Evolutionary relevance and experience contribute to face discrimination in infant macaques (*Macaca mulatta*)

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Abstract

In human children and adults, familiar face types—typically own-age and own-species faces—are discriminated better than other face types; however, human infants do not appear to exhibit an own-age bias, but instead better discriminate adult faces, which they see more often. There are two possible explanations for this pattern: Perceptual attunement, which predicts advantages in discrimination for the most-experienced face types; additionally or alternatively, there may be an experience-independent bias for infants to discriminate own-species faces, an adaptation for evolutionarily relevant faces. These possibilities have not been disentangled in studies thus far, which did not control infants' early experiences with faces. In the present study, we tested these predictions in infant macaques (*Macaca mulatta*) reared under controlled environments, not exposed to adult conspecifics. We measured newborns' (15–25 days; *n* = 27) and 6- to 7-month-olds' (*n* = 35) discrimination of human and macaque faces of three ages—young infants, old infants, and adults—in a visual paired comparison task. We found that 6- to 7-month-olds were the best at discriminating adult macaque faces; however, in the first few seconds of looking, additionally discriminated familiar face types—same-aged peer and adult human faces—highlighting the importance of experience with certain face categories. The present data suggest that macaque infants possess both experience-independent and experientially tuned face biases. In human infants, early face skills may likewise be driven by both experience and evolutionary relevance; future studies should consider both of these factors.

Humans appear better at discriminating facial identity for certain face types, including faces of familiar races relative to other races (for reviews see Anzures et al., 2013; Meissner & Brigham, 2001), faces of familiar ages relative to other ages (for a review see Rhodes & Anastasi, 2012), faces of a familiar gender relative to the other gender (e.g., Wright &

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Sladden, 2003), and faces of their own familiar species relative to other species (for a review see Scott & Fava, 2013). However, the way in which this expertise develops in human and primate infants remains largely unknown, as does the extent to which the quality, quantity, and timing of experiences with different face types contribute to this skill.

Experience May Drive Face Biases: Perceptual Attunement of Face Discrimination

Face biases may reflect perceptual attunement, a developmental pattern in which discrimination improves to a greater extent for face types with which infants have more experience—typically the same species, gender, race and age as the primary caretaker (Maurer & Werker, 2013; Rennels & Davis, 2008; Sugden, Mohamed-Ali, & Moulson, 2013). This improvement in discrimination may also be coupled with a decline in discrimination for uncommon face types (Nelson, 2001; Pascalis, de Haan, & Nelson, 2002; although see Flom, 2014; Simpson, Jakobsen, Fragaszy, Okada, & Frick, 2014). Empirical evidence supports this model in humans: between 3 and 6 months of age, infants appear to discriminate a variety of face types equally, including faces of other species, but by 9 months there is an apparent decline in discrimination of uncommon face types (Scott & Fava, 2013). Similarly, while 3-month-old infants discriminate adult and infant faces, 9-month-old infants appear to only discriminate adult faces (Cassia, Bulf, Quadrelli, & Proietti, 2014). In addition, 3-year-olds with older siblings equally discriminate child and adult faces, while children without older siblings better discriminate adult faces (Cassia, Pisacane, & Gava, 2012). In fact, a recent review concludes that there is little evidence of an own-age bias across ages, and that biases for differently aged faces reflect participants' experiences with individuals of those ages (Macchi Cassia, 2011).

A few studies have systematically manipulated infants' face experiences, such as through training with unfamiliar face categories (e.g., species: Pascalis et al., 2005; races: Heron-Delaney et al., 2011a). For example, infants exposed daily to individually named monkey faces retain discrimination of novel monkey faces at 9 months, whereas infants exposed to faces without individual names fail to retain this discrimination (Scott & Monesson, 2009), demonstrating plasticity in face discrimination. Perhaps more importantly, it appears that exposure must be accompanied by individuation, identifying faces at an individual level (e.g., individual names).

Functionalist Approach: Evolutionary Predispositions in Face Discrimination

Alternatively or additionally, there may be predispositions to discriminate certain face types independently of experience. The so-called functionalist theory suggests that face-processing skills reflect age-appropriate developmental goals (Scherf & Scott, 2012). Young primate infants are highly dependent on the primary caregiver (usually the mother), and their biggest threat is the absence of caregivers or the presence of strangers (Boyer & Bergstrom, 2011; Hrdy, 1979; Scarr & Salapatek, 1970). Thus, young infants may be sensitive to adult female faces due to a need to distinguish the mother's face from strangers' faces. Indeed, human

