Brain oscillation and connectivity during a chemistry visual working memory task

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ABSTRACT

Many studies have reported that frontal theta and posterior alpha activities are associated with working memory tasks. However, fewer studies have focused on examining whether or not the frontal alpha or posterior theta can play a role in the working memory task. This study investigates electroencephalography (EEG) dynamics and connectivity among different brain regions' theta and alpha oscillations. The EEG was collected from undergraduate students (n = 64) while they were performing a Sternberg-like working memory task involving chemistry concepts. The results showed that the frontal midline cluster exhibited sustained theta augmentation across the periods of stimulus presentations, maintenance, and probe presentation, suggesting that the frontal midline theta might associate with facilitating the central execute function to maintain information in the working memory. Study of the central parietal and the occipital clusters revealed a sequence of theta augmentation followed by alpha suppression at constant intervals after the onset of stimulus and probe presentations, suggesting that the posterior theta might be associated with sensory processing, theta gating, or stimulus selection. It further suggests that the posterior alpha event-related de-synchronization (ERD) might be linked to direct information flow into and out of the long-term memory (LTM) and precede stimulus recognition. An alternating phasic alpha event-related synchronization (ERS) and ERD following the 1st stimulus and probe presentations were observed at the occipital cluster, in which alpha ERS might be linked to the inhibition of irrelevant information.

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1. Introduction

In the past decade, many studies have explored neural correlates, measured by electroencephalogram (EEG) power spectra, of working memory. For example, several studies reported that the power of the frontal theta increased during active maintenance of working memory information until the information is retrieved (Jensen and Tesche, 2002; Raghavachari et al., 2001; Klimesch et al., 2005). Fewer studies showed that the parietal and occipital theta are associated with the working memory task (Kawasaki and Yamaguchi, 2012; Raghavachari et al., 2006). Several studies also reported that posterior alpha suppression is associated with working memory tasks (Klimesch et al., 2007; Meltzer et al., 2008). Sauseng et al. (2005) reported an increase in frontal alpha during working memory tasks. Our most recent study showed that the frontal midline cluster exhibited theta and alpha augmentation during a working memory task. The posterior regions also underwent

theta augmentation during a working memory task, though this was followed by an alpha decrease (Lai et al., 2012). Further study is needed to explore how the EEG dynamics and connectivity among or between different brain regions vary during the course of working memory tasks.

This study uses a Sternberg task to examine the spatio-temporal brain dynamics during the different phases of working memory tasks. The Sternberg task is a popular paradigm in cognitive neuroscience that can evaluate the speed and efficiency of information processing in working memory (Meltzer et al., 2008). In the Sternberg task, subjects try to memorize a list of items. After a delayed period, a probe picture/word is presented to the subjects who are then asked whether or not the probe is on the list. They indicate their response by pressing a button. In addition, the event-related spectral perturbation (ERSP) transforms and reaction-time sorted spectral perturbation (RSSP) plots were used to reveal the power dynamic changes across different brain regions and dynamic spectral changes at a certain frequency (or frequency band) of the selected components sorted according to subjects' reaction times. This study aims to uncover how EEG oscillatory activities and connectivity across different brain regions associate with working memory tasks involving chemistry concepts.

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1.1. Frontal and posterior theta in working memory tasks

Earlier studies employing EEG to study working memory have consistently reported that theta activity plays a major role in working memory tasks (Gevins and Smith, 2000; Sammer et al., 2007). Several studies have found that frontal theta activities increase during the encoding of working memory tasks (Jensen and Tesche, 2002; Mitchell et al., 2008; Onton et al., 2005; Sederberg et al., 2003). It appears that the frontal theta is involved with the active maintenance of working memory information until the information is retrieved (Jensen and Tesche, 2002; Raghavachari et al., 2001; Kawasaki and Yamaguchi, 2012). It may also be involved with the execution of cognitive control such as rehearsal or focused attention (Klimesch et al., 2005). To date, few studies have explicitly reported that parietal and occipital theta oscillations rather than frontal theta were involved in working memory tasks (Kawasaki and Yamaguchi, 2012; Raghavachari et al., 2006). Kawasaki and Yamaguchi (2012) observed occipital theta activity during the delay of a visual working memory task. Raghavachari et al. (2006) showed that theta power rose sharply, continued throughout all phases of the trial, and decreased sharply after the participant's response. They postulated that the parietal and occipital theta serve a gating function. However, the possible connectivity among or between different brain regions' theta during a working memory task remains unclear.

1.2. Frontal and posterior alpha in working memory tasks

More recently, Freunberger et al. (2009) reported that working memory encoding involves alpha activity. Klimesch et al. (2007) showed that the alpha power decreased over posterior areas during the retention of working memory, while Meltzer et al. (2008) observed that posterior (parietal–occipital) alpha decreased during the encoding and delay periods of working memory tasks. In Sauseng et al.'s (2005) study event-related de-synchronization (ERD) in the alpha band in the posterior area was associated with carrying out mental operations during a visual working memory task. Other studies found that the alpha ERD reflected excitatory processes which were sensitive for recognizing stimuli, accessing meaningful information, retrieving information from long-term memory, and evaluation of memory traces (Khader et al., 2009; Klimesch et al., 2011; Meeuwissen et al., 2011). It appears that posterior alpha ERD is associated with a number of brain functions such as stimulus recognition, mental operation with visual stimuli, long-term memory retrieval, and information maintenance, all of which occur during working memory tasks.

