



The steady-state visual evoked potential reveals neural correlates of the items encoded into visual working memory



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ABSTRACT

Visual working memory (VWM) capacity limitations are estimated to be ~4 items. Yet, it remains unclear why certain items from a given memory array may be successfully retrieved from VWM and others are lost. Existing measures of the neural correlates of VWM cannot address this question because they measure the aggregate processing of the entire stimulus array rather than neural signatures of individual items. Moreover, this cumulative processing is usually measured during the delay period, thereby reflecting the allocation of neural resources during VWM maintenance. Here, we use the steady-state visual evoked potential (SSVEP) to identify the neural correlates of individual stimuli at VWM encoding and test two distinct hypotheses: the *focused-resource* hypothesis and the *diffuse-resource* hypothesis, for how the allocation of neural resources during VWM encoding may contribute to VWM capacity limitations. First, we found that SSVEP amplitudes were larger for stimuli that were later remembered than for items that were subsequently forgotten. Second, this pattern generalized so that the SSVEP amplitudes were also larger for the unprobed stimuli in correct compared to incorrect trials. These data are consistent with the diffuse-resource view in which attentional resources are broadly allocated across the whole stimulus array. These results illustrate the important role encoding mechanisms play in limiting the capacity of VWM.

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1. Introduction

The goal of the current experiment was to elucidate why we are able to retrieve certain items from visual working memory while others are forgotten. Visual working memory (VWM) refers to the encoding, maintenance, manipulation and retrieval of visual representations for immediate use. Despite the importance of VWM in both simple and complex cognitive tasks, capacity limitations associated with VWM are well documented (Cowan, 2001; Luck & Vogel, 2013). In addition, VWM capacity is further constrained by stimulus factors such as complexity (Alvarez & Cavanagh, 2004), saliency (Melcher & Piazza, 2011), similarity (Awh, Barton, & Vogel, 2007), and set size (Anderson, Vogel, & Awh, 2011; Bays & Husain, 2008; Bays, Catalao, & Husain, 2009; Fukuda, Awh, & Vogel, 2010). At a basic level, these capacity limitations indicate that when trying to encode, maintain, and retrieve a set of items in and from VWM,

only a subset will ultimately be accessible. Although progress has been made in recent years, much remains unknown regarding the origins of this capacity limitation. In the current paper, we propose that constraints on capacity may manifest, in part, during the allocation of VWM resources at the time of encoding. We examine this hypothesis by examining neural signals associated with individual items during VWM encoding, and investigate whether modulations in these signals correlate with the success or failure of the corresponding item being subsequently retrieved from VWM.

Much of the existing research examining the neural correlates of VWM has focused on the delay-period or maintenance-phase of VWM tasks. Electrophysiological and neuroimaging findings indicate that VWM is mediated in part by elevated and sustained neural activity during the delay-period of VWM tasks. Evidence in support of this view emerged from electrophysiological recordings from the prefrontal cortex (PFC) of nonhuman primates. PFC neurons increase firing rates during stimulus presentation and maintain elevated firing rates during the VWM maintenance period of delayed response tasks (e.g., Fuster & Alexander, 1971; Funahashi, Bruce, & Goldman-Rakic, 1990). Neuroimaging studies in humans have identified sustained neural activity during the

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delay-period of VWM tasks (fMRI: Magen, Emmanouil, McMains, Kastner, & Treisman, 2009; Todd & Marois, 2004; Xu & Chun, 2006); event-related potentials (ERP: Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). Moreover, in regions such as the intraparietal sulcus, the magnitude of the delay-period activity increases parametrically with set size (Todd & Marois, 2004; Xu & Chun, 2006) and asymptotes at an individual's VWM capacity limit (Todd & Marois, 2005). Similarly, ERP studies deriving the contralateral delay activity (CDA) from posterior electrode sites show sustained maintenance-phase activity that parametrically varies in amplitude with set size and asymptotes as capacity limits are reached (Vogel & Machizawa, 2004). These converging patterns of evidence are consistent with neural models of VWM that emphasize the importance of sustained maintenance-related patterns of elevated activity within posterior parietal cortex (PPC) and PFC regions. Moreover, these perspectives implicitly and explicitly suggest that the VWM capacity limitation arises due to these maintenance-phase processes.

