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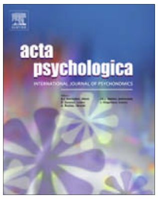

Interactions between working memory, attention and eye movements

Jan Theeuwes *, Artem Belopolsky, Christian N.L. Olivers

Vrije Universiteit, Department of Cognitive Psychology, Van der Boechorststraat 1, 1081 HV Amsterdam, The Netherlands

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ABSTRACT

This paper reviews the recent findings on working memory, attention and eye movements. We discuss the research that shows that many phenomena related to visual attention taking place when selecting relevant information from the environment are similar to processes needed to keep information active in working memory. We discuss new data that show that when retrieving information from working memory, people may allocate visual spatial attention to the empty location in space that used to contain the information that has to be retrieved. Moreover, we show that maintaining a location in working memory not only may involve attention rehearsal, but might also recruit the oculomotor system. Recent findings seem to suggest that remembering a location may involve attention-based rehearsal in higher brain areas, while at the same time there is inhibition of specific motor programs at lower brain areas. We discuss the possibility that working memory functions do not reside at a special area in the brain, but emerge from the selective recruitment of brain areas that are typically involved in spatial attention and motor control.

1. Introduction

In every-day life we often make use of our ability to temporarily store information until our task is completed. Working memory – which refers to the process of actively maintaining relevant information in mind for brief periods of time – is thought to underlie this ability. One of the most influential conceptualizations of working memory is the multiple component model of Baddeley and colleagues (e.g., Baddeley, 1986; Baddeley & Hitch, 1974). In the original model, Baddeley and colleagues suggested two independent buffers for the storage of verbal and visuospatial information. In a later version of the model, an additional buffer was added called "episodic buffer" which was assumed to link information across domains to form integrated units of visual, spatial, and verbal information (Baddeley, 2000). The Central Executive makes it possible to manage information in and between the different buffers. The present paper focuses on the visuospatial aspect of working memory. It refers to the process that allows retention and manipulation of information that is no longer available in the environment.

While it is possible to direct attention to information that is held in working memory, it is also possible to direct attention to relevant information that is still present in the environment. A long line of research has demonstrated that the allocation of visual attention to locations in visual space results in enhancement of processing of information that is presented at the attended location on both behavioral and neural levels (Mangun et al., 2001; Munneke, Heslenfeld, & Theeuwes, 2008; Peelen, Heslenfeld, & Theeuwes, 2004; Posner, 1980).

Recent work by Awh and colleagues (Awh & Jonides, 2001; Awh, Jonides, & Reuter-Lorenz, 1998) indicates that, at least for visuospatial memory, there is a close link between working memory and visual attention. They showed that when a location is kept in working memory, processing of stimuli at the memorized location is facilitated relative to other locations (Awh & Jonides, 2001), 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 (Awh et al., 1998). Brain imaging studies of working memory confirm the notion that rehearsal of spatial information modulates early sensory areas (Awh et al., 1999), and that the same fronto-parietal network is involved as in attention-related tasks (Kastner & Ungerleider, 2000).

In the present paper, we review the recent findings on working memory and attention. We mainly focus on the research from our own laboratory. We discuss the relationship between the allocation of visual attention and working memory. We show that many phenomena related to visual attention taking place when selecting relevant information from the environment also occur when those stimuli are kept active in working memory. We show that maintaining a location in working memory not only may involve attention rehearsal, but also may recruit the oculomotor system. We discuss some recent findings suggesting that remembering a location may involve attention-based rehearsal in higher brain areas, while at the same time there is inhibition of specific motor

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* Corresponding author. Tel.: +31 20 598 8790; fax: +31 20 598 8971.
E-mail address: J.Theeuwes@psy.vu.nl (J. Theeuwes).

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programs at lower brain areas. We discuss the possibility that working memory functions do not reside at a special area in the brain, but emerge from the selective recruitment of brain areas that are typically involved in spatial attention and motor control, a view consistent with the notion of Grounded Cognition (e.g., Barsalou, 2008).

2. Working memory and attention

As a metaphor visual attention has been compared to a spotlight that "selects" parts of the visual world around us (e.g., Posner, 1980). Visual attention allows people to select information that is relevant for their ongoing behavior. Providing information about the location of an upcoming target usually involves a cueing procedure in which a cue indicates with a high probability (e.g., in 80% trials the information provided to the participant is valid) the location of the upcoming target. Such a cue may consist of a centrally presented arrow (or a word or digit) indicating with a high probability the likely target location (e.g., Posner, 1980; Theeuwes, 1989; Theeuwes & Van der Burg, 2007; Theeuwes & Van der Burg, 2008). In this way, cueing is typically referred to as "endogenous" or top-down because participants are instructed to use this information in a top-down way to improve their performance.

In the so-called exogenous version of the location cueing paradigm, the cue has no predictive value regarding the location of the upcoming target (e.g., Jonides, 1981). Typically, before the appearance of the target an uninformative peripheral event (usually an abrupt increase in luminance) is presented either at the location of the target or at a location where the target does not appear. The important finding is that when the cue happens to be valid (i.e., the target happens to appear at the cued location) response times are fast and accuracy is high relative to a condition in which the cue is invalid (the target appears at the uncued location). The finding that a cue which has no predictive value regarding the upcoming target can induce spatial cueing effects is considered to be evidence that exogenous cueing is bottom-up and automatic (Jonides, 1981; LaBerge, 1981; Yantis & Jonides, 1990).

2.1. Attention is used to maintain information in working memory

Studies investigating visuospatial working memory use a procedure that is similar to the exogenous cueing task used in attention research. Typically, a peripheral onset cue is presented with abrupt onset somewhere in the visual field (see, for example, Awh et al.'s 1998 classic result). However, instead of responding to a target, the main task of the participant is to remember the location of the abrupt onset cue. During the retention interval (which could last up to 5 sec), participants are required to make a speeded response to a probe stimulus presented somewhere in the visual field. In 25% of the trials, the probe stimulus happens to appear at the location that was kept in memory. The crucial finding is that when the probe happened to match the location kept in memory, probe reaction time (RT) was about 15 ms faster then when the probe was presented elsewhere in the visual field. It is important to note that the effect only occurs when participants had to keep the location of the cue in memory, not when they had to remember its identity.

