



The when and where of spatial storage in memory-guided saccades

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ARTICLE INFO

Article history:

Received 22 October 2009

Revised 12 February 2010

Accepted 13 May 2010

Available online 21 May 2010

Keywords:

memory-guided saccades

parietal cortex

frontal eye fields

spatial working memory

ERP

sLORETA

ABSTRACT

The memory-guided saccade paradigm is an ideal experimental model for studying spatial working memory. Both the posterior parietal cortex and frontal cortex are known to play a role in working memory; however, there is much debate about the degree of their involvement in the retention of information. We used event-related potentials and electromagnetic tomography to clarify the precise time course and location of the neural correlates of spatial working memory during a memory-guided saccade task in humans. We observed sustained activity in the inferior parietal lobe and extrastriate areas that persisted for the entire duration of the sensory- and memory-phases. This time course reveals that these regions participate in both initial sensory processing of visual cues and in the short-term maintenance of spatial location memory. Similar sustained activation was also observed in the anterior cingulate cortex, probably reflecting attentive control during the task. Differential activity between conditions was also recorded in the dorsolateral prefrontal cortex and in the frontal eye fields, but only during the initial part of the memory-phase. This finding suggests that these areas are not involved in the storage of spatial information, but rather in response selection and in transformation of spatial information into a motor coordinate framework, respectively. By exploiting techniques that provide exquisite temporal resolution and reasonably precise anatomical localization, this study provides evidence supporting the key role of inferior parietal lobe in the storage of spatial information during a working memory guided saccade.

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Introduction

Spatial working memory (WM) refers to the ability to temporarily retain spatial information that is not currently accessible in the perceptual domain and to use that information to effectively interact with the external environment (Baddeley, 1986; D'Esposito, 2007). The saccadic oculomotor system is an ideal experimental model for the study of spatial WM, since it permits to isolate the activity related to the maintenance of information from that related to the visual processing of the cue and to the response execution.

Generally, in a memory-guided saccade (MS) paradigm (Hikosaka and Wurtz, 1983), subjects remember the location of a briefly flashed visual cue and perform a saccade toward it at the end of a delay interval. Cortical areas showing persistent activity throughout the duration of the memory interval are thought to be directly involved in the active maintenance of the information hold in WM (Curtis and D'Esposito, 2003). During the retention of spatial information, a broad range of frontal–parietal cortical areas exhibit persistent neural activity (D'Esposito, 2007; Postle, 2006). Their involvement in the active maintenance of information, however, depends on the type

of information to be remembered and on the response modality required in the task. In an MS paradigm, it is thought that frontal eye fields (FEFs) are largely involved when subjects are biased toward the use of a prospective motor code, such as in the maintenance of the motor plan as oculomotor coordinates (Curtis et al., 2004; Fuster, 1995; Postle and D'Esposito, 2003). Conversely, a greater contribution of parietal cortex is expected when subjects maintain a retrospective perceptual code, in which attention is allocated to regions of the extrastriate and parietal cortex responsible for the perception of location (Awh and Jonides, 2001; Curtis et al., 2004; Postle et al., 2004). However, a recent study has provided evidence that is inconsistent with these assumptions, raising doubts concerning the nature of the code carried by the persistent delay period activity (Srimal and Curtis, 2008). These authors (Srimal and Curtis, 2008) used event-related functional magnetic resonance imaging to identify cortical areas with a persistent activity throughout the WM delays and tested if this activity was related to the metrics of the MS response. They found that during the delay period, activity in the FEFs did not differ from activity in the parietal area, even when saccades were never made, challenging therefore the assumption that neurons in the FEFs maintain the metrics for saccades.

In the present study, we exploit the high temporal resolution of event-related potentials (ERPs) to understand the mechanisms of maintenance during spatial WM delays in humans. Indeed, an important step toward revealing the specific contribution of the

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frontal–parietal areas may come from determining the relative timing of their sustained activation. To our knowledge, two other studies investigated ERPs during memory-guided saccade paradigm (Evdokimidis et al., 2001; Rama et al., 1995), but they did not address this issue of the nature of the code carried by the persistent delay period activity nor tried to localize the cortical areas involved.

A substantial difficulty in interpreting neural differences between a memory-guided saccade and a control condition is that there are numerous processes that occur while a subject is performing a simple memory task that have little or nothing to do with WM *per se*. These non-specific, task-general processes (e.g., arousal, sustained attention, general response preparation, etc.) may have directly contributed to the contradictory results reported in literature. In addition, the timing of neural modulation can be influenced by the specific intervals used between stimuli and the temporal expectations that these engender (Nobre et al., 2007). In the study of ERPs, then, also the least physical differences between the perceptual attributes of cueing stimuli may have a large impact on the ERP waveform morphology (Hillyard and Picton, 1979).

