# Multifaceted pattern of neural efficiency in working memory capacity

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## ARTICLE INFO

## ABSTRACT

The objective of the present study was to investigate whether neural efficiency can be observed in visual working memory performance. Thirty low- and thirty high-performers were selected from a larger cohort of students based on performance on a visual WM task. Electroencephalogram (EEG) data during performance on this task was analyzed with event-related desynchronization/synchronization (ERD/ERS) and event-related coherence (ErCoh) in individually determined theta, alpha, and gamma frequency bands. The results demonstrated that high-performers in comparison to low-performers showed significantly different brain oscillatory responses in all three cognitive processes identified in the WM task – encoding, maintenance and retrieval. High-performers displayed: (1) Increased alpha ERD during encoding and increased gamma ERD during encoding and maintenance, which did not depend on set size, as well as (2) increased theta band ErCoh in fronto-parietal networks during maintenance and retrieval. To some extent, neural efficiency was observed in the gamma frequency band (ERD) and in theta coherence (ErCoh). The results tentatively lend support to the continuous single resource model assuming that working memory capacity is a flexible resource that can be spread among all elements in the sensory input as opposed to the model of discrete slots.

## 1. Introduction

The construct of working memory (WM) refers to a system that temporarily holds or manipulates information that we have just experienced or retrieved from long-term memory (Baddeley, 2012; Baddeley, Allen, & Hitch, 2011; Cowan, 2000; Miyake & Shah, 1999). Since working memory capacity accounts for a substantial portion of variance in general intelligence (Conway, Kane and Engle (2003), studying the neural basis of working memory can improve our understanding of individual differences in cognitive ability. In particular, measures of working capacity are strongly linked to measures of fluid intelligence (Ackerman, Beier, & Boyle, 2005; Harrison, Shipstead, & Engle, 2015; Unsworth & Engle, 2005; Wiley, Jarosz, Cushen, & Colflesh, 2011).

Probably the most popular and enduring conceptualization of WM is the one proposed by Baddeley and Hitch (1974) – the multi component model of WM. In its original form, it consisted of 3 components: the central executive and two slave systems, the visuo-spatial sketch pad and the phonological loop. To increase the explanatory power of the model a third storage system was introduced – the episodic buffer, a temporary interface between short and long-term memory (Baddeley, 1986, 2012). In yet another updated version, the episodic buffer received a more central position: it was still defined as a passive system but with the crucial function of integrating information from different sources and modalities into chunks or episodes (Baddeley et al., 2011).

More recently, state-based models of working memory have gained prominence (D'Esposito & Postle, 2015). These models assume that allocation of attention to different representations in long term memory (either semantic, sensory or motor) governs temporary retention in working memory. The most well-known among these models is Cowan's embedded-processes model in which working memory is defined as a cognitive condition that retains information in an accessible state (Cowan, 1999). Activation occurs in long-term memory, is temporary, and fades unless maintained by verbal rehearsal or continued attention. In the core of this new theoretical framework are two constructs: focus of attention and its capacity – scope of attention (Cowan, 1999; Cowan et al., 2005).

In state-based models as well as in the multi component model, attention is the process that is used to explain the main functions of working memory: bringing information from perception into the focus of attention – encoding, keeping this information in an active state – maintenance (removal of interfering information), and bringing it back to attention when needed – retrieval (Jonides et al., 2008). Contemporary cognitive research of working memory has favored state-based models because they accommodate well to neuroscience data (e.g., D'Esposito & Postle, 2015; Sreenivasan, Curtis, & D'Esposito, 2014).

