

Selection within visual memory representations activates the oculomotor system

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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

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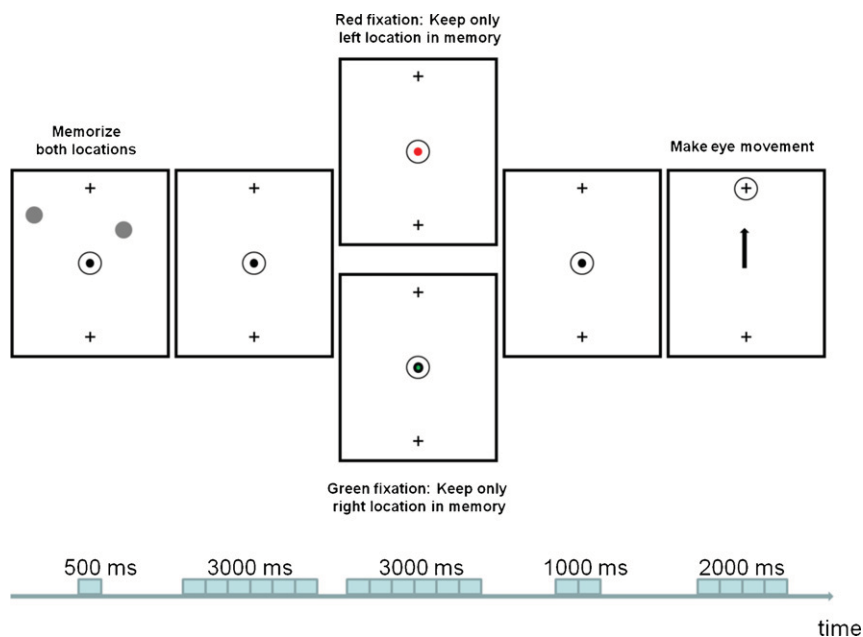


Fig. 1. Illustration of events occurring on a typical trial in Experiment 1. The open circle was not present in the actual display and indicates where participants had to fixate during the trial.

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

saccade trajectory to curve away from that location, but no curvature was expected in the control condition.

2.1. Methods

2.1.1. Participants

Eight naïve participants (7 females, age range 18–32 years) with normal or corrected to normal vision participated in the experiment.

2.1.2. Apparatus

The stimuli were presented on a 21-in. monitor running at 75 Hz with a 1024 × 768 pixels resolution. Eye movements were recorded with the head-mounted EyeLink-II system (SR research, Mississauga, Ontario, Canada) with 500 Hz temporal and 0.2° spatial resolution. An automatic algorithm detected saccades using minimum velocity and acceleration criteria of 35°/s and 9500°/s² respectively.

2.1.3. Stimuli, design & procedure

Each observer was seated 75 cm from a computer screen, with head positioned on a chinrest. The stimuli were presented on a black background. The trial began with the participants fixating the dot (0.5° in diameter) at the center of the screen and pressing a spacebar to start. After 500 ms, two gray dots (1° in diameter) appeared for 500 ms (Fig. 1). In the memory condition, the participants had to memorize the exact locations of the two dots. In the no-memory condition the dots were presented, but did not need to be memorized.

The dots' positions were selected out of 48 possible locations (16 locations on each of the three imaginary circles with the radius of 6°, 6.8°, and 7.6°). Each quadrant contained 12 locations, chosen to be at 30°, 40°, 50° and 60° of arc. The constraint was that the two dots were always presented in the opposite horizontal hemifields, but always in the same vertical hemifield.

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After a blank interval of 3000 ms, the fixation point changed color for another 3000 ms. When fixation point turned red (3.2 cd/m²), it indicated that observers only needed to keep the left location in memory and forget about the location on the right; when fixation point turned green (3.2 cd/m²), it indicated that observers only needed to keep the right location in memory and forget about the location on the left. After a blank interval of 1000 ms, during which the fixation point turned gray, an arrow (1.5°) pointing either straight up or straight down was presented at the central location for 2000 ms. Participants were instructed to immediately make a saccade in the direction of the arrow to a marker placed at the top or bottom of the display 9° from the central fixation (these markers were visible throughout the whole trial). Saccades were always made to the marker located in the same hemifield as the dots have been presented earlier. Memorized location was equally likely to occur in each quadrant of the display.

