Published in final edited form as:

Brain Topogr. 2009 September ; 22(2): 83–96. doi:10.1007/s10548-009-0086-5.

An Investigation of the Relationship Between fMRI and ERP Source Localized Measurements of Brain Activity during Face Processing

Neva M. Corrigan,

Department of Radiology, University of Washington, 1100 NE, 45th Street, Suite 555, Seattle, WA 98195, USA

Todd Richards,

Department of Radiology, University of Washington, Seattle, WA, USA

Sara Jane Webb,

Department of Psychiatry and Behavioral Sciences, University, of Washington, Seattle, WA, USA

Michael Murias,

Department of Psychiatry and Behavioral Sciences, University, of Washington, Seattle, WA, USA

Kristen Merkle,

UW Autism Center, University of Washington, Seattle, WA, USA

Natalia M. Kleinhans,

Department of Radiology, University of Washington, Seattle, WA, USA

L. Clark Johnson,

Department of Psychosocial and Community Health, University of Washington, Seattle, WA, USA

Andrew Poliakov,

Department of Biological Structure, University of Washington, Seattle, WA, USA

Elizabeth Aylward, and

Department of Radiology, University of Washington, Seattle, WA, USA

Geraldine Dawson

Department of Psychiatry and Behavioral Sciences, University, of Washington, Seattle, WA, USA;
Department of Psychology, University of Washington, Seattle, WA, USA

Neva M. Corrigan: nevao@u.washington.edu

Abstract

Brain activity patterns during face processing have been extensively explored with functional magnetic resonance imaging (fMRI) and event-related potentials (ERPs). ERP source localization adds a spatial dimension to the ERP time series recordings, which allows for a more direct

comparison and integration with fMRI findings. The goals for this study were (1) to compare the spatial descriptions of neuronal activity during face processing obtained with fMRI and ERP source localization using low-resolution electro-magnetic tomography (LORETA), and (2) to use the combined information from source localization and fMRI to explore how the temporal sequence of brain activity during face processing is summarized in fMRI activation maps. fMRI and high-density ERP data were acquired in separate sessions for 17 healthy adult males for a face and object processing task. LORETA statistical maps for the comparison of viewing faces and viewing houses were coregistered and compared to fMRI statistical maps for the same conditions. The spatial locations of face processing-sensitive activity measured by fMRI and LORETA were found to overlap in a number of areas including the bilateral fusiform gyri, the right superior, middle and inferior temporal gyri, and the bilateral precuneus. Both the fMRI and LORETA solutions additionally demonstrated activity in regions that did not overlap. fMRI and LORETA statistical maps of face processing-sensitive brain activity were found to converge spatially primarily at LORETA solution latencies that were within 18 ms of the N170 latency. The combination of data from these techniques suggested that electrical brain activity at the latency of the N170 is highly represented in fMRI statistical maps.

Keywords

Face processing; LORETA; Source localization; fMRI; Coregistration

Introduction

Face processing is a fundamental aspect of social cognition. Temporal and spatial patterns of brain activity associated with face processing have been studied extensively using functional magnetic resonance imaging (fMRI) and event-related brain potentials (ERPs). Due to differences in data acquisition technology as well as the fact that these instruments measure signals generated from very different physiological processes, the two techniques produce different but complementary types of information.

Event-related potential (ERP) recordings reveal the rapid and complex spatial and temporal nature of brain electrical activity involved in a cognitive task. ERPs are thought to reflect the post-synaptic potentials of synchronously firing pyramidal cells oriented perpendicular to the surface of the scalp (Lopes daSilva and Van Rotterdam 1982). Brain activity causes voltages measured on the scalp to fluctuate on the order of milliseconds, and topographical maps demonstrate large shifts in the location of maximal activity over even very brief time periods. ERP studies have identified a peak in the ERP signal over the posterior temporal scalp at a latency in the range of 130–190 ms post-stimulus onset (the N170 or “face-sensitive” peak) that is greater in amplitude and faster in latency to faces than to other stimuli (Bentin et al. 1996; Eimer 1998, 2000; George et al. 1996; Itier et al. 2006b; Itier and Taylor 2004a; Rossion et al. 2000). ERP recordings, and topographical maps, however, provide only very coarse information regarding the locations of the neuronal generators of observed fluctuations in scalp voltages.

Functional neuroimaging techniques are used to produce spatial maps of physiological measures that are associated with brain activity. fMRI specifically detects localized signal fluctuations caused by changes in blood flow and blood oxygenation associated with the hemodynamic response. fMRI studies have provided valuable information regarding the spatial location of brain regions involved in face processing. A convergent finding across a number of fMRI studies has been the identification of a region in the bilateral middle fusiform gyrus that is preferentially activated for the viewing of faces compared with other objects, often referred to as the “fusiform face area” (Halgren et al. 1999; Kanwisher et al. 1997; McCarthy et al. 1997). Other areas, such as the superior temporal sulcus, the inferior temporal gyrus and the inferior occipital gyrus have additionally been reported to be preferentially activated by the viewing of faces based on fMRI studies (Ishai et al. 2005; Puce et al. 1995). However, although fMRI yields relatively highly detailed spatial information (with a resolution on the order of millimeters), the temporal resolution of fMRI, on the order of seconds, at best provides only coarse measurement of the timing of neuronal activity.

In summary, both fMRI and ERP studies have demonstrated characteristics in brain activity signal patterns that are sensitive to the viewing of faces. A number of methods have been developed to integrate ERP and fMRI findings to take advantage of the fact that they have complimentary strengths. These include the comparison of fMRI BOLD waveforms to EEG spectral components (Martinez-Montes et al. 2004), and integration with information provided by ERP source localization (Menon et al. 1997; Mulert et al. 2004; Schulz et al. 2008; Vitacco et al. 2002). Source localization algorithms estimate the locations of the neuronal generators of scalp voltage changes at any time point in the ERP recording by solving what is termed the “inverse problem.” A number of algorithms exist, and each requires its own set of a priori assumptions to localize sources of electrical activity measured on the scalp. Despite the fact that these algorithms generally yield solutions with relatively low spatial resolution compared to fMRI, they do provide a more complete description of the complex spatial and temporal nature of brain activity during a cognitive process that is otherwise unavailable. Dipole modeling algorithms model neural generators of brain activity with a small number of discrete point sources. Source localization algorithms based on linear distributed source models, including low-resolution electromagnetic tomography (LORETA, Pascual-Marquis et al. 1994), yield spatial maps of current density which are similar to the activation maps generated with fMRI. fMRI analysis has also been used to guide the process of selecting the number and approximate position of sources in dipole analysis (for example, Stancak et al. 2005). Both dipole representations of sources and current density maps can be directly coregistered and integrated with fMRI maps to provide a simultaneous visualization of information. Other investigators have coregistered LORETA current density maps directly with fMRI activation maps, including Vitacco et al. (2002) for a visual language processing task and Mulert et al. (2004) for a target detection task. Both of these latter studies reported a high spatial correspondence between the findings from the two techniques.

