

## The neural correlates of visual working memory encoding: A time-resolved fMRI study

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### ABSTRACT

The encoding of information into visual working memory (VWM) is not only a prerequisite step for efficient working memory, it is also considered to limit our ability to attend to, and be consciously aware of, task-relevant events. Despite its important role in visual cognition, the neural mechanisms underlying visual working memory encoding have not yet been specifically dissociated from those involved in perception and/or VWM maintenance. To isolate the brain substrates supporting VWM encoding, here we sought to identify, with time-resolved fMRI, brain regions whose temporal profile of activation tracked the time course of VWM encoding. We applied this approach to two different stimulus categories – colors and faces – that dramatically differ in their encoding time. While several cortical and subcortical regions were activated during the VWM encoding period, one of these regions in the lateral prefrontal cortex – the inferior frontal junction – showed a temporal activation profile associated with the duration of encoding and that could not be accounted for by either perceptual or general attentional effects. Moreover, this region corresponds to the prefrontal area previously implicated in ‘attentional blink’ paradigms demonstrating attentional limits to conscious perception. These results not only suggest that the inferior frontal junction is involved in VWM encoding, they also provide neural support for theories positing that VWM encoding is a rate-limiting process underlying our attentional limits to visual awareness.

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### 1. Introduction

Visual working memory (VWM), the temporary storage and manipulation of visual information, has been the subject of numerous behavioral and neurobiological studies (e.g., Baddeley & Logie, 1999; Funahashi, Bruce, & Goldman-Rakic, 1989; Haxby, Petit, Ungerleider, & Courtney, 2000; Jolicœur & Dell’Acqua, 1998; Luck & Vogel, 1997; Miller, Erickson, & Desimone, 1996; Munk et al., 2002; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Postle, Zarahn, & D’Esposito, 2000; Todd & Marois, 2004; Wheeler & Treisman, 2002; Vogel, Woodman, & Luck, 2001). These studies, along with many others, have led to a rich understanding of VWM (Luck & Hollingworth, 2008), including its relationship with attention (e.g., Awh, Jonides, & Reuter-Lorenz, 1998; Cowan, 2001; Corbetta, Kincade, & Shulman, 2002; de Fockert, Rees, Frith, & Lavie, 2001; Downing, 2000; Fougny & Marois, 2006; LaBar, Gitelman, Parrish, & Mesulam, 1999; Mayer et al., 2007; Oh & Kim, 2004; Rensink, 2000;

Woodman & Luck, 2004; see this special issue). By comparison, the initial process by which information is encoded into working memory is much less understood. Yet, there is evidence that VWM encoding is functionally dissociable from the storage of information in working memory (Woodman & Vogel, 2005), and may therefore rely on at least partly distinct neural processes. Moreover, VWM encoding is capacity-limited (Jolicœur & Dell’Acqua, 1998; Vogel, Woodman, & Luck, 2006), and it has been suggested that that this capacity limit impairs our ability to consciously perceive multiple, temporally proximate events (Akyürek & Hommel, 2005; Akyürek, Hommel, & Jolicœur, 2007; Chun & Potter, 1995; Jolicœur, 1998). The latter suggestion has been drawn from studies of the attentional blink (AB), which reveals a deficit in the conscious registration of the second of two targets presented among distractor items when the second target (T2) is presented close in time to the first target (T1) (Raymond, Shapiro, & Arnell, 1992). According to the VWM encoding account of the AB, T2 may not be encoded – and consciously perceived – until T1 encoding is complete. In support of this model, the AB is contingent on the rate of encoding of the T1 display (Ouimet & Jolicœur, 2007). However, other studies have proposed that it is not WM encoding, but the control of selective attention, that is ultimately responsible for the AB (Di Lollo, Kawahara, Shahab Ghorashi, & Enns, 2005; Olivers, van

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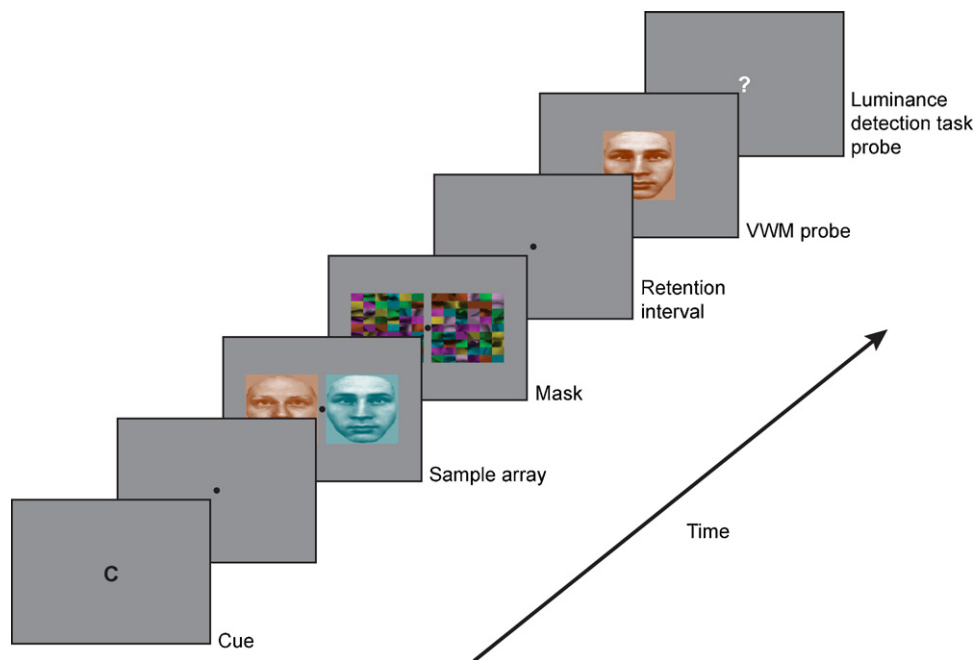
der Stigchel, & Hulleman, 2007, see also Nieuwenstein & Potter, 2006). Dux and Marois (2009) have proposed a reconciliation of these different viewpoints by arguing that it is selective attention to the encoding process that maybe the capacity-limited process underlying the AB.

