Sex and rank affect how infant rhesus macaques look at faces

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We investigated how differences in infant sex and mothers' dominance status affect infant rhesus macaques' (*Macaca mulatta*) interest in visually exploring emotional facial expressions. Thirty-eight infants were presented with animated avatars of macaque facial expressions during the first month of life. Sons of high-ranking mothers looked more at faces, especially the eye region, than sons of low-ranking mothers, but no difference in looking duration was found for daughters. Males looked significantly more at eyes than females, but this effect was reversed in infants who were reared without mothers in a primate nursery facility. In addition, in mother-infant interactions, mothers of sons were more likely to gaze at their infant's face compared to mothers of daughters. Combined with previous research indicating that rhesus macaque mothers interact differently with infants based on their own rank and infant's sex, these results support the view that social experiences shape early face preferences in rhesus macaques.

Key words: dominance rank, early experience, eyetracking, rhesus macaque, sex difference, visual social attention

Short title: Sex and rank affect visual social attention

People care about the attentional state of others: named visual social attention, it refers to a preference to look at other people's faces, particularly the eyes (Guillon, Hadjikhani, Baduel, & Roge, 2014). Newborns, starting within minutes after birth, already show a bias towards faces and face-like stimuli (Goren, Sarty, & Wu, 1975; Simion, Farroni, Macchi Cassia, Turati, & Dalla Barba, 2002; Vinette, Gosselin, & Schyns, 2004; Johnson, Dziurawiec, & Durston, 2005), which is thought to produce biased input, resulting in processing advantages for the most commonly encountered types of faces. For example, infants with female primary caregivers prefer female faces over male faces, whereas infants with male primary caregivers prefer male faces over female faces (Slater & Quinn, 2001). In addition, infants with a female primary caregiver only (as opposed to both male and female caregivers) show greater expertise in discriminating female faces (Rennels, Juvrud, Asperholm, Gredeback, & Herlitz, *in press*), suggesting that visual social attention is affected by the infant's experience and environment.

Given that face processing is likely equally important for non-human primates (hereafter: primates) who live in large and complex social groups, it has been argued that there may be a primate face recognition system common to all primates (Tsao, Moeller, & Freiwald, 2008). Past research has revealed that rhesus macaques (*Macaca mulatta)* also preferentially attend to eyes (Dahl, Wallraven, Bülthoff, & Logothetis, 2009; Leonard, Blumenthal, Gothard, & Hoffman, 2012; Gothard, Brooks, & Peterson, 2009; Guo, Robertson, Mahmoodi, Tadmor, & Young, 2003), a preference that is already apparent in infancy (Muschinski, Feczko, Brooks, Collantes, Heitz & Parr, 2016; Paukner, Simpson, Ferrari, Mrozek, & Suomi, 2014; Mendelson, Haith, & Goldman-Rakic, 1982).

Some face biases appear to be independent of experience. A recent study with human toddlers reported greater similarity in visual social attention in identical twins compared to non-identical twins and randomly paired children, which suggests that visual social behavior is influenced by genetic factors (Constantino et al., 2017). In primates, Paukner, Huntsberry and Suomi (2010) report a preference for adult female monkey faces over adult male monkey faces in 3-wk old infant rhesus macaques who lacked prior exposure to adult monkey faces. Furthermore, rhesus infants reared without mothers in a primate nursery facility show sex differences with regard to visual interest in faces: females look more at emotional facial expressions than males (Simpson, Nicolini, Shelter, Suomi, Ferrari & Paukner, 2016), similar to sex differences in social interest reported in human infants (Hittelman & Dickes, 1979; Connellan, Baron-Cohen, Wheelwright, Batki & Ahluwalia, 2000). These studies suggest that some facial preferences are likely present from birth and independent of individual experiences.

