Published in final edited form as:

Neuropsychologia. 2007 October 1; 45(13): 3087–3091. doi:10.1016/j.neuropsychologia.2007.05.020.

Face Processing without Awareness in the Right Fusiform Gyrus

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Abstract

We investigated brain activity evoked by faces which were not consciously perceived by subjects. Subdural electrophysiological recordings and functional neuroimaging studies have each demonstrated face-specific processing in the fusiform gyrus (FFG) of humans. Using pattern masks, a stimulus can be presented but not consciously perceived, and thus can be used to assay obligatory or automatic processes. Here, using event-related functional magnetic resonance imaging and pattern masking, we observed that masked faces but not masked objects activated the right FFG. Other regions activated by consciously perceived unmasked faces were not activated when faces were masked. These data provide strong evidence for an automatic face processing region in the right FFG.

A briefly exposed visual stimulus may not be consciously perceived if it is preceded and followed by a dissimilar visual pattern, or mask. Masked facial expressions have been shown to influence the activation of the amygdala by subsequent visible faces (Whalen et al., 1998) thus demonstrating that some aspects of face processing can occur without conscious awareness. It has been suggested in these studies that the amygdala is responding to a primitive face representation that bypasses processing in extrastriate cortical regions such as the fusiform gyrus (FFG). Functional MRI studies have demonstrated that visible faces selectively activate focal regions of the FFG (e.g., Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Puce, Allison, Gore, & McCarthy, 1995); however, whether masked faces similarly activate these regions has not yet been examined. Here, we compared activation evoked by masked and unmasked faces and non-face objects to determine whether the FFG and other brain regions are activated by faces without a subject's awareness.

Methods

Subjects

Twenty healthy young adults (10 males) served as subjects in the fMRI study. Two groups of 10 additional healthy young adults (9 male) participated in two separate behavioral

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studies that were conducted outside the scanner. All subjects provided written informed consent.

Materials and Procedure

Subjects were informed that they would be participating in a color discrimination task. Subjects wore LCD goggles through which they viewed a continuous stream of stimuli in which a different mosaic pattern was presented every 100 ms. Most of the mosaics were gray and white, but a colored mosaic occurred infrequently and required a button press. Unknown to the subjects, gray-scale faces and non-face objects (sports equipment such as soccer balls) appeared in intermixed order every 12 – 18 seconds and were exposed for 33 ms. Critical stimuli were locked to the onset of the refresh of the LCD display.

One-hundred stimuli (50 faces, 50 objects) were presented in the seven masked runs that each subject experienced. After the completion of the masked runs, each subject was presented with three additional runs in which the same faces and objects presented at the same duration and with the same intervals, but with the mosaics replaced by a black rectangle. Thus, the faces and objects were consciously perceived. These unmasked runs were used as functional localizers to identify face-specific regions that could be compared to the masked trials.

In the first behavioral task conducted outside the scanner, subjects were told that they would be presented with masked faces and objects on an LCD monitor, and that they were to press one button when they thought they saw a face and a second button when they thought they saw an object. The stimulus durations were the same as those used in the fMRI experiment, and were verified by connecting a photocell to the LCD monitor. However, the intertrial intervals were shorter than those used in the fMRI study, so that more stimuli could be presented more rapidly. Subjects were not cued as to when the stimuli would be presented. For the purposes of analysis, we considered responses that occurred within 2 sec after the onset of any stimulus as a “detection”. The second behavioral task used the same methodology but stimuli were presented on the same LCD goggles used in the fMRI experiment.

Functional Magnetic Resonance Imaging

Scanning was performed on a General Electric Health Technologies, 4T LX NVi MRI scanner system equipped with 41 mT/m gradients. A quadrature birdcage radio frequency (RF) head coil was used to transmit and receive. The subject's head was immobilized using a vacuum cushion and tape. Sixty-eight high resolution images were acquired using a 3D fast SPGR pulse sequence (TR = 500 ms; TE = 20 ms; FOV = 24 cm; image matrix = 256²; voxel size = 0.9375 × 0.9375 × 1.9 mm) and used for coregistration with the functional data. These structural images were aligned in the near axial plane defined by the anterior and posterior commissures. Whole brain functional images were acquired using a gradient-recalled inward spiral pulse sequence (Glover & Law, 2001) sensitive to blood oxygenation level dependent (BOLD) contrast (TR, 1500 ms; TE, 35 ms; FOV, 24 cm; image matrix, 64²; α = 62°; voxel size, 3.75 × 3.75 × 3.8 mm; 34 axial slices). These functional images were also aligned with the plane defined by the anterior and posterior commissures. A semi-automated high-order shimming program ensured global field homogeneity. Runs consisted of the acquisition of 206 successive brain volumes and began with 4 discarded RF excitations to allow for steady state equilibrium. An experimental session contained 10 runs.