On the other hand, a growing number of recent studies note an increase in frontal alpha oscillations in working memory tasks. Sauseng et al. (2005) reported frontal alpha synchronization during top-down processing in a working memory task. Klimesch et al. (2011) further proposed that visual stimuli elicited event-related synchronization (ERS) in the alpha band, reflecting the inhibitory top-down control to block the retrieval of items from previous trials during the perception and encoding of new items. Jensen and Tesche (2002) suggested that alpha synchronization could prevent incoming external input from interfering with ongoing memory processes. In other words, prefrontal alpha ERS is related to controlling and inhibiting irrelevant activities, although no study has examined posterior alpha ERS or the interaction between posterior alpha ERD and posterior alpha ERS.

1.3. Connectivity between the frontal theta and posterior alpha in working memory tasks

The concept of brain connectivity offers a methodological and conceptual basis for a possible mechanism whereby the transient synchronization of brain operations may construct unified and relatively stable neural states (Fingelkurts et al., 2004). Rippon et al. (2007) has proposed to use functional connectivity, measured by a cross correlation between time series, to study the temporal relationship between two or more neuronal assemblies acting synchronously. Fingelkurts et al. (2004) suggested that connectivity was the mechanism for the coordination of activity between different neural assemblies in order to achieve a complex cognitive task or perceptual process. The concept of brain connectivity offers a methodological and conceptual basis for a possible mechanism whereby the transient synchronization of brain operations may construct unified and relatively stable neural states (Fingelkurts et al., 2004). They postulated that neuron assemblies are critical for particular brain operations (local functional connectivity), but that cognitive operations arise from combined synchronous actions/operations of many neural assemblies (remote functional connectivity). Other studies reported that frontal theta increased as posterior alpha decreased (Klimesch et al., 1997; Klimesch et al., 1994; Schack et al., 2005). These studies suggested that during the processing of information, distributed neuronal networks transiently interacted via reciprocal connections. However, no study has investigated the connectivity of theta and alpha between or within the frontal and posterior areas when the brain encodes or retrieves scientific concepts during the Sternberg-like working memory task. This study aims to disclose the functional connectivity between and within frontal and posterior brain regions and to provide new insights into complex spatial–temporal brain dynamics associated with visual working memory processes involving chemistry concepts.

1.4. Main aims

Antonenko and Niederhauser (2010)) reviewed two case studies in educational research which were associated with cognitive load in working memory and suggested that employing EEG and relating them to educational psychology can be helpful in understanding the cognitive processes of learning. Previous working memory studies predominately studied frontal theta and posterior alpha activity, but rarely focused on these oscillatory activities in both the frontal and posterior regions. This study investigates EEG dynamics and connectivity among different brain regions' theta and alpha oscillations during a visual working memory task involving chemistry concepts. Our research questions are: (1) What are the patterns of theta and alpha dynamics during a chemistry visual working memory task across the frontal midline, central, central parietal, and occipital regions? (2) Do theta oscillations differ between the frontal and posterior regions? (3) Do alpha oscillations differ between the frontal and posterior regions? (4) What are the connectivity existed between and within different brain regions?

2. Methods

2.1. Subjects

The participants in this study include 64 (36 males, 28 females) undergraduate students between the ages of 18 and 22 (M = 19.06, SD = 0.98) who were recruited from two major universities in northern Taiwan. All subjects were right-handed, had normal or corrected-to-normal vision, and were free of any disorders and medications. All participants provided written informed consent before the experiment and received a monetary reward for their participation. The study was approved by the Institutional Review Board of China Medical University Hospital.

2.2. EEG instrumentation

EEG data were recorded by a SynAmps2 amplifier (Compumedics Inc., Australia), and the stimuli were delivered using STIM2, a presentation software. The EEG data were sampled at 1000 Hz with an analog band-pass filter from 0.01 to 100 Hz. The electrode impedance was kept below 5 kΩ. The EEG data were recorded from 64 electrodes

placed according to the International 10–20 system, all referenced to linked mastoids (A1 and A2).

2.3. Experimental design and procedure

The modified Sternberg (1966) paradigm was used to study how students encode chemistry concepts. The set of chemistry concepts, knowledge of which all participants acquired in high school, consisted of 60 colored pictures. Each color picture appeared 4 times for the stimuli and once for the probe. The size of each picture was 727 × 648 pixels. All participants were asked to encode the 4 presented stimuli, remember them during a short retention period, and respond as soon as the probe presentation appeared. Each participant performed 60 trials at a viewing distance of 60 cm. Each trial started with an 800 ms fixation, followed by a 400 ms resting period. Then, four chemistry concept items were each displayed for 200 ms with an inter-stimulus interval of 200 ms. After the last item was displayed, a blank screen signaled the beginning of an 800 ms memory maintenance (retention) period during which subjects silently rehearsed the identities of the stimuli. A probe picture then appeared for 200 ms (see Fig. 1), prompting the subject to note whether it had been included in the trial's picture set. Subjects were provided with practice questions in order to acquaint them with the procedure for responding (clicking the left mouse button for "Yes" responses, and the right mouse button for "No" responses). Subjects were given 2000 ms to respond to each trial. The inter-trial interval (ITI) was 500 ms. The probability that a participant would provide a 'yes' or 'no' response was 70% and 30%, respectively. Response time was defined as the duration between the probe onset and the subject's button press.

