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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 faces by a 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.

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.

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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 170ms after stimulus onset (Bentin et al., 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 (Botzel, Schulze, & Stodieck, 1995; Bentin et al., 1996; Rossion et al., 2000; Itier & Taylor, 2004; Rousselet et al., 2004). The N170 is typically lateralized over right posterior scalp (Bentin et al., 1996; Rossion et al., 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 et al., 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 (Jacques & Rossion, 2006; Jacques, d'Arripe, & Rossion, 2007; Heisz, Watter, & Shedden, 2006; Itier et al., 2006; Itier & Taylor, 2002; Batty & Taylor, 2003; 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 et al., 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; under review), 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; under review) 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; under review) 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 et al., 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 100ms 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 et al., 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 140–200ms 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., Haxby et al., 2001; Cox & Savoy, 2003), 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 temporally distributed pattern of activity elicited by faces reliably differed from that elicited by non-faces on a trial-by-trial basis; and 2) the patterns of activity differed among non-faces that varied in how face-like they were.

Method

Participants

Twenty-three adults (11 females) over the age of 18 participated in this experiment. An additional eight adults were tested but were excluded from final data analysis due to excessive EEG artifact. All adults had normal or corrected-to-normal vision, and none had a history of neurological abnormalities.

Stimuli

Our stimulus set consisted of 300 images taken from natural scenes (Meng et al., 2008, under review). Sixty of these were true face images and 60 more were images taken at random from natural scenes that were devoid of faces. False alarms (180 images) from a state-of-the-art computational face detection system developed at Carnegie Mellon University, and recently commercialized by Pittsburgh Pattern Recognition Inc. (Rowley et al., 1998), served to bridge the extremes of non-faces to faces. The computational face-detection system has been trained on tens of thousands of face and non-face images and has learned regularities that enable it to detect faces with high accuracy in natural images. On rare occasions, however, the system generates false-alarms: non-faces that embody some attributes which cause the face detection system to mistake them for genuine faces (Figure 1).

The 180 “false alarm” images were split into three categories of increasing resemblance to genuine faces. Ten observers naïve to the purpose of the study were asked to compare paired images chosen at random from the full set of images and to determine which image of the pair was more face-like. These pair-wise comparisons were then used to calculate a rating, which represented how “face-like” each image was. This was accomplished via an algorithm that is widely employed for rating chess players based on their performance in pair-wise match-ups (Elo, 1978). Each pair-wise comparison performed by a human observer was treated as a competition between the two images being displayed, and the image selected as being more face-like was treated as the “winner,” with the ratings of both images adjusted accordingly. We established “low,” “medium,” and “high” face-similarity categories by splitting the set of 180 images into three groups based on the final rating obtained for each image.

Procedure

Participants saw all 300 pictures in random order. The pictures were presented against a uniform gray background. Each trial consisted of stimulus presentation (500ms) and a post-stimulus recording period (1000ms). The inter-trial interval, during which a black fixation cross was presented on a gray background, varied randomly between 1500–2000ms. Participants were required to determine whether each stimulus was a face or a non-face, and responded using two buttons on a button box. Participants were instructed to make their responses as quickly and accurately as possible, and they had 1500ms from stimulus onset to do so.

Electrophysiological Recording and Processing

While participants were performing the above task, continuous EEG was recorded using a 128-channel Geodesic Sensor Net (Electrical Geodesics, Inc.), referenced online to vertex (Cz). The electrical signal was amplified with 0.1 to 100Hz band-pass filtering, digitized at a 250 Hz sampling rate, and stored on a computer disk. Data were analyzed offline using NetStation 4.2 analysis software (Electrical Geodesics, Inc.). The continuous EEG signal was first filtered with a 30Hz low-pass elliptical filter, then segmented into 600ms epochs, starting 100ms prior to stimulus onset. Data were then baseline-corrected to the mean of the 100ms period before stimulus onset. NetStation's automated artifact detection tools combed the data for eye blinks, eye movements, and bad channels. Segments were excluded from further analysis if they contained an eye blink (threshold $\pm 70\mu\text{V}$) or eye movement (threshold $\pm 50\mu\text{V}$). In the remaining segments, individual channels were marked bad if the difference between the maximum and minimum amplitudes across the entire segment exceeded $80\mu\text{V}$. If more than 10% of the 128 channels (i.e., 13 or more channels) were marked bad in a segment, the whole segment was excluded from further analysis. If fewer than 10% of the channels were marked bad in a segment, they were replaced using spherical spline interpolation. Average waveforms for each of the five stimulus categories were calculated for each participant and re-referenced to the average reference configuration.

