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Human Oscillatory EEG Activities Representing Working Memory Capacity

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1. Introduction

We can flexibly process and make decisions regarding multiple types of information in daily situations such as driving and cooking. However, human error is increased in complex or combined tasks (relative to simple tasks) because our information processing capacity is limited. This limited cognitive function is associated with working memory (WM), which is proposed to be a higher-level human ability to memorize, maintain, and manipulate mental representations in the mind for a short time (Baddeley, 1986). Most theorists think that WM function includes active manipulation as well as passive short-term maintenance. An often-used metaphor for working memory is "the blackboard of the mind." For example, imagine that you are rearranging the furniture in your room. You can move around the furniture in your mind, that is, transform the imagination any number of times. To guide behavior and make decisions about what to do next, WM temporarily selects and retains task-relevant information such as recently processed sensory input, retrieved information from long-term memory, or mentally manipulated images. Thus, WM is directly linked to any and all other brain functions, including perception, movement, emotion, and problem solving.

Baddeley & Hitch (1974) proposed a basic psychological model in which WM is divided into separate components, the "storage system" and the "central executive". The "storage system" consists of 2 temporary storage buffers for visual information (visuospatial sketch pad, i.e., visual working memory) and auditory-verbal information (phonological loop, i.e., verbal working memory) and an episodic buffer for long-term memory, whereas the "central executive" controls the allocations of attention, selects relevant information, and manipulates information held in the storage systems (Baddeley, 1986; Baddeley & Hitch, 1974; Phillips, 1974; Baddeley, 2000). Extensive experimental evidence from behavioral performance of normal subjects, lesion studies, and neuroimaging studies supports this view. For example, performance in dual tasks requiring 2 separate perceptual domains (i.e., a visual and a verbal task, or a mental processing task and a maintenance task) is nearly as efficient as performance of individual tasks (for a review, Cowan, 2001; Della Sala & Logie, 1993). These findings indicate that the visual and verbal WM are separated.

Both visual and verbal WM have 3 phases: encoding, which imports the relevant information in memory; maintenance, which stores the encoded information; and retrieval (or rehearsal), which briefly uses the information for a task. To investigate the neural substrate for WM, previous electrophysiological studies in nonhuman primates and human

neuroimaging studies have shown sustained neural activity over the retention interval in distributed brain regions including frontal, parietal, occipital, and temporal areas during maintenance of relevant information (e.g., Chafee & Goldman-Rakic, 1998). If these brain regions are actually involved in maintaining mental representations, their activities are thought to be correlated with WM capacity. In fact, brain activity has been reported to increase with increasing number of objects to be remembered and saturated below the limited WM capacity (Todd & Marois, 2004; Vogel & Machizawa, 2004). Frontal regions also represent the limitation of executive functions, since activity there is increased during engagement in dual tasks (Marois & Ivanoff, 2005). These results suggest that frontal regions are associated with executive functions and posterior regions are involved in maintenance of mental representations. Thus, although much is known concerning the brain areas involved in various WM functions, understanding how these brain areas temporally communicate is more difficult.

To address this issue, measuring electrophysiological (EEG) data during WM tasks and analyzing the synchronizations in local areas and between different areas has proved particularly useful (Varela et al., 2001). Our previous EEG studies used mental calculation as the auditory WM task and mental spatial manipulation as the visual WM task (Kawasaki et al., 2010). The EEG results clearly demonstrated that the frontal theta (4–6 Hz) activity increased during the manipulation periods on both WM tasks, and the parietal and temporal alpha activities were enhanced only during the maintenance periods on the auditory and visual WM task, respectively. Phase synchronization analysis revealed significant theta synchronizations between the frontal and parietal regions for visual WM and between the frontal and temporal regions for auditory WM. These results indicated that long-range theta synchronizations could connect the different brain regions to manipulate task-relevant representations. Interestingly, the concurrent theta and alpha phases were significantly synchronized in task-relevant storage areas, which suggests the presence of gating mechanisms to extract stored information. Theta and alpha activities thus play an important role in several WM functions; however little is known regarding how these oscillations represent WM limitations.

