



Research article

The different oscillation patterns of alpha band in the early and later stages of working memory maintenance



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HIGHLIGHTS

- Two patterns of alpha band oscillations were observed in the early and late stage of working memory maintenance.
- Alpha power decreased in the early stage of working memory maintenance may involve in focused attentional.
- Whereas alpha power increased in the later stage of working memory maintenance may reflect intentional suppression.

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ABSTRACT

A putative functional role for alpha oscillations in working memory remains controversial. However, recent evidence suggests that such oscillation may reflect distinct phases of working memory processing. The present study investigated alpha band (8–13 Hz) activity during the maintenance stage of working memory using a modified Sternberg working memory task. Our results reveal that alpha power was concentrated primarily in the occipital cortex and was decreased during the early stage of maintenance (0–600 ms), and subsequently increased during the later stage of maintenance (1000–1600 ms). We suggest that reduced alpha power may be involved in focused attention during the working memory maintenance, whereas increased alpha power may reflect suppression of visual stimuli to facilitate internal processing related to the task. This interpretation is generally consistent with recent reports suggesting that variations in alpha power are associated with the representation and processing of information in the discrete time intervals during the working memory maintenance.

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1. Introduction

Working memory (WM) involves the ability to maintain and manipulate information in a brief period and use it for further cognitive tasks [27]. There have been considerable electrophysiology studies that concentrate on WM, to investigate how the brain represents internal information when lacking input about external stimuli. These studies have provided evidence of a relationship between neuronal oscillations (e.g., alpha, theta and gamma bands) and the WM maintenance in humans [15,38]. However, the functional significance of these oscillation frequencies remains unclear.

To illustrate, alpha band activity (8–13 Hz) is a dominant oscillation rhythm in the resting state, traditionally thought to reflect passive or idling states of the brain, but a modern views implicates

this activity in basic cognitive processes, including sensory, motor, and memory processes [13,43]. In line with this perspective, alpha oscillation has been observed in WM. For example, Jensen and colleagues [31] examined EEG data during the maintenance stage of visual WM using a modified Sternberg task and found that alpha band activity increased in the WM maintenance. Similarly, alpha band oscillations have also been found in auditory and somatosensory modalities during the WM maintenance [20,36]. In addition, a memory load-dependent change has been demonstrated [31,37], wherein alpha peak proportionally rises with the number of items maintained in WM.

Despite the consistent view that alpha band oscillations are involved in WM maintenance, the functional interpretation is inconsistent. Some authors have suggested that the alpha fluctuations in the WM maintenance are involved in the functional inhibition of tasks in irrelevant brain areas [10,31,33], while others linked alpha band activity directly to processes underlying WM maintenance [37,39]. Furthermore, there are some differences in alpha band oscillation patterns during the WM maintenance. Con-

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current strong frontal alpha power and weak occipital alpha power have been reported in the maintenance stage of WM [22,34]. In addition, alpha band enhancement in the cuneus and reduction in the precuneus have been observed during the WM maintenance [25]. Others have reported augmentation of alpha band power [30,31] and suppression of alpha band power [46] in the parieto-occipital regions over whole stage of WM maintenance.

The controversy between these findings and prevailing interpretations may reflect the existence of discrete stages existing in the WM maintenance. WM maintenance has been proposed to consist of two different levels of processing: an early stage during which the perceptual representation is rehearsed and a later stage involving deeper analysis of the stimulus [16]. The behavioral and neuroimaging studies supported this proposition. For example, by performing interference task in the maintenance stage, Bergmann et al. [18] found a possible functional distinction in the early and later stages of WM maintenance. The early stage may relate to the construction of a mental representation, whereas the later stage may reflect the retention of stored information. Moreover, these discrete stages of WM maintenance have been found to exhibit different activities in brain regions in an fMRI study [8]. Specifically, activity in the left dorsolateral prefrontal cortex and hippocampus increased during the early stage, while excitability of the posterior parietal and occipital areas occurred in later stage. In addition, Heinrichs-Graham and Wilson [14] observed a transition in alpha band activity during the WM maintenance stage using high-density MEG. They indicated that alpha band activities decreased in the early stage (2.2–2.6 s) and increased during the middle and later stage (3.0–3.4 s) in the bilateral occipital cortices. These results suggested that processing during the early and late stages of WM maintenance might be qualitatively discriminated. Then, the possible functional dissociation during the WM maintenance means that the different time courses of neuronal oscillations might be involved in different cognitive functions. However, this perspective has not been given much attention in previous research, WM maintenance is seen as an intact process rather than functional separation. This may result in controversy about the functional activities of alpha band oscillation during the WM maintenance stage.

