

Neural oscillations involved in self-referential processing

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ABSTRACT

Human adults remember better trait words that are referenced to the self than those referenced to others. To investigate whether non-phase-locked neural oscillations engage in the self-reference effect, we recorded electroencephalogram (EEG) from healthy adults during trait judgments of the self and a familiar other. The wavelet analysis was used to calculate non-phase-locked time–frequency power associated with encoding of trait adjectives referenced to the self or the familiar other at theta (5–7 Hz), alpha (8–13 Hz), beta (14–27 Hz) and gamma (28–40 Hz) bands. We found that, relative to other-referential traits, self-referential traits induced event-related synchronization of theta-band activity over the frontal area at 700–800 ms and of alpha-band activity over the central area at 400–600 ms. In contrast, event-related desynchronization associated with self-referential traits was observed in beta-band activity over the central–parietal area at 700–800 ms and in gamma-band activity over the fronto-central area at 500–600 ms. Moreover, valence of traits referenced to the self and self-relevance of traits respectively led to modulations of theta/alpha- and beta/gamma-band activity. Finally, event-related synchronization of frontal theta-band activity at 700–800 ms positively correlated with the self-reference effect observed during memory retrieval. Our results indicate that non-phase-locked neural activity is involved in self-reflexive thinking. In addition, low and high-frequency neural oscillations play different roles in emotional and cognitive aspects of self-reference processing.

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Introduction

Human adults remember better trait words that are referenced to themselves than those referenced to others (Symons and Johnson, 1997). This self-reference effect has been interpreted by assuming enhanced elaborative encoding of stimuli that are processed in relation to the self (Klein and Loftus, 1988; Klein et al., 2002). Recently, neural correlates of the self-referential processing have been studied extensively using functional magnetic resonance imaging (fMRI) (Kelley et al., 2002; Fossati et al., 2003; Zysset et al., 2002; Macrae et al., 2004; Zhu et al., 2007; Han et al., 2008; see Northoff et al. (2006) for review). Most of the studies employed the self-reference task (Rogers et al., 1977), in which subjects are first asked to judge whether a number of trait words can describe the self or others and then recall as many of the words as they can in a later memory test. Kelley et al. (2002) reported that hemodynamic responses in the medial prefrontal cortex (MPFC) and posterior cingulate cortex (PCC) increased to trait judgments of the self relative to a public person. Macrae et al. (2004) further sorted trait words used in self-judgments based on the subjects' performances during encoding ('yes' or 'no' responses) and memory retrieval ('remembered' or 'forgotten'). They found that, relative to the trait

words with 'no' responses, those followed by 'yes' responses evoked greater MPFC activity. In consistent with this, Moran et al. (2006) found that highly self-descriptive trait words were associated with greater MPFC activity relative to low self-descriptive ones. The MPFC also showed enhanced activations to remembered trait words compared to forgotten ones (Macrae et al., 2004), suggesting that the MPFC engages in elaborative cognitive processing of self-related stimuli that facilitates later memory retrieval of self-relevant information.

The emotional aspect of self-referential processing has been assessed by examining modulations of neural activity by the valence of traits linked to the self. Fossati et al. (2003) found that, while the MPFC activity related to self-referential processing was present regardless of the valence of trait words, negative words induced more reductions in several brain areas including the insula and the inferior parietal regions relative to positive ones. Moran et al. (2006) also reported activations in the ventral anterior cingulate to positive than negative trait words, which, though, was evident only with highly self-descriptive trait words. Fossati et al. (2004) showed that, relative to self-related positive words, retrieval of self-related negative words during the memory test resulted in increased activations in the right dorsolateral prefrontal cortex, the right post-central gyrus, the right occipital cortex, and the left cerebellum. Accordingly, personality relevant words may signal important emotional clues and engage in a widely distributed neural network when maintaining the concepts of the self (Fossati et al., 2003; 2004).

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Although the fMRI findings suggest that the processes of cognitive and emotional aspects of the self are mediated by distinct neural structures, the results provide little information regarding the temporal course of self-referential processing because of the low time resolution of blood oxygen level dependent (BOLD) signals. This has been examined by recording event-related potentials (ERPs) that are both time- and phase-locked to stimulus onset. Magno and Allan (2007) recorded ERPs to cue words that prompted recollection of episodes that were either personal or relevant to a friend or prompted facts relevant to the self or a friend. They found that, relative to friend related processes, self-referential processing induced positive-going shifts of ERPs recorded over the midline scalp sites. The ERPs differentiating between self- and friend-referenced processing occurred at 100–1944 ms after the onset of cue words in the task to recollect episodes but at 800–1200 ms in the task of recollect general facts, suggesting temporal dissociation between retrieval of self-specific episodes and facts. Watson et al. (2007) recorded the ERPs to trait words from subjects who performed either an emotional judgment task (positive/negative) or a self-referential task (like me/not like me). They found a significant main effect of valence at the centro-parietal electrodes between 400 and 550 ms and an interaction between self-reference and valence at 450–600 ms over the fronto-central electrodes. These ERP findings imply an interaction between the recognition of self-relevant material and the recognition of emotional valence of trait words.

Besides phase-locked ERPs, non-phase-locked neural oscillations, which reflect neural rhythm changes of ongoing EEG that is time-locked but not phase-locked to stimulus onset, may provide information about the time course of self-referential processing. Non-phase-locked neural oscillations are greatly attenuated by the additive averaging technique that is necessarily used to quantify ERPs (Kalcher and Pfurtscheller, 1995). Both external stimuli and internal mental events can induce event-related synchronization (ERS)/desynchronization (ERD) of non-phase-locked oscillations that are identified by the increase/decrease of spectral power at specific frequency band (Pfurtscheller and Lopes da Silva, 1999). Low-frequency non-phase-locked oscillations (e.g., alpha band rhythms) can arise from coherent activity in large neuronal pools whereas high-frequency non-phase-locked oscillations (e.g., gamma band rhythms) may stem from synchrony in localized neuronal pools (Lopes da Silva et al., 1973; Lopes da Silva and Pfurtscheller, 1999; Pfurtscheller and Lopes da Silva, 1999). Theta band activities (4–7 Hz) contribute to memory encoding (Klimesch et al., 1996) and are associated with emotional discrimination of visual displays (Aftanas, et al., 2001a,b; 2003b; Krause et al., 2000) and empathy for others' pain (Mu et al., 2008). Alpha (8–14 Hz) oscillations serve as an inhibition mechanism in a variety of cognitive processes (see Knyazev (2007) and Klimesch et al. (2007) for review). The high-frequency band activity such as gamma oscillation is involved in attention and memory processes (Tiitinen et al., 1994,1997;Gruber et al., 1999; Müller et al., 2000; Herrmann and Knight, 2001; Fell et al., 2001; Haenschel et al., 2000).

More relevant to the current work, it has been documented that non-phase-locked neural oscillations engage in multiple-level self-related process such as self-pace movement (Leocani et al., 1997), face-specific visual self-representation (Miyakoshi et al., 2010), reconstitution of the experience of the self (Lehmann et al., 2001), and self-control (Walsh et al., 2010). The current work tested the hypothesis that non-phase-locked neural oscillations are also involved in neural representations of the mental aspect of the self (i.e., one's own trait) by recording electroencephalogram (EEG) in association with trait judgments of the self or a familiar other. To address this issue would help to clarify the functional role of non-phase-locked neural activity in high level social cognition. We employed wavelet analysis to calculate EEG spectral power with high time–frequency (TF) resolution in order to clarify the time course of neural oscillations involved in self-referential processing. We

disentangled the neural oscillations that are respectively linked to the encoding of self-relevance of traits and encoding of valence of traits related to the self by comparing EEG activity induced by trait words followed by 'yes' and 'no' responses and EEG activity induced by positive and negative traits associated with self-judgments. We also assessed whether TF power of non-phase-locked neural oscillations can predict self-advantage in memory of self-related trait words in order to understand the dynamic neural basis of the self-referential effect.