The interpretation of these findings is that during the retention interval attention is endogenously shifted to the location of the abrupt onset cue. This active shift of focal spatial attention to a specific location in space is assumed to allow an active maintenance of this location in working memory. The idea that spatial attention plays a functional role in the active maintenance of location information is also known as the attention-based rehearsal hypothesis (Awh, Armstrong, & Moore, 2006). Note, however, that a recent behavioral study challenged the classic attention-based rehearsal hypothesis of Awh et al. (2006). Belopolsky and Theeuwes (this issue) showed that depending on the task demands, keeping a location in working memory is accompanied by either facilitation or inhibition of visual processing. Facilitation of processing comes from the maintenance of endogenous attention (attention-based rehearsal), while inhibition is most likely a result of suppression of an oculomotor program. Even though this recent study challenged the classic hypothesis, there is also physiological evidence suggesting a role for attention as a rehearsal mechanism (Awh et al., 1998; Smyth & Scholey, 1994). For example, several studies showed a strong overlap between frontal and parietal brain regions that participate in spatial working memory on the one hand, and in spatial selective attention on the other (Awh, Smith, & Jonides, 1995; Awh et al., 1998; Awh et al., 1999; Jha, 2002).

Directing attention to a location in space to keep this location active in memory is related to the research area of mental imagery in which participants actively form a mental image of an object (see Farah, 1985). Mental imagery refers to the capacity to reactivate previous visual experiences in a quasi perceptual format. Visual images may reflect objects and object properties as well as the spatial relations among these objects. The on-line generation of a visual image representing spatial relations among objects may be identical to keeping a location in visual spatial working memory. It is intuitively plausible that scanning a scene kept in working memory occurs in a way similar to scanning a scene presented in the real world. Therefore, keeping the location of the cue active in memory may be nothing else than imagining the cue in an empty display. If a probe is presented near the imagined location it is to be expected that RT would be fast; if the probe is presented at a location far away from the imaged location, RT is relatively slow.

It should be noted, however, that the overlap between imagery and visual spatial working memory may only exist in conditions in which the memory representation is encoded in a visuospatial format. If an object is encoded in a verbal, non-spatial code (see also the experiment described in Section 2.2) then the generation of a visual image will be based on the previously stored verbal representations. In this respect, it is important to note that neuroimaging studies have shown that when conceptual knowledge of objects is represented, modal areas for the properties become active including brain areas for shape, color, size, and action (e.g., Goldberg, Perfetti, & Schneider, 2006). However, activation in these modal areas may not necessarily contribute to the active building of mental representations as which occurs during imagery.

The present review paper discusses aspects of visuospatial working memory referring to one of the buffer systems of the multiple component model of Baddeley (2000). Even though it is recognized that spatial components are a crucial part of the visuospatial working memory, visual subcomponents representing the properties of the object's appearance such as its color, its shape and its orientation are also part of the visuospatial sketch pad as defined by Baddeley (2000). Both these spatial and visual subcomponents are closely related to particular aspects of visual attention. However, it seems that the visual part of the visuospatial working memory is closely related to perception and visual imagery, while the spatial part of visuospatial working memory (which is the focus of this review) is closely related to aspects of attention and action (see Repovs & Baddeley, 2006).

2.2. Attention is used to store and retrieve information from working memory

The work of Awh and colleagues suggests that spatial attention is used to keep information in working memory. Research conducted by Schmidt, Vogel, Woodman, and Luck (2002) showed that focusing attention exogenously or endogenously on a spatial location increases the probability that information at that location will be transferred into visual working memory. In these experiments, participants were required to memorize six different colors presented on an imaginary circle. When attention was summoned by an abrupt onset cue to one of the locations in the array, the probability that the color presented at this location was memorized was higher than the colors presented at any of the other locations. The results indicate that spatial attention controls the transfer of perceptual representations into visual working memory (see. e.g., Belopolsky, Kramer, & Godijn, 2008; Bundesen, 1990; Duncan & Humphreys, 1989: Sperling, 1960:).

Along similar lines, Theeuwes (unpublished data) investigated the role of visual spatial attention when retrieving information from visual working memory. In this experiment, participants were required to hold four distinctly colored circles in visual working memory. Each circle was positioned at one of the corners of the display. Since the storage capacity for visual working memory is about 3 to 4 items (e.g., Sperling, 1960; Vogel, Woodman, & Luck, 2001), we assumed that visual working memory was full. To ensure that the four colored circles were encoded in visual working memory and not recoded into a verbal code, we used a concurrent verbal load task identical to the one used by Schmidt et al. (2002). After storing these four items in visual working memory, we asked observers whether one of the colors was present in the memory array (e.g., “was red present?”). In some trials, a visual probe dot was presented on the (empty) computer screen at a location that previously was occupied by one of the four circles. The probe dot location could, at chance probability, coincide with the location of the colored circle that had to be retrieved from visual working memory. See Fig. 1 for an example of a trial.

In this experiment, we were interested in reaction time to the probes. We found that when we asked whether a particular color was present in the memory array (“was red present?”) and the probe happened to be presented at the location of the color that participants had to retrieve (the probe was presented at the location that happened to contain the red circle), probe RTs were reliably faster (M = 385 ms) than when the probe was presented at any other location (M = 399). This difference was statistically reliable ($t(7) = 3.3$; $p < 0.05$).

This study shows that when selecting information from visual working memory observers allocate visual attention to the location in space that contains the information to be retrieved. Even though there was no reason to allocate spatial attention to the location of the previously presented colored objects (i.e., we did not ask to report a color at a particular location), observers did so anyway. It seems that selecting information from visual working memory is similar to selecting information from an actual visual representation.

It should be noted that our findings critically depend on the verbal suppression task. A pilot experiment in which no verbal suppression task was applied showed no probe validity effect. Apparently, only when visual working memory is utilized does spatial attention play a role in retrieving information. When the opportunity is provided to verbally recode the colors, spatial attention appears to play no role. Our findings suggest that accessing information from memory is not much different from accessing information from the outside world. In both cases, spatial visual attention plays a key role in accessing this information.

