



'Faceness' and affectivity: Evidence for genetic contributions to distinct components of electrocortical response to human faces



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ABSTRACT

The ability to recognize a variety of different human faces is undoubtedly one of the most important and impressive functions of the human perceptual system. Neuroimaging studies have revealed multiple brain regions (including the FFA, STS, OFA) and electrophysiological studies have identified differing brain event-related potential (ERP) components (e.g., N170, P200) possibly related to distinct types of face information processing. To evaluate the heritability of ERP components associated with face processing, including N170, P200, and LPP, we examined ERP responses to fearful and neutral face stimuli in monozygotic (MZ) and dizygotic (DZ) twins. Concordance levels for early brain response indices of face processing (N170, P200) were found to be stronger for MZ than DZ twins, providing evidence of a heritable basis to each. These findings support the idea that certain key neural mechanisms for face processing are genetically coded. Implications for understanding individual differences in recognition of facial identity and the emotional content of faces are discussed.

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Introduction

Though it is undisputed that humans are experts at perceiving and recognizing other human faces, research over the last several decades has generated considerable debate over the neural bases of this ability (Bentin and Carmel, 2002; Carmel and Bentin, 2002; Gauthier and Logothetis, 2000; Kanwisher and Yovel, 2006; Kanwisher et al., 1999; McKone et al., 2006; Nelson, 2001; Tarr and Gauthier, 2000; Yovel and Kanwisher, 2004). It is clear from neuroimaging studies that there are structures within the brain that are preferentially responsive to face stimuli—including the fusiform face area (FFA), the superior temporal sulcus (STS), and the occipital face area (OFA); however, the field is divided as to whether the “face-specific” capacity of these neural structures has a constitutional basis, or develops through experience (Gauthier and Logothetis, 2000; Kanwisher and Yovel, 2006). At the forefront of this debate is whether face-processing abilities reflect a domain-specific mechanism, involving face-specific cognitive and neural processes encoded at a basic gene level (i.e., domain-specificity; Carmel and Bentin, 2002; Wilmer et al., 2010; Yovel and Kanwisher, 2004; Zhu et al., 2010), or if instead they result from an experience-dependent mechanism, involving neural changes arising from repeated exposure to human face stimuli that facilitate processing of such stimuli (Diamond and Carey, 1986; Gauthier and Logothetis, 2000; Tarr and Gauthier, 2000). Alternatively, it is possible that face processing ability, analogous to the capacity for speech, arises

from factors of both types—with inborn, genetically based domain-specific mechanisms requiring specific exposure to faces during a critical period in development (experience-expectant) for face-specific modules to be established and maintained into adulthood (Nelson, 2001).

Recent research investigating the heritability of face processing has attempted to shed light on this debate. For example, Zhu et al. (2010) evaluated whether face-processing abilities are heritable by examining three different cognitive/face-processing phenomena (face-specific recognition ability, face inversion effect, composite-face effect) in monozygotic (MZ) and dizygotic (DZ) twins. Importantly, the tasks these authors employed allowed for specific face-processing abilities to be measured separately from lower level visual processes, attention, or decision-making. Face processing specificity was accomplished by including and contrasting matched non-face stimuli (e.g., houses) in each of the three cognitive/face-processing tasks. Face-specific abilities were quantified based on the difference in performance between the face and non-face conditions. In addition, Zhu et al. (2010) collected measures of high-level cognitive functions (e.g., IQ and global visual processing measures) to contrast and similarly factor out the heritability of so-called “generalist gene” effects. Results of this study clearly demonstrated a prominent genetic component to face processing, distinct from either low-level visual processes or more general cognitive functions.

Similarly, Wilmer et al. (2010) tested whether face processing is a heritable ability, separate from broader visual and memory functions. In this large-sample study, performance scores for same-sex twins MZ and DZ were compared across three different tasks: (1) the Cambridge Face Memory Task (CFMT), which tested subjects' ability to process and

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remember facial features in the absence of external head/hair shape and color cues, (2) a newly developed Abstract Art Memory test (AAM), which served as a non-face visual memory control, and (3) the Verbal Paired-Associates Memory test (VPAM), which assessed subjects' ability to remember non-visual cues. The observed concordance for MZ twins on the CFMT was over twice that for DZ twins, indicating a high degree of genetic contribution to face processing. Results from the other two tasks indicated that this contribution was not attributable to heritability of non-face or non-visual memory abilities.

In another work, Polk et al. (2007) investigated the heritability of functionally defined regions of the ventral visual cortex using functional magnetic resonance imaging (fMRI). In this study, MZ and DZ twins performed a "one-back task" while viewing black and white pictures from five visual categories (faces, places [images of houses], pseudowords, objects [chairs], and phase-scrambled control images) known to activate differing regions of the ventral visual cortex. Though functionally defined regions were not localized with high degrees of selectivity, these authors found higher concordance of activations to face and place stimuli (but not pseudoword or object stimuli) for MZ as compared to DZ twins in the ventral visual cortex.