newborns—whose primary caregiver is the mother—prefer their mother's face to a stranger's face (e.g., Field, Cohen, Garcia, & Greenberg, 1984). According to this approach, infants may be born with an attraction to own-species adult faces. Consistent with this hypothesis, human newborns attend more to pictures of humans than nonhuman primates (Di Giorgio, Leo, Pascalis, & Simion, 2012; Heron-Delaney, Wirth, & Pascalis, 2011b) and attend more to pictures of adult faces compared to child faces (unpublished data). Such early preferences might be a consequence of infants' face templates, present from birth (Johnson, Dziurawiec, Ellis, & Morton, 1991), which may resemble adult faces more than infant or child faces. With age, as infants become more mobile, they need to distinguish a wider variety of faces, as they interact with an increasing number of individuals. To our knowledge, there are no studies of facial identity discrimination of own-species or own-age biases in infant populations with controlled postnatal exposure to own-species faces, which could disentangle the contributions of experience and adaptive predispositions.

Nonhuman Primate Infant Model

A limitation in previous studies with human infants is that the face types that are the most evolutionarily relevant to infants—adult human faces—are also the face types that they are exposed to the most, making it challenging to disentangle the contributions of evolutionary predispositions that may be independent of experiences, with those contributions of their early social environments (e.g., exposure to certain species or ages). This challenge of controlling individuals' experiences is one that can be overcome in studies with nonhuman primates. Infant macaques are a good species for exploring early face processing, because, like human infants, they spend much time looking at the eye regions of faces (Mendelson, Haith, & Goldman-Rakic, 1982) and imitate facial gestures (Ferrari et al., 2006). By adulthood, like humans, they demonstrate an own-species face bias (Humphrey, 1974; Pascalis & Bachevalier, 1998) and spend more time scanning internal than the external features of conspecifics' faces (Keating & Keating, 1982).

Developmental studies in macaques thus far have not clearly supported either experience-driven biases or evolutionary predispositions. Consistent with perceptual attunement, macaque infants prevented from seeing faces for the first 6–24 months of life discriminated human and monkey faces equally prior to face exposure, but after exposure to either human or monkey faces for one month, infants retained discrimination for only the familiar species (Sugita, 2008). This finding demonstrates plasticity and suggests perceptual attunement may be delayed without relevant input. However, there is also evidence of genetically determined own species preferences in macaques (Fujita, 1990; Pascalis, Petit, Kim, & Campbell, 1999; Sacket, 1970; Scott & Fava, 2013). For example, macaque newborns exposed only to the faces of same-aged peers prefer adult macaque faces with normally arranged features compared to linearly arranged features, but do not show this preference for human faces (Paukner, Bower, Simpson, & Suomi, 2013). Furthermore, these infants prefer adult female to male macaque faces, but do not show a sex preference for human faces (Paukner, Huntsberry, & Suomi, 2010). Given this conflicting evidence, the relative contributions of experience and evolutionarily predispositions in infancy are unclear, and studies with infant macaques examining own-face biases under controlled environments could be valuable, allowing us to test the contribution of experience.

Purpose and Predictions

We tested face discrimination biases in infant rhesus macaques with controlled, atypical exposure to faces (i.e., exposure to same aged peers, but not adults). Our primary goal was to test whether developmental changes in face discrimination are consistent with perceptual attunement (i.e., experience-driven) and/or the functionalist approach (i.e., evolutionary predispositions), each of which makes different testable predictions. Specifically, if experience drives early face biases, infants would exhibit superior discrimination of familiar face types: adult human faces and same-aged peer faces. Alternatively or additionally, the functionalist approach predicts that infants of both ages would exhibit superior discrimination of own-species adult faces, compared to other face types, independent of early experience. We also predicted that differences in discrimination across face types may be the consequence of differential face viewing patterns during the familiarization (i.e., increased proportion of time looking to more informative regions of the face, such as the eyes). To test these predictions we measured discrimination and viewing patterns of faces varying in their evolutionary-relevance and familiarity: infant and adult faces of macaques and humans. This is the first study, to our knowledge, to test these models in infants with controlled early experiences.

Methods

The study was carried out in accordance with the Guide for the Care and Use of Laboratory Animals and the Animal Welfare Act.