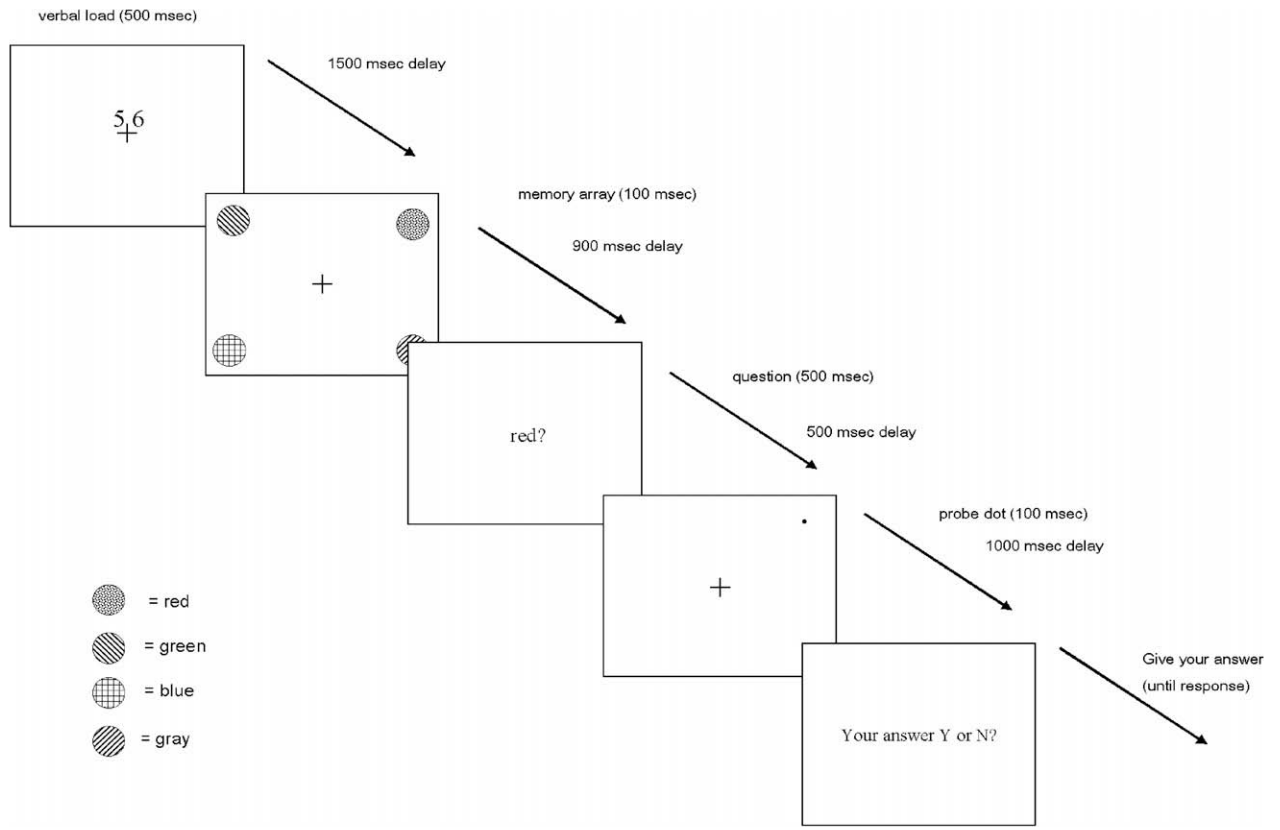

Fig. 1. An example of a probe trial. Participants had to memorize the memory array while saying aloud the number “56”. After receiving the question “red?” participants were required to consult the memorized array and determine whether red was present in the array. In probe trials, a white probe was presented at any of the four locations in the visual field. Participants had to respond as fast as possible to the presentation of the probe. In this example – a valid probe trial – the location at which the probe is presented coincides with the location containing the ‘retrieved’ information (i.e., the probe is presented at the same location where the red circle was presented in the memory array). After the probe trial, participants gave a non-speeded response to the question whether “red?” was present. Note that different fill patterns are used to represent different colors (unpublished data from Theeuwes).

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2.3. Distraction in visual working memory

As is clear from the discussion above, there are many similarities between the spatial attention and working memory. In several previous studies, we, among others, have demonstrated that abrupt onsets have the ability to capture spatial attention in an exogenous way (Schreij, Owens, & Theeuwes, 2008; Theeuwes, 1991; Theeuwes, 1994; Theeuwes, 1995). There is also evidence that task-irrelevant onsets can increase saccade latencies (Walker, Deubel, Schneider, & Findlay, 1997), influence saccade trajectories (Van der Stigchel, Meeter, & Theeuwes, 2006), and capture attention and capture the eyes (Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). Given the influence of abrupt onsets on visual spatial attention, in a recent study we addressed the question whether irrelevant onsets would affect working memory (Van der Stigchel, Merten, Meeter, & Theeuwes, 2007). In this experiment, participants had to memorize the location of a dot. During the retention interval, a task-irrelevant stimulus was presented with abrupt onset somewhere in the visual field. We asked the question whether the memory representation would be affected by the occurrence of this completely irrelevant onset. Results showed that the working memory was affected by the occurrence of the external irrelevant event relative to a control condition in which there was no external event. Specifically, the memorized location was shifted toward the location of the task-irrelevant stimulus. This effect was only present when the onset was close in space to the memory representation. Consistent with the notion that working memory and spatial attention are closely related, these findings suggest that the "internal" spatial map used for keeping a location in spatial working memory and the "external" spatial map that is affected by exogenous events in the outside world are either the same or tightly linked. Van der Stigchel et al. (2007) concluded that an exogenous event in the "outside world" can affect a mental memory representation in the "internal world." An exogenous abrupt onset that is known to capture attention caused a shift in the memory representation in the direction of the onset location.

Recently, a discussion arose addressing another question regarding the role of mental representation on the exogenous capture of attention (see Olivers, 2008; Olivers, in press). The discussion revolves around the question whether a memorized object held in visual working memory would capture attention. In other words, are we more likely to attend to objects that we keep active in working memory? A recent study from our laboratory provides strong evidence for memory-driven attentional capture. In this study, Olivers, Meijer, and Theeuwes (2006) used the classic additional singleton paradigm as developed by Theeuwes (1991), Theeuwes (1992). In this task, participants have to search for a shape singleton (for example, a diamond between circles) while another irrelevant singleton was present (e.g., a red circle between green circles). Theeuwes (1991), Theeuwes (1992, Theeuwes (1994) showed that irrelevant singletons capture attention irrespective of any top-down goals. Olivers et al. (2006) used this very same paradigm and tested whether a singleton that is kept in working memory would cause more capture of attention than a singleton not kept in memory. In Olivers et al. (2006), observers were asked to remember a particular color (red, green, blue or yellow). At the end of the trial, their memory was tested by asking them to choose the original color from a set of three alternatives (see Fig. 2). We used two versions of the memory task. In what is called the "more verbal" version, the memory test consisted of easily distinguishable alternatives for which verbal labels are readily available, for example, red, green, and blue. For this type of memory, one can use the verbal label (e.g., green or red) without any effort in trying to create a visual memory of the exact shade of red. In contrast, in the "more visual" version, the to-be-remembered color had to be distinguished from highly similar colors from the same category. For example, a particular shade of red had to be distinguished from other shades of red. In this condition, we assumed that observers would use their visual working memory.

