



Selection within visual memory representations activates the oculomotor system

Artem V. Belopolsky*, Jan Theeuwes

Dept. of Cognitive Psychology, Vrije Universiteit, Van der Boechorststraat 1, 1081 BT Amsterdam, The Netherlands

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ABSTRACT

Humans tend to create and maintain internal representations of the environment that help guiding actions during the everyday activities. Previous studies have shown that the oculomotor system is involved in coding and maintenance of locations in visual–spatial working memory. In these studies selection of the relevant location for maintenance in working memory took place on the screen (selecting the location of a dot presented on the screen). The present study extended these findings by showing that the oculomotor system also codes selection of location from an internal memory representation. Participants first memorized two locations and after a retention interval selected one location for further maintenance. The results show that saccade trajectories deviated away from the ultimately remembered location. Furthermore, selection of the location from the memorized representation produced sustained oculomotor preparation to it. The results show that oculomotor system is very flexible and plays an active role for coding and maintaining information selected within internal memory representations.

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1. Introduction

Close your eyes and imagine that you are standing at a doorstep of your kitchen. Do you know whether the fridge is on your right or on your left? And if you wanted to make a cup of tea, where would you look to locate the tea-pot? Although you might be miles away from your kitchen it is probably not very difficult to create a rather vivid representation of this familiar environment and to be able roughly indicate the locations of the most commonly used objects.

This example illustrates that besides interacting with the external world, we can also interact with an internal memorized representations of the environment. These internal representations span from simple visual working memory representations that help us to retain the relevant information for short periods of time (Baddeley & Hitch, 1974) to more complex and long-lasting internal representations of the world such as visual long-term memory representations and visual imagery (Kosslyn, Ball, & Reiser, 1978).

Visual attention is the mechanism by which information is selected from the external visual environment and its behavioral and neural underpinnings have been a topic of extensive research for many years (Kastner & Ungerleider, 2000). Interestingly, more recent studies have shown that visual attention might also be involved in selection and maintenance of information in the internal representations (Awh & Jonides, 2001; Awh, Vogel, & Oh, 2006; Postle, 2006; Theeuwes, Belopolsky, & Olivers, 2009). For example, it has been demonstrated that attention facilitates the transfer

of information into the working memory (Belopolsky, Kramer, & Godijn, 2008; Schmidt, Vogel, Woodman, & Luck, 2002; Sperling, 1960). Furthermore, research by Awh and colleagues (Awh, Anillo-Vento, & Hillyard, 2000; Awh, Jonides, & Reuter-Lorenz, 1998) indicated that there is a large overlap between the mechanisms involved in visuo-spatial memory and in attentional selection. They showed that when a location is kept in working memory, processing of stimuli at the memorized location is facilitated relative to other locations, just like attending to a location improves the processing of information at that location (Posner, 1980). Conversely, when attention to memorized locations is interrupted, the ability to remember these locations is impaired (but see Belopolsky & Theeuwes, 2009b). Furthermore, brain imaging studies of working memory confirm the notion that rehearsal of spatial information modulates early sensory areas (Harrison & Tong, 2009; Munneke, Heslenfeld, & Theeuwes, 2010; Postle, Awh, Jonides, Smith, & D'Esposito, 2004).

Studies by Nobre and colleagues (Griffin & Nobre, 2003; Kuo, Rao, Lepsien, & Nobre, 2009; Nobre et al., 2004) have shown that behavioral and neural mechanisms of attentional selection within internal representations are very similar to the mechanisms that operate on the perceptual representations. Direct comparison of cueing of attention to the locations in the internal and perceptual representations revealed a largely overlapping network of frontal, parietal and visual areas (Nobre et al., 2004). In a more recent study (Kuo et al., 2009) participants were first asked to memorize a layout of several shapes or colors and then after a retention interval they were asked to search in memory through this set of objects for a specific target object. The results demonstrated that selection of a target within an internal representation elicited an

* Corresponding author. Tel.: +31 20 598 8714; fax: +31 20 598 8971.
E-mail address: A.Belopolsky@psy.vu.nl (A.V. Belopolsky).

