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NEURAL OSCILLATORY CORRELATES OF DURATION MAINTENANCE IN WORKING MEMORY

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Abstract—Working memory (WM) is a core element of temporal information processing, but little is known about the internal representation and neuronal underpinnings of the duration maintenance in WM. The neural oscillations during maintenance of duration in WM were examined using electroencephalogram (EEG) recordings. The EEG results showed that theta amplitude was not modulated by the length of duration retained in WM, while alpha amplitude decreased in a 4-s duration condition compared with 1-s, 2-s, and 3-s duration conditions. The amplitude of alpha power positively correlated with accuracy for the 3-s duration condition. The results suggest that alpha activity is involved in duration maintenance in WM. Our study provides electrophysiological evidence that different internal representations are retained in WM for durations below and above about 3 s.

Key words: temporal information, duration, working memory, neural oscillation.

INTRODUCTION

Although there is no specific biological system that senses time, as there is for sight, hearing, and taste, we can perceive and process temporal information, and effectively use timing in our daily activities(Buhusi and Meck, 2005; Meck et al., 2013; Merchant et al., 2013). Working memory (WM), the short-term storage and online manipulation of information (Baddeley, 1992), is possibly a core element of temporal information processing. The internal representation of the external event duration must be stored in WM before it is transferred into long-term reference memory; the representation of reference duration can be temporally held in the WM after it is retrieved from long-term memory (Gibbon, 1977; Gibbon et al., 1984; Allan, 1998; Coull et al., 2008). Previous studies have confirmed that visual durations are retained in the visuospatial sketchpad, and auditory durations are retained in the phonological loop (Franssen et al., 2006; Rattat, 2010; Rattat and Picard, 2012). The neural networks underlying duration maintenance in WM are mainly cortico-striatal circuits involving frontal, parietal, and striatal regions (Sakurai et al., 2004; Coull et al., 2008; Genovesio et al., 2009; Harrington et al., 2010). However, more research is needed to understand the internal representation of duration retained in WM.

Some researchers have argued that separate mechanisms process durations below and above about 3 s. Perception of duration below about 3 s is based on the subjective present (Fraisse, 1984). A low-frequency binding mechanism integrates sensory inputs into a coherent experience or temporal gestalt (Pöppel, 1997). Durations above about 3 s can no longer be perceived as a unit, and estimation of longer duration is based on memory and cognitive reconstruction (Fraisse, 1984). There is some evidence to support this theory (Kagerer et al., 2002; Szelag et al., 2002; Ulbrich et al., 2007). One event-related potential (ERP) study found that temporal reproductions were accurate for durations up to 3 s, and accompanied by a slow negative wave named contingent negative variation (CNV), whereas the CNV was reduced or absent when durations longer than 3 s were processed (Elbert et al., 1991). Furthermore, a functional magnetic resonance imaging (fMRI) study revealed that the motor system and the default mode network process durations below and above 2 s, respectively (Morillon et al., 2009). Based on these theoretical and experimental findings, we hypothesized that different internal representations were retained in WM for durations below and above about 3 s.

The synchronous activity of neural oscillation is a critical link between single-neuron activity and behavior (Engel et al., 2001; Buzsáki and Draguhn, 2004). Theta and alpha band frequencies serve distinct functional roles during WM maintenance. It is widely reported that the oscillatory power in the theta band (4–8 Hz) over the prefrontal region increases with the number of items maintained in WM, such as locations (Gevins et al., 1997), letters (Gevins et al., 1997; Onton et al., 2005), and digits (Jensen and Tesche, 2002; Meltzer et al., 2007). Research shows that theta oscillation reflects the organization of sequentially ordered WM items (Hsieh et al.,

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Abbreviations: ACC, accuracy; ANOVA, analysis of variance; CNV, contingent negative variation; EEG, electroencephalogram; EOG, electrooculogram ; ERPs, event-related potentials; ERSP, event-related spectral perturbation; ICs, independent components; WM, working memory.

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2011; Roberts et al., 2013; Roux and Uhlhaas, 2014). Alpha band activity (8–12 Hz) over the parieto-occipital region increases with the number of items maintained in WM, such as locations (Gevins et al., 1997; Johnson et al., 2011), letters (Jensen et al., 2002), digits (Meltzer et al., 2007), shapes (Johnson et al., 2011), and faces (Jokisch and Jensen, 2007; Tuladhar et al., 2007). However, the precise role of the alpha band in WM is still under debate. Some scholars have proposed that oscillatory alpha activity reflects the inhibition of cortical areas representing task-irrelevant information (Jokisch and Jensen, 2007; Klimesch et al., 2007; Tuladhar et al., 2007; Manza et al., 2014), while others have suggested that alpha oscillation is related to successful maintenance of item information (Jensen et al., 2002; Palva and Palva, 2007; Hsieh et al., 2011; Johnson et al., 2011). Duration maintenance in WM has received much less attention compared with non-temporal stimulus properties, and the relationship between neural oscillation and duration maintenance in WM has yet to be identified.

