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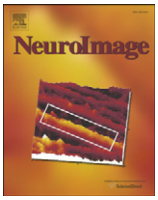

Neural oscillations involved in self-referential processing

Yan Mu, Shihui Han *

Department of Psychology, Peking University, 5 Yiheyuan Road, Beijing 100871, P.R. China

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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– 00 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– 00 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.

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. (200) 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. (200) 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. (200) 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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* Corresponding author. Fax: +8 10 27 1081.
E-mail address: shan@pku.edu.cn (S. Han).

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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– 00 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., 199) 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).

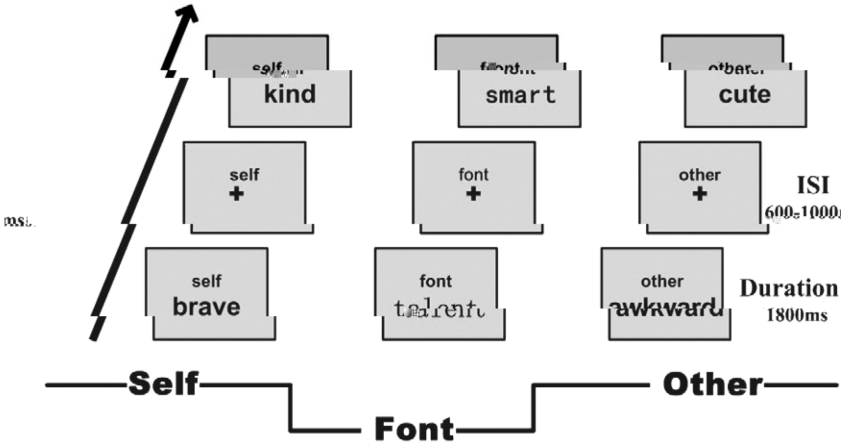

Fig. 1. Illustration of the stimuli and procedure of self-, other- and font-judgments used in the current study. Both the cue and stimuli words were in Chinese.

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 ±50 μV at any electrode and trails 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: 8/70/ 8, $F(2,2\ )=0.\ 13, p>0.5$).

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 trails 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 σ_t) and frequency (SD σ_f) domains around its central frequency f_0:

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

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: $\left(\sigma_t\sqrt{\pi}\right)^{-1/2}$. 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. 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, $t(13)=10.8\ \ , p<0.0001$; 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 ($F(2,2\ )=72.0\ 2, p<0.0001$). However, both the main effect of valence ($F(1,13)=0.020, p>0.05$) and the interaction of Task×Valence were not significant ($F(2,2\ )=1.854, p>0.05$), 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 × 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 (85 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 ($F(2,2\ \ )=95.9\ 3$, $p<0.001$), as the recognition scores were higher for judgments associated with deep semantic processing (self- and other-judgments: 47.0% and 3 .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 ($t(13)=\ .331$, $p<0.001$), 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: $t(13)=-3.\ 7$, $p<0.01$; 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)=-4.4\ $, $p<0.001$; 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: $t(13)=-5.\ 1$, $p<0.001$). However, other-judgment generated a positive shift relative to font-judgment at 500–800 ms at the frontal areas (Fz: $t(13)=2.8\ $, $p<0.05$; 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: $t(13)=3.37$, $p<0.01$; F : $t(13)=3.34$, $p<0.01$; F8: $t(13)=3.12$, $p<0.01$) and a late larger P3 over the fronto-central area at 500–700 ms (FCz: $t(13)=2.\ 9$, $p<0.05$; 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– 00 ms; T4: 00–800 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 00–800 ms (FCz: 4. 3%; FC2: 0.27%). 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: −31.5 %) and ERS at 00–1000 ms at the central areas with the maximum amplitudes at 00–800 ms (FCz: 25.15%; FC2: 23.3 %). 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 (PO : −38.7%; P : −38.25%). Self-judgment induced widespread ERD with the maximum amplitudes at 200–400 ms in the beta1band (PO : −27. 5; PO8: −2 .85%), at 200–400 ms in the beta2 band (C1: −21.17%; FC1: −20.58%), and at 00–800 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 (CP : 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%; P : −32.08%) and alpha2 band ERD at 400– 00 ms (PO4: −40.11%; P : −37.5 %). Widespread ERD was observed at 200– 00 ms over the central and posterior electrodes with the maximum amplitudes at 400– 00 ms in beta1 band (PO4: −2 .82%; PO8: −25.71%) and beta2 band (C : −1 .9%; C4: −19. 7%). The maximum amplitudes of gamma band ERD was observed at 00–800 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– 00 ms (FCz: 87.89%; FC2: 87.15%) and yielded alpha1 band ERS at the central regions with the maximum amplitudes at 400– 00 ms (F1: 30.59%; Fz: 30.19%). Font-judgment also elicited centro-posterior ERD at 200–400 ms in the alpha1band (P5: −23.55%; P : −23. 9%), at 200–400 ms in the alpha2 band (PO : −39.38%; P : −38.35%), at 200–400 ms in the beta1band (PO : −2 .43%; PO8: −2 .27%) and at 400– 00 ms in the beta2 band (C4: −15.90%; C3: −15.85%). The maximum amplitudes of gamma ERD to font-judgment was observed at 00–800 ms at the frontal regions (AF7: −9.21%; F7: −9. %).