Method

Subjects

Fourteen healthy adults (11 males, 3 females, aged 18–26 years, mean = 22.4, SD = 2.28) participated in this study as paid volunteers. All subjects were right-handed, had normal or corrected-to-normal vision. Informed consent was obtained from each subject before the study. This study was approved by a local ethics committee.

Stimuli and procedure

360 Chinese trait adjectives were selected from an established personality trait adjective pool (Liu, 1990). The adjectives were classified into 9 lists of 40 words (half positive and half negative). Each adjective consisted of two characters. Six lists of words were pseudorandomly selected for judgment tasks while the remaining three lists of words were used as new words for the memory test. The assignment of words to different tasks was counterbalanced across subjects.

In three judgment tasks, subjects were asked to judge whether a trait adjective was appropriate to describe the self, a familiar other (e.g. Liu Xiang, a well known Chinese athlete), or to judge the font of a trait word (bold- vs. light-faced). There were two blocks of trials for each judgment task. Each block of 40 trials began with the presentation of an instruction (e.g. "Are the following adjectives appropriate to describe you?"). Each trial consisted of a "cue" word ("self", "other" or "font", black on a gray background) above a fixation cross presented randomly between 600–1000 ms at the center of the screen. A trait adjective then overlaid the fixation cross with a duration of 1800 ms while the "cue" word stayed on the screen (Fig. 1). Subjects responded to each stimulus by pressing one of the two buttons with the left and right thumbs. Each of the Chinese characters subtended a visual angle of $0.65^\circ \times 0.86^\circ$ (width \times height) for the "cue" word or $2.0^\circ \times 2.3^\circ$ for trait adjectives at a viewing distance of 90 cm. Trait words in each block of trials were presented in a random order. The order of different judgment tasks was counterbalanced across subjects using a Latin Square design.

After the judgment tasks, subjects watched a video clip of 50 min and was then given an unexpected memory test. The 240 personality traits used in the judgment tasks were intermixed with 120 new trait adjectives and presented in a random order. Subjects were required to identify whether the adjective presented was old or new by pressing one of two buttons using the right or left thumbs. Each trait word was presented for 2000 ms followed by a fixation with the duration of 800–1600 ms.

EEG data recording and analysis

While subjects performed trait judgment tasks, EEG was continuously recorded from 62 scalp electrodes that were mounted on an elastic cap according to the extended 10–20 system. EEG was referenced to the electrodes at the right mastoid that is the most common reference site used in ERP studies (Luck, 2005). The electrode impedance of each electrode was kept less than 5 k Ω . Eye

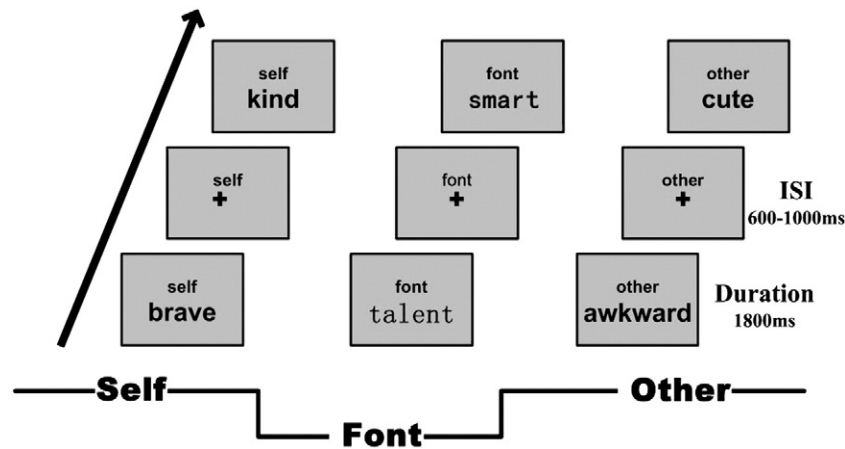


Fig. 1. Illustration of the stimuli and procedure of self-, other- and font-judgments used in the current study. Both the cue and stimuli words were in Chinese.

blinks and vertical eye movement were monitored with electrodes located above and below the left eye. The horizontal electro-oculogram was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. The EEG was amplified (band pass 0.01–45 Hz), digitized at a sampling rate of 250 Hz and stored for off-line analysis. The EEG data were then re-referenced to the algebraic average of the electrodes at the left and right mastoids in order to reduce the influence of reference site on hemispheric asymmetry of any effects. Trials contaminated by eye blinks, eye movements, or muscle potentials exceeding $\pm 50 \mu\text{V}$ at any electrode and trials containing behavioral errors (in the font-judgment task) were excluded from the further analysis. ERPs were calculated separately in each condition (self-judgment, other-judgment and font-judgment) with averaging epochs beginning 200 ms before stimulus onset and continuing for 1200 ms. There was no significant difference in the number of rejected trials between different judgment tasks (self/other/font: 68/70/68, $F(2,26) = 0.613$, $p > 0.5$).

In order to conduct time–frequency analysis, we first subtracted ERPs in each stimulus condition from the corresponding EEG epoch to remove phase-locked EEG activity. Neural oscillations were quantified based on the TF wavelet decomposition of the signal between 5 and 40 Hz. The power of each single trial was averaged across trials in the same condition to obtain non-phase-locked components. The signal was then convoluted by the complex Morlet's wavelet $w(t, f_0)$ (Kronland-Martinet et al., 1987) with a Gaussian shape in time ($SD \sigma_t$) and frequency ($SD \sigma_f$) domains around its central frequency f_0 :

$$w(t, f_0) = A \exp(-t^2 / 2\sigma_t^2) \exp(2i\pi f_0 t)$$

with $\sigma_f = 1/2\pi\sigma_t$. Wavelets are normalized so that their total energy is 1. The normalization factor A was equal to: $(\sigma_t \sqrt{\pi})^{-1/2}$. As a wavelet family is characterized by a constant ratio (f_0/σ_f), which should be chosen in practice greater than ~ 5 (Grossmann et al., 1989), the wavelet family was defined by $f_0/\sigma_f = 5$ (wavelet duration $2\sigma_t$ of about 1.6 periods of oscillatory activity at f_0), with f_0 ranging from 5 to 34 Hz in 1 Hz steps. The time-varying energy $E(t, f_0)$ was defined as the square norm of the result of the convolution of a complex wavelet $w(t, f_0)$ with the signal $s(t)$: $E(t, f_0) = |w(t, f_0) \times s(t)|^2$. Convolution of the signal by a family of wavelets provides a TF representation of the signal.

The mean TF energy in a pre-stimulus window (-200 to 0 ms) calculated as the baseline power was subtracted from the pre- and post-stimulus TF power in each frequency band (theta: 5–7 Hz; alpha: 8–13 Hz; beta: 14–27 Hz; gamma: 28–40 Hz). Alpha, beta, and gamma

band activities were further separated in sub-band activity (alpha1: 8–10 Hz; alpha2: 11–13 Hz; beta1: 14–20 Hz; beta2: 21–27 Hz; gamma1: 28–34 Hz; gamma2: 34–40 Hz). As statistic analyses did not show significant effects on gamma2-band activity, only the results of gamma1-band activity were reported. The signal of power in successive 100-ms windows in each condition was aggregated for statistically analysis. To examine the main effect of judgment tasks, a repeated measures analysis of variance (ANOVA) of the behavioral data was conducted with Task as a within-subject variable (self-/other-/font-judgment). Then phase-locked/non-phase-locked neural activity in each condition (self-/other-/font-judgment) was then compared using paired sample t-tests. To investigate whether neural oscillations related to the self-referential task was modulated by the valence of trait adjectives, a two-way ANOVA was conducted with Task (self- vs. other-judgment) and Valence (positive vs. negative trait) as independent within-subjects variables. To examine the effect of self-relevance on non-phase-locked neural activity, the TF power was calculated respectively for trials followed by 'yes' and 'no' responses during self- and other-judgment tasks. Traits followed by 'yes' responses were relevant to the target person whereas those followed by 'no' responses were irrelevant to the target person. A two-way ANOVA of TF power was then conducted with Task (self- vs. other-judgment) and Relevance ('yes' vs. 'no' response) as independent within-subjects variables.