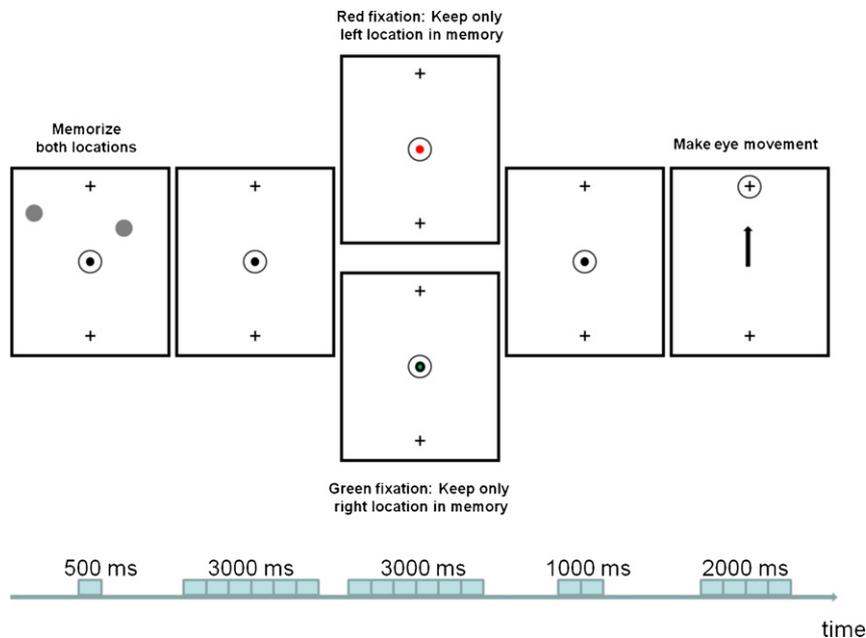


Fig. 1. Illustration of events occurring on a typical trial in Experiment 1. The open circle was not present in the actual display and indicates where participants had to fixate during the trial.

N2pc component in the event-related potential (ERP), which time-course and topography was very similar to the N2pc elicited during a search through a visible array of objects (see also Dell'Acqua, Sessa, Toffanin, Luria, & Jolicoeur, 2010). Converging behavioral evidence has recently been provided by Theeuwes, Kramer, and Irwin (2010), who showed that instruction to retrieve an object from an internal representation resulted in a faster detection of probes occurring at the empty location that was occupied by this object.

Recent studies indicate that there is also a close relationship between visual-spatial working memory and the eye movement system (Belopolsky & Theeuwes, 2009a; Theeuwes et al., 2009; Theeuwes, Olivers, & Chizk, 2005; Theeuwes, Van der Stigchel, & Olivers, 2006; Tremblay, Saint-Aubin, & Jalbert, 2006; Van der Stigchel & Theeuwes, 2006). For example, it has been demonstrated that saccades curve away from the remembered locations, much in the same way as they curve away from visible locations (Theeuwes et al., 2005; Theeuwes et al., 2006). Saccade curvature has been attributed to competition in the oculomotor map for potential saccade targets located in the intermediate layers of superior colliculus (SC, Sparks & Hartwich-Young, 1989). Saccade trajectory deviation away is typically explained by inhibition of the oculomotor program produced by a visible distractor or an attended location, which disturbs the overall activation in SC and shifts the saccade vector away from the distractor location (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; see for a review Van der Stigchel, Meeter, & Theeuwes, 2006). The fact that covertly attended locations and saccade targets are coded on the same motor map provides strong evidence for a close relationship between attention and saccades as postulated by the premotor theory of attention (Rizzolatti, Riggio, & Sheliga, 1994; Sheliga, Riggio, & Rizzolatti, 1994). The observation that saccades also curve away from an empty location that was held in memory indicates that a mere act of remembering a location (note that saccades were never executed to the memorized location) generates competition in the oculomotor system. This shows that attention, visual-spatial working memory and the oculomotor system are very closely related. This led us to propose that visual-spatial working memory may be nothing else than covert preparation for an oculomotor action (Theeuwes et al., 2009).

The current study explored whether the oculomotor system is also involved in selection of information within the memory representations. In previous studies (Theeuwes et al., 2005, 2006), a single dot was presented on the screen and participants were required to select the location of the dot. While encoding the location of the dot, it was extinguished and its location was further maintained in memory. In the current study, two dots were presented on the screen and before participants knew which of the locations had to be maintained in memory the dots were extinguished. While keeping both locations active in memory, participants had to select one of these locations. In other words, in previous studies selection of the relevant location took place on the screen (selecting the location of a dot presented on the screen) while in the current study selection took place within a memory representation (selection of the location of a dot held in working memory).

In Experiment 1 we investigated whether such selection of location within the context of memory representation generated activity on the oculomotor map by measuring whether saccades deviate away from the ultimately remembered location. In Experiment 2 in addition to measuring saccade curvature, we probed the oculomotor activation by cueing participants on some trials to make a saccade to either the remembered or to the ignored location.

2. Experiment 1

The goal of the present experiment was to investigate whether selection of a location within the memorized representation results in saccade curvature away from that location. Participants were asked to simultaneously remember two locations on the left and on the right side of the screen (see Fig. 1). After a retention interval a color change at the fixation told them which location to keep remembering and which location to forget. After the second retention interval participants had to make a saccade and trajectory of this saccade was used to measure the curvature away. We also included a control condition, which was identical to the memory condition, except that participants did not have to keep the locations in memory. If selection of a location within a memorized representation activated the oculomotor system then we expected

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