On the other hand, since it is possible to control many aspects of the environment of infant primates, some of the strongest evidence of the effects of the environment on visual social attention comes from captive primate studies. For example, Sugita (2008) reported that infant macaques without any kind of face experience preferred to look at faces (human and monkey) rather than objects, which is likely an experience-independent preference. Once exposed to either human or monkey faces, monkeys preferred the species' faces that they were first exposed to, for up to a year later, even though all subjects were housed with other monkeys at this point (Sugita, 2008). Other studies report a preference for unfamiliar (heterospecific) over familiar (conspecific) faces in socially housed infant macaques in the first week of life, which reverses at around 5-6-wks of age (Parr, Murphy, Feczko, Brooks, Collantes & Heintz, 2016), suggesting that facial exposure significantly shapes visual preferences.

Undoubtedly for rhesus monkeys, mothers represent a significant influence in their infants' lives. After giving birth, mothers carry, nurse, and protect their infants from other group members for many weeks, thus affecting the quality and quantity of facial experience infants receive. Individual differences in mothers' caregiving style can be traced back to individual differences in mothers' life history. For example, low-ranking mothers tend to be more protective of their infants than high-ranking mothers (White & Hinde, 1975). Differences in infant rearing have also been noted with regards to infant sex: mothers of male infants gaze more at their infants (Dettmer, Kaburu, Byers, Murphy, Soneson, Wooddell & Suomi, 2015), respond more to their infants' separation vocalizations (Tomaszycki, Davis, Gouzoules & Wallen, 2001), and are more likely to encourage their independence (Jensen, Bobbitt & Gordon, 1976) compared to mothers of female infants. These differences in rearing experience are likely to affect infants' visual social attention: for example, at 9-mos old, infants of high-ranking mothers are more vigilant towards threat faces than infants of low-ranking mothers (Mandalaywala, Parker & Maestripieri, 2014).

In the present study, we aim to further elucidate the role mothers play in shaping rhesus macaque infants' visual social attention. We focus on the effects of two factors of individual variability, namely infant sex and mother's dominance rank. We sought to determine the effects of these variables on infants' visual social attention by measuring mother-reared infant rhesus macaques' looking behavior when presented with emotional facial expressions (lipsmacking, fear grimace, threat gesture) performed by an animated avatar. In a previous study, the same stimuli were presented to rhesus macaque infants reared without mothers in a neonatal primate nursery (Simpson et al., 2016); by comparing our results here with these previous data, we are able to infer the influence of mothers on infants' visual social attention. In addition, we observed infants' interactions with their mothers over the first 30-d of life, focusing on gazing episodes between each pair to obtain a measure of infants' facial experience.

Methods

Subjects

Subjects were 38 infant rhesus macaques (*Macaca mulatta*), 23 males and 15 females, aged 7-30 days at the time of testing. Infants were mother-reared and housed in social groups of 8-12 adult females, 1 adult male, and 1-6 other infants of similar age. The home enclosures provided indoor-outdoor access and were enriched with multiple perches, swings, and toys. Each indoor pen measured 2.44m x 3.05m x 2.21m, and each outdoor pen measured 2.44m x 3.0m x 2.44m. Monkeys were fed Purina High Protein Monkey Chow (#5038, St. Louis, MO) twice daily, with ad libitum access to water. Supplemental fruit and other foraging materials such as sunflower seeds were provided daily. We attempted to test an additional 11 infants but either could not calibrate them (N=6) or obtained insufficient data for analysis (N=5, i.e., no data were obtained for a phase of a trial).

Procedure

As part of an unrelated study, infants were briefly separated from their mothers for biobehavioral assessments during the first month of life. Twenty infants were separated four times (age 7, 14, 21, and 30 days, +/- 2 day; eye tracking data were only collected on days 7 and 21) and 18 infants were separated twice (age 14 and 30 days, +/- 2 days; eye tracking data were collected on both days). Mothers were separated from the social group and were lightly sedated with ketamine (10mg/kg IM). Infants were tested using the Infant Neurobehavioral Assessment Scale (Schneider & Suomi, 1992), a behavioral battery that assesses motor, emotional, and perceptual development, and takes approx. 30-min to complete. Following this assessment, the eye tracking data was collected.

