looking behavior

FIGURE 1 Direct gaze (top left) and averted gaze (top right) sample stimuli. Areas of interest (AOI) are shown around the head and eye zone regions (bottom)

can be assessed with remote eye tracking (e.g. Paukner, Simpson, Ferrari, Mrozek, & Suomi, 2014). Such studies have revealed that, by 3 weeks of age, macaques can efficiently detect and look longer at faces compared with nonfaces (Simpson et al., 2017). Further, socially reared macaque infants exhibit early preferences for direct-gaze faces soon after birth (Muschinski et al., 2016) followed by the rapid development of gaze following in the first year of life (Rosati, Arre, Platt, & Santos, 2016), much like human infants. We therefore sought to examine whether macaque infants with fewer species-typical early social experiences (i.e. reared by humans in a neonatal nursery) would exhibit different early patterns of attention to direct and averted-gaze faces, compared to infants with more species-typical, rich social experiences, reared by their mothers in social groups.

2 | METHODS

The *Eunice Kennedy Shriver* National Institute of Child Health and Human Development Animal Care and Use Committee approved the procedures. We conducted the study in accordance with the Guide for the Care and Use of Laboratory Animals and complied with the Animal Welfare Act.

2.1 | Subjects

Subjects were 16 healthy, full-term infant rhesus macaques (*Macaca mulatta*), nine females and seven males, born in 2015. Infants were healthy and were separated from their mothers on the day of birth (typically by 8 a.m.) and reared in a nursery facility by human caretakers for ongoing, unrelated research studies.

In the first months of life, these infants had limited exposure to faces generally, including human and NHP faces. Infants could see other infants housed in adjacent cages, but lacked species-typical exposure to adult conspecifics' faces. Human caretakers were present for 13 hr each day and interacted with infants every 2 hr for feeding and cleaning purposes. Caregivers wore personal protective equipment, including goggles, masks covering the nose and mouth, and hats, so only their eyes were visible (see Paukner, Huntsberry, & Suomi, 2010). While difficult to estimate precisely, these infants had limited face exposure generally (to faces of any species), and especially to conspecifics, compared to infants reared by their mothers in social groups.

Infants were raised identically for the first 5 weeks of life. Once the youngest infant reached 36 days of age, infants were placed into small, same-aged peer groups. Infants were randomly assigned to one of two rearing conditions for unrelated research studies: low-socialization infants (n = 8; four females) and high-socialization infants (n = 8, five females). Low-socialization infants continued to be individually housed but assigned to playgroups composed of 3–4 peers and put together for 2 hr a day, 5 days a week. High-socialization infants were raised in groups with 3–4 peers (for details: Simpson, Miller, et al., 2016; Simpson, Nicolini, et al., 2016; Simpson, Suomi, et al., 2016). Therefore, by 3 months of age, infants had extensive experience with same-aged conspecifics, though still lacking species-typical exposure to adult conspecifics.

Infants were tested longitudinally in the 13 weeks after birth. Testing occurred weekly in the first month (days 10, 17, 24, 30), then every-other-week in the second and third months after birth (days 44, 58, 72, 86), for a total of 8 time-points. Infants were individually housed in incubators (51 cm × 38 cm × 43 cm) for the first 2 weeks of life and in larger cages (65 cm × 73 cm × 83 cm) thereafter. Both housing arrangements contained an inanimate surrogate mother covered with fleece fabric as well as loose pieces of fleece fabric and various toys. Infants were fed Similac infant formula from birth and additionally Purina Monkey chow (#5054) starting at 2 weeks old. Additional food enrichment (fruit, seeds, nuts) was introduced twice daily when infants were 2 months old. Water was available ad libitum.

We compared these nursery-reared infants to a group of mother-reared infants (n = 20), all males, healthy, full-term, and tested with eye tracking using the same stimuli (for details, see Muschinski et al., 2016). The notable difference from the nursery-reared infants was that the mother-reared infants had enriched species-typical environments, reared by their mothers in large social groups (~50–100 individuals). Mother-reared infants were tested longitudinally across 14 test sessions, starting after the third day of life and continuing through approximately 5 months of age, so their testing also extended over a longer period than that for the nursery-reared infants.