In the present study, a matching-to-sample task was adopted to study the neural oscillatory correlates of duration maintenance in WM. This experimental paradigm is widely used to investigate the brain substrates of retention of duration in WM (Sakurai et al., 2004; Coull et al., 2008; Genovesio et al., 2009; Harrington et al., 2010). A sample stimulus and a probe stimulus are presented in succession, separated by a delay. Subjects are asked to judge whether the durations of the probe stimulus and the sample stimulus are identical or different. An advantage of this paradigm is that the encoding (timing), maintenance, and decision for temporal information can be separated (Coull et al., 2008; Harrington et al., 2010). To our knowledge, no previous study has reported the oscillatory correlates of duration maintenance in WM. We focused on the relationship between duration maintenance in WM and neural oscillations in theta and alpha bands, because previous studies on WM have delineated these bands well. In the present study, participants were required to retain one duration (1 s, 2 s, 3 s, or 4 s) in WM. As the theta band reflects the organization of sequentially ordered WM items (Hsieh et al., 2011; Roberts et al., 2013; Roux and Uhlhaas, 2014), the temporal order was equal for four duration conditions; thus, we predicted that the amplitude of the theta band would not be modulated by the length of duration retained in WM. As previously stated, we hypothesized that different internal representations would be retained in WM for durations below and above about 3 s. We inferred that if alpha oscillation is related to successful maintenance of item information (Palva and Palva, 2007; Hsieh et al., 2011; Johnson et al., 2011), then the alpha band activity would reflect different internal representations of durations below and above about 3 s retained in WM. If alpha oscillation reflects inhibition of task-irrelevant information (Jokisch and Jensen, 2007; Klimesch et al., 2007; Tuladhar et al., 2007; Manza et al., 2014), and there is no relationship between alpha band activity and internal representation of duration retained in WM, we would observe no significant alpha band difference between durations above and below about 3 s.

EXPERIMENTAL PROCEDURES

Participants

Eighteen right-handed undergraduates (six male), 20.67 ± 1.33 years of age, were paid for participation in the experiment. Each participant had normal or corrected-to-normal visual acuity and reported having normal hearing. Participants were not taking medications and did not suffer from any central nervous system abnormality or injury. The study was approved by the local institutional review board (RIB), and written informed consent was obtained from each participant. The experimental procedure was in accordance with the Declaration of Helsinki (World Medical Association, 2013).

Experimental material and apparatus

The visual stimuli were displayed on a black background in the center of a computer screen. There were two types of visual stimuli: a red circle and a question mark. The red circle was 3 cm in size (2.29°), its RGB values were [255, 0, 0], and its luminance was 48.5 cd/m^2. The question mark was white and 2 cm in size (1.53°). The refresh rate of the computer monitor was 85 Hz, and the computer screen was placed about 75 cm in front of participants.

Procedure

There were seven blocks of a matching-to-sample task in the experiment. Each block contained 48 trials. There were 84 trials for one duration condition in the experiment. As shown in Fig. 1, in each trial, two red circles (the sample stimulus and the probe stimulus) were presented in tandem, separated by an interstimulus interval of 3 s (the delay/maintenance phase). Each circle was presented randomly for one of four durations (1 s, 2 s, 3 s, or 4 s). After an interval of 1 s, a question mark (response signal) was presented in the center of the screen, and terminated by a key press, or after 2 s had elapsed. Participants had to estimate the duration of the second red circle (probe) as shorter, equal to, or longer than the first circle (sample). During the response period, participants pressed 1, 2, or 3 on the keyboard using the index, middle, or ring finger, respectively (1 denoted shorter, 2 denoted equal to, 3 denoted longer). Half of the participants responded with the left hand, and the other half responded with the right hand. An intertrial interval of 2 s was used.

Electrophysiological recording

Continuous electroencephalogram (EEG) was acquired from Ag/AgCl electrodes mounted in an elastic cap (Brain Products GmbH, Gilching, Germany). Sixty-four electrodes were positioned according to the extended 10–20 system. Additional electrodes were placed on the mastoids. The horizontal electrooculogram (EOG) was acquired using a bipolar pair of electrodes positioned at the external ocular canthi, and vertical EOG was recorded from electrodes placed below the left eye. The EEG and EOG were digitized at 500 Hz with an