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Brief Communication

Experience-dependent neural specialization during infancy

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ABSTRACT

The ability to recognize the difference among faces of another race or species declines from 6 to 9 months of age. During this time, perceptual biases are formed, leading to lasting deficits in recognizing individuals of other races and species. However, little is known about how early infant experience shapes the neural structures underlying face processing. Here we found neural specialization, in infants who received 3 months of training with six individually labeled monkey faces. However, neural specialization was not found after an equal amount of training with the same six faces labeled at the category-level (i.e., all faces labeled "monkey") or when infants were exposed to faces without labels. These results suggest that neural specialization for faces requires learning at the individual level during infancy.

1. Introduction

Infants enter the world with broad abilities to detect similarities and differences among faces, languages, and music (Scott, Pascalis, & Nelson, 2007). During the first year of life, these broad abilities decline as infants learn more about their surrounding environment, and create efficient and finely tuned perceptual capacities (Scott et al., 2007). In face perception, the ability to recognize differences among faces of another race or species appear to decline from 6 to 9 months of age (Kelly et al., 2007; Pascalis, de Haan, & Nelson, 2002; Pascalis et al., 2005; Scott & Monesson, 2009). For example, 6-month-old infants equally distinguish between two monkey faces and between two human faces, whereas 9-month-old infants and adults are better at distinguishing among human faces relative to monkey faces (Pascalis et al., 2002). This developmental process, called *perceptual narrowing*, is thought to shape adult expertise for faces; allowing adults to effortlessly accomplish a variety of everyday activities, including identifying and differentiating individuals, emotions, gender, race, attractiveness, age, and intentions (Scott et al., 2007). However, little is known about the specific experiences that lead to expert face processing or how early perceptual experience contributes to the specialization of the neural structures underlying face processing.

Recently, it was reported that 6-month-old infants maintained the ability to discriminate monkey faces after learning to recognize monkey faces individually (i.e., each face was individually labeled; Scott & Monesson, 2009). However, infants who learned these same faces categorically (i.e., all faces were labeled "monkey") or were simply exposed to these faces (i.e., faces were not labeled) showed a decline in the ability to discriminate monkey faces. These results suggest that the specificity of face representations is driven by individual-level learning during the first year of life.

Faces are typically perceived as a single holistic unit, whereas objects are perceived in a piecemeal fashion and are easily broken down into separable parts (Farah, Wilson, Drain, & Tanaka, 1995). One of the most robust markers of holistic face processing in adults is the face-inversion effect (FIE), or impaired recognition and delayed responses, when faces are presented upside-down relative to upright (Rossion & Curran, 2010; Yovel & Kanwisher, 2005). The FIE is associated with neural activity in regions of the occipital and temporal cortices, including the fusiform face area (FFA) and the occipital face area (OFA) (Yovel & Kanwisher, 2005). In adults, the N170 event-related potential (ERP) component, recorded over occipital and temporal regions of the scalp, differentiates faces and objects (Carmel & Bentin, 2001) and is enhanced to inverted relative to upright faces as well as objects of expertise (de Haan, Pascalis, & Johnson, 2002; Gajewaki, Schlegel & Stoerig, 2008; Rossion et al., 1999). However, the adult N170 inversion effect is specific to face categories for which adults have extensive experience and is absent in response to upright and inverted monkey faces (de Haan et al., 2002) as well as other race faces (Gajewaki et al., 2008). These results suggest that holistic face processing, as indexed by the adult N170, may arise during development and be experience dependent.