Results

Behavior results

Reaction times (RTs)

The ANOVA of RTs associated with trait and font-judgment tasks showed significant main effect of Task ($F(2,13) = 82.32$, $p < 0.0001$). Post-hoc analysis confirmed that both RTs to self- and other-judgment were longer than that to font-judgment (self-judgment vs. font-judgment: 871 vs. 570 ms, $t(13) = 10.866$, $p < 0.0001$; other-judgment vs. font-judgment: 852 vs. 570 ms, $t(13) = 9.259$, $p < 0.0001$). However, there was no significant difference between RTs to self- and other-judgments ($t(13) = 1.01$, $p > 0.05$).

We also performed a 3×2 ANOVA with Task (self-/other-/font-judgment) and Valence (positive/negative) as independent within-subject variables. This also showed a significant main effect of Task ($F(2,26) = 72.062$, $p < 0.0001$). However, both the main effect of valence ($F(1,13) = 0.020$, $p > 0.05$) and the interaction of Task \times Valence were not significant ($F(2,26) = 1.854$, $p > 0.05$), suggesting comparable RTs to positive and negative traits. The ANOVA of RTs with

Task (self-/other-judgment) and Relevance (relevant/irrelevant words) as independent within-subject variables showed a significant main effect of Relevance ($F(1,13)=5.87$, $p<0.05$) as RTs were longer to irrelevant traits than to relevant traits. There was also a significant interaction of Task \times Relevance ($F(1,13)=4.95$, $p<0.05$). Post-hoc analyses showed that responses to self-relevant traits were faster than those to self-irrelevant ones (856 vs. 918 ms, $t(13)=-3.30$, $p<0.01$). However, RTs did not differ between other-relevant and other-irrelevant adjectives (858 vs. 885 ms, $t(13)=-1.28$, $p>0.05$).

Recognition scores

The recognition scores of the memory test were defined as the proportion of hits minus the proportion of false alarm in each condition. The ANOVAs of the recognition performance showed a significant main effect of Task ($F(2,26)=95.963$, $p<0.001$), as the recognition scores were higher for judgments associated with deep semantic processing (self- and other-judgments: 47.0% and 36.1%) than that for font-judgment (8.2%). In addition, the recognition score was significantly higher for traits related to self compared to those related to others ($t(13)=6.331$, $p<0.001$), indicating a reliable self-reference effect.

The recognition scores in memory test were further analyzed separately for trait words associated with 'yes' and 'no' responses during encoding phase. The ANOVAs of the recognition performance with Task (self-/other-judgment) and Relevance (relevant/irrelevant words) only showed a similar main effect of Task ($F(1,13)=38.33$, $p<0.001$). Neither the main effect of Relevance nor the interaction between these two factors was significant ($p>0.05$). Paired t-test confirmed that the recognition score was higher for self-relevant than for self-irrelevant trait words (49.1% vs. 43.9%, $t(13)=2.25$, $p<0.05$). No such difference was observed for the recognition score of other-relevant and other-irrelevant trait words (33.5% vs. 31.8%, $t(13)=0.59$, $p>0.05$).

Electrophysiological results

Phase-locked neural activity

Fig. 2 illustrates phase-locked ERPs elicited by different judgment tasks. Relative to font-judgment, self-judgment induced a larger P2 wave at 200–300 ms over the frontal regions (Fz: $t(13)=3.01$, $p<0.01$; F3: $t(13)=2.92$, $p<0.05$; F4: $t(13)=3.18$, $p<0.01$). However, the P3 component elicited by self-judgment was of smaller amplitude and peaked later than that elicited by font-judgment, resulting in significant difference in the ERP amplitudes between the two tasks at 300–500 ms over the centro-parietal electrodes (Cz: $t(13)=-3.93$, $p<0.01$; C3: $t(13)=-5.31$, $p<0.001$; C4: $t(13)=-4.83$, $p<0.001$; Pz: $t(13)=-3.67$, $p<0.01$; P3: $t(13)=-4.91$, $p<0.001$; P4: $t(13)=-3.95$, $p<0.01$) and at 800–1000 ms over the parietal-occipital area (POz: $t(13)=-4.32$, $p<0.001$; PO3: $t(13)=-4.24$, $p<0.001$; PO4: $t(13)=-4.02$, $p<0.01$). The frontal P3 wave showed a different pattern. Self-judgment induced a more positive shift than font-judgment at the late time window of 500–1000 ms (Fz: $t(13)=3.27$, $p<0.01$; F3: $t(13)=3.14$, $p<0.01$; F4: $t(13)=5.01$, $p<0.001$).

Similarly, the P3 component elicited by other-judgment was of smaller amplitude and peaked later than that elicited by font-judgment at fronto-centro-parietal electrodes at 300–500 ms (FCz: $t(13)=-4.46$, $p<0.001$; FC3: $t(13)=-2.90$, $p<0.05$; FC4: $t(13)=-3.23$, $p<0.01$; Pz: $t(13)=-5.15$, $p<0.001$; P3: $t(13)=-4.72$, $p<0.001$; P4: $t(13)=-5.61$, $p<0.001$). However, other-judgment generated a positive shift relative to font-judgment at 500–800 ms at the frontal areas (Fz: $t(13)=2.86$, $p<0.05$; F3: $t(13)=2.70$, $p<0.05$; F4: $t(13)=4.85$, $p<0.001$).

Interestingly, relative to other-judgment, self-judgment elicited an enhanced P2 from 200 to 1000 ms over the right frontal area (F4: $t(13)=3.37$, $p<0.01$; F6: $t(13)=3.34$, $p<0.01$; F8: $t(13)=3.12$, $p<0.01$) and a late larger P3 over the fronto-central area at 500–700 ms (FCz:

$t(13)=2.69$, $p<0.05$; FC1: $t(13)=2.18$, $p<0.05$; FC2: $t(13)=3.17$, $p<0.01$).

Non-phase-locked neural activity

To examine whether there is any difference between each condition in the pre-stimulus time, we compared TF power of the baseline EEG (−200 to 0 ms) in the self/other/font conditions but did not find significant difference in the baseline TF power between any two conditions ($p>0.05$). Then we investigated the percentage of TF power changes associated with trait and font-judgment tasks in five consecutive time windows (T1: 0–200 ms; T2: 200–400 ms; T3: 400–600 ms; T4: 600–800 ms; T5: 800–1000 ms after stimulus onset) relative to baseline TF power (−200 to 0 ms) within each sub-band. Fig. 3 shows the time-frequency representation of each band ERD/ERS at the frontal/central/parietal electrodes related to self-, other-, and font-judgments. Fig. 4 showed the percentage changes of the theta/alpha1/alpha2/beta1/beta2/gamma neural activity involved in self-/other-/font-judgment tasks in the five time windows.

ERD/ERS related to self-judgment. Relative to the pre-stimulus baseline, self-judgment induced theta band ERS from 400 ms to 1000 ms at the frontal and central areas with the maximum amplitudes at 600–800 ms (FCz: 64.63%; FC2: 60.27%). In the alpha1 band, self-judgment yielded ERD at 200–800 ms over the posterior regions with the maximum amplitudes at 200–400 ms (P4: −35.55%; Pz: −31.56%) and ERS at 600–1000 ms at the central areas with the maximum amplitudes at 600–800 ms (FCz: 25.15%; FC2: 23.36%). Similarly, alpha2 band ERD was observed at 200–800 ms over the parietal and occipital regions with the maximum amplitudes at 200–400 ms in association with self-judgment (PO6: −38.7%; P6: −38.25%). Self-judgment induced widespread ERD with the maximum amplitudes at 200–400 ms in the beta1 band (PO6: −27.65%; PO8: −26.85%), at 200–400 ms in the beta2 band (C1: −21.17%; FC1: −20.58%), and at 600–800 ms in the gamma band (C4: −18.98%; CP4: −18.95%).