Results

Behavioral results

We first examined observers' ability to accurately distinguish between faces and non-faces during the ERP recording session. Specifically, we determined whether or not it is more difficult for our participants to reject non-faces as their similarity to faces increases. This is an important validation of the original assignment of non-face images into "low," "medium," and "high" similarity categories. The average proportion correct across subjects in these conditions is plotted in Figure 2.

We ran a one-way repeated-measures ANOVA on the proportion correct responses from all non-face categories (NF0-NF3). This analysis revealed a main effect of stimulus category ($F(3, 66) = 8.88, p < 0.01$). Post-hoc tests with a Bonferroni correction for multiple comparisons revealed that the NF3 ("high" similarity) category ($M = .80$) differed from the other three non-face categories (all p 's $< .05$), but the NF0, NF1, and NF2 categories ($M = .90, M = .88, M = .87$, respectively) did not differ from each other (all p 's $> .10$). This supports the conclusion that observers did find it harder to reject non-faces as they came to resemble our face stimuli more closely. This result is a critical starting point for our analysis of the ERP data. Behaviorally, a gradient of "faceness" is evident across the "non-face" categories as we have defined them. The question is whether or not this gradient is also evident in the neural data. We continued by examining the ERPs collected in this task in two ways. First, we examined the amplitude and latency of the P1 and N170 components across stimulus categories. Second, we used single-trial classification to measure the amount of

“face signal” in individual trials without targeting specific components of the ERP waveform.

ERP Waveform Analysis

Grand-averaged ERP waveforms were inspected to identify components of interest. Consistent with previous research, there were prominent P1 and N170 peaks over occipitotemporal electrodes. The peak amplitude and latency of the P1 component were determined within a time window of 80–120ms post-stimulus onset, and averaged across clusters of six sensors over the left hemisphere (electrodes 58, 59, 64, 65, 69, 70) and the right hemisphere (electrodes 90, 91, 92, 95, 96, 97). The peak amplitude and latency of the N170 were determined within a time window of 140–200ms post-stimulus onset, and averaged across these same clusters of sensors. These sensors were chosen because they are located around T5 and T6 in the international 10–20 system, where the N170 has been found to be maximal in previous studies (Bentin et al., 1996). Figure 3 displays the grand-averaged ERP waveforms for each stimulus category (NF0, NF1, NF2, NF3, Face) over the left and right hemispheres.

For both the P1 and N170 components, we initially compared subjects' responses to genuine faces (Face category) to their responses to true non-faces (NF0 category) to establish the face-sensitivity of these components. We then compared subjects' responses to the graded non-face stimuli (NF1–NF3 categories) to determine if either component displayed sensitivity to the gradient of faceness present in the non-face stimuli.

P1—We ran separate repeated-measures ANOVAs on the peak amplitude and latency of the P1, with stimulus category (NF0, Face) and hemisphere (left, right) as factors. There were no main effects or interactions for either P1 amplitude or latency, indicating that the response to faces and true non-faces did not differ for this component. We then ran separate repeated-measures ANOVAs with stimulus category (NF1, NF2, NF3) and hemisphere (left, right) as factors. There were no main effects or interactions for either P1 amplitude or latency. Thus, there was no evidence that the P1 component was sensitive either to the face/non-face distinction or to the gradient of faceness present in our stimulus set. These results also provide important validation that our five stimulus categories do not differ in their low-level image properties.