In infants face processing is indexed by two ERP components, the N290 and P400 (de Haan et al., 2002; Halit, de Haan, & Johnson, 2003; Scott & Nelson, 2006; Scott, Shannon, & Nelson, 2006). The present investigation examined the influence of experience on the development of the infant ERP face-inversion effect. Specifically, we

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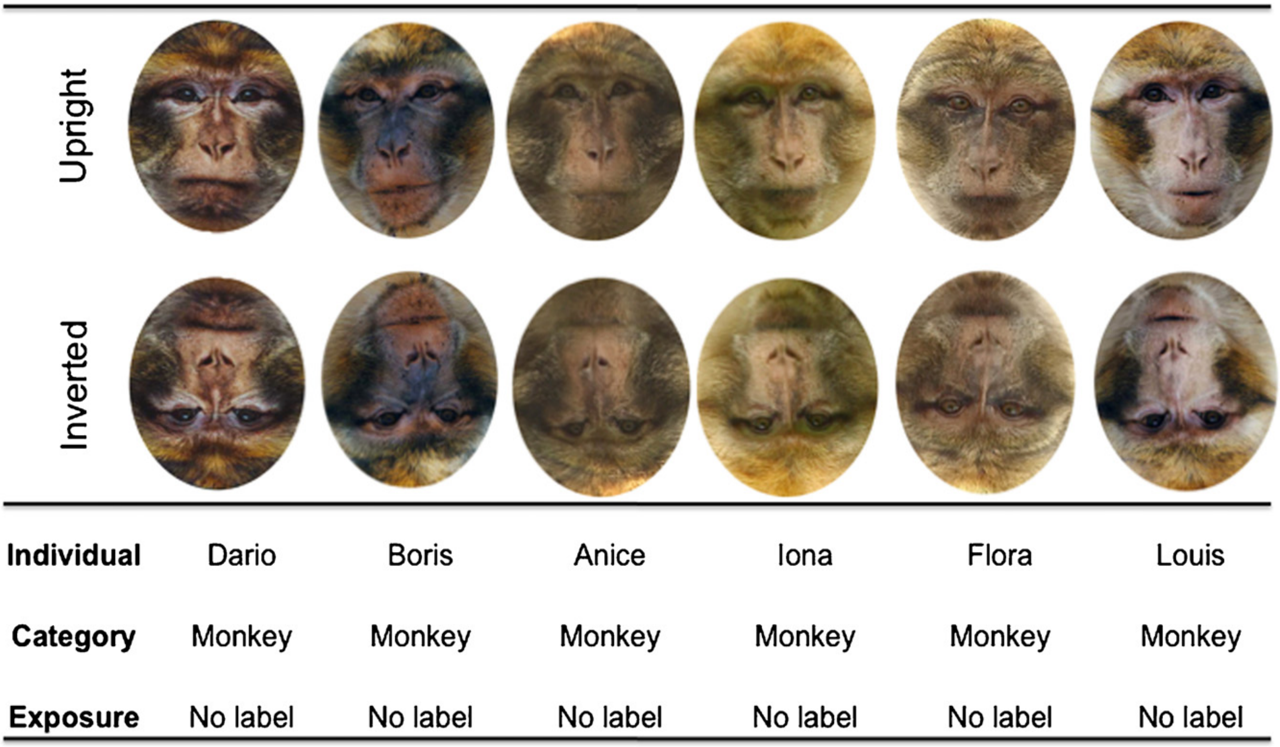

Fig. 1. Experimental stimuli. Color photographs of Barbary macaques (Macaca sylvanus), were used as stimuli for the pre- and posttest assessments. Six of these images were used for training and were presented within a picture book.

examined whether individual-level face learning, during the first year of life, is necessary for face-specific neural specialization as measured by ERPs. ERP responses to upright and inverted monkey faces were measured before (at 6 months) and after (at 9 months) 3 groups of infants ($n = 31$) completed 3 months of training with six monkey faces labeled at either the individual level (i.e., “Boris”, “Fiona”), the category-level (i.e., all faces labeled “Monkey”), or without labels (See Fig. 1).

