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Electrophysiological evidence for separation between human face and non-face object processing only in the right hemisphere

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ABSTRACT

Scalp event-related potential (ERP) studies have demonstrated larger N170 amplitudes when subjects view faces compared to items from object categories. Extensive attempts have been made to clarify face selectivity and hemispheric dominance for face processing. The purpose of this study was to investigate hemispheric differences in N170s activated by human faces and non-face objects, as well as the extent of overlap of their sources. ERP was recorded from 20 subjects while they viewed human face and non-face images. N170s obtained during the presentation of human faces appeared earlier and with larger amplitude than for other category images. Further source analysis with a two-dipole model revealed that the locations of face and object processing largely overlapped in the left hemisphere. Conversely, the source for face processing in the right hemisphere located more anterior than the source for object processing. The results suggest that the neuronal circuits for face and object processing are largely shared in the left hemisphere, with more distinct circuits in the right hemisphere.

1. Introduction

Among the scalp electrophysiological activity that accompanies face recognition, the negative event-related potential (ERP) component in the occipito-temporal cortex that takes place 170 ms after stimulus onset (N170) exhibits the largest and most stable difference between the potentials in responses to human faces and non-face objects (Bentin et al., 1996; Eimer, 2000; Rossion et al., 2000). The face selectivity of the N170 has been extensively studied and discussed. Most studies have demonstrated the sensitivity of N170 to both human faces and non-face objects, but with relatively larger peak amplitudes to human faces (Bentin et al., 1996; Jeffreys, 1996; Eimer, 2000; Watanabe et al., 2003; Itier and Taylor, 2004a, 2004b). Rossion et al. (2003) further showed a hemispheric difference based on the amplitude information of N170 and the strength information of the dipole model. The right hemisphere was shown to be dominant in human face processing, while the processing of other categories of objects was bilateral. However, the direct comparison between N170 signal sources for faces and non-face objects, which has potential to better relate the N170 ERP component to functional magnetic resonance imaging (fMRI) and neuroanatomical findings, is lacking. Hemispheric differences and the relative spatial locations of face- and non-face-evoked N170 dipoles in each hemisphere remain unclear.

fMRI studies have revealed that face perception is mediated by a neural system distributed throughout the human brain that comprises multiple bilateral regions (Haxby et al., 2000). Face perception in humans is a function of a bilaterally organized neural system with a stronger activation in the right hemisphere (Sergent et al., 1992; Puce et al., 1996; Kanwisher et al., 1997), which was proposed to emerge during cognitive function development (Le Grand et al., 2003). Recent ERP investigations indicate that hemispheric asymmetries in face processing may be due to a higher degree of functional lateralization in males compared to females (Proverbio et al., 2010). An increased amplitude of the face-specific N170 ERP component in the right hemisphere was only confirmed in male subjects, with no such laterality effect in females. With whole-head magnetoencephalography (MEG), a larger right-lateralized M170 amplitude was noted in males, as well as asymmetric strength of the underlying dipole, whereas a bilateral response was observed in females (Tiedt et al., 2013). Behavioral studies on face processing demonstrated a higher degree of functional lateralization in the right hemisphere of the male brain, with a more bilateral ability in female subjects (Bourne, 2005; Godard and Fiori, 2010).

Physiological recordings from the superior temporal sulcus and inferotemporal cortex in macaques have identified neurons that selectively respond to faces (Desimone, 1991; Gross et al., 1972; Perrett et al., 1991; Wang et al., 1996, 1998). Brain imaging studies demonstrated that the core of the human neural system for face perception consists of three bilateral regions in the occipito-temporal visual extrastriate cortex, i.e., the inferior occipital gyri, lateral fusiform gyrus, and superior temporal sulcus (Sergent et al., 1992; McCarthy et al., 1997; Halgren et al., 1999; Ishai et al., 1999; Hoffman and Haxby, 2000). To date, the

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neural sources for N170 are controversial. Some found the N170 source corresponded to the fusiform gyrus (Schweinberger et al., 2002; Deffke et al., 2007). It has also been localized to the superior temporal sulcus (Itier and Taylor, 2004a,2004b; Nguyen and Cunnington, 2014).

The present study was designed to investigate the spatial differences between N170 dipole sources during human face and non-face object processing. We presented images of human faces and those for other categories to the subjects during ERP recording. We performed a paired comparison between the N170 source locations accompanying human face processing and non-face object processing for each individual subject. We found that human face and non-face object processing elicited responses in similar areas in the left hemisphere. In contrast, a significant spatial difference in source locations for N170s was consistently observed in the right hemisphere when subjects viewed human faces and other objects.

2. Methods

2.1. Subjects

Of the 22 university students who participated, 2 subjects failed to show a consistent peak 100–200 ms after image presentation regardless of category, with no statistically significant difference between the means for the peak values detected in the range of 100–200-ms time window and for that averaged over −100–0 ms ($p > 0.05$, paired t-test). Excluding these two subjects, we ultimately included data from 20 subjects (10 male and 10 female, aged 18–25 years, mean age 21.7 ± 3.0 years). All the subjects were right-handed, had no previous history of neurological or psychiatric diseases, were not taking any medication, and had normal or corrected-to-normal vision.