N170—As above, we ran a repeated-measures ANOVA on the peak amplitude of the N170, with stimulus category (NF0, Face) and hemisphere (left, right) as factors. There was a main effect of stimulus category, $F(1, 22) = 65.68, p < .001$. The N170 amplitude was significantly larger in response to genuine faces ($M = -4.18 \mu\text{V}$) than true non-faces ($M = -1.78 \mu\text{V}$). There were no other main effects or interactions for N170 amplitude. To determine whether there was evidence of sensitivity to the gradient of faceness in our stimulus set, we then ran a repeated-measures ANOVA on N170 amplitude, with stimulus category (NF1, NF2, NF3) and hemisphere (left, right) as factors. There were no main effects or interactions for N170 amplitude when only these ambiguous non-face stimulus categories were included in the analysis. This suggests that although the N170 is clearly face-sensitive, as it was significantly larger in response to faces compared to genuine non-faces, it was not sensitive to the continuum of faceness present in our stimulus set.

Similarly, we ran a repeated-measures ANOVA on N170 latency, with stimulus category (NF0, Face) and hemisphere (left, right) as factors. There was a main effect of stimulus category, $F(1, 22) = 9.01, p < .01$. The N170 latency was significantly longer in response to genuine faces ($M = 169 \text{ ms}$) than true non-faces ($M = 164 \text{ ms}$). There were no other main effects or interactions. A repeated-measures ANOVA including only the ambiguous non-

face categories (NF1, NF2, NF3) and hemisphere (left, right) as factors revealed a main effect of stimulus category, $F(2, 44) = 6.01$, $p < .05$. Post-hoc tests with a Bonferroni correction for multiple comparisons revealed that N170 latency was significantly longer for the NF3 ($M = 169$ ms) category, than NF1 ($M = 164$ ms) or NF2 ($M = 164$ ms) categories.

Single-trial classification of face/non-face ERPs

We continued by using a statistical classifier to analyze single-trial ERPs elicited by our face and non-face stimuli. This analysis offers an alternative means of examining the neural signal for evidence of a graded response to increasingly “face-like” stimuli by considering the entire ERP waveform measured over multiple sensors as a single multivariate observation.

We used the pre-processed ERP data described in the previous section. Consequently, all ERP data were subjected to 30Hz low-pass filtering, segmentation into 500ms trials, artifact detection and bad channel replacement, baseline correction, and re-referencing. To build classifiers for individual subjects, we concatenated the waveforms measured at the previously defined sensors of interest into a single vector per hemisphere for each trial. We chose to restrict our classification analyses to the same sensors that we used for the component analyses in order to provide a direct comparison between the information obtained from traditional component-based analyses and information obtained from classification analyses at sensors that have reliably demonstrated face-sensitive effects in previous research. In one set of analyses, we considered the entire waveform measured from stimulus onset (0 ms) to stimulus offset (500ms after the stimulus appeared). Additionally, we conducted an independent classification analysis using only the time points within the 140–200ms window that we used to analyze the N170. By conducting single-trial classification in both of these cases, we can compare the results of the classifier to the waveform results more directly by matching the time window under consideration, while also examining how much information we can read out from a more temporally extended signal.

In both of these cases, we continued by training a linear support vector machine (SVM) on the vectors belonging to Face (F) and Non-Face (NF0) trials. We used the SVM-KM toolbox for Matlab, which is freely available online. Next, we tested the trained classifier on the ambiguous (NF1-NF3) stimuli to determine whether the responses elicited on those single trials resemble F or NF0 responses. For each subject (and each hemisphere), we were thus able to determine the proportion of single trials in each category that were labeled as faces.

The NF1, NF2, and NF3 trials are all considered non-face trials, and thus should ideally be classified as such by the classifier. However, if the “faceness” of these stimuli leads to systematic differences in the neural response, it is possible that images that resemble faces strongly may be harder to classify correctly as non-faces. Should this be the case, we would expect a systematic increase in “Face” classification as face resemblance increases (NF3 error > NF2 error > NF1 error). By contrast, if the level of face resemblance is not reflected in the neural signal measured at these sensors, we would expect no differences in classification rates across these stimulus categories.

