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Plasticity of face processing in infancy

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Experience plays a crucial role for the normal development of many perceptual and cognitive functions, such as speech perception. For example, between 6 and 10 months of age, the infant's ability to discriminate among native speech sounds improves, whereas the ability to discriminate among foreign speech sounds declines. However, a recent investigation suggests that some experience with nonnative languages from 9 months of age facilitates the maintenance of this ability at 12 months. Nelson has suggested that the systems underlying face processing may be similarly sculpted by experience with different kinds of faces. In the current investigation, we demonstrate that, in human infants between 6 and 9 months of age, exposure to nonnative faces, in this case, faces of Barbary macaques (Macaca sylvanus), facilitates the discrimination of monkey faces, an ability that is otherwise lost around 9 months of age. These data support, and further elucidate, the role of early experience in the development of face processing.

development | early experience | monkey | recognition

A mong the numerous visual inputs that we receive each moment, the human face is perhaps one of the most salient. The importance of the many signals it conveys (e.g., emotion, identity, direction of eye gaze, etc.) and the speed and ease with which adults typically process this information are compelling reasons to suppose that brain circuits specialized for processing faces may exist (1). However, there is still considerable debate as to whether face processing is a truly special perceptual process and is organized as such at birth, or, instead, has its origin in a more general-purpose perceptual system that becomes specialized with experience (2).

Developmental studies can provide important information to constrain the claims of the different sides of this debate. It is well documented that experience is crucial for the normal development of many perceptual and cognitive functions, such as speech perception. For example, before 6-8 months of age, infants are able to discriminate among a wide range of phonemes (3). This ability tends to narrow with repeated exposure to phonemes in the infant's native language, and a lack of exposure to phonemes outside the native language (4-6). However, Kuhl et al. (7) recently demonstrated that some experience with nonnative languages from 9 months of age facilitates the maintenance of this ability at 12 months. The same pattern of results is observed in infants raised in a bilingual environment (8). Nelson (9, 10) has suggested that the systems underlying face processing may be similarly sculpted by experience with different kinds of faces. Although the pattern of development across speech and face processing may be similar, it is unlikely that the mechanisms and developmental trajectory underlying these different perceptual systems are the same.

Indeed, recent developmental studies have underscored the importance of visual experience in the development of face processing. For example, patients with congenital cataracts who were deprived of patterned visual input for the first months of life demonstrate intact object processing but subtle deficits in face processing (11, 12). Moreover, when patients whose visual input had been restricted mainly to one hemisphere during infancy were examined, it was found that visual input to the right hemisphere, but not the left hemisphere, was critical for expert

levels of face processing to develop. This result is consistent with a model put forth by de Schonen and Mathivet (13) concerning the precocity of the development of the right hemisphere and its involvement in face processing.

In addition, Quinn *et al.* (14) demonstrated that the social environment also influences the tuning of face processing during the first months of life. They have shown that 3-month-old infants prefer to look at female faces when paired with male faces. This preference may reflect a gender bias of the face prototype toward the primary caregiver, which in most cases is female. Importantly, they have identified a population of infants for whom the father was the primary caregiver; such infants demonstrate a bias for male faces when tested in the same manner.

The face-processing system is also influenced by the type of face experienced during the course of development. One example is the well known "other-race effect" (ORE), in which adults find it easier to differentiate faces from their own ethnic group (15). Children demonstrate the same effect (16–22), although reports differ regarding the onset of the effect, ranging from 3 months (23) to 8 years (18, 19). Recently, Sangrigoli et al. (21) reported that native French adults and Korean adults who had moved to France during adulthood both demonstrated the ORE. Conversely, Korean adults adopted by French families during childhood (3-9 years old at time of adoption) performed identically to the native French adult population (21). This finding indicates that the face-processing system remains relatively plastic throughout childhood, allowing the ORE observed at 3 months of age to be reversed. Furthermore, intensive training with other-race faces can extinguish the ORE in adults who initially demonstrate the effect (24–26).