This chapter describes investigations into the neural dynamics of EEG oscillatory activities that underlie the capacity limitations for executive functions and storage buffers in WM, particularly for visual information. To advance understanding of the detailed brain networks involved, the use and interpretation of EEG time-frequency analyses such as wavelet analysis and the role of each EEG oscillatory activity in WM functions is discussed, and 2 experiments are described. Visual storage systems were investigated using delayed-matching-to-sample tasks with visual stimuli, and a dual WM task with visual and auditory representations was used to identify the bottleneck of the central executive function. These EEG findings may contribute to understanding the causes of human error.

2. Capacity limitations of working memory

To investigate the limitation of visual WM (VWM) storage capacity, previous behavioral and neuroimaging studies used a change detection paradigm, namely, delayed matching to sample (DMS) tasks with a visual stimulus. In this paradigm, multiple visual items are presented (sample display) and participants are required to memorize and retain these items

over retention intervals. The number of items within the sample display is manipulated. Following the retention interval, one probe item (test display) or multiple probe items (whole display) are presented at one location within the sample array, and participants are then required to judge whether a change has occurred or not. These 2 tests have shown different performance scores, since VWM storage capacity is vulnerable to visual interference created during the encoding period (Wheeler & Treisman, 2002). Therefore, many behavioral and neuroimaging studies have applied the single-probe test. To avoid the possibility of using verbal strategies, most studies involving the DMS task used very short exposure duration for the sample display (about 150 ms), and require participants to engage in phonological tasks simultaneously, e.g., repeating a word during the sample display and retention intervals (Baddeley, Lewis & Vallar, 1984).

Many previous studies have proposed a VWM capacity of 3 or 4 items (Luck & Vogel, 1997) because the accuracy rates for many DMS tasks systematically decrease as the number of items increases beyond 3 or 4. More recently, one study demonstrated that VWM capacity decreases as object complexity increases, and proposed that VWM capacity varies by the type of features (Alvarez & Cavanagh, 2004). The authors used complex items, Chinese characters, which are thought to be a combination of simple shapes. Although the issue retains some controversy, many studies have demonstrated consensus on the existence of large individual differences in VWM capacity.

To estimate the capacity of VWM in terms of objects stored in DMS tasks, Cowan (2001) has proposed a model that takes both hit rates (accurately detecting a change) and correct rejection rates (accurately reporting no change when none occurred) into account. The model estimates hit rates and correct rejection rates with the following equations:

$$H = \frac{K}{N} + \frac{(N - K)}{N} \times g \quad (1)$$

$$CR = \frac{K}{N} + \frac{(N - K)}{N} \times (1 - g) \quad (2)$$

where K denotes the estimated number of items stored in VWM, N is the total number of items presented in the sample display, H is the probability of a hit rate, CR is the probability of a correct rejection rate, and g is the guessing rate for coincidentally giving a correct answer. The theory assumes that when one of the items within the VWM capacity (K/N ; Fig. 1 purple area) changed, subjects could detect whether the change occurred. In contrast, they could not detect whether a change occurred in objects exceeding the capacity ($(N - K)/N$; Fig. 1 green area).

However, in some cases subjects happened to answer correctly on some portion of the trials (g) under an alternative forced-choice paradigm or, in another portion of the trials ($1 - g$), coincidentally report correctly that no change occurred in the no-change trial, although they could not detect this. This guessing rate could not be estimated from the performance of the DMS tasks. Thus, given the hit rates and correct rejection rates for a particular set size, these equations (1) and (2) can be solved for the set size:

$$K = N \times (H + CR - 1) \quad (3)$$

The Cowan's *K* value is obtained from the set size of each sample display as each subject's VWM capacity for a given material.