Subjects

We tested two groups of infant rhesus macaques (*Macaca mulatta*): 15- to 25-day-olds ($n = 27$, 16 males; hereafter referred to as newborns), and 6- to 7-month-olds (179–209 days; $n = 35$; 21 males). Infants were healthy and were separated from their mothers on the first day of life, after which they were reared in a nursery facility for unrelated studies. Infants were individually housed in incubators (51 cm × 38 cm × 43 cm) for the first two weeks of life and in metal cages thereafter. Both housing arrangements contained an inanimate surrogate covered with fleece fabric as well as loose pieces of fleece fabric and various rubber toys. For the first month of life, infants could see and hear, but not physically contact, other infants of similar age. From 37 days of age until ca. 8 months of age, infants were either housed in small groups (3–5 individuals; peer-reared; $n = 19$), or were housed individually and received 2 hours per day of playtime in small groups (3–5 individuals; surrogate-reared; $n = 16$), 5 times a week (for further rearing practices see Shannon, Champoux & Suomi, 1998). In both rearing conditions, infants had visual access to all other infants in the nursery, typically 18 to 20 individuals. For the first month, human caretakers were present for 13 hours each day, and interacted with infants every 2 hours for feeding and cleaning. Caregivers wore personal protective equipment, including goggles, masks covering the nose and mouth, and hats, so only the eyes were visible (see Figure 1 in Paukner, Huntsberry, & Suomi, 2010). Infants were tested in a variety of socio-cognitive assessments, which involved exposure to full-face human caretakers. Infants in the present study had no exposure to adult macaques. While the newborns had very little face exposure, primarily

only to same-age peers (i.e., young macaque infants), 6- to 7-month-olds had more face experiences, especially with older infant macaques.

Apparatus

We recorded infants' eye movements using corneal reflection, detected by a Tobii T60XL eye tracker, a remote 24-inch monitor with integrated eye tracking technology and sampling rate of 60 Hertz. We collected and summarized the data using Tobii Studio software (Tobii Technology, Sweden).

Stimuli

Infants viewed 60 distinct faces total, 10 unique individuals from each of six face types: human adult (age 20–40 years; all females), older human infant (age 1–3 years; 5 female), younger human infant (age 1–4 months; 5 female), macaque adult (age 5–29 years; all females), older macaque infant (age 5–9 months; 5 female), and younger macaque infant (7 days old; 5 female). These ages were chosen for the face stimuli because humans and macaques are comparable in their neural development at these ages (e.g., Clancy, Darlington, & Finlay, 2001; Workman, Charvet, Clancy, Darlington, & Finlay, 2013). Subjects viewed each image in only one test session. Monkey faces were from a colony at the National Institutes of Health Animal Center in Poolesville, Maryland. Some stimuli were used in previous studies (Bower, Suomi, & Paukner, 2012; Paukner et al., 2010). All individuals were unfamiliar to subjects. Human adult faces were from the NimStim database (Tottenham et al., 2009), and faces of young and older human infants were collected from internet searches. Images were in color, forward facing, exhibiting neutral closed-mouth expressions, and making eye contact with the camera. Photos were paired to match as closely as possible (e.g., color, brightness, contrast), standardized on interpupil distance, sized 800 pixels or 15.2 cm tall (ca. 14.4° visual angle), and cropped in a circle to ensure inner facial features were visible but outer contours (e.g., chin, ears) were not, Figure 1A.

Procedure

One experimenter held the infant 60 cm from the screen. Each infant was calibrated for each test session using animated short videos with sounds displayed at five points on the screen, attracting infants' attention (without training).

Infants viewed one of the six face types per day, in a predetermined counter-balanced order. Each infant received five face pairings per day, each one once, within each of six face sets, for a total of 30 trials across six days. Testing continued daily until infants viewed all face sets. A visual paired comparison task (Fagan, 1970) was employed using the continuous familiarization technique (Fantz, 1964): infants were first familiarized with a face for 10 sec of cumulative looking, and then viewed that familiar face next to a novel face (of the same species and age) for 5 sec of cumulative looking. We counterbalanced the viewing order of each face type, each face's role as familiar or novel and left-right positions. Trial order was semi-random (four differently ordered sets for each face type; 24 conditions).

Data Analysis

We created areas of interest (AOIs) around each face (Figure 1B). We extracted data using the Tobii filter in Tobii Studio (velocity: 35 pixels/window; distance threshold: 35 pixels). In test trials we measured infants' look durations to the novel and familiar faces—a measure of visual recognition memory in infants (Fagan, 1970)—to determine whether discrimination varied as a function of the infants' face experience. We also explored the initial time course of infants' looking by measuring the proportion of time looking to the novel face during the first three seconds of looking as this sometimes yields early encoding preferences that are not evident when looking across the entire trial duration (Hunter & Ames, 1988; Méary, Li, Li, Guo, & Pascalis, 2014). Finally, given that the eyes, relative to other facial features, appear to carry the most relevant information for facial identity discrimination (de Lissa, McArthur, Hawelka, Palermo, Mahajan, & Hutzler, 2014), we examined whether infants' viewing patterns on faces during the familiarization predicted their subsequent face discrimination by measuring the relative duration of time fixating on the eye and mouth regions with an eye-mouth index (EMI) (Merin, Young, Ozonoff, & Rogers, 2007) and testing whether the EMI during encoding predicted face discrimination (Goldinger & Papesh, 2009; Kawakami, Williams, Sidhu, Choma, Rodriguez-Bailón, Cañadas, Chung, & Hugenberg, 2014). We predicted that there would be a positive association between EMI for face types that were higher, compared to lower, in ecological validity (adult monkey > adult human) or familiarity (infant monkey > infant human), and that the association for ecologically relevant stimuli would be higher in newborns, whereas the familiarity association would be stronger in 6- to 7-month-olds who have more extensive experience.