In the memory condition after another blank interval of 1000 ms a memory test was presented. A memory probe (a ring with the same outer diameter as the circle) was presented either at the to-be-remembered location (probability of .5) or at a slightly different location (shifted 1°, 1.5°, or 2° along the horizontal axis either toward or away from fixation). The direction and distance of the memory probe offset was selected randomly. The participants indicated whether the memory probe location was the same ("m" key) or different ("v" key).

Each observer performed 120 trials with and 120 trials without the memory task. The order of the tasks was counterbalanced across the participants. Before the start of each task participants completed a practice block (24 trials). After each block (24 trials), participants received feedback about their average memory accuracy and saccade latency. On each trial, the participants received auditory feedback for memory and eye movement errors.

2.2. Results and discussion

Trials with saccades faster than 80 ms and slower than 600 ms, saccades that did not start within 1° away from fixation point, and saccades that did not land within 30° of arc from the center of the saccade target were discarded from further analyses. Furthermore, saccades that were smaller than 3° were also excluded. This resulted in an average loss of 9% of trials (range 2–18%).

To determine the effect of the memorized location on saccade trajectory, we calculated the angular deviation of the saccade path for each 2-ms sample point that was greater than 0.5° from the central fixation and smaller than 0.5° from the endpoint of the saccade, relative to a straight line from the starting point of the saccade to the saccade endpoint. A median of these deviations was calculated for each saccade, averaged across saccade direction and normalized to the top left hemifield (curvature for memorized location on the left minus curvature for memorized location on the right, for a similar method see Van der Stigchel, Meeter, & Theeuwes, 2006).

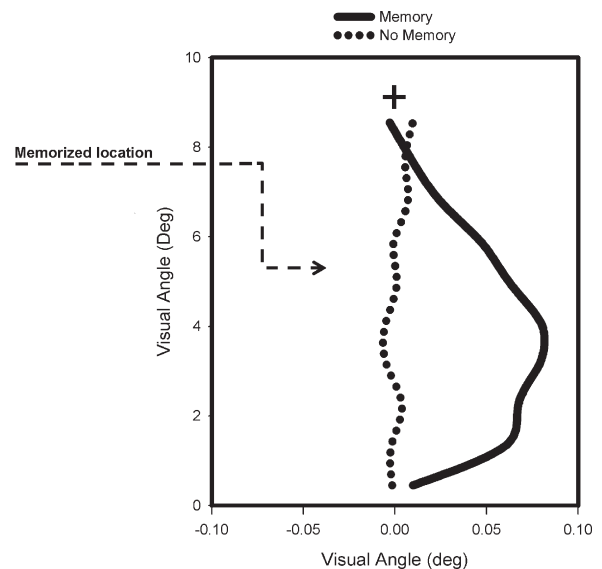


Fig. 2. Plot of mean saccade trajectories used for calculation of curvature in Experiment 1 for the memory and no memory conditions. Trajectories were normalized to the memorized location occurring on the top left side and averaged across saccade directions and participants.

Mean of saccade trajectories used for calculation of curvature are presented in Fig. 2. Curvature away from the memorized location was significantly different from zero when the location had to be kept in memory (0.83° ; $t(7) = 3.48$, $p < 0.05$) and was not significantly different from zero when the location had to be simply observed (0.1° ; $t(7) = 1.08$, $p = .3$). Curvature away from the memorized location was also greater when it had to be kept in memory than when the dots had to be simply observed ($t(7) = 3.70$, $p < .01$). There was no difference in saccade latency between the memory and no memory conditions (334 and 338 ms, respectively, $t(7) = 0.19$, $p = 0.8$).

Although the memory task was rather challenging, participants were overall quite accurate in performing it (68.2% correct responses). When the memory probe did not fall on the memorized location, the accuracy was dependent on the distance of the memory probe from the memorized location. Basically, the closer the memory probe was to the memorized location, the more difficult it was to detect the difference and to respond correctly (49%, 58%, and 77% for close, medium, and far memory probe locations, respectively; $F(2, 14) = 15.0$, $p < 0.001$).

The results suggest selection of location within the context of the memory representation generated oculomotor activity that had to be inhibited in order to execute a saccade to a different location. This inhibition led to saccade curvature away from the location that had to ultimately be held in memory.

