



Neural correlates of spatial working memory load in a delayed match-to-sample saccade task

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ABSTRACT

We propose a new way to identify the neural correlates of memory load in a delayed match-to-sample saccade task with a constant perceptual load. Two conditions were compared with low and high memory loads. In the low-load condition, a rectangular shaped probe defined by its color and orientation was presented centrally. After a delay period, four stimuli were presented peripherally, one in each quadrant. The participants were instructed to saccade to the stimulus that matched the previously viewed sample on both color and orientation. In the high-load condition, the order of stimulus presentation was reversed: first four eccentric stimuli were presented and after a delay the central probe. In the high-load condition, the participant executed a saccade to the remembered location of the stimulus that matched the central probe in color and orientation. The behavioral results indicate that greater working memory load is associated with prolonged saccadic reaction times. A general linear model revealed regions in prefrontal cortex (left anterior insula, right superior and middle frontal gyrus, anterior medial cingulum), and bilaterally along the intraparietal sulcus extending into surrounding areas (precuneus, superior and inferior parietal lobe) that were more activated when participants had to conjointly remember the locations, colors and orientations of four objects (load-4) compared to when they only had to remember the features of a single object (load-1). Specific responses for greater working memory load are focused on regions responsible for feature binding (occipital-temporal cortex) and allocation of attention (anterior insular cortex). Multivariate pattern analysis during the retrieval period of a trial revealed voxel clusters in the ventral visual pathway and the frontal eye fields that correctly classify the target location during the retrieval period of both tasks.

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Introduction

Extensive work has been conducted over the last 60 years to understand how neurons in primary visual cortex (V1) in primates and humans analyze basic visual features such as orientation, color, and spatial frequency (for a review see [Chalupa and Werner, 2003](#)). It is now well established that information concerning object-defining features of visuospatial stimuli is further transmitted from primary visual cortex to visual areas in the ventral and dorsal pathways to segment objects from the background and further classify them ([Kravitz et al., 2011](#); [Roelfsema, 2006](#)). To interact with the environment it often becomes necessary to briefly store the gathered information in memory and keep it available for sensory-guided behavior.

Although we have much information concerning the encoding of visual stimuli, we know little about the mechanisms that underlie our ability to hold this information in working memory. Electrophysiological and functional imaging studies on visual working memory have focused on the specificity of different brain regions for an object's

identity and spatial location ([Harrison et al., 2010](#); [Ungerleider et al., 1998](#)) and on the capacity of visual working memory (e.g. [Todd and Marois, 2004](#); for reviews cf. [Fukuda et al., 2010](#); [Jonides et al., 2008](#); [Pasternak and Greenlee, 2005](#)). Current results point towards a capacity limit of three to four objects that can be reliably stored ([Fukuda et al., 2010](#); [Magnussen, 2000](#); [Pasternak and Greenlee, 2005](#); [Todd and Marois, 2004](#)). The effective storing capacity can be enhanced by employing binding strategies like grouping or chunking ([Cowan, 2001](#)). However the efficiency of storing objects defined by the conjunction of stimulus features like color and shape should depend on the ability to create a bounded representation of the constituting features ([Luria and Vogel, 2011](#)). These authors ([Luria and Vogel, 2011](#)) examined object binding in visual short term memory and found that adding extra features to an object did not lead to an increase in the contralateral delay amplitude (CDA), an electrophysiological marker of working memory activity, whereas the CDA increased with the number of objects. These findings support the assumption that bounded features can be efficiently stored. Hence working memory capacity appears to be limited by the number of objects to be memorized rather than by the number of features that constitute these objects.

Generally, working memory tasks consist of an encoding phase, in which the relevant stimuli are perceived and stored in memory, a

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delay period in which the stored stimuli are maintained and a retrieval period in which the previously maintained information is accessed. A recent series of studies on delay-period activity in working memory tasks for orientation (Harrison and Tong, 2009; Sneve et al., 2012), spatial frequency (Sneve et al., 2012) and color (Serences et al., 2009) was carried out, using fMRI and multivariate pattern analysis (MVPA; Kamitani and Tong, 2005; Norman et al., 2006). To our knowledge none of these earlier studies was able to find delay-period activity during the retention period of a working memory task (e.g. Offen et al., 2009), suggesting that excitatory and inhibitory processes within visual cortex might cancel each other out. Other authors mostly relate parietal and frontal lobe regions to memory maintenance processes (Jonides et al., 2005, 2008; Kravitz et al., 2011; Linden, 2007; Ungerleider et al., 1998). A further study (Bledowski et al., 2006) focused on the working memory retrieval period combining functional MR imaging and EEG event related potentials. These authors argue that responses in the inferior temporal cortex for perceptual evaluation can be temporally dissociated from those in the parieto-frontal network for memory storage, active retrieval and response execution.

The common approach in functional imaging is to investigate visual working memory in the participants' ability to detect and localize a change in the stimulus display (Buschman et al., 2011; Song and Jiang, 2006) or in delayed matched to sample tasks (Todd and Marois, 2004, 2005). In such studies, during the retrieval period, participants compare the current stimuli to those presented during the encoding phase of the same trial. The manipulation of the memory load is achieved by varying the absolute number of objects that needs to be compared. Consequently, in such tasks the perceptual load, defined as increasing number of different items (Lavie, 2005), increases with increasing memory loads. Hence, differences in neural responses (especially in primary sensory areas) to high and low memory loads may be confounded by the increasing number of objects that need to be perceptually encoded prior to storage in memory.

