

Spatiotemporal cortical activation underlying self-referential processing evoked by self-hand

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ABSTRACT

Event-related potentials (ERPs) were recorded to explore the electrophysiological correlates of self-referential processing when subjects were asked to judge whether the stimuli (their hands) were their own or not. ERP results showed that: first, own hand elicited a greater positive component (P350–500) than did other hand in the time window of 350–500 ms, and the generator of P350–500 was localized in the anterior cingulate cortex (ACC), which might be related to retrieval and identification of self-referential information due to their sensitivity to self-hand. Second, own hand elicited a more positive component (LPC) than did other hand in the later time window. Dipole analysis revealed that the generators were localized in the parahippocampal gyrus and the medial frontal gyrus, which might be involved in making a self-referential decision based on retrieval of self-hand information.

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1. Introduction

The question of the self has been one of the most prominent problems throughout the history of philosophy and psychology (e.g., Churchland, 2002; Damasio, 2003; Northoff and Bermpohl, 2004; Gillihan and Farah, 2005; Northoff et al., 2006; Chen et al., 2008). Early researches on this topic demonstrated a mnemonic advantage for information that was processed in a self-referential manner (Rogers et al., 1977; Kelley et al., 2002; Chen et al., 2008). In Chen et al.'s study (2008), they summarized, “Two putative explanations have been proposed for the self-reference effect in memory (Gillihan and Farah, 2005; Kelley et al., 2002). One suggests that the self is a unique cognitive structure that possesses extraordinary or additional mnemonic abilities (e.g., Northoff et al., 2006; Northoff and Bermpohl, 2004; Craik et al., 1999; Rogers et al., 1977). The other proposes that the memory enhancement afforded to self-reference can be interpreted as an extension of the basic depth-of-processing effect (e.g., Symons and Johnson, 1997; Klein and Loftus, 1988; Ferguson et al., 1983; Bower and Gilligan, 1979).”

Moreover, the past few years had brought a remarkable increase in research on the neural basis of visual perception of the human body. For example, some previous studies had indicated that

the frontal and parietal lobes were somehow involved in the self-attribution of limbs, the cognitive and neural processes underlying self recognition remained inconsistent (e.g., Feinberg, 1997; Meador et al., 2000; Ehrsson et al., 2004). In addition, some studies were used to explore the physical self, such as face recognition (Turk et al., 2002; Platek et al., 2006), and recognition of one's own voice (Kaplan et al., 2008), whereas some studies employed trait adjectives (Craik et al., 1999; Kelley et al., 2002; Serino et al., 2008) and autobiographical memory (Fink et al., 1996; Gray et al., 2004; Summerfield et al., 2009) could be used to explore the psychological self.

In a word, some methods had been applied in studies of self-processing, such as behavioral, neuropsychological, neuroimaging and electrophysiological (e.g., Craik et al., 1999; Keenan et al., 1999; Kelley et al., 2002; Turk et al., 2002; Gray et al., 2004; Gunji et al., 2008). The early studies were mainly behavioral and neuropsychological, and demonstrated some potential neural bases of self-related processing, such as laterality (Platek et al., 2003; Uddin et al., 2004). With the development of neuroimaging techniques, more specific brain structures such as the anterior cingulate cortex (ACC) and the posterior cingulate cortex (PCC) in self-referential processing had been reported (e.g., Northoff and Bermpohl, 2004; Gillihan and Farah, 2005; Uddin et al., 2007; Han et al., 2009). Recent fMRI studies had demonstrated that, like emotional faces, images of emotionally expressive bodies and body parts increase activation in the visual cortex when compared with neutral controls (e.g., Peelen et al., 2007; Urgesi et al., 2007). Meanwhile, Peelen et al. (2007)

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pointed out that a focal region of the lateral occipitotemporal cortex responded strongly and selectively to static images of human bodies and body parts, but weakly to faces, objects and object parts.