Source localization techniques have been used to identify the locations of the neural generators of the N170 and the M170 (a similar face-sensitive component detected with MEG). Both the fusiform gyrus (Halgren et al. 2000; Itier et al. 2006a; Rossion et al. 1999,

2003) and the superior temporal sulcus (Itier et al. 2007; Itier and Taylor 2004b) have been identified as possible primary sources. Other source localization studies report the involvement of occipital extrastriate areas (Itier et al. 2006a) or a relatively extensive network of sources located in the both the temporal and occipital lobes (Watanabe et al. 2003). Dale and Halgren (2001) emphasize the challenge to interpreting the integrated findings from fMRI and EEG due to the fact that the coupling between the electrical and hemodynamic signals is poorly understood. This in part arises from the fact that the mechanisms that underlie the generation and propagation of signal measured by the two techniques are vastly different and not fully characterized. One question related to this coupling is whether fMRI activation maps for face processing reflect activity occurring during a particular stage of face processing, or reflect a summation of all of the sources involved during all stages represented in the typical ERP epoch, which can extend to up to 1 s after stimulus onset. Based on findings from an attentional study of individuals using stimuli of faces and houses, using fMRI and MEG, Furey et al. (2006) suggest that the hemodynamic response reflects neuronal activity occurring later in face processing, after the latency of the M170.

In this study, fMRI and high-density ERP data were acquired from 17 healthy volunteers in separate sessions during performance of a face and object processing task. Activity during the viewing of faces was compared to that for the viewing of houses for each technique in order to isolate face-sensitive visual processing activity. Source localization of the ERP data was performed using LORETA, and the findings from the two techniques were compared and integrated by coregistration and superim-position of statistical maps. Our objectives were (1) to compare the spatial locations of generators of face processing activity provided by the two techniques, and (2) to investigate whether fMRI activation maps reflect activity occurring at a specific latency during the ERP epoch. Similarities in results from previous studies of face processing using fMRI or ERP indicated that we would find spatial overlap between the solutions. The findings from Furey et al. (2006) suggested we would find this overlap relatively late in the ERP epoch, after the latency of the N170.

Materials and Methods

Participants

Subjects for this study were a subset of a sample recruited for a larger study investigating differences in fMRI and ERP responses to various visual stimuli. Data from 17 neuropsychiatrically healthy adult males were included in this analysis. The same subjects participated in both the fMRI and ERP experiments. Subjects ranged in age from 18 years to 40 years, with an average age of 22.9 years. All but two of the subjects were right-handed. Exclusionary criteria included birth or developmental abnormalities, psychotropic medication usage, seizures, significant sensory or motor impairment, major physical abnormalities, serious head injury, or a first degree relative with autism spectrum disorder. The study was approved by the University of Washington Human Subjects Institutional Review Board and all subjects consented to the procedures.

ERP

Stimuli—The ERP stimuli consisted of gray-scale digital images, each with a gray background, presented on a computer monitor. Stimuli were presented randomly in four blocks composed of 58 trials of five different stimulus categories: upright faces (50), inverted faces (50), upright houses (50), inverted houses (50), and scrambled faces (32). All facial images were standardized so that the center of the eyes was presented at the center of the screen; visual angle for the faces was 11° (height) by 7.6° (width). The ethnicity of the face images reflected regional demographics. All house pictures were taken from local neighborhoods, or from stimulus sets provided by N. Kanwisher and M. Eimer. The houses in the images were symmetrical and the visual angle for the houses was 7.1° (height) by 7.1° (width). To control for attention, participants were instructed to press a button upon the appearance of each scrambled face. Only the recordings corresponding to the presentation of upright faces and upright houses were used in the current analysis. ERP analysis for the larger study is reported elsewhere (Webb et al. 2009).

Data Acquisition—ERP data were acquired in an electronically shielded, sound-attenuated and darkened room. Participants were seated approximately 75 cm from the computer monitor on which the stimuli were presented. A 128 channel Geodesic sensor net (EGI; Eugene OR) was dipped in a potassiumchloride electrolyte solution, placed on the participant's head, and fitted according to the manufacturer's specifications. The electrodes were evenly spaced and symmetrically covered the scalp from nasion to inion and from left to right ears. Amplification was $1,000\times$ and impedances were kept below $40\text{ k}\Omega$. A sampling rate of 500 Hz was used. Data were filtered with both a 0.1 Hz high-pass filter and a 200 Hz elliptical low-pass filter and the vertex electrode was used as a reference. The trial structure consisted of 500 ms baseline recording with presentation of a central fixation cross followed by 300 ms of stimulus presentation, and a random inter-trial interval of between 1,000 and 1,300 ms. The inter-stimulus interval ranged from 1,500 ms to 1,800 ms.

Data Processing—All ERP data were processed using NetStation 4.0. Data were first low-pass filtered at 30 Hz, and then trials with fast amplitude exceeding $100\text{ }\mu\text{V}$, differential average amplitude exceeding $50\text{ }\mu\text{V}$, or zero variance were marked as bad. Electrodes with more than 20% trials marked as bad were rejected and replaced using spline interpolation of the signal from the neighboring leads. Trials with eye movement artifact were additionally identified and excluded. Data were averaged for each stimulus type and re-referenced to an average reference. In this analysis, only data from the 124 electrodes located on the scalp (and not on the face) were used.

