

Oscillatory activity during maintenance of spatial and temporal information in working memory

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ABSTRACT

Working memory (WM) processes help keep information in an active state so it can be used to guide future behavior. Although numerous studies have investigated brain activity associated with spatial WM in humans and monkeys, little research has focused on the neural mechanisms of WM for temporal order information, and how processing of temporal and spatial information might differ. Available evidence indicates that similar frontoparietal regions are recruited during temporal and spatial WM, although there are data suggesting that they are distinct processes. The mechanisms that allow for differential maintenance of these two types of information are unclear. One possibility is that neural oscillations may differentially contribute to temporal and spatial WM. In the present study, we used scalp electroencephalography (EEG) to compare patterns of oscillatory activity during maintenance of spatial and temporal information in WM. Time-frequency analysis of EEG data revealed enhanced left frontal theta (5–8 Hz), enhanced posterior alpha (9–12 Hz), and enhanced left posterior beta (14–28 Hz) power during the delay period of correct temporal order trials compared to correct spatial trials. In contrast, gamma (30–50 Hz) power at right lateral frontal sites was increased during the delay period of spatial WM trials, as compared to temporal WM trials. The present results are consistent with the idea that neural oscillatory patterns provide distinct mechanisms for the maintenance of temporal and spatial information in WM. Specifically, theta oscillations are most critical for the maintenance of temporal information in WM. Possible roles of higher frequency oscillations in temporal and spatial memory are also discussed.

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1. Introduction

Working memory (WM) is a core cognitive function that supports the active maintenance and manipulation of various domains of information in order to complete complex and everyday tasks (Baddeley, 1992). A major breakthrough in understanding the neural mechanisms of WM originated from studies in monkeys, which demonstrated that single neurons in the prefrontal cortex (PFC; Fuster & Alexander, 1971; Funahashi, Chafee, & Goldman-Rakic, 1993; Kojima & Goldman-Rakic, 1982; Sawaguchi & Yamane, 1999) and posterior parietal cortex (Chafee & Goldman-Rakic, 1998, 2000; Curtis, Rao, & D'Esposito, 2004; Gnadt & Andersen, 1988) show persistent, location-specific activity during tasks that require the active short-term retention of spatial locations in WM. Building on this research, much of the literature on neural mechanisms for WM in humans has focused on spatial WM, and, in contrast, little is

known about the neural underpinnings of memory for temporal order information.

Behavioral evidence suggests that the processes which support WM for temporal order may be different from those that support WM for spatial location information (Delogu, Nijboer, & Postma, 2012a,b; Gmeindl, Walsh, & Courtney, 2011). These findings seemingly conflict with physiological and neuroimaging studies, which indicate that the same frontal and parietal cortical regions that support spatial WM also support WM for temporal order. For instance, single neuron activity in frontal and parietal regions has been associated with the maintenance of temporal information (Funahashi, Inoue, & Kubota, 1997; Ninokura, Mushiaki, & Tanji, 2003, 2004). Furthermore, human neuroimaging studies have shown that activity in PFC and posterior parietal cortex is increased during tasks that require WM for temporal order (Amiez & Petrides, 2007; Marshuetz, Smith, Jonides, DeGutis, & Chenevert, 2000; Marshuetz & Smith, 2006).

One possible explanation that may resolve these inconsistencies in the literature is that, although similar brain regions might support maintenance of spatial and temporal information, it is conceivable that neural oscillations could differentially support

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these forms of WM. These oscillatory patterns might represent distinct mechanisms for maintaining these different types of information. Work in computational neuroscience has led to the idea that theta oscillations (5–8 Hz) might play an essential role in the retention of temporal order information (Cutsuridis & Hasselmo, 2012; Lisman & Idiart, 1995; Lisman & Buzsaki, 2008; Jensen, 2006; Wallenstein & Hasselmo, 1997). Neural oscillations in the theta band have been shown to increase at frontal sites with WM load or difficulty (Gevins, Smith, McEvoy, & Yu, 1997; McEvoy, Pellouchoud, Smith, & Gevins, 2001; Meltzer, Negishi, Mayes, & Constable, 2007; Schmiedt, Brand, Hildebrandt, & Basar-Eroglu, 2005; Jensen & Tesche, 2002), and with successful memory performance (Klimesch, Doppelmayr, Pachinger and Ripper (1997); Haenschel et al., 2009; Rutishauser, Ross, Mamelak, & Shuman, 2010; Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011). Furthermore, Hsieh, Ekstrom, & Ranganath (2011) compared oscillatory activity during tasks that required either active maintenance of temporal order or active maintenance of visual object details. They found that frontal theta oscillations were enhanced during maintenance of temporal order relative to visual object information.