2.4. Data analysis

Independent component analysis (ICA) refers to a family of related algorithms (Bell and Sejnowski, 1995; Lee et al., 1999) that exploit independence to perform blind source separation. ICA is an effective method for removing artifacts and separating sources of brain and non-brain signals from these recordings. ICA has been widely used to analyze signals from the brain recorded using EEG, MEG and fMRI (Jann et al., 2008; Jung et al., 2001; Neumann et al., 2008). ICA algorithms may help identify which temporally independent activations compose the collected scalp recordings without specifying directly where in the brain these activations arise. That is, ICA could isolate the mixed sources and coefficients from the observed data to solve the blind source separation problem and obtain a single component to identify EEG activities sources. It is also an effective method to filter out artifacts from eye muscle movements or other noise (Jung et al., 2001).

The recorded whole time-window EEG data in this study were first digitally filtered with a band-pass filter of 0.5–52 Hz and down-sampled to 250 Hz. The data were then submitted to extended infomax ICA (Lee et al., 1999) using the binica function (Makeig et al., 1997) from the EEGLAB toolbox for the MATLAB® platform. Default extended-mode binica training parameters were used with a stopping criterion (total weight changes) set to 1e−7. A Fast Fourier Transformation (FFT) was then used to transform the EEG activity into a power spectrum in the following frequency bands: theta (θ, 4–7 Hz), alpha (α, 8–12 Hz), and low beta (β, 13–18 Hz). Data were analyzed by custom MATLAB scripts built on the open source EEGLAB toolbox (Delorme and Makeig, 2004) (http://sccn.ucsd.edu/eeglab). EEGLAB could assess event-related spectral amplitude from single electrodes and/or in ICA components. This study selected some behaviorally relevant components to further analyze for more specific source identification of ICA components.

2.4.1. Component selection

Activation time courses of all independent components (ICs) decomposed from each subject's EEG data were first categorized into brain or non-brain activity by visual inspection of their activation spectra, time courses, and scalp topographies. Subsequently, an equivalent current dipole model was computed for each selected brain IC using a boundary element head model (BEM) as implemented in the DIPFIT toolbox (Oostenveld and Oostendorp, 2002). ICs with bilaterally distributed scalp maps were fitted with a dual equivalent dipole model with a positional symmetry constraint. Only ICs with equivalent dipole models accounting for more than 85% of actual IC scalp map variance and ICs with model equivalent dipole(s) located inside the head sphere were included in the further analysis.

2.4.2. Component power spectra and event-related spectral perturbation (ERSP)

The data were separated into non-overlapping epochs of 5.7 s after ICA decomposition. Each epoch was taken 1 s before the onset of the first stimulus as baseline to 4.7 s after the onset, giving sufficient time to include subjects' responses. The IC activation for each trial was then transformed into a spectrographic image (called event-related spectral perturbation, ERSP, in EEGLAB, Makeig, 1993) using three-cycle Morlet wavelets in a frequency range between 3 and 50 Hz. The purpose of the ERSP measures is to visualize mean event-related spectral changes over time relative to an experimental event in a broad frequency range. Calculating an ERSP requires averaging the power spectrum of brief, overlapping data windows and normalizing by the average spectral power in the pre-stimulus baseline period (1000 ms in this study). The ERSP results are then plotted as relative spectral log amplitude from the baseline on a 2-D time-frequency plane with the different colors representing power variations (Delorme and Makeig, 2004; Makeig, 1993).

2.4.3. Independent component clustering

All selected ICs were then clustered using a K-means clustering algorithm as implemented in EEGLAB. It is to group highly similar activity together from as many subjects as actually express the relevant IC(s) and their characteristic activity. We included various measures into the clustering algorithm to identify homogenous groups of components across subjects (Onton et al., 2006). With the exception of dipole locations (with only three dimensions), each of the measures (spectrum, ERP, ERSP, inter-trial coherence, and scalp topography) was compressed into a 10-dimensional feature vector. Subsequently, all measures were combined and further compressed by principal component analysis (PCA) into a 53-dimensional feature vector for
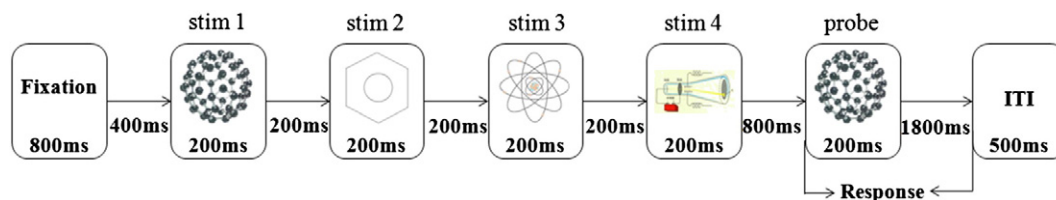

Fig. 1. Materials and procedures. The modified Sternberg paradigm was used in this study. All of the participants were asked to encode the four sequentially presented stimuli consisting of chemistry concepts presented as pictures. The probe picture then appeared, prompting the subject to respond by pressing buttons to indicate whether the probe picture had appeared in the set of that trial.

each IC. Due to the characteristics of the different measures in the feature vector, such as dimension and variance, the different measures were weighted by different factors to equalize their respective influence: The equivalent dipole location measure was inherently three-dimensional and was weighted by a factor of 20 to make it more influential. ERSP was given a weight of 9, while spectrum, ERP, inter-trial coherence, and scalp topography were all given a weight of 1. All ICs from all subjects were grouped into 40 clusters. The results of clustering were then re-clustered by removing the ICs whose distances to their cluster centroid were greater than three standard deviations. The experimenters finally examined the resultant clusters and manually removed improper ICs from each cluster according to their dipole locations, ERSPs, scalp maps, and power spectra.