Global Field Power Calculation—The global field power, or spatial standard deviation of the scalp potentials, provides a comprehensive summary of electrical activity across the entire scalp. For this analysis, it was computed as a function of time from the ERP recordings using the following equation:

$$GFP(t) = \sqrt{\frac{1}{n} \times \sum_{i=1}^n \left(u_i(t) - \frac{\sum_{j=1}^n u_j(t)}{n} \right)^2}$$

In this equation, u represents the voltage at a single electrode, n represents the total number of electrodes, and t represents the time sample.

fMRI

Stimuli—The face and house images presented in the fMRI experiment were similar in all respects to those used for the ERP experiment with the exception that different individual people and houses were pictured. Participants viewed photographs of neutral faces and houses in alternating blocks of 36 s each for a total of eight blocks. Each individual image was presented for a duration of 3 s with no inter-stimulus interval. Eighteen seconds of fixation (crosshair) were included at the beginning, the middle, and the end of the fMRI data acquisition. Data from the full fMRI analyses are presented elsewhere (Kleinhans et al. 2007). Attention was assessed using a one-back working memory task, whereby subjects were asked to press a button if the exact same stimulus was presented twice in a row. All images were presented to the subject via a mirror on the head coil that allowed for a view of a projection screen placed at the foot of the scanning table.

Data Acquisition—MR imaging was performed on a 1.5T Signa Horizon system (General Electric, WI). Axial plane fMRI images were collected using an echo-planar pulse sequence (TR/TE 3,000/50 ms, 21 slices, 6 mm thick, 1 mm gap, 64×64 matrix, 114 volumes total). High-resolution sagittal spoiled gradient-recalled echo (SPGR) images were also collected for fMRI registration and anatomical localization (TR/TE 11.1/2 ms, with voxel dimensions of $0.97 \times 1.1 \times 1.2$ mm).

Data Processing—All fMRI data processing and analysis were performed using the Centre for Functional MRI of the Brain (FMRIB) Software Library version 3.3 (FSL; www.fmrib.ox.ac.uk/fsl). The following steps were performed in the pre-processing of the fMRI data: the first two volumes of each fMRI experiment were discarded, motion correction was performed with Motion Correction FMRIB's Linear Registration Tool (MCFLIRT, Jenkinson et al. 2002); non-brain structures were removed using Brain Extraction Tool (BET, Smith 2002); data were filtered spatially with a Gaussian kernel of FWHM 5 mm and temporally with a Gaussian high-pass filter of $\sigma = 72$ s. Motion related components, identified using Multivariate Exploratory Linear Optimized Decomposition into Independent Components (MELODIC, Beckmann and Smith 2004), were filtered from the data prior to statistical analyses.

Individual fMRI data were registered to the high-resolution 3D SPGR images, transformed into the MNI152 standard space using FLIRT (FMRIB's Linear Image Registration Tool) and resampled to 2 mm^3 voxels. MNI152 space is defined by a template generated at the Montreal Neurological Institute, where 152 T1-weighted and stereotactically normalized

scans were averaged to form a standardized human brain volume. This standard template is distributed with FSL. Analysis was carried out using FEAT (fMRI Expert Analysis Tool) Version 5.63, part of FSL. Higher-level analysis was carried out using OLS (ordinary least squares) simple mixed effects (Worsley et al. 1992). This analysis produced group z (Gaussianised T/F) maps for the contrast between viewing faces and houses. We report data where z score exceeds a value of 3.0, corresponding to a significance level P of 0.001. fMRI statistical maps were masked to show activation only in regions for which the source localization algorithm computed a solution.

Source Localization

Current density maps of activity for both the face and house conditions were generated from the ERP recordings of all subjects individually with the LORETA-Key software package (Pascual-Marquis 1999). The LORETA algorithm implementation is based on a distributed source model, which does not require a priori assumptions about the number and locations of neuronal generators of the electrical activity measured on the scalp. It assumes a model of the brain as a three-dimensional matrix of point sources, and attributes electrical activity, termed current density and expressed in units of $\mu\text{V}/\text{mm}^2$, to each of these points. As there is an infinite number of source configurations that can generate the voltages measured on the scalp (the system is underdetermined), distributed source models require the a priori application of constraints in order to select a unique solution. LORETA specifically utilizes a Laplacian weighted minimum norm algorithm to compute the configuration that provides the smoothest solution, meaning that the current density at any point is as similar as possible to that of its closest neighbors. This “smoothness constraint” is consistent with physiological models that assume that the generation of ERP potentials requires coherent firing of groups of neighboring neurons and results in a solution with a relatively low spatial resolution. The LORETA-Key implementation of this algorithm limits the solution to the cortical gray matter and hippocampus according to digital probability atlases provided by the Montreal Neurological Institute. The solution produces a time series of three-dimensional volumes, each with a spatial resolution of 7 mm^3 and containing 2,394 voxels. Source localization computations are based on a three-shell spherical head model registered to the Talairach human brain atlas (Talairach and Tournoux 1988). EEG electrode coordinates provided by EGI in online documentation for the Geodesic Sensor Net were used to calculate the transformation matrix using a regularization constant of 1e^{-4} . The temporal resolution of the LORETA solution in the current study was 2 ms, the same as the original ERP recording, and the solution was computed for the epoch extending from 100 ms prior to the onset of face stimulus presentation to 400 ms after face stimulus onset. Statistical t value maps for differences in electrical source activity between the viewing of faces and houses were generated using the LORETA-Key software package statistical non-parametric mapping voxel-wise comparison calculation tool for paired comparisons (Nichols and Holmes 2002). This tool computes statistical maps based on the individual current density maps for all subjects for each of the stimulus conditions. The resulting statistical volumes summarize the findings of face-sensitive activity for the group of subjects as a whole. Thus, the LORETA statistical tool allowed for the computation of statistical maps for the contrast between faces and houses that were analogous to the statistical (activation) maps generated in the fMRI analysis, even though the original ERP waveforms did not directly provide a contrast

between the two conditions. The LORETA t value maps were thresholded at a value of 3.0. We chose this threshold because it provided maps that demonstrated reasonable correspondence with the fMRI without large amounts of spurious noise (activity not confined to large clusters) as determined by visual inspection.

