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Neural Correlates of Visual Recognition in 3-Month-Old Infants: The Role of Experience

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Abstract

Early experiences contribute powerfully to the development of neural systems that underlie various perceptual and cognitive abilities in humans. In one of the first studies to systematically control infants' exposure to a familiar object, we examined the effects of controlled experience on the neural correlates of visual recognition in two groups of infants. One group received 1 month of in-home familiarization to a 3D model of a female face. Another group received 1.5 min of in-lab familiarization to the 3D model of a female face, creating two conditions that differed in the amount and, importantly, the context of exposure to a familiar stimulus. Following familiarization, event-related potentials (ERPs) were recorded at 3 months of age while infants viewed pictures of the familiar face and an unfamiliar face. Results demonstrated that while both groups of infants discriminated between the familiar and unfamiliar faces, the pattern of neural processing was reversed for the two groups. Thus, the amount and context of visual exposure altered the neural correlates of recognition processes in young infants.

Keywords

visual recognition; development; event-related potentials; infancy; early experiences; face recognition

Introduction

Early experiences have a profound influence on the development of perceptual, cognitive, and social systems. Studies of visual deprivation reveal that early patterned visual input is necessary for the development of both low-level and high-level visual abilities (Le Grand, Mondloch, Maurer, & Brent, 2001; Lewis & Maurer, 2005; Maurer, Mondloch, & Lewis, 2007); studies of language acquisition indicate that infants retain the ability to discriminate phonemes with which they have experience, but lose the ability to discriminate phonemes with which they have little experience (Kuhl, Tsao, & Liu, 2003; Werker & Tees, 2002); and studies of psychosocial deprivation demonstrate that the opportunity to form stable relationships with adults is essential for the typical development of socioemotional

capabilities (Ghera et al., 2008; Kreppner, O'Connor, Dunn, & Andersen-Wood, 1999; Zeanah, Smyke, Koga, & Carlson, 2005). Despite the growing body of knowledge about the role of experience in development, questions remain regarding how much and what kinds of experiences are necessary to drive typical development, largely due to the practical and ethical complexities involved in studying humans. Researchers interested in understanding the role that experience plays in shaping the developing human brain have traditionally been limited to relating variations in normal experience to variations in outcome and relying on unfortunate situations in which individuals have been deprived of species-typical experiences.

In this study, we introduce a novel approach to investigating the effects of experience on development. Rather than relying on natural, non-quantified variations in experience, here we used an “enrichment” approach, in which we systematically manipulated infants' exposure to a particular stimulus that they would not otherwise experience. The specific question under investigation in this study was whether the amount of experience with a particular object alters the neural representation of that object in relation to a novel object. We measured a 3-month-old infants' neural processing of a familiar face and a novel face under two different exposure conditions—brief versus extended—to determine whether the neural representation of a familiar face depended on how much exposure to that face infants received. For practical reasons, the context for these exposures also differed, with the former occurring in a laboratory setting, and the latter in the infant's home.

Although in principle this question could be examined using any object category, we chose to use faces for two reasons. First, faces are ecologically relevant and perhaps the most salient visual stimulus in the young infant's world. In fact, the ability to recognize individual faces develops very early in infancy. For example, Pascalis and de Schonen (1994) demonstrated that 3- to 4-day-old infants recognize a face to which they have been habituated, and Pascalis, de Schonen, Morton, Derulle, and Fabre-Grenet (1995) demonstrated that infants show a spontaneous visual preference for their mother's face compared with a female stranger's face at the same age. In addition to being observed in behavior, individual face recognition is also reflected in the differential brain activity that infants show in response to familiar and unfamiliar faces. Studies using event-related potentials (ERPs), a non-invasive measure of the brain's electrical activity, have demonstrated that (1) The positive slow wave—an ERP component that is thought to reflect memory updating (Nelson, 1994)—is larger in response to a novel face compared to either mother's face (de Haan & Nelson, 1997) or a briefly familiarized face (Pascalis, de Haan, Nelson, & de Schonen, 1998) in young infants; and (2) The Nc—an ERP component thought to reflect the allocation of attention (Courchesne, Ganz, & Norcia, 1981; Richards, 2003)—is larger in response to mother's face compared to a female stranger's face (de Haan & Nelson, 1997).