If encoding of information into working memory is the rate-limiting step underlying the AB, then one might expect the neural substrates of VWM encoding to overlap with those underlying the AB. Neuroimaging, electrophysiological, and lesion studies of the AB have consistently implicated a network of lateral prefrontal and parietal cortical areas as the neural underpinnings of our limited capacity to consciously perceive multiple targets in RSVP streams (Feinstein, Stein, Castillo, & Paulus, 2004; Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Marcantoni, Lepage, Beaudoin, Bourgouin, & Richer, 2003; Marois, Chun, & Gore, 2000; Marois, Yi, & Chun, 2004; see also Cooper, Humphreys, Hulleman, Praamstra, & Georgeson, 2004; Gross et al., 2004; Hein, Alink, Kleinschmidt, & Müller, 2009; Kessler et al., 2005; Kihara et al., 2007; Kranczioch, Debener, Maye, & Engel, 2007; Martens, Munneke, Smid, & Johnson, 2006; Sergent, Baillet, & Dehaene, 2005; Williams, Visser, Cunningham, & Mattingley, 2008). According to the encoding bottleneck account of the AB, these regions should therefore be involved in the encoding of information into VWM. Despite the contribution of the rate-limited process of VWM encoding to attentional limitations in conscious perception, and to working memory in general, the neural mechanisms underlying this process are not well established. Several neuroimaging studies have ascribed the encoding of information into VWM to specific brain regions, most notably the parietal and frontal/prefrontal cortices (Andersen, Essick, & Siegel, 1985; Courtney, Ungerleider, Keil, & Haxby, 1997; Linden et al., 2003; Majerus et al., 2007; Munk et al., 2002; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Petrides, 1994, 1996; Postle et al., 2000; Roth, Serences, & Courtney, 2006; Rypma and D'Esposito, 1999; Todd & Marois, 2004, 2005; Zarahn, Aguirre, & D'Esposito, 1997). However, these studies did not provide a pure measure of VWM encoding because the encoding activity could not be dissociated from either perceptual or

maintenance-related activity due to the limited temporal resolution of fMRI.

The goal of the present study was to isolate VWM encoding-specific brain activity, and to determine whether this activity is consistent with neuroimaging studies of the AB. Our experimental strategy for isolating the brain substrates of VWM encoding consisted in using fMRI to identify brain regions whose temporal profile of activation tracked the time course of VWM encoding. To achieve this aim, we took advantage of the fact that the duration of WM encoding increases proportional to increasing object complexity (Alvarez & Cavanagh, 2004; Awh, Barton, & Vogel, 2007; Curby & Gauthier, 2007; Eng, Chen, & Jiang, 2005; Ouimet & Jolicœur, 2007). While fMRI cannot reveal the absolute duration of a neurophysiological process, it can be informative about the relative duration of such process (Dux, Ivanoff, Asplund, & Marois, 2006; Formisano & Goebel, 2003; Henson, Price, Rugg, Turner, & Friston, 2002; Liao et al., 2002; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). Hence, brain regions involved in WM encoding should show differential durations of activity depending on the time it takes to encode objects of different complexity. These latency effects can be estimated by assessing the differences in the time it takes for the hemodynamic response to reach its peak, as time-to-peak is a reliable measure of duration of brain activity (Dux et al., 2006; Henson et al., 2002).

We applied this time-resolved fMRI approach to the encoding of two different stimulus categories that differ extensively in the duration of encoding: colors, which can be encoded in about 50 ms (Vogel et al., 2006), and faces, which may take about ten times longer to be fully encoded (Curby & Gauthier, 2007). Subjects were instructed to encode, in separate trials, either the color or the face identity of a pair of stimuli (Fig. 1). Because encoding a pair of colors should take approximately 100 ms while encoding a pair of faces should take about 1000 ms, the 900 ms difference in peak latency between these two conditions should be readily resolved with fMRI. In a pilot behavioral experiment, we demonstrated that two colors were fully encoded in about 300 ms, whereas approximately 1200 ms was needed to encode two faces into VWM (see



**Fig. 1.** Trial design. At trial onset, a cue reminded the subject of the task-relevant feature (C, color; F, face). While performing an articulatory suppression task, the subject encoded the task-relevant feature from the memory array, which was presented for 500 or 1500 ms. Concurrent with encoding the memory array, the subject monitored for a brief change in the luminance in either memory array stimulus. Following a mask and then a 9000 ms retention interval, the memory probe was presented. Finally, a question mark appeared in the center of the display and the subject indicated if there was (not) a luminance change in the memory array.

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