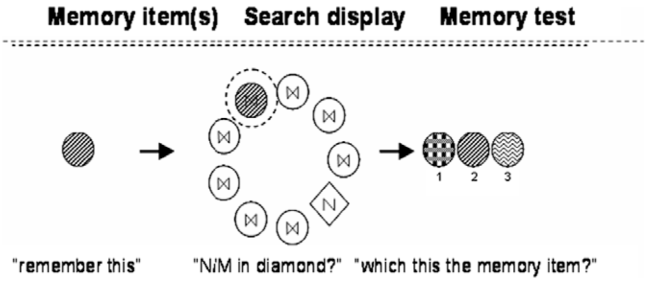

Fig. 2. The main procedure of Olivers et al., 2006. Participants had to memorize the color of a circle. When searching for the shape singleton (the diamond) an irrelevant color singleton was present. The color of the singleton could match the color kept in working memory. After the search, participants received a memory test in which they had to indicate the color they had kept in working memory. The results provide evidence for memory-driven capture: when the color of the irrelevant singleton matched the color held in memory, there was more capture than when it did not match (from Olivers et al., 2006).

After memorizing the color for a few seconds, participants had to search for a grey diamond among grey circles. Participants responded to the identity of the letter presented inside the diamond. In many trials, however, one of the distractors carried a unique color. The important finding here was that the interference was stronger for distractors that matched the content of memory than for unrelated color distractors. The other important finding was that this was only the case for the "more visual" memory condition. In the "more verbal" condition, there was no effect of the relationship between the visual distractor and the contents of memory. Note that participants had no reason to attend to the distractor: It only interfered with the goal of responding to the grey diamond. Thus, these results are consistent with the idea that visual working memory and visual attention share the same content. Moreover, follow-up experiments excluded a number of alternative explanations in terms of implicit perceptual priming, perceptual encoding, strategic memory updating, and delayed attentional disengagement. Even though our work clearly indicates an interaction between working memory and visual search, it should be noted that others have failed to find such an interaction (see e.g, Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Woodman & Luck, 2007). In a recent study, Olivers (in press) compared the various paradigms used in the previous studies, and indicated that particular aspects of the task and stimulus material may explain the discrepancy in finding direct interactions between working memory and attention.

3. Working memory and eye movements

As described above, there appears to be a strong link between visual working memory and attention. In turn, an equally strong link exists between spatial attention and eye movements. Previous research has shown that the eyes typically move to the location where attention is allocated, and, vice versa, attention is allocated at possible saccade targets (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995).

In a study conducted in our laboratory, we showed that just before executing a saccade sequence attention appears to reside at both saccade target locations simultaneously (Godijn & Theeuwes, 2004). In this study, we presented four location markers at the corners of the display. By means of a centrally presented cue which pointed to two of the four markers, participants were told to execute a saccade sequence to the locations indicated by the central cue in the order participants preferred. For example, the cue could indicate both the top-left and top-right locations, suggesting that the participants had to execute a saccade sequence from the center to top-left than to top-right and then back to the center. Participants were instructed to execute a saccade sequence as fast as possible. Just before the eyes started to move, we flashed letters up near the potential target locations (the location markers). After executing the saccade, participants were asked to indicate which of two letters shown in the center of the display they thought they had seen in the display. The results showed above-chance performance for both saccade target locations. For locations to which the eyes did not have to go to, the performance was at chance level. Subsequent experiments showed that spatial attention must have been allocated at the two locations simultaneously just before the saccade was executed. Even though this study mainly focused on the relationship between attention and eye movements, the measure we used to determine to which locations attention was allocated was related to working memory. In fact, we used a forced-choice recognition test. Our results indicate that eye movement, attention and working memory are related. Attention precedes an eye movement, and attention is the vehicle by which information is stored in working memory (as concluded by Schmidt et al., 2002).

Other studies also showed a strong link between working memory and eye movements. A number of studies have shown that eye movements disrupt spatial working memory (e.g., Baddeley & Lieberman, 1980; Smyth & Scholey, 1994). For example, Smyth and Scholey (1994) demonstrated that additional tasks that require shifts of spatial attention disrupt performance of the Corsi Blocks Task, a typical clinical measure used to determine spatial memory span. The underlying notion is that attention is needed both to maintain locations active in spatial working memory and for the execution of eye movement. Because both processes make use of the same attentional mechanism, working memory performance deteriorates when eye movements have to be executed.

3.1. Working memory is the same as programming an eye movement

In a recent study conducted in our laboratory, we found evidence for even a tighter link between visuospatial working memory and eye movements (Theeuwes, Olivers, & Chizk, 2005). We showed that while maintaining a location in working memory the eyes curve away from the remembered location (See Fig. 3b). While previous research has shown that eyes may deviate away from *visible* stimuli (e.g., Godijn & Theeuwes, 2002; Sheliga, Riggio, & Rizzolatti, 1994), Theeuwes et al. (2005) were the first to demonstrate that the eyes also curve away from *remembered* stimuli. The study provides evidence for a direct link between working memory and the oculomotor system. In our study, we used saccade curvature as a measure to determine the effect of remembered stimuli on the eye movement system. Saccade curvature (and eye movement deviations in general) has been attributed to competitive interactions of activity within intermediate layers of the SC involved in encoding stimuli as potential saccade targets (Sparks & Hartwich-Young, 1989). The SC is a lower level structure which operates as a motor map for the generation of eye movements. Its intermediate layers have direct projections to and from the posterior parietal cortex (Paré & Wurtz, 1997), a region closely related to attentional selection (see Kastner & Ungerleider, 2000 for a review). Competitive interactions within SC have been shown to operate between separate populations of neural activity in the SC. In some situations, populations of activity which are close in space may merge, thus facilitating the averaging of saccades (the well-known 'global effect') while more remote populations inhibit one another (Munoz & Istvan, 1998). The competitive interactions are central to models of saccade curvature effects. Curvature away from a distractor has been attributed to the distractor-related activity being inhibited (presumably by a top-down signal), so the overall population of activity produces a saccade vector that deviates away from the distractor location (e.g., Doyle & Walker, 2001; Godijn & Theeuwes, 2002). For example, in Godijn and Theeuwes (2004), saccade deviations were observed in the oculomotor capture task (e.g., Theeuwes et al., 1998). In this task, observers have to make an eye movement to a predefined target while ignoring a distractor singleton. This creates a situation in which there is a competition between an endogenous signal and an exogenous signal. The results showed that the eyes curved away from the distractor location, suggesting that the location of the distractor was inhibited. This inhibition was necessary to prevent the eyes from going to the distractor location. The inhibition hypothesis is also consistent with the results from Aizawa and Wurtz (1998) which showed similar saccade trajectory deviations after local inactivation of a region of the SC.