A second reason to use faces is that previous research has demonstrated the key role that early experiences play in shaping the development of face perception. Three-month-old infants show a preference for faces to which they have been more extensively exposed, such as faces from their own race (Bar-Haim, Ziv, Lamy, & Hodes, 2006; Kelly et al., 2005) and faces that match the sex of their primary caregiver (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002). In addition, 3-month-old infants show an advantage for own-race face recognition versus other-race face recognition (Sangrigoli & de Schonen, 2004). Nine-month-old infants also show an advantage for own-race and own-species face recognition, in that they have lost the ability to discriminate faces with which they have little experience (Anzures, Quinn, Pascalis, Slater, & Lee, 2010; Kelly et al., 2007; Pascalis, de Haan, & Nelson, 2002). Studies of early visual deprivation (e.g., congenital cataract) have demonstrated that even a brief period of deprivation during the first year of life results in long-term deficits in subtle

aspects of face processing (Le Grand et al., 2001). Additionally, children who have experienced early psychosocial deprivation (i.e., children raised in institutions for orphaned and abandoned children) show altered neural processing of faces (Parker & Nelson, 2005; Moulson, Fox, Zeanah, & Nelson, 2009; Moulson, Westerlund, Fox, Zeanah, & Nelson, 2009), and children who are raised in abusive or neglectful households show altered facial emotion processing (Pollak, Cicchetti, Hornung, & Reed, 2000; Pollak & Sinha, 2002; Pollak & Kistler, 2002; Pollak, Messner, Kistler, & Cohn, 2009). Thus, the role of early experiences in shaping the development of face perception is well established.

In the current study, we used ERPs to examine the neural representations of familiar and novel faces after brief versus extended exposure to the familiar face. The strengths of using ERPs to investigate perceptual and cognitive functions in infants and young children have been discussed extensively by a number of authors (Nelson & Monk, 2001; Nelson, de Haan, & Thomas, 2006; Johnson & Mareschal, 2001). In general, these strengths include the ability to measure with millisecond resolution the chronometry of mental events; the ability to capture the various stages of information extraction that occur over the first few hundred milliseconds after a stimulus has been presented; and the ability to capture a response that occurs so rapidly that a behavioral assay (e.g., looking time) is insensitive to what has transpired. In the context of the current study, we chose to use ERPs because they often provide a more sensitive measure of responding than looking time in young infants (e.g., Nelson & Collins, 1991) and our understanding of the underlying neural representations of familiar and novel faces is currently unclear.

To examine the neural representations of familiar and novel faces after differing amounts of exposure to the familiar face, infants were assigned to one of two groups. Infants in the “experience” group received 1 month of at-home exposure to a realistic 3D model of a female face beginning at 2 months of age. One month of exposure was chosen because we felt it was a sufficient amount of time to approximate the amount of exposure young infants get with other familiar faces (e.g., siblings, grandparents) in their natural environment.¹ Infants in the “no-experience” group received 1.5 min of in-lab exposure to a 3D model of a female face at 3 months of age. This exposure time was chosen to mimic previous lab-based studies using habituation and familiarization procedures to investigate face and object recognition. At 3 months of age, ERPs were recorded while infants viewed pictures of the familiar face and a novel face.

Method

Participants

The final sample included 35 infants (“experience” group: $n = 16$; “no-experience” group: $n = 19$). All infants were born at term (± 2 weeks of their due date) and had no history of vision or neurological problems. Thirty-four infants were White, and one infant was biracial. Infants were tested within 1 week of their 3-month birthday. An additional 55 infants were tested, but were excluded from final data analysis due to fussiness ($n = 25$), excessive EEG artifact ($n = 28$), experimenter error ($n = 1$), or drop out ($n = 1$). This attrition rate is typical of ERP studies with infants this age (Halit, de Haan, & Johnson, 2003).