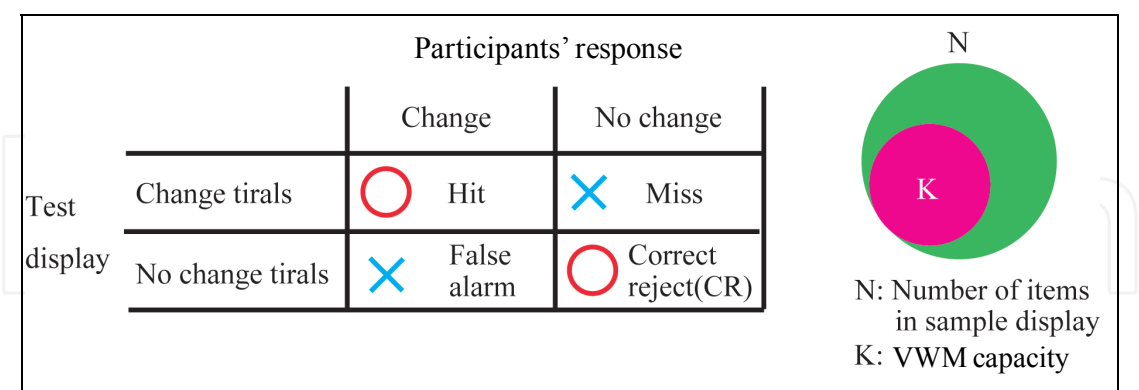


Fig. 1. Combination of participants' response and trial type (change or not) in change detection paradigm (left) and a model of Cowan's formula (right).

Unlike VWM, the WM capacity for executive functions has been evaluated using dual WM tasks. Although no interference exists between independent storage components such as visual and verbal storage, simultaneously processing more than 2 information sources that require mental manipulation and reactions is thought to be difficult. Previous studies have revealed a psychological refractory period, in which a second task elicits a longer reaction time when the interval between the first and second tasks (i.e., stimulus onset asynchrony; SOA) is short (Marois & Ivanoff, 2005). That is to say, if the 2 tasks seem to be processed simultaneously, the performance is degraded. This phenomenon is known to be a bottleneck of the central executive function.

3. Neural substrates for working memory

Over many years, numerous researchers have attempted to localize and characterize the neural implementation of VWM and dissociate its functions. Lesion studies have reported that damage to the prefrontal cortex (PFC) in monkeys impairs performance on DMS tasks with a short delay, but not on visual discrimination tasks that do not require maintenance of information (Goldman-Rakic, 1987). Likewise, electrophysiological recording studies of nonhuman primates have revealed sustained neuronal firing in the PFC during the retention interval of DMS tasks, and interpreted the activity as maintaining the previously presented representations (Fuster & Alexander, 1971; Kubota & Niki, 1971). Therefore, the PFC was believed to be the neural substrate for VWM over a longer period. Since then, numerous physiological studies have shown neurons specifically active during the delay period in a vast network of brain regions including the PFC (e.g., Funahashi, Bruce, & Goldman-Rakic, 1989), the posterior parietal cortex (e.g., Chafee & Godman-Rakic, 1998), and visual processing cortices (Bisley & Pasternak, 2000; Miyashita & Chang, 1988). Consistent with this interpretation, human neuroimaging studies have also revealed that the blood flow in these regions continually increased during the retention interval (Courtney et al., 1997, 1998; Postle & D'Esposito, 1999). Although considerable evidence supports the sustained delay-period activity, DMS tasks include many requirements (e.g., preparation of actions) in addition to maintenance. Therefore, recent fMRI studies have assumed that the blood oxygen level-dependent (BOLD) signal captures a population of neuronal activity that

may reflect the representation of multiple items to be maintained, and have indeed shown that a subset of the distributed network demonstrated delay-period activity sensitive to the number of items in the sample display (Diwadkar et al., 2000; Glahn et al., 2002; Jha & McCarthy 2000; Linden et al., 2003). The VWM load-sensitive network includes the frontal, parietal, and visual cortices. Notably, some studies have revealed that activity in the posterior parietal cortex is correlated with the number of items to be remembered (Cowan's *K* value) and indicated that this area actually stored the representations (Kawasaki et al., 2008; Todd & Marois, 2004, 2005; Vogel & Machizawa, 2004; Xu & Chun, 2006).

In contrast to the posterior parietal and visual cortices, anterior regions including the frontal cortex have also been associated with executive processes such as attentional selection and manipulation of information (Curtis & D'Esposito, 2003). For instance, in studies using a spatial WM task that requires participants to memorize the spatial locations of simultaneous or sequentially presented items and, after a delay, select one relevant location, the prefrontal cortex has been reported to show transient activity during the selection period and no sustained activity during the retention interval (Rowe et al., 2000). Furthermore, the frontal cortex is particularly sensitive to the number of listed items to be maintained in VWM in the *n*-back task, which requires participants to maintain a series of items and their order, select a relevant item from VWM, and compare it with the earlier item (Smith & Jonides, 1999). Moreover, the frontal cortex is proposed to serve in maintaining task-specific goals (Miller & Cohen, 2001; Passingham & Sakai, 2004) and assist in maintaining high loads and/or long retention intervals (Braver et al., 1997; Linden et al., 2003).