Eye movements were recorded via corneal reflection using either a Tobii T60XL (n = 20) or a Tobii TX300 (n = 18) eye tracker, remote 61cm and 58.4cm monitors, respectively, both with integrated eye tracking technology and a sampling rate of 60 Hertz. We used Tobii Studio software (Tobii Technology, Sweden) to collect and summarize the data. Three silent video stimuli were used, depicting an animated adult macaque (based on a female template) looking at infants and exhibiting either lipsmacking (LPS; an affiliative gesture), fear grimaces, or threats. The macaque, making eye contact with the viewer, displayed a 5-s expression (LPS, fear grimaces, or threats), followed by a 5-s neutral face (eye blinks and small head movements were included to maintain an animated impression). The macaque then turned away at a 45° angle, breaking eye contact before turning back to the viewer. This sequence was shown a second time, for a total duration of 30-s. All videos were created using Maya and Zbrush software. Screen and video resolution were set to 1280 x 800 pixels (Tobii T60XL), or 1280 x 720 pixels (Tobii TX300). See supplemental materials for examples.

One experimenter held each infant wrapped in soft fleece fabric at a distance of approximately 62 cm from the screen. Each infant was calibrated using a 5-point calibration procedure to Tobii Studio's pre-set locations; individual calibration points that were judged to be unreliable were repeated until an acceptable calibration was obtained. Following calibration, all three videos were presented in random order.

Mothers’ rank assessment

Social groups were observed bi-weekly in 30-min sessions in which all instances of dyadic dominance interactions (supplant, threat, chase, attack, submissive) were recorded by 3-5 observers (inter-rater reliability ≥85%). Spreadsheets were generated for each group with a winner column (initiator of aggression or recipient of submissive behavior) and loser (recipient of aggression or initiator of submissive behavior) column. Dominance hierarchies were constructed via Elo-rating, a numerical system that continuously updates values based on wins and losses and the expected outcome, with higher Elo-ratings reflecting a higher dominance rank (Albers and de Vries, 2001; Neumann et al., 2011; Wooddell, Kaburu, Suomi, & Dettmer, 2017).

Using R software (v 3.1.2), the *elo.sequence* function (Neumann et al., 2011) generated Elo-ratings, with each animals' initial value set at 1000, and the k factor (a weighted constant based on the probability of winning) set at 200. Ranks were extracted at the beginning of the birth season. A median split of the Elo-ratings divided mothers into high or low rank for their respective cohort of females. Infants were assigned the same dominance rank as their mothers, as macaque infants inherit their mothers' rank (Missakian, 1972).

Infant Observations

A subset of mother-reared infants (N=20, 11 male) were observed within their social group for the first 30-d of life by three observers (inter-rater reliability ≥ 85%). Observations occurred three times per week between 900 and 1700 for 15-min (range 6-17 sessions, mean = 12), during which time the entire social group was locked in the outer portion of the enclosure for a maximum of one hour. Data collection began only if both mother and infant were awake and alert. If mother and/or infant fell asleep for more than 50% of the session, the session was aborted, and the data were not used for analysis. During each data collection session, observers recorded the frequencies of gazing between infants and the mother (mother initiate gaze at infant,

infant initiate gaze at mother, and mutual gaze). Gazing was recorded when lasting at least 3-s; the end of gazing occurred when the behavior ceased for approximately 3-s or longer (Dettmer et al., 2016).

Data analysis

For 12 infants, we were only able to achieve an eye tracking calibration on one test day; for the remaining 26 infants, we calibrated and collected data on both test days. In Tobii Studio, we created two Areas of Interest (AOIs) for analysis: a Face AOI (700 x 700 pixel) and an Eye AOI (400 × 150 pixel). For each AOI, data from both test days (where available) were averaged for each infant. Data were trimmed between subjects to remove outliers greater than two standard deviations from the mean.

