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Sensitivity to first-order relations of facial elements in infant rhesus macaques

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Abstract

Faces are visually attractive to both human and nonhuman primates. Human neonates are thought to have a broad template for faces at birth and prefer face-like to non-face-like stimuli. To better compare developmental trajectories of face processing phylogenetically, here we investigated preferences for face-like stimuli in infant rhesus macaques using photographs of real faces. We presented infant macaques aged 15–25days with human, macaque, and abstract faces with both normal and linear arrangements of facial features, and measured infants' gaze durations, number of fixations, and latency to look to each face using eye-tracking technology. There was an overall preference for normal over linear facial arrangements for abstract and monkey faces, but not human faces. Moreover, infant macaques looked less at monkey faces than at abstract or human faces. These results suggest that species and facial configurations affect face processing in infant macaques, and we discuss potential explanations for these findings. Further, carefully controlled studies are required to ascertain whether infant macaques' face template can be considered as broad as human infants' face template.

Keywords

Rhesus Macaque; Infant; Face Perception; Eyes; Eye Tracking

Faces convey a large amount of significant information such as the identity, gender, and attentional state of another individual. Not surprisingly, human adults are sensitive to these types of information and are experts at processing faces under a variety of environmental conditions (Gliga &Csibra, 2007). Two types of facial recognition processing are commonly studied: Feature-based processing is recognition based on characteristics of individual facial features (e.g., eyes, mouth), such as their size, shape, or color. Configural processing is based on sensitivity to three things: (1) *first-order relations*, or the relative position of the features (e.g., the eyes are above the nose, which is above the mouth); (2) *second-order relations*, or the spacing among the features; and (3) *holistic processing*, or perceiving the face as a single figure with integrated parts(Maurer, Le Grand,& Mondloch,2002). These three configural processing strategies can be distinguished with behavioral marker tasks, and may be based on different neural pathways (Maurer et al., 2002).

It seems intuitive that detection of faces based on first-order relations is achieved before detection of second-order relations and holistic processing can occur. Past research has

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shown that human neonates already prefer normally configured facial features, and are more likely to track a face-like pattern than a non-face-like pattern (Goren, Sarty, & Wu, 1975).Further experiments have shown that newborns not only prefer faces, but more generally top-heavy patterns (Valenza, Simion, Cassia, & Umilta, 1996) and specifically, top-heavy patterns with a curvilinear external contour (Simion, Farroni, Cassia, Turati, & Dalla Barba,2002). This initial attentional preference towards faces is thought to produce biased input, resulting in processing advantages for the most commonly encountered types of faces. For example, Quinn, Yahr, Kuhn, Slater, & Pascalis (2002) demonstrated that 3-month-old infants prefer female faces over male faces, unless the primary caregiver is male. Other effects stemming from environmental exposure may include processing advantages for own race faces (Kelly et al., 2005), and for own species faces(Pascalis et al., 2005). This increasing face specialization may be driven by a process known as perceptual narrowing (Nelson,2001): infants are thought to have an initial, broad face template, which becomes gradually more focused throughout development. Therefore, the face perception system is often considered an evolutionary inheritance, but one that can be influenced by environmental factors after birth (Pascalis &Kelly, 2009).

Studying perceptual narrowing in human infants has unique challenges. For example, the lack of control over infants' environment due to ethical and practical reasons can make it difficult to ascertain the types of stimuli to which infants are exposed. A suitable animal model, whose environmental experiences can be under complete control, might offer an appropriate solution to this issue. Non-human primates may be an ideal choice given their close evolutionary history with humans. Rhesus macaques offer a particularly intriguing model in this respect because like humans, they live in large and complex social networks, and they exhibit intimate mother-infant bonds(Herman, Paukner, & Suomi, 2011). Newborn macaques have good visual acuity, which develops rapidly in the first weeks of life (Ordy, Latanick, Samorajski, & Massopust, 1964). Finally, rhesus macaques are thought to share a last common ancestor with humans ca. 25 million years ago (Gibbs et al., 2007), and comparisons of human and macaque infants' early face processing strategies could reveal whether there may be phylogenic continuity of early developmental processes – in other words, whether faces are special not only to human infants, but also to other non-human primate infants.