A final example of the importance of early experience is the "other-species effect," in which both monkey and human adults are better at recognizing faces from their own species as assessed with the visual paired comparison (VPC) task (27) or with a forced-choice task (28). Many researchers attribute the ORE and other-species effects to the relatively common experience of having greater exposure to faces of one's own race compared with other races (15) and greater experience with faces within one's own species compared with other species. Thus, it appears that these effects can be accounted for by the notion that we are best at recognizing faces similar to those we see most often (i.e., faces of individuals with whom we have most contact, be they of the same race or the same species). However, it is important to differentiate between other-race faces, which belong to the same face category as own-race faces (i.e., human faces), and otherspecies faces, which belong to a separate face category (i.e., nonhuman primate). Whereas the face-processing system remains flexible for the category of faces to which we are most exposed, this plasticity may not extend to other face categories.

Collectively, these studies suggest that visual input during early infancy and childhood influences the development of many

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Abbreviations: ORE, other-race effect; VPC, visual paired comparison.

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aspects of face processing. However, the exact nature and origins of this experience and its effect on the development of face processing has been the subject of considerable discussion. According to Valentine's (29) model, faces are encoded as individual points within a multidimensional face space defined by a set of dimensions (gender, eye color, etc.). Valentine proposes a norm-based coding model, whereby faces are encoded as vectors according to their deviation from the central tendency, or prototypical average of the face space. Nelson (9, 10) has proposed that this face prototype is broadly tuned at birth and that the dimensions this prototype encodes may differ both qualitatively and quantitatively in infants compared with adults. One way to think about the development or formation of a face prototype is based on the experience or kinds of faces one encounters. For example, if this prototype is thought of as a continuum of all incoming faces, then the more a face deviates from the prototype (other-race and other-species faces), the less this face is easily discriminated, compared with faces that are more similar to the prototype. The development of the face prototype is most likely influenced by a number of factors, including, but not limited to, exposure time (number of faces seen), dynamic and emotionally salient information provided within the face, the timing and preferences of the development of the visual system, and changes in the categorization of individuation of people (i.e., the mother's face may have more "weight" in the formation of the prototype). Combined, these experiences gradually lead to the face prototype becoming more

Early in life, infants possess a remarkable ability to discriminate among and between a large corpus of different faces, such as faces from an unfamiliar species or an unfamiliar race. With experience, the infant's face-representation system becomes more precise and increasingly restricted to faces with which infants are most familiar. This, in turn, results in the development of expertise, in which the ability to discriminate between faces that one has not had exposure to (or has had less exposure to) is not as good as discrimination between faces with which one has had experience.

An example of this specialization of the face processing system was demonstrated in a previous study (30), in which we reported that although 6-month-olds, 9-month-olds, and adults are all equally good at discriminating two human faces, only 6-montholds can also discriminate two monkey faces. Thus, it seems that some time after 6 months of age the face prototype becomes less generalized and more specific to faces commonly experienced in one's environment. Furthermore, uncommon faces, or faces that differ on the defined prototypical dimensions, are no longer easily discriminated. This observation led us to ask how flexible this representation is, and whether we can maintain its early, more general nature by exposing infants to other-species faces between the ages of 6 and 9 months.

In our investigation, 6-month-olds were exposed regularly to Barbary Macaque monkey faces during a 3-month period, and their ability to discriminate monkey faces was then assessed at 9 months. Their discrimination performance was compared with a control group of 9-month-olds who received no training. We hypothesize that if the ontogeny of the face-processing system progresses from being very broadly tuned to more specific and narrowly tuned, then exposure to the monkey faces should extend the ability to discriminate faces from another species.

Experimental Procedures

Infants were tested at 6 and 9 months of age. Each infant was tested three times. On his/her first visit, the 6-month-old's pretraining ability to discriminate between monkey faces was assessed with a VPC task. Parents were then provided with a folder for training purposes, which contained six labeled monkey images (each monkey had a name) that were different from those used in the baseline test. Parents of the infants were asked to present the pictures in the folder to their child for 1–2 min every day for 2 weeks and then less frequently following a fixed schedule of exposures during the 3-month period. The infants returned after the 3-month training period, and their ability to recognize the monkey faces from the folders was measured by using a Visual Preference task. During the third test, the infant's ability to discriminate between novel monkey faces (i.e., those not previously seen) was assessed during a posttraining recognition test by using the same recognition task used during their first visit. A separate group of 9-month-olds, with no previous exposure to monkey faces, was used to assess an infant's ability to discriminate between monkey faces without experience.