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Performance on working memory tasks has been associated with activity in the fronto–parietal network (e.g., Chein & Fiez, 2010; Jonides et al., 2008; Palva, Monto, Kulashekhar, & Palva, 2010; Posner, 1990; Schumacher et al., 1996). It has been suggested that the central executive function of WM is linked to the frontal lobes, whereas the WM storage component is associated with parietal areas (Collette and Van der Linden, 2002; Champod & Petrides, 2010; Olson & Berryhill, 2009; Sauseng, Klimesch, Doppelmayr, et al., 2005; Sauseng, Klimesch, Schabus, and Doppelmayr, 2005; Sauseng et al., 2009; Sauseng et al., 2010; for a review see D'Esposito & Postle, 2015; Sreenivasan et al., 2014). Based on evidence from several brain imaging studies, the left intraparietal sulcus has been identified as a unique area responsible for amodal or multimodal storage of information (Xu and Chun, 2006; Majerus et al., 2006, 2010; Cowan et al., 2011). Support for a fronto–parietal distinction related to processing and storing of information in WM comes also from research employing neuro-electric brain imaging methods (Klimesch, 1999; Klimesch, Freunberger, Sauseng, & Gruber, 2008; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010).

Likewise, Jung and Haier's (2007) Parieto-Frontal Integration Theory (P-FIT) assumes that human intelligence is underpinned by interactions within parietal and frontal cortical regions, linked by white matter structures. Early processing of sensory information within temporal and occipital lobes also represents an important part of the model. A more recent meta-analysis of functional brain imaging studies by Basten, Hilger, and Fiebach (2015) found overlap with P-FIT mainly for frontal and parietal brain regions, but less support for the involvement of temporal and occipital sensory regions.

One of the most prominent findings in studies investigating the neural basis of intelligence is that brighter individuals display more efficient operation of the brain (e.g., Haier et al., 1988), which became known as the neural efficiency hypothesis. As a whole, brighter individuals use fewer energy resources to cope with task demands because they focus the energy on smaller (task-relevant) brain areas and make less use of task-irrelevant brain areas (for a review see Neubauer & Fink, 2009). Neural efficiency has been observed mainly when participants work on tasks of low to medium complexity and is particularly prominent in frontal brain regions (Doppelmayr, Klimesch, Hödlmoser, Sauseng, & Gruber, 2005). Given the strong relationship between intelligence and WM (Buehner, Krumm, & Pick, 2005; Colom, Abad, Quiroga, Shih, & Flores-Mendoza, 2008; Deary, 2012; Engle, Tuholski, Laughlin, & Conway, 1999; Unsworth & Engle, 2007), it is reasonable to assume that neural efficiency would also be observed in working memory. Individuals with high working memory capacity should display less cortical activity during performance on a WM task compared to individuals with low working memory capacity, particularly on the low to medium difficulty levels. Although two studies del Río et al. (2012), Nussbaumer, Grabner & Stern (2015) found some confirmation for neural efficiency in WM performance, it is difficult to link the findings directly to WM, or to neural efficiency. The study by Nusbaumer et al. (2015) employed the *n*-back task with increasing complexity (*n*-back level) as a measure of task difficulty. As stressed by Kane et al. (2004) the *n*-back has received little empirical justification as a working memory measure. Thus, the cognitive mechanisms involved in its performance are not well understood, and its relationship to other complex WM tasks is also unclear (Shipstead, Hicks, & Engle, 2012). On the other hand, the study by del Río et al. (2012) based the neural efficiency claims on magnetoencephalic (MEG) resting state connectivity related to individual differences on a verbal memory span task. However, neural efficiency is usually determined in relation to differences between resting and cognitive load conditions (e.g., Neubauer & Fink, 2009; Pfurtscheller, 1999), hence further research is needed to clarify this relation.

Few studies have focused on the neural underpinning of individual differences in WM performance. Studies based on the neuro-electric approach have revealed mixed results (Angelakis, Lubar, and Stathopoulou, 2004; Angelakis, Lubar, Stathopoulou, and Kounios,