2.2 | Materials

2.2.1 | Stimuli

At each age, infants viewed two novel pairs of unfamiliar faces, for a total of 16 unique trials per infant (eight time-points × two trials at each age). These faces were randomly selected for each test from a larger set of 42 female monkey faces. Each infant saw each face only once. The stimuli were the same as those used previously in mother-reared rhesus macaque infants (Muschinski et al., 2016). In each trial, two photographs of the same adult female monkey were shown for 10 s, one with direct gaze and one with averted gaze, side-by-side, cropped closely around the head, presented on a black background (Figure 1; also, see figure 2 in Muschinski et al., 2016). The direct-gaze faces were facing forward, with eyes looking straight into the camera. The averted-gaze faces' heads and eyes were angled away from the camera at about 45° to either the left or right. The location of the direct and averted-gaze faces was balanced, so they were equally likely to appear on the left and right side of the screen. Faces appeared on a black screen, sized 28 × 51 cm (1,280 × 720 pixels).

2.2.2 | Eye tracking

Eye movements were recorded via corneal reflection using a Tobii TX300 eye tracker with a remote 58.4 cm monitor and integrated eye-tracking technology and a 60 Hertz sampling rate. We used Tobii Studio software (Tobii Technology, Sweden) to collect and summarize the data. An area of interest (AOI) was drawn around each face and each eye region (see the bottom panel of Figure 1). The sizes of the AOIs did not vary systematically across direct and averted face conditions, for either the face or eye AOIs, $t(19) = 1.49$, $p = 0.152$ and $t(19) = 1.16$, $p = 0.262$, respectively. We used the Tobii Filter to extract fixations, defined as occurring within a window of 37 pixels for at least 50 ms.

2.3 | Procedures

An experimenter held the infant wrapped in soft fleece fabric at a distance of approximately 60 cm from the screen. Each infant was calibrated prior to each test using a 5-point calibration procedure to Tobii Studio's pre-set locations; individual calibration points judged to be unreliable were repeated until acceptable. Following calibration, each infant viewed two face pairs (four face images total) each day.

2.4 | Data analysis

Overall, we followed the general data analysis strategy used by Muschinski et al. (2016). We calculated two dependent variables for each AOI (face and eyes) separately: (a) the proportion[1] of total looking time (the sum of fixation times) to the AOI out of the total time looking to the screen; and (b) the sum of fixation times (in seconds) to a AOI (see Supporting Information Appendix S1, including Supporting Information Figures S1, S2 and S3, and Supporting Information Tables S1 and S2). We analyzed these data with linear mixed models in SPSS v.23. All models included a fixed effect for stimulus category of gaze direction (direct vs. averted gaze); a random intercept for subject, a random slope for age, and an unstructured covariance matrix were used for the random effects.

3 | RESULTS

3.1 | Main effects of stimulus category

First, we ran models using this basic structure to test for main effects of stimulus category (gaze direction) on our dependent variables in the nursery-reared infants. Stimulus category was dummy coded 1 for direct gaze, 0 for averted gaze.

In the model predicting proportion of total looking time to the face, the intercept was statistically significant, $b = 0.26$, $SE = 0.01$, 95% CI: (0.23, 0.29), $p < 0.001$, indicating that infants spent approximately a quarter of the time they were looking at the screen looking at the face AOI of averted-gaze faces. The coefficient for gaze direction was also significant, $b = 0.05$, $SE = 0.02$, 95% CI: (0.02, 0.85), $p = 0.005$, indicating that infants spent more of their time looking at direct-gaze faces than averted-gaze faces (Figure 2). Similarly, in the model predicting proportion of total looking time to the eyes, both the intercept ($b = 0.06$, $SE = 0.01$, 95% CI: [0.05, 0.08], $p < 0.001$) and the coefficient for gaze direction ($b = 0.03$, $SE = 0.01$, 95% CI: [0.01, 0.05], $p = 0.006$) were significant, indicating that infants spent more of their time looking at the eyes on direct-gaze faces than they did looking at the eyes on averted-gaze faces.

