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Magnetoencephalographic Analysis of the Neural Responses in the Perception of Ambiguous Body Figures

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INTRODUCTION

In the past few years, there has been a remarkable increase in research on the neural basis of visual perception of the human body. Downing et al. found a body-selective region in the brain in the right and left lateral occipital-temporal cortex and has designated it as the extrastriate body area (EBA). Recent findings indicate that the observation of body parts produces an ERP that is similar to the N170 (Stekelenburg and de Gelder, 2004), shows greater response to bodies and peaks at 190 ms (Thierry et al., 2006). In our previous Magnetoencephalography (MEG) studies, we used realistic and abstract images of bodies to show that the M2 component (M190) which peaked at around 190 ms reflected the neural processing of body images, and we suggested that, analogous to faces, the perception of bodies is a special category of the human-recognition system.

The results of several studies for face perception suggest that simple or abstract stimuli, such as realistic minute figures or 'ambiguous' face figures, induce the face-selective neural responses when the participants recognise them as faces. However, Bentin et al. (2002) reported that when participants fail to recognise the

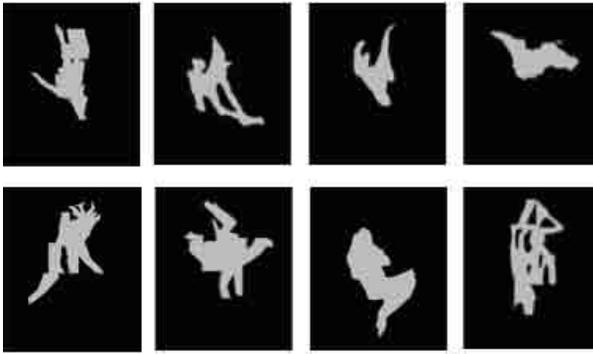


Figure 1. Stimulus examples; ambiguous body figures.

stimuli as a ‘face’, the expression of the face-selective N170 (or M2 for faces) component was remarkably diminished. It means the face-selective N170 is strongly linked with low-level perceptual features as well as conscious recognition of faces. Therefore, it would be interesting to determine whether the body-selective M2 component (M190) is also affected by participants’ conscious recognition of the visual stimuli. In the current study, we investigated the neural responses associated with the relationship between the body-selective components and the participants’ conscious recognition. We presented ambiguous images to subjects and used MEG to record the activities in specific body-selective (M190) and object-selective components (M2) when the subjects did or did not perceive an ambiguous image as a body. If body perception is represented by the activity of a specific brain module, the increased activity associated with the perception of an ambiguous body should be specific to body-selective responses.

MATERIALS AND METHODS

Subjects: Nine healthy right-handed volunteers without any history of neurological or psychiatric disorders (5 males, 4 females; age range, 24–28 years) participated in this study.

Stimuli: 53 ambiguous body images that were identified as bodies by approximately 50% of 20 naive observers were used as stimuli. These ambiguous body images may be perceived as bodies or as a collection of black and white blobs (see Figure 1).

Procedure: The subjects were instructed to indicate the perception of a body by

pressing 1 of 2 buttons with the right hand. The subjects performed 4 blocks of experiments: each block contained 35 trials for both the body and object silhouettes; thus, there were a total of 140 trials. The duration was 500ms. The intertrial interval (ITI) was 1500 ms (± 100 ms). The stimuli were sequenced using STIM2 (Neuroscan, Texas, USA) and subtended to a maximum of $4^\circ \times 5^\circ$ of the visual angle. The presenting orders were randomised across subjects.

MEG recordings: The magnetic signals in the brain were measured using a 306-channel whole-scalp MEG system (Vectorview; ELEKTA Neuromag, Helsinki, Finland) in a magnetically shielded room. The event trigger was synchronised to the onset of stimulus presentation. The MEG signals were band-pass filtered at 0.01–100 Hz, sampled at 1000 Hz. Trials with error responses or those contaminated with eye blinking or body movements were excluded from the averaging. A total of at least 100 epochs for each test category were recorded for averaging.