Self- vs. font-judgment. Relative to font-judgment, self-judgment induced greater theta band ERD at 300– 00 ms over the fronto-central and posterior regions (FCz: $t(13)=-4.\ 5$, $p<0.001$; 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

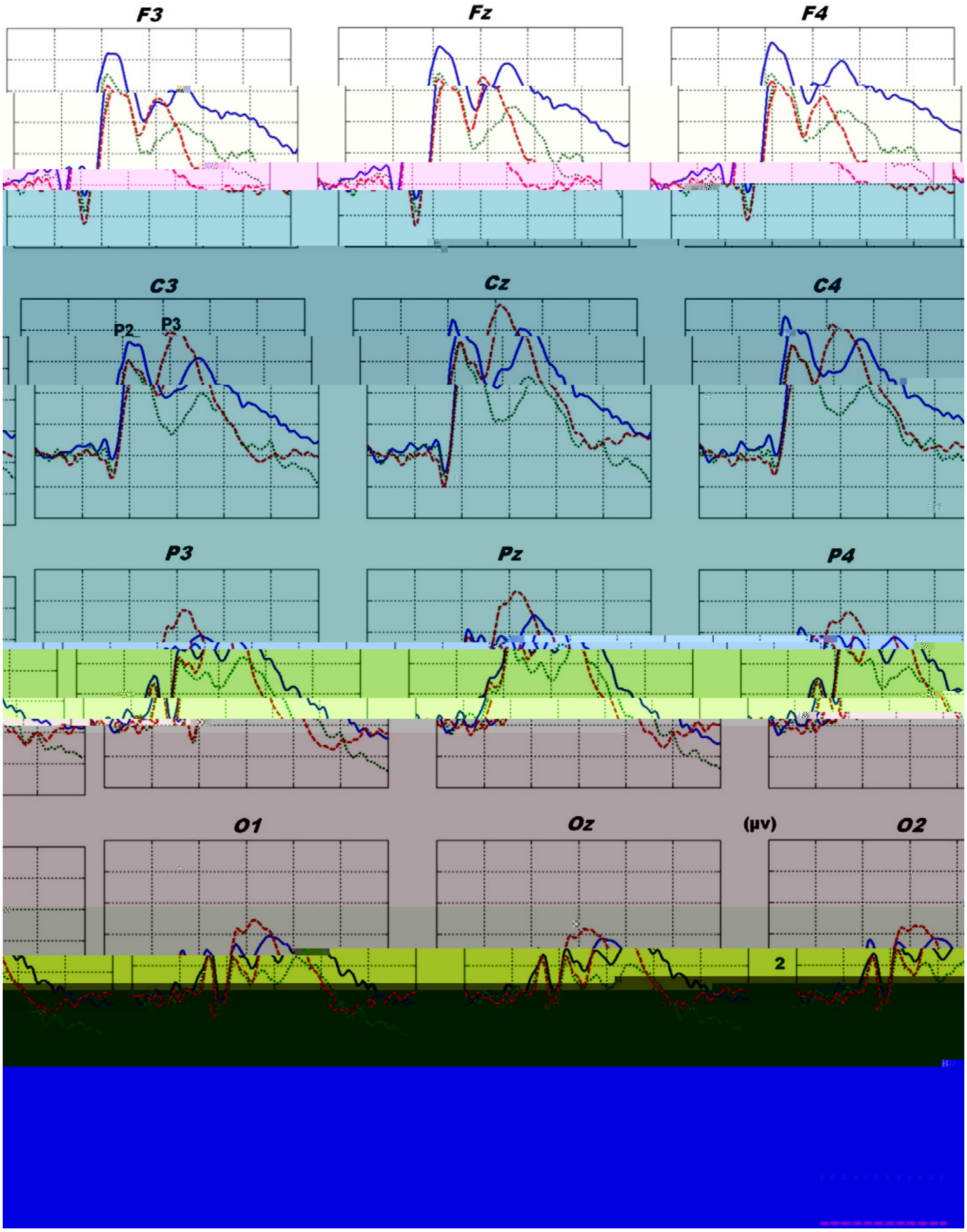

Fig. 2. Grand-average ERPs recorded at the frontal/central/parietal/occipital electrodes elicited by self-, other-, and font-judgments.

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: $t(13)=-2.\ 8$, $p<0.02$; 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: $t(13)=-2.\ 1$, $p<0.05$; FC3: $t(13)=-3.43$, $p<0.01$) and at 00–900 ms over the posterior region (POz: $t(13)=-2.53$, $p<0.05$; PO3: $t(13)=-2.9\ $, $p<0.01$; 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 00–1000 ms over the frxontal–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 