2.4.4. Reaction-time sorted spectral perturbation (RSSP) and inter-trial coherence (ITC)

A reaction-time sorted spectral perturbation (RSSP) plot was used to reveal the dynamic spectral changes at a certain frequency (or frequency band) of the selected components. An RSSP plot is a 2-D transformed stacked spectral representation in which the power spectra at a certain frequency of data epochs were first sorted according to reaction time, then color-coded, stacked, and finally smoothed across adjacent trials (optional) to form a 2-D image. In addition, inter-trial coherence (ITC) was computed at a certain frequency and displayed beneath an RSSP image. ITC refers to the event-related phase coherence in the EEGLAB function and it is a frequency-domain measure of the partial or exact synchronization of activity at a particular latency and frequency to the experimental events to which EEG data trials are time locked. A value of ITC near 1 indicates perfect EEG phase reproducibility across trials at a given latency (Delorme and Makeig, 2004).

3. Results

3.1. Theta and alpha oscillations across frontal midline, central, central parietal and occipital areas

The frontal midline, central, central parietal and occipital clusters recruited 44, 40, 53, and 76 ICs from 41, 40, 51, and 50 subjects (out of 64), respectively. Note that some ICs might be missing from some subjects' ICA decomposition results, and that some subjects might contribute more than one component to the same IC cluster. Fig. 2A–D shows the average scalp maps for these four clusters along with the dipole locations. Fig. 2E–H shows the ERSPs of the four IC clusters, and Fig. 2I–L shows the corresponding time course of theta and alpha power over time.

The ERSP of the frontal midline cluster showed theta and alpha power augmentation after the onset of stimuli, during the maintenance periods, during probe presentation, and after the participants' responses (Fig. 2E). The spectral time courses of the frontal cluster showed strong frontal theta and alpha augmentation after probe presentation (Fig. 2I). The central cluster's ERSP showed brief theta augmentation after the first stimulus and probe presentation, and alpha suppression across each of the stimulus and probe presentations (Fig. 2F and J). The central parietal ERSP showed greater theta augmentation after the first stimulus and probe onset along with alpha suppression across each stimulus and probe onsets (Fig. 2G). Fig. 2K further shows that the central parietal theta augmentation and alpha suppression were time-locked to stimulus and probe presentations. The occipital cluster ERSP revealed a sequence of theta augmentation followed by alpha suppression at constant intervals after the onset of stimuli and probe presentations (Fig. 2H). Furthermore, the magnitudes of theta augmentation decreased gradually from the 1st to the 4th stimulus, and the magnitude of theta augmentation after probe presentation was about the same as after the 1st stimulus (Fig. 2L). The occipital alpha suppression was very strong following the 1st stimulus presentation

and then alternated to the same lower bound following subsequent stimulus presentations (Fig. 2L).

3.2. Frontal and posterior theta

Fig. 3A–C shows the RSSP plots for theta activity in the frontal midline, central parietal and occipital areas. Theta bursts were found across the frontal and the posterior areas, but were more salient in the occipital area. The occipital theta augmentation was time-locked to stimulus and probe presentations, and a similar pattern was found in the central parietal area (Fig. 3B–C). The ITC of the occipital theta was salient following each stimulus and probe presentation (Fig. 3C). The RSSP indicated that the theta power peaked at about 200 ms in the occipital cluster (Fig. 3C). The frontal midline theta augmentation clearly time-locked to the probe presentation and revealed a greater theta ITC after the 1st stimulus and probe presentation (Fig. 3A).

The changes in theta power among the four clusters differed largely and reached a .05 significance level in a one-way ANOVA for most of the time courses. The post hoc analysis revealed that the most significant differences existed between the frontal midline and occipital, and between the central parietal/central and occipital (Fig. 4A). The frontal midline cluster exhibited sustained theta augmentation across the sequential stimulus presentations, the maintenance period, and after the probe presentation. The power of the central parietal cluster resembled that of the occipital cluster, which exhibited a momentary increase at the beginning and an abrupt decrease near the end of each stimulus and probe presentation. In addition, the levels of theta power augmentation gradually declined from the 1st to the 4th stimulus. The magnitude of the theta augmentation following the probe presentation was comparable to that following the 1st stimulus onset.

3.3. Frontal and posterior alpha ERS and ERD

Fig. 3D–F shows the RSSP plots of alpha activities of the frontal midline, central parietal and occipital clusters. Alpha bursts were found across the frontal and the posterior areas, but were more salient in the occipital area. The occipital alpha ERS appeared immediately after the 1st stimulus and probe presentation, followed by alpha ERD. A similar alternating ERS/ERD pattern was also found in the central parietal cluster (Fig. 3E). The occipital and central parietal clusters' alpha ERD time-locked to each stimulus and probe presentation (Fig. 3F). The greater occipital alpha ITC was salient for each stimulus and probe presentation (Fig. 3F, bottom traces), supporting the time- and phase-locked nature of alpha. The ERSP trace showed that the alpha time course peaked at about 100 ms after stimulus and probe onsets (visual P1 component), followed by the alpha ERD before the next stimulus onset (Fig. 3F). Similar patterns were also found in the central parietal cluster (Fig. 3E).

