



EEG correlates of categorical and graded face perception

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ABSTRACT

Face perception is a critical social ability and identifying its neural correlates is important from both basic and applied perspectives. In EEG recordings, faces elicit a distinct electrophysiological signature, the N170, which has a larger amplitude and shorter latency in response to faces compared to other objects. However, determining the face specificity of any neural marker for face perception hinges on finding an appropriate control stimulus. We used a novel stimulus set consisting of 300 images that spanned a continuum between random patches of natural scenes and genuine faces, in order to explore the selectivity of face-sensitive ERP responses with a model-based parametric stimulus set. Critically, our database contained “false alarm” images that were misclassified as face by computational face-detection system and varied in their image-level similarity to real faces. High-density (128-channel) event-related potentials (ERPs) were recorded while 23 adult subjects viewed all 300 images in random order, and determined whether each image was a face or non-face. The goal of our analyses was to determine the extent to which a gradient of sensitivity to face-like structure was evident in the ERP signal. Traditional waveform analyses revealed that the N170 component over occipitotemporal electrodes was larger in amplitude for faces compared to all non-faces, even those that were high in image similarity to faces, suggesting strict selectivity for veridical face stimuli. By contrast, single-trial classification of the entire waveform measured at the same sensors revealed that misclassifications of non-face patterns as faces increased with image-level similarity to faces. These results suggest that individual components may exhibit steep selectivity, but integration of multiple waveform features may afford graded information regarding stimulus appearance.

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1. Introduction

Adults are experts at processing faces. We excel at detecting faces in cluttered natural scenes that contain a wealth of visual information. We reliably distinguish human faces from other categories of objects. We quickly and accurately recognize faces across large image transformations and degradations. Perhaps most importantly, we are able to use information from faces that varies moment-by-moment to guide our social behavior.

Several components of the event-related potential (ERP) have been implicated in various aspects of face perception (i.e., face detection, face identification, emotion identification). The most well-established marker for face perception is the N170, a prominent negative-going component of the ERP waveform that occurs approximately 170 ms after stimulus onset (Bentin, Allison, Puce,

Perez, & McCarthy, 1996). In general, human faces elicit larger N170s than other object categories, including houses, cars, butterflies, flowers, hands, chairs, shoes, animal faces, and novel shapes such as Greebles (Bentin et al., 1996; Botzel, Schulze, & Stodieck, 1995; Itier & Taylor, 2004; Rossion et al., 2000; Rousselet, Mace, & Fabre-Thorpe, 2004). The N170 is typically lateralized over right posterior scalp (Bentin et al., 1996; Rossion, Joyce, Cottrell, & Tarr, 2003) and reflects certain hallmarks of face expertise observed in behavior. For example, the N170 is consistently larger in amplitude and longer in latency for inverted faces compared to upright faces (Rossion et al., 2000; Itier, Latinus, & Taylor, 2006; Jacques & Rossion, 2007; Sagiv & Bentin, 2001), an effect that is not observed for other classes of objects (Rossion et al., 2000).

Based on these findings, the general consensus is that the N170 component primarily reflects face detection, although there is evidence that it is also sensitive to differences within the face category, such as face identity and facial emotion (Batty & Taylor, 2003; Heisz, Watter, & Shedden, 2006; Itier & Taylor, 2002; Itier et al., 2006; Jacques & Rossion, 2006; Jacques, d'Arripe, & Rossion, 2007;

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Leppanen, Moulson, Vogel-Farley, & Nelson, 2007). Another line of research using ambiguous stimuli also suggests that the N170 reflects face detection, or the perceptual awareness of a face. Bentin and colleagues found that when ambiguous stimuli were preceded by a schematic face, and therefore were more likely to be perceived as faces or face parts, the ambiguous stimuli elicited N170s of equal magnitude to the face stimuli themselves (Bentin & Golland, 2002; Bentin, Sagiv, Mecklinger, Friederici, & von Cramon, 2002). When the same ambiguous stimuli were not primed by a schematic face, they elicited much smaller N170s. Similarly, George and colleagues found that when ambiguous two-tone “Mooney” images were perceived as faces in an explicit face detection task, they elicited larger N170 responses than when they were perceived as non-faces. Additionally, they found an orientation (upright vs. inverted) effect only for the Mooney images perceived as faces (George, Jemel, Fiori, Chaby, & Renault, 2005).

Despite these findings, the precise selectivity of the N170 for faces is still somewhat unclear, because the answer hinges on finding an appropriate control stimulus. The N170 is elicited not only by face stimuli, but also by all other classes of object stimuli that have been tested to date and its amplitude varies widely among non-face object categories (Rossion et al., 2000). The general strategy in previous research exploring the response properties of the N170 has been to choose as comparison stimuli separate categories of real or nonsense objects that share some feature(s) with faces (e.g., bilateral symmetry, animacy, biological significance, etc.). The rationale behind this approach is that by choosing stimuli that are similar to faces in ways that we think might evoke a larger N170 response, we can determine if the N170 is specific to faces or to the particular feature(s) that they share with the comparison stimuli. While this strategy has proved fruitful, the large space of possible alternative object categories makes it difficult to say definitively that the N170 is highly selective for faces *per se*. Each selection of a particular control stimulus category represents a comparison between faces and another very small portion of “image space,” relying on the experimenter’s ingenuity (and subjective judgments regarding appropriate controls) to traverse an extremely high-dimensional space a few very small steps at a time.