Another important question is whether the oculomotor preparation at the ultimately memorized location is maintained or inhibited. For example, Belopolsky and Theeuwes (2009a) showed inhibition of saccades to locations in working memory. They suggested that locations maintained in working memory are always coded in the oculomotor system, but can be either activated or inhibited depending on the task demands (see also Belopolsky & Theeuwes, 2009b). To investigate this issue on some trials in Experiment 2 participants had to make a saccade either to the remembered or to the ignored location.

3. Experiment 2

The goal of the present experiment was to measure the oculomotor preparation at the remembered location. On half of the

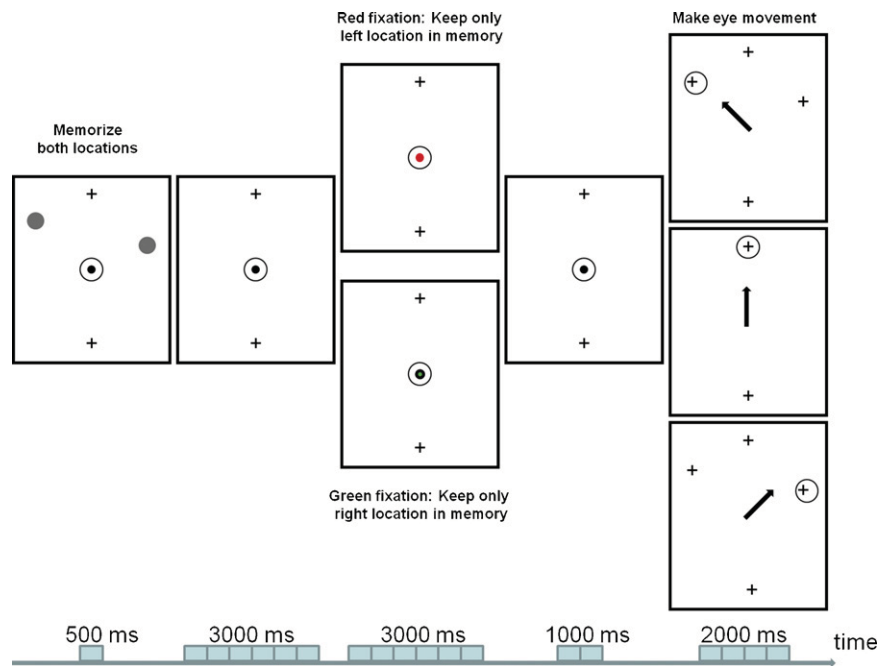


Fig. 3. Illustration of events occurring on a typical trial in Experiment 2. The open circle was not present in the actual display and indicates where participants had to fixate during the trial.

trials the task was identical to the memory condition of Experiment 1 and these trials were used to calculate saccade curvature and to replicate the findings of Experiment 1. On the other half of the trials markers appeared at the remembered and ignored locations and participants were cued to make a saccade towards one or the other location (see Fig. 3). If oculomotor preparation is maintained at the remembered location, we expected that the latency of saccades to that location would be shorter than the latency of saccades to the ignored location. Alternatively, if oculomotor orienting to the remembered location is suppressed this would be evident in longer latency of saccades to that location.

3.1. Methods

3.1.1. Participants

Eight naïve participants (6 females, age range 18–28 years) with normal or corrected to normal vision participated in the experiment.

3.1.2. Stimuli, design & procedure

The experiment was very similar to Experiment 1 but with a few exceptions. Only a memory condition was used (Fig. 3).

The locations of the memory dots were chosen to always be equidistant from the fixation point (e.g. on the same imaginary circle, but not necessarily mirrored). The timing of the events was the same as in Experiment 1. On half of the trials, the experiment was identical to the memory condition of Experiment 1, with the arrow indicating the saccade direction pointing either up or down. Importantly, on the other half of trials two additional markers were presented at the locations previously occupied by the memory dots and the arrow was now pointing to one of those markers. As before, participants had to make a saccade to the marker indicated by the arrow. The arrow was equally likely to point to the location that had to be maintained in memory, as to the location that had to be ignored. The memory test for the to-be-remembered location was identical to the one used in Experiment 1.

Each observer performed 224 trials divided across 7 blocks. Before the start of each task participants completed a practice block (32 trials).