The frontal midline alpha augmentation was more pronounced following the probe presentation (Fig. 3D). Unlike the occipital cluster, the frontal midline cluster did not show any alpha ERD. The alpha perturbations among the four clusters differed largely and reached a .05 significance level in a one-way ANOVA for most of the time courses. The post hoc analysis revealed that the significant differences existed on almost all Pairwise comparisons, with the exceptions of the frontal midline and central clusters (Fig. 4B). The frontal midline cluster exhibited sustained alpha augmentation across all four stimuli, during maintenance, and after probe presentations. On the other hand, the central parietal and occipital clusters showed strong alpha ERD across each stimulus and alternating phasic alpha ERS/ERD following the 1st stimulus and probe presentations (Fig. 4B).

3.4. Connectivity between brain regions

Fig. 4 summarizes the time courses of theta and alpha power across the four component clusters. The frontal midline cluster maintained its
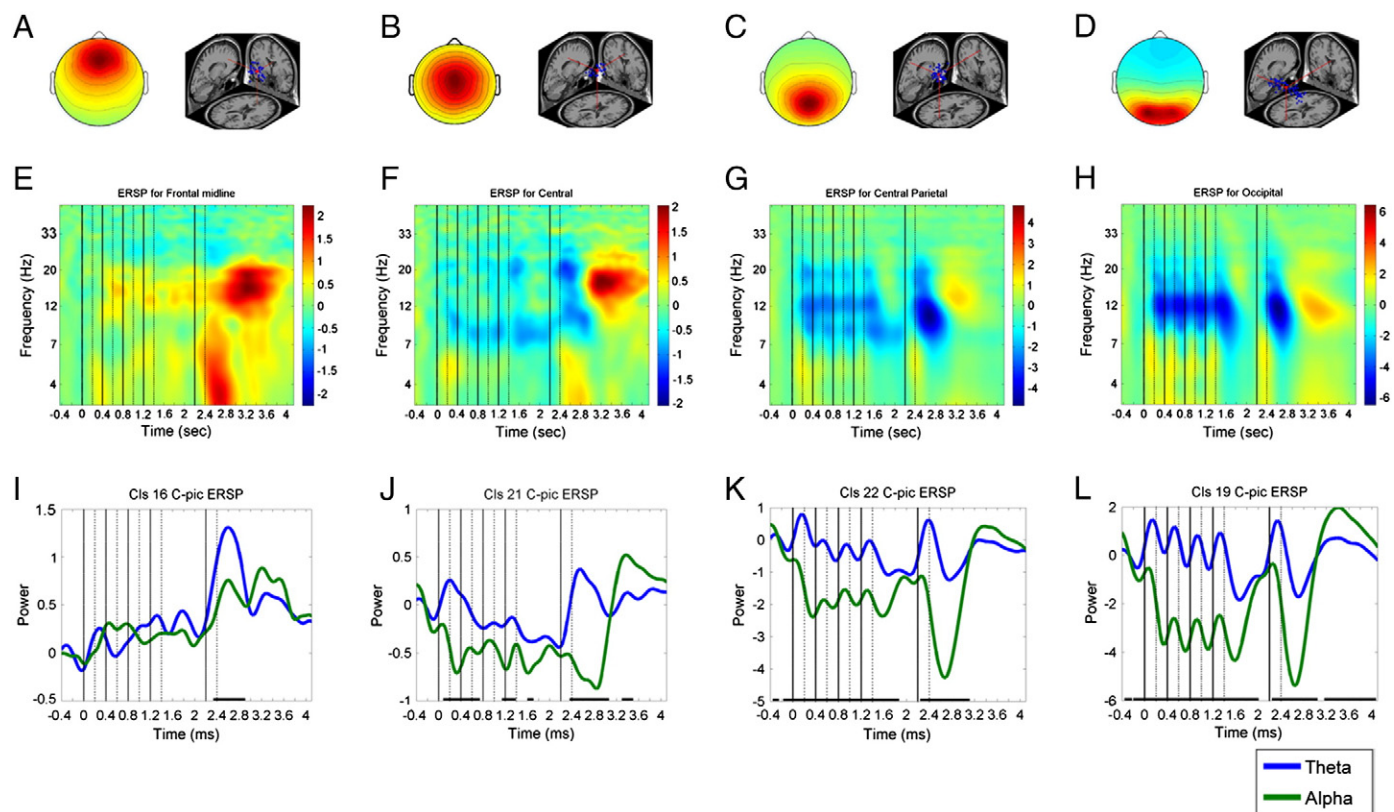
Fig. 2. Scalp maps, dipole models, ERSP images and ERSP transforms. (A–D) The mean cluster scalp maps and the respective equivalent dipole models of all independent component processes (blue spheres) and the cluster centroid (red sphere) projected onto the Montreal Neurological Institute (MNI) head model for frontal midline, central, central parietal and occipital clusters. (E–H) The average ERSP image showed the time-frequency results during stimulus presentation, probe presentation, and response periods for each cluster. (I–L) ERSP transforms were computed to show the changes of theta and alpha power across different clusters. A t-test was conducted to examine whether there were statistically significant differences in frontal midline (I), central (J), central parietal (K), and occipital (L) clusters between theta and alpha power. Which the t-test reached a .05 significance level was presented by a solid line at the bottom of the image. (E–L: The solid lines were used for the onsets of the stimuli and the probe; the dotted lines were used for the offsets of the stimuli and the probe.)