Apparatus and Procedure

Infants in both groups were familiarized to one of eight 3D models of a female face (Fig. 1A; created by Lars Carlsson, Makeup-FX, Gothenburg, Sweden), counterbalanced across

¹Of course, we do not claim that the 3D models provide the same naturalistic experience that the infant would receive from observing real faces that move, emote, and interact with the infant.

participants. The 3D models were static, life-sized, and posed neutral facial expressions. All of the models were White. For infants in the “experience” group, the 3D model was brought to the infant's house at 2 months of age and mounted on a wheeled cart so that it could be moved easily throughout the house. Parents were instructed to expose their infant to the 3D model for approximately 1 hr/day, but not to allow their infants to touch the 3D model. They were told that “exposure” included both direct interactions with the 3D model as well as the 3D model being present in the infant's immediate environment. Parents kept a log of the times and broader contexts (e.g., play-time, tummy-time, and feeding) in which their infant saw the 3D model. The average exposure time per day was 96 min (range = 30–213 min, SD = 52.14). Since we relied on parental report, it was impossible to determine exactly how this exposure time was accumulated (i.e., how much time the infant spent interacting with the 3D model compared to the 3D model simply being in the infant's immediate environment). However, anecdotal reports from parents suggested that the majority of them spent at least some time each day having their infants interact directly with the 3D model. Infants in the “no-experience group” were familiarized to the 3D model in the lab at 3 months of age. While seated on their parent's lap in a darkened, sound-attenuated room, they saw the 3D model in a full-frontal view for six trials lasting for 15 s each, for a total of 1.5 min of possible exposure to the 3D model. Looking times during this familiarization period were not recorded.

Both groups of infants underwent ERP testing at 3 months of age with the familiar and a novel model (across participants, each of the eight 3D models served as the familiar stimulus and the novel stimulus an approximately equal number of times). The delay between the familiarization and test periods was approximately 15 min for infants in the no-experience group; the delay between the familiarization and test periods was more variable for infants in the experience group, but generally these infants had seen the familiar 3D model earlier in the day on the day of test. Infants were seated on their parent's lap approximately 60 cm in front of a computer monitor that was 48 cm wide by 31 cm high in a darkened, sound attenuated room. After application of the sensor net, infants passively viewed color photographs of the familiar and a novel 3D model. Stimuli were presented for 500 ms each, and each presentation was preceded by a fixation cross in order to direct the infant's attention to the center of the computer screen. An experimenter watched the infant in order to present the pictures when the infant was looking at the screen. The familiar and novel stimuli were presented with equal probability, and stimulus presentation continued until the infant became too fussy or bored to continue, or the maximum number of trials (120) was reached.

Electrophysiological Recording and Processing

Continuous EEG was recorded from a Geodesic Sensor Net (V2.0—Electrical Geodesics, Inc., Eugene, OR), consisting of 64 electrodes evenly distributed across the scalp. During collection, EEG data were referenced to vertex, amplified with a .1–100 Hz band-pass filter, and digitized at a 250 Hz sampling rate. Continuous EEG data were processed offline using NetStation 4.0.1 (Electrical Geodesics, Inc.). The continuous EEG data were first digitally filtered with a 30 Hz low-pass elliptical filter, then segmented into trials with a 100 ms baseline, 500 ms stimulus presentation, and 700 ms post-stimulus recording period. Trials were then baseline corrected and subsequently edited for artifact. Artifact detection on individual trials was accomplished via visual inspection for eye blink, eye movement, motion artifact, and drift. Trials were excluded if more than 15% of the channels were marked as bad. For the remaining good trials, individual bad channels were replaced using spherical spline interpolation. Infants were excluded from final data analysis if they had fewer than 10 artifact-free trials in each condition. This cut-off is commonly used in infant ERP studies (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Csibra, Tucker, &

Johnson, 1998; Farroni, Johnson, & Csibra, 2004). The mean number of trials per condition was 24. Individual subject averages were computed and then re-referenced to an average reference configuration.