3.2. Results and discussion

Trials with saccades faster than 80 ms and slower than 800 ms, saccades that did not start within 1° away from fixation point, and saccades that did not land within 30° of arc from the center of the saccade target were discarded from further analyses. Further-

more, saccades that were smaller than 3° were also excluded. This resulted in an average loss of 14% of trials (range 5–25%).

Saccade curvature was calculated in the same way as in Experiment 1. Mean of saccade trajectories used for calculation of curvature are presented in Fig. 4. Curvature away from the memorized location was again significantly different from zero (1.22° ; $t(7)=4.28$, $p < .005$). This finding replicates the result from Experiment 1 and shows that selection of a location within working memory representation results in oculomotor activity that makes saccades curve away from that location.

To determine whether selection within the working memory representation also has consequences for initiating a saccade we compared saccade latencies of saccades executed to the remembered location and saccades executed to the ignored location. The results are plotted in Fig. 5. Saccades were initiated faster to the

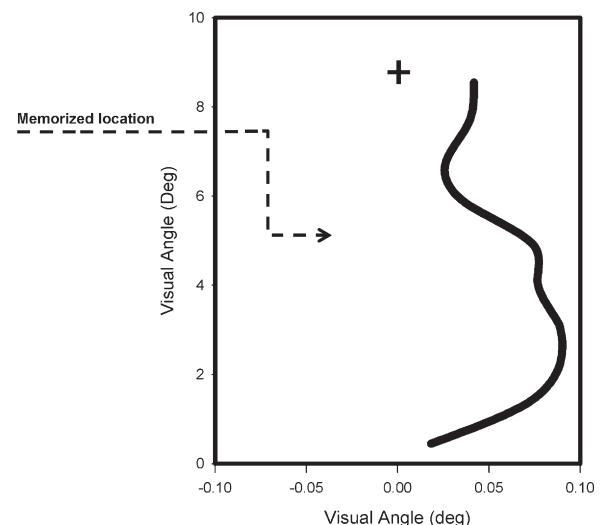


Fig. 4. Plot of mean saccade trajectories used for calculation of curvature in Experiment 2. Trajectories were normalized to the memorized location occurring on the top left side and averaged across saccade directions and participants.

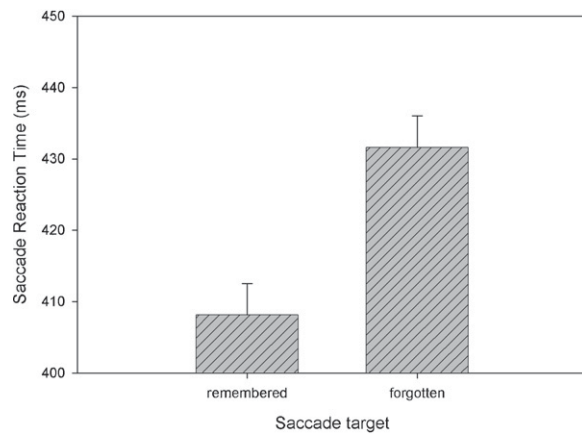


Fig. 5. Mean correct saccade RT in Experiment 2 as a function of the whether saccade was made to the same location as the remembered location or to the ignored location. Error bars show ± 1 SEM for within-subjects design (Loftus & Masson, 1994).

remembered location than to the ignored location (408 ms and 432 ms, respectively, $t(7) = 2.65$, $p < .05$). This implies that selecting and remembering a location within a working memory representation is associated with preparation and maintenance of a saccade program to that location.

The mean latency of the vertical saccades was 430 ms. Note, that these saccades cannot be directly compared to the saccades to the remembered or ignored locations since they were longer than the oblique saccades and used different ocular muscles.

Participants were again quite accurate in performing the memory task (70.5% correct responses). When the memory probe did not fall on the memorized location, the closer it was to the memorized location, the more difficult it was to detect the difference and to respond correctly (49%, 67%, and 83% for close, medium, and far memory probe locations, respectively; $F(2, 14) = 43.6$, $p < .001$).

Additional analysis showed that memory performance was slightly improved when saccades were directed to the remembered or ignored locations than to the visible markers at the top or bottom of the screen (74% vs 67%, respectively; $t(7) = 2.0$, $p = 0.09$). This result is not surprising since in the former case the memorized location was always re-stimulated through appearance of saccade markers. As shown in Belopolsky and Theeuwes (2009a), such re-stimulation of the memorized location leads to memory improvement. Further illustration of this fact is that memory performance for the remembered and ignored locations were not significantly different from each other (73.9 vs 73.6%, $t(7) = 0.12$, $p = .91$).