Recently, Kontaris et al. (2009) had used fMRI to examine the extrastriate body area (EBA), the fusiform body area (FBA), and an area in the posterior superior temporal sulcus (PSTS) that responded to patterns of human biological motion. Frassinetti et al. (2009) also found that visual information from self body-parts in motion might be processed independently in patients with impaired static self-processing, thus pointing to a modular organization of the mechanisms responsible for the self/other distinction. Hodzic et al. (2009) found the existence of a cortical network for the extraction of body-related information and another cortical network for the extraction of self-related body information. In addition, the classical EBA is only involved in the analysis of body-related information but not in the assignment of body identity. Although fMRI studies provided many important results to explore the brain mechanism of self-referential, the time course of cortical activation could not be studied with precision. As Gillihan and Farah (2005) proposed, "If some methodological difficulties could be overcome, the hypothesis of a different response to the self could be examined better".

Fortunately, it is well known that the methods of event-related potential (ERP) recordings and voltage maps could provide critical temporal information for analyzing the functional neuroanatomy of cognitive processes of self-referential processing. As for now, previous ERP studies had used some different stimuli and subjects to invest self-referential processing. For example, two studies on self face recognitions showed similar self-effect for face: enhanced late positivity (P300 time window) for self face compared to familiar faces, both in attended than unattended conditions (Sui et al., 2006; Gunji et al., 2008). Miyakoshi et al. (2008) investigated the effect of viewpoint-independence for familiar-face recognition, and found that facial angle differences were reflected by N170 latency and N250 amplitude. Furthermore, the N250 difference was attenuated in the left hemisphere for famous faces and in the right hemisphere for one's own face. Also, some studies found that "self effect" was observed very early on 170 ms over posterior and fronto-central sites and marked at 250 ms where P2/N2 amplitude was significantly reduced for self-faces (Caharel et al., 2002; Keyes et al., 2009). Moreover, Miyakoshi et al. (2007) used ERP to investigate the self-referential effect in object recognition, and found left-lateralized N250 activity differentiated self and familiar from unfamiliar, and then self was dissociated from familiar in the later interval. Recently, Chen et al. (2008) also explored the temporal features and underlying brain structures of self-referential processing, and the results showed that other handwriting elicited a greater negative component than own handwriting in the time window of 200–500 ms.

To some extent, these previous ERP studies investigated the temporal features of self-referential processing, and get some interesting spatiotemporal patterns of brain activity during the performance of self-referential tasks (Miyakoshi et al., 2007, 2008; Chen et al., 2008). However, we found that their results were not consistent because they might use different self-referential stimuli. That is to say, we thought that the neural bases and the temporal features of self-referential processing might be different when people performed different self-referential tasks. Therefore, in the present study, high-density (64 channels) ERP recording was used to explore the temporal course and underlying neural substrates of self-referential processing, and determined whether the ERP components elicited by own and other hand were different. Moreover, we predicted that our ERP results would be also different from the findings by using other self-referential stimuli because the stimuli were not the familiar self faces but the stranger self hands. In our experiment, subjects were required to judge whether the hand

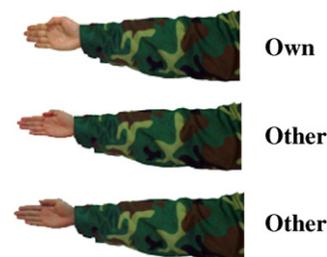


Fig. 1. The example of the picture of the subject's hand.

was their own or not. We believed that responses to own hand in the experiment were related to more primary cognitive processes, such as attention, perception, and memory. Therefore, we hypothesized that own hand would elicit a greater positive component (e.g., P300) than did other hand. The anatomic specificity data of fMRI mapping obtained from previous studies and the time resolution of ERP recordings would enable the characterization of the functional roles of specific brain areas in the context-dependent self-referential processing.

2. Method

2.1. Subjects

Twelve soldier undergraduates (12 men) aged 18–21 years (average age, 19.4 years) from Southwest University in China participated in the experiment as paid volunteers. All subjects gave written informed consent, were right-handed, had no current or past neurological or psychiatric illness, and had normal or corrected-to-normal vision.

2.2. Stimuli and procedure

Twelve subjects were asked to wear uniform, and stimuli were photographs of own and other right hands which were photographed with a digital camera. The subjects were asked to close hand and straighten their arm. The backgrounds of all the photos were white. The height and the width of hand stimuli were 2.4 cm and 5.7 cm. The distance of subjects from the monitor was about 60 cm, and thus the visual angle of the stimuli were about 2.3° and 1.2°, respectively.