00–700 ms over the right posterior regions (PO4: $t(13)=-2.35$, $p<0.05$; PO : $t(13)=-2.51$, $p<0.05$; 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– 00 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– 00 ms over the left fronto-centro-temporal regions (FC5: $t(13)=-3.5\ $, $p<0.01$; F7: $t(13)=$

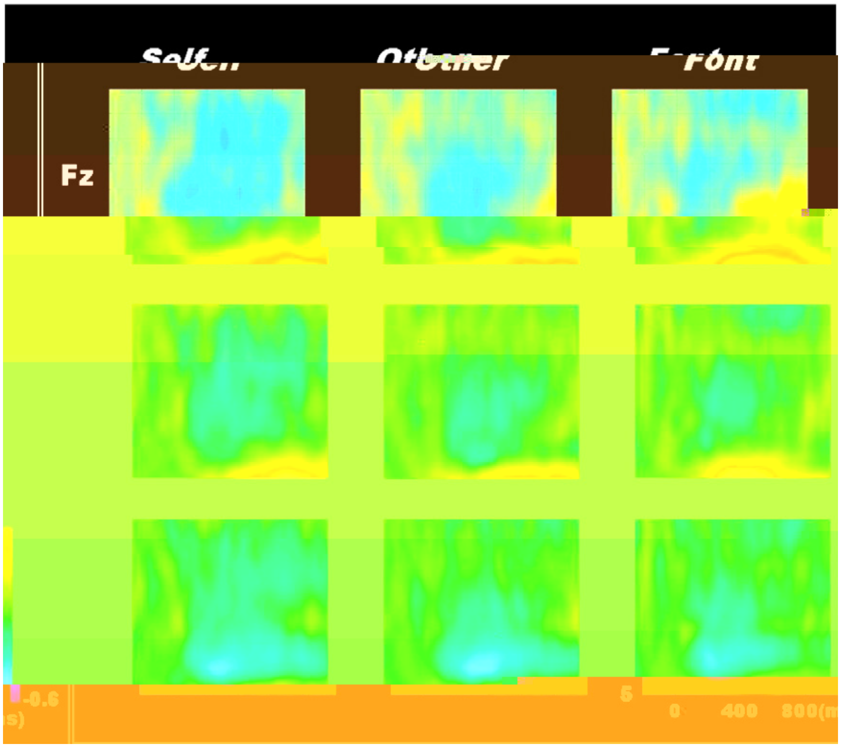

Fig. 3. The time–frequency representation of each band ERD/ERS at the frontal/central/parietal electrodes related to self-, other-, and font-judgments.

-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– 00 ms over the fronto-central regions (FCz: $t(13)=-2.27$, $p<0.05$; FC5: $t(13)=-2.24$, $p<0.05$; FC : $t(13)=-2.44$, $p<0.05$) and at 00–700 ms over the right parietal region (P2: $t(13)=-2.22$, $p<0.05$; P4: $t(13)=-2.17$, $p<0.05$; P : $t(13)=-2.57$, $p<0.05$).

