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

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\begin{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, 1997; Miller, Erickson, & Desimone, 1996; Munk et al., 2002; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Postle, Zarahn, & D’Esposito, 2000; Todd & Marois, 2004; Wheeler & Treisman, 1997; 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, 2000; de Fockert, Rees, Frith, & Lavie, 2001; Downing, 2000; Fournig & Marois, 2006; LaBar, Giteman, 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 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...
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 may be 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 Hulleman, Praamstra, & Georgeson, 2004; Gross et al., 2004; Hein, Alink, Kleinschmidt, & Müller, 2009; Kessler et al., 2005; Kihara Hulleman, Praamstra, & Georgeson, 2004; Gross et al., 2004; Hein, Alink, Kleinschmidt, & Müller, 2009; Kessler et al., 2005; Kihara Hulleman, Praamstra, & Georgeson, 2004; Gross et al., 2004; Hein, Alink, Kleinschmidt, & Müller, 2009; 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