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A multifunctional method (ERP and fMRI) of analysis on facial expression

Three pilot studies

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ABSTRACT

As social primates, one of the most important cognitive tasks we conduct, dozens of times a day, is to look at a face and extract the person's identity. During the last decade, the neural basis of face processing has been extensively investigated in humans with event-related potential (ERP) and functional MRI (fMRI). These two methods provide complementary information about the temporal and spatial aspects of the neural response, with ERPs allowing high temporal resolution of milliseconds but low spatial resolution of the neural generator and fMRI displaying a slow hemodynamic response but better spatial localization of the activated regions. Despite the extensive fMRI and ERP research of faces, only a few studies have assessed the relationship between the two methods and no study to date have collected simultaneous ERP and fMRI responses to face stimuli. In the current paper we will try to assess the spatial and temporal aspects of the neural response to faces by simultaneously collecting functional MRI and event-related potentials (ERP) to face stimuli. Our goals are twofold: 1) ERP and fMRI show a robust selective response to faces. In particular, two well-established face-specific phenomena, the RH superiority and the inversion effect are robustly found with both ERP and fMRI. Despite the extensive research of these effects with ERP and fMRI, it is still unknown to what extent their spatial (fMRI) and temporal (ERP) aspects are associated. In Study 1 we will employ an individual differences approach, to assess the relationship between these ERP and fMRI face-specific responses. 2) Face processing involves several stages starting from structural encoding of the face image through identity processing to storage for later retrieval.

This representation undergoes several manipulations that take place at different time points and in different brain regions before the final percept is generated. By simultaneously

recording ERP and fMRI we hope to gain a more comprehensive understanding of the time-course that different brain areas participate in the generation of the face representation.

Keywords: fMRI; ERP; facial expression; emotion

1. INTRODUCTION

Face recognition is essential for our daily social interactions. The ease in which we discriminate among the thousands of faces we encounter throughout our life is remarkable, given the very similar structure and features that all faces share. Indeed, there is ample evidence from studies that have applied behavioral and neurophysiological techniques, which suggest that faces are processed by specialized mechanisms that are not used for the processing of other objects, where we rarely need to discriminate among many different members of the same category (e.g., thousands of different chairs).

The central role of faces in our daily life and the robust neural responses they elicit have led to an extensive and productive research of the neural basis of face processing in humans with both functional MRI (fMRI) and event-related potentials (ERPs) techniques. These two methods provide complementary information about the temporal and spatial aspects of the neural response, with ERPs providing electrophysiological data with higher temporal resolution (milliseconds) but lower spatial resolution and functional MRI allowing relatively higher spatial resolution (millimeters) but a much lower temporal resolution due to the time scale of the hemodynamic response (several seconds). Thus, whereas ERPs can reveal *when* different stages of face processing take place, it is hard to determine which brain regions are involved at these different stages of processing. In contrast, whereas fMRI can reveal the different brain regions that are involved in the processing of faces, it is hard to assess at which stages of face processing these different brain regions participate. Thus, only by combining the two methods we can get a full understanding of the neural basis of cognition.

So far, ERP and fMRI studies of face perception have been mostly done in parallel by separate research groups. A few recent studies, reviewed below, have collected fMRI and ERP in separate sessions under the same experimental conditions to try to assess the relationship between them. The goal of the current proposal is to learn about the temporal and spatial aspects of the neural response to faces by simultaneously collecting ERP and

fMRI data. Such simultaneous recording with faces has not been reported yet mostly due to the technical challenges in extracting EEG data that is collected simultaneously with fMRI data acquisition (but see our pilot data).

1.2. Event-related potential and functional MRI studies of face processing

During the mid 90's, studies of the neural basis of face processing in humans revealed a face-selective response (i.e., a significantly higher response to faces than non-face stimuli) with both fMRI and ERP techniques. Functional MRI studies revealed several face-selective regions in the human occipital-temporal lobe, including a region in the mid-fusiform gyrus that is known as the "fusiform face area" (FFA); a more posterior region in the lateral occipital cortex known as the "occipital face area" or "OFA"; and a face-selective region in the posterior part of the superior temporal sulcus (STS), the face STS (fSTS). In parallel, event-related potential studies have revealed a negative component that appears 170 ms after stimulus onset (N170), which shows a much higher amplitude to faces than non-face stimuli (Bentin et al., 1996). Although many properties of the N170 have been reported (e.g., Bentin and Deouell, 2000; Campanella et al., 2000; Eimer, 2000; Rossion et al., 2000), its anatomical source and the processes underlying it are still uncertain. Studies that employed a source localization technique, have suggested that the N170 originates in the inferior posterior temporal gyrus and the fusiform and lingual gyri (e.g., Shibata et al., 2002). However, it is not possible with source localization techniques alone to assess whether the N170 originates from face-selective cortical regions, such as the FFA or OFA, which are functionally defined for each subject based on his/her selective response to faces rather than based on anatomy per se.