Coregistration of Current Density Maps with fMRI Activation Maps

In order to directly compare the LORETA statistical maps with the fMRI statistical maps, it was necessary to coregister the LORETA solution volumes to the same space as the fMRI volumes. To do this, the MNI coordinates for each LORETA voxel, as provided in supplementary materials of the LORETA-Key software package, were used to map each of the 2,394 voxels into the same space as the fMRI activation maps: MNI152 space, which has dimensions of $91 \times 109 \times 91$ pixels. To do this, the statistical value for each LORETA voxel was positioned at the same coordinate in MNI152 space. Due to the smaller number of voxels in the LORETA solution compared to the number of voxels in the MNI152 space, this resulted in large gaps between voxels with LORETA values. To fill in this volume, the t value for each data point was duplicated to the surrounding data points in order to fill in the entire volume, essentially resulting in an expansion of each LORETA voxel to a larger size. This resulted in a LORETA statistical map matrix that was coregistered with the fMRI activation volume. Whereas the functional activation volume included only three-dimensional spatial information, the temporal dimension of the LORETA solution was maintained by combining volumes for all time points into a four-dimensional ANALYZE file. The resulting file thus included three spatial dimensions and one temporal dimension. In order to compare the activation by each technique in each brain region, the Automatic Anatomic Labeling Map (AAL) anatomical atlas (Tzourio-Mazoyer et al. 2002) available in the MRIcro software package (<http://www.sph.sc.edu/comd/rorden/mricro.html>) was also coregistered to the standard MNI152 brain. FSL was used to view the overlaid images, and custom software was developed in the laboratory to compare the volumes on a pixel-by-pixel and regional anatomy basis.

Results

ERP

The configuration of the 128 lead Geodesic sensor net used in data acquisition for this study is shown in Fig. 1a. Electrodes that were considered in this analysis to be situated in close proximity to the posterior temporal lobe are marked in red. Figure 1b shows the grand-averaged signal across all subjects measured from these posterior temporal electrodes for both hemispheres and stimulus types. The grand-averaged ERPs for the face condition demonstrate a P100 at 88 ms in both hemispheres and N170 right and left hemisphere latencies of 142 and 138 ms, respectively. The grand-averaged ERPs for the house condition show P100 positivities at right/left hemisphere latencies of 100/104 ms and right/left hemisphere N170 latencies of 156/158 ms. The global field power is shown for each stimulus type in Fig. 1c. Peak latencies of the global field power waveforms represent times of maximal cortical brain activity that are unbiased by assumptions as to the locations of the neuronal generators. The viewing of faces produces peaks in global field power at latencies of 90, 136, and 216 ms after stimulus onset. The two earliest peaks correspond closely in

time with the P100 and N170 component latencies measured from the posterior temporal scalp electrodes. For the viewing of houses, the global field power demonstrates peaks at 100 and 222 ms after face stimulus onset. The latency of the earliest global field power peak for the house condition corresponds closely with the timing of the P100 as measured on the scalp for the same condition. The absence of a corresponding peak in the global field power for the house condition suggests that the peak at 136 ms for the face condition reflects activity across the brain that is sensitive to face processing.

fMRI

fMRI z score maps for the contrast between faces and houses superimposed on the MNI152 standard brain for slices in the axial plane are shown in the left panel of Fig. 2. In this panel, the yellow-orange color corresponds to the magnitude of the z score for the contrast of faces versus houses for the fMRI BOLD signal. Prominent fMRI activity is evident in multiple regions, including the bilateral fusiform gyri, the bilateral hippocampus, the bilateral amygdalae, the right middle temporal gyrus, the bilateral cuneus, and the bilateral precuneus.

LORETA

LORETA *t* value maps for the contrast between faces and houses superimposed on the MNI152 standard brain are shown in the right panel of Fig. 2. The blue color corresponds to the magnitude of the *t* value for the contrast of faces versus houses for the LORETA solution. The images correspond to the solution at 136 ms post-stimulus presentation onset. Prominent activity is evident in regions including the bilateral fusiform gyri, the bilateral inferior temporal gyri, the bilateral middle temporal gyri, the right superior temporal gyrus, the bilateral inferior occipital gyri, the right insula, the right rolandic operculum, the bilateral precuneus, and the bilateral middle cingulate gyri. A more comprehensive spatial and temporal description of brain activity generated from the LORETA analysis is provided in the Supplementary Materials as Fig. S1.

Correspondence of fMRI and LORETA Results

Brain activity as measured by functional MRI and LORETA at three different LORETA solution latencies is shown superimposed on the MNI152 standardized brain in Fig. 3. The latencies were chosen as those corresponding to maximal overlap of regions between the two techniques. The locations of activity in the fMRI maps coincide maximally with the source localized activity at 134 ms poststimulus onset in the bilateral precuneus. At 142 ms there is maximal overlap of activity in the left fusiform gyrus as well as the left inferior temporal gyrus. Maximal overlap in activity in the right fusiform gyrus, the right superior temporal gyrus, and the right middle temporal gyrus occurs at a latency of 146 ms post-stimulus onset. Overlays of fMRI and LORETA spatial findings for five individual subjects are presented in the Supplementary Materials as Figs. S2 and S3.

A list of all regions demonstrating overlap between the two techniques, along with the latencies of maximal overlap, the number of voxels overlapping, and the statistical values and MNI coordinates of the voxels with the maximal statistical value in the regions of overlap is presented in Table 1. In this table the number of overlapping voxels is also shown

as a percentage of the number of voxels in each region, the total number of suprathreshold LORETA voxels for the region and the total number of suprathreshold fMRI voxels in the region. The figures in this table reflect the following: (1) the regions of overlap are relatively small compared to the size of the overall anatomical regions, (2) the clusters of LORETA activation are larger than the clusters of fMRI activity, (3) for more than half of the regions of overlap, more than 50% of the fMRI suprathreshold voxels converge with the LORETA solution for the thresholds used, and (4) the numbers of overlapping voxels is relatively small for each region compared to the total number of suprathreshold LORETA voxels. These are consistent with a visual inspection of the statistical maps in Fig. 2 and the overlays in Fig. 3.

Waveforms representing LORETA t value changes over time for regions demonstrating overlap in the LORETA and fMRI statistical maps are shown in Fig. 4. For a given plot, each individual waveform represents a single voxel in the image volume. Dashed vertical lines indicate the time of stimulus onset as well as the latencies of the peaks in the global field power for the face condition. Voxels in the left fusiform as well as the left inferior temporal gyrus demonstrate prominent peaks proximal in latency to the earliest peak in the global field power peak for the face condition. The waveforms for most regions demonstrate local peaks that are proximal to the latency of global field power peak at 136 ms. Latencies of overlap between the LORETA and fMRI statistical maps are indicated by gray shading. All spatial overlap, except for one instance of very early overlap in the left postcentral gyrus (excluded from this figure for space considerations) occurs within 18 ms of the global field power peak at 136 ms.

Another representation of the duration and relative latency of overlap of the LORETA statistical maps with the fMRI maps for regions demonstrating overlap is shown in Fig. 5. Dashed vertical lines in this figure demark the latencies of the peaks in the global field power for the face condition. The exact latencies of the onset and end of overlap, illustrated graphically in Fig. 5, are listed in Table 2.

