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Neuromagnetic evidence that the right fusiform face area is essential for human face awareness: An intermittent binocular rivalry study

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ABSTRACT

When and where the awareness of faces is consciously initiated is unclear. We used magnetoencephalography to probe the brain responses associated with face awareness under intermittent pseudo-rivalry (PR) and binocular rivalry (BR) conditions. The stimuli comprised three pictures: a human face, a monkey face and a house. In the PR condition, we detected the M130 component, which has been minimally characterized in previous research. We obtained a clear recording of the M170 component in the fusiform face area (FFA), and found that this component had an earlier response time to faces compared with other objects. The M170 occurred predominantly in the right hemisphere in both conditions. In the BR condition, the amplitude of the M130 significantly increased in the right hemisphere irrespective of the physical characteristics of the visual stimuli. Conversely, we did not detect the M170 when the face image was suppressed in the BR condition, although this component was clearly present when awareness for the face was initiated. We also found a significant difference in the latency of the M170 (human < monkey < house). Taken together, our findings indicate that face stimuli are imperative for evoking the M170 and that the right FFA plays a critical role in human face awareness.

1. Introduction

Humans have specialized processes for recognizing faces that are distinct from those used for general object recognition (Haxby et al., 2000). Faces are a rich source of important social information, allowing us to discern the identity, age, and emotional state of those around us. Before this information can be accessed, however, the presence of a face in a visual scene must be detected. Recent models of face perception have incorporated a distinct initial stage: face detection is gated by an obligatory detection process though which holistic processing begins (Tsao and Livingstone, 2008). Functional magnetic resonance imaging (fMRI) studies have identified a face-selective neural network that consistently shows greater activation in response to faces compared with non-face stimuli. This face-selective network includes the occipital face area (OFA) and the fusiform face area (FFA), the ventral surface of the occipital and temporal lobes, and the posterior region of the superior temporal sulcus (STS) (Rajimehr et al., 2009). Additionally, neural responses to faces in these regions, particularly in the FFA, appear to have right hemispheric predominance (Collins and Olson, 2014; Watanabe et al., 1999, 2003; Yovel and Kanwisher, 2004).

In the last decade, several studies have focused on face awareness during dichoptic presentation (Stein et al., 2014; Sterzer et al., 2014; Suzuki and Noguchi, 2013). When dissimilar images are presented simultaneously to each eye, awareness of one image can dominate such that the other image is imperceptible (Blake and Logothetis, 2002; Blake and Wilson, 2011; Lin and He, 2009; Tong et al., 2006). This is so-called binocular rivalry (BR) and such visual perception can be temporary. Several researchers have proposed that these phenomena reflect the outcomes of competitive neuronal interactions that take place on multiple levels of the visual system (Blake and Logothetis, 2002; Kallenberger et al., 2014; O'Shea et al., 2013; Persike et al., 2014; Pitts et al., 2010; Sandberg et al., 2014; Sterzer et al., 2009; Zhang et al., 2011). fMRI can be used to produce activation maps showing which parts of the brain are involved in a particular mental process. BR can occur even at the earliest stages of visual processing, as evidenced by blood oxygenation level dependent (BOLD) responses during fMRI (Tong et al., 2006; Watanabe et al., 2011; Wunderlich et al., 2005; Yuval-Greenberg and Heeger, 2013). Several fMRI studies have

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reported that face-selective high-level visual areas (i.e. FFA and STS) are activated in response to visible faces, however, activity in FFA was much reduced when face images became invisible (Blake and Logothetis, 2002; Fang and He, 2005; Jiang and He, 2006; Sterzer et al., 2008). Although spatial resolution of fMRI is excellent, temporal resolution is sub-second order. Thus, when and where the obligatory facial detection process is consciously initiated is unclear.

Regarding the electroencephalographic responses, the N170 component is known to reflect the face-specific visual processing in the human brain. It appears to be maximal over the right occipito-temporal region (Bentin et al., 1996; Rossion and Jacques, 2008) and has amplitudes that are significantly more negative in response to faces compared with other objects (Allison et al., 1999; Rossion and Jacques, 2008). Although the relationship between the N170 and activity in face-selective brain regions has been elusive, recent multimodal studies in which electroencephalography (EEG) and fMRI signals were simultaneously acquired revealed that N170 amplitudes elicited by faces were strongly associated with BOLD responses in the FFA (Horovitz et al., 2004; Nguyen and Cunnington, 2014; Sadeh et al., 2010).