4. General discussion

The present results clearly demonstrate that the oculomotor system is intimately involved in selection of information from the internal representations of space. Its involvement is analogous to selection of visible stimuli. We show that just as during the selection of information in external space, selection of a location within a memorized representation leads to saccade trajectories deviated away from that location. Furthermore, saccades were initiated faster to the remembered location than to the ignored location, suggesting that the oculomotor program to that location was maintained (Belopolsky & Theeuwes, 2009c). Note that in both experiments there was no need to program an eye movement to the remembered location: in Experiment 1 saccades were never made to these locations and in Experiment 2 the probability of making a saccade to the remembered location was very small (25% of trials). Nevertheless, selection in the memory space was able to gener-

ate a spatially specific activity in the oculomotor system, while the external space was empty.

The current findings are consistent with our proposal regarding a strong overlap between visual working memory, spatial attention, and the oculomotor system (Theeuwes et al., 2009). However, our findings provide an important extension of this proposal. While previous studies have shown that shifts of spatial attention (Belopolsky & Theeuwes, 2009c; Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Sheliga et al., 1994) and locations maintained in working memory (Belopolsky & Theeuwes, 2009a; Theeuwes et al., 2005; Theeuwes et al., 2006) are coded on the oculomotor map, we show that oculomotor map flexibly codes all operations of spatial selection and maintenance, whether they occur in the external space or internal memory space.

The most likely candidate for such a map is the superior colliculus (SC) – a midbrain structure that operates as a motor map for the generation of eye movements. The intermediate layers of the SC have direct projections to and from the posterior parietal cortex (Pare & Wurtz, 1997), a region closely related to attentional selection (Kastner & Ungerleider, 2000). Neural activity in SC encodes the locations of potential saccade endpoints that compete with each other. When a saccade is initiated the eyes start moving in the direction of the mean vector of these activities (Godijn & Theeuwes, 2002; Van der Stigchel et al., 2006). If there is not much time to apply inhibition to the location of the distractor the mean vector of activity would be shifted in the direction of the distractor. However, given enough time inhibition can be applied to the distractor location (McSorley, Haggard, & Walker, 2006; Theeuwes & Godijn, 2004), which would lead to a shift in the mean vector of activity, resulting in the eye movement deviating away from the distractor (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Sheliga et al., 1994). Neurophysiological evidence for the inhibition account of curvature away has been provided by Aizawa and Wurtz (1998) who showed saccade trajectories deviating away from the region in SC that was locally inactivated. Our results suggest memory-based activity can generate competition within the oculomotor system and in order to allow for an accurate saccade to the target location, the oculomotor activity associated with the remembered location in the SC needs to be inhibited. Most importantly, activation in SC has to be very flexible: observers first had to maintain both locations in memory and only later on select one location for further maintenance. Therefore, the oculomotor map in SC can be very flexibly modulated offline.

In addition to finding curvature away from the location selected within a memory representation we also found that the oculomotor preparation was maintained at the ultimately remembered location. Note that this result is unlike previous findings in which we found a delay in initiation of saccades to a memorized location (Belopolsky & Theeuwes, 2009a; Theeuwes et al., 2006). One possible explanation why in the current study there is oculomotor facilitation while in previous studies there was inhibition is that in the previous studies selection of the relevant location took place on the screen (the location was stored in memory while the dot was still physically on the screen) while in the present study selection took place within the memory representation (the relevant location was selected after the dots were no longer on the screen). In other words, the current study deals with selection within a memory representation. It is feasible that when the initial selection takes place on the screen inhibitory effects resembling inhibition of return (IOR) are observed (Klein, 2000). As in the current study selection takes place within a memory representation inhibitory effects are not seen but instead facilitatory oculomotor (and possibly attentional) effects are observed.