Only a few studies have attempted to assess the relationship between ERP and fMRI response to faces. One of the first reports by Henson et al., (2003) assessed the fMRI and ERP repetition effects (i.e., the difference in response to first vs. repeated presentation of the same face) to familiar and unfamiliar faces (Henson et al., 2003). Based on the fSTS laterality to faces and its pattern of response to familiar and repeated faces, Henson et al. (2003) concluded that the N170, which showed similar patterns, is associated with the activation to faces in the STS but not in the fusiform gyrus. Notably, because the data was collected on separate groups of subjects, it was not possible to perform direct correlations between the measures. Recently, Horovitz et al., (2004) collected ERP and fMRI data in separate sessions on the same group of subjects in a study that parametrically manipulated the noise level of a face stimulus and found a similar pattern of res-

ponse in the N170 and the FFA. Thus, in contrast to Henson and colleagues' conclusions, Horovitz et al. argued that the N170 may be associated with the fusiform face activation. Finally, Iidaka et al. (2006) performed a correlational analysis across subjects on fMRI and ERP data to faces and houses that were collected in the same group in separate sessions but did not find correlations between the face-selective N170 and face-selective fMRI activations (Iidaka et al., 2006). A voxel-by-voxel exploratory analysis revealed correlations between the two measures in occipital and temporal regions outside face-selective regions (see Study 1 for a more theoretically based approach).

In summary, the few studies that explored the relationship between ERP and fMRI response to faces reported inconsistent findings. Importantly, none of these studies have employed simultaneous data collection of the two measures, which is an ideal procedure to link the two methods.

2. RESEARCH OBJECTIVES

The goal of the current research is to integrate the spatial and temporal aspects of the neural response to faces using simultaneous ERP and fMRI data collection.

We will apply two techniques to reveal the link between early and later ERP components and different brain regions that play a role at different stages of face processing:

- 1) we will assess the duration the identity of a face is maintained for further processing at different time-points (with ERPs) and different brain regions (with fMRI). This will not only reveal how long identity information is maintained at different stages of face processing but will allow us to link different ERP components with different brain regions that show a similar pattern of response (*parametric approach*);

- 2) To more directly assess the relationship between various ERP components and brain activations, we will use the paradigm-induced amplitude modulation approach (Eichele et al., *PNAS*, 2005), in which single-event ERPs are extracted and their amplitude variance at different components is correlated with the fMRI response in a voxel-by-voxel basis. This novel procedure will allow us to reveal which voxels show fMRI activations that covary with the amplitude modulation of early or late ERP components during a task that manipulates categorization or identification of faces. In summary, examination of the neural basis of visual processing opens up a window to the evolvement of the mental image from initial encoding of the

input to the generation of its mental representation.

Specific Aim 1. To assess the relationship between *face-selective* ERP (i.e. N170) and *face-selective* fMRI responses (FFA, OFA, STS) using an individual differences approach. In particular, we will focus on two well-established face-specific phenomena: the right hemisphere superiority for faces and the face inversion effect (FIE). Each of these phenomena is robustly and reliably found in both ERP and fMRI. By performing a correlational (multiple regression) analyses across individuals, we hope to reveal which of the face-selective brain regions may be the source of the N170 right hemisphere superiority and which is the source of N170 face inversion effect. Importantly, in contrast to standard source localization techniques that estimate an *anatomical* source of the ERP response, our goal here is to link the face-selective N170 to functionally defined face-selective brain regions that are generated under the same experimental conditions (Study 1).

In contrast to Specific Aim 1, which focus on face-selective neural responses, in Specific Aims 2 we will employ a whole-brain approach and examine the entire time-course of the ERP response to faces.