The same participants were recalled approximately 2 months after the images were photographed. Each trial was initiated with a small black cross presented randomly for 300–400 ms; next, a picture of hand was presented 2000 ms after the offset of the little black cross. The subjects were required to answer the question: "Is the presented hand yours?", and to press "1" if they thought the hand in the picture was their own hand and to press "2" if not (other hand). The index and middle fingers of right hand were used to respond to the visual stimuli and the effector used was counterbalanced across subjects.

The subject was required to respond as fast and as accurately as possible. Each response was followed by a white, blank screen lasting for 1000 ms (Fig. 1).

The total experiment was divided into a practice phase and a test phase. To familiarize the subjects with the procedure of this task and pressing of the response buttons, a practice phase was designed during which subjects had to finish 14 practice trials (7 trials of their own hand and 7 of others' hand). The test phase was divided into two blocks: the first were 42 trials (21 trials were their own hand and 21 were others' hand), whereas the second block consisted of 40 trials (20 trials were their own hand). In this way, a total of 41 formal trials were included in each condition. The visual presentation of self and other's hands pictures within the two ERPs recording blocks were randomly presented.

2.3. Electrophysiological recording and analysis

Brain electrical activity was recorded from 64 scalp sites using tin electrodes mounted in an elastic cap (Brain Product), with the reference on the left and right mastoids. The vertical electrooculogram (EOG) was recorded with electrodes placed above and below the left eye. All interelectrode impedance was maintained below 5 k Ω . The EEG and EOG were amplified using a 0.05–80 Hz bandpass and continuously sampled at 500 Hz/channel for off-line analysis. Eye movement artifacts (blinks and eye movements) were rejected offline and 16 Hz low pass filter was used. Trials with EOG artifacts (mean EOG voltage exceeding $\pm 80 \mu\text{V}$) and those contaminated with artifacts due to amplifier clipping, bursts of electromyographic activity, or peak-to-peak deflection exceeding $\pm 80 \mu\text{V}$ were excluded from averaging.

The ERP waves for both conditions were overlapped and averaged. As seen in the grand-averaged waveforms and topographical maps, the ERPs elicited by the own and other conditions showed prominent differences from each other in the experiment and these differences were largest at frontal and central regions (see