Numerous studies have shown that as adults, rhesus macaques are particularly sensitive to facial stimuli. For example, eye tracking studies have demonstrated that when scanning conspecific or human faces, rhesus macaques are especially attracted to the eye region (Nahm, Perret, Amaral, & Albright, 1997; Keating & Keating, 1993; Gothard, Brooks, & Peterson,2009). Furthermore, macaques can identify faces by individual features as well as by the distances among individual features (Keating & Keating, 1993; Leopold & Rhodes, 2010). However, not all faces are processed in the same way, and macaques show better recognition and discrimination of macaque faces than human faces (Guo, Robertson, Mahmoodi, Tadmor, & Young, 2003; Dahl, Wallraven, Bulthoff, & Logothetis, 2009; Gothard et al., 2009). This own-species face specialization is suggestive of perceptual narrowing, but developmental studies are required to investigate this issue in detail. In a landmark study, Sugita (2008) demonstrated that exposure to different types of faces can significantly impact species preferences in infant and juvenile macaques. Moreover, prior to exposure to any faces at all, macaque infants showed preferences for both human and monkey faces over non-face objects when tested at 6 months old. These findings suggest that in the absence of suitable input, the primate face recognition system exhibits a high degree of plasticity and may be based on a broad template for faces.

Further evidence for a broad face template at birth comes from studies showing that infant monkeys are sensitive to first-order relations among facial features, i.e., within the first weeks of life they significantly prefer line drawings of face-like stimuli to non-face-like stimuli (Lutz, Lockard, Gunderson, & Grant, 1998; Kuwahata, Adachi, Fujita, Tomonaga, & Matsuzawa, 2004). However, these previous studies are limited by their exclusive use of line drawings and abstract shapes as stimuli. Such stimuli provide high-contrast input and therefore may be easier to perceive than real faces, which may have less intense contrast configurations. Mendelson, Haith, and Goldman-Rakic (1982) reported that nursery-reared infant rhesus macaques' fixate inner and outer features of an infant macaque photograph equally across the first 7 weeks of life, suggesting that in the absence of high contrast elements infant macaques may not be particularly attentive to inner facial elements. Thus, it remains an open question whether infant macaques' preference for facial configurations over non-facial configurations is indeed based on a broad face template that can be generalized to a variety of facial stimuli.

In the present study, we investigated infant rhesus macaques' visual preferences for faces and face-like stimuli using eye tracking technology. In particular, we were interested in assessing their sensitivity to first-order relations among facial features by comparing the relative salience of top-heavy facial configurations to linear facial configurations. We presented nursery-reared infant macaques with photographs of human faces, monkey faces, and abstract facial stimuli consisting of contours of monkey heads with high-contrast abstract shapes replacing inner elements. We used three dependent measures: total looking time, number of fixations, and latency to look at each stimulus. While latency may be interpreted as a measure of attention capture, looking time and number of fixations may be considered measures of subsequent engagement of attention (Nummenmaa, Hyona, & Calvo, 2006).Based on previous findings, we hypothesized that if infant macaques have a broad template for faces at birth, they would show shorter latencies as well as longer total looking time and more frequent fixations towards normally-configured faces compared to linearly-configured faces.

Methods

Subjects

Subjects were 24infant rhesus macaques (*Macaca mulatta*),8female and 16male. All infants appeared to be at term, and all birth weights fell within normal parameters. All infants were separated from their mothers on the first day of life (typically by 8am)and 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 mother covered with fleece fabric as well as loose pieces of fleece fabric and various rubber toys (see Shannon, Champoux, & Suomi [1998] for further details on rearing practices). For the first month of life, infants could see and hear, but not physically contact, other infants of similar age. Human caretakers were present for 13h a day, and they interacted with infants every 2h for feeding and cleaning purposes. Caretakers always wore a hair cover, safety glasses, and a face mask that covered the entire face with the exception of a small area around the eyes (ca. 2 inches vertically exposed). In addition, infants were tested in a variety of socio-cognitive assessments which involved exposure to full-face human caretakers for ca. 15 minutes a day for the first week of life, and for ca. 5 minutes a day, twice a week, between weeks 2 and 4. For the current study, we report data from infant ages 15days to25days. An additional 5infants were tested but excluded from the analysis due to insufficient data.