Participants. Eighteen 6-month-olds (7 boys and 11 girls; mean age = 186 days, ranging from 83 to 194 days) were included in the training group. Three infants at 6 months of age were not included because of crying or fussing. Two infants were excluded because they did not return for testing at 9 months of age. All infants included for analysis returned at 9 months of age (mean age = 274 days, ranging from 268 to 292 days). Thirteen 9-month-olds (8 boys and 5 girls; mean age = 274 days, ranging from 269 to 283 days) were included in the control group. One infant was excluded from the control group because of excessive

Stimuli. The face stimuli used were 24 color pictures (12 in the training group and 12 in the control group) of Barbary macaques (M. sylvanus) presented against a white background (Fig. 1). Four different series of faces, containing six faces in each, were used for the experiment. Folders were made for each of the four series of faces, each containing the images and names of six test stimuli. Faces were presented in a frontal orientation, with the most neutral expression possible. All of the pictures were cropped in a standard oval, removing salient cues (e.g., ears). Stimulus size and brightness were kept uniform by using PHO-TOSHOP (Adobe Systems, San Jose, CA). The pairing of the pictures was completed by the experimenters on the basis of pictures being similar but distinguishable. When projected onto the screen, each picture was 15 cm high and 10 cm wide (14° of visual angle). Only one stimulus was projected in the center of the screen for the familiarization period, and two stimuli were projected side by side separated by a 12-cm gap during the retention tests.

General Method. VPC was used to assess facial discrimination in infants both before and after an exposure/training period with monkey faces. The VPC task developed by Fantz (31, 32) is commonly used to measure visual recognition memory in preverbal and nonverbal individuals. The VPC task exploits an infant's attraction to novelty to assess his/her recognition memory for previously seen stimuli. In this task, infants are first presented with a stimulus for a familiarization period. Thereafter, the participant is presented with the same stimulus paired simultaneously with a novel stimulus. The key dependent measure is the length of time spent fixating each of the two stimuli. Longer duration of looking to one stimulus, generally the novel one, indicates discrimination and recognition memory.

Detailed Procedure. Half of the infants were tested in Minneapolis and the other half in Sheffield, U.K. All testing took place in a sound-attenuated chamber. Infants were seated on their mother's lap in front of a screen onto which the images were projected. A black-and-white CCD camera (Maplin Electronics, U.K.) (specialized for low-light conditions) was used to film the infant's eye movements. This eye movement was displayed to the experimenters, during recording, on an ITC control monitor. Time was recorded and displayed on the control monitor by using a



Fig. 1. Examples of stimuli used. Two different pairs of stimuli were used in each condition.

HORITA (Mission Viejo, CA) TG-50 time code generator at 25 frames per second. The film was then digitized to be analyzed frame by frame on a computer by using specialized software.

Pretraining Testing. During the experiment, parents were asked to look above the screen to avoid influencing their infants looking to either stimulus. Infants were familiarized to the monkey face for 20 s of cumulative looking. Stimulus fixation was assessed by corneal reflection of the stimuli. An observer hidden from the infant's view examined the eyes on a TV monitor and controlled the time for the presentation of different stimuli during the familiarization, the intertrial intervals, and the preference tests. A computer algorithm determined when 20 s of cumulative looking time was reached. The discrimination tests started when the infant looked at one of the two stimuli, and they ended after 5 s had elapsed. After the first 5-s test, the side on which the images were presented was reversed, and a second 5-s test was completed. After the pretraining session, parents were sent home with a folder containing six images of Barbary macaques, each with individual names. These six images were different from the one used during the pretraining test.

Parents were advised to note the date when testing began in the "Date Started" box and then check the relevant box after each presentation, working through the weeks as shown. The experimenters ensured that all parents understood exactly what was expected of them and how to complete the training schedule. Parents were also supplied with detailed written information along with contact information.

Posttraining Testing. Three months later, the infant's ability to recognize the folder's pictures was assessed. There were six trials, and for each trial, a familiar image from the learned series was presented with a novel image for 5 s, followed by a blank screen for 5 s. After a short break, a posttraining VPC test was conducted in the same way as the pretraining task by using a new set of pictures with completely novel monkey images. Only one trial was conducted for each infant.