Results

The time to reach the cumulative look duration did not vary across face types (age or species), $ps > .10$. We assessed whether there were effects of rearing (peer-reared, surrogate-reared) or sex. We found no effects of these factors ($ps > .05$), so subsequent analyses excluded them.

To determine whether discrimination varied as a function of face type, we examined the total time looking to novel and familiar faces, using a 2 (Face type: novel, familiar) × 2 (Face species: human, macaque) × 3 (Face age: adult, old infant, young infant) × 2 (Infant age: newborn, 6- to 7-month-old) mixed design ANOVA, which revealed a main effect of Face type, $F(1, 60) = 26.67$, $p < .001$, $\eta^2_p = .31$, in which there was, overall, more looking to the novel faces ($M = 1.46$ sec, $SD = .40$) compared to the familiar faces ($M = 1.25$ sec, $SD = .33$). To explore further, we assessed within each age group whether looking to each face type differed between novel and familiar faces with paired-sample t tests (Bonferroni correction: p = .05/6 = .008). While newborns' looking did not differ from chance for any face type, $t(26) < 2.51$, $ps > .01$, the 6- to 7-month-olds looked for a greater proportion of time at the novel adult macaque faces, $t(34) = 3.04$, $p = .005$, $d = .51$, but no differences from chance for other face types, $ps > .01$ (Bonferroni criteria: $p < .008$), Table 1. There were no other significant main effects or interactions, $ps > .05$.

Next, we explored the time course of viewing preferences by calculating the proportion of cumulative looking to the novel face, out of the total looking to both faces, for the first three

seconds of looking (three time points: first 1 sec, first 2 sec, and first 3 sec), Table 2. We then carried out one-sample t tests to determine at which times, if any, looking differed from chance (Bonferroni correction: $p = .05 / 18$ [6 face types × 3 time points] = .003). While there were no looking preferences in newborns, 6- to 7-month-olds looked to the novel faces a greater proportion of the time for the first one and two seconds of looking, for human adult faces ($t(33) > 3.57$, ps ≤ .001, $ds > .61$), and in the first two seconds of looking for monkey adult faces ($t(32) = 3.28$, $p = .003$, $d = .57$), and same-aged peer (older infant) monkey faces ($t(34) = 4.03$, $p < .001$, $d = .68$). There were no other significant differences, $ps > .003$.

To test whether differences in the viewing patterns during the familiarization may account for differences in face discrimination, we examined infants' looking durations to the eye and mouth regions during the familiarization. We created an eye-mouth-index (EMI), using Eyes / (Eyes + Mouth), to compare looking durations to both areas concurrently (Merin, Young, Ozonoff, & Rogers, 2007). A value of 0.5 indicates equal looking to the eye and mouth regions, while values closer to 1 indicate more looking to the eyes and values closer to 0 indicate more looking to the mouth. We examined the EMI using a 2 (Face species: human, macaque) × 3 (Face age: adult, old infant, young infant) × 2 (Infant age: newborn, 6- to 7-month-old) mixed design ANOVA, which revealed an interaction between Face age × Infant age, $F(2, 120) = 4.29$, $p = .016$. To explore further, we assessed within each age group and face type whether the EMI differed from chance with one-sample t-tests (Bonferroni correction: p = .05/6 = .008). This analysis revealed that EMIs were greater than chance for newborns only for adult faces (human adult: $M = .69$, $SD = .21$; monkey adult $M = .66$, $SD = .21$), but for 6- to 7-month-olds, EMIs were greater than chance across all face types ($M = .63$ to .67, $SD = .15$ to .21), $ps < .008$, Table 1. There were no other significant differences, $ps > .05$.