ERD/ERS related to other-judgment. Other-judgment induced theta ERS at 400–1000 ms at the central and parietal regions with the maximum amplitudes at 800–1000 ms (CP6: 81.13%; P8: 78.71%), alpha1 band ERD at 200–800 ms at the posterior region with the maximum amplitudes at 200–400 ms (P4: −32.47%; P6: −32.08%) and alpha2 band ERD at 400–600 ms (PO4: −40.11%; P6: −37.56%). Widespread ERD was observed at 200–600 ms over the central and posterior electrodes with the maximum amplitudes at 400–600 ms in beta1 band (PO4: −26.82%; PO8: −25.71%) and beta2 band (C6: −16.9%; C4: −19.67%). The maximum amplitudes of gamma band ERD was observed at 600–800 ms at the frontal and centro-parietal regions (AF7: −11.01%; F8: −11.12%) to other-judgment.

ERD/ERS related to font-judgment. The font-judgment induced widespread theta ERS over the fronto-central regions with the maximum amplitudes at 400–600 ms (FCz: 87.89%; FC2: 87.15%) and yielded alpha1 band ERS at the central regions with the maximum amplitudes at 400–600 ms (F1: 30.59%; Fz: 30.19%). Font-judgment also elicited centro-posterior ERD at 200–400 ms in the alpha1 band (P5: −23.55%; P6: −23.69%), at 200–400 ms in the alpha2 band (PO6: −39.38%; P6: −38.35%), at 200–400 ms in the beta1 band (PO6: −26.43%; PO8: −26.27%) and at 400–600 ms in the beta2 band (C4: −15.90%; C3: −15.85%). The maximum amplitudes of gamma ERD to font-judgment was observed at 600–800 ms at the frontal regions (AF7: −9.21%; F7: −9.66%).

Self- vs. font-judgment. Relative to font-judgment, self-judgment induced greater theta band ERD at 300–600 ms over the fronto-central and posterior regions (FCz: $t(13)=-4.65$, $p<0.001$; Cz: $t(13)=-5.08$, $p<0.001$; Pz: $t(13)=-3.51$, $p<0.01$) but greater ERS at 700–1000 ms over the

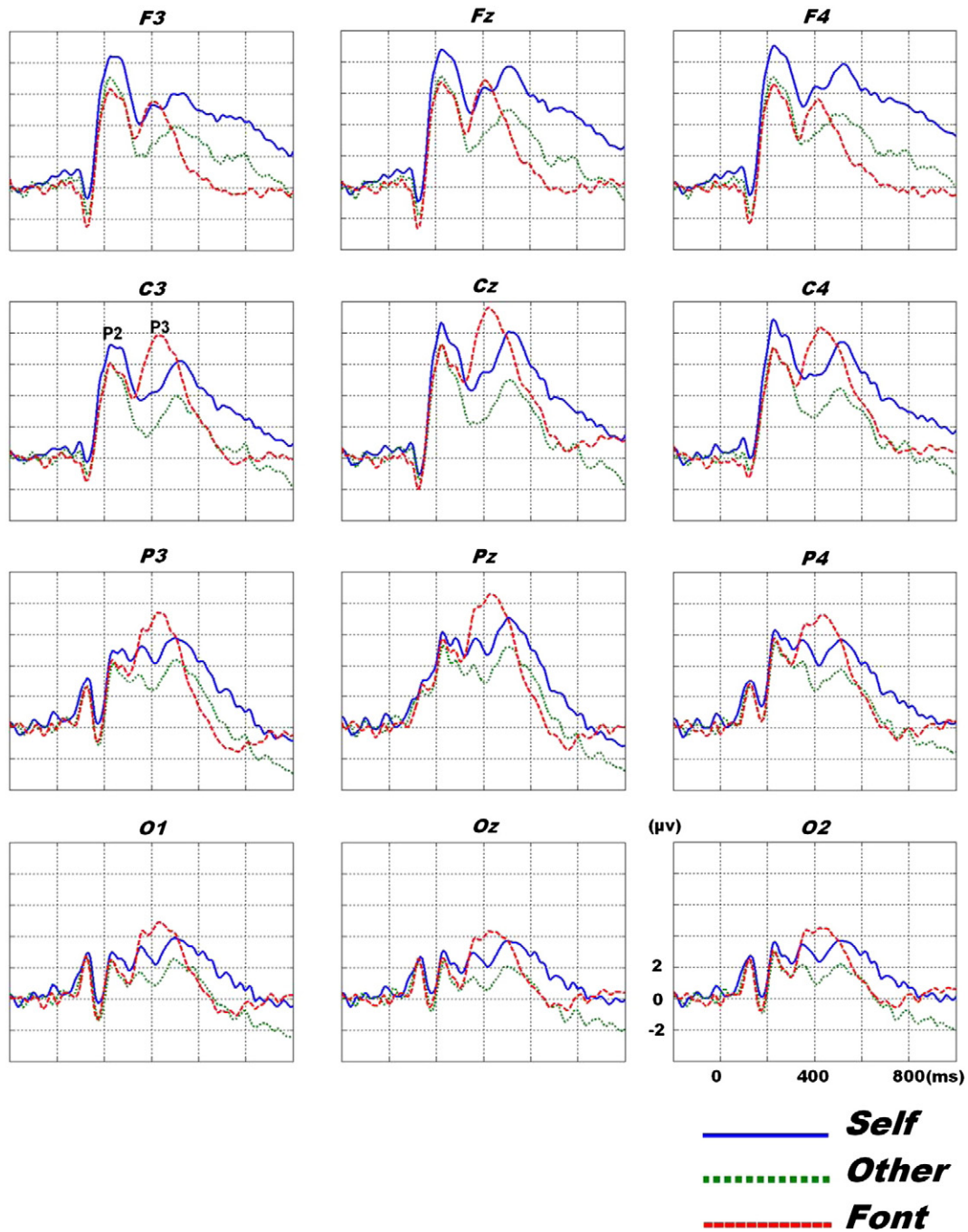


Fig. 2. Grand-average ERPs recorded at the frontal/central/parietal/occipital electrodes elicited by self-, other-, and font-judgments.

frontal and central areas (FCz: $t(13) = 3.98, p < 0.01$; FC3: $t(13) = 3.22, p < 0.01$; FC4: $t(13) = 2.55, p < 0.05$). Self-judgment also induced greater ERD in alpha1-band activity at 300–500 ms over the fronto-central areas (FCz: $t(13) = -3.71, p < 0.01$; FC3: $t(13) = -3.19, p < 0.01$; FC4: $t(13) = -2.73, p < 0.05$) and at 500–900 ms over the posterior region (POz: $t(13) = -3.13, p < 0.01$; PO3: $t(13) = -2.68, p < 0.02$; PO4: $t(13) = -3.24, p < 0.01$). Increased ERD in alpha2-band activity was also observed in association with self vs. font-judgment at 300–500 ms over the fronto-central areas (Fz: $t(13) = -2.92, p < 0.05$; FCz: $t(13) = -2.61, p < 0.05$; FC3: $t(13) = -3.43, p < 0.01$) and at 600–900 ms over the posterior region (POz: $t(13) = -2.53, p < 0.05$; PO3: $t(13) = -2.96, p < 0.01$; PO4: $t(13) = -2.47, p < 0.05$). Greater ERD associated with self-judgment, compared to font-judgment, was observed in beta1-band activity at 600–1000 ms over the fronto-central areas (FCz: $t(13) =$

$-3.10, p < 0.01$; FC3: $t(13) = -3.34, p < 0.01$; FC4: $t(13) = -2.72, p < 0.05$) and in gamma-band activity at 600–700 ms over the right posterior regions (PO4: $t(13) = -2.35, p < 0.05$; PO6: $t(13) = -2.51, p < 0.05$; PO8: $t(13) = -2.53, p < 0.05$).