ERP Waveform Analysis

Inspection of the grand-averaged ERP waveforms revealed two components of interest: the P400 and the Nc. The P400, located over occipitotemporal regions, is thought to reflect face-sensitive processing, in that it peaks earlier in response to faces compared to other objects (de Haan & Nelson, 1999) and its amplitude is larger for upright than inverted faces (de Haan et al., 2003). The Nc, located over frontocentral regions, is thought to reflect the allocation of attention (Courchesne et al., 1981; Nelson, 1994; Richards, 2003) and previous studies have shown that it is larger in response to mother's face compared to a stranger's face (de Haan & Nelson, 1997). The choice of time windows and electrode groupings to capture the components of interest was guided by previous literature and visual inspection of the averaged ERP waveforms. The average amplitude of the P400 was determined within a time window of 350–675 ms (electrode groupings: Left Hemisphere—32, 33, 28, 29; Midline—34, 38, 37, 40; Right Hemisphere—42, 46, 41, 45), and the average amplitude of the Nc was determined within a time window of 300–700 ms (electrode groupings: Left Hemisphere—13, 16, 9; Midline—8, 3, 4; Right Hemisphere—62, 58, 57) (see Supplementary Fig. 1 for electrode groupings). The average amplitude, rather than the peak amplitude, was chosen as our dependent measure because inspection of the ERP waveforms revealed that both components were broadly distributed, not sharply peaked.

Results

Inspection of the grand-averaged ERP waveforms (Fig. 1B) revealed that infants' neural processing of the familiar face versus the novel face was strikingly different depending on their exposure condition. Infants who had received 1 month of in-home exposure showed larger average amplitudes in response to the familiar face compared to the novel face for both the P400 (Familiar: $M = 6.75 \mu\text{V}$, $SD = 4.64$ vs. Novel: $M = 4.30 \mu\text{V}$, $SD = 3.41$) and the Nc (Familiar: $M = -5.11 \mu\text{V}$, $SD = 4.97$ vs. Novel: $M = -3.40 \mu\text{V}$, $SD = 3.15$). In contrast, infants who had received 1.5 min of in-lab exposure showed larger average amplitudes in response to the novel face compared to the familiar face for both the P400 (Familiar: $M = 6.15 \mu\text{V}$, $SD = 4.79$ vs. Novel: $M = 8.21 \mu\text{V}$, $SD = 3.82$) and the Nc (Familiar: $M = -5.22 \mu\text{V}$, $SD = 4.70$ vs. Novel: $M = -6.88 \mu\text{V}$, $SD = 3.84$) (see Fig. 1C). To capture the opposite pattern of results shown by the two groups, we conducted 2 (Group: experience vs. no-experience) $\times$ 2 (Condition: familiar vs. novel) $\times$ 3 (Laterality: left, midline, and right) mixed-model ANOVAs, separately for the P400 and Nc components.

For the P400, there were no main effects of group or condition; however, there was a significant interaction between these variables, $F(1, 33) = 9.35$, $p = .004$. Follow-up paired t -tests revealed that within the experience group, the P400 was significantly larger in response to the familiar face than the novel face, $t(15) = 1.94$, $p = .036$ (one-tailed), whereas in the no-experience group the P400 was significantly larger in response to the novel face than the familiar face, $t(18) = -2.23$, $p = .020$ (one-tailed). Additionally, there was a main effect of laterality, $F(2, 66) = 8.16$, $p = .001$, that was qualified by a significant condition $\times$ laterality interaction, $F(2, 66) = 4.77$, $p = .013$. To follow up this interaction, one-way repeated measures ANOVAs were conducted examining the effect of laterality within each condition separately. The P400 response to the familiar face was significantly larger over right and midline leads than over left leads, $F(2, 68) = 10.61$, $p < .001$; however, the P400 response to the novel face did not differ across leads, $F(2, 68) = 2.03$, $p = \text{ns}$.

Similar to the P400, the Nc showed no main effects of group or condition, but a significant interaction, $F(1, 33) = 4.34, p = .045$. Follow-up paired t -tests revealed that within the no-experience group, the Nc was significantly larger in response to the novel face compared to the familiar face, $t(18) = 1.74, p = .049$ (one-tailed); however, in the experience group, the Nc amplitude did not differ between the groups, $t(15) = -1.26, p = \text{ns}$. There was no main effect of laterality (left, midline, and right) or interactions involving laterality for the Nc component, indicating that these effects were not lateralized.

Overall, these findings indicate that although both groups of infants distinguished between the familiar and a novel face, the amount and type of exposure to the familiar face significantly altered the neural representation of that face in relation to a novel face.