Results

Separating infant monkeys from their mothers has the potential to significantly alter infants' behavior towards their mothers (e.g. Suomi, Mineka, & DeLizio, 1983). Since some infants were separated more frequently than others in the current study, we analyzed whether this difference in separation frequency could potentially have affected visual social attention. However, we found no difference in looking duration between the two groups for either AOI (all $p > .3$), and thus did not control for this factor in subsequent analyses.

Face AOI

We ran a repeated measure ANOVA with Gesture (LPS, Fear grimace, Threat) and Phase (Expression, Still, Turn) as within subjects factors and Infant Sex (Male, Female) and Rank (High, Low) as between subjects factors. We found a main effect for Rank ($F (1, 28) = 5.35$, $p = .028$, $\eta_p^2 = .16$) as well as an interaction between Rank and Infant Sex ($F (1, 28) = 4.42$, $p = .045$,

η_p^2 = .14). While rank did not appear to affect looking time to faces in female infants (p = .89), high-ranking male infants (M = 1.57) looked significantly more at faces than low-ranking males (M=.80, p = .002, d = 1.20; Figure 1).

Isolating the Expression phase, a repeated measure ANOVA with Gesture (LPS, Fear grimace, Threat) as within subjects factors and Infant Sex (Male, Female) and Rank (High, Low) as between subjects factors showed a main effect for Gesture (F (2, 56) = 4.68, p = .013, η_p^2 = .14). Post-hoc comparisons revealed that infants looked significantly more at LPS (M=1.38, p = .008, d = .62) and Threat gestures (M = 1.32, p = .013, d = .60) compared to Fear (M = .93). There were no other main effects or interactions.

Eye AOI

We next analyzed looking to the eye region only. A repeated measures ANOVA with Gesture (LPS, Fear, Threat) and Phase (Expression, Still, Turn) as within-subjects factors and Infant Sex (Male, Female) and Rank (High, Low) as between subjects factors showed an interaction between Infant Sex and Rank (F (1, 27) = 9.11, p = .005, η_p^2 = .25). Similar to Face AOIs, high-ranking males (M=.60) looked significantly more at the eyes than low-ranking males (M = .23, p = .001, d = 1.52), but there was no difference between high- and low-ranking females (M = .23 and M = .34, p = .37; Figure 2). There were no other main effects or interactions. Isolating the Expression phase showed similar results: we observed a main effect for Infant Sex (F (1, 78) = 6.09, p = .020, η_p^2 = .18) and an interaction between Infant Sex and Rank (F (1, 27) = 4.85, p = .036, η_p^2 = .15). High-ranking males looked more at the eyes of the avatar during the expression phase than low-ranking males (M = .58 vs. M = .33, p = .017, d = 1.05), but there was no difference between high- and low-ranking females (M = .21 vs. M = .30, p = .45).

Comparison to Nursery-Reared Infant Macaques

We compared these data described above with the previously collected data on 48 nursery-reared infants (Simpson et al., 2016). These infants were separated from their mothers on the day of their birth, and they were reared in a nursery facility for unrelated studies where they had constant visual, auditory, and olfactory, but not physical contact, to other infants of similar age until ~37 days old (for details on rearing and testing procedures of nursery-reared infants, see Simpson et al., 2016.). Infants were tested between 10-28 days old using the same procedure described for mother-reared infants, the only difference being that nursery-reared infants were shown only one video per day. Data trimming of values greater than two standard deviations from the mean left a total of 40 infants for analysis. Mother's rank information was available on 33 infants. The final data set contained 16 infants from low-ranking (7 female) and 17 infants from high-ranking (6 female) mothers. Only analyses that involved effects or interactions with rearing condition are reported below.