Other- vs. font-judgment. Similarly, relative font-judgment, other-judgment induced greater theta band ERD at the 300–600 ms over the frontal, central and parietal regions (FCz: $t(13) = -5.42, p < 0.001$; Cz: $t(13) = -4.75, p < 0.001$; CPz: $t(13) = -3.74, p < 0.01$). Greater ERD associated with other-judgments was also observed in alpha1-band activity at 300–500 ms over the fronto-central areas (FCz: $t(13) = -4.53, p < 0.001$; FC3: $t(13) = -4.10, p < 0.01$; FC4: $t(13) = -3.31, p < 0.01$), at 400–600 ms over the left fronto-centro-temporal regions (FC5: $t(13) = -3.56, p < 0.01$; F7: $t(13) =$

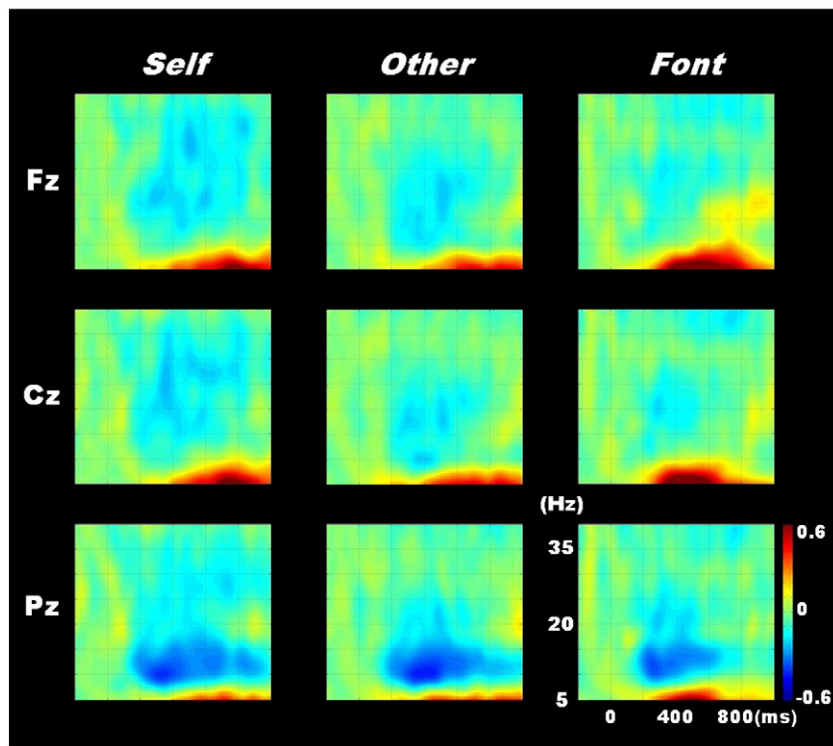


Fig. 3. The time–frequency representation of each band ERD/ERS at the frontal/central/parietal electrodes related to self-, other-, and font-judgments.

–3.29, $p < 0.01$; FT7: $t(13) = -3.19$, $p < 0.01$), and at 500–700 ms over the occipital region (Oz: $t(13) = -3.11$, $p < 0.01$; O1: $t(13) = -2.32$, $p < 0.05$; O2: $t(13) = -2.48$, $p < 0.05$). Alpha2-band activity also showed greater ERD associated with other-judgments at 300–500 ms over the frontal electrodes (Fz: $t(13) = -3.08$, $p < 0.01$; F1: $t(13) = -2.78$, $p < 0.01$; F2: $t(13) = -3.02$, $p < 0.01$). The beta2-band activity showed larger ERD related to other-judgment at 500–600 ms over the fronto-central regions (FCz: $t(13) = -2.27$, $p < 0.05$; FC5: $t(13) = -2.24$, $p < 0.05$; FC6: $t(13) = -2.44$, $p < 0.05$) and at 600–700 ms over the right parietal region (P2: $t(13) = -2.22$, $p < 0.05$; P4: $t(13) = -2.17$, $p < 0.05$; P6: $t(13) = -2.57$, $p < 0.05$).

Self- vs. other-judgment. As can be seen in Fig. 5, relative to other-judgment, self-judgment induced greater theta band ERD at 300–400 ms over the right parieto-occipital region (P4: $t(13) = -3.06$, $p < 0.01$; P6: $t(13) = -3.32$, $p < 0.01$; P8: $t(13) = -3.31$, $p < 0.01$) but produced larger theta band ERS at 700–800 ms over the left fronto-central region (F3: $t(13) = 2.46$, $p < 0.05$; FC3: $t(13) = 2.50$, $p < 0.05$; C3: $t(13) = 2.53$, $p < 0.05$). Similarly, self-judgment resulted in enhanced alpha1 band ERS at 400–600 ms over the central regions relative to other-judgment (Cz: $t(13) = 3.32$, $p < 0.01$; C1: $t(13) = 2.70$, $p < 0.05$; C2: $t(13) = 3.03$, $p < 0.01$). Beta2 band showed greater ERD in association with self- vs. other-judgment at 700–800 ms over the right centro-parietal areas (CP5: $t(13) = -2.91$, $p < 0.05$; P5: $t(13) = -2.53$, $p < 0.05$; PO5: $t(13) = -2.18$, $p < 0.05$). Enhanced ERD was also observed in gamma-band activity linked to self- compared to other-judgment at 500–600 ms over the fronto-central and the left parieto-occipital electrodes (FCz: $t(13) = -2.36$, $p < 0.05$; Fz: $t(13) = -2.25$, $p < 0.01$; P3: $t(13) = -2.96$, $p < 0.05$; PO3: $t(13) = -2.65$, $p < 0.05$).

Interaction of Task \times Valence. To assess if neural oscillations engaged in the processes of trait judgment task are modulated by the valence of trait words, we conducted the ANOVA with Task (self- vs. other-judgments) and Valence (positive vs. negative traits) as independent variables. The main effect of Valence was not significant at any

frequency band activity ($p > 0.05$). However, there was a significant interaction of Task \times Valence at theta-band activity at 700–800 ms over bilateral frontal areas (F3: $F(1,13) = 5.68$, $p < 0.05$; F4: $F(1,13) = 4.94$, $p < 0.05$; AF3: $F(1,13) = 9.25$, $p < 0.01$; AF4: $F(1,13) = 8.47$, $p < 0.05$), suggesting that, relative to positive traits, negative traits elicited increased theta band TF power in self-judgment whereas a reverse pattern was observed for other-judgment (see Fig. 6). Post-hoc analyses confirmed the significant valence effect for self-judgment (AF3: $t(13) = -2.222$, $p < 0.05$; F4: $t(13) = -2.225$, $p < 0.05$; AF4: $t(13) = -2.959$, $p < 0.05$) but not for other-judgment ($ps > 0.05$). There was also a significant interaction of Task \times Valence at alpha2-band activity at 300–600 ms over the parietal region (Pz: $F(1,13) = 5.48$, $p < 0.05$; P1: $F(1,13) = 5.36$, $p < 0.05$; P2: $F(1,13) = 6.21$, $p < 0.05$), suggesting that the negative traits induced increased alpha2 band ERS relative to positive traits during self-judgment whereas a reverse pattern was present for other-judgment. However, post-hoc analyses did not reveal significant valence effect for both self- and other-judgments ($ps > 0.05$).

Interaction of Task \times Relevance. The ANOVA with Task (self- vs. other-judgments) and Relevance ('yes' vs. 'no' response) as independent variables showed a significant main effects of Relevance at theta-band activity at 300–600 ms and 800–1000 ms over the fronto-central area (Cz: $F(1,13) = 17.54$, $p < 0.01$; FCz: $F(1,13) = 24.80$, $p < 0.001$; Fz: $F(1,13) = 22.46$, $p < 0.001$), suggesting that trait words followed by 'yes' response induced more theta ERS than trait words followed by 'no' response. Gamma-band activity also showed significant main effect of Relevance at 700–800 ms over the central-parietal area (Cz: $F(1,13) = 5.22$, $p < 0.05$; CPz: $F(1,13) = 5.93$, $p < 0.05$; Pz: $F(1,13) = 11.70$, $p < 0.01$), suggesting that trait words followed by 'yes' response induced less gamma ERS compared to trait words followed by 'no' response.