Here, we adopted magnetoencephalography (MEG) to probe neuromagnetic responses associated with awareness of the human face by using an intermittent BR paradigm because of its excellent temporal and spatial resolution. Like the continuous BR paradigm, two competitive visual stimuli were rendered perceptible or imperceptible in the intermittent BR condition. With continuous BR, the time intervals between the perceptual changes themselves and the reports of such changes are likely to vary from trial-to-trial by tens to hundreds of milliseconds. This temporal jitter between percept is likely to affect MEG responses such as M170 (a magnetic counter part of N170). In addition, the intermittent BR method has several advantages compared with continuous BR paradigm (Pitts and Britz, 2011). First, perception of the stimuli in the left or right eye is much clearer than in the continuous method. Second, in this paradigm, temporal jitter of perceptual responses can be disregarded. Third, it is possible to record event related fields (ERFs) that are time-locked to the stimulus onset of the reported percept. Therefore, we hypothesized that differing responses in perceptual dominance periods under the intermittent BR condition would reveal new information about face recognition processing and face awareness. We also expected that responses to human faces to be distinct from responses to monkey faces because humans are human face recognition experts (Itier et al., 2011; Rossion, 2014).

2. Methods

2.1. Participants

In this study, 24 healthy young adults (6 female, mean age 25.1 ± 5.8 years old, all right handed) participated. They had normal or corrected-to-normal vision and normal stereo-depth perception. After being given a complete description of the study, all participants gave written informed consent in accord with the regulations of the Ethics Committee of the Graduate School of Medical Sciences, Kyushu University (approval number 424).

2.2. Visual stimuli

The stimuli consisted of three images (8 cm × 10 cm: 72 ppi): a human face, a monkey face and a house (Fig. 1(a)). In the monocular condition, the luminance of each stimulus was somewhat comparable: 8.5 or 9.8 cd/m^2 through the green or red filter, respectively. In the BR condition, the luminance of the overlaid images was nearly equivalent: 9.7 or 9.5 cd/m^2 through the green or red filter, respectively. Each stimulus was presented at a viewing distance of 200 cm (visual angle, 2.3° × 2.9°). A black cross was used as a fixation point (visual angle, 0.9° × 0.9°). This was presented in the center of the monitor throughout the visual experiment.

2.3. Procedures

The participants wore non-corrective spectacles with one lens exchanged for a red filter and the other exchanged for a green filter [Kodak Wratten Filters; 25 (red) and 58 (green); Edmund Industrial Optics, Barington, NJ] to view each stimulus separately through the right or left eye. These filters were the same as those used in a previous study (Williams et al., 2004). The placement of the filters (green on the left and red on the right or vice versa) was counter balanced across the participants. The color of the images (green face and red house or vice versa) was also counterbalanced within the participants. All stimuli were presented on a 27-in. liquid crystal display (CG-L19 DSWV2; Corega Inc., Japan) in a dark magnetically shielded room.

Before the MEG experiment, all participants were given instructions about how to discriminate between normal perception (i.e. faces or objects, see Fig. 1(a)) and piecemeal perception (i.e. a mixture of two images, see Fig. 1(b)) (Carmel et al., 2010). Following this instruction, they practiced reporting precise information about dominant perception under conditions of BR (Fig. 1(b)). In the training session, the stimuli were the same as those used in the MEG experiment. The practice trials were repeated until it was clear that the participants fully understood our instructions.

Our experiment included two experimental MEG conditions: the "BR condition" and the "the monocular physical alternate condition" (Fig. 1(c)). We defined the latter as the pseudo-rivalry (PR) condition. In the BR condition, we presented overlaid images (i.e. "a human face and a house (HF/H)" and "a monkey face and a house (MF/H)"). In the PR condition, we presented one of the images from a given stimuli pair. These stimuli were presented in random order. Each condition comprised four blocks: Two HF/H and two MF/H blocks. All stimuli were presented for 800 ms with an inter-stimulus interval that ranged from 500 to 700 ms. The mean luminance of the blank screen shown during the inter-stimulus interval was the same as that of each stimulus (Fig. 1(c)).

2.4. MEG recording

The MEG signals were acquired using a whole-head 306-channel sensor array (Vectorview; Elekta Neuromag, Helsinki, Finland). Prior to recording, we attached four head position indicator (HPI) coils to the scalp of each participant, and used a 3D digitizer (Fastrak; Polhemus, Colchester, VT, USA) to measure three fiducial points and the locations of the HPI coils. The sampling rate was 1000 Hz and we filtered the signal online using a bandpass of 0.1–330 Hz. We performed head localization prior to MEG measurement for each run, which comprised two blocks.

2.5. Behavioral testing

We conducted the behavioral experiment while collecting MEG measurements. The participants were instructed to report which image appeared to be dominant by pressing the left or right mouse button as fast as they were able. They were instructed not to press any buttons if they saw an image they deemed to be ambiguous, i.e. they could not distinguish between two images that were being simultaneously presented (Fig. 1(b)). The stimuli were presented until we received at least 120 responses in a block.