The first goal of the current study was to probe the selectivity of the N170 for faces in adults using an alternative approach to selecting non-face comparison stimuli. This approach was motivated by research using single-unit recordings in non-human primates, in which the response properties of neurons are often explored by creating sets of stimuli that vary parametrically along a dimension or dimensions of interest. For example, the response properties of neurons in IT have been investigated with sets of stimuli that vary along simple shape dimensions, such as curvature (Kayaert, Biederman, Op de Beeck, & Vogels, 2005). These parametric studies allow researchers to isolate specific stimulus features that may drive the neuron’s response. Although this parametric approach is common in single-unit work, it is rarely applied to ERP research where it could be used to determine the response properties of specific components. In our case, instead of creating a set of stimuli that varied parametrically along sets of low-level features, we employed a set of stimuli, compiled by Meng et al. (2008, submitted for publication), that varied along the complex dimension of “faceness.” This is obviously a great deal more complicated than parametrically varying a more basic perceptual quality like contrast or curvature. To realize this goal, Meng et al. (2008, submitted for publication) adapted tools from computer vision and graphics to objectively describe the “faceness” of arbitrary images.

They started by selecting 60 images of genuine faces and 60 images taken at random from natural scenes containing no faces. These 120 images represented the two extreme ends of our dimension of faceness. To create a continuum of faceness between these two sets of images, Meng et al. (2008, submitted for publication)

obtained false alarms – non-face images that were mistaken for faces – from a state-of-the-art computational face detection system that detects faces in natural images with high accuracy (Rowley, Baluja, & Kanade, 1998). These false alarm images represent a convenient means of bridging the gap between genuine faces and non-faces. Parametrically varying the “faceness” of the comparison stimuli allows us to determine the nature of the function that determines the N170’s selectivity for faces—i.e., a steep, step-wise response that distinguishes faces and non-faces unambiguously or a response that varies smoothly along the continuum of faceness built in to our stimulus set.

To examine the possibility that any observed effects at the N170 might be a function of basic low-level image differences across our continuum of facial resemblance, we also examined the P1, an early visual component that is maximal over occipital regions and occurs approximately 100 ms after stimulus onset. Several studies have reported that the amplitude and latency of the P1 component are modulated by the category to which the visual stimulus belongs; specifically, some studies have found that it is larger in amplitude and shorter in latency in response to faces compared to other object categories (Eimer, 1998, 2000; Itier & Taylor, 2004). Other studies have reported that the amplitude and latency of the P1 are also modulated by particular aspects of faces (e.g., facial emotion—Batty & Taylor, 2003). Although these results suggest that the P1 component reflects face-sensitive processing, many other studies have failed to find amplitude or latency differences between faces and non-faces for this early component (Rossion et al., 2003; Rousselet, Husk, Bennett, & Sekuler, 2005, 2007). Indeed, the P1 is notoriously sensitive to low-level visual features (e.g., luminance, color, spatial frequency content, contrast) that likely differ between faces and other objects, and in studies in which these low-level variables are explicitly controlled, P1 differences are not evident (Rousselet et al., 2005, 2007). Additionally, a recent study has provided direct evidence that the purported P1 sensitivity to faces is entirely the result of low-level image characteristics, rather than the perception of a face (Rossion & Caharel, 2011). For our purposes, an analysis of the P1 is a useful means of establishing that low-level variables are well-matched in images across our continuum, suggesting that differences observed for the N170 are more likely a function of how face-like a pattern is rather than more basic image properties.

In the current study, we also pursued an alternative approach to describing how face selectivity manifests in the ERP waveform. Traditional component-based analyses reduce ERP data to particular time windows and regions of interest. For example, the N170 is usually defined by only two values—the amplitude and latency of the most negative peak within a window from approximately 140–200 ms and occurring at small clusters of sensors over occipitotemporal scalp regions. By restricting the ERP analysis in this way, we are necessarily losing potentially valuable information contained in the distributed pattern of activity present across the entire waveform and the whole scalp. It is possible that face sensitivity or selectivity might manifest itself not only in the amplitude and latency of ERP components like the N170, but also in differences between the overall patterns of brain activity elicited by faces compared to other visual stimuli.

Neuroimaging research has successfully used statistical classification approaches to demonstrate that objects in different categories elicit reliably different patterns of hemodynamic response across large swaths of ventral temporal cortex (e.g., Cox & Savoy, 2003; Haxby et al., 2001), but these approaches have not been as widely applied to ERP data. In the current study, we recorded high-density (128-channel) ERPs as adults performed a face/non-face detection task while viewing images from our stimulus set that varied on a continuum of faceness. In addition to performing traditional waveform analyses for the P1 and N170 components, we used statistical classifiers to determine if (1) the

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