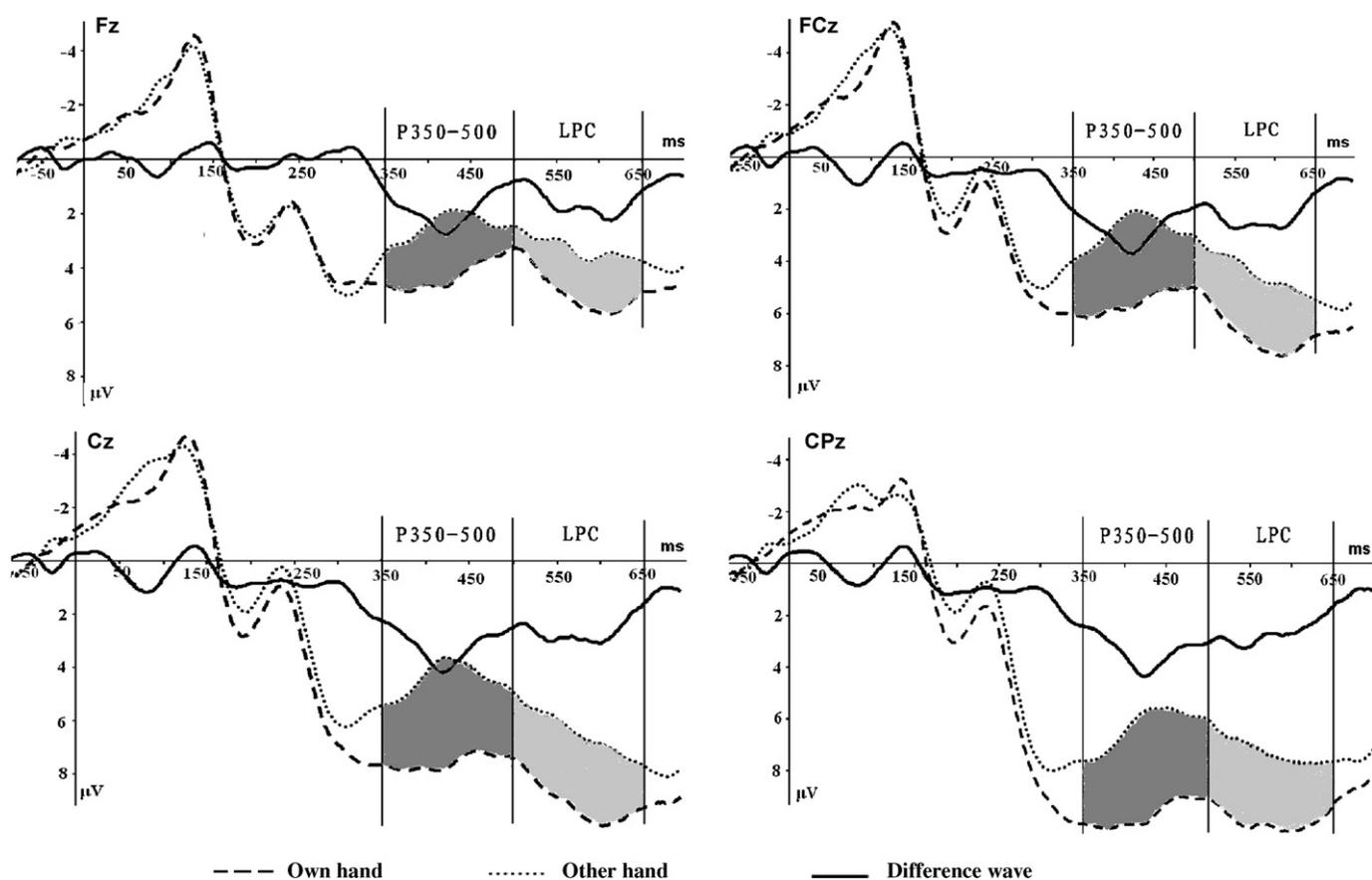


Fig. 2. Grand average event-related potentials at Fz, FCz, Cz, CPz for own, other hands including 11 other hands (the shadow regions were most significantly different).

Fig. 3). Thus, the following 15 electrode sites were selected for statistical analysis: F3, F4, C3, C4, P3, P4, Fz, Cz, Pz, FC3, FC4, CP3, CP4, FCz and CPz. The major aims were to measure and analyze the amplitudes and latencies of N1 (100–150 ms), P2 (P150–220 ms), and N2 (200–250 ms). Analysis of variance (ANOVA) was conducted on the amplitudes (from baseline to peak) and peak latencies of N1, P2, N2, and the mean amplitudes in the 350–500 and 500–650 ms interval, with factors of condition (own hand and other hand) and electrode sites (15 electrode sites). Mean amplitudes in the time window of 350–500 and 500–650 ms were analyzed using two-way repeated-measures Analyses of variance (ANOVA). The ANOVA factors were stimulus type (own hand and other hand) and electrode site. For all analyses, p -values of all main and interaction effects were corrected using the Greenhouse-Geisser method for repeated-measures effects.

2.4. Dipole source analysis

Brain Electrical Source Analysis program (BESA, Version, 5.0, Software) was used to perform dipole source analysis. For dipole source analysis, the four-shell ellipsoidal head model was used. The difference wave was obtained by subtracting the averaged ERPs of own hand from that of other hand trials. Principal component analysis (PCA) was employed for the ERP difference wave in order to estimate the minimal number of dipoles. After the minimal dipole numbers were determined, the software automatically determined the dipole locations according to the related residual variance criterion.

3. Results

3.1. Behavioral results

The error rate of judging one's own hand was 1.6 ± 0.2 (% \pm SE), whereas the error rate of judging others' hand was 4.4 ± 0.5 . The result of repeated measures showed that there is no significant difference between the two error rates [$F(1, 11) = 1.76$, $p > 0.05$]. In addition, the mean reaction time (RT) for own hand was 710 ± 37 ms (mean \pm SE), whereas the mean RT for other hand was 771 ± 38 ms. The repeated-measures ANOVA for the mean RTs

showed a significant difference between the two hand conditions [$F(1, 12) = 11.19$, $p < 0.001$].