theta power during the stimulus, maintenance, and probe presentation periods. Both theta and alpha increased considerably after the probe presentation. The occipital cluster exhibited a precise stimulus-locked

theta augmentation, followed by alpha ERD, which corresponded to the onsets of the stimulus presentations at 0, 400, 800, and 1200 ms (Fig. 2L). The occipital theta augmentation and alpha ERS both appeared
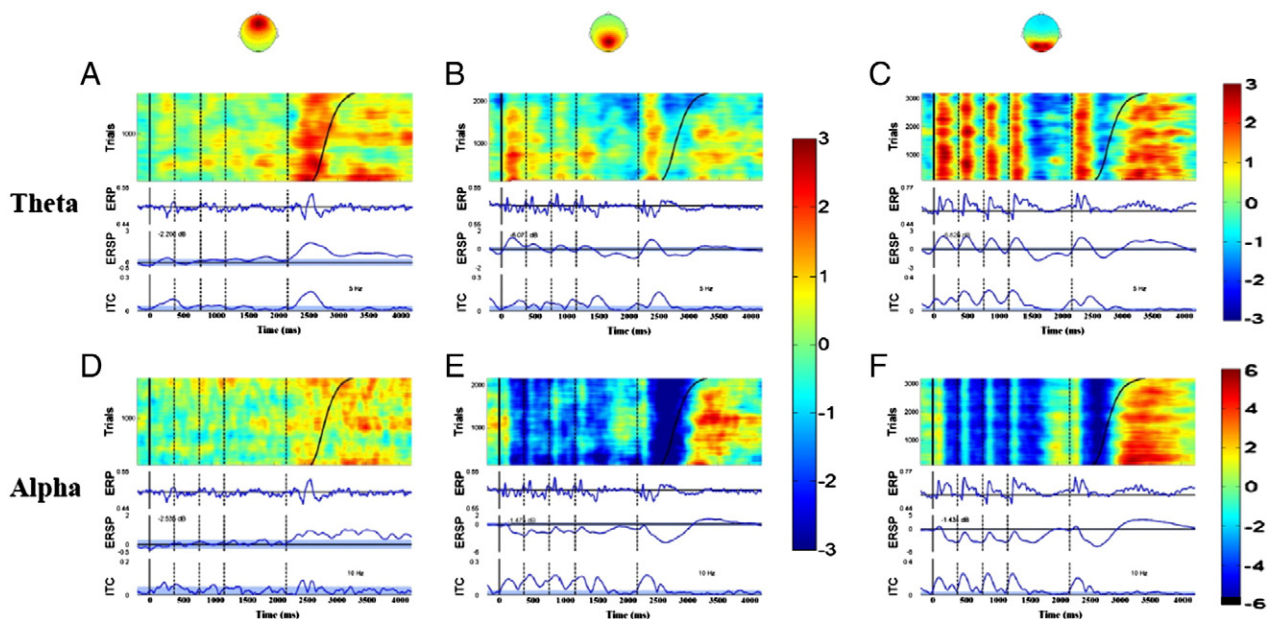

Fig. 3. RSSP images. The reaction-time sorted spectral perturbation (RSSP) image was sorted by reaction time and smoothed adjacent trials to reveal the dynamic spectral changes at theta (5 Hz) and alpha band (10 Hz) for the frontal midline, central parietal and occipital clusters.
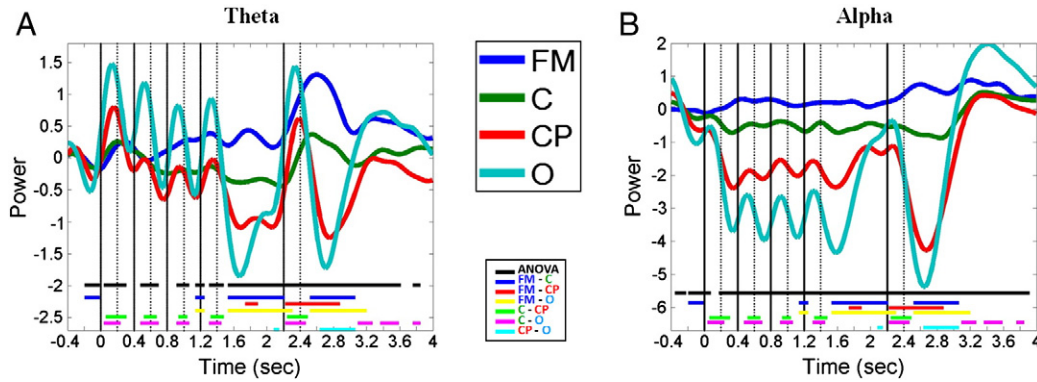
Fig. 4. The dynamics of theta and alpha power. The ERSP transforms were computed to show the dynamics of theta and alpha power for the frontal midline (FM), central (C), central parietal (CP), and occipital (O) clusters. A one-way ANOVA was conducted to examine whether there were statistically significant differences in theta (A) or alpha (B) power among the 4 different clusters. Which the ANOVA and all pairwise comparisons reached a .05 significance level were presented by solid lines in different colors at the bottom of the image. (A–B: The solid lines were used for the onsets of the stimuli and the probe; the dotted lines were used for the offsets of the stimuli and the probe.)