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: $t(13)=-3.0$, $p<0.01$; P : $t(13)=-3.32$, $p<0.01$; 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: $t(13)=2.4$, $p<0.05$; 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– 00 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– 00 ms over the fronto-central and the left parieto-occipital electrodes (FCz: $t(13)=-2.3$, $p<0.05$; Fz: $t(13)=-2.25$, $p<0.01$; P3: $t(13)=-2.9$, $p<0.05$; PO3: $t(13)=-2.$ 5, $p<0.05$).

Interaction of Task × 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 × Valence at theta-band activity at 700–800 ms over bilateral frontal areas (F3: $F(1,13)=5.$ 8, $p<0.05$; 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.). 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 × Valence at alpha2-band activity at 300– 00 ms over the parietal region (Pz: $F(1,13)=5.48$, $p<0.05$; P1: $F(1,13)=5.3$, $p<0.05$; P2: $F(1,13)=$ .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 × 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– 00 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: $F(1,13)=22.4$, $p<0.001$), 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 × 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

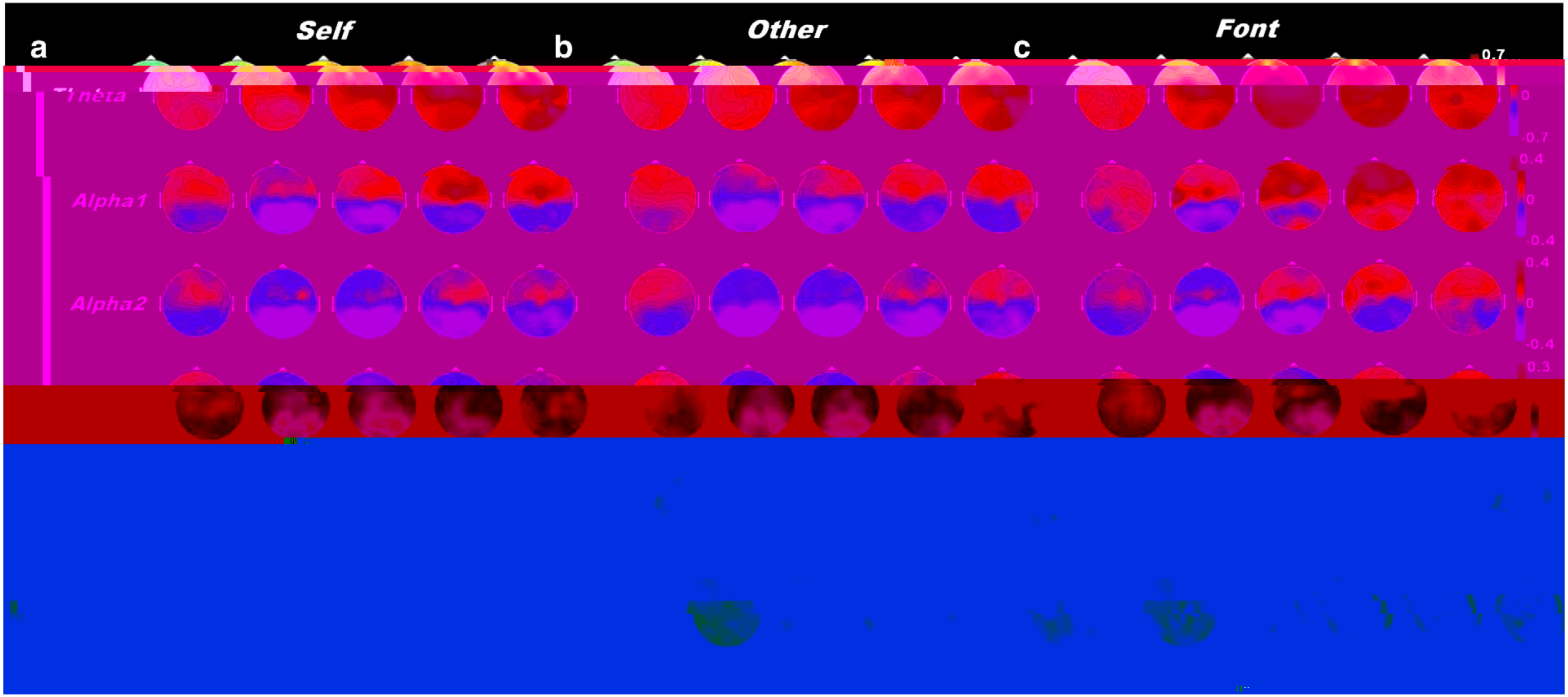

Fig. 4. Topographies of theta, alpha, beta, and gamma band ERD/ERS in each condition. a) The topographies of ERD/ERS related to self-judgment; b) the topographies of ERD/ERS related to other-judgment; c) the topographies of ERD/ERS related to font-judgment. ERD/ERS was calculated relative to a baseline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