3.2. Electrophysiological scalp data

Fig. 2 showed that the experimental conditions produced remarkable N1, P2 and N2 components. Topographical maps were shown separately for self and other's hand in Fig. 3. A two-way ANOVA was conducted on the amplitudes (from the baseline to the peaks) and peak latencies of N1, P2 and N2, as well as on the mean amplitudes in the 350–500 and 500–650 ms interval. The results of the ANOVA on mean amplitudes in the 350–500 ms interval showed that other hand elicited a significantly greater negativity than own hand [$F(1, 11) = 12.712$, $p < 0.01$], and the main effect of electrode site was significant [$F(14, 154) = 14.394$, $p < 0.001$]. However, the interaction between condition and electrode sites were not significant [$F(14, 154) = 1.565$, $p > 0.05$]. In the 500–650 ms interval, the result of the ANOVA also showed that other hand elicited a significantly greater negativity than own hand [$F(1, 11) = 5.657$, $p < 0.05$], and the main effect of electrode site was extremely significant [$F(14, 154) = 8.549$, $p < 0.001$]. However, the interaction between condition and electrode sites were not significant [$F(14, 154) = 1.356$, $p > 0.05$]. In summary, the amplitude and latency effects were not significantly different between the two conditions at N1, P2 and N2, but there were significantly different between the two conditions in the time windows of 300–500 and 500–650 ms.

3.3. ERP data of a control experiment

In our study, we used 1 own hand and 11 other hands, considering that the different stimulus familiarity/probability for the two

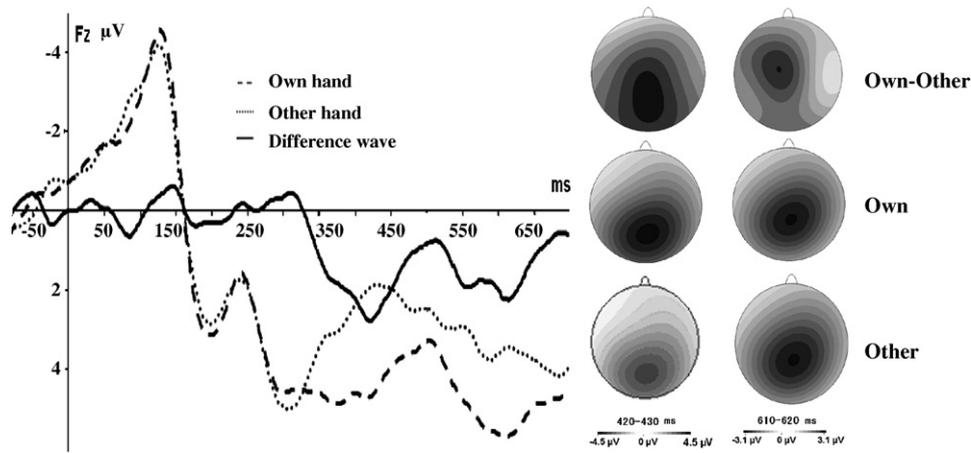


Fig. 3. Grand average ERP to own, other right hand and the difference wave (own–other) at Fz. Topographical maps of the voltage amplitudes for own, other and own vs. other hands difference wave in the 420–430 ms and 610–620 ms.

conditions might influence the result, so we added a control experiment to exclude the possible elements. In the control experiment, 13 soldier undergraduates (13 men) aged 18–21 years (average age, 19.6 years) from Southwest University in China participated in the experiment as paid volunteers. The method was the same as the main experiment. The only difference was that there was one other hand in the “other condition” (see Fig. 4).

Fig. 5 showed that the experimental conditions produced remarkable N1, P2 and N2 components. A two-way ANOVA was conducted on the amplitudes (from the baseline to the peaks) and peak latencies of N1, P2 and N2, as well as on the mean amplitudes in the 350–500 and 550–700 ms interval. The results of the ANOVA on mean amplitudes in the 350–500 ms interval showed that other hand elicited a significantly greater negativity than own hand [$F(1, 12) = 8.506, p < 0.01$], and the main effect of electrode site was significant [$F(14, 154) = 7.403, p < 0.05$]. However, the interaction between condition and electrode sites were not significant [$F(14, 154) = 0.797, p > 0.05$]. In the 550–700 ms interval, the result

of the ANOVA also showed that other hand elicited a significantly greater negativity than own hand [$F(1, 12) = 52.918, p < 0.05$], and the main effect of electrode site was extremely significant [$F(14, 154) = 7.048, p < 0.01$]. However, the interaction between condition and electrode sites were not significant [$F(14, 154) = 1.048, p > 0.05$].

