



The developmental time course and topographic distribution of individual-level monkey face discrimination in the infant brain

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ABSTRACT

The ability to discriminate between faces from unfamiliar face groups has previously been found to decrease across the first year of life. Here, individual-level discrimination of faces within a previously unfamiliar group was investigated by measuring neural responses to monkey faces. Six- and 9-month-old infants ($n = 42$) completed a Fast Periodic Visual Stimulation (FPVS) task while steady state visual evoked potentials (ssVEPs) were recorded. Using an oddball task design (e.g., infrequent changes in face identity) faces were presented at a 6 Hz (1 face approximately every 167 ms) stimulation rate and every 1.2 Hz different individual monkey faces were presented. Significant SNRs at 1.2 Hz in both 6- and 9-month-old infants suggest that neural responses, recorded over posterior scalp regions, remain sensitive to individual-level differences within an unfamiliar face group despite previous behavioral evidence of decreased discrimination. However, the topographic distribution of the 1.2 Hz response varied by age, suggesting that 6- and 9-month-old infants are using different neural populations to discriminate unfamiliar faces at the individual level.

1. Introduction

Faces are arguably one of the most important stimuli infants experience during the first year of life. They not only provide important social information such as referential attention (Striano et al., 2006) and emotional cues (for review, see Leppänen and Nelson, 2006), but also scaffold learning in a variety of domains (e.g., speech perception and production, Lewkowicz and Hansen-Tift, 2012; learning gaze-cued objects, Pickron et al., 2017). People are also extraordinarily good at recognizing faces; however, this expertise is often diminished for faces of another species or for faces of people within less familiar groups (e.g., other-race groups). These biases arise over the course of the first year of life and contribute to deficits in recognizing and identifying individuals within unfamiliar and infrequently experienced groups (e.g., Kelly et al., 2009, 2007, Pascalis et al., 2005, 2002).

While newborns do not show a visual preference for own- over other-race faces, 3- month-olds exhibit a spontaneous preference for own-race faces (Kelly et al., 2005). Across the first year of life, infants move from equally discriminating faces within both familiar and unfamiliar groups to failing to discriminate faces within unfamiliar groups, a pattern called “perceptual narrowing” (Scott et al., 2007). At 9 months of age infants continue to easily differentiate faces within the

most frequently experienced groups (e.g., Kelly et al., 2009, 2007; Pascalis et al., 2002).

In a recent proposal, perceptual narrowing and perceptual tuning effects were hypothesized to reflect a shift from primarily bottom-up processing of stimulus features/salience to a combination of bottom-up and top-down influences across the first year of life (Hadley et al., 2014). For face processing, proposed important top-down influences include: the socio-cultural developmental context, language development and word learning, category and concept formation, learned attention to relevant stimulus features (Hadley et al., 2014), and other salient developmental tasks such as motor development and the formation of an attachment relationship (Scherf and Scott, 2012). However, many of these bottom-up and top-down factors are confounded by familiarity and general experience which limits our understanding of these important contributions. Other-species faces have previously been used to examine the developmental trajectory of perceptual narrowing and reduce pre-experimental familiarity/experience confounds (e.g., Pascalis et al., 2005, 2002, Scott and Monesson, 2010, 2009). Scott and Fava (2013) argue that monkey faces are useful stimuli for understanding face learning and recognition because it can be assumed that participants will have little to no prior experience and the results can therefore be attributed to the experimental manipulations and not

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individual differences in levels of pre-experimental face experience. Previous research using monkey face stimuli suggests infants exhibit decreased discrimination of monkey faces from 6 to 9 months of age (Pascalis et al., 2002), but that the top-down experience of listening to parents name individual monkey faces leads to continued discrimination at the individual level (Scott and Monesson, 2009).

To complement the behavioral literature showing perceptual narrowing for faces across the first year of life, a handful of studies have examined the neural correlates of own- versus other-race face processing in infancy using event-related potentials (ERPs). For example, 9-month-olds exhibited differential ERP responses to own- versus other-race faces (Balas et al., 2011; Vogel et al., 2012), whereas 5-month-olds did not differentially respond to own- and other-race faces (Vogel et al., 2012). Investigations examining infants' neural responses to own- and other-species faces report increased neural specificity, as measured by ERPs, to human faces relative to monkey faces (de Haan et al., 2002; Halit et al., 2003; for review, see de Haan et al., 2003). In addition, when infants are given three months of experience (from 6 to 9 months of age) with individually-labeled monkey faces, neural specialization for monkey faces increases (Scott and Monesson, 2010).