Interestingly, significant interactions of Task \times Relevance were found in beta2-band activity at 800–900 ms over the left fronto-central areas (FCz: $F(1,13) = 8.53$, $p < 0.05$; Fz: $F(1,13) = 5.15$, $p < 0.05$; FC3: $F(1,13) = 4.85$, $p < 0.05$; F3: $F(1,13) = 8.05$, $p < 0.05$), as trait

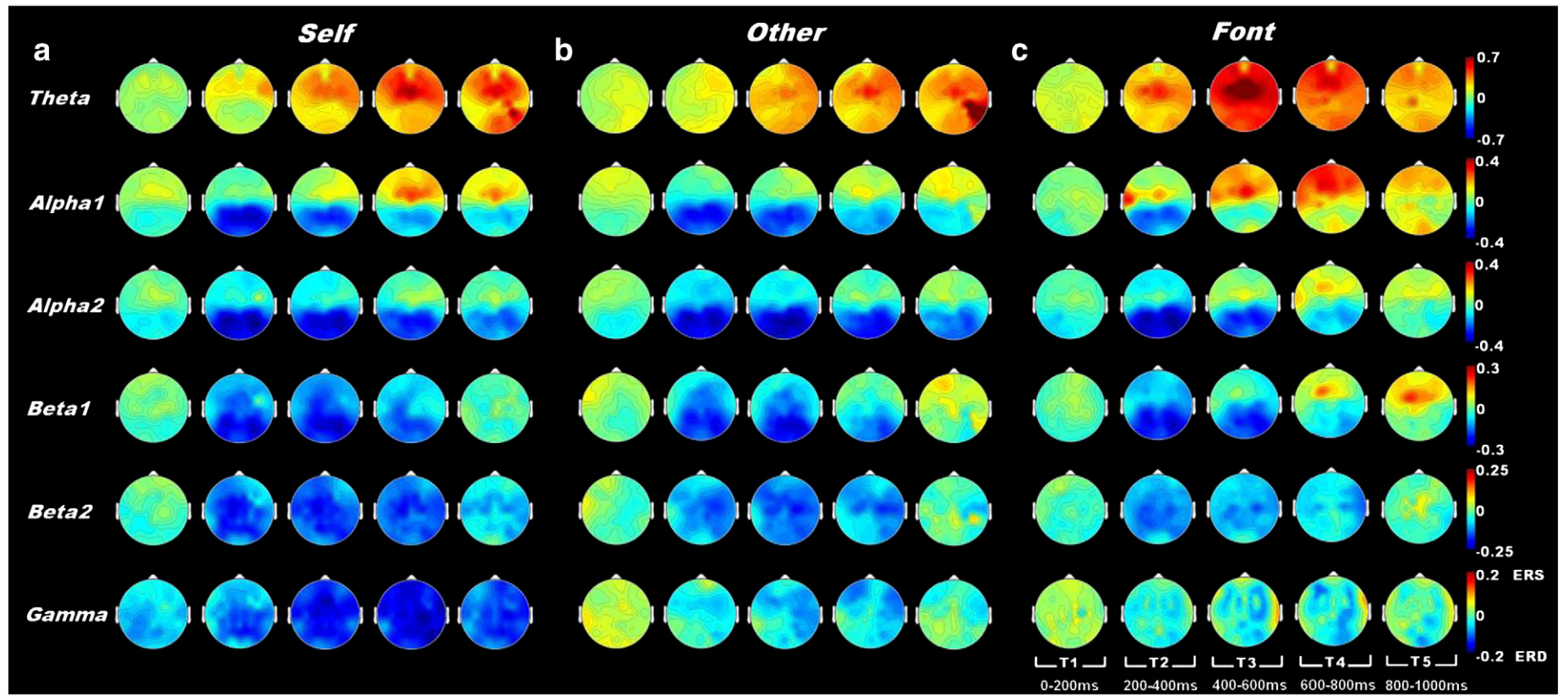


Fig. 4. Topographies of theta, alpha, beta, and gamma band ERD/ERS in each condition. a) The topographies of ERD/ERS related to self-judgment; b) the topographies of ERD/ERS related to other-judgment; c) the topographies of ERD/ERS related to font-judgment. ERD/ERS was calculated relative to a baseline of -200 to 0 ms. Topographies were plotted in 5 time windows of 200 ms.

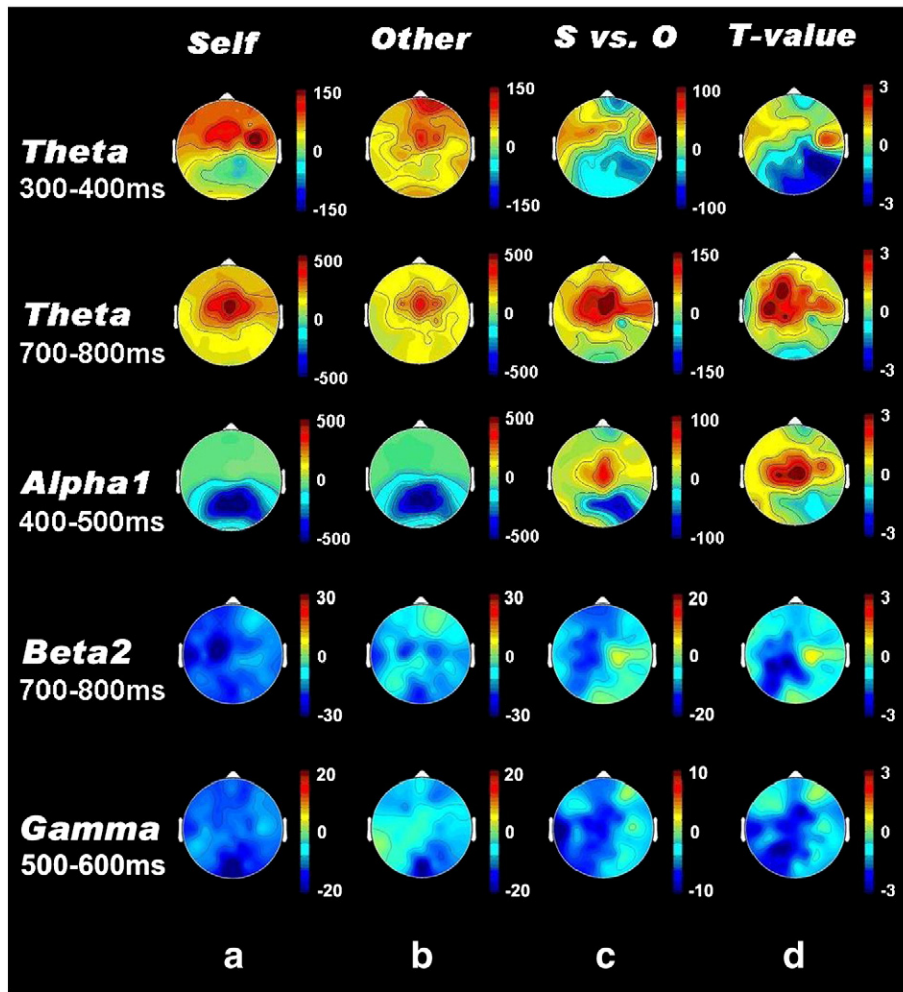


Fig. 5. a) Topographies of TF power related to self-judgment; b) topographies of TF power related to other-judgment; c) topographies of differential TF power between self- and other-judgments; d) topographies of the t-values differentiating self and other encoding.

words judged as relevant to the self induced more ERS than trait words judged as irrelevant whereas a reverse pattern was true for other-judgment (Fig. 7). Similarly, there was a significant interaction of Task × Relevance at gamma-band activity at 200–300 ms over the right parietal region (Pz: $F(1,13) = 5.13, p < 0.05$; POz: $F(1,13) = 6.28, p < 0.05$; P4: $F(1,13) = 9.10, p < 0.01$; PO4: $F(1,13) = 7.21, p < 0.05$), suggesting that the self-relevant words induced greater ERS than irrelevant ones, whereas the other-judgment exhibited a reverse pattern for relevant words and irrelevant ones.