An alternative view of VWM is sometimes termed the *sensory-recruitment* model of VWM (Awh & Jonides, 2001; D'Esposito, 2007; Postle, 2006). This view is derived from a recent wealth of evidence that cortical regions involved during perception are reactivated to aid in the storage and retrieval of stimuli encoded into VWM (e.g., Albers, Kok, Toni, Dijkerman, & de Lange, 2013; Ester, Serences, & Awh, 2009; Emrich, Riggall, LaRocque, & Postle, 2013; Ester, Anderson, Serences, & Awh, 2013; Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009). To examine the sensory-recruitment perspective, recent fMRI experiments have leveraged univariate and multivariate (multivoxel pattern analysis, MVPA) techniques to measure BOLD responses and decode sub-threshold activation patterns to improve our understanding of the mechanisms underlying VWM. Even in the absence of sustained, elevated patterns of maintenance-related activity in visual cortex (e.g., V1–V4, hMT+), decoding procedures reveal that the same sensory regions (e.g., V1–V4, hMT+) that are initially engaged in stimulus perception are involved in storing representations of those task relevant features during the delay-period of VWM tasks (Ester et al., 2009; Emrich et al., 2013; Ester et al., 2013; Harrison & Tong, 2009; Offen, Schuppeck, & Heeger, 2009; Riggall & Postle, 2012; Serences et al., 2009). In addition to the role of early visual regions, intermediate dorsal (V3a/b) and ventral (LO1/2) visual areas become significantly more active when engaged in effortful VWM encoding (Sneve, Alnaes, Endestad, Greenlee, & Magnussen, 2012). Thus, according to this view, limitations in VWM capacity may arise due to the inability to reactivate and maintain the perceptual representations of the multiple items present in the stimulus display. Experiments examining the *sensory-recruitment* model largely focus on the maintenance phase of VWM tasks. However, to maintain a representation of a stimulus in VWM it must first be encoded. As such, capacity limitations that arise during encoding may become apparent during the maintenance phase and contribute in general to the overall capacity limitation of VWM.

Several studies have examined the correspondence between encoding and maintenance related VWM activity within both visual cortex and higher-order regions of the brain. Successful encoding and maintenance of visual information relies on intracortical communication (e.g., Fuster, Bauer, & Jervey, 1985; Gazzaley, Rissman, & D'Esposito, 2004; McIntosh, Grady, Haxby, Ungerleider, & Horwitz, 1996). Recent fMRI evidence shows that greater correspondence in neural activity between encoding and maintenance processes in cortical regions (e.g., lateral PFC) is associated with successful VWM performance (Cohen, Sreenivasan, & D'Esposito, 2012). Importantly, enhanced functional connectivity between the lateral PFC and extrastriate cortex (EC) during VWM encoding and maintenance is associated with

successful VWM performance (Cohen et al., 2012). These findings further stress the importance of accurate perceptual representations and successful encoding of the items to be maintained in and retrieved from VWM. Any limitation in the capacity to represent and encode the to-be-retrieved items will necessarily contribute to the overall capacity limitation of VWM.

In the current investigation of VWM, we were concerned with the fundamental question of why certain stimulus items are selected and subsequently retrieved from VWM while others are forgotten. This selection process must begin during encoding and impose a fundamental limitation in our ability to subsequently maintain and successfully retrieve information from VWM. The experiment described below reveals that neural processing associated with the encoding of a specific item in a VWM display can indeed influence whether or not that item will be subsequently retrieved. Moreover, the experiment tests two alternative hypotheses for how and why some items are successfully encoded while others may not be (Fig. 1A). First, participants may deliberately attempt to encode only a subset of items in a given memory array. This could happen, for example, if participants selectively allocate attentional resources to a subset of items in the display. We term this the *focused-resource* hypothesis. It predicts that if one of the items from the encoded subset is later probed, attempts at retrieval will be successful, but if the probed item was not in the subset at encoding, a retrieval failure will occur. The intuition behind this hypothesis is similar to the notion that providing a predictive attentional pre-cue would facilitate the VWM encoding, maintenance, and retrieval of the cued item. In this case, one may predict that neural signatures at the time of encoding of probed items successfully retrieved from working memory will be greater than those that are forgotten. In contrast, neural signatures of unprobed items would be expected to be greater on trials in which the probed item was forgotten than when it was successfully retrieved (Fig. 1A).

Alternatively, it may be the case that observers attempt to encode all of the items in a VWM display, but on a trial-by-trial basis they will not always succeed. This *diffuse-resource* hypothesis proposes that participants try to encode all items, but sometimes, due to distraction, lower motivation, or fluctuation in the overall amount of available attentional resources on a given trial, VWM performance suffers. According to this hypothesis, neural signals of both probed and unprobed items should be greater when the probed item is subsequently remembered than when it is forgotten (Fig. 1B).

We investigated these hypotheses using the steady-state visual evoked potential (SSVEP; Regan, 1989). The SSVEP is an electrophysiological signal derived from the EEG in response to temporally-periodic stimuli (i.e., stimuli flickering at a specific rate). In research investigating human cognition (e.g., visual attention), the SSVEP has been most commonly considered in the frequency domain and is used specifically when analyzing signal power in the EEG at frequencies associated with the flicker rates of experimental stimuli (Appelbaum & Norcia, 2009; Hillyard et al. 1997; Morgan, Hansen, & Hillyard, 1996; Muller et al. 1998; Muller & Hubner, 2002). One simple way to conceptualize the SSVEP is that a flickering stimulus will produce an EEG signal with increased power at the flicker frequency and/or one of its harmonics.

In the current experiment, we investigated the hypotheses described above by examining SSVEPs in response to the items present at the encoding phase of a VWM change detection task. This was accomplished by having the to-be-remembered items flicker at unique frequencies (3 Hz, 5 Hz, 12 Hz, 20 Hz). This allowed us to examine power in the SSVEP at frequencies corresponding to each item ($f_1=3$ Hz; $f_2=5$ Hz, $f_3=12$ Hz, $f_4=20$ Hz) and their second harmonics ($2f_1=6$ Hz, $2f_2=10$ Hz,

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