3.2 | Longitudinal effects of stimulus category

Next, we added a fixed effect for week and a week × stimulus type (gaze direction) interaction to the models to test for longitudinal changes. We rescaled week by subtracting a constant of 2 so that the intercepts in the following models correspond to week 2, the earliest week of testing. Following Muschinski et al. (2016), we fit three full-factorial models of this type for each analysis: one with a linear growth term, one that added a quadratic growth term, and one that added a cubic growth term. Then, we used chi-square deviance tests to determine which of the nested models best fit the data. In all cases except for one, the model with the linear growth term fits the data best, so those are the models we report here. The one exception was the cubic model predicting percentage of time looking at the face—however, none of the terms in this model were statistically significant,

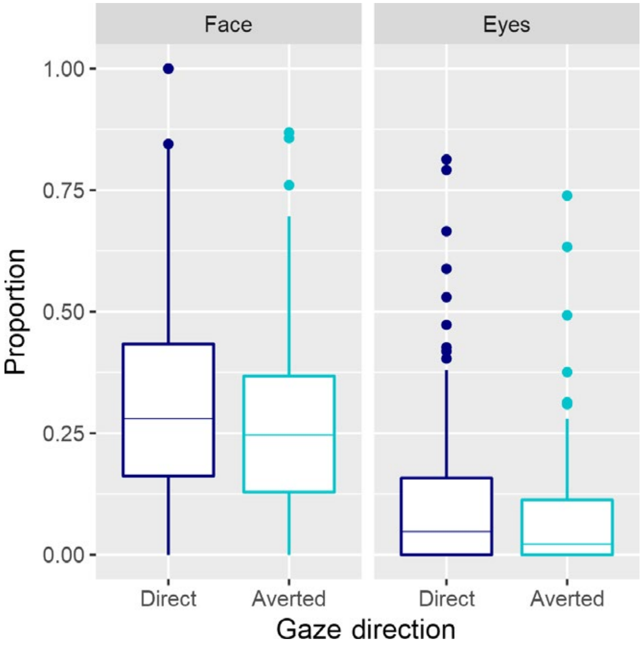

FIGURE 2 Overall fixation proportion collapsed across age in nursery-reared infants. Infants looked for a greater proportion of time to the direct (dark blue) compared with averted (light blue) gaze faces, for both the face region (left plot) and the eye region (right plot), *ps* < 0.05. Solid horizontal lines indicate medians, the bottom and top of the boxes indicate 25th and 75th percentiles, respectively, and whiskers indicate the most extreme data point that is no more than 1.5 × interquartile range (IQR) below the lower quartile and above the upper quartile. Dots indicate outliers, more than 1.5 × IQR

indicating that the model was simply overfit due to the large number of included terms. Therefore, we retained the linear model instead.

Full model results are presented in Tables 1 and 2. In the model predicting the proportion of time looking to the face, there were significant main effects for both week ($b = 0.008$, $p = 0.026$) and gaze direction ($b = 0.08$, $p = 0.014$). Thus, in addition to a predicted increase in looking proportion over time generally, the model predicts that subjects spent an additional 8% of their time looking at direct-gaze faces than at averted-gaze faces. The interaction between gaze direction and week was not significant, indicating that the effect of gaze direction did not change over development (Figure 3). In the model predicting the proportion of time looking to the eyes, neither week ($b = 0.005$, $p = 0.070$) nor gaze direction ($b = 0.03$, $p = 0.114$) was statistically significant, but they trended in the same direction as in the face model.

3.3 | Comparison with mother-reared infants

In all of their longitudinal analyses for mother-reared infants, Muschinski et al. (2016) found significant interactions between age and gaze direction in predicting fixation time and proportion of looking time. In some of their models, they also found significant nonlinear effects of age (i.e. quadratic and cubic). In contrast, we found no significant interactions or nonlinear effects of age for our longitudinal analyses in nursery-reared infants, which indicate that there may be differences in developmental trajectories between mother-reared and nursery-reared infants. We obtained the raw data from Muschinski et al. (2016) for the first 13 weeks of testing their mother-reared infants (*N* = 20), and we combined these data with our more recently collected nursery-reared infant data to directly test for overall effects of mother- versus nursery-rearing. That is, beyond the apparent differences in growth trajectories between the two data sets, do mother-reared infants and nursery-reared infants differ in their overall preferences for direct and averted-gaze faces?