Based on previous behavioral findings (Scott & Monesson, 2009) we predicted that individual-level training would lead to increased holistic processing resulting in ERP differences between upright and inverted faces at 9 months. However, neither category-level nor exposure training were expected to lead to ERP inversion effects. Prior to training we expected infants in all three groups to treat upright and inverted monkey faces similarly. Previous behavioral findings suggest that infants' ability to discriminate monkey faces decreases between 6 and 9 months of age without experience matching faces with individual-level labels (Pascalis et al., 2005; Scott & Monesson, 2009). Therefore two patterns of change are possible. First, consistent with previous behavioral results, infants in all three training groups may exhibit ERP inversion differences at 6 months which are maintained after individual-level training and abolished after either category or exposure training. This finding would support the hypothesis that perceptual narrowing is characterized as a “loss” in ability to perceptually discriminate faces within unfamiliar groups during development. Alternately, if the perceptual narrowing is not due to a loss, but instead to increased specialization for familiar groups of faces, infants should only exhibit ERP inversion effects after 3 months of individual-level training. No differences between upright and inverted monkey faces should be present prior to training or after category or exposure training. This latter pattern of results would suggest that previously reported behavioral effects are not due to a loss in ability but instead to increased neural specialization for commonly, relative to uncommonly, experienced face groups.

2. Materials and methods

The University of Massachusetts Amherst Institutional Review Board approved all methods and procedures used in this study.

2.1. Participants

Parents of all infants gave informed consent prior to testing. Participants were thirty-one 6-month-old infants (17 males, 14 females) who were randomly assigned to the individual-, category-, or exposure-training groups. Twelve infants completed individual-level training, 11 infants completed category-level training, and 8 infants completed exposure training. An additional 32 participants were excluded because they never returned for the posttest or were noncompliant with the training ($n = 15$), became fussy during testing at either session ($n = 5$), did not contribute enough artifact free trials to each condition ($n = 7$), or their mean amplitude or latency was 1.5 standard deviations away from the mean of all participants for the conditions of interest ($n = 5$). All infants were born full term and had no visual or neurological abnormalities. Participants were tested at 6 months (mean age = 185.89 days, $SD = 8.30$) and 9 months (mean age = 276.03 days, $SD = 8.98$ days) of age. At each session, the families of participants were paid $10 and given a small toy for their participation.

2.2. Stimuli and apparatus

Twelve digitized color photographs of Barbary macaques (Macaca sylvanus), presented on a dark gray background at a visual angle of approximately 13°, were used as stimuli for the pre- and posttest assessments. Six of these images were used for training and were presented within a picture book (see Fig. 1).

2.3. Procedure

2.3.1. Electrophysiological procedure

At pre- and posttest infants passively viewed trained and untrained monkey faces while seated on their parents' lap. Each image was presented for 500 ms. Half of the images included the six trained monkey faces (from the book) and half of the images were of six untrained monkey faces. An experimenter observed infants' gaze direction and only presented trials when infants were attending to the screen. Each trial consisted of a 100 ms baseline, a 500 ms stimulus presentation, and a 1000–1500 ms inter-trial interval. Infants completed an average of 97 ($SD = 35.11$) trials at pretest and 115 ($SD = 45.21$) trials at posttest.

ERPs were collected with a 128-channel Geodesic Sensor Net connected to a DC-coupled 128-channel, high input impedance amplifier (Net Amps 300 TM, Electrical

Geodesics Inc., Eugene, OR). Amplified analog voltages (.1–100 Hz bandpass) were collected continuously and digitized at 500 Hz. Individual electrodes were adjusted until impedances were less than 50 kΩ.