Specific Aim 2. Processing of unfamiliar faces involves several stages starting from structural encoding of the face image through identity processing to storage for possible later retrieval. We will apply two procedures to reveal the link between early and later ERP components and different brain regions that play a role at different stages of processing of unfamiliar faces: 1) We will employ a repetition-effect procedure to assess the duration the identity of a face is maintained for further processing at different time-points (with ERPs) and different brain regions (with fMRI). Based on prior research we hypothesize that early components and more posterior brain regions, which are primarily involved in encoding of the stimulus, retain the visual image for very short durations (few milliseconds), whereas later components and more anterior brain regions, which are involved in identity processing for possible later retrieval, maintain the visual image for longer durations (seconds-minutes and beyond). A systematic examination of repetition lags will allow us to link specific ERP components to specific brain regions that show a similar pattern of retention of the face image. 2) A more direct way to correlate ERP and fMRI signals will employ the paradigm-induced amplitude modulation that was recently reported by Eichele et al. (2005). In particular, single trial ERPs are extracted and their modulation during a blocked-design task is correlated with the BOLD modulation in a voxel-by-voxel manner.

Here we will apply this novel procedure to reveal which brain regions are associated with the amplitude modulation of early or late ERP components during a task, which manipulate categorization and identification of faces.

As mentioned above, ERP and fMRI provide complementary information about the temporal and spatial aspects of the neural response. Simultaneous ERP-fMRI recording is a cutting-edge technique, which has been applied so far in only few laboratories around the world (e.g., Eichele et al., 2005; Liebenthal et al., 2003). Currently, there are no reports on application of such simultaneous recording for the study of face processing.

We believe that our studies will significantly advance our understanding of the neural basis of face processing by finally combining the two extensively productive lines of research on the temporal and spatial aspects of the neural response to faces that have so far been conducted mostly in parallel. Such combined analysis will hopefully reveal which brain regions participate at the different stages of face processing.

3. STUDY 1: INDIVIDUAL DIFFERENCES OF ERP AND FMRI FACE-SELECTIVE RESPONSES

The aim of Study 1 is to apply an individual differences approach to assess whether *face-selective* fMRI and *face-selective* ERP responses are associated. Our working hypothesis is that the robust face-selective effects that we obtain with both measures (higher response to faces than non-faces) suggest that at least one of the face-selective fMRI regions (OFA, FFA, STS) might be associated with face-selective N170 component.

Importantly, rather than simply correlating the magnitude of the fMRI and ERP responses to faces (Iidaka et al., 2006), we will focus on two face-selective phenomena that are reliably found with both measures: the *RH superiority* for faces, that is the overall stronger response to faces over the right than the left hemisphere (Yovel and Kanwisher, 2004; Yovel et al., 2003), and the *face inversion effect (FIE)* the difference in response to upright than inverted faces (Rossion et al., 2000; Yovel and Kanwisher, 2005). By focusing on neural phenomena that are found reliably with both measures, rather than performing an exploratory analysis of their overall responses as in Iidaka et al. (2006), we increase statistical power and therefore are more likely to detect associations between the two measures. Furthermore, pilot data we collected show that the N170 and the FFA laterality measures were each correlated with a behavioral measure of laterality for faces. These find-

ings suggest that we may find a similar positive relationship between the two neural measures. In addition, simultaneous collection of fMRI and ERP data eliminates across-session variance and is therefore a better method to reveal reliable co-variance between the two methods. Notably, the FIE pattern of correlations are not expected to necessarily generate similar findings to the RH asymmetry study. In fact, these two phenomena may have different underlying neural mechanisms. Finally, to assess whether these findings are specific to faces, we will also present non-faces and localize object general regions (Lateral Occipital Complex) (Malach et al., 1995).

3.1. Methodology

Stimuli and Procedure

1. A blocked-design Localizer, which includes faces, objects and scrambled images of objects will be presented to localize face-selective and general object regions (LOC).
2. A rapid event-related design with faces and chairs will be presented in a pseudo-randomized order that allows deconvolution of the single events. These protocols have been used by the PI repeatedly to identify face-selective regions with fMRI (Yovel and Kanwisher, 2004; Yovel and Kanwisher, 2005). The same event-related design can be also used to elicit the face-selective N170. To obtain a measure of the FIE, the face and non-face stimuli will be presented either upright or inverted.