Many regions demonstrated suprathreshold activity in both the fMRI and LORETA statistical maps, but occurred in spatial areas that did not overlap. A list of these regions of non-overlapping activity is given in the left column of Table 3. A list of regions demonstrating suprathreshold activity in the fMRI statistical maps alone is shown in the right column of Table 3.

Discussion

The ERP findings are consistent with the literature, showing an N170 that is faster and larger in amplitude for face stimuli than for house stimuli. The finding of a peak in the global field power corresponding to the latency of the N170 that is more prominent for the face condition than the house condition is consistent with other reports global field power differences for faces compared to objects (Caldara et al. 2003; Itier and Taylor 2004a; Rousselet et al. 2004). Both the fMRI and LORETA results demonstrate the expected prominent activity of the fusiform gyrus with this face processing task. The LORETA t value waveforms shown in Fig. 4 additionally reflect peaks in fusiform activity at the time

of the face-sensitive global field power peak, providing evidence for a link between the N170 as measured on the scalp and fusiform activity. The presence of a large number of other active regions in the results from both techniques, however, suggests that the fusiform gyrus is likely not the single or most important source of face processing-sensitive activity in the brain, nor the sole generator of the N170 negativity measured on the scalp. Indeed, all of the regions shown in Fig. 4 demonstrate local maxima in differences between activity for the face and house conditions proximal to the time of the N170. This finding is consistent with the involvement of a network of brain areas in face processing at the time of the N170. Our findings include involvement of the lateral temporal cortex, as reported by Watanabe et al. (2003) and the superior temporal sulcus, as reported by Itier et al. (2007) and Itier and Taylor (2004b).

The most striking result from this analysis is that, with the exception of very early activity in the left post-central gyrus, the spatial convergence of fMRI and LORETA solutions occurs within 18 ms of the N170 latency as measured on the scalp. These results suggest that although activity shifts between different brain regions in the 400 ms after an individual views a face, the activity that occurs at the latency of the face processing-sensitive ERP component is highly represented in the fMRI maps. These results are contrary to the findings of Furey et al. (2006), which based on results from an MEG and fMRI face processing study, concluded that the fMRI activation maps reflected activity occurring in the later stages of the MEG epoch, after the latency of the M170. An important note in considering the respective results from these two studies, however, is that the study designs differed greatly. Although both studies contrasted activity for the viewing of faces and houses, the findings of Furey et al. (2006) were based on activity measured when subjects focused attention towards a single stimulus type when two stimulus categories were presented in double-exposed images. The current findings represent a direct comparison of measured activity when individuals were viewing each stimulus type alone in turn. Inclusion of information provided by calculation of the source localized solution in the current study may have also contributed to the differences in findings.

The maximal overlap in left hemisphere fusiform gyrus and inferior temporal gyrus, as well as in the right hemisphere fusiform gyrus, superior temporal gyrus and middle temporal gyrus, occurs 4 ms after the latency of the N170. Of all of the regions of overlap, these are the most commonly associated with face processing. After inspection of the LORETA solution, summarized in Supplementary Fig. S1, it is evident that these regions are active at latencies prior to the N170 as well. These results indicate that for these regions, the fMRI solution is best representing activity that occurs a few milliseconds after the latency of the N170 component. The regions demonstrating the most overlap between solutions in terms of number of voxels are the left hemisphere precuneus, inferior temporal gyrus, and fusiform gyrus. This finding is notable considering that face processing is thought to more predominantly engage right hemispheric regions, and the precuneus is not a region typically considered to be integral to the processing of unfamiliar faces. However, the precuneus is known to be involved in a wide spectrum of highly integrated tasks, including visuo-spatial imagery (Cavanna and Trimble 2006).

Our interest for this study was to determine what combined information from face processing experiments with ERP source localization and fMRI might reveal about our understanding of face processing as well as about the relative meaning of the fMRI and ERP findings. The data was derived from a larger study in which fMRI and ERP experiments were performed independently and the stimulus presentation and acquisition parameters were tailored for each technique to elicit robust face-sensitive activity based on previous experience with the data acquisition systems used. Although both experiments involved recording data for the viewing of face and house stimuli from the same group of subjects, a number of details in stimulus presentation and data acquisition differed. These included the duration of presentation of the individual stimuli, the use of a block design for the fMRI acquisition and an event-related design for the ERP acquisition, the use of different attentional tasks, and the presentation of stimuli of additional categories in the ERP experiment. Despite these differences, analysis of the data for the respective experiments demonstrated robust face-sensitive activation for each of the two techniques, and the individual findings were found to be consistent with reports from face processing studies in the literature. In this study, we integrated the information to determine what additional information it would provide about the spatial and temporal dynamics of face processing in the brain as well as the meaning of the respective findings. Despite the differences in the experimental details, integration of fMRI activation maps with maps from ERP data source localization yielded spatial convergence of the findings primarily proximal to the latency of the N170.

The effect of the differences in experimental constraints are unclear. As noted above, fMRI and ERP measure signals from processes that evolve on different time scales and are produced by different physiological phenomena. However, the use of identical stimulus paradigms would have been preferable. Timing differences and the fact that the data were not acquired simultaneously also likely had an effect on the results of this study, although Sadeh et al. (2008) report a high degree of correlation between ERP data acquired outside the MRI scanner during a session on a different day to be highly correlated with ERP data acquired during simultaneous recording with fMRI, indicating that these effects may be minimal. Differences in the details of the techniques, however, would most likely have decreased the likelihood of finding convergence between the descriptions of face processing for the two techniques.

The use of different attentional task for the two experiments may have also affected the results for this study. However, all comparisons between the results for the two techniques were based on statistical maps, which were designed to isolate solely differences in activity between the face and house stimulus conditions. In such a design, the effect of any variable that is constant during the two conditions, including attentional task, theoretically should not be represented in the calculated statistical maps. This approach would likely have minimized the effect of the attentional task on the study findings, even though they differed across the two experiments.