MEG analysis: We calculated the differences between the MEG signals for the events in which a body was perceived and the events in which ‘no body’ was reported. Significant deflections ($2 \times$ S.D. of the fluctuation level in the baseline period), which peaked at around 110 ms (90–120 ms) and 190 ms (160–200 ms) after the target onset, were identified in all the participants. These deflections were observed in 2 areas: the occipital and occipital-temporal regions. We labelled the 2 components as M100 and M190, respectively. In this study, we focused on the M190 component, which peaked at around 190 ms, because our previous studies confirmed that the M2 component is tightly associated with body perception.

To obtain the source activity of the visual evoked magnetic-fields (VEFs), we conducted multisource localisation analysis for each subject. The cerebral sources of the responses were modelled as equivalent current dipoles (ECDs) in a spherical conductor for each hemisphere. The peak latencies, amplitudes, and ECD locations for each MEG response, and their associations with category (body and no-body) and hemisphere (left and right) were analysed by repeated-measures analysis of variance (ANOVA).

RESULTS

Behavioural results

A total of 54.2% ($\pm 3.4\%$) of the subjects perceived the ambiguous stimuli as bodies, and 43.8% ($\pm 4.8\%$) of the subjects perceived the stimuli as ‘no body’.

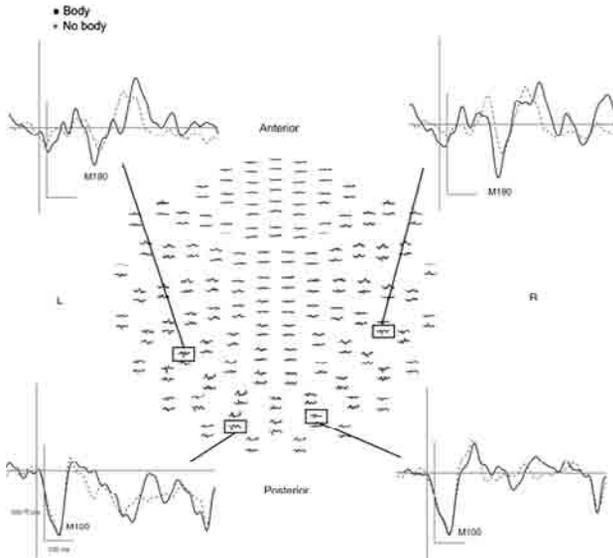


Figure 2. M100 and M190 responses to body and no body in a representative subject. The largest responses in each hemisphere are enlarged. Body, solid line; no body, red dotted line.

MEG results

All the subjects showed prominent deflections peaking at around 190 ms in the occipital-temporal regions (M2) in both hemispheres. Figure 2 shows the whole-scalp-recorded sensors and individual VEF waveforms for ‘body’ and ‘no body’ responses. Figure 3 indicates the VEF amplitudes and latencies of both responses.

Amplitude: We observed a significant main effect of category ($F = 17.57, p < 0.01$) on the amplitude of the M2 component. The mean amplitude of the responses when the participants perceived the ambiguous figures as bodies was larger than the corresponding amplitudes for the ‘no body’ responses. Furthermore, there was a significant difference between the amplitudes in the 2 hemispheres. The mean amplitude in the right hemisphere was larger than that in the left hemisphere. In addition, we observed a significant interaction between category and hemisphere ($F = 12.64, p < 0.05$). In the case of the ‘body’ responses, the M2 component in the right hemisphere was more pronounced than that in the left hemisphere ($p < 0.001$), while there were no interhemispheric differences with regard to the ‘no body’ responses.

Latency: In the case of the M2 component, there was a significant main effect

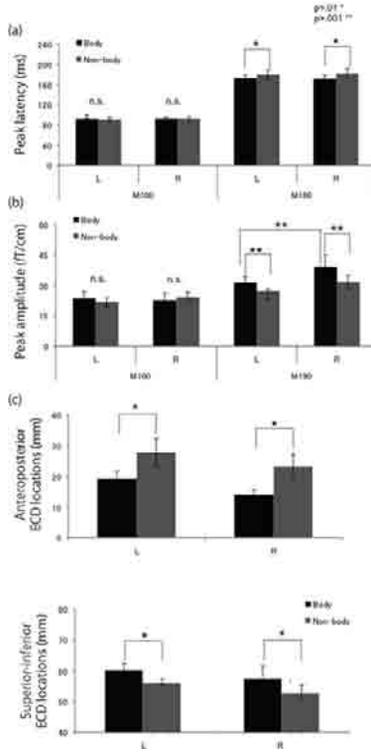


Figure 3. Mean (\pm SEM) of M100 and M190 peak latency (a) and amplitude (b) for two categories. (c) Mean (\pm SEM) of posteroanterior and superior-inferior ECD location (y-axis, z-axis) of M190 for two categories.

of category on the latency ($F = 11.23, p < 0.01$). The peak latencies for ‘body’ responses were lower than those for ‘no body’ responses.