Although, thus far, many neuroimaging studies have identified the neural substrate for the storage systems and central executive of WM, they have not dealt with how these brain areas temporally communicate. To address this issue, some studies have investigated the dynamic relationships governing brain activity by focusing on electroencephalograph (EEG) oscillations, which are closely related to synchronization of a large number of neurons underlying a particular function (Varela et al., 2001). Previous human scalp-recorded EEG studies have revealed modulated theta (about 4–8 Hz) and alpha (about 9–12 Hz) rhythms in distributed brain regions and phase synchronization between them during various WM tasks (Jensen & Tesche, 2002; Kawasaki & Watanabe, 2007; Klimesch et al., 2008; Mizuhara et al., 2004; Sauseng et al., 2005). Frontal theta activity in particular has been associated with the mental manipulation of WM, because these oscillations were enhanced in tasks such as mental calculation and image transformation (Kawasaki et al., 2010). In contrast, posterior alpha activities are thought to be involved in the WM storage systems, because these oscillations are mainly observed in the retention intervals of many WM tasks. However, whether these oscillatory activities are increased or decreased during each WM period remains controversial. Furthermore, little is known regarding how these oscillations represent WM limitations; therefore, their detailed mechanisms have not yet been identified. To clarify the functional role of the theta and alpha oscillations in WM, the study described in the following 2 sections used EEG data measured during DMS and dual WM tasks to demonstrate 2 types of EEG activity that were correlated with the WM capacities for visual storage and central executive systems.

4. EEG oscillations for visual storage capacity

This section describes the investigation of EEG oscillatory activity correlated with VWM capacity, which aimed to identify the roles of different oscillations in the VWM storage

systems (e.g., maintenance of high or low VWM demands). EEG data was measured during the DMS task.

4.1 Delayed matching to sample task

Fourteen healthy, right-handed volunteers (10 male and 4 female; mean age = 25.6 ± 4.2 years, range 21–38 years) with normal or corrected-to-normal visual acuity, normal hearing acuity, and normal motor performance took part in the delayed matching to sample tasks. All participants gave written informed consent, which was approved by the Ethical Committee of the RIKEN (in accordance with the Declaration of Helsinki), before the experiments were performed. Participants faced a computer screen and were asked to memorize the colors of 3 or 6 colored disks (size, 1° × 1°; color, white, red, green, blue, yellow, magenta, cyan, or orange) that were distributed at random locations within an invisible 3 × 3 cell matrix in a black rectangle (size, 10° × 10°) for 0.2 s (Fig. 2, sample display). After a 2-s retention interval, one disk was presented at one location within the sample array (test display), and participants were asked to judge whether its color matched the disk at the same location in the sample display via a button press while the fixation point was red for 2 s. In one trial, the color of the probe disk matched the sample disk, and in a second trial, the color of the probe disk did not match. After the judgment, a feedback stimulus indicating whether the answer was correct (O) or incorrect (X) was presented. The duration of the inter-trial interval (ITI) was 2 s. Each participant completed 4 separate sessions which consisted of 48 trials. A behavioral training session before the EEG-measurement sessions was provided for all participants.

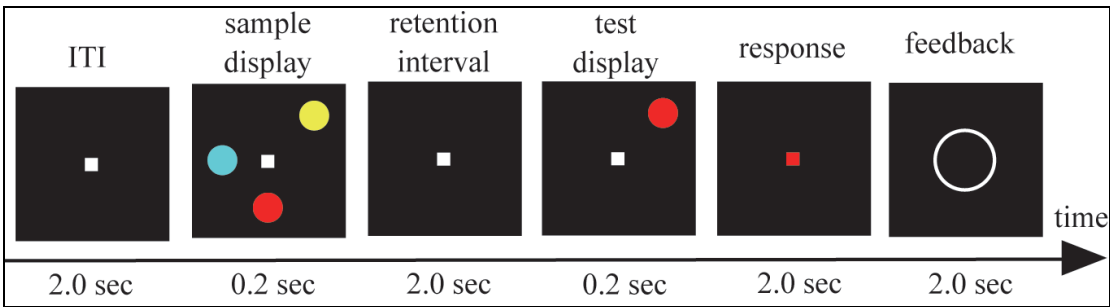


Fig. 2. Task procedure for 1 trial of the delayed-matching-to-sample task.