3.4. Results of dipole source analysis

The ERP wave elicited by other hand was subtracted from that elicited by own hand to obtain a difference wave. Fig. 2 showed that the difference wave displayed a remarkable negative component in the 350–500 and 500–650 ms interval. Thus, PCA was conducted on the difference wave in the 350–500 and 500–650 ms interval.

In the 350–500 ms interval, the result showed that one principal component accounted for 95.1% of the variance, and the remaining components accounting for no more than 5%. Thus, one dipole fitted the data (Fig. 6). When the dipole’s orientation and place was not limited, the dipole for principal component was localized in the

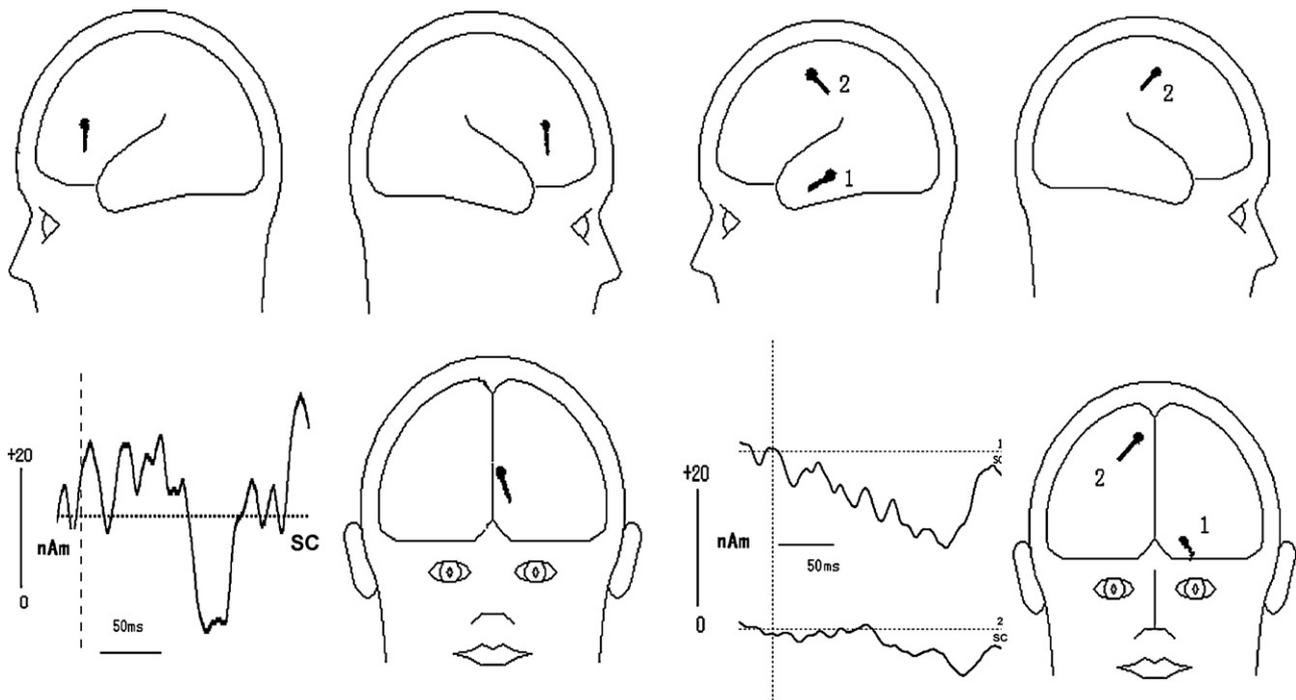


Fig. 4. The example of the pictures of the subject's hand. The own hand and the other hand (the hand was not included in the 13 subjects).



Fig. 5. Grand average event-related potentials of the control experiment at Fz, FCz, Cz, CPz for own, other hand including only one other hand (the shadow regions were most significantly different).

ACC ($x = -2.4$, $y = 16.7$, and $z = 19$), and the maximal dipole moment strength was at about 420 ms. At the moment of the dipoles' peak activation, this model can best account for the data in the interval, and accounts for the most variance, with a residual value of 19.5%.