We propose a way to overcome these possible drawbacks by designing a working memory task with high and low memory loads, while the perceptual load is kept constant across the entire trial. We compared neural responses during a saccadic delayed match to sample task with a high memory load (four objects to be remembered, load-4) to those evoked by a task with low memory load (one object to be remembered, load-1). The objects were composed of rectangular-shaped stimuli defined by color and orientation. In the load-4 task, subjects had to encode four of these objects and, after a 2-s delay, to saccade to the remembered location of the object that matched a centrally presented cue. The sensory input (perceptual load) over a trial was kept constant by reversing the presentation order of the cue and test stimuli during our load-1 condition. Hence, in the load-1 condition, subjects encode the features of a single stimulus, store this information and then saccade to one of the 4 quadrants depending on the location of the matching object.

We aim to identify the neural correlates that underlie visual working memory load using fMRI. We assume that higher working memory load should be associated with greater activations in parietal and prefrontal brain regions and prolonged saccadic reaction times. We apply multivariate pattern analysis (MVPA) on the dataset to gain insights into the pattern of brain activation. We test which voxels significantly contribute to the retrieval period of our working memory task by testing for the successful prediction of the correct target quadrant.

Methods

Participants

Fourteen naïve participants gave informed written consent and participated in the experiment (eight males, age: 20–28 years). All participants had normal or corrected-to-normal vision and none had a history of neurological or psychiatric illness. Their eye-movement traces showed normal saccadic and fixational eye movements. Data

from two subjects had to be discarded from further analysis due to poor signal-to-noise ratio of the eye-tracker signal in the scanner.

Stimuli and stimulus presentation

All stimuli were presented with a prototype of the “MRI Live!” projection system (Cambridge Research Systems, Ltd, Rochester, UK). Participants viewed two dichoptically presented high-resolution (1280×1024 pixels) displays through a custom built optical system (www.crsrtd.com/mri-live), which yielded a display size of 45 by 30° to each eye. The luminance and color contrasts of the stimuli were clearly visible for all participants at the presented eccentric locations. Luminance of the visual stimuli was 11.1 (for the red stimuli), 13.2 (green), 1.4 (blue) and 26 (yellow) cd/m². The stimuli were depicted on a gray background (luminance 12.7 cd/m²). Using the same device we recorded the fixation and saccadic eye movements of the participant with a high-speed (250 Hz) video-based eye tracker (see below). The stimuli were geometric rectangles each subtending 0.5° by 3° of visual angle and a radius of 6° visual angle between the fixation and the center of the stimulus. The rectangles varied across two dimensions (color and orientation) each with four possible randomly chosen characteristics (possible color variations: red, green, blue, yellow; possible variations in orientation: vertical, horizontal, tilted 45 deg left, tilted 45 deg right). From the possible characteristics, the randomization algorithm generated four unique rectangle stimuli. Exact replications of a particular combination of color and orientation within one trial were excluded. Consequently subjects always had to perform a conjoint encoding of position, color and orientation to perform a trial in both conditions correctly. Color and orientation during load-1 and load-4 tasks were further randomized in such a way that possible color and orientation combinations were balanced across the experiment. Accordingly, each possible color-orientation combination was presented equally often in each visual quadrant.

Participants had to perform a saccadic delayed match-to-sample task with high memory load (load-4 task) and with low memory load (load-1 task). Both categories of trials started with a jittered inter-trial interval of 6700 ms on average (the jitter resulted in durations of 5700, 6700 or 7700 ms to yield a virtual MR sampling rate of 1 Hz). In the load-4 task, four rectangle cue stimuli had to be encoded (one located in each quadrant). They were presented simultaneously for 200 ms followed by a memory delay period (2000 ms) and a centrally presented target (200 ms), which initiated the memory retrieval. In the retrieval period subjects had to remember the previously presented location of the cue that matched the target in color and orientation and had to execute a saccade to this position as quickly and accurately as possible. In the load-1 condition, first one central stimulus was presented as a cue (200 ms) followed by a memory delay (2000 ms). Subsequently the four stimuli were presented simultaneously, one stimulus per quadrant. Subjects had to saccade to the stimulus that exactly matched the previously encoded cue in color and orientation as quickly and accurately as possible. In the experimental and control conditions subjects were given visual feedback with respect to the correct location of the saccade target. This was done by introducing tiny (4 pixel) dots at the location of the stimuli, which were green at the correct location and red at the three distractor locations. These tiny dots were only visible when viewed with central foveal vision. Subjects were instructed to maintain fixation on the feedback dots for 3000 ms, after which the central fixation for the next trial was presented. The total trial duration was 12, 13 or 14 s, depending on the jitter. The experiment was divided into 12 blocks of load-4 and 12 blocks of load-1 tasks, each block containing 6 trials. The blocks were presented in a randomized sequence. Fig. 1 shows a schematic overview of both tasks.

Eye movement data analysis

Using a velocity threshold we could analyze the resulting eye traces offline, detect artifacts like eye blinks and extract the saccades

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