The curvature observed in the Theeuwes et al. (2005) study in which the eyes curved away from a *remembered* location can be explained in similar terms. One could regard the process of remembering a location similar to the process of programming an eye movement to that location. Accordingly, remembering a location will generate corresponding activity in the SC. However, note that in our task, observers remember the location of the dot, but this is a location to which they should not make an eye movement. Instead, 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. Just like the inhibition assigned to a visible distractor location, the inhibition assigned to a location in memory then causes a saccade curvature away from the memorized location. Thus, memory-based activity can generate competition within the oculomotor system.

In the Theeuwes et al.. (2005) study, we investigated the effect of keeping one location in memory on saccadic eye movements. Obviously, it is possible to keep more than one location in memory up to a certain maximum (most likely up to four locations). It is likely that multiple object locations are stored in memory on the basis of the storage of a sequence of eye movements. Similar ideas were suggested by Tremblay, Saint-Aubin, and Jalbert (2006) who showed that eye movements play a crucial role in visual-spatial rehearsal. (see also Guérard, Tremblay, & Saint-Aubin, this issue). They argued that eye movements represent an *overt* form of rehearsal; while our study suggests that the programming of saccades may also be the mechanism by which *covert* rehearsal is maintained. Future studies using multiple object locations will reveal the viability of the hypothesis that multiple locations are stored in working memory by means of a saccade sequence.

The fact that remembered items are represented even at an oculomotor level raises some interesting questions about the nature of memory representations. For one, there is the possibility that working memory is "nothing more" than the preparation to perform an action, be it oculomotor, manual, verbal, or otherwise in nature, a notion that fits well with the idea of working memory as an emergent property (e.g., Postle, 2006) and the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987; Sheliga et al., 1994). According to these notions, attention and motor preparation should be unified into a single concept. Our data suggest that working memory should join them.

3.2. Inhibition in working memory

The studies discussed above show that attention, eye movements and working memory are tightly coupled. The experiment discussed in the previous section even suggests that working memory is basically the same as programming a saccade to a location. If there is so much overlap between the various mechanisms,

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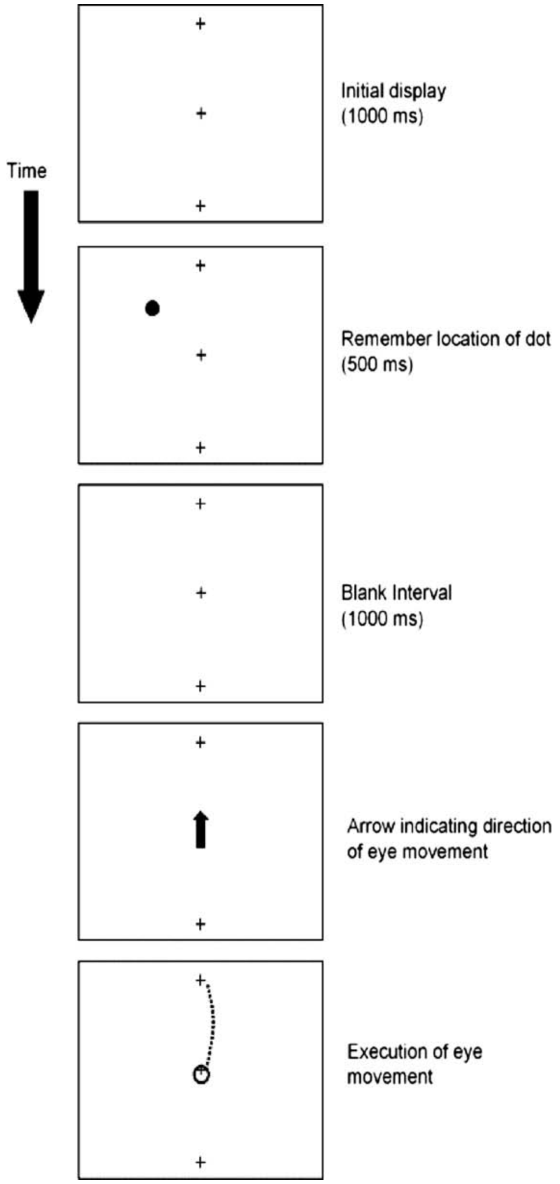

Fig. 3a. Typical task sequence. After the initial display, a dot was presented somewhere in one of four quadrants (in this example top, left). In the memory condition, observers had to remember the location of the dot. In the no-memory condition, observers ignored the dot. After a blank interval of 1000 ms, an arrow indicated the direction in which a saccade had to be made. The direction of the saccade could be to the same half (top or bottom) as where the dot was presented (e.g., upwards when the dot was in the top half of the screen) or to the opposite half as where the dot was presented (e.g., downwards when the dot was in the top half of the screen).

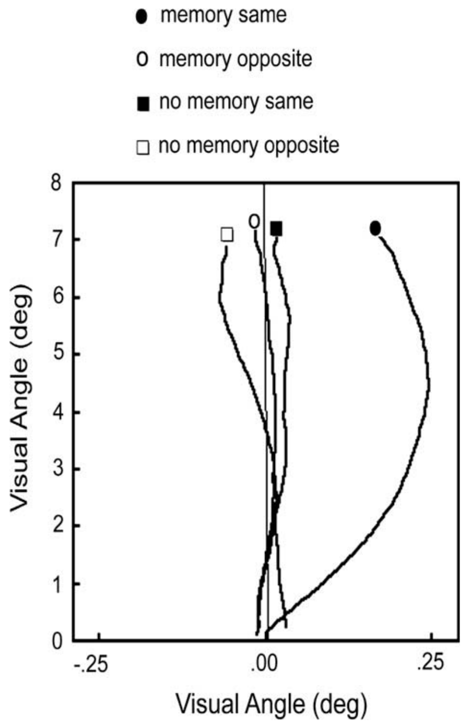

Fig. 3b. Eye movement trajectories. When observers kept a location in working memory and the eyes moved in the same direction as the memorized location, a clear saccadic trajectory deviation was observed (memory same condition). When observers did not keep the location in memory ('no memory' condition) or moved their eyes towards an opposite location ('opposite' condition) in space, there was no saccadic deviation (from Theeuwes et al., 2005).

one can ask the question whether other phenomena which are typically related to visual attention interact with working memory.