To test this, we reran our four main effects models—fixation proportion and fixation time for face and eyes AOIs—on the combined data set with an added predictor for rearing condition (for fixation time results, see Supporting Information Appendix S1). Each model contained a dummy-coded predictor for gaze direction (1 = direct gaze, 0 = averted gaze), rearing condition (1 = mother-reared; 0 = nursery-reared), and their interaction. Muschinski et al. (2016) began testing in the first week of life, but we rescaled the week variable to match our own (i.e. we subtracted a constant of 2 across both data sets). Thus, the intercept in each model referred to nursery-reared infants looking at averted faces in their second week of life. Full model results are displayed in Table 3 (face AOI) and Table 4 (eyes AOI). Particularly noteworthy is that for fixation proportion to the face AOI (Figure 4), mother-reared infants, compared to nursery-reared infants, showed an increased preference for direct-gaze faces, as indicated by the significant gaze direction × rearing condition interactions. Rerunning the model with the dummy code for rearing condition switched confirmed that, in mother-reared infants, there was a significant preference for direct-gaze faces compared

TABLE 1 Longitudinal results for face

	Fixation time				Fixation proportion			
Parameters	*b*	*SE*	95% CI	*p*	*b*	*SE*	95% CI	*p*
Intercept	0.62	0.12	0.37, 0.86	<0.001	0.22	0.02	0.17, 0.26	<0.001
Week	0.06	0.02	0.03, 0.10	0.001	0.008	0.003	0.001, 0.014	0.026
Direct	0.16	0.15	−0.13, 0.44	0.292	0.08	0.03	0.02, 0.13	0.014
Week × direct	−0.01	0.02	−0.06, 0.03	0.630	−0.005	0.005	−0.014, 0.005	0.314

Notes. Results of two linear mixed models, one predicting fixation time and one predicting fixation proportion. Models included a random intercept for subject, and a random slope for age (week), and an unstructured covariance matrix was used for the random effects. “Direct” refers to a dummy code for gaze direction (1 = direct gaze; 0 = averted gaze).

TABLE 2 Longitudinal results for eyes

	Fixation time				Fixation proportion			
Parameters	***b***	***SE***	**95% CI**	***p***	***b***	***SE***	**95% CI**	***p***
Intercept	0.14	0.07	0.01, 0.28	0.036	0.05	0.01	0.02, 0.07	0.001
Week	0.03	0.01	0.003, 0.05	0.028	0.005	0.003	−0.0004, 0.01	0.070
Direct	0.06	0.10	−0.12, 0.25	0.509	0.03	0.02	−0.007, 0.07	0.114
Week × direct	0.008	0.02	−0.02, 0.04	0.620	0.00	0.003	−0.006, 0.006	0.974

Notes. Results of two linear mixed models, one predicting fixation time and one predicting fixation proportion. Models included a random intercept for subject, and a random slope for age (week), and an unstructured covariance matrix was used for the random effects. “Direct” refers to a dummy code for gaze direction (1 = direct gaze; 0 = averted gaze).