ECD location: A source-localisation analysis was performed to locate the generator for each component. Figure 4 shows the representative estimated ECD locations of M2 on the two-dimensional brain images developed using an anatomical MR image of a representative subject. Figure 3(c) represents the mean ECD locations for the responses to each category of stimuli in both hemispheres.

In the case of the M2 for ‘body’ responses, all the subjects showed the ECDs that seemed to lie in the proximity of the occipital temporal area. These ECDs seemed to be located around the region of the EBA, where we identified the ECDs for bodies in previous studies. In the case of M2 for the ‘no body’ responses, the ECDs were estimated to be present in a more posterior site around the occipital temporal area. Within the occipital-temporal area, the ECDs for ‘no body’ responses

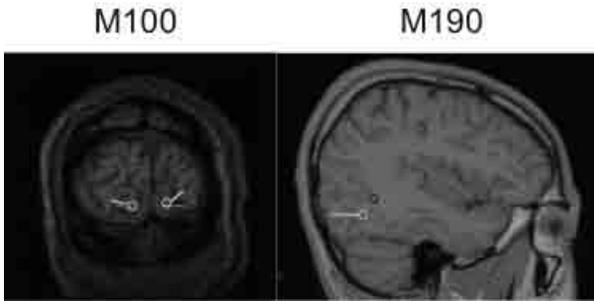


Figure 4. Anatomical MRI scans depicting the location of M100 in the occipital cortex and M190 in the occipital-temporal region. Body, red circles; no body, yellow circles.

seemed to lie more posterior than those for body responses, probably in the lateral occipital region (LO).

DISCUSSION

We aimed to investigate the magnetoencephalographic correlates of the perception of ambiguous figures as ‘body’ or ‘no body’ by performing MEG focusing on the M2 component that relates to body perception. The M2 component was clearly identified in both ‘body’ and ‘no body’ responses. We observed significant differences between the amplitudes and latencies of the M2 components of the ‘body’ and ‘no body’ responses. The activities induced by ‘body’ responses were higher than those induced by ‘no body’ responses, and the right hemisphere was predominant in comparison with the left hemisphere. In several previous studies on ambiguous-face perception, the amplitude of the N170 (M2) components for ‘face’ responses were higher than those for ‘no face’ responses (Dolan et al., 1997; Andrews et al., 2004). In this study, we confirmed that the M2 components for the stimuli perceived as bodies were larger than those that were not perceived as bodies. These results indicate that this component is tightly linked with the subjective perception of bodies and is important for the subject’s overt perception of a body in the M2-generation process.

The latencies induced by the ‘no body’ responses were delayed than those induced by ‘body’ responses. These results for latencies are consistent with those observed in our previous studies.

The ECDs of the M2 components induced by ‘body’ responses were estimated to be located around the EBA in the middle temporal area in both hemispheres.

However, the ECDs for ‘no body’ responses were estimated to be located in a more posterior region in the occipital area. These ECD locations are consistent with the results obtained in study 2, where we discussed the differences between bodies and objects. Previous fMRI-based studies on ambiguous stimuli have reported that the relevant visual processing areas, such as the fusiform face area for faces, show greater activities when the subjects perceive a stimulus as a face and they suggested that the fusiform gyrus is tightly linked to the awareness of faces. (Andrews et al., 2004; McKeef and Tong, 2007). In the current study, our results indicate that, analogous to face perception, the EBA shows a strong relationship with the subjective perception of bodies.

CONCLUSION

In the current study, we presented ambiguous images to subjects to determine the representation of the body perception in the brain. We investigated modulation of the M190 component by using ambiguous body figures, and indicated that the M190 is closely linked to the participant’s perception of bodies, just as N170 or M2 is closely linked to faces. These results indicate that body perception induces a consistent and selective neural activity in the human brain, as an analogy to face perception.

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