Data analysis

SPM2 will be used for fMRI analysis. EEGLab will be used for artifact rejection and data analysis of ERP. In fMRI data analysis face-selective areas will be defined as voxels producing a significantly higher response to faces than to objects (t-test, $p < .001$, uncorrected); of these regions, the mid-fusiform region will be considered the FFA, lateral occipital cortex, the OFA, and lateral STS region the fSTS. Voxels showing higher response to objects than scrambled images of objects will be identified as object selective regions (LOC). The response to upright and inverted faces and chairs will be examined within these regions of interest.

ERP data analysis will involve high-pass filtering (45 Hz) and averaging of segments of time locked EEG (-100ms – 1000ms) to faces and chairs. The peak amplitude of the N170 to faces and chairs will be measured for each individual.

1) Measures of the RH superiority

- *fMRI*. Two measures will be used to assess hemispheric asymmetry of face-selective regions in each subject. A normalized asymmetry score $[(RH - LH) - \text{sum}(RH, LH)]$ of: 1) The volume of each face-selective region (see pilot data 1); 2) The magnitude of the *selectivity* to faces $[(\text{facechairs})/\text{sum}(\text{face, chairs})]$ (that are presented in the event-related task) in face-selective regions that are independently defined by the localizer. The same measures will be collected for object general regions (LOC).
- *ERP*. We will measure the amplitude of the N170 over the right and left occipito-temporal electrodes and compute a normalized RH superiority measure $[(RH - LH) - \text{sum}(RH, LH)]$ as well as the difference in selectivity to faces $[(\text{face- chairs})/\text{sum}(\text{faces, chairs})]$ for the right and left temporal N170.
- *Correlational analysis*. Based on Pilot data 1 we will assess the correlation between the amplitude of the N170 and the volume of face-selective regions. In addition we will assess the correlation between the laterality of the ERP and fMRI selectivity measures. In addition to zero-order correlations, a multiple regression analysis will be used to assess the contribution of the asymmetry of each of the three face-selective regions (predictors) to variance in the N170 asymmetry (predicted). Similar measures will be computed for non-face stimuli to assess the specificity of the fMRI/ERP laterality for faces (Rossion et al., 2000).

2) Measures of the Face inversion effect:

- *fMRI*. Measures for the fMRI-FIE will be the normalized difference in fMRI response (% signal change) to upright and inverted faces $[(\text{upright} - \text{inverted})/\text{sum}(\text{upright, inverted})]$ that are presented in the event-related tasks in each of the face-selective regions, which will be determined independently based on the localizer.
- *ERP*. The amplitude and latency of the N170 to upright and inverted stimuli will be calculated. A normalized FIE score will be calculated for each subject for face and chair stimuli.
- *Correlational and regression analyses* of the FIE measures will be similar to the analysis of laterality measures discussed briefly above. Examination of non-face stimuli will assess the specificity of the effect to faces.

In summary, in Study 1 we will employ an individual differences approach to try to reveal whether and how the well-established ERP and fMRI face-selective responses are correlated. In studies 2 and 3 reported below, we plan to explore the relationship between ERP and fMRI responses to faces beyond face-selective responses, by assessing the entire time course of the

ERP as well as brain areas that are not restricted to the face-selective regions in order to examine the temporal and spatial aspects of the neural response at different stages of face processing.

4. STUDY 2: THE DURATION OF THE FACE REPRESENTATION AT DIFFERENT STAGES OF FACE PROCESSING

The goal of this study is to associate between fMRI areas and ERP components that are involved in early or late stages of face processing by measuring the duration they maintain information about the identity of unfamiliar faces. Numerous studies have shown that a second presentation of the same stimulus modulates the neural response relative to the first presentation (i.e. repetition/adaptation effect). This procedure has been extensively used with fMRI and ERP (as well as behavioral priming study) to learn about the nature of the representation of the stimulus (for review see, Grill-Spector et al., 2006). However, this procedure can be also used to learn how long the image is maintained at different stages of face processing. Specifically, by manipulating the lag between the first and second presentation of the same stimulus, we can assess which ERP components and brain regions revealed by fMRI maintain the image for only shorter duration (show repetition effects for shorter but not longer lags) and which store it for a longer duration (show repetition effects for longer lags) that will allow later retrieval.