4.2 EEG measurements and analyses

An EEG was continuously recorded using 60 scalp electrodes embedded in an electrode cap in accordance with the extended version of the International 10/20 System of Electrode Placement. The sampling rate was 500 Hz. Reference electrodes were placed on the right and left earlobes. Artifacts due to eye blinks and movements were detected by electro-oculogram (EOG) electrodes placed above and below the left eye to monitor eye blinks and vertical eye movements, and electrodes placed 1 cm from the right and left eyes to monitor horizontal eye movements. Trials in which the amplitude of any electrode of an EEG epoch exceeded plus or minus 100 μV were rejected from the offline analysis. These EEG data were amplified using NeuroScan equipment (Compumedics NeuroScan Corp., Charlotte, NC) and filtered with a band-pass range from 0.1 Hz to 50 Hz.

We analyzed the EEG data for the correct trials. These epochs were subjected to infomax independent component analysis (ICA) with the use of EEGLAB (Delorme & Makeig, 2004;

Institute for Neural Computation, University of California, San Diego, CA) running under Matlab (Mathworks, Natick, MA). ICA components that were significantly correlated with vertical or horizontal EOGs were regarded as components related to eye movement or other artifacts and were reduced or eliminated from the data. The ICA-corrected data were recalculated using regressions on the remaining components.

To accurately evaluate cortical activity under the scalp EEG electrodes without error due to volume conduction, we used a current source density analysis at each electrode position. The spherical Laplace operator was applied to the voltage distribution on the surface of the scalp using the following parameters: the order of the spline, $m = 4$, and the maximum degree of the Legendre polynomial, $n = 50$, with a precision of 10^{-5} (Perrin et al., 1989).

Time-frequency (TF) amplitudes and phases were calculated by wavelet transforms based on Morlet's wavelets, having a Gaussian shape in the time domain ($SD \sigma_t$) and frequency domain ($SD \sigma_f$) around a center frequency (f) (Tallon-Baudry et al., 1997). The TF amplitude $E(t, f)$ for each time point of each trial was the squared norm of the result of the convolution of the original EEG signal $s(t)$ with the complex Morlet's wavelet function $w(t, f)$:

$$w(t, f) = (\sigma_t \sqrt{\pi})^{-1/2} \exp(-t^2 / 2\sigma_t^2) \exp(i2\pi ft) \quad (4)$$

$$E(t, f) = |w(t, f) \otimes s(t)|^2 \quad (5)$$

where $\sigma_t = 1/(2\pi\sigma_f)$. The wavelet used was characterized by a constant ratio ($f/\sigma_f = 7$), with f ranging from 1 Hz to 40 Hz in 0.5-Hz steps. The TF amplitude was averaged across single trials for events and conditions. The event-related TF amplitude was calculated by subtracting the baseline data measure in the ITI for each frequency band. For all statistical analyses, a nonparametric Wilcoxon signed-rank test was used across the events or conditions because the distributions of the TF amplitude populations were far from Gaussian.

4.3 Results

Accuracy rates (percent correct) for lower numbers of presented objects were higher than those for larger numbers of presented objects (3 objects: $90.2 \pm 2.0\%$; 6 objects: $72.6 \pm 2.8\%$). A one-factor analysis of variance (ANOVA) revealed a main effect of the number of objects ($F_{1, 26} = 24.3$, $P < 0.01$) and the accuracy rates demonstrated a significant difference (Wilcoxon signed-rank test; $Z = 3.71$, $P < 0.01$).

The VWM capacity was estimated by Cowan's K formula (see Section 2; 3 objects: $K = 2.41 \pm 0.12$; 6 objects: $K = 2.71 \pm 0.33$). A one-factor ANOVA revealed no main effect of the number of objects ($F_{1, 26} = 0.64$, $P = 0.43$), and no significant difference between K -values was detected between 3 and 6 objects ($Z = 1.18$, $P = 0.24$). These results suggested that the VWM capacity in our experiments was limited to approximately 2.7 objects.

