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Functional connectivity among multi-channel EEGs when working memory load reaches the capacity

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ABSTRACT

Evidence from behavioral studies has suggested a capacity existed in working memory. As the concept of functional connectivity has been introduced into neuroscience research in the recent years, the aim of this study is to investigate the functional connectivity in the brain when working memory load reaches the capacity. 32-channel electroencephalographs (EEGs) were recorded for 16 healthy subjects, while they performed a visual working memory task with load 1–6. Individual working memory capacity was calculated according to behavioral results. Short-time Fourier transform was used to determine the principal frequency band (theta band) related to working memory. The functional connectivity among EEGs was measured by the directed transform function (DTF) via spectral Granger causal analysis. The capacity was 4 calculated from the behavioral results. The power was focused in the frontal midline region. The strongest connectivity strengths of EEG theta components from load 1 to 6 distributed in the frontal midline region. The curve of DTF values vs load numbers showed that DTF increased from load 1 to 4, peaked at load 4, then decreased after load 4. This study finds that the functional connectivity between EEGs, described quantitatively by DTF, became less strong when working memory load exceeded the capacity.

1. Introduction

Working memory (WM) refers to a limited-capacity memory system that provides temporary storage and manipulation of the information necessary for complex cognitive tasks such as comprehension, reasoning, planning and learning (Baddeley, 1992). WM capacity refers to the amount of information that can be maintained and manipulated in WM. Accumulated behavioral studies have found WM capacity was approximately four items (Cowan, 2001; Fukuda et al., 2010; Luck and Vogel, 1997, 2013). Asking observers to detect changes among arrays of colored squares following a brief retention period, Luck and Vogel found that the performance was nearly perfect for arrays for 1–3 items and then declined systematically as the set size increased from 4 to 12 items, which indicated that observers could hold about four items worth of information in WM (Luck and Vogel, 1997).

The neural mechanism underlying the capacity limitations in WM has attracted much interest. A handful of studies have systematically determined WM load-related effects in brain activity (Callicott et al., 1999; Leung et al., 2004; Linden et al., 2003). Two distinct responses have been identified to

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reflect the effect of WM capacity on WM load-related brain activity: (i) capacity-unconstrained responses, where brain activity increases as a function of WM load, and (ii) capacity-constrained responses, where brain activity increases with WM load until the load approaches the capacity and then levels off or decreases thereafter.

Electrophysiological (Li et al., 2011; Vogel and Machizawa, 2004) and neuroimaging studies (Callicott et al., 1999; Fusser et al., 2011; Linden et al., 2003; Mitchell and Cusack, 2008; Nyberg et al., 2009; Sauseng et al., 2009; Todd and Marois, 2004; Xu and Chun, 2006) have supported the capacity-constrained responses in WM load-related brain activity. Previous study found that the amplitude of event-related potential (ERP) was modulated by WM load. However, it approached a plateau when the load met or exceeded the capacity (Vogel and Machizawa, 2004). Using a parametric n-back working memory task, Callicott et al. (1999) reported that activities in the dorsolateral prefrontal cortex as well as in the parietal cortex evinced a capacity-constrained response, with activity decreasing from 2- to 3-back. Across numerous neuroimaging studies in humans, maintaining more information in WM leaded to larger activation in the frontal (e.g., dorsolateral prefrontal cortex, frontal eye fields) and parietal regions (e.g., intra-parietal sulcus) until WM load reached the capacity and then leveled off or declined, in consistent with the capacity-constrained responses.