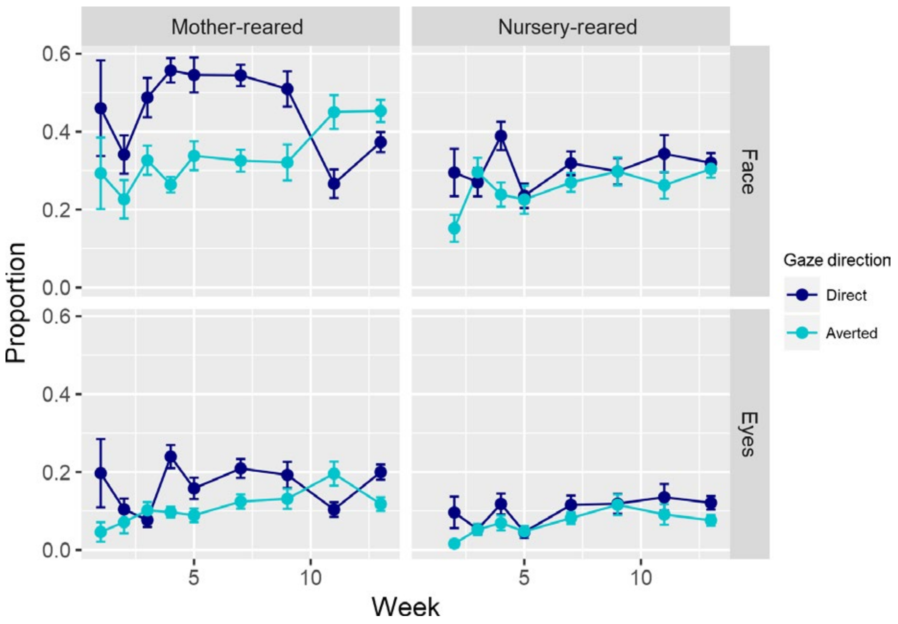

FIGURE 3 Fixation proportion across development (in weeks) in mother-reared (left graphs) and nursery-reared (right graphs) infants. Infants displayed increases in their proportions of time looking to the areas of interest (AOI) in the zones around the face (top graphs) and eyes (bottom graphs) with age, *ps* < 0.05. Direct-gaze faces are represented with dark blue, and averted-gaze faces are represented with light blue. Points reflect means, and error bars reflect standard errors of the means

TABLE 3 Face area of interest overall comparison with mother-reared infants

	Fixation time				Fixation proportion			
Parameters	***b***	***SE***	**95% CI**	***p***	***b***	***SE***	**95% CI**	***p***
Intercept	0.90	0.09	0.71, 1.08	<0.001	0.26	0.02	0.23, 0.29	<0.001
Direct	0.10	0.10	−0.09, 0.29	0.312	0.05	0.02	0.01, 0.09	0.023
Mother	0.21	0.12	−0.03, 0.46	0.085	0.08	0.02	0.04, 0.12	<0.001
Direct × mother	0.32	0.12	0.08, 0.56	0.008	0.08	0.03	0.02, 0.13	0.005

Notes. Results of two linear mixed models, one predicting fixation time and one predicting fixation proportion. Models included a random intercept for subject, and a random slope for age, and an unstructured covariance matrix was used for the random effects. “Direct” refers to a dummy code for gaze direction (1 = direct gaze; 0 = averted gaze). “Mother” refers to a dummy code for rearing condition (1 = mother-reared; 0 = nursery-reared).

with averted-gaze faces ($b = 0.13$, $SE = 0.02$, 95% CI: [0.09, 0.16], $p < 0.001$).

Additionally, the significant simple effects of rearing condition in both of the fixation proportion models (face and eyes AOIs) indicate that mother-reared infants spent a greater portion of their time looking at averted-gaze faces than did nursery-reared infants (recall that the intercepts of these models refer to nursery-reared infants looking at averted faces). Taken together with the interaction results mentioned above, this indicates a general tendency for mother-reared infants to spend a greater proportion of their time than nursery-reared infants looking at faces and eyes *in general*, with mother-reared infants also having an even greater preference for direct-gaze faces *in particular*.

Finally, we directly tested for differences in growth trajectories between mother-reared and nursery-reared infants by rerunning the models with an added fixed effect for week, as well as its

TABLE 4 Eyes area of interest overall comparison with mother-reared infants

	Fixation time				Fixation proportion			
Parameters	***b***	***SE***	**95% CI**	***p***	***b***	***SE***	**95% CI**	***p***
Intercept	0.29	0.06	0.17, 0.40	<0.001	0.07	0.01	0.05, 0.10	<0.001
Direct	0.10	0.06	−0.01, 0.21	0.070	0.03	0.01	0.003, 0.06	0.028
Mother	0.08	0.08	−0.07, 0.23	0.310	0.04	0.02	0.01, 0.08	0.012
Direct × mother	0.10	0.07	−0.04, 0.23	0.173	0.03	0.02	−0.003, 0.07	0.072

Notes. Results of two linear mixed models, one predicting fixation time and one predicting fixation proportion. Models included a random intercept for subject, and a random slope for age, and an unstructured covariance matrix was used for the random effects. “Direct” refers to a dummy code for gaze direction (1 = direct gaze; 0 = averted gaze). “Mother” refers to a dummy code for rearing condition (1 = mother-reared; 0 = nursery-reared).