A few studies reported a systematic investigation of the effect of different lags on the ERP and fMRI signal with objects (Henson et al., 2004) and with familiar and unfamiliar faces (Henson et al., 2000; Henson et al., 2002). Overall, repetition effects for unfamiliar faces are usually weak (Henson et al., 2002) or absent with fMRI (Henson et al., 2003) and elicit relatively late repetition effects, 400-600 ms after stimulus onset with ERPs (Henson et al., 2004). Most of these studies have used relatively long lags of seconds or minutes with intervening stimuli between the first and second presentation. However, a lag of 1 second with no intervening stimuli or an absence of lag elicits ERP repetition effects effect at 250ms (Schweinberger et al., 2004) and the N170 (Jacques and Rossion, 2004), respectively. Similarly with fMRI, robust repetition effects for unfamiliar faces are clearly revealed in the FFA for lags of 500ms (Fang et al., 2006; Yovel and Kanwisher, 2005) but not for longer lags (Henson et al., 2003).

In summary, by examining the effects of lag on repetition effects of various ERP components and fMRI regions, we can assess how long face

identity information is maintained at different stages (ERP) and different regions (fMRI). Our *working hypothesis* is that the representation of unfamiliar faces at early stages of face processing, during structural encoding, is shorted-lived (a few milliseconds) and therefore earlier components (Jacques and Rossion, 2004) and posterior brain regions will be modulated by repetition of shorter lags of few milliseconds (see Kourtzi and Huberle, 2005 for an fMRI study with novel hierarchical patterns), but not longer lags (seconds-minutes) that have been employed in most previous reports. Longer lags will elicit repetition effects only in later components and more anterior regions, where the representation is kept for longer duration for further processing and possibly later retrieval. Importantly, a similar pattern of repetition effects for different ERP components and fMRI regions to parametric manipulation of the lag, may allow us to link specific time points in stimulus processing (ERPs) with specific brain regions (fMRI) (for a similar rationale see Horowitz et al., 2004). Finally, studies have shown that familiar and unfamiliar faces elicit different patterns of neural repetition effects (Henson et al., 2000; Henson et al., 2003). Thus, because the proposed study focuses on repetition effects for unfamiliar faces, simultaneous recording is important so subjects see the face exemplars for the first time during both ERP and fMRI sessions, rather than exposed to the different exemplars in separate sessions.

4.1. Methodology

We will employ a procedure that can be used to measure short-lag repetition (adaptation) with event-related fMRI (e.g., Yovel and Kanwisher, 2005). Five hundred pairs of same or different faces will be randomly presented with 5 different SOAs ranging from 0, 50, 400, 1000, 2000ms. We will compare the amplitude for the first and second presentation for each lag. In addition, we will also examine effects of longer lags, by presenting some of the faces after 5mins and 30 mins delays.

Stimuli and Procedure

The time lags that will show different influence on early versus late ERP components will be used in this study. We will employ an event-related fMRI-adaptation design that has been used by the PI (see also, Kourtzi and Huberle, 2005; Yovel and Kanwisher, 2005) to examine the effect of lag on the BOLD response to pairs of different versus identical faces.

5. STUDY 3: PARADIGM-INDUCED MODULATION OF ERP AND fMRI RESPONSE TO FACES

A more direct way to link between different ERP components and brain regions was recently employed by Eichele et al. (2005) who measured the amplitude modulation of single trial ERPs during alternating blocks that differed in a task relevant parameter (Eichele et al., 2005). The novelty of this approach is that it is based on assessment of the variance of the amplitude of different ERP components across single ERP trials (Jongsma et al., 2006; Quian Quiroga et al., in press; see pilot data 3) rather than only focusing on the average ERP, as in most ERP studies. By designing a task that generates amplitude modulation (AM) that corresponds with the slow time course of the BOLD, one can examine the correlation between the pattern of AM of each component with the BOLD on a voxel-by-voxel basis. Such analysis may reveal in which brain regions the BOLD covary with the AM of different ERP components.