Materials

Apparatus

Eye movements were recorded via corneal reflection using a Tobii T60XL eye tracker, a remote 24" monitor with integrated eye tracking technology and a sampling rate of 60 Hertz. Tobii Studio software (Tobii Technology, Sweden) was used to collect and summarize the data. Since the infants' interpupilar distance was smaller than standard human interpupilar distance, data from only one eye were available during calibration and data collection.

Stimuli

Stimuli included 3 pairs of abstract faces, 3 pairs of adult female human faces, and 3 pairs of adult female macaque faces. Human and macaque faces were unfamiliar to infants, and were depicted with neutral facial expressions and gaze directed at the observer. All faces were standardized for inter-pupilar distance(height =ca.14.25 degrees visual angle), cropped around the outer contours of the head, and displayed in grey scale on a black background. Each pair contained a normal face and a linear face with the position of each face (left-right) randomized for each trial. To create a linear face, we digitally manipulated each normal face to re-arrange its inner features in a vertical line in the center of the face. Abstract faces consisted of the outline of an adult female macaque face but with eyes and mouth represented by black, abstract shapes (square, circle, or plus sign; see Figure 1).While we did not control for image contrast, we examined luminosity histograms of the eye region of all stimuli, and used the standard deviation as an approximation of contrast. Average standard deviation values for abstract, human, and monkey faces were 64.0, 49.5, and 36.5 respectively.

Procedure

At the beginning of each session, one experimenter held the infant wrapped in soft fleece fabric at a distance of approximately 60 cm in front of the screen. Each infant was calibrated using a 5-point calibration procedure to Tobii Studio's pre-set locations using the software's standard infant calibration routine. This routine consists of colorful, animated short videos and sound effects displayed at calibration point locations, which were sufficient to attract the infants' attention; no training was necessary to obtain successful calibrations. Individual calibration points that were judged to be unreliable were repeated until reliability was obtained. For seven infants, the same calibration was used throughout the study; all other infants were newly calibrated for each test session. Following calibration, each stimulus pair (i.e., one normally configured and one with linearly arranged features) was presented once per session for 10sec in random order. To sustain interest in the task, we presented short video clips of colorful, animated toys and objects accompanied by sound effects between stimuli. Infants were tested in1 session once a day for an average of 6.6 sessions total (range 5–9 sessions).

Data Analysis

An Area of Interest (AOIs) was created for each face, containing the entire face as well as a small area surrounding each face (25.0% of total screen area).Tobii Studio was used to extract data with a fixation filter set to50 pixels radius and 100ms duration to define a fixation. We only used trials in which infants looked at both normal and linear faces at least once; if only one face was looked at, that particular trial was discarded. All reported Ps are two-tailed except where indicated.

Results

Latency to look

A repeated measures ANOVA assessing the latency to look at each face with Species (abstract, human, monkey) and Configuration (normal, linear) as within-subject factors revealed a main effect for configuration (F(1, 23)=6.63, P=0.017), but no effect for species (F(2, 46)=0.02, P=0.98), and no interaction (F(2, 46)=0.34, P=0.72). Infants were consistently faster to look at normal faces than at linear faces (Figure 2).

Duration of looking

A repeated measures ANOVA assessing the total duration of looking to each face with Species (abstract, human, monkey) and Configuration (normal, linear)as within-subject factors showed a main effect for Species (F(2, 46)=6.46, P=0.003) and a main effect for Configuration (F(1, 23)=7.37, P=0.012), but no interaction (F(2, 46)=2.15, P=0.13). Infants looked significantly longer at abstract faces (P=0.007) and at human faces (P=0.001) than at monkey faces (Figure 2). Infants also looked significantly longer at normal configurations than at linear configurations(Figure 2).As a further measure of preference, we divided looking time at each normal face by the total looking time at both normal and linear faces [normal/(normal + linear)], and compared this proportion against chance levels (0.5). As we predicted a preference for normal faces, we used one-tailed one-sample t-tests. Infants looked significantly above chance levels at the normal configuration for abstract faces (mean=0.58, P=0.006) and for monkey faces (mean=0.57, P=0.028), but not human faces (mean=0.51, P=0.40).