Data Analysis

Image preprocessing was performed with custom programs and SPM 99 modules (Wellcome Department of Cognitive Neurology, UK). Head motion was detected by center

of mass measurements. No subject had greater than a 3-mm deviation in the center of mass in any dimension. Images were time-adjusted to compensate for the interleaved slice acquisition and realigned to the tenth image to correct for head movements between scans. The realigned scans were then normalized to the Montréal Neurologic Institute (MNI) template found in SPM 99. The functional data were high-pass filtered and spatially smoothed with an 8 mm isotropic Gaussian kernel prior to statistical analysis. These normalized and smoothed data were used in the analysis procedures described below.

The first step in our analysis was to determine where faces evoked greater activity than objects during unmasked presentation. This analysis consisted of the following steps: (1) The epoch of image volumes beginning 2 images before (−3.0 s) and 8 images after (13.5 s) the onset of each trial was excised from the continuous time series of volumes. (2) The average intensity of the HDR at expected peak was computed and averaged from the two peak timepoints (4.5 and 6 sec). This peak was the same for both faces and objects. A *t*-statistic was then computed at each voxel within the brain to quantify the HDR differences between faces and objects. (3) The individual *t*-maps created in the preceding step were then subjected to a random-effects analysis that assessed the significance of differences across-subjects.

For each brain region showing a significantly larger response ($p < .01$) for the presentation of unmasked faces compared to unmasked objects we created a functional region of interest (ROI). This ROI was then used as the basis for our primary analysis of the unmasked trials. Furthermore, because we expected that the functional ROIs defined during conscious perception would have a larger spatial extent of activation than the masked trials, we also identified the voxel within each ROI which had the largest effect for each subject.

Results

Behavioral Tasks

In the first behavioral task, detections (as described in methods) occurred on 8.2% of stimulus trials. For those detections, subjects accurately assigned category membership 52.7% of the time, a value not significantly different than chance. In the second behavioral study that used the same LCD goggles as used in the fMRI study, detections occurred on 9.4% of all stimulus trials and subjects accurately assigned category membership on 55.4% of detections – a value not significantly different from chance. From these data, we can conclude that if subjects truly detected the presence of a stimulus, such detections were infrequent and subjects were not in any case able to accurately report what it was that they did detect.

We further explored the probability of making a detection in this study. The proportion of 2-sec windows following masked stimuli comprised 39% of all possible 2-sec windows in this behavioral task and, thus, we should expect that a subject responding at chance would have ~39% of his or her responses defined operationally as “detections”. In this study, 34.7% of all responses occurred during 2-sec windows following masked stimuli, a value not different from chance. Thus, we make the stronger conclusion that our subjects’ operationally defined detections reflected chance and were not true detections of masked stimulus events.

These behavioral results verified that our masking procedures were effective at preventing conscious awareness of the face and non-face object stimuli even when subjects were forewarned that such stimuli were being presented. Subjects were not similarly warned in the fMRI study and, during debriefing, no subject in the fMRI experiment reported seeing either a face or an object during the masked runs.

Functional MRI

Unmasked faces engaged the right FFG, the posterior superior temporal sulcus (STS), the left amygdala, and the parahippocampal gyri (PPG) (see Figure 1). Within these ROIs we identified the voxel with the largest face > object difference for each individual. Figure 2A displays each subject's most face-specific voxel within the ROI determined by the unmasked trials plotted on a line-drawing of the ventral occipitotemporal cortex. Our primary analysis of the masked data quantified the activity of these voxels at the mean of the three consecutive time points which encompassed the peak of the hemodynamic response for the unmasked trials. Activity in the right FFG was greater for masked faces compared to masked objects at these locations, $t = 2.92$, $p < .01$. Masked faces evoked numerically greater activity than objects in the left FFG and right STS, but these differences were small and did not reach statistical significance. The effect sizes, plotted as t -values, for the comparisons between masked faces and objects for each of our target brain regions are displayed in Figure 2B. The average hemodynamic response difference waveform for the comparison between masked faces and masked objects at each subject's most face specific voxel is plotted in Figure 2C.

Discussion

A focal region of the right FFG was selectively activated by both masked and unmasked faces. The right STS, right amygdala, and bilateral parahippocampal gyri were activated by unmasked, but not masked, faces. The current findings thus identify important differences in responses among the network of brain regions activated by faces.

The current results support the notion that automatic processes in the FFG reflect the operations of a face detector, necessary for rapid discrimination between faces and non-face objects. In a prior investigation, Grill-Spector and her colleagues (Grill-Spector, Knouf, & Kanwisher, 2004) used a backward masking procedure that impeded subjects' ability to detect approximately one-third of trials to test the hypothesis that the face selective region of the FFG was involved in both detection and identification of faces, but not within-category discrimination of other objects. Activity in the face-selective region of the FFG was correlated with detection of faces, but not with the detection of objects for trials that were consciously perceived (Grill-Spector, Knouf, & Kanwisher, 2004). The current results extend this finding by demonstrating that this initial response from the FFG is capable of discriminating faces from other objects even when all trials occur outside of conscious awareness.