Using the Face AOI, we ran a repeated measure ANOVA using Gesture (LPS, Fear, Threat) and Phase (Expression, Still, Turn) as within-subjects factors and Infant Sex (Male, Female), Rank (High, Low), and Rearing (Mother, Nursery) as between subjects factors. We found a main effect for Rearing (F (1, 57) = 58.14, p < .001, η_p^2 = .51), with nursery-reared infants (M = 2.17) looking significantly more than mother-reared infants (M = 1.16). Using just the Expression data (LPS, Fear, Threat), a repeated measure ANOVA with Infant Sex (Male, Female), Rank (High, Low), and Rearing (Mother, Nursery) as between subjects factors again showed a main effect for Rearing (F (1, 57) = 54.11, $p < .001$, $\eta_p^2 = .49$) as well as an interaction between rearing and infant sex (F (1, 57) = 5.26, p = .026, $\eta_p^2 = .08$). Post-hoc comparisons showed that nursery-reared females' looking duration at faces was significantly longer than nursery-reared males' (females: M = 2.51, males: M = 2.03, p = .020, d = .85) but there was no difference in looking duration between mother-reared females and males (females: M = 1.12, males: M = 1.30, p = .39).

When considering data just from the eye region, a repeated measure ANOVA using Gesture (LPS, Fear, Threat) and Phase (Expression, Still, Turn) as within-subjects factors and Infant Sex (Male, Female), Rank (High, Low), and Rearing (Mother, Nursery) as between subjects factors again showed a main effect for Rearing (F (1, 56) = 30.93, $p < .001$, $\eta_p^2 = .36$) and an interaction between Infant Sex and Rearing (F (1, 56) = 8.71, p = .005, $\eta_p^2 = .14$). Nursery-reared females (M = .82) looked more at the eyes than nursery-reared males (M = .58, p = .008, d = 1.00) but there was no difference between mother-reared females (M = .28) and males (M = .41, p = .16). Isolating the expression phase, a repeated measure ANOVA with Gesture (LPS, Fear, Threat) as within subjects factor and Infant Sex (Male, Female), Rank (High, Low), and Rearing (Mother, Nursery) as between subjects factors showed a main effect for Rearing (F (1, 56) = 23.15, $p < .001$, $\eta_p^2 = .29$) and an interaction between Infant Sex and Rearing (F (1, 56) = 13.36, p = .001, $\eta_p^2 = .19$). Nursery-reared females (M = .79) looked significantly more at the eyes than nursery-reared males (M = .52, p = .004, d = 1.08), but mother-reared females (M = .26) looked significantly less at the eyes than mother-reared males (M = .45, p = .034, d = .80; Figure 3).

Infant observations

To determine whether mother-reared infants' exposure to faces was associated with their sex and rank, we ran three linear regressions on a subset of infants (N=20) using mothers' gazing at infants, infants' gazing at mothers, and mutual gaze between mothers and infants as outcomes, and mother's rank and infant sex as predictors. Only mothers gazing at infants rendered a significant model ($R^2 = .308$, $F(2,19) = 3.79$, $p = .044$). Male infants were associated with significantly more gazing from mothers ($\beta = 1.867$, $t(17) = 2.70$, $p = .015$), but there was no effect of rank ($\beta = .352$, $t(17) = .51$, $p = .62$). Unfortunately, avatar data were available from only N=12 infants, giving us insufficient statistical power to investigate any direct associations with mother-infant gaze interactions.

Discussion

Our results indicate that individual differences in mother's rank and infant sex affect how infants view emotional facial expressions. Male infants may be more susceptible to certain environmental influences – particularly certain social influences – than females: while no effect of dominance rank was found for female infants, male infants looked more at faces, especially the eye region, if their mothers were high-ranking rather than low-ranking. Previous studies have reported that high-ranking rhesus macaque mothers are often less restricting towards their infants than low-ranking mothers (White & Hinde, 1975), and that high-ranking mothers are less likely to suffer reproductive costs compared to low-ranking mothers (Redondo, Gomendio, & Medina, 1992). Previous studies have also suggested that in rhesus macaques, maternal investment is greater in sons than in daughters (Bercovitch, Widdig, & Nürnberg, 2000; Hinde, 2007; Tomaszycki, Davis, Gouzoules, & Wallen, 2001), likely due to skewed male reproductive output

