Not all attention orienting is created equal: Recognition memory is enhanced when attention orienting involves distractor suppression

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A B S T R A C T

Learning through visual exploration often requires orienting of attention to meaningful information in a cluttered world. Previous work has shown that attention modulates visual cortex activity, with enhanced activity for attended targets and suppressed activity for competing inputs, thus enhancing the visual experience. Here we examined the idea that learning may be engaged differentially with variations in attention orienting mechanisms that drive eye movements during visual search and exploration. We hypothesized that attention orienting mechanisms that engaged suppression of a previously attended location would boost memory encoding of the currently attended target objects to a greater extent than those that involve target enhancement alone. To test this hypothesis we capitalized on the classic spatial cueing task and the inhibition of return (IOR) mechanism (Posner, 1980; Posner, Rafal, & Choate, 1985) to demonstrate that object images encoded in the context of concurrent suppression at a previously attended location were encoded more effectively and remembered better than those encoded without concurrent suppression. Furthermore, fMRI analyses revealed that this memory benefit was driven by attention modulation of visual cortex activity, as increased suppression of the previously attended location in visual cortex during target object encoding predicted better subsequent recognition memory performance. These results suggest that not all attention orienting impacts learning and memory equally.

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1. Introduction

Visual exploration involves active scanning of the environment for information gathering. Visual attention during exploration has been traditionally studied as a mechanism that supports resource allocation in a cluttered visual world. We argue that the well-established spatial and temporal dynamics of attention orienting *additionally* play a critical role in learning and memory during natural visual search and exploration. We present converging eye tracking and neuroimaging data showing that the attention mechanism underlying orienting to a spatial location, and particularly whether suppression of competing information at the previously attended location is engaged, is a determining factor in how well information at the attended location is encoded for subsequent recognition memory.

Evidence of attention/memory interactions at encoding comes from laboratory studies showing enhanced recognition memory for attended versus ignored information (Ballesteros, Reales, Garcia, & Carrasco, 2006), as well as improved encoding when attention is directed to the location of objects prior to their appearance (Broadway, Hilimire, & Corballis, 2011; Hauer & MacLeod, 2006). Neuroimaging studies have identified a distributed network including medial temporal, parietal, and prefrontal regions that are engaged during memory encoding and subsequent retrieval (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Kahn, Davachi, & Wagner, 2004; Kim, 2013; Konishi, Wheeler, Donaldson, & Buckner, 2000; McDermott, Jones, Petersen, Lageman, & Roediger, 2000; Qin, van Marle, Hermans, & Fernandez, 2011; Wagner, Shannon, Kahn, & Buckner, 2005). Parallel research has similarly identified a dorsal attention network that supports attentional selection of relevant stimuli and suppression of distracting or competing information (Corbetta & Shulman, 2002; Squire, Noudoost, Schafer, & Moore, 2013). A recent meta-analysis found that positive subsequent memory effects (i.e., activity elicited during memory encoding that is associated with correct responses at subsequent test) were predominantly associated with involvement of this dorsal attention network, suggesting that top–down attention selection promotes effective encoding (Uncapher & Wagner, 2009).

Growing evidence suggests that modulation of visual cortex activity via the dorsal attention network may mediate the link

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between attention and enhanced memory encoding (Kim, 2013; Qin et al., 2011; Uncapher & Wagner, 2009). For example, selective attention to specific stimulus features (i.e., color, location) enhanced activity in visual cortical regions dedicated to processing those features, which in turn elicited more effective encoding by medial temporal lobe systems (Uncapher & Rugg, 2009). The authors proposed that selective attention enhanced cortical processing in favor of goal-relevant stimuli, resulting in propagation of higher-fidelity representations to the hippocampus and increased efficacy of memory encoding (Uncapher & Rugg, 2009).

Selective attention involves both this stimulus enhancement and *suppression* of competing information (Dosher & Lu, 2000; Smith, Singh, & Greenlee, 2000). Thus, activation of dorsal frontoparietal selective attention networks results in enhanced visual cortex activity associated with the attended stimulus (i.e., excitation/enhancement) (Gandhi, Heeger, & Boynton, 1999; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999) as well as concurrent suppression of the signal associated with information appearing in the surrounding unattended locations (Slotnick, Schwarzbach, & Yantis, 2003; Smith et al., 2000). This distractor suppression can influence the quality of object representations in visual regions such as inferior temporal cortex (IT). Neurophysiological recordings have shown that the neural signal in IT conveys reduced object information in the presence of distractors, relative to when the object was presented in isolation (Zhang et al., 2011). However, when selective attention modulated neural activity, with signal enhancement for the attended object and suppression of the distractors, the object representation was restored to a level as if the object had been presented in isolation (Zhang et al., 2011). The suppression of neural activity elicited by selective attention effectively eliminated the noise introduced by the distractors.