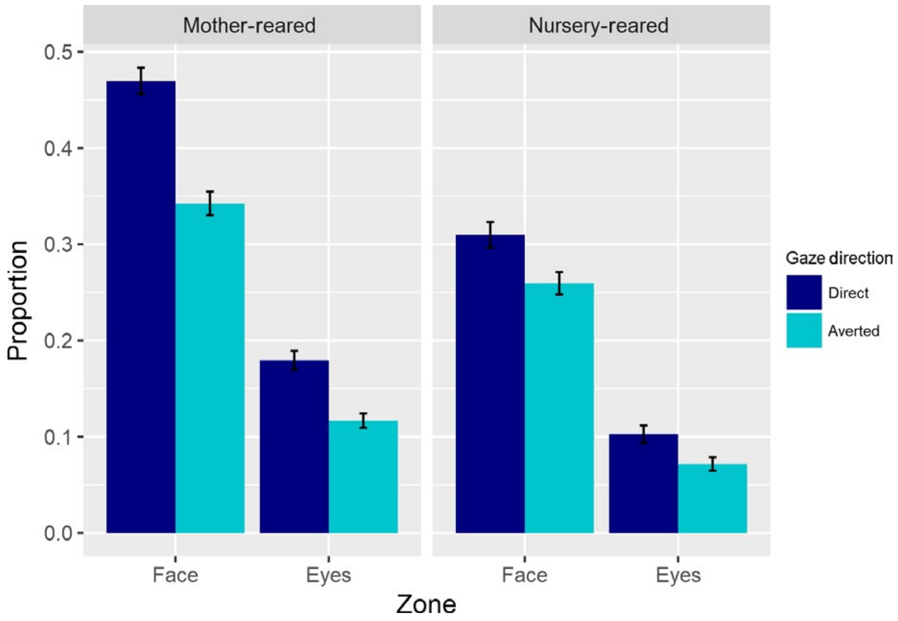

FIGURE 4 Mean fixation proportion collapsed across age in mother-reared (left graph) and nursery-reared (right graph) infants, for the areas of interest (AOI) in the zones around the face and eyes, for direct-gaze (dark blue) and averted-gaze (light blue) faces. There was a stimulus type × rearing interaction for the face looking time proportion, *ps* < 0.05, indicating that mother-reared infants displayed a larger difference in attention between direct and averted-gaze faces compared with nursery-reared infants. Error bars reflect standard error of the mean

interactions with gaze direction and rearing condition. We note that given our relatively small sample size here, the results of these models should be interpreted with caution. In the proportion of looking time model for the face AOI, there was a small but significant week × stimulus type × rearing condition interaction ($p = 0.005$) indicating that mother-reared infants had a stronger preference for direct-gaze faces than did nursery-reared infants that gradually decreased (about 3% per week) over time (which can be seen in the upper-left panel of Figure 3). None of the other three models indicated differences in growth trajectories between datasets (full results in Supporting Information Tables S1 and S2). Hence, our models do not conclusively provide evidence that mother-reared and nursery-reared infants differ in their growth trajectories in preferences for direct-gaze faces over the first 13 weeks of life, though these models may be underpowered to detect these differences.

4 | DISCUSSION

The present study explored whether early experiences influence attraction to eye contact in infant rhesus macaques. Using remote eye tracking, we examined infants’ attention patterns to face pairs varying in their gaze direction (direct or averted) longitudinally across the first 13 weeks of life. We found that infants who were raised by human caretakers, and therefore had limited contact with conspecifics, spent longer (and a greater proportion of time) looking to direct gaze compared with averted gaze conspecific faces, and especially the eyes. In addition, regardless of gaze direction, nursery-reared infants’ looking to faces, and especially the eyes, increased with age. These findings parallel those reported previously in infant monkeys raised with their mothers in rich social environments with conspecifics (Muschinski et al., 2016). These findings suggest that there may be an initial preference for direct-gaze faces, and eyes, from birth that is present even when opportunities for social interactions are limited (Sugita, 2008), although some minimal level of face exposure may still be necessary. These results are consistent with the proposal that there may be an “eye direction detector” mechanism (Baron-Cohen & Ring, 1994) that develops even with very limited social experience.

However, we did not find evidence that nursery-reared infants had an increased interest specifically in direct-gaze faces with age, suggesting that, while there may be an initial preference for direct-gaze faces from birth, social experiences seem to support this attraction and may be necessary for it to grow stronger across the first weeks of life. Further, nursery-reared infants appeared overall less attentive to the faces and eyes compared with mother-reared infants, suggesting overall decreased social interest in conspecifics among infants with more limited social experiences. Similarly, chimpanzees with impoverished early social environments attended less to videos of conspecifics (and instead attended more to nonsocial videos) compared with chimpanzees reared with more socialization (Kano, Shepherd, Hirata, & Call, 2018). These findings are in line with a functional architecture account of development, which proposes that infants' initial predispositions may be supported through early social experiences with caregivers (Murray et al., 2016). For face processing, more specifically, our findings support the conspec–conlearn two-process theory (Johnson et al., 2015; Morton & Johnson, 1991). That is, infant monkeys appear to be born with a preference for direct-gaze faces over averted-gaze faces, but early social experiences can boost this preference in the first weeks and months of life. In a limited social context, infants may not have as many opportunities to learn the value of direct-gaze faces, so they do not show growing interest in them with age, as do the infants who had more enriched social experiences.