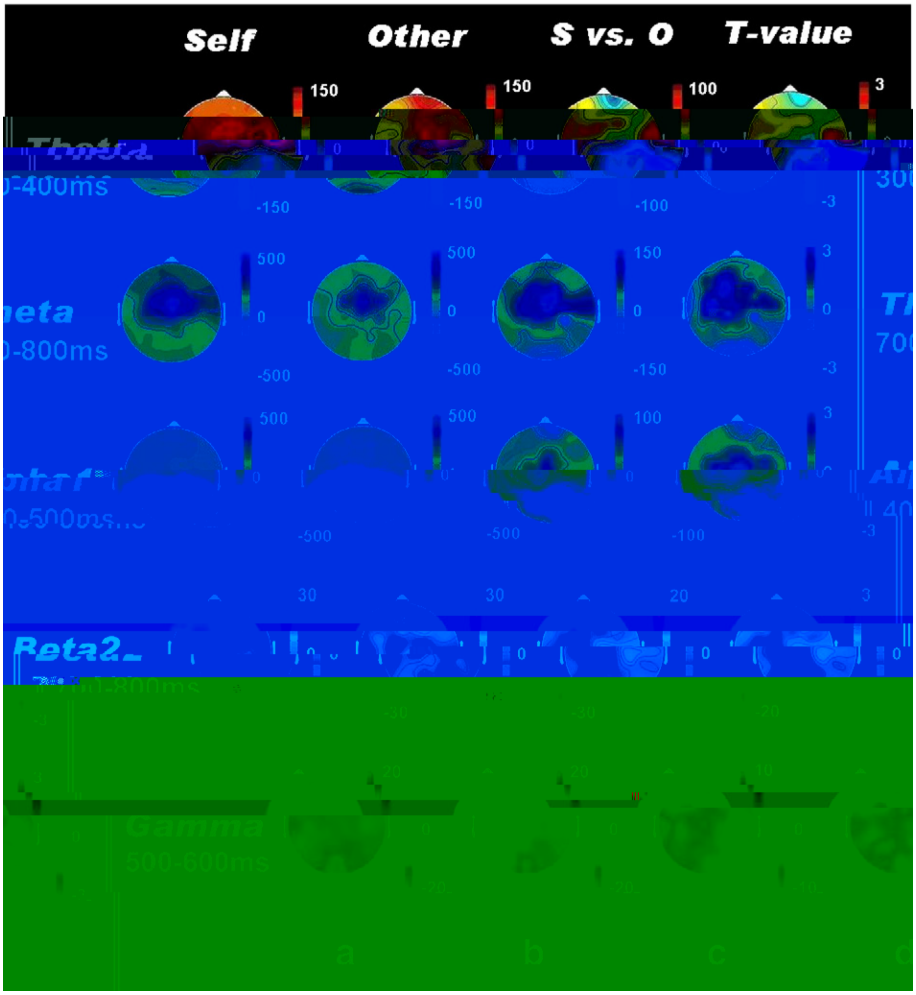

Fig. 5. a) Topographies of TF power related to self-judgment; b) topographies of TF power related to other-judgment; c) topographies of differential TF power between self- and other-judgments; d) topographies of the t-values differentiating self and other encoding.