In principle, this procedure should allow us to assess the correlation between ERP and fMRI modulation in a standard block-design task. Because this procedure has been only used so far in one experiment that presented an odd-ball auditory task (Eichele et al., 2005), in the first set of experiments we will use a visual version of the task used by Eichele. In follow up studies we will examine the effect of other types of alternating blocks on the AM at different components. For example, we will examine the effect of alternating blocks of faces and non-faces (categorization) and of unfamiliar and familiar faces (identification) on the AM of different components. This set of experiments will be done with ERPs outside the scanner (Study 3 – ERP pilot). Once we obtain reliable patterns of AM, in Study 3 we will simultaneously collect fMRI-ERP data to find voxels that show correlation with the pattern of the AM of the different components.

In summary, we hope that this procedure will allow us to reveal which brain regions are associated with the sensitivity of early or late ERP components to category and identity discrimination of faces. The success of this approach depends on our ability to extract single trial ERPs, first by following procedures that were reported in the literature (Eichele et al., 2005; Quian Quiroga and Garcia, 2003) as well as developing our own tools. This effort will be conducted in collaboration with Prof. Nathan Interator from the Department of Computer Sciences at Tel Aviv University.

5.1. Methodology

Stimuli and Procedure

We will design a visual version of the design used by Eichele et al (2005) with auditory stimuli. An odd-ball paradigm, in which faces are presented as standards and either a chair or a face of different identity is used as a deviant in random or regular intervals. Each block will last 96 seconds during which 6 deviants are presented among standards in a random deviant to deviant interval (4-22 seconds) during one half of the block and 6 deviants are presented in a regular 8 seconds interval during the second half of the block. A total of 18 blocks will be presented. We will first compare the auditory and visual version. Once we are able to obtain reliable AM, in follow up experiments we will use a similar design and examine AM for alternating blocks of faces and objects in one experiment, familiar and unfamiliar faces in another experiment.

6. GENERAL METHODS FOR EXPERIMENT 1-3

Functional MRI: Visual Stimulation. The scanner at the Wohl imaging Center is equipped with a computer LCD projection system and mirror system for presenting high-resolution color images to the subject. Subjects will lie on their backs inside the scanner magnet, viewing the stimuli (via a mirror near their forehead) on a rearprojection screen attached to the inside of the magnet bore.

- *fMRI Acquisition.* fMRI data will be recorded using GE 3T Signa scanner (GE, Milwaukee, USA). For the functional scans, a gradient echo pulse sequence will be used. We typically use twenty 4-mm-thick axial slices (no skip) for full brain coverage, with a TR of 2 seconds, TE = 35 ms and flip angle 90°.
- *fMRI data analysis.* fMRI data analysis will involve motion correction, detrending, and smoothing on the native brain space for Study 1. For whole-brain analysis in Studies 2&3 the data will be normalized.
- *ERP: Apparatus.* EEG signal will be recorded using BrainAmp MR-compatible EEG recording system with 32-electrode cap (Brain Products, Munich, Germany). Brain analyzer is used for data recording.
- *EEG Acquisition.* EEG signals will be amplified with a 0.1 to 100 Hz band pass and digitized on-line with a sampling rate of 5000 Hz that is required for gradient artifact removal. To get a good measure of the posterior temporal N170, the reference electrode will be located on the nose

(Bentin et al., 1996; Eimer, 1998; Eimer, 2000; Eimer and McCarthy, 1999; Jemel et al., 1999).

- *ERP Data Analysis.* For ERP averaging, the EEG will be segmented into epochs of 1024 ms, starting 100 ms before stimulus onset. Trials with artifacts due to blinks or eye movements will be excluded prior to averaging. The N170 will be defined for each subject as the most negative peak within the 140-200 ms interval. Latency will be defined as the time from stimulus onset to the peak point. Artifact removal for ERP data collected in the scanner will be performed with algorithm implemented in the FMRIB plug-in for EEGLAB

7. PRELIMINARY FINDINGS

7.1. Pilot data 1: A simultaneous ERP/fMRI study of face-selective responses

Procedure

The experiment was comprised of 6 consecutive recording sessions in which images of faces and chairs were presented in an rapid-presentation event-related design. EEG data was recorded during all sessions and fMRI data – during the first, third and fifth sessions. Such a setup allowed us to assess the effect of the MR artifacts on the quality of EEG data.