Discussion

Our findings indicate that the amount of exposure to a familiar stimulus (in this case, a face)—and/or the context in which that stimulus was experienced—altered the neural response to that stimulus in relation to a novel stimulus. Infants who received only brief in-lab exposure to the familiar face showed larger amplitude brain activity in response to the novel face compared to the familiar face. In contrast, infants who received extensive in-home exposure to the familiar face showed larger amplitude brain activity in response to the familiar face compared to the novel face. Both patterns of brain activity are consistent with the infants being able to discriminate between the familiar and novel faces. However, the opposite direction of effects in the two different exposure conditions suggests that the neural representation of the familiar face was altered by the increased exposure time (and potentially the context of exposure and the delay between last exposure and test).

That the neural correlates of visual recognition are sensitive to the amount of exposure to a familiar stimulus is consistent with previous research. Habituation and oddball paradigms have demonstrated that after brief familiarization to one object, infants' brain activity tends to be larger for a more novel object (Courchesne et al., 1981; Karrer & Ackles, 1987), which parallels the finding here for the no-experience group. In contrast, other studies have demonstrated that infants show increased amplitude brain activity in response to objects that have become very familiar over the course of the infant's day-to-day experiences (e.g., mother's face, favorite toy—Carver et al., 2003; de Haan & Nelson, 1997, 1999), which parallels the finding here for the experience group. In addition to studies that have examined the neural correlates of visual recognition following brief or extended exposure, there is, of course, a whole body of literature examining infants' behavioral responses to familiar and novel objects. Numerous studies have demonstrated that young infants show a consistent novelty preference (i.e., preferential attending to a novel stimulus over a familiar stimulus) following brief familiarization (Fagan, 1970, 1971, 1972; Fantz, 1964). Other studies have demonstrated that young infants show familiarity preferences (i.e., preferential attending to a familiar stimulus over a novel stimulus) in certain circumstances. Most notably, young infants show a familiarity preference for the mother's face compared to a stranger's face (Pascalis et al., 1995).

In concert with findings that extremely brief familiarization results in behavioral familiarity preferences (Roder, Bushnell, & Sasseville, 2000), the results from this and previous studies suggest a U-shaped function of exposure time on the behavioral and neural responses to familiar objects. That is, extremely brief exposure results in a behavioral preference for familiarity (Roder et al., 2000); brief exposure results in a behavioral preference for novelty (Fantz, 1964) and increased brain activity to a novel object (i.e., the pattern of activity observed in the “no-experience” group in the current study; see also Pascalis et al., 1998; Reynolds & Richards, 2005); and extended exposure results in a behavioral preference for

familiarity (Pascalis et al., 1995) and increased brain activity to the familiar object (i.e., the pattern of activity observed in the “experience” group in the current study; see also de Haan & Nelson, 1997; 1999; Carver et al., 2003). Since few studies have directly examined the neural correlates of recognition after very short familiarization times (although see Nelson & Collins, 1991 for an exception), it is unclear whether the familiarity preference observed in this situation indicates an underlying increase or decrease in brain activity in response to the familiar object. This remains an area for future investigation. Despite the intriguing correspondence between the behavioral and neural responses to familiar versus novel objects under different exposure conditions, future research is required to determine exactly how these two measures are related (e.g., does the size of a novelty preference correlate with the amplitude of the Nc component—see Reynolds, Courage, & Richards, 2010, for a recent investigation into this issue).

The current findings extend previous results in two key respects. First, by using the same stimuli in both the brief and extended exposure conditions (unlike previous studies, which have generally examined the effects of either brief or extended exposure, but not both), we can be more certain that the difference in neural responses between the two conditions is due to the difference in amount of exposure time and not to differences among the stimuli used in previous studies. Second, the majority of previous studies investigating the effects of extended exposure on the neural representations of familiar and novel objects have taken advantage of the naturalistic, non-quantified exposure that occurs over the course of the infants' day-to-day life. In these studies, it thus becomes difficult to disentangle the effects of exposure time and other variables, like the affective significance of the objects involved (e.g., mother's face, a favorite toy). Because the stimuli used in the current study were unlikely to have become affectively significant to the infants, it is more likely that the difference between conditions was due to differences in exposure time. It is important to note, however, that the context in which infants experienced the familiar object in the current study did differ between the brief and extended exposure conditions. Therefore, it is possible that the observed condition differences had their origins not only in the amount of exposure the two groups of infants received, but also in the context in which that exposure occurred (i.e., home vs. lab).