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: $F(1,13) =$ .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

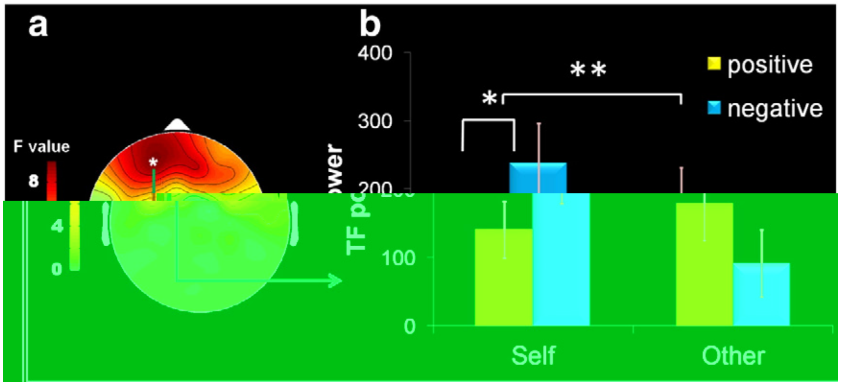

Fig. 6. a) The topographies of F-value of the interaction of Valence × Task; b) the histograms show the theta band power values (700–800 ms) associated with each stimulus condition at AF3.

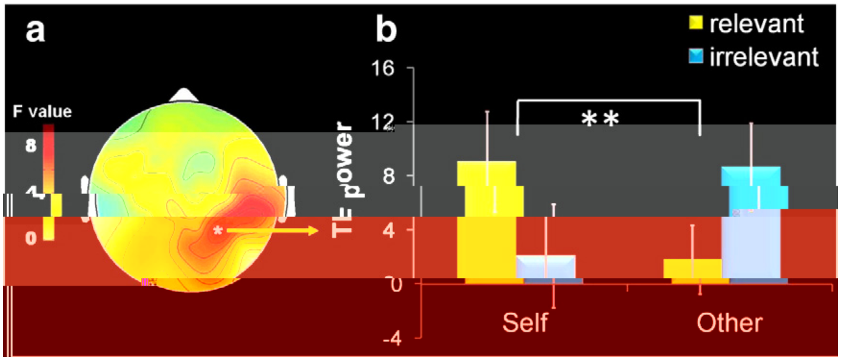

Fig. 7. a) The topographies of F-value of the interaction of Relevance × Task; b) the histograms show the gamma band power values (200–300 ms) associated with each stimulus condition at P4.

700–800 ms over the left fronto-central area positively correlated with the differential recognition scores across subjects (FC3: $r = 0.\ 17$, $p < 0.02$; FC1: $r = 0.\ \ 24$, $p < 0.02$; 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.

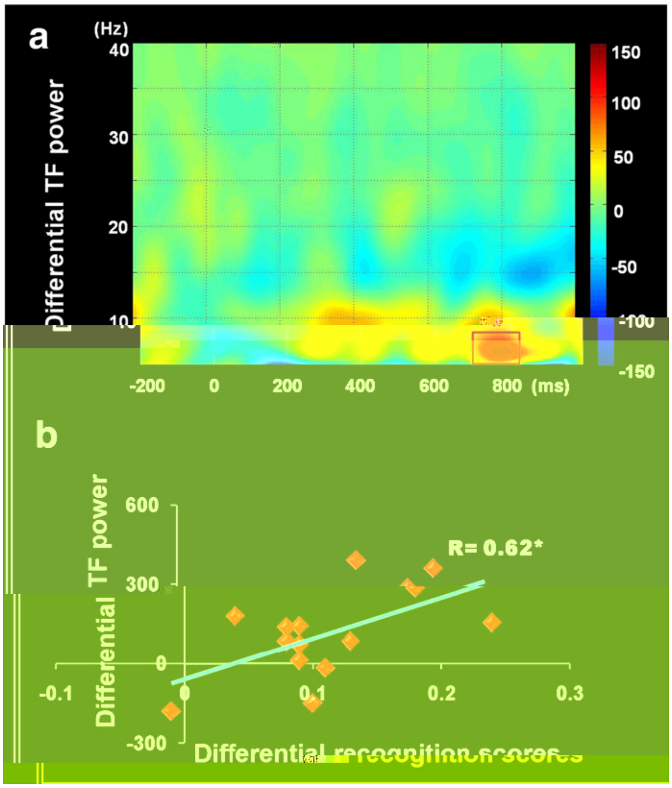

Fig. 8. a) The time–frequency representation of the differential power between self- and other-judgments at FC3; b) differential recognition scores (self vs. other) correlated positively with differential left frontal theta-band activity at FC3.

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., 199) 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. (199) 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.

Previous studies suggest that the frontal theta rhythm can be localized in the anterior cingulate or the medial frontal cortex (Asada 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., 200). 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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