(Trivers & Willard, 1973; Widdig, Bercovitch, Streich, Sauermann, Nuernberg, & Krawczak, 2004). Thus, it appears that high-ranking mothers are not only in a better position to invest in their offspring, they are also more likely to invest in their male offspring – which can not only affect infants' physiology (Bercovitch, Widdig, & Nürnberg, 2000), but also, as we show here, infants' attention.

Our observations on mother-infant interactions partially confirm this idea: mothers of sons were more likely to look at their infants than mothers of daughters, but we did not find an effect of rank on mother-infant interactions, similar to previous reports (Dettmer et al., 2016). Increased facial contact is likely to have led to increased familiarity and experience with faces in male infants, thereby affecting infants' processing strategies. These strategies may be of value in their later life: given the risk of mortality following male dispersal (Trefilov, Berard, Krawczak, & Schmidtke, 2000), enhanced socio-cognitive abilities may be advantageous when trying to integrate into a new social group. Even as adults, male rhesus macaques show sensitivity to facial information: males will forego a juice reward to view pictures of high-ranking monkeys, but not low-ranking monkeys (Deaner, Khera, & Platt, 2005). These skills may be based on perinatal experience and reinforced through mother-infant interactions.

Even though there was some indication that infants looked more at affiliative (lipsmacking) and aggressive (threat) facial displays than fearful facial displays, infants largely appeared to treat all facial displays in the same way, and there were no interactions with infant sex or rank. The risk of receiving aggression in neonatal infant rhesus macaques is close to zero (Kulik, Amici, Langos, & Widdig, 2015), indicating that young infants are buffered from aggression. Previous research has reported increased vigilance to threat faces in high-ranking and more protective mothers compared to low-ranking and less protective mothers in 9-mo old, but not 3-mo old infant macaques (Mandalaywala et al., 2014). Other studies have observed behavioral reactions to threatening faces emerging at about 3-mos old (Sackett, 1966). These findings suggest that at 1-mo old, infants in the current study were simply too young to be expected to show behavioral responses to threat faces, potentially due to not having had enough experience with facial gestures. In humans, vigilance towards threat is apparent by 6-12-mos old (Grossman, Striano, & Friederici, 2007), but newborns already show a preference for happy faces (Farroni, Menon, Rigato, & Johnson, 2007). This preference for happy faces may not be surprising since this facial expression is likely common around newborns (Farroni et al., 2007). Yet in rhesus macaques, mothers are known to frequently lipsmack at their infants in the first month of life (Ferrari, Paukner, Ionica, & Suomi, 2009) which as the current study shows, did not result in preferential looking at lipsmacking faces. Future research should address how processing of emotional facial displays develops, taking into account individual differences in infants and mothers.

When compared to infants who were reared by human caregivers in a primate nursery setting (Simpson et al., 2016), mother-reared monkeys showed an interesting contrast. First, longer overall looking times in nursery-reared monkeys can likely be attributed to nursery-reared infants' daily interactions with human caretakers, including familiarity with the testing situation. In addition, monkey facial gestures as displayed by the avatar were likely to have higher novelty value for nursery monkeys compared to mother-reared monkeys, which could also have affected their interest in these gestures. Second, unlike mother-reared infants, nursery-reared monkeys showed no effects of maternal dominance rank on looking patterns. Even though dominance rank can affect monkeys' behavioral tendencies and glucocorticoid regulation (Kohn, Snyder-Mackler, Barreiro, Johnson, Tung, & Wilson, 2016), immune regulation (Snyder-Mackler, Sanz, Kohn, Brinnkworth, Morrow, Shaver, Grenier, Pique-Regi, Johnson, Wilson, Barreiro, & Tung, 2016), learning (Bunnell, Kenshalo Jr, Allen, Manning & Sodetz, 1979), and even epigenetic changes during prenatal development (Massart, Suderman, Nemoda, Sutti, Ruggiero, Dettmer, Suomi, & Szyf, 2017), this lack of an effect for dominance rank in nursery-reared monkeys in the current study suggests that 1) postnatal rank inheritance is more of a social rather than a biological construct (Wooddell et al., *in press*); and 2) facial processing may be influenced by social rather than biological mechanisms, particularly via interactions with the mother or caregiver.