Although the current findings have helped to elucidate the effects of exposure time on the neural representation of familiar objects, they do not speak directly to our understanding of how early experiences shape the development of the face processing system. However, the novel approach introduced in the current study has the potential to do so. Although there are some notable exceptions (Pascalis et al., 2005; Kuhl et al., 2003), the majority of previous studies that have attempted to examine this issue have relied on either variations in infants' natural environments (e.g., studies that contrast face perception in infants exposed to different race faces; see Bar-Haim et al., 2006; Kelly et al., 2007) or cases of early deprivation (e.g., studies that examine face perception in children who have experienced visual or psychosocial deprivation—Le Grand et al., 2001; Moulson et al., 2009). Although these approaches have been informative, the specific advantage of the current approach is that it has the potential to elucidate precisely how much and what kinds of experience are necessary to drive the development of particular abilities (again, note that we are not arguing that the current findings demonstrate the effects of experience on the development of face perception per se, only that the approach presented here has the potential to do so). In the domain of other-race face processing, for example, if we could expose infants to varying amounts of precisely controlled exposure to other-race faces, we could determine exactly how much (and what kind of) experience is necessary to maintain the ability to discriminate other-race faces in infancy, and when during development this experience must occur. Of course, the current study is only a first step towards quantifying how much exposure is required to alter the neural representation of a familiar object (the particular question of

interest in the current study), and future studies are necessary to delineate the boundaries of “very brief,” “brief,” and “extended” amounts of exposure. However, this study is an important proof of principle that this approach can be used fruitfully to explore how experience shapes the development of infants' perceptual capabilities.

The use of only one stimulus category in the current study makes it impossible to determine how generalizable these findings are (i.e., whether these findings are specific to faces or also hold true for other object categories). Future studies should take this question under investigation by examining the effects of exposure time on recognition using multiple different stimulus categories. Additionally, although we would argue that the face stimuli used in the current study were more naturalistic than those used in most lab-based studies of face recognition in that they were three-dimensional, obviously they were not real faces that moved and interacted with the infants. However, it is still interesting to speculate about how our findings fit with the existing face processing literature. Although the difference was not statistically significant, infants who received extensive exposure to the familiar face in the current study showed a larger Nc (and a significantly larger P400) to the familiar than to the novel face. This is similar to studies that have demonstrated that 6- and 18- to 24-month-old infants show a larger Nc when viewing their mother's face compared to a stranger's face (Carver et al., 2003; de Haan & Nelson, 1997, 1999). This suggests that the neural responses to familiar and novel faces in the infant's day-to-day life may be driven more by the visual structure of faces than their affective significance, although this remains a question for future investigation.

Despite the limitations of the current study, these findings are an important contribution to our understanding of the neural correlates of visual recognition in young infants. In addition, the “enrichment” approach used in the current study—i.e., systematically controlling infants' experience with particular stimuli—is a novel way to examine the role of early experience in the development of infants' perceptual abilities, one that can be applied to many different domains of development.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

(A) Grayscale photographs of two 3D models used in this study. (B) Grand-averaged ERP waveforms depicting the P400 (averaged across the 12 occipital electrodes included in the analyses) and the Nc (averaged across the nine frontocentral electrodes included in the analyses) for both the experience group and the no-experience group. The y-axis represents average amplitude in microvolts (μV); the x-axis represents latency in milliseconds (ms). Solid lines represent responses to the familiar face; dotted lines represent responses to the novel face. (C) Average amplitudes in microvolts (μV) for the P400 and Nc components. Bars represent the differential response to the familiar versus novel face (familiar minus novel) for the experience group (black bars) and the no-experience group (striped bars).

Error bars represent the standard error of the mean. For the P400, values above 0 μV indicate that familiar > novel, while values below 0 μV indicate that novel > familiar. For the Nc, values below 0 μV indicate that familiar > novel, while values above 0 μV indicate that novel > familiar. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]