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Face Processing: The Interplay of Nature and Nurture

Joonkoo Park, Lee I. Newman, and Thad A. Polk

A number of behavioral and neuroscientific studies suggest that face processing is qualitatively different from the processing of other visual stimuli. Why? Is face processing in some sense innate? What role does experience play in the development of face processing? The authors review recent evidence related to these questions. They begin by identifying some of the ways in which face processing is special. They then consider findings that demonstrate a crucial role for experience-independent genetic mechanisms in the development of face

processing and its neural substrates. Finally, the authors review studies demonstrating the crucial role played by experience-dependent mechanisms. These findings support the hypothesis that there is a genetic predisposition for a special face processing mechanism, but that experience plays a crucial role in tuning this mechanism during development.

Keywords: face perception; genetics; environment; ventral visual cortex

Face processing is a crucial cognitive ability. Recognizing faces provides one of the most fundamental ways of identifying individuals, and interpreting facial expression and eye gaze is required for social interaction and emotion perception. Accumulating evidence suggests that processing faces is qualitatively different from processing other visual stimuli (Farah and others 1998; McKone and others 2007), but whether face recognition is an innate human capability or is an acquired skill is a matter of debate. However, a simple binary view of the role of nature versus nurture in face processing is both problematic and unnecessary. In this review, we discuss a variety of empirical evidence for the subtle interplay between genetics and experience in the development of face processing.

Evidence That Face Processing Is Special

Faces appear to be processed differently than other visual stimuli. In particular, a number of phenomena have been shown to apply to the processing of faces, but not other visual stimuli (see Box 1). These empirical findings suggest that faces, unlike other objects, are processed in a holistic and configural manner (see Diamond and Carey 1986; Gauthier and Tarr 1997, for arguments that such configural processing can also develop for nonface stimuli with sufficient practice and expertise).

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Evidence for face-specific visual processing has also been found in neuroimaging studies that show domain-specific activations in the ventral visual cortex. Functional magnetic resonance imaging (fMRI), positron emission tomography (PET), and electroencephalography (EEG) studies have shown that part of the mid-fusiform gyrus, particularly on the right, is selectively activated when participants are viewing faces compared with other objects such as houses or man-made objects (Allison and others 1994; Haxby and others 1994; Kanwisher and others 1997; Puce and others 1995). Converging evidence now suggests that a network of multiple brain areas is involved in face perception. These areas appear to correspond to different subcomponents of face processing (e.g., identification, gaze direction, or facial expression; Haxby and others 2000; Ishai 2008).

The Role of Nature

The developmental trajectory of face processing offers insight into how genetics and experience might interact to produce this important cognitive ability. Previous studies have shown that even newborns have some ability to discriminate facelike stimuli from nonface stimuli, suggesting that face processing may have a prenatal component (Johnson 1991; Mondloch and others 1999; Box 1). One interpretation is that infants are born with an innate subcortical mechanism for detecting faces and that this mechanism is later replaced by cortical mechanisms that support more sophisticated face processing (Morton and Johnson 1991). The idea that face recognition may be innate and independent from experience is also supported by the neuropsychological finding that brain damage at 1

Box 1. The uniqueness of faces

A number of studies have found that faces are processed qualitatively differently than other visual stimuli. For example, newborns as young as 17 minutes old have a tendency to orient toward facelike stimuli presented in the periphery of the visual field (Johnson 1991; Morton and Johnson 1991). The infants were found to be selectively sensitive to stimuli with blobs that were arranged in a facelike fashion. Adults also process faces in unique ways. For example, adults are much worse at recognizing previously studied faces (Fig. 1A) when they are upside-down (bottom) than upright (top) (Yin 1969). Critically, this inversion effect does not apply to other complex objects such as houses and airplanes. An inversion effect is also observed in the processing of face parts. When the top and bottom halves of different familiar faces are combined to form a single novel face (Fig. 1B), identification of the component parts is impaired. However, this effect is unique to upright faces and disappears when the same stimuli are inverted (Young and others 1987). People are also better at recognizing a part of a face when it is presented in the context of a whole face than when it is presented in isolation (Fig. 1C). This effect is also unique to upright faces and does not apply to scrambled faces, inverted faces, or houses (Tanaka and Farah 1993).