This study describes correspondence between the LORETA t value maps and fMRI z score maps. Any approach to comparing the results from the two techniques requires the selection of thresholds. This selection of thresholds may introduce subjectivity, as criteria are

confirmed by the researcher's estimations of reliable and interpretable signal in the presence of noise. Previous studies reporting correspondence between LORETA findings and fMRI activation maps have compared LORETA current source density (CSD) maps (with values in units of $\mu\text{V}/\text{mm}^2$) to fMRI statistical maps. In a study of correspondence for a language processing task, Vitacco et al. (2002) selected LORETA CSD thresholds that ensured that the number of LORETA Amaxima never exceeded the number of activated clusters in the fMRI activation maps. In a study of brain activity during target detection, Mulert et al. (2004) evaluated correspondence of functional MRI maps and LORETA maps at latencies that were determined by visual inspection of CSD values for different brain regions. In those reports, the choice of threshold level for the LORETA CSD values were not based on a measure of statistical significance. In this study, we have instead compared statistical maps generated by the two analyses. Our decision to compare LORETA t value maps instead of current density maps was driven by the desire to limit findings to face-sensitive visual processing, as opposed to visual processing associated with the viewing of objects, a distinction that would not be possible with the analysis solely of CSD values for the face stimulus condition. We recognize that there are differences in the distributions and significance levels associated with the statistics reported here for the two techniques (LORETA t values and fMRI z scores). We have selected a threshold value for the LORETA t values that we considered to be appropriate for the current analysis.

There are a number of additional possible reasons for differences in findings between the two techniques in this study. The LORETA statistical maps have low spatial resolution compared to the fMRI statistical maps and many regions may artificially demonstrate suprathreshold statistical values as a result. This may account for the much larger number of regions demonstrating face-sensitive activity as compared to the fMRI findings. It is probable that apparent activity observed in some areas is a result of contamination of signal from surrounding active regions. Discrepancies in findings involving deeper cortical structures, such as the amygdala and hippocampus, may be a result of the distance of these structures from EEG recording electrodes, or the orientation of pyramidal cells within these regions. The use of a spherical head model instead of one based on individual subject anatomy for the LORETA solution calculation may also have introduced error and could be a source of offset between face-sensitive LORETA and fMRI activity. When evaluating the correspondence between fMRI and LORETA results, however, it is also important to keep in mind that they measure different physiological processes thought to be related to neuronal activity, so dissimilar findings do not necessarily indicate erroneous calculations by either technique.

In summary, findings from this study are likely affected by a number of factors which would likely decrease the chances of finding spatial or temporal convergence. Given these factors and also the challenges inherent in integrating data acquired using different techniques, the findings of temporal convergence of fMRI activation and the N170 ERP component from this study are highly notable and suggest that electrical brain activity at the latency of the N170 is highly represented in fMRI statistical maps.

Conclusion

We report correspondence between fMRI and LORETA source localization measures of neuronal activity in a number of brain regions for a face processing task. Overlapping activity between the fMRI maps and the LORETA solution at the latency of the N170 was found in a number of areas in the occipital and temporal lobes, and included the bilateral fusiform gyrus and the right inferior, middle and superior temporal gyri. For all regions where activity for the two techniques overlapped, overlap occurred at LORETA solution latencies within 18 ms of the latency of the N170 as measured on the scalp. This study demonstrates that integration of information provided by fMRI and source localization can aid our understanding of the temporal relationship between the activity measured by the two techniques.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

This research was funded by a program project grant from the NIMH Studies to Advance Autism Research and Treatment (U54MH066399). The Murdock Trust provided funds for purchase of the system for recording electroencephalographic activity. This work was also facilitated by grant no. P30 HD02274 from the National Institute of Child Health and Human Development. We gratefully acknowledge the contributions of these funding sources, the UW Autism Clinical and Statistical Cores of this project, and the individuals who participated in this study. We additionally thank Jenée O'Brien for her assistance in acquiring the MR data for this study.

References

- Beckmann CF, Smith SM. Probabilistic independent component analysis for functional magnetic resonance imaging. *IEEE Trans Med Imaging*. 2004; 23:137–152. [PubMed: 14964560]
- Bentin S, Allison T, Puce A, Perez E, McCarthy G. Electrophysiological studies of face perception in humans. *J Cogn Neurosci*. 1996; 8:551–565. [PubMed: 20740065]
- Caldara R, Thut G, Servois P, Michel CM, Bovet P, Renault B. Face versus non-face object perception and the 'other-race' effect: a spatio-temporal event-related potential study. *Clin Neurophysiol*. 2003; 114:515–528. [PubMed: 12705432]
- Cavanna AE, Trimble MR. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain*. 2006; 129:564–583. [PubMed: 16399806]
- Dale AM, Halgren E. Spatiotemporal mapping of brain activity by integration of multiple imaging modalities. *Curr Opin Neurobiol*. 2001; 11:202–208. [PubMed: 11301240]
- Eimer M. Does the face-specific N170 component reflect the activity of a specialized eye processor? *NeuroReport*. 1998; 9:2945–2948. [PubMed: 9804295]
- Eimer M. The face-specific N170 component reflects late stages in the structural encoding of faces. *NeuroReport*. 2000; 11:2319–2324. [PubMed: 10923693]
- Furey ML, Tanskanen T, Beauchamp MS, Avikainen S, Uutela K, Hari R, Haxby JV. Dissociation of face-selective cortical responses by attention. *Proc Natl Acad Sci USA*. 2006; 103:1065–1070. [PubMed: 16415158]
- George N, Evans J, Fiori N, Davidoff J, Renault B. Brain events related to normal and moderately scrambled faces. *Brain Res Cogn Brain Res*. 1996; 4:65–76. [PubMed: 8883920]
- Halgren E, Dale AM, Sereno MI, Tootell RB, Marinkovic K, Rosen BR. Location of human face-selective cortex with respect to retinotopic areas. *Hum Brain Mapp*. 1999; 7:29–37. [PubMed: 9882088]