In the 500–650 ms interval, the result showed that two principal components accounted for 96.5% of the variance, with principal component 1 accounting for 86.8%, principal component 2 accounting for 10.7%, and the remaining components accounting for no more than 4.0%. Thus, two dipoles fitted the data (Fig. 6), the dipole for principal component 1 was localized in the parahippocampal gyrus ($x = -19.2$, $y = -16.0$, and $z = -8.8$). The dipole for principal component 2 was localized in the medial frontal gyrus ($x = 11.2$, $y = -9.8$, and $z = 54.3$), and the maximal dipole moment strength was at about 620 ms. At the moment of the dipoles' peak activation, this model could best account for the data in the interval, and accounts for the most variance, with a residual value of 14.8%.

4. Discussion

In the present study, we used right hands as our experimental materials to explore the electrophysiological correlates of self-referential processing. Observing from the grand averaged waveforms and topographical maps, we found that the ERP components elicited by the two kinds of stimuli were not significantly different in either the latencies or amplitudes of N1, P2 and N2. These results suggested that the early processing of the two kinds of stimuli was similar. However, the ERPs elicited by own and

other hand appeared significantly different in these time windows (350–500 and 500–650 ms). In addition, our control experiment also suggested that the different stimulus familiarity/probability for the two conditions had no effect on these ERPs components effect. We would discuss the implications of these findings.

First, own hand elicited a greater positive component (P350–500) than did other hand in the time window of 350–500 ms. According to the difference wave, the P350–500 might be an obvious P300 component. In general, P300 amplitude reflected the amount of attentional resources employed in a given task (e.g., Donchin and Coles, 1988; Ilan and Polich, 1999), and was also thought to represent “context updating” processes (e.g., the current perceptual/motor context needs to be updated) in visual short-term memory (VSTM; Donchin and Coles, 1988; Luck, 2005; Picton, 1992). Specifically, Berlad and Pratt (1995) found that P300 amplitude was larger in response to a participant's own name compared to other words, which suggested that stimulus relevance had an additional effect on P300 amplitude. Ninomiya et al. (1998) also found that P300 amplitude in response to a subject's own face was significantly larger than that of an unfamiliar face or red square, suggesting that his or her own face caused an emotional response other than an orientation response. In addition, in Gray et al.'s study (2004), P300 amplitude elicited by self-referential stimuli was larger than that elicited by control stimuli and P300 latency indicated that self-referential processing might happen at a higher level of cognitive processing involving selective attention. Based on these findings, we suggested that the P350–500 might reflect identifying target stimuli (attentional effects) and retrieving of much more self-referential information in the early processing of judgment.

To better understand P300 modulation in the present study, a dipole analysis was conducted on the difference wave in the 350–500 ms time window. One dipole which fitted to the data in this time window was located in the ACC. Earlier studies had indicated that the ACC might be involved in action selection based on the expected outcome of an action (e.g., Bush et al., 2002; Hadland et al., 2003; Shima and Tanji, 1998) integrating information regarding a motor response and its potential outcome (e.g., Williams et