N170 time window (140-200ms)—The training data (F and NF0 trials only) were correctly classified 100% of the time in both hemispheres of all subjects. This is not a surprising result, but does indicate that these responses are separable by a linear SVM. A 3×2 repeated-measures ANOVA with stimulus category (NF1, NF2, NF3) and hemisphere (left, right) as factors revealed no main effects or interactions. Thus, there is no evidence in the N170 time window for sensitivity to the increasing “faceness” in our stimulus set.

Entire waveform (0-500ms)—As above, the training data (F and NF0 trials only) were correctly classified 100% of the time in both hemispheres of all subjects. A 3×2 repeated-measures ANOVA with stimulus category (NF1, NF2, NF3) and hemisphere (left, right) as factors revealed a main effect of stimulus category, $F(2, 44) = 3.36, p < .05$. Post-hoc comparisons revealed that “face” classification rates were significantly higher for NF3 than NF1 stimuli ($p < .05$), significantly higher for NF2 than NF1 stimuli ($p < .05$), and did not differ for NF3 and NF2 stimuli. There were no other main effects or interactions. Thus, ambiguous non-face stimuli that resembled faces more closely (NF2, NF3) were more difficult to accurately classify as non-faces than ambiguous stimuli that were less face-like (NF1).¹ In Table 1, we list the “face” classification rates for stimuli in categories NF1-NF3 in each hemisphere, with 95% confidence intervals for the mean across subjects.

Discussion

The goals of the current study were two-fold. First, we probed the face-selectivity of the N170 component, using a unique stimulus set containing images that varied in how face-like they were. Second, we investigated whether there was evidence for a gradient of sensitivity to face-like structure in the temporally distributed pattern of neural activity elicited in single ERP trials. We found that the N170, the classic neural marker for face perception (Bentin et al., 1996), was larger in response to face images compared to genuine non-face images; we also found that the N170 did not differ in amplitude among non-face categories that differed in their image-level similarity to faces. Thus, the amplitude of the N170 seems to exhibit a steep, step-wise response that distinguishes faces and non-faces unambiguously. It should be noted that this face-selective response for the N170 amplitude did not seem to be driven by low-level visual features that differed between our face and non-face stimuli, since we found no differences among any of the stimulus categories for the P1 component. Results for N170 latency were more complex. First, contrary to previous findings, the N170 was slower in response to face images compared to genuine non-face images. Second, the N170 was slower in response to non-face images that resembled faces more closely. Although this suggests that sensitivity to the “faceness” of non-face images may be contained in the latency of this classic neural marker of face perception, this finding is somewhat difficult to interpret given that the N170 response to faces compared to genuine non-faces was reversed from what has been found previously.

In contrast to the findings for the N170 component, single-trial classification of the entire ERP waveform from stimulus onset to offset showed unambiguous evidence of sensitivity to the continuum of faceness built in to our stimulus set. We found that ambiguous non-face images became harder to classify as non-faces as their image-level similarity to faces increased. However, when single-trial classification was performed on just the time window of the N170 component, we found no evidence of sensitivity to how face-like the ambiguous images were. Thus, both strict selectivity for the face category during the N170 time window and sensitivity to graded face similarity across the whole waveform were evident in our ERP data.

That the amplitude of the N170 was highly selective for genuine faces in this stimulus set extends previous research demonstrating that the N170 is larger for faces than all other object categories tested to date (Bentin et al., 1996; Itier & Taylor, 2004; Rossion et al., 2000). This finding supports the hypothesis that the N170 reflects the categorization of an

¹A linear SVM has only one free parameter that can be manipulated, which is a “Cost variable” usually denoted C , that determines how willing the classifier is to trade-off perfect performance on the training data against rigid decision boundaries between classes. We found that our results were quantitatively robust to changes in C over a wide range of values and so we do not have reason to think that the results displayed in Table 1 depend critically on fine-tuning classifier parameters.