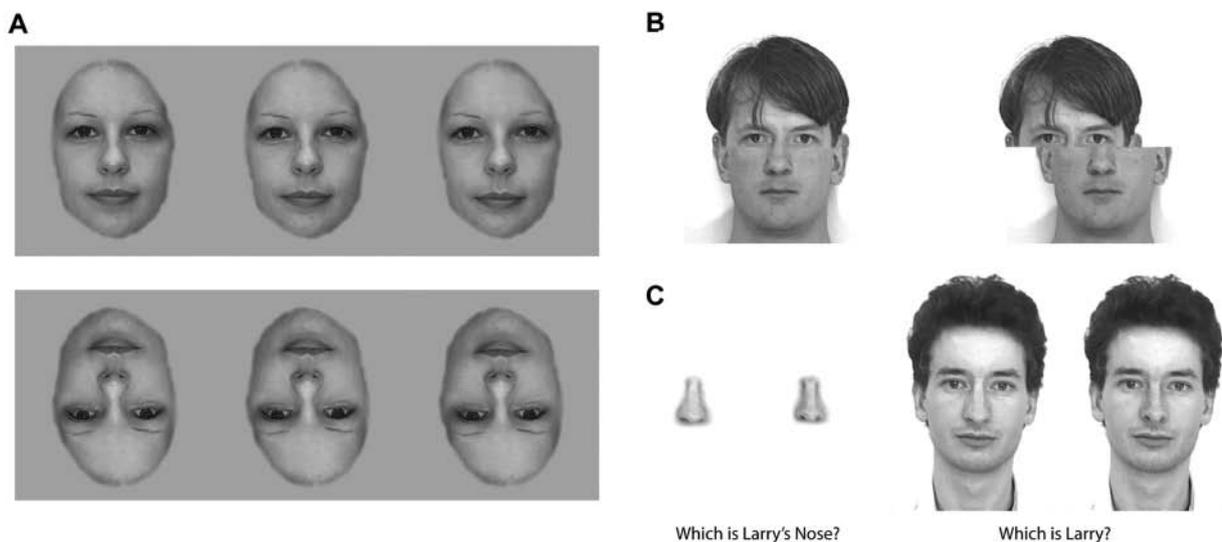


Figure 1. The uniqueness of face processing. (A) The face inversion effect: People are much better at recognizing familiar upright faces than familiar inverted faces, and this effect is larger for faces than for other visual stimuli. (B) When the top and bottom halves of different familiar faces are combined to form a single novel face, identification of the component parts is impaired. This effect is unique to upright faces. (C) People are also better at recognizing a part of a face when it is presented in the context of a whole face than when it is presented in isolation. This effect does not apply to scrambled faces, inverted faces, or houses.

day of age can lead to a lasting visual recognition deficit that disproportionately affects faces (Farah and others 2000).

A recent monkey study provides even stronger evidence for a genetic predisposition for face processing (Sugita 2008). In this study, infant monkeys were reared in a visually rich environment but with no exposure to either monkey or human faces for up to 24 months. The face-processing abilities of these monkeys were then assessed with a preferential looking technique and a visual paired-comparison procedure during and after the face-deprivation period.

Control monkeys that were reared in a normal environment showed a selective preference for monkey faces relative to nonface objects as expected. Surprisingly, the face-deprived monkeys also showed

strong preferences for both human and monkey faces even though they were never exposed to faces of any kind. Their preference not only for monkey faces but also for human faces, as well as their ability to discriminate not only individual monkey faces but also human faces, further suggests that this seemingly innate capability is not restricted to processing faces of their own species. Overall, these results demonstrate a significant role for experience-independent maturation in the development of face processing.

Evidence for such a genetic influence has also recently been observed at the neural level. Polk and others (2007) found evidence for an innate bias in the functional organization of face processing by studying twins. Identical or monozygotic (MZ) twins share the same genotype, whereas fraternal or dizygotic

(DZ) twins are no more genetically similar than are other siblings. Therefore, traits that are significantly more similar in MZ twins than in DZ twins are typically assumed to be significantly influenced by heredity. Neuroimaging studies using twin participants can therefore provide insights into the role that genetics plays in both neuroanatomy and neural function (Box 2).

In the study by Polk and others (2007), MZ and DZ twins performed a visual one-back task with gray-scale pictures of faces, houses, pseudowords, chairs, and phase-scrambled control stimuli in a blocked design as their brain activity was scanned using fMRI. The similarity of the normalized activation patterns elicited by faces (defined by the contrast face > phase-scrambled control or face > house) were calculated between twin pairs by computing a correlation coefficient. These patterns were significantly more similar in the MZ twins than in the DZ twins (Fig 2B). (The activation patterns elicited by houses were also more similar in MZ than DZ twins.) In contrast, the activation patterns elicited by words and chairs were no more similar in MZ twins than in DZ twins (Fig 2B). Furthermore, the interaction between zygosity and stimulus category was significant, indicating that the effect is not simply due to differences in structural similarity. The study therefore suggests a genetic influence on the functional organization of face processing and that heredity has a larger influence on the neural substrates underlying the recognition of faces compared with other stimulus categories. This interpretation is plausible from an evolutionary perspective in that visual processing of faces may have provided an important adaptive advantage for survival, whereas processing of relatively new manmade objects such as chairs would not have been as adaptively important.