In one study from our laboratory (Theeuwes, Van der Stigchel, & Olivers, 2006), we examined whether the classic inhibition effect known as Inhibition of Return (IOR, Posner & Cohen, 1984) would also occur for locations kept in working memory. IOR is a visual attention phenomenon characterized by delayed responses to targets presented at recently cued or recently fixated locations (see Klein, 2000 for an overview). In a typical IOR experiment, an exogenous abrupt onset cue is presented at one of two locations. The cue is not predictive of the location of the subsequent target. Typically, detecting a target presented at the cued location is faster than detecting a target at the uncued location. However, when the interval between the abrupt onset cue and the target is relatively long, the opposite pattern of results is observed; i.e., responses to targets presented at the cued location are slower than those presented at the uncued location (Posner & Cohen, 1984).

In this study, we addressed the question whether keeping a location active in working memory would abolish the occurrence of IOR. Given the claim that an object is kept in working memory by directing spatial attention to its location, it is feasible that IOR does not occur for locations kept in memory. At the outset, it seems unlikely that inhibition and activation, both related to spatial attention, can co-occur at the very same location. In our experiment, as in Theeuwes et al. (2005), we asked observers to retain the location of a laterally presented onset while executing a saccade to another location (see Fig. 3a.). Again we measured saccade trajectories. To measure IOR, in some trials observers were required to execute an additional saccade to either the cued (and memorized) location or an equidistant uncued location at the opposite side of space. The difference in saccade latency between cued and uncued locations was our measure of IOR. Both the trajectory deviation and the IOR effect were compared to a control condition in which the cue needed not be memorized.

Our results showed that the abrupt onset cue caused IOR; yet, surprisingly IOR occurred with equal magnitude whether the return-to-location was kept in memory or not. Identical to Theeuwes et al. (2005), we showed that keeping the location in memory systematically influenced the saccade trajectory such that the eyes deviated away from the memorized location. These results suggest that working memory and IOR do not interact. Keeping a location in memory does not modulate the strength of IOR. Theeuwes et al. (2006) concluded that IOR is the result of the initial short-lived exogenous activation caused by the initial abrupt onset dot, while the saccade deviations observed in the memory condition are the result of inhibiting the sustained endogenous activation necessary to keep the location in memory. Note that these findings are consistent with the studies that have shown that IOR is independent of the endogenous orientation of spatial attention (e.g., Chica, Lupiáñez, & Bartolomeo, 2006; Riggio & Kirsner, 1997).

In a recent study, we addressed this issue again (Belopolsky & Theeuwes., in press) by investigating the time course of the occurrence of IOR. Unlike Theeuwes et al. (2006), in this new study we let participants make a saccade directly to the memorized location. To ensure that there was no abrupt onset which could cause IOR in one of our experiment (see Fig. 4), we presented two circles on each side of fixation and a central pointer indicated which location should be kept in memory. In other words, the location to be kept in memory was indicated in an endogenous way, suggesting that a classic IOR effect would not occur. If anything we expected that the saccade latency to the memorized location would be faster than the saccade latency to the non-memorized location, because in order to keep this location in memory attention was needed to be directed to its location. Contrary to our expectations we found that at both time intervals (1000 and 2000 ms) making a saccade to the memorized location was slower than making a saccade to the non-memorized location. Even though the performance on the memory task indicated that participants held this location actively in memory, they were slower to execute a saccade to this location.

Our findings present somewhat of a puzzle because the results seem to suggest that keeping a location in memory resulted in the inhibition of saccades to the memorized location. Inhibition of saccades to the memorized location was present even though the location to be kept in memory was indicated endogenously by a central pointer. It is known that classic IOR cannot be produced by an endogenous cue, unless it is used to prepare and inhibit a saccade (Rafal, Calabresi, Brennan, & Sciolto, 1989). In our task, participants were never instructed to make a saccade towards the memory cue, and the direction of the upcoming saccade in response to the central cue was not known in advance. In fact, in half of the trials no saccade had to be made.

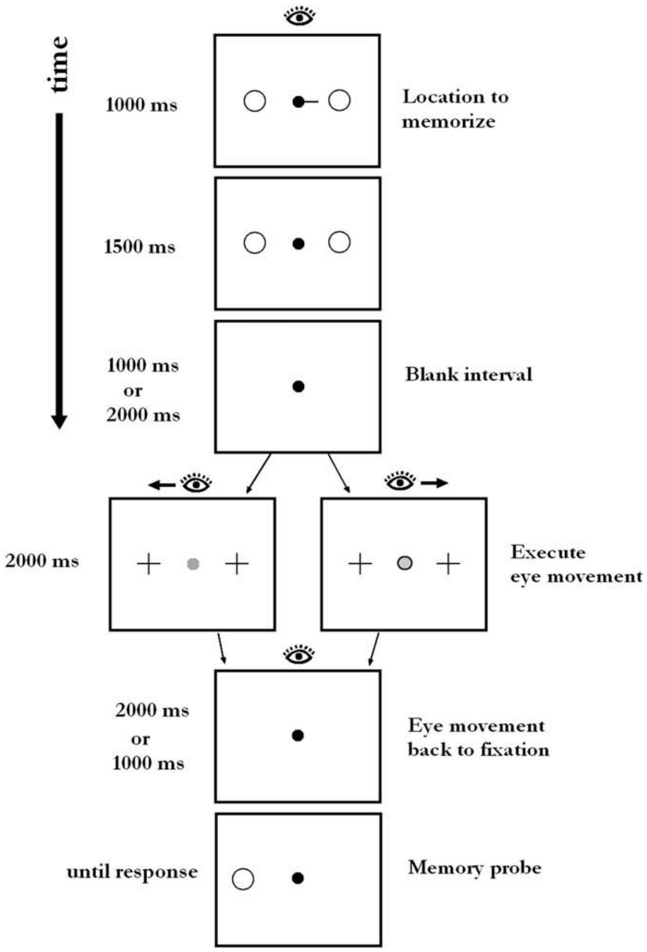

Fig. 4. Participants had to memorize the location indicated by the central cue (in this case the right location), after a retention interval (either 1 or 2 s) participants had to make a saccade to one of two locations. After they made a saccade back to the middle, they had to perform a memory test. A memory probe was presented and participants had to indicate whether this probe matched the location kept in memory or not (from Belopolsky & Theeuwes, in press).