1. *EEG Analysis.* EEG data was split into two sets – the 3 sessions recorded simultaneously with fMRI and the 3 sessions recorded without fMRI. The data recorded simultaneously with fMRI was then subjected to the gradient and cardiobalistic artifact removal. After the artifact removal, both data sets were processed in an identical fashion. For each set, the EEG data was segmented into windows of [-200 – 600] milliseconds around stimulus presentation, baseline-corrected and averaged across trials and sessions for each stimulus type (faces and chair) separately.
2. *fMRI Analysis.* fMRI data analysis was performed using the SPM2 software (see General methods). A simple effect contrast of face versus chairs was performed on deconvolved fMRI signals. fMRI analysis revealed selective activations for faces in lateral occipital and fusiform gyrus, which is compatible with previous results. ERP analysis revealed a larger N170 amplitude for faces than chairs. Importantly, there is no observable degradation of the ERP signal quality attributable to the gradient artifacts.

7.2. Pilot data 2: Individual differences in the behavioral and neural aspects of the LVF/RH superiority

1. *ERP and Behavioral studies.* ERP data was collected for faces presented centrally from 11 subjects at Northwestern University (IL, US). The N170 amplitude was larger over the right than the left temporal electrode ($t(10) = 2.85, p < .05$). In addition, subjects matched pairs of sequentially presented faces presented in the left or right visual field (Figure 2AII). Performance was better for faces presented in the left than right visual field ($t(10) = 2.65, p < .05$). The behavioral laterality (difference in performance for left and right side presentations) was positively correlated with the N170 asymmetry (difference in amplitude over right and left temporal-occipital electrodes) ($r(9) = .69, p < .02$).
2. *fMRI and Behavioral studies.* A different group of 11 subjects was presented with a face localizer in the fMRI scanner at the MGH/Martinos imaging center, US. The FFA was identified in each subject (Figure 2B) and was larger over the right (1621 mm³) than the left hemisphere (803 mm³) ($t(10) = 2.99, p < .01$). The behavioral left visual field superiority was measured in a separate session. Results show a positive correlation ($r = .59, p = .05$) between these two measures. Taking together these data imply that the N170 and FFA asymmetry, which are both correlated with the behavioral left visual field superiority, may be correlated. This hypothesis will be examined in Study 1.

7.3. Pilot data 3: Extraction of single-trial ERP using a wavelet denoising procedure

A single subject was presented with 48 faces and 48 chairs in a randomized order during ERP recording. The average amplitude of the N170 to faces was higher than chairs. We then applied the wavelet denoising procedure (Quian Quiroga and Garcia, 2003) to extract single trial ERPs. Briefly, the average ERP is decomposed in different scales (i.e. frequency bands) and times by using the wavelet multiresolution decomposition; Quadratic bi-orthogonal B-Splines are chosen as the basic wavelet functions due to their similarity with the ERP. Each level of decomposition corresponds to its Wavelet coefficients. Wavelet coefficients correlated with the ERPs are identified and the remaining ones (which contain unwanted frequencies) are set to zero. The chosen coefficients should cover a time range in which the single-trial ERPs are expected to occur. The inverse transform is applied, thus obtaining a denoised average ERP; the denoising scheme defined by

the previous steps (keeping the coefficients chosen) is applied to the single-trials; the result is single ERP trials filtered from unwanted information in the time-frequency domain.

REFERENCES

- Bentin, S., Allison, T., Puce, A., Perez, E., and et al. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8, 551-565
- Bentin, S., and Deouell, L. Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology*, 17, 35-54.
- Campanella, S., Hanoteau, C., Depy, D., Rossion, B., Bruyer, R., Crommelinck, M., and Guerit, J. M. (2000). Right N170 modulation in a face discrimination task: an account for categorical perception of familiar faces. *Psychophysiology*, 37, 796-806.
- Eichele, T., Specht, K., Moosmann, M., Jongsma, M. L., Quiroga, R. Q., Nordby, H., and Hugdahl, K. (2005). Assessing the spatiotemporal evolution of neuronal activation with single-trial event-related potentials and functional MRI. *Proceedings of the National Academy of Science of U S A*, 102, 17798-17803.
- Eimer, M. (1998). Does the face-specific N170 component reflect the activity of a specialized eye processor?. *Neuroreport*, 9, 2945-2948.
- Eimer, M. (2000). The face-specific N170 component reflects late stages in the structural encoding of faces. *NeuroReport*, 11, 2319-2324.
- Eimer, M., and McCarthy, R. A. (1999). Prosopagnosia and structural encoding of faces: evidence from event-related potentials. *Neuroreport*, 10, 255-259.
- Fang, F., Murray, S. O., and He, S. (2006). Duration-Dependent fMRI Adaptation and Distributed Viewer-Centered Face Representation in Human Visual Cortex. *Cerebral Cortex*.
- Grill-Spector, K., Henson, R., and Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in Cognitive Science*, 10, 14-23.
- Henson, R., Shallice, T., and Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, 287, 1269-1272.
- Henson, R. N., Goshen-Gottstein, Y., Ganel, T., Otten, L. J., Quayle, A., and Rugg, M. D. (2003). Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cerebral Cortex*, 13, 793-805.
- Henson, R. N., Rylands, A., Ross, E., Vuilleumier, P., and Rugg, M. D. (2004). The effect of repetition lag on electrophysiological and haemodynamic correlates of visual object priming. *Neuroimage*, 21, 1674-1689.
- Henson, R. N., Shallice, T., Gorno-Tempini, M. L., and Dolan, R. J. (2002). Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cerebral Cortex*, 12, 178-186.
- Horovitz, S.G., Rossion, B., Skudlarski, P., and Gore, J.C. (2004). Parametric de-