2004; Bashivan, Bidelman, & Yeasin, 2014; Clark et al., 2004; del Río et al., 2012; Dong, Reder, Yao, Liu, & Chen, 2015; Gulbinaite, Johnson, de Jong, Morey, & van Rijn, 2014; Klimesch, Schimke, & Pfurtscheller, 1993; Lebedev, 1994; Stam, 2000; Vogel & Machizawa, 2004; Wiegand et al., 2016). This diversity is further enlarged by the variety of methodological approaches used, which were based on resting state eyes closed/open EEG recordings (e.g., Angelakis, Lubar, and Stathopoulou, 2004; Angelakis, Lubar, Stathopoulou, and Kounios, 2004; del Río et al., 2012), data obtained under cognitive load (e.g., Gulbinaite et al., 2014), or a combination of both (e.g. Klimesch et al., 1993; Pahor & Jaušovec, 2016). An additional source for conflicting results are the different computational algorithms used for the derivation of brain activity measures and biomarkers, ranging from linear (e.g., Bashivan et al., 2014; Vogel & Machizawa, 2004) to nonlinear (e.g., del Río et al., 2012; Stam, 2000), analyzed in time (e.g., Gulbinaite et al., 2014; Wiegand et al., 2016) or frequency domains (e.g., Stam, 2000), or in a combination of both (e.g., Dong et al., 2015). In general, increased event-related potential (ERP) amplitudes were observed in individuals with high visual WM capacity as compared to low ones (e.g., Dong et al., 2015; Vogel & Machizawa, 2004; Wiegand et al., 2016). ERP responses capture the time-locked activity of the brain and therefore fail to detect induced brain activity, which is best analyzed with event-related synchronization/desynchronization (ERD/ERS) as demonstrated by Pfurtscheller and Lopes da Silva (1999). Bashivan et al. (2014) applied this methodology to the same tasks as used by Vogel and Machizawa (2004), yet did not replicate their findings.

The objective of the present study was to investigate whether neural efficiency can be observed in visual working memory performance. For that purpose, we adopted the ERD/ERS methodology, which is not directly phase-locked (Pfurtscheller & Lopes da Silva, 1999). ERD/ERS was determined as the percentage change of band power relative to average power in the resting reference interval preceding the stimulus onset. It should be noted that a positive ERD indicates the percentage of power decrease or desynchronization and a negative ERD indicates the percentage of power increase or synchronization – ERS (Pfurtscheller, 1999). The analysis was performed in three frequency bands (alpha, theta, and gamma) for which there is robust evidence that they are related to cognitive processes contained in the WM construct (Gevins, Smith, McEvoy, & Yu, 1997; Huang et al., 2000; Klimesch, 2012; Roux & Uhlhaas, 2014; Sauseng, Klimesch, Doppelmayr, et al., 2005; Sauseng, Klimesch, Schabus, and Doppelmayr, 2005; 2009; 2010). In addition, connectivity between different brain areas was analyzed with induced event-related coherence (ErCoh). This was motivated by research showing that long-range synchronization between different neuronal assemblies supports WM-related top-down processes. Inter-regional synchronization during WM tasks has been reported for alpha, theta, and gamma frequencies (Crespo-Garcia et al., 2013; Lutzenberger, Ripper, Busse, Birbaumer, & Kaiser, 2002; Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998; Sauseng et al., 2010; Sauseng, Klimesch, Schabus, and Doppelmayr, 2005; 2004; Palva et al., 2010; Payne & Kounios, 2009). Since the main objective of the study was to characterize specific dimensions of individual differences in WM capacity rather than to estimate the exact effect size, an extreme-groups design was used (Yarkoni & Braver, 2010).

Scalp alpha rhythms result from sequences of inhibitory and excitatory post-synaptic potentials at the dendrites of cortical pyramidal neurons. These potentials depend mainly on the influence of near and distant cortical modules (Nunez, Wingeier, & Silberstein, 2001), as well as on the interactions of excitatory cortico-thalamo-cortical relay fibers and inhibitory thalamic reticular fibers (Lopes da Silva, Vos, Mooibroek, & Van Rotterdam, 1980). Alpha power reflects the number of neurons that discharge synchronously in these integrated cortico-cortical and cortico-thalamo-cortical systems (Hindriks & van Putten, 2013; Klimesch, 1999). Its activity desynchronizes in relation to task performance (Pfurtscheller & Aranibar, 1977). Alpha synchronization used to be considered a cortical idling phenomenon (Pfurtscheller,