Brain activity was evaluated using the averaged time-frequency amplitudes of the EEG data obtained during the DMS task. The EEG results demonstrated that parietal alpha amplitudes (about 12 Hz) sustainably and significantly increased during the retention intervals (POz electrode: $Z = 2.11$, $P < 0.04$), whereas enhancement of the frontal theta delay-period amplitudes (about 6 Hz) was not observed (Fz electrode: $Z = 0.18$, $P = 0.85$). Frontal theta activity during maintenance of 6 objects was significantly higher than that for maintenance of 3 objects (3 objects: $-0.28 \pm 0.21 \mu V$; 6 objects: $0.55 \pm 0.40 \mu V$; $Z = 2.12$, $P < 0.04$). In contrast, parietal alpha activity demonstrated an opposing pattern (3 objects: $2.06 \pm$

0.66 μV ; 6 objects: $0.45 \pm 0.45 \mu\text{V}$; $Z = 1.97$, $P < 0.05$). Interestingly, frontal theta activity was significantly and positively correlated with the VWM capacity of the individual (Fz electrode: $r(14) = 0.39$, $P < 0.05$), whereas the parietal alpha activity was negatively correlated with the VWM capacity (Poz electrode: $r(14) = -0.44$, $P < 0.05$).

4.4 Discussion

The observed VWM capacity was about 3 objects, which is consistent with many previous findings using simple visual features (Luck & Vogel, 1997). In relation to the behavioral results, the EEG results revealed that the frontal theta and parietal alpha amplitudes were sustainably enhanced during the retention interval of the DMS task. Interestingly, frontal theta activity demonstrated a positive correlation with individual WM capacity, whereas parietal alpha activity demonstrated a negative correlation.

In addition to confirming previous reports that these oscillations are involved in VWM (; Klimesch et al., 2008; Jensen & Tesch, 2002; Jensen et al., 2002), the present study was able to dissociate their functions. Frontal theta activities have been associated with central executive functions including mental manipulation and calculation tasks (Kawasaki et al., 2010) and in supporting VWM storage during high-VWM loads and demands (Curtis & D'Esposito, 2003; Kawasaki & Watanabe, 2007; Sakai et al., 2002). Parietal alpha activity has been proposed to reflect simple WM storage. Indeed, many neuroimaging studies using the DMS task with simple visual features (e.g., color) have shown that parietal activity was correlated with VWM capacity and decreased beyond the limit of VWM capacity, unlike increased frontal activity (Linden et al., 2003; Rypma et al., 2002). These results suggested that parietal alpha activity may be involved essentially only in the maintenance of limited visual information, whereas the frontal theta activity seems to assist in VWM storage under high VWM demand, as if instead of the suppressed alpha activity.

5. EEG oscillations for central executive

This section describes the investigation of EEG oscillatory activities that represent the WM limitations for executive functions by comparing dual and single WM tasks. The dual tasks required 2 separate perceptual domains: mental manipulation with visual stimuli and the mental calculations with auditory stimuli.

5.1 Dual WM task for visual and auditory representations

Fourteen healthy volunteers (10 male and 4 female; mean age = 27.92 ± 6.76 years, range 21–41 years; 13 right-handed) with normal or corrected-to-normal visual acuity, normal hearing acuity, and normal motor performance took part in the single visual and dual WM tasks. All participants gave written informed consent, which was approved by the Ethical Committee of the RIKEN (in accordance with the Declaration of Helsinki), before the experiments were performed.

For the single VWM task, at the beginning of each trial, 5×5 gridded squares and a red circle included within one of those squares were presented on the computer screen as the visual stimulus for 1 s (Fig. 3A). The participants were required to memorize and then maintain the position of the red circle for 2 s after the visual stimulus disappeared. A white arrow designating a direction (up, down, right, or left) to which the participants should move the red circle in their minds was then presented at the center of screen for 1 s. The participants manipulated the mental representations for 2 s. Like the auditory working