immediately after the 1st stimulus and probe presentations, and the theta augmentation lasted slightly longer than the alpha ERS (Fig. 3C and F). The occipital alpha ERD and theta power returned to the baseline at about the same time before the next stimulus onset. Comparing the occipital theta and alpha patterns indicates that occipital theta increases and appears earlier than occipital alpha ERS for the first stimulus, followed by the appearance of occipital alpha ERD (Fig. 5). Similar spectral perturbations were found for each stimulus and probe presentation (Fig. 2L). The central parietal cluster exhibited similar theta augmentation and alpha ERS/ERD patterns following the 1st stimulus and probe presentations (Fig. 2K). It also revealed that occipital theta arises earlier and is stronger than the frontal midline (Figs. 4A and 5). The power amplitude of the frontal theta is less than that of the occipital theta during the stimulus periods, but it rises to a relatively higher level during the maintenance periods compared to the occipital theta (Fig. 4A). The theta patterns in the occipital and central parietal regions resemble each other, while the pattern of the frontal midline resembles that of the central region. In addition, the alpha ERD was clearly observed for the occipital, central parietal for all four stimuli, and at the central cluster for only the first stimulus. Their alpha patterns differ from that of the frontal midline, the alpha augmentation pattern of which is observed across the different periods.

4. Discussion

4.1. Frontal and occipital theta

One of the aims of this study is to investigate the frontal and occipital theta oscillations during a visual working memory task involving

chemistry concepts. The experimental results of this study showed a theta augmentation for the frontal midline cluster after stimulus onsets, during the maintenance periods and after probe presentations. This is consistent with Raghavachari et al.'s (2001)) study, which reported a strong increase in theta oscillation during the encoding of a verbal working memory task, and that this increased theta activity was sustained during the retention period until information had been retrieved. Klimesch et al. (2005) also reported that either the maintenance of information in short-term memory or the execution of control processes (e.g. rehearsal or focused attention) was reflected by a sustained theta-power increase. Other researchers reported that theta oscillations are involved in the active maintenance and recall of working memory representations (Jensen and Tesche, 2002; Kahana et al., 1999; Klimesch, 1999; Doppelmayr et al., 1998), and that fontal midline theta activity is more pronounced (Inanaga, 1998; Jensen and Tesche, 2002; Mitchell et al., 2008). Many studies indicated that the most pronounced theta activity most likely emanates from (or near) the dorsal anterior cingulate cortex (dACC) (Ishii et al., 1999) during the encoding phase (Sederberg et al., 2003). Miller and Cohen (2001) suggested that the role of the prefrontal cortex is mainly associated with the executive control of the task. The results of this study were in line with previous studies in finding that the stronger frontal midline theta oscillations were responsible for actively maintaining information and facilitating the central executive function for working memory tasks.

This study also showed theta activity at both the central parietal and the occipital clusters, which was strongly associated with stimulus onsets and probe presentations. Raghavachari et al. (2006) similarly reported a strong theta-power increase in the occipital, parietal, and temporal lobes during a Sternberg working memory task. Rizzuto et al.
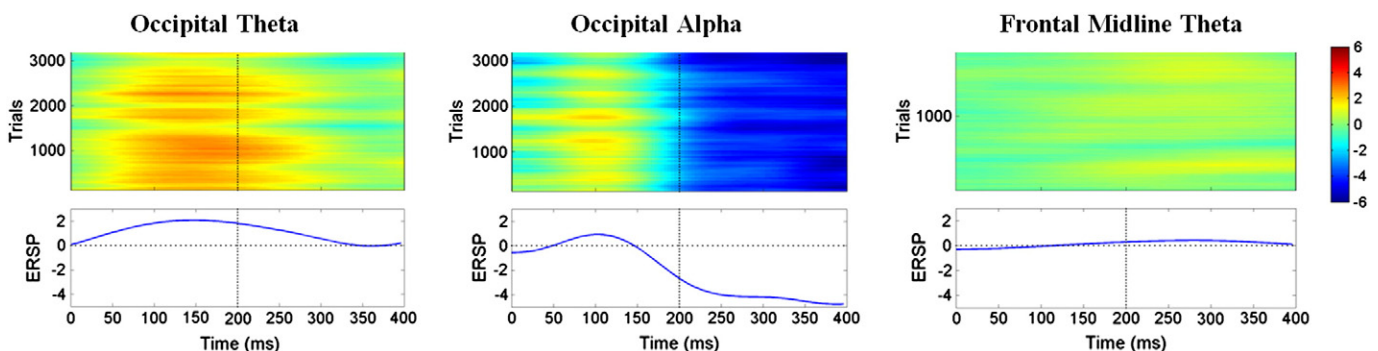

Fig. 5. The connectivity of theta and alpha power. The RSSP images and the ERSP plots showed dynamic spectral changes during the first stimulus for the occipital theta (5 Hz), occipital alpha (10 Hz) and frontal midline theta (5 Hz).

(2003) found that stimulus-induced phases reset in the theta-band activities in many brain regions, but not in the prefrontal cortex, which was exactly what the current study found. Raghavachari and Lisman (2004) suggested that activation in the occipital cortex might be related to sensory rather than memory processing. Raghavachari et al. (2001, 2006) studied gated brain oscillations and found that they increased dramatically at the beginning of the trial, continued through all phases and decreased sharply at the end. They further observed these oscillations throughout the brain cortex and noted that they were more pronounced in the parietal area. They suggest that gated theta cannot be a simple consequence of the sensory and motor components of the task. Rather, they play an important role in organizing multi-item working memory to precisely control the cognitive demands of the working memory task. Other studies found that the parietal lobe is responsible for the capacity limit of short-term memory (Postle et al., 2004) or memory load (Vogel and Machizawa, 2004). Fries et al. (2002) hypothesized that neuronal synchronization correlates with stimulus selection, which increases the firing of postsynaptic neurons. The novel onset of a rivalrous stimulus leads to the selection of this stimulus and at the same time to the suppression of the already presented competing stimulus. Their earlier study reported that synchronization in the primary and secondary visual cortices correlates with stimulus selection (Fries et al., 1997). They suggested that the firing rate was slightly lower when the stimulus was new (Fries et al., 2002).