image as a face or non-face (i.e., the perceptual awareness of a face). Additional evidence that the N170 reflects the categorization of an image as a face comes from other studies that have used ambiguous non-face stimuli. In the current study, we demonstrated that ambiguous stimuli that were perceived as non-faces - i.e., non-face images that were correctly classified behaviorally as non-faces - elicited smaller N170s than genuine faces. In contrast, previous studies have demonstrated that when ambiguous stimuli were preceded by a schematic face (and therefore were more likely to be perceived as faces) or were explicitly categorized as faces, they elicited face-like N170s (Bentin & Golland, 2002; Bentin et al., 2002; George et al., 2005). In the current study we were unable to examine this phenomenon - whether non-faces would elicit face-like N170s if they were perceived as faces - because there were too few trials on which subjects made this behavioral error. However, the complementary findings that ambiguous stimuli that are perceived as non-faces elicit small N170s (the current study), whereas ambiguous stimuli that are perceived as faces or face parts elicit face-like N170s (Bentin & Golland, 2002; Bentin et al., 2002; George et al., 2005) strongly suggest that the N170 reflects the categorical decision between face and non-face that is observed in behavior. However, not all studies using ambiguous stimuli have found this clear distinction. For example, Churches and colleagues found that "face-like" objects elicited larger amplitude N170s than "non-face-like" objects, although genuine faces elicited larger N170s than both object classes (Churches, Baron-Cohen, & Ring, 2009). This contrasts with our finding that the N170 was not sensitive to the faceness of our non-face images. However, in the task used by Churches et al., participants were required to explicitly classify objects as "face-like" or "non-face-like." This may have biased participants to look for and perceive faces among the objects (similar to the findings of Bentin and colleagues described above), leading to larger amplitude N170s for "face-like" objects.

Our results from traditional component analyses and single-trial classification converge nicely for the N170 time window. Both analysis approaches revealed strict selectivity for veridical face stimuli within this time window. In contrast, single-trial classification performed on the pattern of activity across the entire waveform did show evidence of a graded response to increasingly face-like stimuli. Although the absence of timing information when using the entire waveform for classification could be construed as a weakness of this analysis, these results nonetheless reveal how much information is available at a particular set of electrodes over an extended period. It is noteworthy that the traditional component analyses and the classification analyses occurred over the same occipitotemporal sensors, yet the two different analysis strategies yielded different interpretations regarding the sensitivity of the neural signal to the continuum of faceness built into our stimulus set. Thus, the combination of component-based analysis and single-trial classification in the current study proved to be a powerful method for examining the representational content of the ERP signal, and future research should consider adopting this approach. Analogously, there is increasing consensus in the fMRI literature that pattern classification approaches are a significant addition to traditional ROI analyses, as they have recently yielded new insights into neural information processing in multiple domains (for a review, see Norman, Polyn, Detre, & Haxby, 2006).

Findings from the current study provide insight into the nature of face processing in the human visual system. The majority of studies that examine the neural correlates of face perception implicitly assume that the neural response to faces is strictly categorical; that is, the brain selectively responds to images classified as faces in a categorically different way than it responds to images classified as non-faces. Here we have shown that the visual system does not discard potentially valuable information about image-level similarity to achieve this selective response to faces; rather, this information about face similarity persists in the EEG signal. Thus, the visual system is flexible enough to accommodate the need for

sharp distinctions among stimulus categories without compromising the ability to make finer-grained judgments.

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Highlights

- In this study we probe the neural correlates of face perception using ERPs
- Unique stimulus set contained images that varied on a continuum of "faceness"
- The N170 component exhibited steep selectivity: larger for faces than all non-faces
- Single-trial classification of whole waveform revealed sensitivity to graded face similarity
- Visual system shows both graded and selective response to faces



Figure 1.

Example images from the stimulus set used in the ERP experiment. The top and bottom rows are unambiguous non-face and face stimuli, respectively (NF0 and F). The remaining images are examples of "false-alarms" made by the computer vision algorithm described in the main text, with degree of resemblance to genuine faces increasing from top to bottom.