Indeed, studies in both human and nonhuman primates suggest that mutual gaze between infants and caregivers may promote the development of healthy social skills (Dettmer et al., 2016; Murray et al., 2016; Rayson, Bonaiuto, Ferrari, & Murray, 2017). Human 4 month olds exhibit more facial mimicry when interacting with social partners engaging in eye contact compared to those without eye contact (de Klerk, Hamilton, & Southgate, 2018). Human infants who engage in more mutual gaze with their parents go on to develop more attentional control (Niedźwiecka, Ramotowska, & Tomalski, 2018), suggesting that sensitivity to eye contact may be an important early marker of healthy social development. Sensitivity to the eyes also helps infants to use others, who may be more experienced, as sources of information, for example, to orient to important things in the environment (e.g. social partners, food, or threats; Emery, Lorincz, Perrett, Oram, & Baker, 1997; Teufel, Gutmann, Pirow, & Fischer, 2010). A rich social environment—particularly one that includes joint attention interactions—provides infants with learning opportunities to understand the links between others' gaze and relevant items in the environmental (Corkum & Moore, 1998; Gredebäck, Fikke, & Melinder, 2010).

Atypical face and eye processing has been linked to heightened risk of psychopathy (Bedford, Pickles, Sharp, Wright, & Hill, 2015) and autism spectrum disorders (ASD; Gangi et al., 2018; Shultz, Klin, & Jones, 2018). For example, newborns at risk for ASD are less attentive to faces, particularly direct-gaze faces, compared with low-risk newborns (Di Giorgio et al., 2016). Further, at 2 months of age, infants who later are diagnosed with ASD attend to the eye region of faces similar to non-ASD infants, but from 2 to 6 months, ASD infants show a decline in attention to the eye region compared with low-risk control infants, who show an increase in attention to the eyes (Jones & Klin, 2013). The present study found that infants with limited early social experience still exhibit normative attentional preferences to face and eye regions of direct-gaze faces initially in the first weeks of life, but that, with age, their attention to direct-gaze faces and eyes specifically did not increase to a greater extent than their interest in faces generally, as in infants with more species-typical social environments. That is, unlike what previous research has found for mother-reared infants (Muschinski et al., 2016), here, we found that nursery-reared infants did not display a pattern of increasing interest in direct-gaze faces with age. It is also worth noting, though, that we did not find statistical support for this rearing difference in growth trajectories, so this finding should be interpreted with caution. While this finding might, at first, seem to signify a dysfunction or unhealthy pattern of attention predictive of later disorder, it may, alternatively, be adaptive for infants to develop phenotypes that best suit their particular environments. Drawing parallels between human disorders and the present findings, therefore, should be done with care, mindful of these limitations. Nonetheless, these findings suggest that the developmental trajectories of different types of social attention may be informative indices of normative social development.

Our findings are also consistent with studies of more general face processing. For example, face-deprived infant macaques—not exposed to faces or face-like stimuli after birth—still exhibit attentional preferences for faces compared with nonfaces, suggesting initial face biases appear intact even in face-deprived environments (Sugita, 2008). However, experience with faces may be necessary for the formation of specialized cortical processing for faces, given that face-deprived infant macaques exhibit impaired neural specialization for faces, lacking face patch regions in the superior temporal sulcus that are selectively responsive to faces (Arcaro, Schade, Vincent, Ponce, & Livingstone, 2017). Thus, while initial attentional predispositions may be present independent of experience, early exposure to faces further refines the specialization of this system.