Post-recording processing was completed using Netstation 4.3 (Electrical Geodesics Inc., Eugene, OR). Stimulus locked ERPs were baseline-corrected with respect to a 100 ms pre-stimulus recording interval and digitally low-pass filtered at 40 Hz. Trials were discarded from analyses if there were more than 12 bad electrodes (changing more than 300 μV in the entire segment). Individual channels that were consistently bad (off-scale on more than 70% of the trials) were replaced using a spherical interpolation algorithm. Following artifact detection, each trial was visually inspected for noise and rejected if a significant amount of noise or drift was present. Participants with fewer than 15 artifact free trials per condition were excluded from analyses. At pretest (6 months) a mean of 24 (*SD* = 8.44) trials contributed to each of the four conditions across all groups. At posttest (9 months) a mean of 29 (*SD* = 12.31) trials contributed to the average of each condition after individual-level training, a mean of 28 (*SD* = 11.10) trials contributed to the average of each condition after category-level training, and a mean of 29 (*SD* = 11.10) trials contributed to the average of each condition after exposure training. An average reference was used to minimize the effects of reference site activity and accurately estimate the scalp topography of the measured electrical fields.

Mean amplitude was measured between 220 and 410 ms after stimulus onset. This window began one standard deviation before the peak of the N290 component and ended one standard deviation after at the peak of the P400 component. Electrodes over the occipital regions of the left and right hemisphere were averaged for analysis (right hemisphere: 83, 82, 88, 89 (corresponding to O1); left hemisphere: 70, 69, 73, 74 (corresponding to O2)). Means were submitted to separate 2 × 2 × 2 × 2 MANOVAs across training groups and for each of the three training conditions, including two levels of test (pretraining at 6 months; posttraining at 9 months), 2 levels of orientation (upright; inverted), 2 levels of training (trained monkey faces; untrained monkey faces), and 2 levels of hemisphere (right, left). Follow-up analyses of significant interactions were conducted using paired sample *t*-tests. Latency analyses were conducted but are not reported here because no significant differences were found across training groups.

2.3.2. Training procedure

After the pretest, participants in the individual-training group were sent home with books in which six images of monkey faces were labeled at the individual level (e.g., “Boris”, “Iona”). Participants in the category-training group were sent home with books in which the same six images of monkey faces were labeled at the category-level (i.e., all were labeled “monkey”), and participants in the exposure condition were sent home with books in which the same six images were not labeled. For each group (individual, category, exposure), there were two different training books, counterbalanced across participants, containing six different monkey faces. The training books were randomly assigned within each group, so half of the infants were trained with one set of 6 faces and the other half were trained with another set of 6 faces. The 6 monkey faces not present in the training book served as untrained images at both pretest and posttest.

After the pretest assessment, parents were given a diary and training schedule with instructions to read the book for 10 min with their infant everyday for the first 2 weeks, every other day for the following 2 weeks, every third day for the next 2 weeks, and every fourth day until their 9-month posttraining assessment. Parents were instructed to only use the provided labels when referring to the images and were given a diary to record their training efforts. Parents were considered compliant with the training if they followed the schedule for at least 75% of the time.

3. Results

To determine whether ERP inversion effects are driven by individual-level face learning during infancy, mean amplitude was