Finally we assessed whether attention to the eyes at encoding predicted subsequent discrimination for face types that were either high or low in ecological validity or familiarity. We computed difference scores for EMIs to compare stimuli that varied in their ecological relevance (EMI_{adult}: adult human subtracted from adult monkey), and familiarity (EMI_{infant}: infant human subtracted from infant monkey). Higher scores on EMI_{adult} therefore indicate a stronger preference for the eyes in an ecologically relevant stimulus (monkey adult faces) relative to an ecologically irrelevant stimulus (human adult faces). In contrast, higher scores on EMI_{infant} indicate a stronger preference for the eyes in a familiar stimulus (monkey infant faces) relative to an unfamiliar stimulus (human infant faces). We then computed indices of face discrimination in test trials, defined as the proportion of time looking to the novel face out of the total time looking to both faces. We computed difference scores for discrimination: one for ecological relevance (adult human subtracted from adult monkey), $PropNov_{adult}$, and one for familiarity (infant human subtracted from infant monkey), $PropNov_{infant}$. Higher scores on $PropNov_{adult}$ therefore indicate a relatively stronger discrimination for an ecologically relevant stimulus (monkey adult faces) relative to an ecologically irrelevant stimulus (human adult faces). In contrast, higher scores on $PropNov_{infant}$ indicate a relatively stronger discrimination for a familiar stimulus (monkey infant faces) relative to an unfamiliar stimulus (human infant faces).

For each subject age group (newborns, 6- to 7-month-olds) we carried out two regressions, one for adult faces and one for infant faces, by entering the respective EMI into a regression to see if it would predict face discrimination, i.e., novelty preferences, for those face types. For the newborns, neither regression was significant, (adult: $b = .088$, $p = .320$; infant: $b = -.149$, $p = .742$). For the 6- to 7-month-olds, there was no effect for the adult faces ($b = .074$, $p = .591$), but there was an effect for the infant faces ($b = .503$, $p = .010$). This indicates that, in the 6- to 7-month-olds, EMI_{infant} (a greater proportion of time looking to the eye region of a familiar face type, infant monkeys, relative to an unfamiliar face type, infant humans), predicted $PropNov_{infant}$ (face discrimination for the familiar face type, infant monkeys, relative to the unfamiliar face type, infant humans).

Discussion

This is the first study, to our knowledge, to attempt to assess facial identity discrimination of own-species and own-age face biases in infants with controlled postnatal face exposure. Our goal was to begin to disentangle some of the contributions of adaptive predispositions and experience to facial identity discrimination in early infancy. We set out to test two developmental models, one that proposes face recognition is experience-driven (i.e., perceptual attunement; Scott & Fava, 2013) and one that proposes face recognition may be attuned for ecologically relevant face types that may aid infant survival, based on a functionalist approach (Scherf & Scott, 2012). We found some support for both models; our results did not clearly favor one model. It seems that both evolutionary-predispositions and experience may play important roles in early face discrimination abilities. In our view, nursery-reared infant monkeys, with controlled postnatal environments, offer a promising population for testing these models and we suggest future avenues for research.

We found that 6- to 7-month-old infant macaques discriminated adult macaque faces despite no experience with adult macaques, while they failed to show strong evidence of discrimination of the other face types, including familiar face types (e.g., adult human faces, same-age peer faces). Given that adult conspecifics are a primary threat for infant macaques, infants may have evolved predispositions to be particularly sensitive to adult macaque faces, a necessity for distinguishing adults who may provide support from those who may be dangerous (i.e., infanticide; Hrdy, 1979; Maestripieri, 1995; Thompson, 1967). Macaque infants are dependent on their primary caregiver (usually the mother) for food and protection (Boyer & Bergstrom, 2011; Hrdy, 1979; Scarr & Salapatek, 1970). In fact, macaque mothers appear aware that other adults may be threats to their infants, even when they are not threats to themselves (Maestripieri, 1995), and during agonistic encounters, mothers and female relatives protect infants (Berman, 1980). Given these selective pressures, infant monkeys may be predisposed to be particularly good at recognizing adult conspecifics' faces.

These findings are consistent with previous reports of own-species biases in nursery-reared infant macaques. For example, infant macaques prefer female compared to male faces when viewing macaque but not human faces (Paukner et al., 2010), and prefer faces with normally configured inner features (i.e., eyes above nose and mouth) compared to linearly arranged features, in macaque but not human faces (Paukner et al, 2013). Moreover, even rhesus macaques reared in isolation demonstrate own-species preferences, suggesting that social

experience may be unnecessary for species-typical responses to conspecifics (Sackett, 1966). The present study extends these findings, offering converging evidence that, independent of experience, infant monkeys are predisposed to better discriminate ecologically relevant types of faces.