Attention to others' attentional states is a foundation precursor for later social cognitive skills, including gaze following (i.e. looking where another individual is looking; Frischen, Bayliss, & Tipper, 2007). While a rudimentary form of gaze following is found in human newborns, it is rather inflexible and limited (e.g. requiring motion of the pupil, as well as mutual gaze prior to the motion; Farroni et al., 2004). In humans and NHP, the capacity to systematically follow the direction of others' attention emerges more consistently in infancy around 6 months of age and continues to improve beyond that, becoming more flexible and accurate well into the second year of life (for a review, see Grossmann, 2017).

Furthermore, social experiences influence later gaze-following abilities. In human infants, own-race faces compared with other-race faces are more reliably followed during gaze-following tasks at 7 months of age (Xiao et al., 2018). Similarly, in the present study, adult monkey faces were arguably more familiar to the mother-reared infants than the nursery-reared infants. Future work with human face stimuli, or same-aged peer faces, oriented with eye contact or averted gaze, could be used to see if nursery infants are more likely to discriminate between these types of stimuli and show stronger preferences for direct-gaze faces in this context.

Previous studies have found that infant monkeys with more social experience with humans are better at following the direction of humans' eye gaze (i.e. looking where another individual looks) at 7 months of age (Simpson, Miller, et al., 2016; Simpson, Nicolini, et al., 2016). Early social experiences appear to support the development of infants' gaze following competence, possibly due to infants' increased exposure to social cues, thereby enhancing infants' interest or skill in social interactions.

A number of questions remain, including the following: Are there long-term consequences of failing to be exposed to social gaze? Studies in rhesus monkeys suggest that infants' early social skills predict their later social relationships. For example, rhesus monkeys with better face recognition and social interaction skills in infancy develop more prosocial behaviors as adults (Sclafani et al., 2016). Similarly, rhesus monkeys with better neonatal imitation skills in the first week of life develop more dominance and higher juvenile social status (Kaburu, Paukner, Simpson, Suomi, & Ferrari, 2016; Wooddell, Simpson, Murphy, Dettmer, & Paukner, 2018). These findings suggest that early social capacities may lay the groundwork for later emerging more complex social competencies (for a recent review in humans, see Shultz et al., 2018).

The present study is not without limitations. Mother-reared infants were all male, limiting our ability to test whether there are sex differences. Previous studies suggest female neonates engage in more eye contact compared with male neonates, in both humans (Hittelman & Dickes, 1979) and macaques (Simpson, Miller, et al., 2016; Simpson, Nicolini, et al., 2016), although the developmental trajectories of each sex remain, to our knowledge, unexplored. While we found no sex differences in the nursery-reared infants (alone or combined with mother-reared infants), we lacked power and therefore cannot conclude that such differences do not exist. We also followed nursery-reared infants for only the first 13 weeks of life, but there may be developmental changes that occur beyond that point. Future research with more balanced sex ratios and over more extended periods of development will therefore be important.

In addition, for our stimuli, we used pictures rather than videos or a live individual, as these enabled us to have more experimental control. However, static images are more limited in their ecological validity and may not produce as strong of effects as interacting with a live partner (e.g. Pönkänen, Alhoniemi, Leppänen, & Hietanen, 2010; Risko, Richardson, & Kingstone, 2016). Furthermore, it is unclear to what extent our findings would extend to other types of stimuli, including male faces and faces of other ages or species. For example, nursery-reared infants, who have more experience with same-aged peer faces, may show superior processing with more familiar types of faces, such as those of conspecific infant faces relative to adult faces (Simpson, Suomi, et al., 2016).

Finally, there were methodological differences in our testing of mother-reared and nursery-reared infants (e.g. different eye-tracking systems) that may have influenced data quality and therefore limit our comparisons. While future research using more comparable equipment across the two groups would be ideal, the present study provides initial evidence of different developmental patterns across these groups.

Nonetheless, the present study suggests that early attentional preferences for direct-gaze faces may emerge independent of early infant experiences, but that social experiences appear to also play an important role in supporting the development of social attention.

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CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

ENDNOTES

[1] Analyzing proportion outcomes in a linear model can lead to model predictions outside the range of 0–1. To verify that this issue did not affect our results here, we reran all of the proportion models with a logit-transformed outcome variable, which circumvents the issue without increasing error rates (Warton & Hui, 2018). None of the effects in the logit-transformed models meaningfully differed from the proportion models, so we report the results of the proportion models here for ease of interpretation and consistency with Muschinski et al. (2011).

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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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