In addition to theta, there is reason to believe that oscillatory activity in other frequency bands might also relate to temporal or spatial WM maintenance. For instance, alpha oscillations (9–12 Hz), often associated with “idling,” (Pfurtscheller, Stancak, & Neuper, 1996), have more recently been associated with cognitive control processes that support active maintenance of information in WM (Hsieh et al., 2011; Johnson, Sutterer, Acheson, Lewis-Peacock, & Postle, 2011; Nenert, Viswanathan, Dubuc, & Visscher, 2012; Palva & Palva, 2007). According to one hypothesis the primary role for alpha oscillations in WM is in the inhibition of irrelevant stimuli (Freunberger, Werkle-Bergner, Griesmayr, Lindenberger, & Klimesch, 2011; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007), or more generally, inhibition of brain regions that are not critical for the relevant task (Jensen & Mazaheri, 2010). This gate-keeping function may allow for more robust and efficient WM maintenance, although it is not clear whether this would differentially support spatial or temporal WM processing. Beta oscillations (14–28 Hz) have been associated with shifts in attention (for review see Wrobel (2000)), as well as filtering irrelevant visual representations (Waldhauser, Johansson, & Hanslmayr, 2012), and gamma oscillations, centered around 40 Hz, have been associated with a variety of cognitive functions, as well as the processing of both temporal (Lisman & Idiart, 1995; Lisman & Buzsaki, 2008; Lisman & Redish, 2009) and spatial (Kaiser & Lutzenberger, 2005; Van Der Werf, Buchholz, Jensen, & Medendorp, 2012) information in cognitive tasks. In light of the findings described above, we sought to determine whether alpha, beta, and gamma activity would be differentially associated with temporal or spatial WM maintenance.

To investigate the role of oscillatory activity associated with temporal and spatial WM processes, we recorded scalp EEG during two tasks that required maintenance of either the temporal order or spatial positions associated with each of four objects, which were selected from a pool of sixteen basic shapes. In this task, temporal and spatial trials were intermixed, and stimuli were presented in randomized order and location on the screen. Each trial began with an instruction that indicated the trial type. During temporal trials, subjects were instructed to maintain the order in which stimuli were presented on the screen, whereas, in spatial trials, they were instructed to maintain the quadrant of the screen in which each stimulus was presented. We anticipated that subjects would incidentally maintain both spatial and temporal information on each trial, as it is natural to do so, and many subjects reported remembering information about both domains even when they were trying to inhibit irrelevant information. However, the critical issue was that participants needed

to place greater emphasis on maintenance of either spatial or temporal information in order to perform a given task accurately. Based on the findings of Hsieh et al. (2011), we predicted that theta power during the delay period of the WM task would be increased during maintenance of temporal, as compared with spatial information. In addition, based on the evidence described above, we investigated activity differences in the alpha, beta, and gamma bands as well, although we did not have strong *a priori* predictions about whether activity in these bands would differentiate between spatial and temporal WM maintenance.

While Hsieh et al. (2011) reported differences in EEG oscillations related to WM for temporal order information, this study only examined the differences in activity between temporal order and visual object WM. Given that meaningful interpretations of EEG require comparison between conditions, this study could only tell us about neural oscillations during temporal WM as it relates to visual object WM, and thus leaving open the question of how oscillatory activity compares between spatial and temporal WM. This is an important question, given that recent studies in auditory WM (Delogu et al., 2012a,b; Gmeindl et al., 2011) indicate that spatial and temporal WM are, in fact, separable processes. Therefore, further research is necessary to provide additional information regarding the role of neural oscillations in temporal WM, and how neural oscillations uniquely contribute to temporal and spatial WM. The aim of this study was to investigate how temporal and spatial information are differentially maintained in WM. Understanding these relationships between neural oscillations is an essential step in characterizing the neural implementation of WM maintenance processes.

2. Materials and methods

2.1. Participants

18 healthy undergraduate subjects were recruited from the University of California, Davis community. Participants ranged in age from 18 to 24 years of age, with an average of 20.6 years of age $\pm$ 0.381 SEM. All participants were right-handed. Seven subjects were female. Data from one subject was excluded due to poor memory performance ($< 50\%$ correct on either trial type), and data from one subject was excluded due to excessive artifacts in the recorded EEG. The study was approved by the Institutional Review Board at the University of California, Davis. Written informed consent was obtained from each subject before the experiment.

2.2. WM task

The paradigm for the WM task is illustrated in Fig. 1. Stimuli consisted of sixteen basic shapes, but the same shapes were never presented in consecutive trials. All shapes were white, and were presented on a black background. Shapes were approximately 3.5×3.5 in. in size. There were no differences in color or luminance across stimuli. Each trial began with a fixation for 1000 ms, followed by an instruction slide for 1000 ms, which indicated “Order” or “Location.”

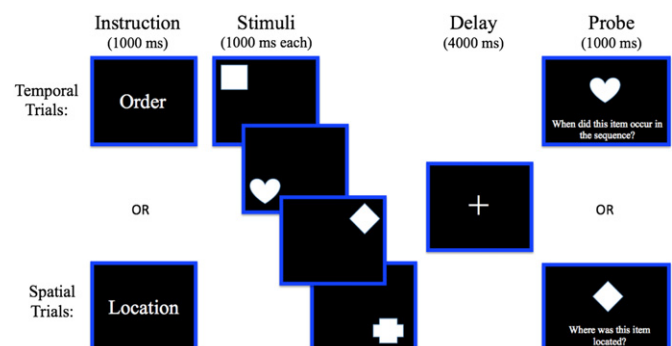


Fig. 1. Schematic depiction of stimuli and timing of trial events in the WM task.

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