Keeping these aspects in mind, we compared ERPs elicited by an MS and a visually guided saccade (VS) task (e.g., Brignani et al., 2007). Both the tasks were built in order to minimize cognitive and perceptual differences unrelated to spatial working memory. Perceptual attributes of cueing stimuli, covert attentional shift and aspecific motor activation were carefully balanced in the two task conditions, all aspects that have not been considered before. In the MS task, subjects had to memorize the specific location of a saccadic target briefly presented during the sensory phase and perform an eye movement toward it at the end of the memory phase. In the VS task, subjects did not know the amplitude of the saccade to be executed, and simply moved toward a visually presented saccadic target at the end of the delay interval. However, also in this condition the direction of the subsequent saccade was provided, forcing subjects to shift spatial attention and to prepare a general motor plan towards the side where the saccadic target would have appeared. If FEFs play a relevant role in the storage of spatial information by maintaining the saccadic plan when the specific oculomotor coordinates are provided before the memory delay, then we expected a larger sustained activity of FEFs in MS than in VS task condition during all the delay period. On the contrary, if no persistent differential activation between the two tasks was found, we should conclude that FEFs do not play a relevant role in the storage of spatial information.

Despite excellent temporal resolution, ERPs lack the spatial discriminatory power to provide an adequate localization of the cortical activity. To overcome this difficulty we also analyzed data using standardized low resolution electromagnetic tomography (sLORETA, Pascual-Marqui, 2002, 2007), a method with zero error localization that seems in some aspects comparable to the classical functional imaging methods, when the analysis is limited to the identification of superficial signal sources within the cerebral cortex.

Materials and methods

Participants

Twenty-four healthy volunteers participated in the study. Four were disqualified from the analysis due to excessive noise in the recording, or because they produced too many anticipatory eye movements. The remaining 20 participants (8 females and 12 males) had a mean age of 23.5 years (range of 20–30). They were right handed (+78.3%) according to the Edinburgh handedness inventory test (Oldfield, 1971) and had normal or corrected to normal visual acuity. The experimental methods were non-invasive and were approved by the Ethics Committee of IRCCS San Giovanni di Dio Fatebenefratelli, Brescia, Italy. All participants gave informed consent.

Behavioral task and procedure

Each participant sat in a dimly illuminated room with his/her head stabilized through a combination of a chin rest and a head support bar. All visual stimuli were rear-projected on a large screen placed at a distance of 1.5 m in front of the subject.

All participants performed an MS and a VS task, arranged in a blocked design and presented in a balanced order across subjects. In the MS task, subjects were required to memorize the position of a peripherally flashed visual target and to execute a saccade towards its position after a delay-phase. In the VS task, subjects did not need to memorize a saccadic target. After a delay interval, in which they were requested to maintain central fixation, they performed a saccade towards a peripheral target presented in the visual hemifield. In this task, information about the direction of the subsequent saccade was also provided, forcing subjects to shift spatial attention and to prepare a general motor plan towards the side where the saccadic target would have appeared.

The tasks are described in greater detail below. Several phases were common to both tasks, and all phases were presented in the same temporal sequence (Fig. 1):

Fixation-phase—Participants fixated on a central point for a period of 2 s.

Sensory-phase—Two horizontal lines were shown for 300 ms on both sides of the central fixation point at $\pm 20^\circ$ of the visual angle, one with the same color as the central fixation point (i.e., cue), the other with a different color (i.e., distracter). In the VS task, the cueing horizontal line informed participants about the direction of the subsequent saccade (i.e., the hemifield containing the line of the same color as the central fixation point), inducing activation of a general motor plan. In the MS task, a dot with a color congruent to the line was superimposed on each horizontal line in one of eight possible positions, equally spaced along the horizontal meridian, within a range of $\pm 20^\circ$ of the visual field (i.e., $\pm 5^\circ$, $\pm 10^\circ$, $\pm 15^\circ$, $\pm 20^\circ$). The point with the same color as the central fixation point (i.e., the cue) was to be memorized, while the point appearing in a non-symmetrical position (i.e., a distracter) in the contralateral visual field was to be ignored. In this condition, the actual amplitude of the saccadic response was provided, allowing participants to program a specific motor plan. The horizontal lines and the distracter were included to reduce the visual differences between the two conditions and the two hemispheres, respectively.

Memory/delay-phase—The central fixation point was shown alone for a delay period of 2 s, during which the subjects were instructed to avoid making eye movements.

Motor-phase—In the MS task, disappearance of the fixation point (i.e., GO signal) was the indication for subjects to execute a saccade to the precise remembered cue position (multiple saccades were allowed). In the VS task, disappearance of the fixation dot was followed by a 300 ms gap, after which a peripheral target (i.e., GO signal) appeared on the same side cued in the sensory-phase. In this task, subjects executed a simple saccade to the new target.

Correction-phase—This phase was present only during the MS task. One second after the GO signal, the memorized target appeared alone for 1 s in order to allow subjects to perform a corrective saccade if needed and additionally to check for possible errors in the response.

In both tasks, reappearance of the fixation point marked the beginning of the next trial.

The central fixation and the peripheral stimuli were red or green dots with a diameter of 0.43° , rendered on a black background. For half of the subjects, the central fixation point and, therefore, the valid cue were red, while, for the other half of the subjects, they were green. Each MS/VS experimental session was divided into four blocks of 64

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