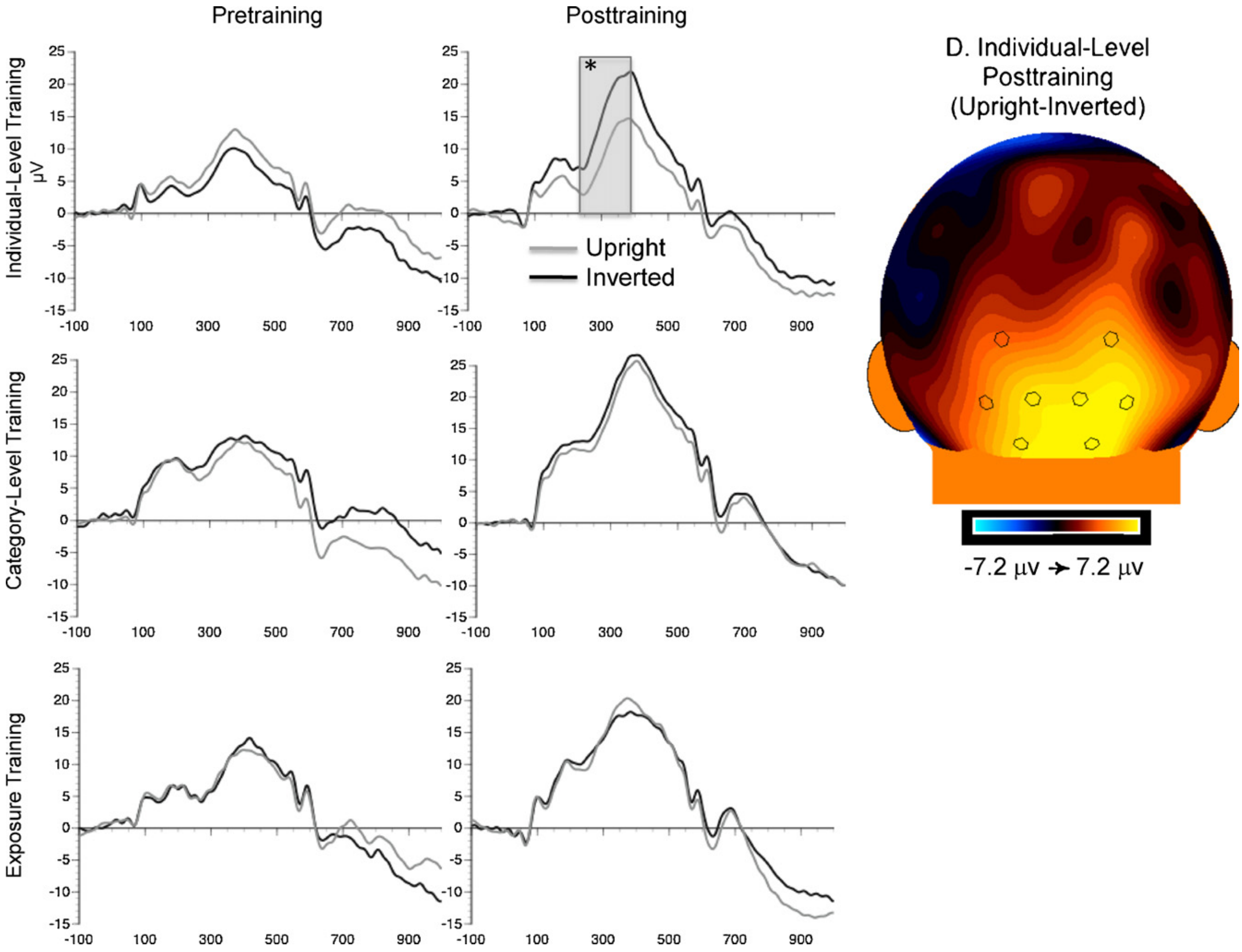

Fig. 2. (A–C) ERP waveforms and topographic maps. ERP responses averaged across hemispheres in response to upright and inverted trained and untrained monkey faces. (A) Mean amplitude (gray box) was greater for inverted relative to upright monkey faces after individual-level training, (B) but not after category-level training or (C) exposure training. (D) Topographic distribution of the amplitude difference between inverted and upright faces before and after individual-level training.

measured from the peak of the N290 (220 ms) to the peak of the P400 (410 ms) over the occipital regions of the scalp before and after training.

3.1. Overall training

In order to determine whether there were any general training effects, participants were first collapsed and into a single analysis. Results revealed a main effect of pretraining/posttraining ($F(1, 30) = 12.8$, $p = .001$, $\eta 2 = .30$) due to a larger peak-to-peak amplitude posttraining relative to pretraining. There was a significant interaction between pretraining/posttraining and whether the faces were trained or untrained ($F(1, 30) = 5.18$, $p = .022$, $\eta 2 = .16$). Follow-up paired *t*-tests showed that this interaction was due to a marginally greater amplitude to untrained faces compared to trained faces posttraining ($t(30) = -1.88$, $p = .07$) a significantly greater amplitude to unfamiliar faces post- compared to pretraining ($t(30) = -4.27$, $p = .001$) and to familiar faces posttraining compared to pretraining ($t(30) = -2.58$, $p = .015$). There was also a significant interaction between pretraining/posttraining and hemisphere ($F(1, 30) = 4.69$, $p = .38$, $\eta 2 = .13$) which was due to a greater amplitude response in both the left and the right hemisphere posttraining compared to pretraining (*p*'s < .01).