Written informed consent was obtained from all subjects prior to their participation. A copy of the written consent form is available for review upon request. The study was approved by the ethics committee at the Graduate School of Science and Engineering, Kagoshima University (permit number: H25SE001).

2.2. Stimuli

The stimuli consisted of 400 gray images, with 100 images for each of the four categories: human face, animals, plant, and car (Fig. 1). Human face images were taken of 50 female and 50 male volunteer Japanese university students randomly selected from other schools of the university. The averaged size of the images was 7.9° × 8.1°, and the subjects for photography were facing and fixating 30° leftward from the lens. A questionnaire administered after electrophysiological recording confirmed that the subjects had not previously seen the human faces in the images. The animal and plant images were downloaded from multiple free image databases. Car images were downloaded from the websites of several car makers. The image sizes were adjusted so that the size along the shortest axis was >7.5° and the size along the longest axis was <16.8°. The luminance was adjusted to be the same across all the images. The stimulus images were presented on a 22-inch MultiSync FP1350 CRT display (NEC, Japan), which was set 57 cm in front of the subject. The screen resolution was 1280 × 1024 with a refresh rate of 85 Hz.

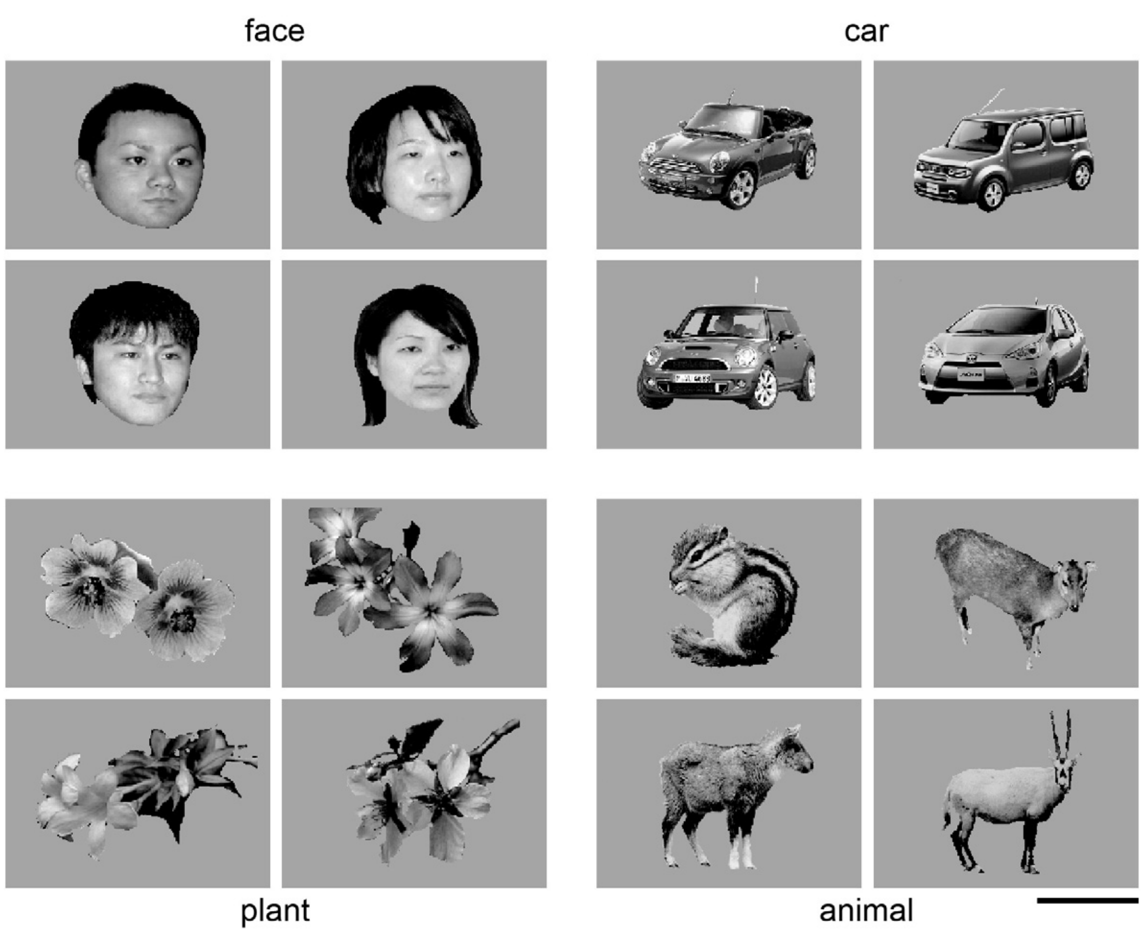

Fig. 1. Sample images of the stimuli. For each of the 4 categories, 4 sample images are selected from the 100 images in each category. Bar: 10 deg.