The main aim of the present study was to investigate the time courses of alpha oscillations during the WM maintenance stage, and to elucidate the possible functions of alpha rhythm within the information representation without external stimulation.

2. Experimental procedures

2.1. Subjects

Twenty adults participated in the study. All subjects were right-handed and had normal or corrected vision. Two of them were excluded because of poor memory performance (<50% correct on either trial type), and two subjects were removed due to extreme artifacts on EEG waveforms. Thus, all analyses were conducted for the remaining 16 participants (10 males, 6 females; mean age = 21.10 years, SD = 5.6 years). Participants gave signed informed consent prior to the study and received financial compensation for participation. The Ethical Committee of the Third Military Medical University approved the protocols conducted in this study.

2.2. Experimental task

The task used in the present study was a modified Sternberg WM task. The subjects were instructed to memorize short lists of the letters (two, four, six and eight), which were in capital letters,

Arial, grey font, size 60, and presented on a 19-in CRT computer monitor. After a brief delay, the probe stimulus was shown and participants were asked to indicate whether the probe item had been on the previous list using a rapid button-press response. During the task processes including maintenance interval, the participant kept eyes open. The task consisted of 4 testing blocks, with 24 trials for each block, for 96 trials. Trials were randomly presented. Within each block, half of probe stimuli were repeatedly presented on the list. The serial position effect was also controlled in the procedure. To ensure that the subjects understood the task, they completed one practice block consisting of 12 trials prior to beginning the testing block. The details of an experimental trial were shown in Fig. 1a.

2.3. EEG data record

EEG signals were recorded from 64 Ag/AgCl electrodes at a sampling rate of 1000 Hz using a SynAmps amplifier (Neuroscan, Compumedics, Inc.). The 64 scalp electrodes were positioned according to the international 10–20 system. Reference electrodes were placed on the bilateral mastoids. The impedance of the electrode was kept below 5 K Ω on average. Additional vertical (from above and below the left eye) and horizontal (from left and right outer canthi) eye movements were recorded. All subjects were instructed to minimize muscle tension, eye movement and blinking.

2.4. Data processing

Offline EEG data processing was performed using the EEGLAB 13.0.3.2b toolbox [1] for the Matlab 2013b platform (MathWorks, Natick, MA, USA). First, continuous EEG data was re-referenced to the average of the right and left mastoid, and band-pass filtered at 1–100 Hz. EEG epochs were extracted for the period of –0.4 s prior to onset to 2 s following the delay end and down-sampled at 250 Hz. Trials showing an unacceptable EEG waveform based on extreme values in a trial ($\pm 100 \mu\text{V}$) were removed from further analysis. An extended informax independent component analysis (ICA) [2], implemented in EEGLAB, was used to obtain 60 independent components (ICs) from each participant (in total $60 \times 16 = 960$ ICs). For all ICs, an equivalent current dipole location was estimated using DIPFIT 2.3. The head model of the Montreal Neurological Institute (MNI) standard coordinate system and Colin27-MRI-average anatomical template were used. ICs displaying greater residual variance than 15% were rejected from further analysis.

To obtain the spectral power and phase at each time point and frequency band, event-related spectral perturbation (ERSP) was calculated using time-frequency analysis. As a default setting of EEGLAB, wavelet zero-padded discrete Fourier transforms using the morlet taper were selected to calculate the power and phase of the signal. K-means clustering was performed to make IC clusters for conducting group analysis, using the criteria of dipole locations (dimension: 3; normalization; weight: 8), ERSP (latency: 0–600 ms and 1000–1600 ms; frequency: 1–100 Hz; dimension: 8; normalization; weight: 8) and scalp topography (dimension: 8; normalization; weight: 5).

3. Results

3.1. Behavior data

Performance was evaluated in terms of correct reaction times (RTs) (including correct hit and correct reject) and accuracy rate (ACC), which was measured for the test arrays relative to all trials presented. Overall, the subjects performed well above chance

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