3.2. Individual-level training

Results revealed no differential ERP response to upright versus inverted or trained versus untrained monkey faces prior to training in 6-month-old infants. Posttraining, infants who were given experience associating monkey faces with individual-level labels exhibited a significant interaction between pre- and posttraining and whether the faces were presented in the upright or inverted orientation ($F(1, 11) = 5.81$, $p = .03$, $\eta 2 = .34$). This interaction was due to a significantly greater peak-to-peak amplitude to inverted relative to upright monkey faces posttraining ($t(11) = -2.18$, $p = .05$; see Fig. 2A and D) and a greater amplitude response to inverted faces posttraining relative to pretraining (($t(11) = -2.42$, $p = .03$). There was also a significant interaction between pretraining/posttraining and whether the faces were trained or untrained ($F(1, 11) = 6.18$, $p = .030$, $\eta 2 = .36$). Follow-up paired *t*-tests showed that this interaction was due to a marginally greater amplitude to untrained faces compared to trained faces posttraining ($t(11) = -2.03$, $p = .07$) and marginally greater amplitude to unfamiliar faces post- compared to pretraining ($t(11) = -2.02$, $p = .07$).

3.3. Category-level and exposure training

Neither category-level nor exposure training, led to differential ERP responses to upright versus inverted monkeys (see Fig. 2B and C) or trained versus untrained monkey faces. Category training led to a significantly greater amplitude response posttraining relative to pretraining ($F(1, 10) = 8.60$, $p = .02$, $\eta 2 = .46$).

4. Discussion

These data suggest that infants tune their visual neural representations to environmentally salient stimuli experienced from 6 to 9 months of age. Previous studies investigating perceptual narrowing in face processing suggest that infants' ability to discriminate among unfamiliar groups of faces declines from 6 to 9 months of age without experience individuating faces within these groups (Pascalis et al., 2005; Scott & Monesson, 2009). The current results suggest that experience individuating faces also leads to more holistic perceptual representations which likely contribute to the ability to discriminate among these faces at 9 months. More specifically, we show that labeling faces individually led to an occipital–temporal ERP inversion effect, not present prior to training. This inversion effect was similar to what has been reported when adults view upright and inverted human faces and was the result of an increased response to inverted monkey faces after individual-level training. Notably, neither category-level nor exposure training resulted in inversion effects, suggesting that the neural mechanisms responsible for face processing are specifically dependent on early experience individuating faces.

Previous developmental ERP studies have found both the N290 and the P400 components to index infant face-processing abilities (de Haan et al., 2002; Halit et al., 2003; Scott et al., 2006; Scott & Nelson, 2006). Here, we find training effects that begin at the N290 component and continue to the P400 component. de Haan et al. (2002) recorded ERPs from 6-month-old infants and adults while they viewed upright and inverted monkey and human faces. Half of the infants viewed monkey faces and half viewed human faces, and they found that whereas infants viewing monkey faces only exhibited an inversion effect in the left hemisphere, infants viewing human faces showed bilateral inversion effects consistent with effects we see after individual-level training in the present investigation. It is notable that unlike de Haan et al. (2002) we did not find any inversion differences for monkey faces, prior to training, in 6-month olds, even when we collapse across all training groups. More work is needed to determine why this discrepancy exists and whether or not infants show consistent inversion effects for unfamiliar groups of faces or objects prior to training.