Recently, studies on brain connectivity have attracted increasingly widespread attentions (Park and Friston, 2013; Rubinov and Sporns, 2010). A large number of studies have used functional connectivity to investigate WM system (Babiloni et al., 2004; Blinowska et al., 2013b; Gazzaley et al., 2004; Grady et al., 2001; Hampson et al., 2006; Lenartowicz and McIntosh, 2005). However, a relatively small number of functional connectivity studies have systematically investigated the effects of WM load, especially when WM load reaches the capacity. Using a modified Sternberg task, Payne and Kounios (2009) found increased WM load (2, 4, and 6 letters) would lead to increasing theta-band coherence between frontal-midline and left temporal-parietal sites, as well as increasing alpha-band coherence between midline parietal and left temporal/parietal sites. A MEEG (combined MEG and EEG) study reported that inter-areal phase synchrony was strengthened with increasing load 1–6 between the fronto-parietal regions in alpha (10–13 Hz), beta (18–24 Hz), and gamma (30–40 Hz) during the visual WM retention period (Palva et al., 2010). The subjects' individual WM capacities were predicted by the WM load values at which the strength of phase synchrony plateaued. However, the methods of coherence and phase synchrony could indirectly investigate functional connectivity. Besides, the capacity-related effect was only reported in the MEEG study. Thus, the WM capacity-related effects in functional connectivity in humans has not been conclusively established.

Directed transfer function (DTF) method has the advantage taking into account multivariate structure of data and different rhythmic activities, accounting for weighted and directed interactions, compared with other methods (Blinowska et al., 2013b). Studies have shown that DTF is one of the most effective methods for evaluating the functional connectivity among neural signals (Blinowska and Kaminski, 2013a; Wilke et al., 2011; Xu et al., 2013).

In this EEG study, we used a visual WM task with parametric variation of WM load from 1 to 6. First, we applied DTF to investigate the effects of increasing load on functional connectivity in the WM network, especially when the load exceeded the capacity. Then, we calculated functional connectivity strengths within and among different brain regions to investigate which region was sensitive to WM load. Thus, it was possible to investigate the neural mechanism underlying the capacity in WM, from the view of functional connectivity (Fig. 1).

2. Results

2.1. Behavioral results

Reaction time (RT) and accuracy for loads from 1 to 6 are shown in Fig. 2. Mean values of RT from load 1 to 6 was 407.25±14.33 ms, 491.83±16.35 ms, 568.96±16.10 ms, 635.76±15.97 ms, 694.30±20.88 ms, 764.88±29.61 ms, respectively ($F_{(5,1242)}=680.52$, $p<0.001$). Mean accuracy from load 1 to 6 was 98.06±0.55%, 96.46±0.93%, 96.18±0.55%, 96.01±0.96%, 87.43±1.39%, and 84.69±1.19%, respectively ($F_{(5,90)}=32.717$, $p<0.001$).

RT increased significantly with the load increasing from 1 to 6 (*Post-hoc* test, $p<0.001$). The decline of the accuracy was not statistically significant until load 5 ($p<0.05$). The averaged memory capacity was 4.13±0.15, in line with earlier data (Palva et al., 2010).

2.2. Time-frequency analysis

To determine which frequency bands contained task-related rhythmic activity during the WM task, we represented the power spectra for individual correctly performed trials and each channel. Task-related power changes were observed in the theta (4–8 Hz) band. Besides, the Fz channel was chosen as a representative, because theta power of this channel was the maximum among the 32 channels. Fig. 3A shows the time-frequency representations of Fz for load 4 during correct trials ($n=208$). The time frequency representations revealed that theta power was sustained through the delay period until the probe was present. Strong theta activity is clearly shown in Fig. 3B. To determine whether the theta activity was affected by WM load, the power spectra during the delay period were investigated ($n=208$). The topographies clearly showed the theta activity associated with the frontal midline region and increased from load 1 to 4, and leveled off thereafter in Fig. 4. Table 1 shows the theta power of the Fz channel for load 1–6. Statistical analysis showed significant differences between load 4 and load 1–3.

2.3. Functional connectivity distributions for each load

To determine in which frequency band functional connectivity strength was stronger, we computed DTF_{global} distribution with the frequency for load 4. Results showed that the DTF_{global} values in theta (4–8 Hz) and high gamma (85–95 Hz)