While infants in the present study appeared to exhibit the strongest face discrimination for adult monkey faces, we also found that, early on in stimulus viewing (i.e., first seconds of face viewing), infants appeared to exhibit greater sensitivity for familiar face types. Specifically, in the first two seconds of cumulative looking, 6- to 7-month-old monkey infants appeared not only to discriminate adult monkey faces, but also to discriminate human adult and same-aged peer (old infant monkey) faces. Same-aged peers are increasingly important to infants of this age, so this result is consistent with an evolutionary perspective; however, human adult faces are not evolutionarily important for infant macaques, so this result appears inconsistent with an experience-independent evolutionary perspective. At first these results may see contradictory with our finding of apparently better discrimination of adult monkey faces when looking across the entire test trial. On the one hand, these viewing preferences in the first couple of seconds suggest infants' experiences with human caretakers and same-aged peers may have improved their discrimination skills for these face types. This interpretation is consistent with reports that human infants' perceptual systems may be tuned by experience with certain face types, including faces of familiar species (Scott & Fava, 2013) and familiar ages (Rhodes & Anastasi, 2012). On the other hand, the fact that these preferences for familiar faces were only evident in the first two seconds of looking, but were not consistently strong across the test trial, may indicate that the infants in the present study simply did not have robust familiarity-driven face discrimination. These infants, who were only 6 to 7 months of age, may not yet have had enough experiences to fully fine-tune their face discrimination skills. Testing macaque infants at a later age, after a year or more of exposure to faces of a certain category, may reveal more robust experience-driven face discrimination abilities.

Unlike the 6- to 7-month-olds, we found no evidence of face discrimination in newborn monkeys. We did, however, find both newborns and 6- to 7-month-olds overall exhibited a preference for novel, compared with familiar faces, suggesting there may be preferences emerging early in development, but they were not strong enough to be evident with the present task. Of course, newborns' failure to discriminate cannot be attributed to a lack of ability, as it may simply reflect that this was an insensitive measure. For example, the familiarization period may have been too short (e.g., Bachevalier, Brickson, & Hagger, 1993), or faces may need to be socially relevant for individuation (e.g., Scott & Monesson, 2009). In addition, while the present study employed a passive task, newborns monkeys appear to distinguish identities of individuals with whom they actively engage (Simpson, Paukner, Sclafani, Suomi, & Ferrari, 2013). A careful inspection of the newborn data revealed that a couple of face types—the young and old infant humans—showed some trends of more looking to the novel faces, which approached but failed to reach statistical significance with Bonferroni corrections. While it is possible that increasing our sample size may have allowed us to detect a small difference here, it is also possible that this is a Type I Error. In our view, rather than expanding our sample size using the present paradigm, future

efforts would be better spent attempting to use different methodologies with newborn infants that may be better suited for their early visual/attentional capacities.

We tested the possibility that infants' face viewing patterns during familiarization might explain their differences in discrimination. That is, if infants were attending to the faces differently during familiarization, this may have allowed them to better recognize some face types. To test this, we analyzed the relative time infants spent looking at the eyes and mouths, an index of attention to the most information region of the face, which revealed that viewing patterns during familiarization could not account for differences in discrimination. In fact, the 6- to 7-month-olds looked more to the eyes across all face types.

We did, however, find that newborns in the present study looked more to the eyes than the mouth only for adult faces, of both humans and monkeys. This result is unlikely to be due to newborns' experiences, since they have no previous experience with adult macaque faces and, at this age, only limited experience with adult human faces (caregivers). Rather, it seems more likely that newborn macaques exhibit experience-independent preferences for the most informative region (eye region) of adult faces, as they are the most evolutionarily relevant face types for newborns.

We also found developmental increases in interest in the eye region of faces. Indeed, while human neonates appear to already possess a specialized mechanism for detecting eyes (e.g., Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000), this eye preferences increases across early infancy (e.g., Maurer & Salapatek, 1976), and appears especially strong for the eyes of conspecifics by 3 months of age (Dupierrix et al., 2014). Previous work in infant macaques likewise demonstrates a preference for the eye region of faces in the first two months of life (Mendelson et al., 1982; Paukner, Simpson, Ferrari, Mrozek, & Suomi, 2014). The present results, however, extend these findings, revealing developmental increases in sensitivity to the eye region in macaque infants, from the newborn period to 6- to 7-months of life.

Finally, because the eyes, relative to other facial features, may carry the most relevant information for facial identity discrimination (de Lissa et al., 2014), we predicted and found some support for our prediction that individual differences in EMIs would predict subsequent differences in face discrimination. While we detected no associations in newborns, we did find that, in the 6- to 7-month-olds, for a familiar relative to unfamiliar face type (infant monkeys relative to infant human), a greater proportion of time looking to the eye region predicted face discrimination. That is, preferentially attending to the eye region may have improved discrimination of familiar more than unfamiliar face types. Our results are consistent with reports that attending more to the eye region of own-race faces is associated with better discrimination of own-race relative to other race faces (Goldinger & Papesh, 2009; Kawakami et al., 2014).