Electrophysiological recordings made from subdural electrodes in the FFG of humans (Allison et al., 1994) have identified a field potential with a peak latency of about 200 ms (N200) that responds selectively to faces. The N200 shows little or no habituation to repeated faces, appears unaffected by the affective qualities of stimuli, and is unaffected by attention, emotional context, familiarity, priming, or learning (McCarthy, Puce, Belger, & Allison, 1999; Puce, Allison, & McCarthy, 1999). However, FFG activations measured in neuroimaging studies are strongly influenced by top-down processes including attention (Clark et al., 1996; Haxby et al., 1994; Wojciulik, Kanwisher, & Driver, 1998), emotional content (Vuilleumier, Armony, Driver, & Dolan, 2001), and familiarity (Henson, Shallice, & Dolan, 2000). We suspect that some of the discrepancies in the literatures for the face-specific N200 directly recorded from the FFG and for functional neuroimaging activations in this same region reflects the fact that the latter integrates the blood oxygenation correlates of brain activity that persists over a long temporal interval. Thus, neuroimaging activations may be more sensitive to sustained and recurrent activation evoked by task-related and strategic processing that occur subsequent to the recognition that a face is in the visual field. This interpretation is consistent with intracranial ERP recordings showing that while the

N200 is insensitive to attention and task demands, longer latency components may be modulated by top-down processing (Puce, Allison, & McCarthy, 1999). Given this logic, we speculate that the BOLD activation observed in the right fusiform gyrus for masked faces reflects the initial activity in a face detector, similar to the process reflected by N200. We also contend that the low amplitude of this right fusiform BOLD activation evoked by masked faces, relative to unmasked faces, reflects the lack of task-related and strategic processing that may be dependent upon feedback from more upstream brain regions.

Several other brain regions were selectively activated by unmasked faces: the lateral occipital cortex including the posterior STS, the parahippocampal gyri, and the amygdala. These regions were not activated by masked faces in the present study, although we recognize that it is possible that they may have been activated below the level of our ability to detect activation, and that more sensitive measurements may demonstrate face activation in the future. We suggest, however, that these areas do not participate in the initial detection of a face, but rather are involved in such processes such as face individuation or identification and expression analysis.

While the current results are consistent with a role of the right FFG in the detection of faces, the notion that this process is active below the level of conscious awareness adds significantly to our understanding of the function that is captured with modern imaging techniques. Furthermore, the activity evoked by implicit processing reflects the importance of this neural mechanism to social information processing. Implicit processing has become a major focus of research dedicated to emotional perception (Killgore & Yurgelun-Todd, 2004; Morris et al., 1996; Whalen et al., 1998). Much of this interest stems from LeDoux's proposal that emotional processing can occur via two a pathway that provides a direct connection from the thalamus to the amygdala and serves as an early evaluation system for the potential of a threat in the environment (LeDoux, 1996). If a visual stimulus is determined to be threatening a series of emotional responses places the organism in a heightened state necessary for survival. Just as the brain has adapted to treat threatening stimuli with an automatic response, encountering a face is sufficient in guiding the organism to prepare for further information with regards to subsequent social behaviors. Our data do not disprove the existence of a non-striatal pathway, but do suggest that the FFG can be engaged during processing of faces presented outside of awareness.

Acknowledgments

This research was supported by NIMH grant MH-05286. J.P. Morris was supported by F32 MH073367. K.A. Pelphrey was supported by K01 MH71284. G. McCarthy was supported by a Department of Veteran Affairs VA Senior Research Career Scientist award. The authors wish to thank M.B. Nebel and X. Li for assistance with stimulus creation and data processing, and C.R. Michelich for help with data analysis.

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Figure 1.

Unmasked trials. Faces and objects were presented for 33 ms and preceded and followed by a static black mask, which allowed for conscious perception. The red/yellow color map reflects the results of a random-effects analysis demonstrating regions of the brain where peak amplitude evoked by faces was significantly greater than that evoked by objects. Regions showing this significant difference included the right fusiform gyrus, right superior temporal sulcus, right amygdala, and bilateral parahippocampal gyrus.

Masked Trials

Figure 2.

Masked trials. Faces and objects were presented for 33 ms and preceded and followed by a pattern mask. The primary analysis for the masked presentation, used face-specific voxels that were identified by unmasked presentation of faces and objects. We found each subject's most face specific voxel within six different ROIs. Panel A shows the location each subject's most face specific voxel, as measured in the unmasked condition, in the right fusiform gyrus plotted in the X and Y dimension (data are collapsed across the Z dimension) in Talairach space on a template brain. Panel B shows the effect size, in t-values, for the peak amplitude difference evoked by masked faces relative to masked objects in voxels

previously identified as face specific. Panel C displays the average hemodynamic response difference between masked faces and objects for each subject's most face specific voxel.

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