Another study by Anokhin et al. (2010) investigated the heritability of affective face processing by analyzing brain event-related potential (ERP) responses to continuous presentations of neutral, happy, and fearful faces in MZ and DZ twins. Results demonstrated heritability of facial-affect response effects for two distinct ERP components, the N240 and the P300. Critically, however, due to the nature of the research questions investigated in this study and the experimental design used to address them, a key ERP component of interest in the face processing literature, the N170, was not evaluated for heritability. The N170 is a negative-going brain response that occurs at temporal-parietal electrode sites approximately 170 ms after the presentation of a visual stimulus, which appears to be maximally responsive to the presentation of faces (Bentin et al., 1996). Although the neural generator of the N170 has not been definitively located, multiple studies utilizing simultaneous EEG-fMRI recordings have established a clear correlation between activations of "face areas" in the ventral visual cortex, including the FFA and STS, and face-selectivity of the N170 (Sadeh et al., 2010; Yovel et al., 2008).

Debate surrounding the N170 centers on whether this response reflects face-specific processing or expertise-specific processing, essentially paralleling the broader domain-specific versus experience-dependent face processing debate (Bentin and Carmel, 2002; Rossion et al., 2002). A focal point of this debate pertains to findings showing that although the N170 is maximally responsive (has greatest negative peak amplitude) to face stimuli as compared to stimuli of other types (houses, cars, etc.), extensive expertise with a particular category of stimuli (e.g., cars, birds, etc.) tends to result in enhanced N170 response to stimuli of that type in comparison to other "non-expert" stimuli. These results point to the idea that maximal N170 responses to face stimuli simply reflect the very high expertise that adult humans have in general, for the processing of faces, due to widespread exposure to faces of differing types from birth (Rossion et al., 2002).

Building on this prior published work, a major aim of the current study was to evaluate the heritability of the N170 in a face processing context by recording ERP responses to face versus non-face stimuli from MZ and DZ twins and comparing concordance of N170 amplitude to stimuli of each type across the two. Based upon findings summarized above, we hypothesized that if amplitude of the N170 response to faces is determined in part by genetic influences, either domain-specific or experience-expected, then N170 enhancement for face as compared to non-face stimuli should show higher concordance for MZ as compared to DZ twin pairs.

In addition to gaining further insight into the heritability of the "faceness" component of stimulus processing as indexed by N170 response enhancement for faces versus nonfaces, the current study also investigated an additional component of face-processing that is arguably

of equal importance—namely, detection of the emotional content of a face. Face processing tasks have been a dominant methodology in affective neuroscience research for many years, and work aimed at understanding the neural correlates and mechanisms of affective face processing and the etiologic origins of this capacity is a clear priority. Regarding ERP correlates of affective face processing, some evidence exists that the N170 is enhanced for affective (e.g., fearful) as compared to neutral faces (Blau et al., 2007; Jiang et al., 2009), however many argue that affective face processing is more strongly represented at midline scalp sites (e.g., P8; Paulmann and Pell, 2009) rather than at temporal-parietal sites. There is also evidence of affective differentiation for later ERP components. For example, Paulmann and Pell (2009) identified an ERP component that appears to reflect processing of the emotional content of a face—specifically, a positive-going component occurring 200 ms after stimulus presentation at midline sites (labeled P200), that was reliably enhanced for affective as compared to neutral face stimuli.

A further ERP component known to be enhanced for visual affective stimuli of differing types—including face stimuli (Eimer & Holmes, 2002) as well as affective non-face stimuli (e.g., Cuthbert et al., 2000; Hajcak et al., 2006; Schupp et al., 2000)—is the late positive potential (LPP). The LPP is broadly defined as a later onset (> 250 ms) midline component that reflects sustained attentional-elaborative processing of affective stimuli, following initial registration of the basic affective significance of the stimulus (Eimer & Holmes, 2002; Schupp et al., 2000).

To further advance our understanding of brain ERP indices of affective face processing, the design of the current study included both emotional (fearful) and nonemotional (neutral) face stimuli along with control (scrambled face) stimuli. The twin feature of the design enabled us to evaluate, for the first time, the role of genetic influences in the predicted affective (fear vs. neutral face) differentiation for the N170, P200, and the LPP. Our primary hypothesis for these later ERP components was that they would show (perhaps even more so than the N170) enhancement for fearful as compared to neutral face stimuli. We also predicted that these two ERP components would exhibit enhancement for face stimuli of both types in relation to non-face (scrambled) stimuli, but to a lesser extent than the N170.

Methods

Participants

Participants were 62 pairs of MZ (25 pairs female) and 65 pairs of DZ (20 pairs female) twins recruited from the Minnesota Twin and Family Study database as part of a larger test protocol examining individual differences in affective and cognitive processing. Prior to testing, subjects were screened for impairments in visual acuity. The study was approved by the Institutional Review Board at the University of Minnesota and all subjects received informed consent and were compensated for their participation. All subjects were naïve as to the aims of the study.

Equipment and procedures

Face stimuli selected from the NimStim face stimulus set (Tottenham et al., 2009), were displayed on a 19" CRT monitor with a resolution of 1024 × 768 pixels and a refresh rate of 85 Hz. Subjects were seated 100 cm from the screen, yielding a viewing angle of 2.91 by 3.88° for stimuli. Stimulus presentation was controlled using the Psychophysics Toolbox (Psychtoolbox; Brainard, 1997; Pelli, 1997). Face stimuli consisted of 8 different fear faces, their neutral counterparts (i.e., same actors posing neutral expressions), and scrambled versions of the same fear and neutral faces. Scrambled face images were constructed by segmenting the face images into grids (18 × 24 pixels) and randomly resorting the grids within the original image dimensions using the MATLAB software package (The MathWorks, Inc.).

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