Number of fixations

For number of fixations, we found a main effect for Species (F(2, 46)=12.29, P<0.001) and a main effect for Configuration (F(1, 23)=5.693, P=0.026), but no interaction (F(2, 46)=0.95, P=0.40). Infants showed significantly more fixations on abstract and human faces than on monkey faces (both P<0.001), and significantly more fixations on normal faces than on linear faces (Figure 2).As an additional analysis, we divided the number of fixations on each normal face by the total number of fixations on both normal and linear faces [normal/(normal + linear)], and compared this proportion against chance levels (0.5) within each species. As we predicted a preference for normal faces, we used one-tailed one-sample t-tests. Results show that infants looked significantly above chance levels at the normal configuration for monkey faces (mean=0.55, P=0.01), approaching significance for abstract faces (mean=0.53, P=0.068), but at chance levels for human faces (mean=0.51, P=0.35).

Discussion

The present study aimed to address the question of preferences for first-order configurational facial arrangements in infant rhesus macaques. We hypothesized that if infant macaques have a broad face template at birth (as has been suggested for human infants), they would show a preference for normal facial configurations over linear facial configurations across all types of face stimuli. Our results confirm that infant macaques are sensitive to first-order relations among facial elements: they showed overall shorter latencies to first look, longer looking durations, and a higher frequency of fixations towards normal facial arrangements compared to linear facial arrangements. However, not all faces were processed equally. Infant macaques showed shorter looking durations and fewer fixations to monkey faces compared to both abstract and human faces.

One potential explanation for this finding may be related to the stimuli's different levels of contrast. Previous studies have shown that adult macaques are particularly attracted to high-contrast features of macaque faces (Wilson & Goldman-Rakic, 1994).Human newborns are thought to be sensitive to high contrast information and low spatial frequencies (de Heering et al., 2008), possibly because high-contrast information is easier to perceive (Hole & Bourne, 2010). In the current study, the eye region of stimuli showed different levels of contrast with abstract faces containing the highest amount of contrast, monkey faces containing the least amount of contrast, and human faces falling between the two. Thus, it is possible that infant macaques looked more at abstract and human faces because they were easier to perceive than monkey faces. Alternatively, the angle at which stimulus faces were presented may have affected infants' preferences. Both human and monkey faces were shown in a frontal pose, neutral expression, and direct gaze seemingly directed at infants (arguably, abstract faces were also presented in a frontal pose, but without conceivable gaze direction). Direct gaze is usually a threat signal in rhesus macaques, signifying aggression; an appropriate (submissive) response is glancing away (van Hooff, 1962). Gaze aversion is therefore a frequently used means for avoiding agonistic interactions (Nahmet al.,1997), and aversion of direct gaze may appear as early as 2 weeks of age (Mendelson et al., 1982).Thus, rather than preferring the high contrast information in abstract and human faces, infants may have avoided the direct gaze of monkey faces. Future studies with better controlled contrast information between stimuli could test these hypotheses directly.

A second finding of the current study further reinforces the view that not all faces are processed equally by infant macaques: while latencies to first fixation were consistently shorter for normal facial configurations across all species faces, looking durations and number of fixations were increased only for normal abstract and normal monkey faces but not normal human faces, suggesting that species and facial configuration may not have an effect on attention capture, but may interact during subsequent engagement of attention. A potential explanation for lack of species effect on latencies may be related to infants' peripheral vision: acuity may not have been sufficient to process stimuli in detail so as to differentiate between species, thus infants may have reacted to a basic face template across species. In terms of attention engagement, previous studies have only used high-contrast line drawings of faces to test infant macaques, and found significant preferences for normal (compared to abnormal) configurations of monkey faces (Lutz et al., 1998) and schematic human and abstract faces (Kuwahata et al. 2004).However, monkey faces in the current study contained the least amount of contrast (and therefore should have been the most difficult to process), thus ruling out contrast as an explanation for the current results. Moreover, a lack of preference for normally configured human faces may indicate that young infant macaques' face template is not as broad as human infants' face template. For example, Di Giorgio, Leo, Pascalis, &Simion (2012) showed human and monkey faces to newborn human infants, and found that they perceive human and monkey faces in a similar way. Human infants typically do not start exhibiting a processing advantage for human faces until6–9 months old, which has commonly been attributed to perceptual narrowing (Pascalis et al., 2005; Pascalis & Kelly, 2009). Instead, infant macaques may be particularly sensitive to own species faces soon after birth as also indicated by another recent study with infant macaques, which reported visual preferences for female macaque faces but not female human faces (Paukner, Huntsberry,& Suomi, 2010).