In sum, given that the posterior (occipital and central parietal) theta oscillation peaked at around 200 ms after stimulus onset and returned to the baseline before the onset of the next stimulus, and further given that the theta power decreased gradually from the 1st to the 4th stimulus, we speculate that the posterior theta might be driven by a combination of the following: (1) sensory processing, (2) theta gating, and (3) stimulus selection. Our findings suggest that the occipital theta might be different from the frontal theta and thus responsible for different functions. However, further studies are still needed to provide the local mechanism for the generation of cortical theta rhythms (including those of the occipital and central parietal lobe).

4.2. Frontal and posterior alpha ERD and alpha ERS

Klimesch et al. (2005) suggested that upper alpha plays an important role in the maintenance of memorized information up to the point when retrieval can actually be performed. Klimesch et al. (2007) further suggested that alpha oscillations play an important role in directing the information flow to task-relevant brain structures on the basis of two general mechanisms: inhibition and timing. Their studies suggested that visual stimuli elicit the alpha ERS that reflects inhibitory top-down control to block retrieval of items from previous trials during the perception and encoding of new items. In short, alpha ERS serves to inhibit task-irrelevant and/or competing information (Klimesch et al., 2011). Alpha ERD indicates the onset of an excitatory status and enables subjects to recognize stimuli, access meaningful information, retrieve information from LTM, and evaluate memory traces (Klimesch et al., 2011; Meeuwissen et al., 2011; Khader et al., 2009). Alpha ERD and ERS were considered to be processing mode controls encoding a stimulus but not responding to a stimulus. In other words, alpha ERS and ERD are not associated with processing new information but are rather associated with already stored and meaningful information in LTM. Our ERP results showed P1 at about 100 ms after stimulus onsets, followed by the alpha ERD that peaked before the next stimulus onset. Klimesch et al. (2011) proposed that sensory information is processed for up to 100 ms after a stimulus, which allows for an early categorization for the encoded stimulus. The P1 and alpha phase responses start at around 100 ms and should be functionally related to early stimulus categorization and the inhibition of irrelevant information. In short, the appearance of P1 reflects an early stimulus categorization (which is reflected primarily by a phase response of alpha at around 100 ms), and the alpha ERD reflects a gradual release from inhibition and

the beginning of a recognition process, which can be understood as the beginning of a memory-accessing process. The early categorization establishes access routes to information stored in the knowledge system and precedes stimulus recognition. Klimesch et al. (2011) also provided an alternative view of alpha: it may reflect a specific type of attention, it controls the flow of information into and out of LTM, and it helps to narrow down the relevant search area in the memory. Taking all of the previous and current studies into consideration, one may surmise that the posterior alpha ERS following the 1st stimulus onset might be associated with early stimulus categorization and inhibit irrelevant information, whereas the alpha ERD might be associated with stimulus recognition and the control of flow of information into and out of LTM.

4.3. Connectivity between brain regions

Fingelkurts et al. (2004) identified connectivity as the mechanism that coordinates activity between different neural assemblies in order to achieve complex cognitive tasks or perceptual processes. The concept of brain connectivity offers a conceptual basis for a possible mechanism whereby the transient synchronization of brain operations may construct unified and relatively stable neural states (Fingelkurts et al., 2004). The mechanism that allows frontal and posterior regions to coordinate to perform working memory tasks still remains unclear. Our results showed that the theta activity of the frontal region is very different from what is found in the posterior region, and theta oscillations in the frontal and posterior regions arise in sequence, which might be attributed to the different functions served by different brain areas. The possible explanation for such connectivity between frontal and posterior activity is discussed below according to the results of this study.

The thalamus is divided into several nuclei that act as specific relays for incoming sensory information. The lateral geniculate nucleus receives sensory signals from retina and then transmits the signals to the primary sensory cortex at the occipital region (Gazzaniga et al., 2009, p. 82; Kropotov, 2009, p. 192; Skinner, 1984, p. 42). The primary sensory cortex located in the occipital region has reciprocal inter-cortical connections with the anterior cortical areas of the executive system which are responsible for involving in the selection of actions and maintaining working memory in order to process sensory information in detail (Gazzaniga et al., 2009, p. 82; Kropotov, 2009, p. 255; Skinner and Yingling, 1977, p. 57). Taking the neurophysiology evidence, that sensory information was transmitted from the thalamus to the occipital and then the prefrontal cortex in sequence, provides a plausible explanation for why the occipital theta arises earlier than the frontal theta. The sensory information sent from the thalamus to the occipital region supports posterior theta gating ideas and helps to explain why our occipital theta increased dramatically at the beginning of the stimulus and decreased sharply after the stimulus vanished. It is well known that frontal lobe is responsible for maintaining working memory to process sensory information in detail. This helps to explain why frontal theta increased slower than occipital theta after stimulus onset, and why frontal theta maintained a relatively higher power level from the beginning of the maintenance periods until the response than did occipital theta.

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