On the other hand, sex differences in visual social attention were apparent in both nursery- and mother-reared infants. In nursery-reared infants, females looked more at faces than males, and especially at the eye region, which, given the carefully controlled environment of these infants, has previously been interpreted to be an experience-independent sex difference (Simpson et al., 2016), i.e., likely to have a biological origin. Similar sex differences in visual social attention have been reported in human infants (e.g. Connellan, Baron-Cohen, Wheelwright, Batki, & Ahluwalia, 2000; Hittelman & Dickes, 1979), although uncertainty still remained as to the degree to which differential treatment by caregivers (Lewis, 1972; Tronick & Cohn, 1989; Lytton & Romney, 1991) may influence infants' behavior. However, in the current study, this influence could be measured: by comparing nursery-reared infants with mother-reared infants, it was revealed that, contrary to nursery-reared infants, mother-reared male infants looked more at the eye region than mother-reared female infants. Thus, the early social environment appears to have had a significant impact on infants' visual social attention in a sex-dependent manner in the first month of life. While factors such as high visual contrast draw infants' attention to the eye region in human infants (e.g., Farroni et al., 2005) and also likely in monkey infants (Wilson & Goldman-Rakic, 1994; Paukner, Bower, Simpson, & Suomi, 2013), the fact that sex x rearing interactions emerged in attention to the eye region suggests a more complex mechanism underlying early visual attention. Future studies should focus on elucidating the exact nature of the biological mechanism driving visual social attention, as well as the ways in which the social environment impacts and shapes not only the mechanism but also future behavioral outputs (e.g., Arcaro, Schade, Vincent, Ponce, & Livingstone, 2017).

Our study provides further evidence that individual variability in infants' environment, can affect infants' cognitive and behavioral development. Thus, these factors are important to consider for studies exploring infants' visual social attention as well as for studies exploring primate evolutionary history or testing animal models of human cognitive processes. Examining how individual differences in visual social attention affect later socio-cognitive behavior and cognition are important directions for future research.

Notes

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Figure captions

Figure 1. Average fixation duration (in seconds) at the avatar's face across all gestures (LPS, fear grimace, threat) by infant sex and rank. All infants were mother-reared. Error bars indicate standard errors, asterisks indicate $p < .01$.

Figure 2. Average fixation duration (in seconds) at the avatar's eyes across all gestures (LPS, fear grimace, threat) by infant sex and rank. All infants were mother-reared. Error bars indicate standard errors, asterisks indicate $p = .001$.

Figure 3. Average fixation duration (in seconds) at the avatar's eyes in the gesture phase across all gestures (LPS, fear grimace, threat) by infant sex and rearing. Error bars indicate standard errors, single asterisk indicates $p < .05$, double asterisks indicate $p < .01$.

Supplemental Files

Video S1. A 29-day-old mother-reared male watches the avatar displaying lipsmacking gestures. Red dots indicate fixations, larger dots indicate longer fixations.

Video S2. A 29-day-old mother-reared male watches the avatar displaying a fear gesture. Red dots indicate fixations, larger dots indicate longer fixations.

Video S1. A 29-day-old mother-reared male watches the avatar displaying a threat gesture. Red dots indicate fixations, larger dots indicate longer fixations.

Supplemental Figure S1. Illustration of the Areas of Interest (AOIs) used for analyses.