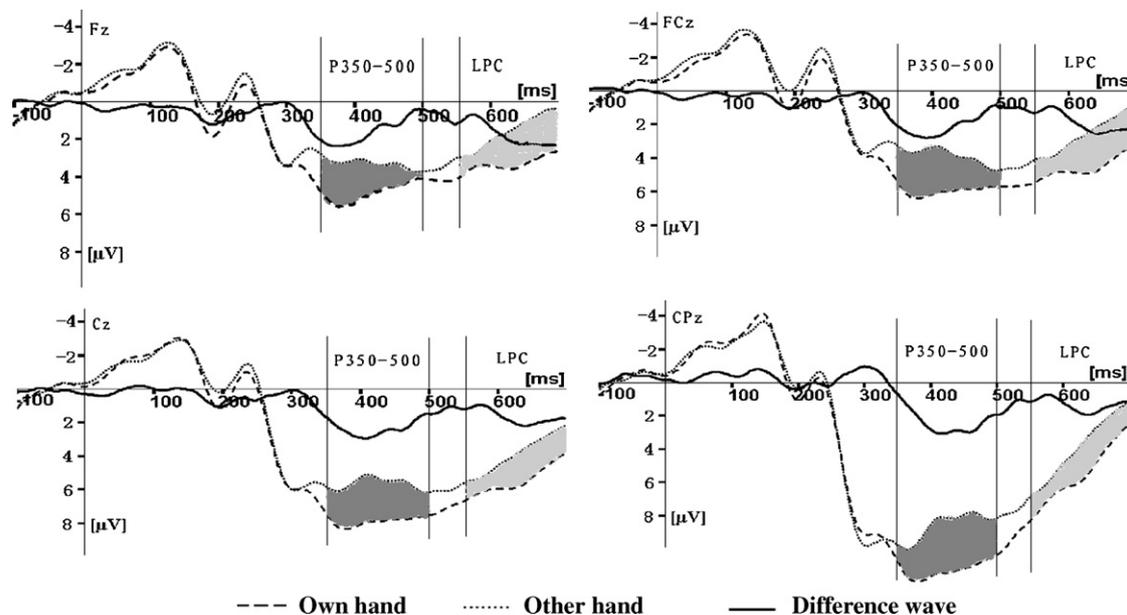


Fig. 6. Results of the dipole source analysis of the difference wave (own right hand vs. other right hand) in the time range of 350–650 ms. The bottom left shows the source activity waveforms, whereas the right figure displays the mean locations of the dipole. Left: between 350 and 500 ms, the dipole is located in the anterior cingulate cortex (ACC) ($x = -2.4$, $y = 16.7$, and $z = 19$). Right: in the time range of 500–650 ms, the first dipole is located in the parahippocampal gyrus ($x = -19.2$, $y = -16.0$, $z = -8.8$), the second in the Medial Frontal Gyrus ($x = 11.2$, $y = -9.8$, $z = 54.3$).

al., 2004; Mars et al., 2005). Moreover, greater ACC activity during encoding of self-referential trait adjectives relative to conditions that were not self-related (Fossati et al., 2003, 2004; Macrae et al., 2004). Therefore, we thought that the ACC might play a central role in automatic processing of self-referential information. On the contrary, when the presented stimulus was other hand, less retrieval of own hand features would be evoked. That is to say, we thought that own hand would evoke various self-related identification and memories, and this most likely contributed to the conspicuous P350–500 and the ACC activities.

Second, own hand elicited a more positive component than did other hand in the time window of 500–650 and 550–700 ms. We thought they might be a late P300 component (or late positive component, LPC). Previous studies had indicated that slow positive/negative waves in the ERP are correlated with rehearsal/retention operations in working memory (e.g., King and Kutas, 1995; Mecklinger and Pfeifer, 1996). Specifically, Donchin and Coles (1988) had suggested tasks that required greater amounts of attentional resources, P300 amplitude was smaller as processing intervening nontarget events engage attention to modify the current neural representation. Also, Some studies revealed that P300 amplitude decreased due to the increasing effects of task difficulty and smaller on the most demanding task. That is to say, P300 amplitude increased due to the decreasing effects of task difficulty (e.g., Bernstein, 2002; Houlihan et al., 1998). Therefore, LPC was larger in the condition of own hand than in other hand. In addition, dipole source analysis of the difference waves (own–other) showed that the LPC was localized near the parahippocampal gyrus and the medial frontal gyrus. Many previous studies had indicated that the hippocampal/parahippocampal regions might contribute to the retrieval of the memory trace related to the representation (e.g., Cabeza et al., 2002; Leube et al., 2001; Bohbot et al., 1998; Epstein and Kanwisher, 1998). Moreover, the medial frontal gyrus might be involved in implementing processes underlying adjustments of performance control (e.g., Carter et al., 1998; Botvinick et al., 2001; Van Veen and Carter, 2006), and might play a central role in the self-monitoring that was necessary for adaptive goal-directed behavior (Paus, 2001; Bush et al., 2000). Therefore, we thought that the LPC (activation of the parahippocampal gyrus and the medial frontal gyrus) might be related to make a decision based on retrieval of self-hand information.

In conclusion, our study compared spatiotemporal cortical activation patterns underlying own hand and other hand using ERP recording and dipole source analysis. The results showed that own hand elicited more positive ERP components (P300 and LPC) than other hand in the time window of 350–650 ms, which might reflect retrieval self-referential information and making a self-referential decision, separately. However, there were still some shortcomings in our study. For example, due to inherent limitations of source localization, the brain areas implied by source localization were only tentative. Regarding the involvement of brain regions in response to own and other hand, the current results only provided a model, rather than empirical data. Therefore, further studies should be done using both ERPs and fMRI to investigate spatiotemporal cortical activation patterns underlying the brain mechanism of self-referential processing due to different self-referential stimuli.

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