Note that it is possible to simultaneously have saccade curvature away from a location which is assumed to represent inhibition while at the same time to have facilitatory processing at that loca-

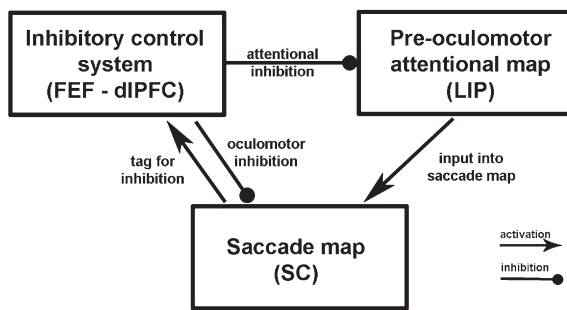


Fig. 6. A framework for understanding the inhibitory control of saccades (adapted from Godijn & Theeuwes, 2004; Theeuwes & Godijn, 2004).

tion. It is thought that saccade curvature is generated within the SC while oculomotor processing (both inhibitory and facilitatory) originates in the preculomotor attentional map located in posterior parietal cortex (most likely the intraparietal sulcus). According to the framework developed by Godijn and Theeuwes (2004), (see also Theeuwes and Godijn, 2004) when a location is attended it is passed from the preculomotor map to the saccade map in the SC (see Fig. 6). In case of inhibition the activation within the saccade map then generates activation in the inhibitory control system (most likely dorsolateral prefrontal cortex and/or the frontal eye fields). Activation in the inhibitory control system in turn generates an inhibitory tag within the preculomotor attentional map, which delays the initiation of saccade. We propose that during selection within a memory representation there is no inhibitory tag passed from the SC to the inhibitory control system. Instead, activation in the preculomotor attentional map in the posterior parietal cortex is sustained.

To summarize, the present study corroborates previous findings suggesting that the process of selecting information from our internal representations resembles the way it occurs for the external world (Kuo et al., 2009; Nobre et al., 2004). Our findings show that oculomotor system is very flexible and plays an active role for coding and maintaining information selected within internal representations.

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References

- Aizawa, H., & Wurtz, R. H. (1998). Reversible inactivation of monkey superior colliculus. I. Curvature of saccadic trajectory. *Journal of Neurophysiology*, *79*(4), 2082–2096.
- Awh, E., Anillo-Vento, L., & Hillyard, S. A. (2000). The role of spatial selective attention in working memory for locations: Evidence from event-related potentials. *Journal of Cognitive Neuroscience*, *12*(5), 840–847.
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, *5*(3), 119–126.
- Awh, E., Jonides, J., & Reuter-Lorenz, P. A. (1998). Rehearsal in spatial working memory. *Journal of Experimental Psychology-Human Perception and Performance*, *24*(3), 780–790.
- Awh, E., Vogel, E. K., & Oh, S. H. (2006). Interactions between attention and working memory. *Neuroscience*, *139*(1), 201–208.
- Baddeley, A. D., & Hitch, G. (1974). Working memory. In G. Bower (Ed.), *The psychology of learning and motivation*, VIII (pp. 47–89). New York: Academic Press.
- Belopolsky, A. V., Kramer, A. F., & Godijn, R. (2008). Transfer of information into working memory during attentional capture. *Visual Cognition*, *16*(4), 409–418.
- Belopolsky, A. V., & Theeuwes, J. (2009a). Inhibition of saccadic eye movements to locations in spatial working memory. *Attention Perception and Psychophysics*, *71*(3), 620–631.