Correlations

To investigate whether the difference of neural oscillations between self- and other-judgment was associated with individual differences in memory advantage of self-related traits, we conducted correlation analyses between the differential TF power defined by the contrast of self- and other-judgment at the significant electrodes and the self-referential effect defined by the differential recognition scores (self- vs. other-judgment). We found that the differential theta-band activity at

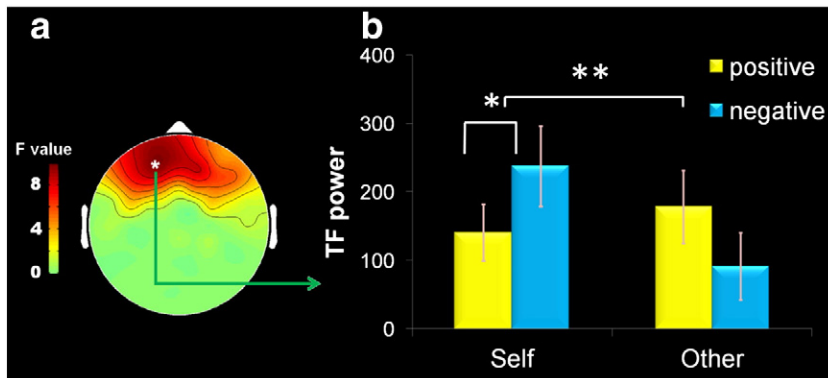


Fig. 6. a) The topographies of F-value of the interaction of Valence × Task; b) the histograms show the theta band power values (700–800 ms) associated with each stimulus condition at AF3.

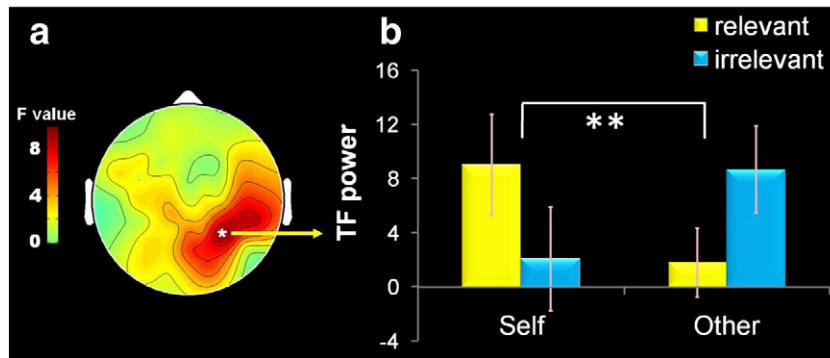


Fig. 7. a) The topographies of F-value of the interaction of Relevance×Task; b) the histograms show the gamma band power values (200–300 ms) associated with each stimulus condition at P4.

700–800 ms over the left fronto-central area positively correlated with the differential recognition scores across subjects (FC3: $r=0.617$, $p<0.02$; FC1: $r=0.624$, $p<0.02$; F1: $r=0.570$, $p<0.05$, Fig. 8), suggesting that the greater the differential theta-band activity, the larger the self-referential effect.

Discussion

RTs did not differ between self- and other-judgment tasks, possibly due to that the instructions in our experiment did not emphasize response speed. However, RTs to self-judgments differentiate between ‘yes’ and ‘no’ responses, suggesting that behavioral performances were sensitive to self-relevant and self-irrelevant trait words during the judgment task. In consistent with the better

memory of self-related compared to other-related trait words, self-judgments enhanced the fronto-central P2 and P3 relative to other- and font-judgments, consistent with previous observations (Magno and Allan, 2007). While the ERP results indicate that phase-locked neural activities are engaged in differentiating between self- and other-judgments, the present study provide evidence that non-phase-locked neural oscillations in multiple frequency bands and time windows are involved in self-referential processing.

Basically, relative to font-judgments, both self and other trait judgments induced ERD in multiple frequency bands, suggesting reduced synchronous non-phase-locked oscillations during enhanced semantic processing of trait words during trait judgment tasks. Moreover, neural oscillations in multiple frequency bands differentiated between trait judgments of the self and others and the magnitudes of non-phase-locked neural activity predict the degree of the self-reference effect across individuals. In addition, the cognitive and emotional aspects of self-judgments are mediated by non-phase-locked neural oscillations in different frequencies and time windows.

Theta oscillations related to self-referential processing

It has been well documented that the self is a well-developed and most often-used construct that promotes elaboration and organization of information during memory encoding (Symons and Johnson, 1997). While our results of the memory test indicate enhanced elaboration of self-related information during trait judgments, our EEG data suggested differential encoding of information related to the self and others during trait judgments. Self-judgments induced more theta band ERS at 700–800 ms over the left fronto-central regions relative to other-judgment. Modulations of theta band oscillations have been associated with general processing demands of the working memory system during language comprehension task (Röhm et al., 2001) and with the encoding of new information (e.g., Klimesch, et al., 1996) and retrieval of episodic information from long-term memory (Klimesch, 1999a). Theta-band activity is also correlated with memory performance (e.g. Doppelmayr et al., 1998; Doppelmayr et al., 2000) and modulated by memory load (e.g. Jensen and Tesche, 2002; Klimesch et al., 1999). Klimesch et al. (1996) compared theta-band activity changes linked to words which were remembered or failed to be recalled during retrieval and found that successfully retrieved words engaged larger extent theta band synchronization during encoding. These findings indicate that theta band ERS is related to working memory that is involved in encoding different new items. Thus the left frontal theta band ERS observed in our study possibly reflected engagement of more working memory resources and enhanced processing of semantic meaning of items in association with the self compared to others.

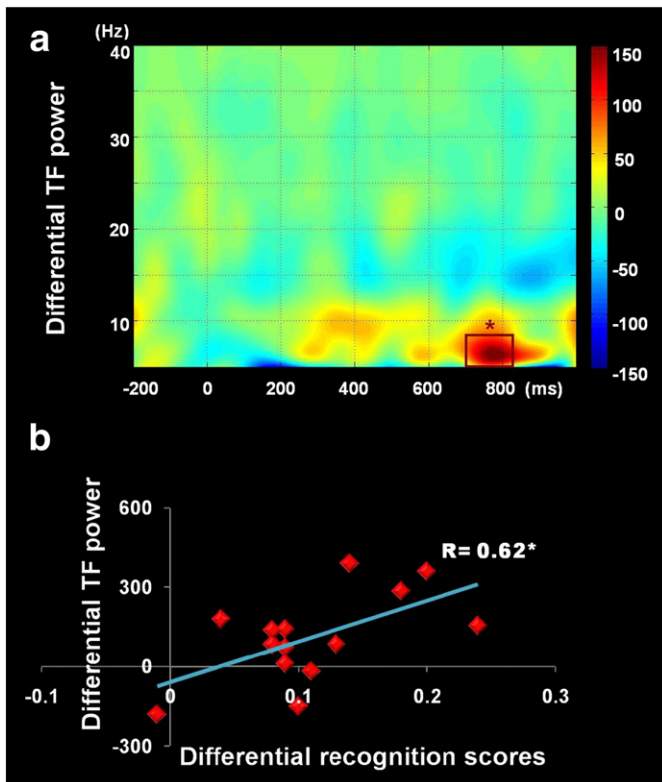


Fig. 8. a) The time–frequency representation of the differential power between self- and other-judgments at FC3; b) differential recognition scores (self vs. other) correlated positively with differential left frontal theta-band activity at FC3.

Previous studies suggest that the frontal theta rhythm can be localized in the anterior cingulate or the medial frontal cortex (Asada et al., 1999; Gevins et al., 1997; Ishii et al., 1999; Onton et al., 2005). Recently, Scheeringa et al. (2008) recorded EEG and fMRI simultaneously and observed significant negative correlations between medial frontal activity and theta oscillations during a resting condition, suggesting that theta activity can be seen as an EEG index of default mode network activity. The modulation of the theta-band activity by the self-referential task observed in our research is consistent with the previous fMRI studies that showed increased activations in the MPFC associated with self-trait judgment (Kelley et al., 2002; Fossati et al., 2003; Zysset et al., 2002; Macrae et al., 2004; Zhu et al., 2007; Han et al., 2008). Thus it may be speculated that the left frontal theta band ERS associated with the encoding of self items in our EEG study may arise from the medial frontal cortex, though this needs to be confirmed in future research.