Even though attention and eye movements and attention and spatial working memory are closely linked, our findings suggest that the allocation of attention at a location does not result in oculomotor facilitation. If anything, we observe oculomotor inhibition which is quite similar to the classic IOR.

4. Discussion

In this paper, we discussed evidence suggesting a strong overlap between visual working memory, spatial attention and the oculomotor system. The premotor theory of attention (Rizzolatti et al., 1987; Sheliga et al., 1994) provides a framework to explain the strong overlap. According to this theory, the activation of neural structures related to attention depends on the required motor action. Thus, spatial attention shifts are considered to be a byproduct of preparing a saccadic eye movement, or in the extreme case, are nothing else but such programming of saccades. Findings discussed above suggest that the premotor theory of attention should be extended to incorporate visuospatial working memory. In this respect, we may regard the process of remembering a location the same as the process of programming an eye movement to that location. Accordingly, remembering a location will generate corresponding activity in the oculomotor systems such as the superior colliculus (SC). Our findings suggest that the oculomotor activity associated with the remembered location in the SC results in inhibition. We have shown that eyes curve away from this inhibited location (Theeuwes et al., 2006), and that saccades are delayed in returning to the inhibited location (Belopolsky & Theeuwes, in press). The original conception of Awh (e.g., Awh & Jonides, 2001) suggesting that maintenance in working memory involves the allocation of spatial attention can only account for part of the observed effects. Our results suggest that at least at an oculomotor level there appears to be an inhibition at the memorized location. In principle, it is possible that inhibition at the SC oculomotor level and activation at a higher level co-exist and both contribute to an accurate memory representation.

4.1. Tentative model

A framework developed by Godijn and Theeuwes (2004; Theeuwes & Godijn, 2004) to account for IOR and saccade curvature may shed some light on the interplay between attention, working memory and eye movements. This framework consists of three subsystems: a preoculomotor attentional map, a saccade map, and an inhibitory control system (see Fig. 5). Within the saccade map (most likely in the superior colliculus), the final stage of saccade programming takes place. 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 preoculomotor attentional map (most likely the lateral intraparietal area).

When the location that needs to be memorized is indicated by presenting an abrupt onset somewhere in the visual field (as in most of Awh et al., studies), the transient will cause exogenous activation in the preoculomotor attentional map and in the saccade

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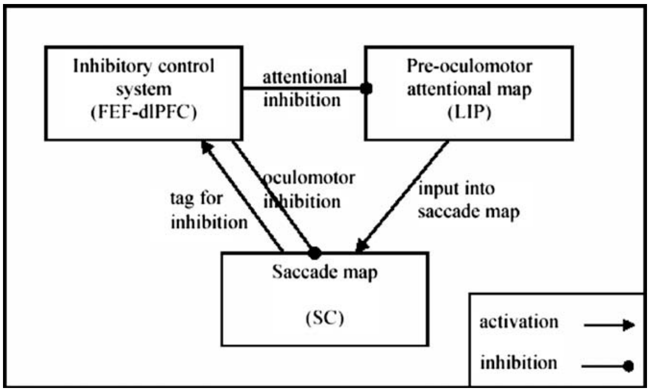

Fig. 5. A framework for understanding inhibitory control of saccades (from Godijn & Theeuwes, 2004; Theeuwes & Godijn, 2004). The framework consists of a network of three subsystems that are involved in inhibitory control of saccades: a preoculomotor attentional map, a saccade map and an inhibitory control system. When a stimulus is presented activation flows through the preoculomotor map to the saccade map. Activation in the saccade map generates an inhibitory tag in the inhibitory control system. This tag is passed on to the preoculomotor attentional map. Inhibition in the preoculomotor attentional map reduces the input into the saccade map at the location at which the original stimulus was presented. This delays the execution of the saccade (IOR). It is speculated that the inhibitory control system is represented by the frontal eye fields (FEFs) and/or by the dorsolateral prefrontal cortex (dlPFC), and that the preoculomotor attentional map is represented by the lateral intraparietal area (LIP) and the saccade map is represented by the superior colliculus (SC).

map corresponding to the location in space where the stimulus was presented. Subsequently, sustained endogenous activation is needed to keep this location in memory. Given previous findings, it is reasonable to assume that the preoculomotor attentional map (the lateral intraparietal area) is able to sustain such a top-down attentional activation (see, e.g., Bisley & Goldberg, 2003). We assume that this endogenous activation initially results in activation within the saccade map and at the same time gives an inhibitory tag delivered to the inhibitory control system. As we have suggested this inhibitory tag will result in what is referred to as the classic IOR effect (Godijn & Theeuwes, 2004; Theeuwes & Godijn, 2004). Our findings suggest that the interplay between these systems may also result in inhibition within the oculomotor system when a location is kept in memory. Even though there is inhibition at the oculomotor level (SC), the sustained activation at the preoculomotor map (LIP) may co-occur, explaining attention-based rehearsal effects showing benefits for responding to target presented at memorized locations (e.g., Awh & Jonides, 2001). It is assumed that dorsolateral prefrontal cortex and the frontal eye fields are responsible for inhibiting a specific location in the SC (e.g., Chelazzi & Corbetta, 2000; Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991). Even though our model assumes different roles for the various substructures such as SC, FEF and LIP, it should be noted that single cell studies show similar activations in the various substructures (e.g., Paré & Wurtz, 1997).