- Belopolsky, A. V., & Theeuwes, J. (2009b). No functional role of attention-based rehearsal in maintenance of spatial working memory representations. *Acta Psychologica*, *132*(2), 124–135.
- Belopolsky, A. V., & Theeuwes, J. (2009c). When are attention and saccade preparation dissociated? *Psychological Science*, *20*(11), 1340–1347.
- Dell'Acqua, R., Sessa, P., Toffanin, P., Luria, R., & Jolicœur, P. (2010). Orienting attention to objects in visual short-term memory. *Neuropsychologia*, *48*(2), 419–428.
- Doyle, D., & Walker, R. (2001). Curved saccade trajectories: Voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research*, *139*(3), 333–344.
- Godijn, R., & Theeuwes, J. (2002). Programming of endogenous and exogenous saccades: evidence for a competitive integration model. *Journal of Experimental Psychology: Human Perception and Performance*, *28*(5), 1039–1054.
- Godijn, R., & Theeuwes, J. (2004). The relationship between inhibition of return and saccade trajectory deviations. *Journal of Experimental Psychology-Human Perception and Performance*, *30*(3), 538–554.
- Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience*, *15*(8), 1176–1194.
- Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*(7238), 632–635.
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, *23*, 315–341.
- Klein, R. M. (2000). Inhibition of Return. *Trends in Cognitive Science*, *4*(4), 138–147.
- Kosslyn, S. M., Ball, T. M., & Reiser, B. J. (1978). Visual images preserve metric spatial information: Evidence from studies of image scanning. *Journal of Experimental Psychology: Human Perception and Performance*, *4*(1), 47–60.
- Kuo, B. C., Rao, A., Lepsien, J., & Nobre, A. C. (2009). Searching for targets within the spatial layout of visual short-term memory. *Journal of Neuroscience*, *29*(25), 8032–8038.
- Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin and Review*, *1*, 476–490.
- McSorley, E., Haggard, P., & Walker, R. (2006). Time course of oculomotor inhibition revealed by saccade trajectory modulation. *Journal of Neurophysiology*, *96*(3), 1420–1424.
- Munneke, J., Heslenfeld, D. J., & Theeuwes, J. (2010). Spatial working memory effects in early visual cortex. *Brain and Cognition*, *72*(3), 368–377.
- Nobre, A. C., Coull, J. T., Maquet, P., Frith, C. D., Vandenberghe, R., & Mesulam, M. M. (2004). Orienting attention to locations in perceptual versus mental representations. *Journal of Cognitive Neuroscience*, *16*(3), 363–373.
- Pare, M., & Wurtz, R. H. (1997). Monkey posterior parietal cortex neurons antidromically activated from superior colliculus. *Journal of Neurophysiology*, *78*(6), 3493–3497.
- Posner, M. I. (1980). Orienting of attention, the VIIth Sir Frederic Bartlett lecture. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*(1), 23–38.
- Postle, B. R., Awh, E., Jonides, J., Smith, E. E., & D'Esposito, M. (2004). The where and how of attention-based rehearsal in spatial working memory. *Cognitive Brain Research*, *20*(2), 194–205.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*, 31–40.
- Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. In C. Umiltà, & M. Moscovitch (Eds.), *Attention and performance XIV*. MIT Press.
- Schmidt, B. K., Vogel, E. K., Woodman, G. F., & Luck, S. J. (2002). Voluntary and automatic attentional control of visual working memory. *Perception and Psychophysics*, *64*(5), 754–763.
- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research*, *98*, 507–522.
- Sparks, D. L., & Hartwich-Young, R. (1989). The deeper layers of the superior colliculus. In R. H. Wurtz, & M. E. Goldberg (Eds.), *Rev. oculomotor res., the neurobiology of saccadic eye movements* (pp. 213–255). Elsevier Science Publishers.
- Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs*, *74*(11), whole issue.
- Theeuwes, J., Belopolsky, A., & Olivers, C. N. L. (2009). Interactions between working memory, attention and eye movements. *Acta Psychologica*, *132*(2), 106–114.
- Theeuwes, J., & Godijn, R. (2004). Inhibition-of-return and oculomotor interference. *Vision Research*, *44*(12), 1485–1492.
- Theeuwes, J., Kramer, A. F., & Irwin, D. E. (2010). Attention on our mind: The role of spatial attention in visual working memory. *Acta Psychologica*, doi:10.1016/j.actpsy.2010.06.011
- Theeuwes, J., Olivers, C. N. L., & Chizk, C. L. (2005). Remembering a location makes the eyes curve away. *Psychological Science*, *16*(3), 196–199.
- Theeuwes, J., Van der Stigchel, S., & Olivers, C. N. (2006). Spatial working memory and inhibition of return. *Psychonomic Bulletin and Review*, *13*(4), 608–613.
- Tremblay, S., Saint-Aubin, J., & Jalbert, A. (2006). Rehearsal in serial memory for visual-spatial information: Evidence from eye movements. *Psychonomic Bulletin and Review*, *13*(3), 452–457.
- Van der Stigchel, S., Meeter, M., & Theeuwes, J. (2006). Eye movement trajectories and what they tell us. *Neuroscience and Biobehavioral Reviews*, *30*(5), 666–679.
- Van der Stigchel, S., & Theeuwes, J. (2006). Our eyes deviate away from a location where a distractor is expected to appear. *Experimental Brain Research*, *169*(3), 338–349.