Alpha oscillations related to self-referential processing

Alpha band oscillations are linked to a variety of high level cognitive tasks such as semantic processing (Klimesch, 1999a; Klimesch et al., 2007), anticipation and processing of affective stimuli (Aftanas et al., 1996; Aftanas et al., 2002), understanding and sharing others' emotion (Mu et al., 2008), and risk perception and evaluation (Qin et al., 2009). Klimesch et al. (2007) proposed that alpha band ERS reflects a state of inhibition which helps to establish a highly selective activation pattern, whereas alpha ERD reflects general attention demand and active cognitive processing.

In the present study self-judgments induced increased alpha synchronization relative to other-judgment at 400–600 ms over the fronto-central areas. Several results support the idea that the alpha band ERS arose from an inner-directed attention demand induced by self-referential processing. First, both self and other trait judgments gave rise to more alpha band ERD relative to font-judgment that engaged semantic processing to a minimum degree. Unlike alpha ERS related to self-referential processing, the alpha band ERD reflected general enhanced task demand of semantic processing involved in trait judgments. Second, the alpha ERS related to self-trait judgments occurred in the low alpha band but not in the high alpha band that is, however, involved in semantic-specific encoding (Klimesch, 1999a). Third, internally directed attention such as mental arithmetic and mental imagery is association with alpha band ERS and reflects an active inhibition necessary for internally driven mental operations (Cooper et al., 2003; Orekhova et al., 2001). Given the functional roles of alpha band ERS, we suggest that alpha ERS related to self-referential processing observed in the current study reflected an inhibition of external attention and increased internally directed attention during self-trait judgment.

High-frequency oscillations related to self-referential processing

Our results showed that the fast frequency band, including beta2 and gamma, exhibited similar late ERD in association with self-judgments. Gamma band oscillations have been assigned with various functions such as attention (Gruber et al., 1999; Müller et al., 2000; Herrmann and Knight, 2001), sensory memory (Haenschel et al., 2000), recollection and the process of familiarity (Burgess and Ali, 2002). Herrmann et al. (2004) propose a framework that relates gamma oscillations to two underlying memory processes, i.e., the comparison of memory contents with stimulus-related information and the utilization of signals derived from this comparison. This memory match-and-utilization model attempts to explain the early gamma band responses in terms of the match between bottom-up and top-down information.

Gamma band oscillations observed in our work can be interpreted by the match processing between trait words shown during the

judgment tasks and the information stored in memory. The suppression of gamma oscillations related to self may reflect less effort for the matching process relative to other-judgments. This is consistent with the idea that self-trait judgment is realized by searching for self-related information from semantic knowledge whereas trait judgment of others is accomplished by searching evidence from episodic memory (Klein et al., 2002). In addition, self-trait judgment may also induce enhanced selective and task-driven attention and resulted in modulation of gamma band oscillations during self-trait judgment. Klimesch et al. (2007) reviewed the functional roles of alpha band and proposed a possibility that phase coupling between alpha and gamma reflects the early top-down influence of alpha on perceptual processes. The gamma ERD in associated with self condition is possibly an extended phenomenon of alpha ERS, suggesting a top-down control for more internally driven attention.

The relationship between neural oscillations during encoding and behavioral performances during retrieval

The present study also examined whether neural oscillations that differentiate between self and other-referential processing at the encoding stage can predict individual performances of retrieval of trait words during the memory test. Only one fMRI study reported that the MPFC activity during encoding can discriminate remembered and forgotten trait words related to the self (Macrae et al., 2004). However, the contrast between remembered and forgotten self-related items uncovered the neural activity involved in encoding processing of traits that led to good and bad performances during self-related memory retrieval but did not reveal the neural activity that affects the magnitude of the self-reference effect. We examined this by assessing the correlation between differential neural oscillations involved in self and other trait judgments and differential memory scores of recollecting words related to the self and others. We found a positive correlation between differential theta-band activity at 700–800 ms over the left fronto-central and differences in recognition scores across subjects. Theta and alpha band activities have been related to individual differences of cognitive performance and can differentiate good and bad performers when performing different cognitive tasks such as visual discrimination (Hanslmayr et al., 2005) and memory (Klimesch et al., 1997; 2000; 2004). Our results suggest that, relative to other-reference encoding, the greater theta ERS induced by items referenced to self exhibited during encoding stage, the better subjects remembered self-related trait words, suggesting that theta band oscillations involved in encoding self-related items influence individual differences in recognition performance.

Low-frequency band and the affective self

Previous fMRI studies have shown that emotional valence of trait words interacts with self-related trait evaluation (Fossati et al., 2003; Fossati et al., 2004; Moran et al., 2006). Such interaction is also evident in phase-locked neural activity as ERPs to self-trait judgment over the fronto-central areas are modulated by emotional valence of trait words (Watson et al., 2007). Our results reinforced previous findings by showing that non-phase locked neural oscillations also engaged in differentiation between positive and negative trait words during self-trait judgment but not during other trait judgment. Specifically, self-related negative trait words induced greater theta band ERS over the frontal area compared to positive trait words. As frontal theta band ERS is a marker of the amount of mental effort (Sauseng et al., 2007), it may be proposed that the processing of negative traits related to the self causes more cognitive effort than that of positive traits. When judging negative trait words, subjects may have to inhibit their emotional responses in order to maintain their positive self mode and to avoid the influence of negative feelings. Similarly, the posterior

alpha2 band showed evidence of modulations of self-referential processing by valence of trait words. Taken together, the EEG results suggest distinct neural oscillations in mediating emotional responses during self- and other-related encoding. We proposed that the self-specific frontal theta activity engages in integrations of cognitive evaluation and emotional responses during self-referential encoding. This analysis is consistent with converging EEG evidence that emotion processing modulates theta and alpha band oscillations. Theta oscillations are related to affective valence discrimination of visual displays (Aftanas et al., 2001b; Aftanas et al., 2003a, 2003b; Krause et al., 2000) and engaged in empathic responses to perceived pain in others (Mu et al., 2008). In addition, alpha rhythm oscillations are associated with processing of affective pictures (Aftanas et al., 2001a; Aftanas et al., 2002), recognition of emotional face expression (Güntekin and Başar, 2007) and perception of others in painful situations (Mu et al., 2008).

High-frequency band and self relatedness

It has been suggested that the relevant and affective components of self-referential processing engage distinct neural network as the MPFC activation is modulated by self-relevance of trait words whereas the valence of items is resolved in an adjacent area of ventral anterior cingulate (Moran et al., 2006). Our EEG results provide further evidence for the dissociation between the relevant and affective components of self-referential processing. While the low-frequency theta and alpha band activities were involved in differentiation of negative and positive traits referenced to the self, the high-frequency beta and gamma band oscillations were engaged in dissociation of self and other trait judgments in terms of relevance of traits to the target person. Interestingly, self-relevant items generated ERS in beta and gamma-band activity compared to self-irrelevant items whereas a reverse pattern was observed for other relevant and irrelevant items. The differential pattern of encoding of relevance occurred as early as 200 ms after stimulus onset. According to Klein et al. (2002), a key component of self-referential processing is to match the input stimulus with semantic knowledge about the self. Herrmann et al. (2004) proposed that high-frequency neural oscillations such as gamma-band activity mediate the comparison of memory contents with stimulus-related information and the utilization of signals derived from this comparison. Therefore, it is possible that the gamma band ERS underlies the match of semantic meaning of trait words with the semantic knowledge about the self. In addition, such process may occur as early as 200 ms after stimulus presentation. In contrast, trait judgments of others are accomplished by comparing semantic meaning of trait words with episodes (Klein et al., 2002), resulting reduced gamma-band activity related to items relevant to the familiar other.

Conclusion

Our EEG results provide the first piece of evidence for the link between non-phase-locked neural oscillations and self-referential processing. Our results indicated that multi-band neural oscillations contribute to the self-referential processing during the trait judgment task. Both low (theta and alpha) and high (beta and gamma) band oscillations were involved in encoding self-related information. In addition, there was a positive correlation between the frontal theta power and self recognition scores. Thus theta band neural oscillations may bridge the gap between encoding and retrieval of self-related information. Finally, our EEG results showed evidence for dissociation of cognitive and affective components of self-referential processing in low and high band neural oscillations, suggesting different functional significance of non-phase-locked neural oscillations in self reflective thoughts.

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