In sum, the present data provides evidence that macaque infants possess both experience-independent and experientially driven face biases. One the one hand, infants exhibited the strongest evidence of face discrimination for the evolutionarily relevant, but entirely novel face category of adult conspecifics. That is, monkey infants exhibit privileged own-species

face processing independent of experience. Infants' face viewing patterns during the familiarization could not explain this difference. Indeed, it makes evolutionary sense for infants to exhibit privileged processing of own-species faces, or to have a face system pre-tuned for own-species adult faces, given infants' need for fast and accurate face recognition to navigate their social world (McKone, Crookes, Jeffery, & Dilks, 2012). The present study challenges the view that primate infants are simply face generalists whose face specialization is exclusively driven by experiences; rather, our data suggest that macaque infants are more efficient at discriminating evolutionarily-relevant faces, even without prior experience with such face types. The present data also highlight the possibility that human infants, like monkey infants, may already possess, from early in infancy, experience-independent biases for own-species faces. A functionalist approach may be particularly fruitful in uncovering these early biases in human infants (Di Giorgio et al., 2012; Heron-Delaney et al., 2011b; Johnson et al., 1991). On the other hand, our data also are consistent with models of perceptual attunement, in which there are developmental improvements in face discrimination for face types with which infants have the most experience (Maurer & Werker, 2013). We found that, in the first couple of seconds of looking, infants showed superior discrimination for familiar face types, including same aged conspecifics and adult humans, relative to unfamiliar face types. Infants' viewing patterns during encoding also predicted their discrimination for familiar relative to unfamiliar faces.

Conclusions and Future Directions

While we agree that there is much evidence supporting the notion that early experiences with various face types (e.g., races: Gaither, Pauker, & Johnson, 2012; species: Pascalis et al., 2005) shape infant face discrimination, we think a focus solely on experience-driven face processing provides an incomplete picture. The present study supports our view, suggesting some aspects of early face specialization may be influenced by experience-independent adaptive mechanisms, sensitive to faces that were recurrent, and posed widespread opportunities and/or threats, over the course of evolution (e.g., LoBue & DeLoache, 2010). That is, there may be some experience-expectant mechanisms, which, even in the absence of environmental input, still may guide visual processing for stimuli of high evolutionary relevance (LoBue, 2010; Lobue & Deloache, 2011; Penkunas & Coss, 2013).

A limitation in previous studies with human infants is that the face types that are the most evolutionarily relevant to infants—adult human faces—are also the face types that they are exposed to the most, making it challenging to disentangle the contributions of evolutionary predispositions that may be independent of experiences, with those contributions of their early social environments (e.g., exposure to certain species or ages). The present study is the first study to attempt to overcome this challenge through the use of a nonhuman primate model.

Acknowledgments

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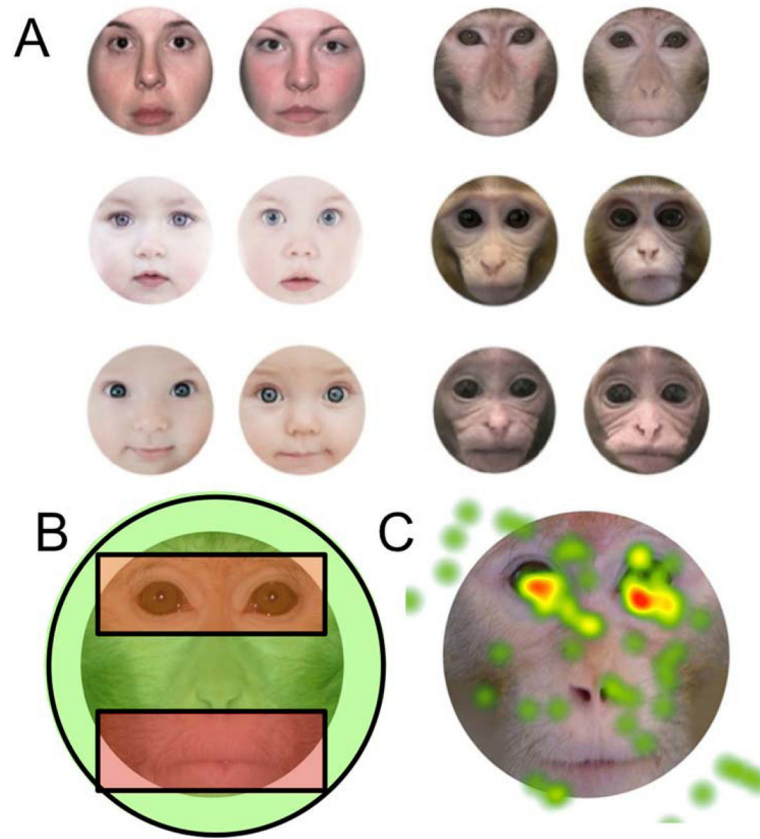
Figure 1.
(A) Sample stimuli. Top row: adult faces, middle row: old infant faces, bottom row: young infant faces. Faces were matched on inter-pupil distance and cropped in a circle. (B) Sample areas of interest (AOI) surrounding faces, eye regions, and mouth regions. (C) Heat map example. Red regions indicate the most looking.