memory condition, the participants were required to repeat the mental manipulation 4 times, and then determine whether the position of the red circle which they mentally moved matched a probe visual stimulus (test display). In half of the trials, the probe stimulus matched the mental representation. In the remaining trials, the wrong probe was presented by changing only the fourth direction of movement from the initial position. The participants were asked to indicate via button press whether the probe stimulus was correct or not while the fixation point was red for 2 s. The duration of the ITI was 2 s. The size of the red circle and gridded squares was $1^{\circ} \times 1^{\circ}$ and $5^{\circ} \times 5^{\circ}$ ($1^{\circ} \times 1^{\circ}$ per square), respectively. For the dual WM task, the participants were asked to complete an auditory WM task simultaneously to the visual task (Fig. 3B). When the visual stimuli described above were presented on the computer screen, a word indicating a one-digit number was simultaneously presented as the auditory stimulus through the headphones of both ears for 1 s (sample display). The auditory WM task required the participants to memorize and maintain the presented number with rehearsal in their minds and, after a 2-s retention interval, to update the number by adding the another presented one-digit number for 2 s. After this a total of 4 incidences of auditory and visual manipulation, auditory and visual stimuli were simultaneously presented again, and participants were required to judge whether or not they were identical to the manipulated mental representation for both auditory and visual tasks (test display). In half of the trials, both the auditory and visual probe stimulus matched the mental representations. In the remaining trials, the incorrect probe for either the auditory or visual stimulus was presented, similar to the single VWM condition. The button press, duration of the inter-trial interval, and creation of the stimuli were identical to the single WM condition.

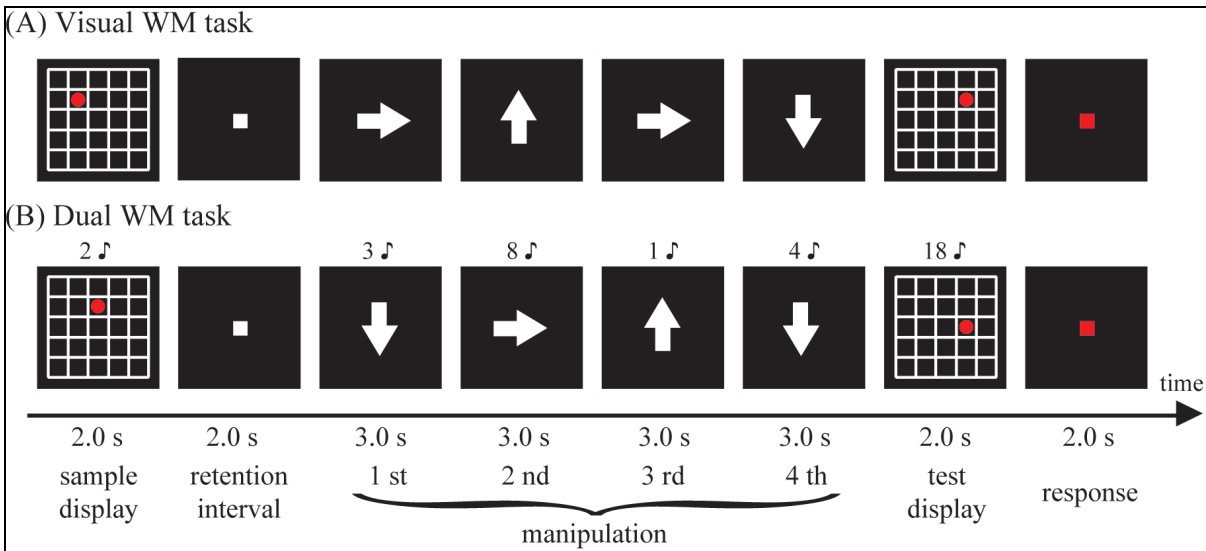


Fig. 3. Task procedure for one trial of the single visual WM (A) and dual WM (B) tasks.

5.2 EEG measurements and analyses

The same methods were used as described in Section 4.2.

5.3 Results

All participants performed all the WM tasks with high accuracy rates (mean accuracy rate (\pm s.d.), $97.3 \pm 4.7\%$ and $91.1 \pm 7.1\%$ for visual and dual WM conditions, respectively).

Significant differences in performance were detected between the single and dual WM conditions (Wilcoxon signed-rank test; $Z = 2.87$, $P < 0.01$), suggesting the presence of dual-task interference, that is, degraded performance of 2 simultaneous tasks relative to a single task (e.g., psychological refractory period) (Logan & Gordon, 2001; Pashler, 1994).

Time-frequency analyses of the recorded EEG data revealed enhanced theta amplitudes (4–6 Hz) of the 4 manipulation periods relative to those of the ITI in the frontal and parietal regions in both the single visual and dual WM conditions (single WM: AF3 electrode, $Z = 3.53$, $P < 0.01$; Pz electrode, $Z = 2.04$, $P < 0.05$; dual WM: AF3 electrode, $Z = 3.71$, $P < 0.01$; Pz electrode, $Z = 3.01$, $P < 0.01$). The increased frontal theta amplitudes during the dual WM conditions were significantly higher than those during the single VWM condition (AF3, $Z = 2.24$, $P < 0.03$), whereas this difference was not observed in the parietal theta activities (Pz, $Z = 0.68$, $P = 0.49$).