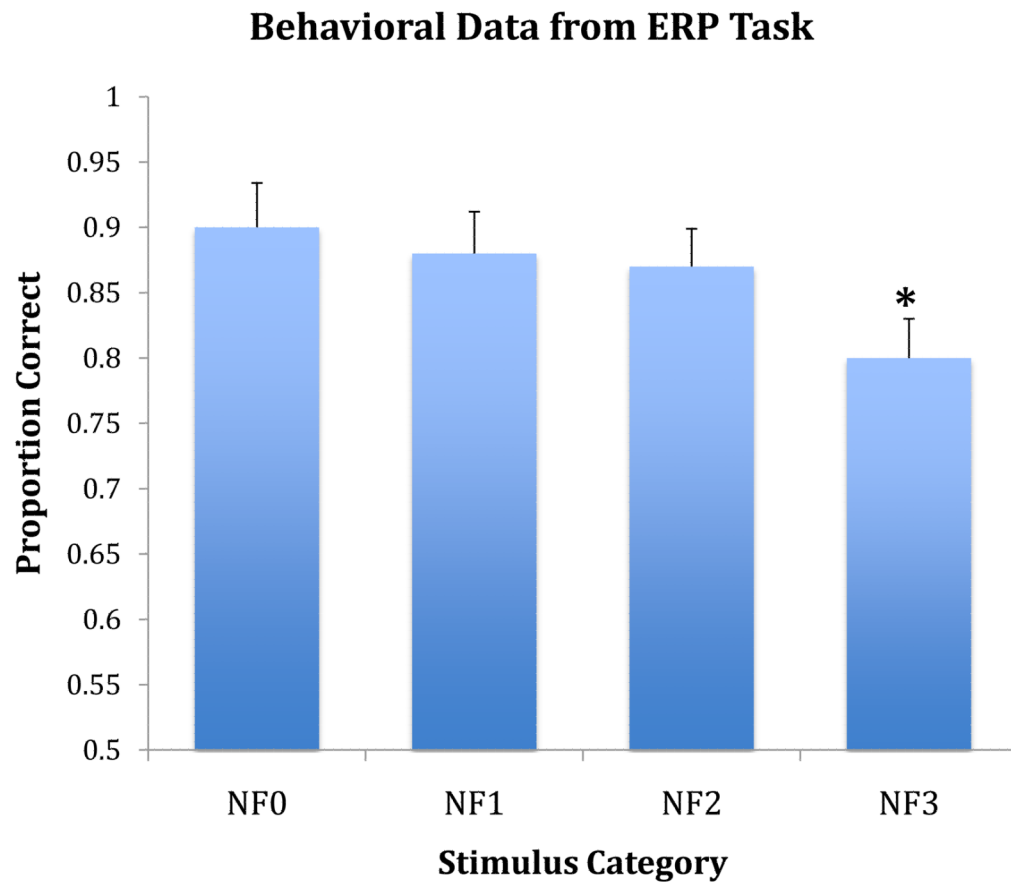


Figure 2.

Average proportion correct in all “non-face” categories across subjects. Error bars indicate standard error of the mean. Asterisk indicates that NF3 category is significantly different from all other stimulus categories ($p < .05$); thus, increased similarity to veridical faces induced more erroneous “face” responses.

Figure 3a.

