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Research Report

Synchronous retinotopic frontal–temporal activity during long-term memory for spatial location

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ABSTRACT

Early visual areas in occipital cortex are known to be retinotopic. Recently, retinotopic maps have been reported in frontal and parietal cortex during spatial attention and working memory. The present event-related potential (ERP) and functional magnetic resonance imaging (fMRI) study determined whether spatial long-term memory was associated with retinotopic activity in frontal and parietal regions, and assessed whether retinotopic activity in these higher level control regions was synchronous with retinotopic activity in lower level visual sensory regions. During encoding, abstract shapes were presented to the left or right of fixation. During retrieval, old and new shapes were presented at fixation and participants classified each shape as old and previously on the "left", old and previously on the "right", or "new". Retinotopic effects were manifested by accurate memory for items previously presented on the left producing activity in the right hemisphere and accurate memory for items previously presented on the right producing activity in the left hemisphere. Retinotopic ERP activity was observed in frontal regions and visual sensory (occipital and temporal) regions. In frontal cortex, retinotopic fMRI activity was localized to the frontal eye fields. There were no significant ERP or fMRI retinotopic memory effects in parietal regions. The present long-term memory retinotopic effects complement previous spatial attention and working memory findings (and suggest retinotopic activity in parietal cortex may require an external peripheral stimulus). Furthermore, ERP cross-correlogram analysis revealed that retinotopic activations in frontal and temporal regions were synchronous, indicating that these regions interact during retrieval of spatial information.

1. Introduction

For over a decade, detailed retinotopic maps have been reported in early visual areas of human occipital cortex (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997; Tootell et al., 1997; Slotnick and Yantis, 2003). While previous studies have focused on retinotopic maps in occipital cortex associated with perception of a rotating checkerboard stimulus, more recent studies have looked for retinotopic maps in higher level cortical regions using more complex stimuli and tasks. Retinotopic maps associated with spatial perception and attention have recently been reported in parietal cortex, within the intraparietal sulcus (Silver et al., 2005; Swisher et al., 2007; Saygin and Sereno, 2008). Saygin and Sereno (2008) separately assessed the effects of spatial perception and spatial attention and found both processes

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produced retinotopic maps in occipital and parietal cortex, but only spatial attention produced retinotopic maps in the frontal cortex, within the precentral gyrus at its junction with the superior frontal sulcus (i.e., the frontal eye fields; Paus, 1996; Corbetta, 1998).

Retinotopic maps have also been reported in occipital cortex, parietal cortex, and frontal cortex during delayed saccade and delayed pointing tasks (Sereno et al., 2001; Schluppeck et al., 2005; Kastner et al., 2007; Hagler et al., 2007). Although such tasks involve both spatial working memory and a motor response, the corresponding retinotopic maps can be attributed to spatial working memory (without the motor component) as spatial working memory alone can produce retinotopic maps in the same regions (Sereno et al., 2001; Hagler and Sereno, 2006; Kastner et al., 2007). Working memory related retinotopic maps have been observed in two regions of the frontal cortex, near the junction of the superior frontal sulcus and the precentral sulcus and near the junction of the inferior frontal sulcus and the precentral sulcus (Hagler and Sereno, 2006; Kastner et al., 2007). The more superior retinotopic activity appears to span two sub-regions, the frontal eye fields (which extend from the central sulcus to the precentral sulcus, including the precentral gyrus, at the junction with the superior frontal sulcus; Paus, 1996; Corbetta, 1998) and the posterior superior frontal sulcus that has been associated with spatial working memory (Courtney et al., 1998; Slotnick, 2005). The more inferior retinotopic activity in ventral frontal cortex has been associated with object working memory (Courtney et al., 1996; Sala et al., 2003).

The existence of retinotopic maps in higher level control regions, particularly in the frontal cortex during spatial attention and working memory, challenges the long held view that only visual sensory regions have retinotopic organization and suggests other tasks might also produce retinotopic maps in frontal and parietal cortex. Moreover, it is unknown whether such higher level retinotopic activity operates independently or interacts with lower level visual sensory retinotopic activity. The first aim of the present event-related potential (ERP) and functional magnetic resonance imaging (fMRI) study was to determine whether spatial long-term memory could produce retinotopic effects in frontal or parietal regions, akin to retinotopic memory effects that have been reported in occipital and temporal regions (Slotnick and Schacter, 2006; Slotnick, 2009). The second aim of the present study was to use ERP cross-correlation analysis to assess the degree to which retinotopic activity in higher level regions was synchronous with retinotopic activity in visual sensory regions. While spatial attention and working memory paradigms require participants to focus on a unique location in the visual field on a trial-by-trial basis which typically translates into very high accuracy, spatial long-term memory paradigms involve storage of many spatial locations across trials which produces relatively lower accuracy (as indicated by an intermediate level of spatial retrieval accuracy; e.g., Slotnick, 2009). This limitation was addressed in the current study by presenting stimuli at only two spatial locations during encoding, either to the left or the right of fixation (Fig. 1A). During retrieval (Fig. 1B), old and new shapes were presented at fixation and participants classified each shape as old and previously presented on the “left”, old and previously presented on the “right”, or “new”. As it is known that retinotopic activity occurs in the contralateral hemisphere, retinotopic effects in the present study would be manifested by accurate memory for items in the left visual field producing activity in the right hemisphere and accurate memory for items in the right visual field producing activity in the left hemisphere.

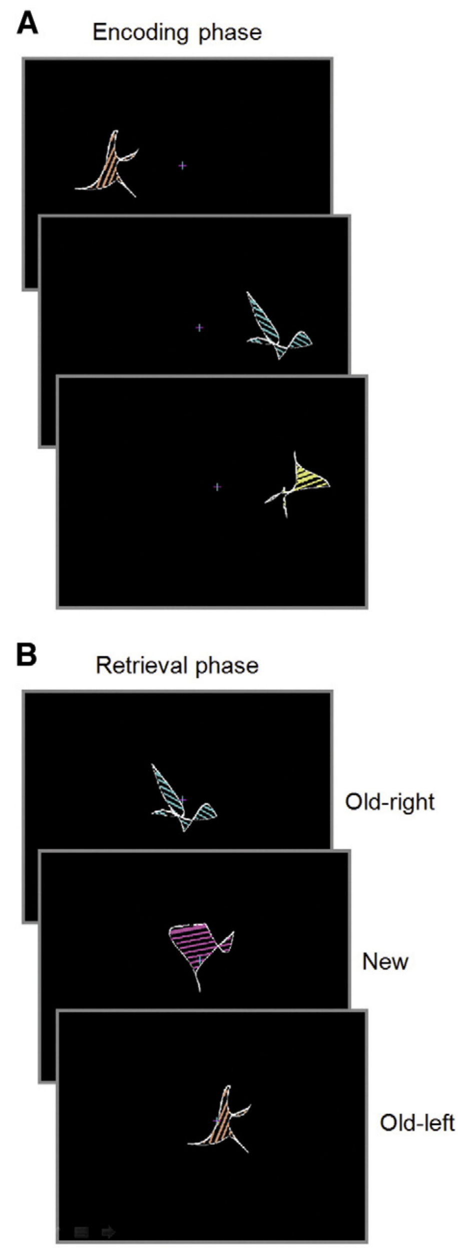

Fig. 1 – (A) During encoding, shapes were presented to the left or right of fixation. (B) During retrieval, shapes previously presented in the left or right visual field (old-left, old-right) and new shapes were presented at fixation and, for each shape, participants responded “old-left”, “old-right”, or “new” (accurate responses are shown to the right).