- sign and correlational analyses help integrating fMRI and electrophysiological data during face processing. *Neuroimage*, 22, 1587-1595.
- Iidaka, T., Matsumoto, A., Haneda, K., Okada, T., and Sadato, N. (2006). Hemodynamic and electrophysiological relationship involved in human face processing: evidence from a combined fMRI/ERP study. *Brain and Cognition*, 60, 176-186.
- Jacques, C., and Rossion, B. (2004). Concurrent processing reveals competition between visual representations of faces. *Neuroreport*, 15, 2417-2421.
- Jemel, B., George, N., Chaby, L., Fiori, N., and Renault, B. (1999). Differential processing of part-to-whole and part-to-part face priming: an ERP study. *Neuroreport*, 10, 1069-1075.
- Jongsma, M. L., Eichele, T., Van Rijn, C. M., Coenen, A. M., Hugdahl, K., Nordby, H., and Quiroga, R. Q. (2006). Tracking pattern learning with single-trial event-related potentials. *Clinical Neurophysiology*, 117, 1957-1973.
- Kanwisher, N., and Yovel, G. (in press). The Fusiform Face Area: A Cortical Region Specialized for the Perception of Faces. *Philosophical Transactions of the Royal Society of London*, B. Galit Yovel PhD 90/07
- Kourtzi, Z., and Huberle, E. (2005). Spatiotemporal characteristics of form analysis in the human visual cortex revealed by rapid event-related fMRI adaptation. *Neuroimage*, 28, 440-452.
- Liebenthal, E., Ellingson, M. L., Spanaki, M. V., Prieto, T. E., Ropella, K. M., and Binder, J. R. (2003). Simultaneous ERP and fMRI of the auditory cortex in a passive oddball paradigm. *Neuroimage*, 19, 1395-1404.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., and Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Science of USA*, 92, 8135-8139.
- Quian Quiroga, R., Atienza, M., Cantero, J., and Jongsma, M. L. (in press). What can we learn from single-trial event-related potentials?
- Quian Quiroga, R., and Garcia, H. (2003). Single-trial event-related potentials with wavelet denoising. *Clinical Neurophysiology*, 114, 376-390.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., and Crommelinck, M. (2000). 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*, 11, 69-74.
- Schweinberger, S. R., Huddy, V., and Burton, A. M. (2004). N250r: a face-selective brain response to stimulus repetitions. *Neuroreport*, 15, 1501-1505.
- Shibata, T., Nishijo, H., Tamura, R., Miyamoto, K., Eifuku, S., Endo, S., and Ono, T. (2002). Generators of visual evoked potentials for faces and eyes in the human brain as determined by dipole localization. *Brain Topography*, 15, 51-63.
- Yovel, G., and Kanwisher, N. (2004). Face perception: Domain specific, not process specific. *Neuron*, 44, 1-20.

- Yovel, G., and Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology*, 15, 2256-2262.
- Yovel, G., Levy, J., Grabowecky, M., and Paller, K. A. (2003). Neural correlates of the left-visualfield superiority in face perception appear at multiple stages of face processing. *Journal of Cognitive Neuroscience*, 15, 462-474.