This hypothesis may appear at odds with Sugita's (2008) finding that 6–24 months old infant macaques reared in complete absence of facial stimuli show equal preferences and discrimination for human and monkey faces. Sugita (2008) argued for a sensitive period for face perception in macaques, which can last as long as 2 years after birth. During this period, specific experiences with face stimuli prime macaques' perceptual narrowing of face processing, leaving a life-long effect on the specific patterns of face processing. Infant macaques in the current study had limited to no experience with adult macaque faces, but they were in visual contact with other macaque infants of similar age. Thus, this early exposure to infant macaque faces could have prompted a processing advantage for macaque faces including adult faces. On the other hand, Scherf and Scott (2012) recently proposed a functionalist approach to developmental trajectories of face processing. Under this framework, face processing strategies may be influenced by age-appropriate tasks or goals given the social, emotional, and contextual milieu of an individual. This approach might consider the face processing strategies employed by a young (<1 month old) infant macaque-which is fully dependent on its mother-as functionally different to the face processing strategies employed by a 6 months old infant macaque -which is considered for the most part weaned from its mother, and which spends considerable time in social contact and play with other groups members(Suomi, 2005).In other words, a functionalist approach could reconcile a bias towards monkey faces at an early age when infants are dependent on the mother as primary care giver, with broader face processing strategies incorporating a variety of faces at an age when infants' social networks expand dramatically in both scope and complexity.

Overall, the results of the current study suggest that infant macaques are sensitive to first-order facial configurations shortly after birth and prefer normal facial arrangements to linear facial arrangements. Our results confirm previous suggestions that infant macaques are born with a template for faces, which is amenable to post-natal experiences(Sugita, 2008; Pascalis &Kelly, 2009). However, further studies are required to ascertain whether infant macaques' template is as broad as that of human infants, or whether there may be early biases towards own-species faces. Caution should also be exercised as images of humans and macaques are necessarily impoverished representations and may not have contained the same amount of information as real-life entities (e.g. contrast, brightness, color). Future studies could systematically explore potential interactions between first-order configurations and feature information on infant macaques' facial processing strategies. Studies in this area contribute broadly to our understanding of experience-expectant components of perception and attention in human and nonhuman primates, and highlight the role of experience during critical periods in infancy and beyond.

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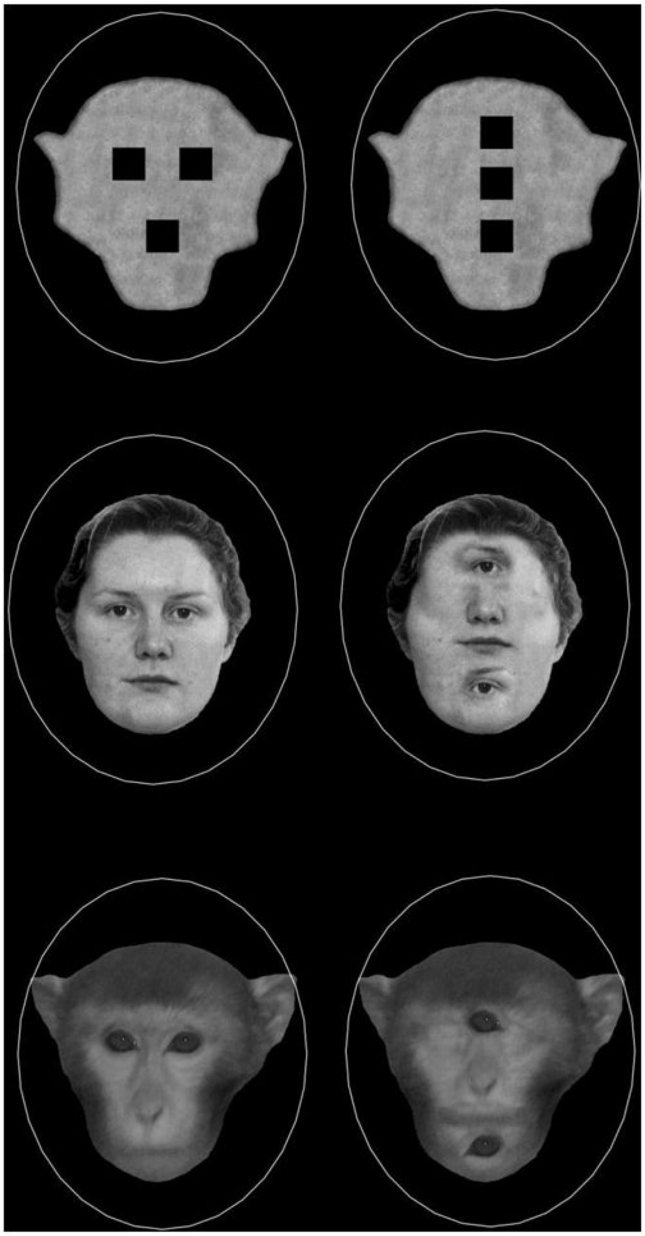