Table 1

Means (*M*) and standard deviations (*SD*) for eye-mouth index (looking duration to Eyes / [Eyes + Mouth]) during familiarization trials, and looking durations (seconds) to novel and familiar faces during test trials.

Subjects	Face Stimulus		Familiarization			Test Trials Look Duration				
	Species	Age	Eye-Mouth Index			Novel Face		Familiar Face		
			M	SD	p	M	SD	M	SD	p
Newborns	Human	Adult	0.69	0.21	< 0.001 *	1.53	1.01	1.39	0.87	0.422
		Old Infant	0.61	0.24	0.022	1.54	1.10	1.14	0.75	0.019
		Young Infant	0.63	0.24	0.009	1.59	1.09	1.18	0.65	0.030
	Monkey	Adult	0.66	0.21	0.001 *	1.25	0.86	1.19	0.88	0.708
		Old Infant	0.55	0.21	0.252	1.52	0.88	1.39	0.95	0.433
		Young Infant	0.55	0.25	0.324	1.23	0.73	1.18	0.67	0.647
6- to 7-month-olds	Human	Adult	0.63	0.15	< 0.001 *	1.46	0.67	1.41	0.78	0.669
		Old Infant	0.64	0.19	< 0.001 *	1.46	0.84	1.25	0.83	0.215
		Young Infant	0.66	0.17	< 0.001 *	1.59	1.12	1.34	0.74	0.042
	Monkey	Adult	0.63	0.21	0.001 *	1.54	0.96	1.16	0.66	0.005 **
		Old Infant	0.67	0.17	< 0.001 *	1.57	0.84	1.33	0.85	0.107
		Young Infant	0.65	0.17	< 0.001 *	1.17	0.75	1.05	0.64	0.397

Significant differences with Bonferroni corrections indicated by:

*
*p*s < .008, one-sample *t* tests;

**
p = .005, paired *t* test (novel vs. familiar).

Table 2

Means (*M*) and standard deviations (*SD*) for the proportion of time looking to the novel face, out of the total time looking to both novel and familiar faces, in test trials. Cumulative looking at three time points is shown: first 1 second, first 2 seconds, and first 3 seconds.

Subjects	Face Stimulus Species	Age	Proportion of Time Looking to Novel								
			0–1 seconds			0–2 seconds			0–3 seconds		
			M	SD	p	M	SD	p	M	SD	p
Newborns	Human	Adult	0.56	0.25	0.202	0.53	0.19	0.440	0.50	0.20	0.928
		Old Infant	0.46	0.23	0.435	0.47	0.18	0.443	0.49	0.17	0.716
		Young Infant	0.55	0.28	0.357	0.53	0.20	0.522	0.54	0.17	0.264
	Monkey	Adult	0.59	0.24	0.087	0.57	0.23	0.123	0.54	0.21	0.343
		Old Infant	0.50	0.27	0.985	0.54	0.21	0.406	0.56	0.15	0.081
		Young Infant	0.47	0.25	0.536	0.46	0.23	0.380	0.47	0.17	0.375
6- to 7-month-olds	Human	Adult	0.63	0.20	< 0.001*	0.61	0.18	0.001*	0.55	0.15	0.055
		Old Infant	0.57	0.22	0.079	0.58	0.18	0.016	0.60	0.20	0.011
		Young Infant	0.50	0.23	0.979	0.56	0.18	0.085	0.54	0.17	0.177
	Monkey	Adult	0.58	0.22	0.054	0.61	0.20	0.003*	0.61	0.20	0.005
		Old Infant	0.55	0.19	0.112	0.60	0.14	< 0.001*	0.58	0.16	0.006
		Young Infant	0.52	0.17	0.531	0.55	0.18	0.144	0.56	0.21	0.152

Significant differences with Bonferroni corrections indicated by:

*
  *p*s .003, one-sample *t* tests (chance .50).