The Role of Nurture

Experience also plays a crucial role in the development of face processing. For example, in the Sugita (2008) study discussed previously, early experience had a significant impact on the face processing of their monkeys. The face-deprived monkeys were taken into a special room for an initial exposure period. For a month, one group of monkeys was exposed to human faces only, and a second group was exposed to monkey faces only. When their preference and recognition ability was tested, monkeys selectively exposed to human faces showed a preference and superior discrimination ability for human faces (compared with monkey faces and nonface objects) and the monkeys selectively exposed to monkey faces showed a preference and superior discrimination ability for monkey faces (compared with human faces and nonface objects). This effect was present even a year after the monkeys were moved into a normal environment,

indicating that the initial experience during the sensitive period had a very significant impact on the monkeys' face-processing abilities.

The existence of a sensitive period for face processing has also been found in human studies. Pascalis and others (2005) exposed a group of 6-month-old human infants to pictures of six labeled monkey faces for 3 months, and recognition memory was tested using a visual paired-comparison task before and after this training period. Another group of 9-month-olds also performed the visual paired-comparison task as a control. The 6-month old infants were able to distinguish different monkey faces even before training; They had significantly longer fixations to the novel compared with the familiar monkey faces. Furthermore, they retained this ability after 3 months of training. In contrast, the 9-month-old infants in the control group looked equally long at both types of stimuli, suggesting that they had lost the ability to distinguish different monkey faces and that the experience of seeing monkey faces from 6 to 9 months had a significant effect on the face-processing abilities of the infants.

The effect of exposure on face processing is not limited to faces from other species. It is now well known that people are better at recognizing faces of their own race than another race (Kelly and others 2007; see Meissner and Brigham 2001, for a meta-analysis). This so-called other-race effect demonstrates the plasticity of face-recognition mechanisms because the effect does not depend on race per se, but rather on cultural experience, especially during infancy and youth (Sangrigoli and others 2005). This preference for own-race (or familiar) faces is known to start as early as 3 months of age (Bar-Haim and others 2006; Sangrigoli and de Schonen 2004). The effects of experience with faces within and across species suggest that experience-independent maturation cannot fully account for the development of face processing. In short, although we may in some sense be genetically wired to recognize faces, experience during the first few years after birth shapes our face-processing ability to support quick and accurate recognition of familiar faces.

How experience influences the neural organization underlying face processing is not well understood. Recent developmental fMRI studies have found age-related changes in fusiform face area (FFA) activity (but not other areas) suggesting an extended neural developmental trajectory of face processing (Golarai and others 2007; Scherf and others 2007). Furthermore, it is known that expertise, acquired from many years of experience, alters the activity of cortical areas known to be involved in face processing. For example, Gauthier and others (2000) recruited participants who were experts at recognizing car models and bird species. Neural activity in these subjects was estimated using fMRI while they performed identity- or location-matching tasks

Box 2. Genetic influences on anatomical and functional brain organization

Twin studies provide a valuable way to disentangle the influences of genetics and the environment in determining traits. In an early neuroimaging study of twins, Thompson and others (2001) investigated how genes might have influenced the structure of the human brain (Fig. 2A). In this study, they scanned 10 monozygotic (MZ) and 10 dizygotic (DZ) twin pairs. They first extracted a high-resolution surface model of the cortex and identified primary gyral patterns for each subject. Then gray matter density was measured at each cortical point for each participant, and intraclass correlation between pairs of MZ and DZ twins was computed for a similarity measure at each cortical point. The within-pair similarity for gray matter density was very high (intraclass correlation coefficient of up to 0.9) in sensorimotor and linguistic cortices (Broca's and Wernicke's areas) in both MZ and DZ pairs. However, the similarity within DZ pairs was significantly lower than MZ pairs in frontal cortex, and the authors suggested that there are substantial genetic influences in the frontal region. (Thompson and other 2001).

Polk and others (2007) used a similar approach to investigate how heredity influences neural function. Specifically, they used multivariate pattern analysis to compute the within-pair similarities of activation patterns (e.g., activation elicited by faces) in the ventral visual cortex in MZ and DZ twin pairs (Fig. 2B). Statistical parametric maps of activation were constructed for each twin pair, for each contrast of interest. A region of interest was predetermined using functional localizers and within this region of interest, similarities between the activation maps for each twin pair were measured using correlation coefficients. The patterns of cortical response for viewing faces (compared with viewing houses or phase-scrambled control stimuli) were more similar in MZ pairs than in DZ pairs, showing an effect of zygosity for face-related activity. There was no zygosity effect for chair-related activity, suggesting that heredity plays a more important role in determining the neural response to faces than chairs.