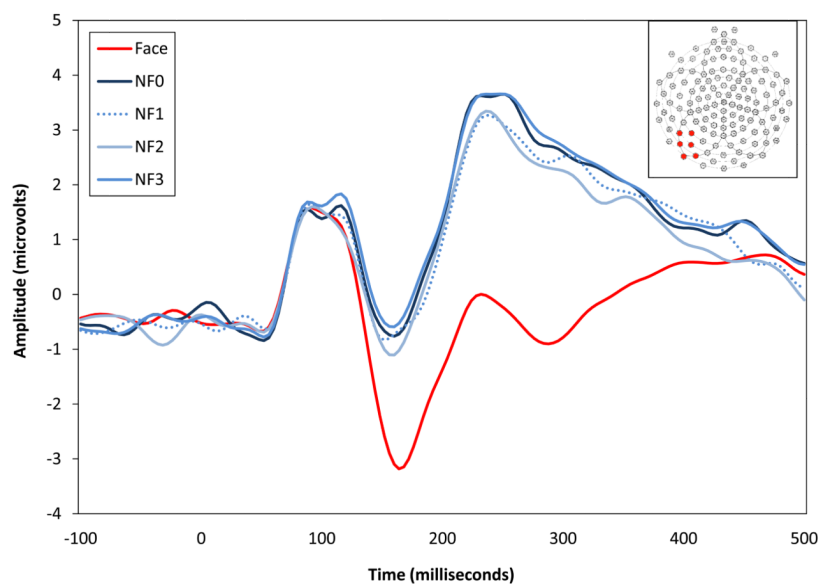


Figure 3b.

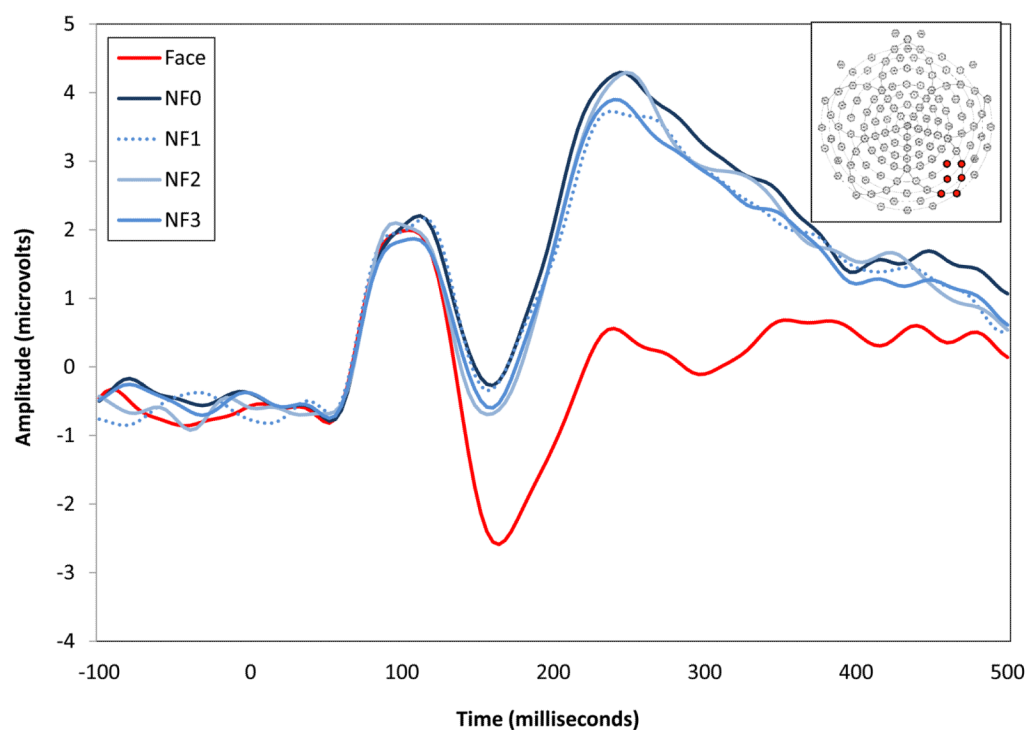


Figure 3. Grand averaged ERP waveforms over the left (a) and right (b) hemisphere. Sensors highlighted in red indicate sensor groupings used for P1, N170, and single-trial classification analyses.

Table 1

“Face” classification rates for single-trial responses across the entire time window to NF1-NF3 stimuli. A main effect of face similarity is observed, such that increasing resemblance to a face elicits a greater rate of “face” classification.

	NF1	NF2	NF3
Left Hemi. – Mean	40.4	44.7	45.2
Left Hemi. – 95% CI	[30.5, 50.3]	[34.4, 55.1]	[36.9, 53.5]
Right Hemi. – Mean	36.2	40.7	38.7
Right Hemi. – 95% CI	[26.6, 45.8]	[31.6, 49.9]	[29.7, 47.7]