One previous study examined the extent to which 9-month-old infants can categorize or individuate previously unfamiliar human and monkey faces using ERPs and found no evidence of individuation of monkey faces (Peykarjou et al., 2014). However, in another study 9-month-old infants demonstrated neural differentiation of experimentally familiarized human and monkey faces (Scott et al., 2006), although the neural responses differed depending on species, suggesting separate mechanisms for discriminating faces within familiar versus unfamiliar groups. The inconsistent results reported by Peykarjou et al. (2014) and Scott et al. (2006) highlight the need for additional work examining the development and neural correlates of familiar and unfamiliar face processing. One important difference between these two investigations was the length of the face familiarization period. Peykarjou et al. (2014) showed infants each individual face for only 1000 ms, whereas Scott et al. (2006) used an infant controlled habituation period, resulting in a longer familiarization time. It is possible that extended familiarization/exposure time allows for increased discrimination. This interpretation is consistent with behavioral work showing that in 12-month-olds, increasing the familiarization time from 20- to 40-s allows for reliable discrimination of monkey faces (Fair et al., 2012). Although these previous findings suggest differential processing of familiar versus unfamiliar groups of faces, the extent to which neural responses discriminate faces within unfamiliar groups is not known. Moreover, if neural evidence of individual-level discrimination is present, the extent to which these responses differ in sensitivity, timing, or topography across the first year of life is also unknown. The goal of the current study was to further investigate individual-level discrimination of faces within a previously unfamiliar group by measuring neural responses over posterior scalp regions while 6- and 9-month-old infants completed a fast periodic visual stimulation (FPVS) task.

In FPVS paradigms, images are presented at a rapid, constant frequency (e.g., 6 faces per second). The resulting neural response, the steady state visual evoked potential (ssVEP), is present at exactly the presentation frequency (for review, see Norcia et al., 2015). Using FPVS and ssVEP techniques, infants can be exposed to hundreds of images and several conditions within minutes, ultimately reducing attrition rates and increasing power. The ssVEP method can be used to measure the brain's differentiation of various stimulus conditions providing a link to behavioral visual discrimination tasks. FPVS has primarily been used to investigate face processing in adults (for review, see Rossion, 2014). For example, in adults, one recent study utilized FPVS and an oddball task design (e.g., infrequent changes in face identity) to examine whether adults exhibited a response to face identity above and beyond a category response to faces (Liu-Shuang et al., 2014). In this task, stimuli were presented at a rate of 6 Hz and every 5th face was a

different individual (1.2 Hz). In addition to the mid occipital 6 Hz response to visually presented faces, Liu-Shuang and colleagues found that adults exhibited a right-lateralized 1.2 Hz response to changes in face identity.

To date, only three published studies have used the ssVEP technique to examine face processing in infancy (de Heering and Rossion, 2015; Farzin et al., 2012; Peykarjou et al., 2017). Two studies focused on the specificity of face and object category representations. Farzin et al. (2012) presented 4- to 6-month-old infants with alternating images (6 Hz) of intact (3 Hz) and scrambled faces and objects. Infants showed face-related neural responses over left, right, and medial occipital regions, whereas object-related responses were only found over the medial occipital region. de Heering and Rossion (2015) also examined 4- to 6-month-old infants' neural discrimination of faces and objects using an oddball design. A significant 1.2 Hz response measured over the right occipital scalp region was found, suggesting that infants form a category representation of faces that is separate from objects. Additionally, Peykarjou et al. (2017) used an oddball design to examine the categorization of human and ape faces in 9-month-old infants. A 1.2 Hz categorization response was found over occipital scalp regions both when ape faces were the oddball (and human faces the standard) and when human faces were the oddball (and ape faces the standard). Combined, these findings suggest that the brain differentiates faces and objects as early as 6 months and that the infant brain differentiates stimuli based on category, both between face and non-face stimuli and within the category of faces. However, it is still unclear whether infants will exhibit individual-level discrimination of faces and whether the topographic distribution of individual-level face processing will differ across age.

Based on previous behavioral evidence for perceptual narrowing (Kelly et al., 2009, 2007; Pascalis et al., 2005, 2002; Scott and Monesson, 2009; Vogel et al., 2012), 6-, but not 9-month-olds should exhibit individual-level discrimination as measured by a 1.2 Hz neural response. However, if neural responses remain sensitive to individual-level differences within unfamiliar face groups (e.g., Scott et al., 2006), both 6- and 9-month-old infants should exhibit a 1.2 Hz face individuation response. Based on previous FPVS findings in adults (Liu-Shuang et al., 2014) the topographic distribution of neural activity will also be examined. If infants exhibit adult-like 1.2 Hz face individuation responses, it is expected to be primarily right-lateralized.

2. Method

2.1. Participants

All parents gave informed consent prior to testing. Analyses included data from 23 6-month-olds (12 males), and 19 9-month-olds (11 males). Four additional infants were excluded from the analyses because they did not contribute enough usable trials per condition (see below, $n = 2$) or because they were a statistical outlier ($n = 2$). All infants were born full-term and had no history of neurological, visual or auditory impairments. Parents of participants were paid \$10 and infants received a small toy for their participation.

2.2. Stimuli and apparatus

Visual stimuli consisted of 12 digitized color photographs of Barbary macaques (*Macaca sylvanus*) and 12 digitized color photographs of Tufted capuchins (*Cebus apella*) cropped into an oval shape and presented at a visual angle of approximately 13° against a white background (Fig. 1). The Barbary macaque faces were used in prior infant face processing studies (Scott and Monesson, 2010, 2009). The Tufted capuchins were from a database of images maintained by the Language Research Center at Georgia State University.

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