After testing, the videotapes were played back, and for each

trial, the time each participant spent looking at both stimuli during the retention tests was recorded by using a frame-by-frame video recorder. Samples of videotapes were analyzed by two observers. The observers were blind to the lateral location of the novel and familiar test items. Interobserver reliability was calculated for 50% of the infants chosen from the sample at random. The amount of time required to reach the familiarization time and the two-test trial were double-scored for each of these infants. Direction of looking (left, right, or blinking/no fixation) was compared for each 40-ms frame. The average level of agreement was 95%.

Results

The looking time toward the novel and familiar stimuli is expressed as the percentage of looking time compared with the total looking time to stimuli (time spent looking at the novel stimulus divided by the time spent looking at the novel stimulus plus the time spent looking at the familiar). The data were analyzed by using a one-tailed t test that compared the fixation toward the novel stimulus with chance (50%).

Pretraining Test. VPC results for 6-month-olds reveal significantly longer fixations to the novel (56.2%) compared with the familiar monkey face (43.7%) (t=2.712, df = 17, P<0.05), thus demonstrating discrimination. These data replicate our previous result (30), suggesting that the effect found at 6 months of age is robust to changes in stimulus type (in this study, we used a new set of monkey faces from a different species).

Recognition of the Folder's Pictures. The average looking time toward the familiar and the novel picture was calculated across the six discrimination trials. The infants demonstrated longer looking time to the novel stimulus (53.8%) compared with the familiar (pictures from the training folder) stimulus (46.2%) (t = 2.994, df = 17, P < 0.05). These results suggest that infants successfully discriminated the six familiar monkey faces from unfamiliar monkey faces.

Discrimination Test Posttraining. Nine-month-old participants with monkey face training looked significantly longer toward the novel monkey face (55.8%) than toward the familiar monkey face (44.2%) (t = 2.963, df = 17, P < 0.05), thus demonstrating recognition.

Thirteen 9-month-old control infants with no previous exposure to monkey faces were tested in the same way. Results indicate that they looked equally long at the novel stimulus (49.8%) compared with the familiar stimulus (51.2%) (t = 0.43, df = 12, P > 0.05), replicating our previous report (30). These findings demonstrate that exposure to monkey faces from 6 to 9 months of age was sufficient to extend the infants' ability to discriminate monkey faces.

Discussion

The experiment reported here examined the effect of exposure to monkey faces on the specialization of the face-processing system to human faces during the first year of life. Our results are consistent with Nelson's hypothesis stating that a broadly defined face prototype exists at birth, and its development is influenced by the visual environment, leading to a more precise face prototype. Specifically, here and in our previous work, we observed a specialization of the face-processing system, as shown by the loss of ability to discriminate between faces from other species. However, with exposure to other species' faces, this loss is prevented in infants. Our results indicate, as hypothesized by Nelson (9, 10), that the development of face processing follows a trend similar to the one observed for speech processing. The duration of this effect has yet to be determined; similarly we also do not know how much exposure 6 month olds need to be able to discriminate monkey faces.

Kuhl et al. (7) have shown that social interaction is an important part of the learning mechanism. In their study, they

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compared a group of American infants passively exposed to a video of a native Mandarin speaker with a group of infants who were read stories by a native Mandarin speaker. Passive exposure did not prevent the loss of discrimination at 10 months of age. In our study, the procedure involved social interaction because the parents were asked to present the pictures of the monkey faces and their labels (or names) in a friendly way. It will therefore be important to replicate this study with passive exposure to monkey faces with and without labels to determine the importance of social interaction and individuation and how they facilitate learning.

These findings have implications for elucidating the role of experience in brain specialization. From our studies, we would speculate that the regions of the inferior temporal cortex (e.g., fusiform gyrus) that are known to be involved in face processing in adults are beginning to come on line during the first year of life. These data combined with our previous report (30) suggest that there may be a sensitive period, during the first year of life, for the development of face processing. However, at this time the nature and specificity of this sensitive period is relatively unknown. These data and the speculation of a sensitive period are consistent with work in early cataract patients who demonstrate a sensitive period for the development of a normal vision and a normal configural face processing (11, 12). Furthermore, the current findings support the notion that experience with faces early in life may influence and shape the development of a face prototype. The development of this prototype leads to biases in discriminating own-race and own-species faces compared with other-race and other-species faces.

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