The present results further implicate both the N290 and P400 as precursors to the adult N170 and suggest that the widely reported N170 inversion effect may be a result of experience learning faces at the individual level during infancy. From these results, we conclude that perceptual narrowing should not be characterized as a "loss" in ability but rather as an increase in neural specialization for faces learned at the individual level.

The present results are also consistent with several studies investigating the acquisition of perceptual expertise in adults. For example, when two groups of adults were trained to either categorize or individuate the same novel objects, individuation but not categorization training led to increased face-like holistic processing of these objects (Wong, Palmeri, & Gauthier, 2009). Combined with previous findings, the results from the present investigation suggest that the manner in which adult perceptual expertise is acquired is similar to the manner in which face expertise is acquired through experience during development.

The present results lead to several questions about the specificity and timing of perceptual narrowing. First, it is unclear whether the period from 6 to 9 months of age marks a sensitive period in development when the maturation of the infant brain is particularly receptive to individual-level learning or whether these neural structures are similarly receptive to experience across the lifespan. Coincident with perceptual narrowing, the brain is experiencing an exuberance of synaptic connections, followed by the pruning of these connections to adult levels (Huttenlocher, de Courten, Garey, & Van der Loos, 1982). It is possible that experience-dependent pruning, within the occipital and temporal cortices, leads to entrenched perceptual abilities and difficulty discriminating among individuals within unfamiliar face groups. However, it is also possible that repeated individual-level perceptual experience with certain groups of faces increases the strength of the neural circuit responding to familiar face groups. This type of increase in synaptic efficacy occurs across the lifespan in the presence or absence of synaptogenesis and pruning.

A recent investigation (Sugita, 2008) reared infant non-human primates in an environment without faces for 6–24 months. After deprivation monkeys did not prefer to look at either human or monkey faces whereas non-deprived monkeys preferred to look at monkey faces. The deprived monkeys were then trained with either human or monkey faces. After training, monkeys only discriminate among trained face types. Monkeys trained with human faces continued to show deficits in monkey face discrimination at least 1-year after placement in a typical environment with other monkeys. Sugita reports that the deprivation effects, as well as the training effects, were not tied to a particular period in development suggesting that although there does appear to be a sensitive period, it can be activated at anytime. These results suggest that the perceptual narrowing is likely linked to increases in synaptic efficacy rather than synaptogenesis and pruning within occipital and temporal brain regions. However, more work is needed to determine whether human perceptual narrowing is tied to a sensitive period in development or whether this type of learning is similar to learning occurring across the lifespan.

Although the present results suggest that individual-level experience drives the development of the face processing system, the nature of this experience is still not completely understood. For example, it is possible that individual-level training led to greater attention allocation or increased perceptual memory (or both) on the part of the infant, which resulted in posttraining inversion effects. Future research should determine whether the development of attention or memory contributes to perceptual narrowing for faces. In addition, the results of the present investigation do not allow us to determine whether or not verbal labeling is a necessary for specialized neural responses for faces to emerge or whether individual-level training, without labels, will lead to similar results. It is possible that verbal labeling drives the development of neural structures related to face processing resulting in highly specialized responses. However, it is also possible that any correlated cue (e.g., unique color) will lead to similar inversion effects, suggesting that verbal labeling is sufficient but not necessary for the development of face processing.

These findings further elucidate the role of experience in the specialization of neural regions underlying face processing. The present data suggest that experience learning individual-level labels for six monkey faces, from 6 to 9 months of age, leads to face-like neural responses at 9 months. However, learning these same six monkey faces labeled at the category-level or without labels results in perceptual narrowing and neural responses more similar to what is seen for non-expert object processing. Moreover, perceptual narrowing is not a “loss” in ability but instead related to an increased focus of faces learned at the individual level relative to faces that are typically categorized. Thus, perceptual narrowing and early indicators of the other race effect, arise because infants do not typically learn to individuate faces of other races.

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