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Spatial working memory effects in early visual cortex

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ABSTRACT

The present study investigated how spatial working memory recruits early visual cortex. Participants were required to maintain a location in working memory while changes in blood oxygen level dependent (BOLD) signals were measured during the retention interval in which no visual stimulation was present. We show working memory effects during the retention period in early visual cortex which were retinotopically organized in the sense that evoked BOLD responses were specific to the position of the remembered location on an imaginary clock. We demonstrate that this activity is similar to activity observed in conditions in which participants have to direct spatial attention to the same location. We suggest that during the retention interval modulation of neurons coding the remembered location evoke a baseline shift, providing converging evidence for the notion that spatial working memory may use spatial attention as a rehearsal mechanism.

1. Introduction

The ability to briefly maintain and interact with information held in memory is one of the pivotal qualities ascribed to “working memory”, and using this ability is functionally important for bridging the gap between perception and action. Over the years multiple models of working memory have been devised in an attempt to explain its many properties and functions (e.g. Baddeley, 1992; Baddeley & Hitch, 1974; Cowan, 1995). A widely accepted concept of working memory entails separate mechanisms for visuospatial and verbal storage of information, both of which have been studied extensively (for an overview see Jonides et al., 1996; Jonides, Lacey, & Nee, 2005). Spatial working memory refers to the ability to store and interact with location-specific information of stimuli presented in the visual field over a brief period of time (see Theeuwes, Belopolsky, and Olivers (2009), for a recent review). Usually this ability is tested with a delayed recognition task (Awh, Jonides, & Reuter-Lorenz, 1998; Postle, Awh, Jonides, Smith, & D’Esposito, 2004; Smith, Jonides, & Koeppe, 1996). In a typical spatial delayed recognition task, participants are instructed to remember the location of an item presented on a display. After a delay during which the item is no longer present, a new item is presented and participants have to indicate whether the new item is presented at the remembered or at a different location. Delayed recognition tasks are used to study the properties and constraints of spatial working memory at a behavioural level, but are also used to study its effects at a neural level by looking at brain activity during the delay period. Due to the absence of visual stimulation during the delay period, observed neural activity is not confounded by sensory processes and therefore the observed neural activity is thought to reflect genuine working memory related processes.

Neural patterns during a working memory delay period are assumed to reflect memory-related maintenance processes, ensuring an active representation of spatial information. Studies investigating the neural correlates of spatial working memory have demonstrated numerous regions in the parietal and frontal cortex which seem to reflect these maintenance processes, such as the prefrontal cortex (PFC), the frontal eye fields (FEF) and the posterior parietal cortex (PPC) (Curtis, 2006; Naghavi & Nyberg, 2005). However, some studies have questioned the interpretation of delay-period activity as purely mnemonic in nature. For example, Lebedev, Messinger, Kralik, & Wise (2004) had two monkeys (Macaca) perform a task in which a saccade had to be made to either an attended or a remembered location. This study showed that neurons in prefrontal cortex of a monkey, that fired during a delay period, reflected maintenance processes only to a small extent, and that most cells in this region represented attended locations. They concluded that activity in prefrontal cortex observed during a delay period may exceed maintenance processes and that these processes may represent a broader scope of cognitive functions including spatial attention.

In line with Lebedev et al. (2004), spatial working memory is not the only source of activation in these areas in humans. Brain responses in the fronto-parietal network have also been observed in tasks involving spatial attention. Converging lines of research have suggested an intimate link between spatial working memory and spatial attention. Evidence for this suggested link comes from both

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behavioural and neuropsychological research. First, at a behavioural level it has been shown that processing visual information occurs more extensively at remembered locations compared to new locations, a finding similar to the observed enhanced processing of attended over unattended locations (Awh, Smith, & Jonides, 1995). Awh et al. showed that choice reaction times (RTs) to targets were faster when these targets were presented at a memorized location, compared to a non-memorized location, claiming that the speeded RTs were due to attentional enhancement of the processing of stimuli at the memorized location. In addition, when participants are unable to direct attention towards the remembered location, memory accuracy is attenuated (Awh et al., 1998; Smyth, 1996) indicating that spatial working memory utilizes spatial attention mechanisms. Second, at a neural level a large overlap is observed in the cortical circuitry active during spatial working memory and spatial attention tasks in the fronto-parietal network (Awh & Jonides, 1998, 2001; Corbetta, 1998; LaBar, Gitelman, Parrish, & Mesulam, 1999). Furthermore, Jha (2002) showed that ERPs (N1 and P1) evoked by non-relevant probe stimuli during a delay-period in a working memory task were of equal magnitude independent of whether the probe stimuli were presented early or late in the delay period, suggesting that attention is deployed during the entire delay period. Taken together, these observations entail that both constructs may be conceptually different, but that the underlying neural mechanisms may be much more intertwined than commonly thought.