- Halgren E, Raij T, Marinkovic K, Jousmaki V, Hari R. Cognitive response profile of the human fusiform face area as determined by MEG. *Cereb Cortex*. 2000; 10:69–81. [PubMed: 10639397]
- Ishai A, Schmidt CF, Boesiger P. Face perception is mediated by a distributed cortical network. *Brain Res Bull*. 2005; 67:87–93. [PubMed: 16140166]
- Itier RJ, Taylor MJ. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. *Cereb Cortex*. 2004a; 14:132–142. [PubMed: 14704210]
- Itier RJ, Taylor MJ. Source analysis of the N170 to faces and objects. *NeuroReport*. 2004b; 15:1261–1265. [PubMed: 15167545]
- Itier RJ, Herdman AT, George N, Cheyne D, Taylor MJ. Inversion and contrast-reversal effects on face processing assessed by MEG. *Brain Res*. 2006a; 1115:108–120. [PubMed: 16930564]
- Itier RJ, Latinus M, Taylor MJ. Face, eye and object early processing: what is the face specificity? *Neuroimage*. 2006b; 29:667–676. [PubMed: 16169749]
- Itier RJ, Alain C, Sedore K, McIntosh AR. Early face processing specificity: it's in the eyes! *J Cogn Neurosci*. 2007; 19:1815–1826. [PubMed: 17958484]
- Jenkinson M, Bannister P, Brady M, Smith S. Improved optimization for the robust and accurate linear registration and motion correction of brain images. *Neuroimage*. 2002; 17:825–841. [PubMed: 12377157]
- Kanwisher N, McDermott J, Chun MM. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci*. 1997; 17:4302–4311. [PubMed: 9151747]
- Kleinhans NM, Johnson LC, Mahurin R, Richards T, Stegbauer KC, Greenson J, Dawson G, Aylward E. Increased amygdala activation to neutral faces is associated with better face memory performance. *NeuroReport*. 2007; 18:987–991. [PubMed: 17558282]
- Lopes daSilva, F.; Van Rotterdam, A. Biophysical aspects of EEG and MEG generation. In: Niedermeyer, E.; Lopes daSilva, F., editors. *Electroencephalography: basic principles, clinical applications and related fields*. Urban and Schwarzenberg: Baltimore, Munich; 1982. p. 15–26.
- Martinez-Montes E, Valdes-Sosa PA, Miwakeichi F, Goldman RI, Cohen MS. Concurrent EEG/fMRI analysis by multiway partial least squares. *Neuroimage*. 2004; 22:1023–1034. [PubMed: 15219575]
- McCarthy G, Puce A, Gore JC, Allison T. Face-specific processing in the human fusiform gyrus. *J Cogn Neurosci*. 1997; 9:605–610. [PubMed: 23965119]
- Menon V, Ford JM, Lim KO, Glover GH, Pfefferbaum A. Combined event-related fMRI and EEG evidence for temporal-parietal cortex activation during target detection. *NeuroReport*. 1997; 8:3029–3037. [PubMed: 9331910]
- Mulert C, Jager L, Schmitt R, Bussfeld P, Pogarell O, Moller HJ, Juckel G, Hegerl U. Integration of fMRI and simultaneous EEG: towards a comprehensive understanding of localization and time-course of brain activity in target detection. *Neuroimage*. 2004; 22:83–94. [PubMed: 15109999]
- Nichols TE, Holmes AP. Nonparametric permutation tests for functional neuroimaging: a primer with examples. *Hum Brain Mapp*. 2002; 15:1–25. [PubMed: 11747097]
- Pascual-Marquis RD. Review of methods for solving the EEG inverse problem. *Int J Bioelectromagn*. 1999; 1:75–86.
- Pascual-Marquis RD, Michel CM, Lehmann D. Low resolution electromagnetic tomography: a new method for localizing electrical activity in the brain. *Int J Psychophysiol*. 1994; 18:49–65. [PubMed: 7876038]
- Puce A, Allison T, Gore JC, McCarthy G. Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J Neurophysiol*. 1995; 74:1192–1199. [PubMed: 7500143]
- Rossion B, Campanella S, Gomez CM, Delinte A, Debatisse D, Liard L, Dubois S, Bruyer R, Crommelinck M, Guerit JM. Task modulation of brain activity related to familiar and unfamiliar face processing: an ERP study. *Clin Neurophysiol*. 1999; 110:449–462. [PubMed: 10363769]
- Rossion B, Gauthier I, Tarr MJ, Despland P, Bruyer R, Linotte S, Crommelinck M. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *NeuroReport*. 2000; 11:69–74. [PubMed: 10683832]

- Rossion B, Joyce CA, Cottrell GW, Tarr MJ. Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *Neuroimage*. 2003; 20:1609–1624. [PubMed: 14642472]
- Rousselet GA, Mace MJ, Fabre-Thorpe M. Spatiotemporal analyses of the N170 for human faces, animal faces and objects in natural scenes. *NeuroReport*. 2004; 15:2607–2611. [PubMed: 15570161]
- Sadeh B, Zhdanov A, Podlipsky I, Hendler T, Yovel G. The validity of the face-selective ERP N170 component during simultaneous recording with functional MRI. *Neuroimage*. 2008; 42:778–786. [PubMed: 18554929]
- Schulz E, Maurer U, van der Mark S, Bucher K, Brem S, Martin E, Brandeis D. Impaired semantic processing during sentence reading in children with dyslexia: combined fMRI and ERP evidence. *Neuroimage*. 2008; 41:153–168. [PubMed: 18378166]
- Smith SM. Fast robust automated brain extraction. *Hum Brain Mapp*. 2002; 17:143–155. [PubMed: 12391568]
- Stancak A, Polacek H, Vrana J, Rachmanova R, Hoechstetter K, Tintera J, Scherg M. EEG source analysis and fMRI reveal two electrical sources in the fronto-parietal operculum during subepidermal finger stimulation. *Neuroimage*. 2005; 25:8–20. [PubMed: 15734339]
- Talairach, J.; Tournoux, P. Co-planar stereotaxic atlas of the human brain. Thieme; Stuttgart: 1988.
- Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage*. 2002; 15:273–289. [PubMed: 11771995]
- Vitacco D, Brandeis D, Pascual-Marqui R, Martin E. Correspondence of event-related potential tomography and functional magnetic resonance imaging during language processing. *Hum Brain Mapp*. 2002; 17:4–12. [PubMed: 12203683]
- Watanabe S, Kakigi R, Puce A. The spatiotemporal dynamics of the face inversion effect: a magneto- and electro-encephalographic study. *Neuroscience*. 2003; 116:879–895. [PubMed: 12573727]
- Webb SJ, Merkle K, Richards T, Aylward E, Dawson G. ERP responses differentiate inverted but not upright face processing in adults with ASD. *Soc Cogn Affect Neurosci*. 2009 (in press).
- Worsley KJ, Evans AC, Marrett S, Neelin P. A three-dimensional statistical analysis for CBF activation studies in human brain. *J Cereb Blood Flow Metab*. 1992; 12:900–918. [PubMed: 1400644]

Fig. 1.