Figure 1.
Illustration of stimuli and AOIs with normal configurations on the left and linear configurations on the right. Top: abstract stimulus, Middle: human stimulus, Bottom: monkey stimulus. Area within white line represents AOI(Area Of Interest).

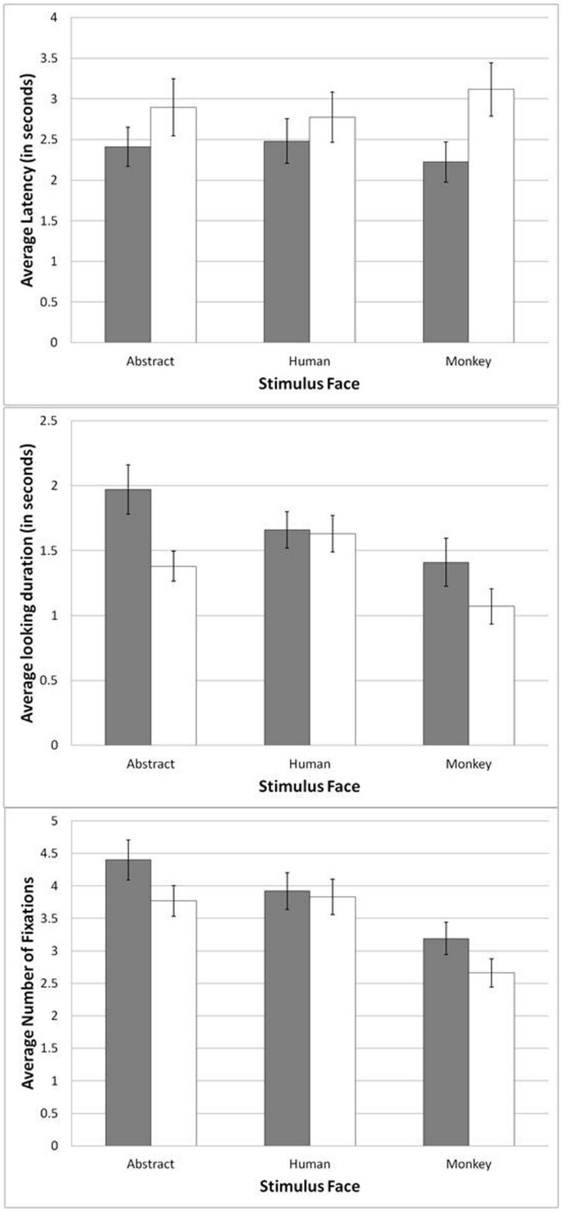

Figure 2.

Summary of results for normal and linear faces from abstract, human, and monkey face stimuli. Top: Average latency to first fixation (in seconds), Middle: Average looking duration (in seconds), Bottom: Average number of fixations. Grey bars indicate normal configurations and white bars indicate linear configurations of each face type. Error bars represent standard errors.