If spatial working memory evokes neural responses similar to spatial attention, then this overlap may not only occur in the fronto-parietal network, but in additional brain regions as well. Recently, an increasing number of studies on spatial attention have focused on the effects of attention on early visual processing in regions of the occipital cortex such as striate and extrastriate cortex. These studies indicate that the neural response to a visual event can be modulated by focused attention in striate and extrastriate cortex in a retinotopic fashion (Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Martinez et al., 1999; Somers, Dale, Seiffert, & Tootell, 1999). Moreover, in the absence of visual stimulation an increase in baseline activity can be observed in early visual cortex prior to the presentation of an expected visual event. Baseline activity refers to the spontaneous firing rate of neurons in the cortex and an attention-induced increase in baseline activity can be observed in both extrastriate cortex (Corbetta et al., 2005; Hopfinger, Buonocore, & Mangun, 2000; Luck, Chelazzi, Hillyard, & Desimone, 1997) and striate cortex (Jack, Shulman, Snyder, McAvoy, & Corbetta, 2006; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Munneke, Heslenfeld, & Theeuwes, 2008; Ress, Backus, & Heeger, 2000). From these and other studies it has become apparent that visual cortex is involved in more than low-level processing of visual information.

If spatial working memory draws on the same neural circuitry as spatial attention, the question is whether visual cortex is also involved when remembering a location. In other words, does maintenance of spatial information in working memory elicit BOLD responses at retinotopic regions in early visual cortex? Previous research has shown some evidence that the visual cortex is modulated by remembering spatial information, but it is not always clear whether the observed activation pattern reflects working memory-related maintenance processes or sensory processes caused by the stimuli presented during the task (Awh et al., 1999). Moreover, the activation patterns observed were not retinotopic in nature, so the question as to what extent the observed effects are spatially specific to the target location remains (e.g. Courtney, Ungerleider, Keil, & Haxby, 1996). Postle, Awh, Jonides, Smith, and D'Esposito (2004) conducted a study which showed effects of spatial working memory in visual cortex; yet these effects did not reach statistical significance in primary visual cortex (V1) during the retention interval, despite being of a similar magnitude compared to effects of spatial working memory observed in extrastriate cortex.

Furthermore, in a recent fMRI study by Serences, Ester, Vogel, and Awh (2009) multi-voxel pattern analyses (MVPA) showed that during the retention period of a working memory task, specific patterns of BOLD activation could be observed in V1 related to a to-be remembered feature of a stimulus (color or orientation). This result suggests that neural activation in early visual cortex may only reflect the coding of relevant features, but not the entire stimulus. A similar result was obtained by Harrison and Tong (2009) who were able to predict which of two gratings was held in working memory by the participant, based on classification of BOLD patterns. These studies show that early visual cortex is capable of maintaining to-be remembered information over a period of time during which the stimulus is no longer in view.

If visual cortex is capable of supporting working memory processes, this will add to the evidence linking the concepts of spatial working memory and spatial attention. A theoretical account of this overlap hypothesizes that maintaining location-specific information in spatial working memory is accomplished by shifts of spatial attention towards the memorized locations (Awh et al., 1998, 1999; Postle et al., 2004; Smyth, 1996). Rehearsal of the stored spatial representation by covert shifts of attention acts as a functional mechanism similar to verbal rehearsal as a mechanism for storing information in verbal working memory (e.g. Baddeley, 1998). In both types of working memory, maintenance of the active representation is established by rehearsal of the task-relevant features of the stimulus. The existence of an attentional rehearsal mechanism in spatial working memory would explain the observation that the performance level in such a task is dependent on the attentional constraints of that particular task. Attentional rehearsal as a means for storage of spatial representations again emphasizes the strong behavioural link between the two concepts. However, at a neural level, the two constructs have mostly been studied separately and many questions concerning the overlap and functionality of observed neural activation during those tasks remain.

Although Awh et al. (1999, 2001), and Postle et al. (2004) observed effects of spatial working memory in early visual cortex; the method used in these studies leaves open some questions concerning the spatial specificity of the observed effects. Awh et al. and Postle et al. used full stimulation of both hemifields in order to define regions of interest in the visual cortex which makes the specificity of the observed effects within a hemifield hard to determine. This leaves open the question of whether the reported effects are truly retinotopic in nature or whether they reflect more general processes such as hemispheric arousal or alerting. In the current study we aim to further specify the effects observed by Awh et al. and Postle et al. investigating the spatial specificity of the observed effects and the role primary visual cortex may play in attention and working memory. This is done by functionally defining the regions of interest (ROIs) in V1, V2 and V3 in a separate task based on target locations. Furthermore, ROIs based on nearby non-target locations were included in order to investigate whether the effects observed at target locations are spatially specific only for these locations or whether a larger part of the visual cortex is involved in spatial working memory.

2. Methods

2.1. Participants

Sixteen paid volunteers participated in an fMRI experiment. All participants were healthy and had normal or corrected-to-normal vision. Based on eye movement data, three participants were ex-