In addition to the theta amplitudes, alpha amplitudes (9–12 Hz) were increased only in the parietal regions during manipulation periods in the single visual WM condition (single WM: AF3, $Z = 1.15$, $P = 0.25$, Pz, $Z = 2.19$, $P < 0.05$; dual WM: AF3 electrode, $Z = 1.11$, $P < 0.27$; Pz electrode, $Z = 2.39$, $P < 0.02$). Parietal alpha amplitudes demonstrated no significant difference between the single and dual WM conditions (Pz, $Z = 1.78$, $P = 0.08$). Moreover, enhanced parietal alpha activity was observed during the retention intervals as well as the manipulation periods (Pz, $Z = 0.49$, $P = 0.62$).

5.4 Discussion

The EEG results concerning oscillatory amplitudes demonstrated the bottlenecks of central executive function in WM. In our recent study using single visual and auditory WM tasks, the frontal theta activity was mainly observed during the manipulation period and not the maintenance periods, whereas posterior alpha activity was enhanced both in the manipulation and maintenance periods (Kawasaki et al., 2010). Building upon those previous findings, the present study demonstrated that frontal theta activity further increased in the dual WM task in comparison to the single VWM task, whereas parietal alpha activity did not differ between the single and dual WM tasks. In this study, the dual WM task required a large amount of mental manipulation compared to the single WM task. However, the amount of visual representations to be remembered for the dual WM task was almost same that required for the single VWM task. Therefore, these results indicate that the bottlenecks for central executive function are represented by frontal theta activity, which is supported by the earlier evidence that the frontal cortex is associated with active manipulation, and the posterior regions are involved in simple maintenance (Curtis & D'Esposito, 2003; Postle et al., 1999; Rowe et al., 2000; Smith & Jonides, 1999; Wager & Smith, 2003). These results suggest that concurrent frontal theta and alpha activity is associated with the hierarchical control structures of the multiple operations involved in dual WM tasks.

6. Conclusion

Using data from 2 EEG experiments, this study has demonstrated the brain oscillations that are related to WM capacities for visual storage and central executive function. Frontal theta and parietal alpha activities represented the storage limitations under conditions of high and low WM demands, respectively. Moreover, frontal theta activity was also related to bottlenecks in central executive function, which is necessary to perform dual WM tasks. In addition to confirming previous findings concerning regional dissociations between WM

functions, the present study further suggests important roles for these brain oscillations, which reflect different local synchronizations within specific cell assemblies, in the WM process: theta for manipulation and alpha for maintenance.

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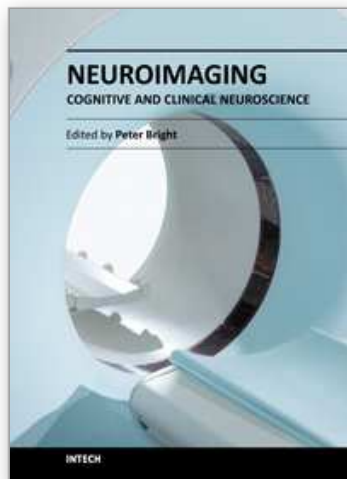
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The rate of technological progress is encouraging increasingly sophisticated lines of enquiry in cognitive neuroscience and shows no sign of slowing down in the foreseeable future. Nevertheless, it is unlikely that even the strongest advocates of the cognitive neuroscience approach would maintain that advances in cognitive theory have kept in step with methods-based developments. There are several candidate reasons for the failure of neuroimaging studies to convincingly resolve many of the most important theoretical debates in the literature. For example, a significant proportion of published functional magnetic resonance imaging (fMRI) studies are not well grounded in cognitive theory, and this represents a step away from the traditional approach in experimental psychology of methodically and systematically building on (or chipping away at) existing theoretical models using tried and tested methods. Unless the experimental study design is set up within a clearly defined theoretical framework, any inferences that are drawn are unlikely to be accepted as anything other than speculative. A second, more fundamental issue is whether neuroimaging data alone can address how cognitive functions operate (far more interesting to the cognitive scientist than establishing the neuroanatomical coordinates of a given function - the where question).

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