We hypothesize that this suppression of competing interference has benefits that extend beyond object representation in IT: specifically, the presence of distractor suppression will reduce noise in the neural signal of the attended object (Zhang et al., 2011), which will improve memory encoding for the target object.

Thus, encoding for subsequent recognition will be improved when target enhancement is paired with distractor suppression. This potential role for suppression in reducing noise and promoting memory encoding may be especially relevant as we execute series of eye movements during visual exploration. With each new eye movement, an attentional trace remains at the previously attended location (Golomb, Pulido, Albrecht, Chun, & Mazer, 2010; Talsma, White, Mathôt, Munoz, & Theeuwes, 2013). Our hypothesis is that suppression of this interference at the previously attended location should enhance the signal at the attended location, in turn benefiting encoding and subsequent recognition memory.

We support this hypothesis with eye tracking and fMRI experiments, all using the spatial cueing task (Posner, 1980). By varying a single timing parameter, the spatial cueing task can be used to compare encoding in the context of attention orienting involving basic target location enhancement versus orienting paired with suppression at the previously attended location. In this task, attention shifts covertly to a peripheral cue, followed by a brief delay and then presentation of a target in either the previously covertly attended 'cued' (cued-target trials) or in the 'noncued' opposing location (noncued-target trials, Fig. 1). The stimulus timing can elicit an orienting bias and enhancement at the cued location (short delay <250 ms), an effect known as facilitation. Extending the cue-target delay (>250 ms) elicits *suppression* at the previously attended, cued location, resulting in the well-characterized inhibition of return (IOR) response in which individuals are biased to orient to the opposite, noncued location (Posner & Cohen, 1984; Posner, Rafal, & Choate, 1985). IOR has long been considered a mechanism relevant for generating non-repetitive sequential eye movements in visual search and exploration, as suppression at previously attended locations promotes orienting to novel locations (Klein, 1988; Klein & MacInnes, 1999; Klein, 2000). Previous fMRI studies examining the neural correlates of IOR have found activity in posterior parietal regions, oculomotor regions (e.g., frontal eye fields, supplementary eye fields), middle temporal gyrus, and several frontal regions, including anterior cingulate, medial frontal gyrus, and middle frontal gyrus (Lepsien & Pollmann, 2002;
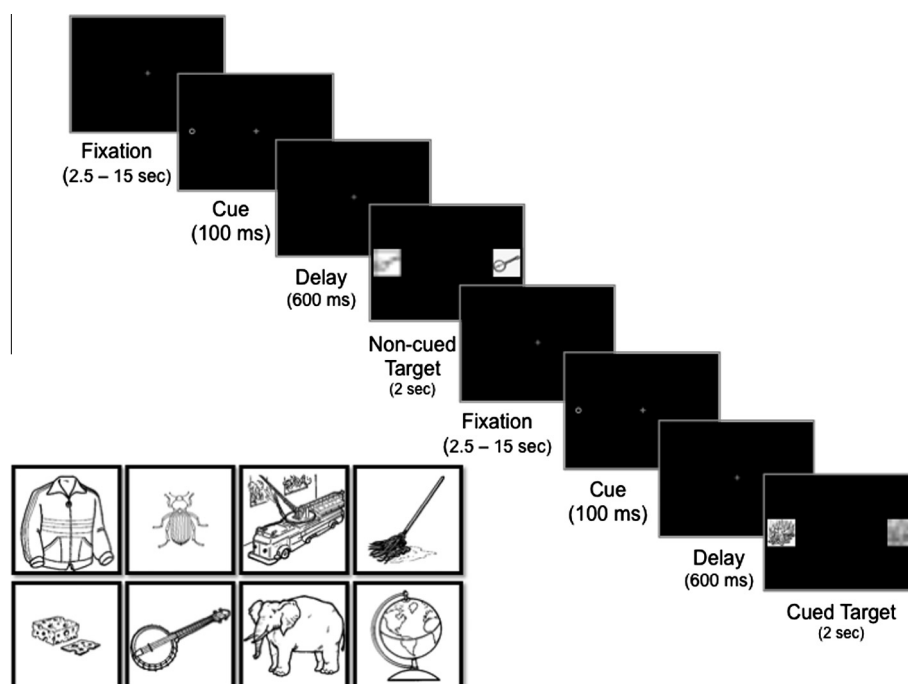

Fig. 1. Schematic depiction of the spatial cueing/encoding task and examples of object images used as target stimuli during the task.