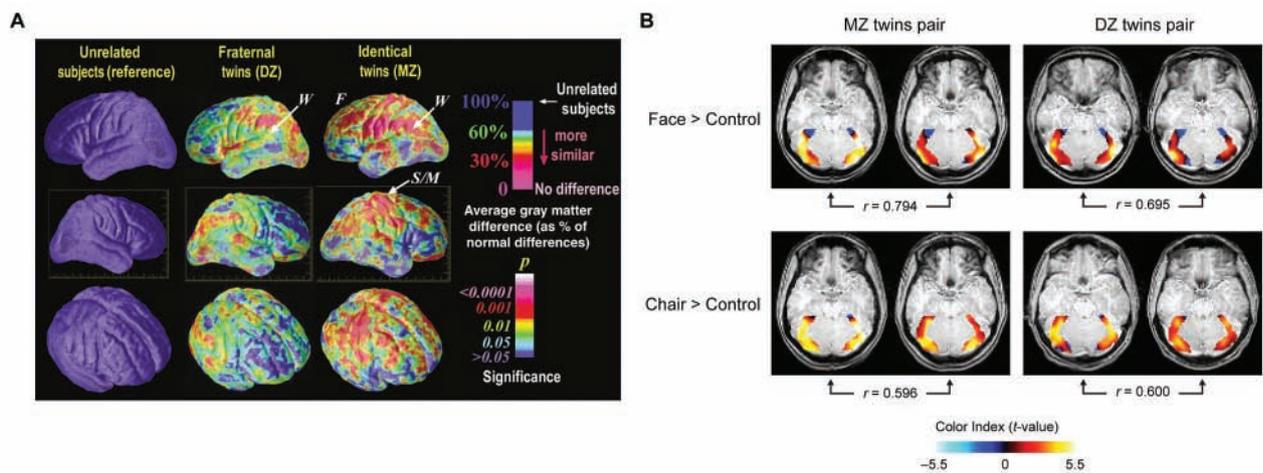


Figure 2. Neuroimaging studies using twins to investigate the role of genetics in determining the structural and functional organization of the human brain. (A) Differences in the quantity of gray matter at each region of cortex were computed for monozygotic (MZ) and dizygotic (DZ) twins, compared with the average differences that would be found between unrelated pairs (modified and reprinted from Thompson and others [2001] with permission from the Nature Publishing Group). F, frontal; S/M, sensorimotor; W, Wernicke's areas. (B) Similarities in the patterns of face-selective and chair-selective activations in the ventral visual cortex in MZ and DZ twin pairs. There is a significant zygosity effect for faces (MZ twins are more similar than DZ twins) but not for chairs (modified and reprinted from Polk and others [2007] with permission from the Society for Neuroscience).

with pictures of cars, birds, and nonface common objects. In an independently defined face recognition area (e.g., right FFA and right occipital face area [OFA]), car experts showed greater activity in response to cars than to birds whereas bird experts showed greater activity to birds than to cars. Based on this interaction between category and expertise, the authors concluded that brain areas known to be involved in processing faces are significantly affected by expertise.

Co-construction of Face Processing by Nature and Nurture

Faces are special among visual stimuli. Not only are they uniquely important for social interactions, they also appear to be processed in a way that is fundamentally different from the way other visual stimuli are processed. Why? Is face processing in some sense innate? What role, if any, does experience play in the development of face processing?

We have reviewed evidence demonstrating that both nature and nurture play a crucial role in the development of face processing and that any simple either/or answer is problematic. There is substantial evidence that both human and nonhuman infants display an innate preference for faces even if they have no exposure to faces at all. Furthermore, even the neural substrates of face processing are more strongly influenced by heredity than are the neural substrates underlying the processing of other visual stimuli. It appears then that we and other species are genetically wired for face processing in a way that does not apply to other visual stimuli.

Nevertheless, the evidence demonstrates that experience also plays a crucial role. Early experience with specific types of faces (e.g., faces of a specific species, faces of a specific race) leads to lasting advantages in the processing of those faces. Furthermore, the activity of face-selective areas is susceptible to experience: Cortical areas that seem specialized for faces can and do become responsive to other categories of visual stimuli with sufficient experience.

In short, the evidence suggests that humans as well as nonhuman primates are genetically wired for face recognition, but that experience, especially early experience, is crucial to fine-tune the mechanisms underlying face recognition and to tailor them to the specific demands of one's own environment. It is important to recognize the critical role played by both nature and nurture and to avoid any simple-minded view that ignores either factor.

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