a Geodesic 128 channel sensor net configuration. Leads considered to be recording signal from the posterior temporal lobes in this analysis are marked in red. **b** Grand-averaged ERP signal from the left and right hemisphere posterior temporal leads for the viewing of upright faces (FU) and for the viewing of upright houses (HU). ERP signals are in units of μV . Each epoch begins with a 100 ms period of baseline recording; the vertical dashed line indicates the time of stimulus onset. For the face condition, the latency of the P100 is 88 ms for both hemispheres and the latencies of the right/left hemisphere N170 are 142/138 ms. For the house condition, the latencies of the right/left P100 are 100/104 ms and the right/left N170 are 156/158 ms. **c** Global field power of the grand-averaged ERP signals, with the time of stimulus onset indicated with a vertical dashed line. Global field power maxima are at 90, 136, and 216 ms for the face condition and at 100 and 222 ms for the house condition

Fig. 2.
 FMRI z score maps and LORETA t value statistical maps for the latency of 136 ms
 superimposed on the MNI152 standard brain. The number below each slice indicates the
 MNI z coordinate

Fig. 3. LORETA t value maps thresholded at a value of 3.0 (*blue*) and fMRI activation maps (*red/yellow*) thresholded at a z score value of 3.0 superimposed on the MNI152 standard brain showing overlap in the precuneus, fusiform gyri, and inferior, middle and superior temporal gyri. LORETA solution time points were selected as those demonstrating maximum overlap for each region with the fMRI maps. The fMRI maps have been masked to only show activation in areas for which a LORETA solution is computed. Top: left and right hemisphere precuneus (PC) overlap at 134 ms. Middle: left fusiform gyrus (FG) and inferior temporal gyrus (ITG) overlap at 142 ms. Bottom: right hemisphere fusiform gyrus, superior temporal gyrus (STG) and middle temporal gyrus (MTG) overlap at 146 ms

Fig. 4.

Time course of t value statistic for comparison between the LORETA solutions for the face and house conditions in regions with LORETA activity spatially overlapped with fMRI activity. Individual waveforms represent the change in the t value statistic over time for a single voxel. Vertical dashed lines indicate the time of stimulus onset, as well as the latencies of the maxima in global field power for the face condition. Gray shading indicates the time points of spatial overlap of voxels in each region with the fMRI statistical map

Fig. 5.

Temporal map of overlap in LORETA and fMRI activity. The location and extent of each gray bar along the x -axis demonstrates time points of suprathreshold (test statistic > 3.0) LORETA and fMRI activity for the corresponding region, listed to the left. Vertical dashed lines indicate the latencies of maxima of the global field power for the face condition

Table 1

Statistics for regions with overlapping activity

Region	Total # voxels in region	Latency (ms)	# voxels overlap	% overlap # AAL region voxels	% overlap # act fMRI voxels	% overlap # act LOR voxels	fMRI # act vox in reg	LORETA					
								# act vox in reg	x	y	z	max t	X Y Z
Postcentral L	3,540	132	3	0.08	15	1	20	298	-44	-14	46	3.14	-46 -14 46
Parietal Inf L	2,396	132	5	0.21	100	10	5	48	-58	-26	46	3.09	-58 -24 46
Precuneus R	3,305	134	13	0.39	4	8	346	170	8	-56	34	3.44	8 -56 38
Precuneus L	3,640	134	33	0.91	9	22	386	148	-10	-54	34	3.18	-8 -52 38
Insula L	1,885	134	1	0.05	100	0.6	1	165	-42	0	10	3.49	-42 0 10
Rolandic Oper L	965	134	3	0.31	100	4	3	74	-44	0	12	3.10	-46 0 12
Cingulum Mid L	1,979	134	4	0.20	44	3	9	136	-12	-50	34	3.41	-4 -48 34
Temporal Inf L	3,205	142	31	0.97	100	2	31	1,318	-42	-48	-20	3.92	-44 -46 -16
Fusiform L	2,314	142	19	0.82	95	6	20	344	-42	-48	-22	3.86	-44 -46 -22
Fusiform R	2,579	146	7	0.27	88	2	8	389	42	-46	-24	3.54	42 -46 -24
Temporal Sup R	3,008	146	11	0.37	55	1	20	846	52	-48	14	4.55	56 -48 16
Temporal Mid R	4,234	146	11	0.26	5	2	205	750	50	-48	12	4.55	56 -48 12
Temporal Inf R	3,444	148	1	0.03	100	0.4	1	267	42	-48	-26	3.24	42 -48 -26

Summary of statistics for regions demonstrating spatial overlap of suprathreshold fMRI and LORETA activity. All statistics correspond to the LORETA Solution at the latency with maximum overlap with the fMRI activation map. (#voxels overlap): number of overlapping voxels; (% overlap #AAL region voxels): number of overlapping voxels as a percentage of the number of voxels in the region; (% overlap #fMRI voxels): number of overlapping voxels as a percentage of suprathreshold fMRI voxels in the region; (% overlap # act LOR voxels): number of overlapping voxels as a percentage of suprathreshold LORETA voxels in the region. The number of suprathreshold voxels for both techniques are also listed along with the Statistical values and MNI coordinates for the voxel with maximal Statistical value in the region of overlap

Table 2
Latencies of Overlapping Activity

Region	Latency of overlap (ms)
Postcentral L	12–16, 130–134
Insula L	120–136
Rolandic Oper L	120–136
Cingulum Mid L	128–138
Precuneus R	130–138
Parietal Inf L	130–134
Temporal Inf R	132–150
Precuneus L	132–136
Fusiform R	132–150
Temporal Inf L	134–148
Temporal Sup R	134–152
Fusiform L	134–148
Temporal Mid R	136–154

Full range of latencies of overlap for all regions, also illustrated graphically in Fig. 5

Table 3
Regions with Non-Overlapping Activity

Regions with non-overlapping LORETA and fMRI activity	Regions with fMRI activity only
Amygdala L	Amygdala R
Angular L	Calcarine R
Calcarine L	Cingulum Post L
Cingulum Ant L	Cingulum Post R
Cingulum Mid R	Cuneus L
Frontal Mid Orb R	Cuneus R
Frontal Sup Medial R	Frontal Mid Orb L
Hippocampus R	Frontal Sup Medial L
Insula R	Hippocampus L
Lingual L	Lingual R
Occipital Mid R	Olfactory L
Olfactory R	
Precentral L	
Rolandic Oper R	
Temporal Mid L	

Regions that demonstrate significant fMRI activity that does not overlap with significant LORETA source localized activity. Left column: regions demonstrating significant, although non-overlapping activity, in both techniques. Right column: regions demonstrating suprathreshold face processing-specific activity only in the fMRI statistical maps