4.2. Working memory as an emergent property

The fact that a target location can be remembered on the basis of activation in an attentional system and/or inhibition in the oculomotor system opens the possibility that working memory functions arise through the recruitment of brain systems that are involved in sensory and action-related functions (see Postle, 2006, for a detailed discussion of this account). In the extreme, there is the possibility that working memory is "nothing more" than the preparation to perform an action, be it oculomotor, manual, verbal, or otherwise in nature (Theeuwes et al. 2006). According to this emergent property viewpoint of working memory, the short term retention of spatial information is not necessarily the result of specialized systems (such visuospatial scratch pad that may or may not reside in prefrontal cortex), but it emerges from the capabilities afforded by spatial attention and motor control (Postle, 2006), an idea that is similar to what has been referred to as "Grounded Cognition" (e.g., Barsalou, 2008). Attention-based rehearsal may be accomplished by allocating attention in "higher centers" such as LIP and the superior prefrontal cortex (Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998) while setting up a motor plan that codes for a specific location and is subsequently inhibited in the SC (at least for oculomotor control). It is conceivable that these two systems work together such that the "lower" system provides the spatial coordinates, while the higher system makes use of this while controlling information flow at these spatial coordinates. Our research suggests that a remembered location can be actively represented in higher cortical regions, while at the same time suppressed in lower regions (in this case the superior colliculus).

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Correspondence concerning this article should be addressed to Jan Theeuwes, Dept. of Cognitive Psychology, Vrije Universiteit, van der Boechorststraat 1, 1081 BT Amsterdam, The Netherlands. Electronic mail may be sent to J.Theeuwes@psy.vu.nl. This research was funded by a grant from NWO (Netherlands organization for Scientific Research), grant to JT and NWO-Vidi grant 452-06-007 to C.N.L.O.

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., Smith, E. E., & Jonides, J. (1995). Human rehearsal processes and the frontal lobes: PET evidence. In J. Grafman, K. Holyoak, & F. Boller (Eds.), *Annals of the New York Academy of Sciences. Structure and functions of the human prefrontal cortex* (Vol. 769, pp. 97–119). New York: New York Academy of Sciences.

Awh, E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection: Links, causes and implications for spatial attention. *Trends in Cognitive Sciences, 10*(3), 124–130.

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., Jonides, J., Smith, E. E., Buxton, R. B., Frank, L. R., Love, T., et al. (1999). Rehearsal in spatial working memory: Evidence from neuroimaging. *Psychological Science, 10*(5), 433–437.

Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences, 5*(3), 119–126.

Baddeley, A. D. (1986). *Working memory*. Cambridge, MA: MIT Press.

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.

Baddeley, A. D., & Lieberman, K. (1980). Spatial working memory. In R. Nickerson (Ed.), *Attention and performance VIII* (pp. 521–539). Hillsdale, NJ: Erlbaum.

Baddeley, A. D. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Science, 4*, 417–423.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology, 59*, 617–645.

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.W., & Theeuwes., J. (in press). Inhibition of saccadic eye movements to locations in spatial working memory. Attention, Perception & Psychophysics.

Belopolsky, A.V., & Theeuwes, J. (this issue). No functional role of attention-based rehearsal in maintenance of spatial working memory representations. *Acta Psychologica*. doi:10.1016/j.actpsy.2009.01.002.

Bisley, J. W., & Goldberg, M. E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science, 299*, 81–86.

Bundesen, C. (1990). A theory of visual attention. *Psychological Review, 97*, 523–547.

Chelazzi, L., & Corbetta, M. (2000). Cortical mechanisms of visuospatial attention in the primate brain. In M. E. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 667–686). MIT Press.

Chica, A. B., Lupiáñez, J., & Bartolomeo, P. (2006). Dissociating inhibition of return from endogenous orienting of spatial attention: Evidence from detection and discrimination tasks. *Cognitive Neuropsychology, 23*(7), 1015–1034.

Courtney, S. M., Petit, L., Maisog, J. M., Ungerleider, L. G., & Haxby, J. V. (1998). An area specialized for spatial working memory in human frontal cortex. *Science, 279*, 1347–1351.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research, 36*(12), 1827–1837.

Doyle, M., & Walker, R. (2001). Curved saccade trajectories: Voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research, 139*, 333–344.

Downing, P. E., & Dodds, C. M. (2004). Competition in visual working memory for control of search. *Visual Cognition, 11*, 689–703.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review, 96*, 433–458.

Farah, M. J. (1985). Psychophysical evidence for shared representational medium for mental images and percepts. *Journal of Experimental Psychology: General, 114*(1), 91–103. Psychological Review, 96, 433-458.

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.

Guérard, K., Tremblay, S., & Saint-Aubin, J. (this issue). The processing of spatial information in short-term memory: Insights from eye tracking the path length effect. *Acta Psychologica.*

Goldberg, R. F., Perfetti, C. F., & Schneider, W. (2006). Perceptual knowledge retrieval activates sensory brain regions. *Journal of Neuroscience, 26*, 4917–4921.

Hoffman, J. E., & Subramaniam, B. (1995). Saccadic eye movements and visual selective attention. *Perception & Psychophysics, 57*, 787–795.

Houtkamp, R., & Roelfsema, P. R. (2006). The effect of items in working memory on the deployment of attention and the eyes during visual search. *Journal of Experimental Psychology-Human Perception and Performance, 32*(2), 423–442.

Jha, A. P. (2002). Tracking the time-course of attentional involvement in spatial working memory: An event-related potential investigation. *Cognitive Brain Research, 15*(1), 61–69.

Jonides, J. (1981). Voluntary versus Automatic Control over the Mind's Eye's Movement. In *Attention and Performance X* (pp. 187–203). Hillsdale, NJ: Erlbaum.

LaBerge, D. (1981). Automatic information processing: A review. In J. B. Long & A. D. Baddeley (Eds.), *Attention and performance IX* (pp. 173–186). Hillsdale, NJ: Erlbaum.

Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience, 23*, 315–341.

Klein, R. (2000). Inhibition of return. *Trends in Cognitive Sciences, 4*(4), 138–147.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*(13), 1897–1916.

Mangun, G. R., Hinrichs, H., Scholz, M., Mueller-Gaertner, H. W., Herzog, H., Krause, B. J., et al. (2001). Integrating electrophysiology and neuroimaging of spatial selective attention to simple isolated visual stimuli. *Vision Research, 41*(10–11), 1423–1435.

Munneke, J., Heslenfeld, D. J., & Theeuwes, J. (2008). Directing attention to a location in space results in retinotopic activation in primary visual cortex. *Brian Research, 1222*, 184–191.

Munoz, D. P., & Istvan, P. J. (1998). Lateral inhibitory interactions in the intermediate layers of the monkey superior colliculus. *Journal of Neurophysiology, 79*(3), 1193–1209.

Olivers, C. N. L., Meijer, F., & Theeuwes, J. (2006). Feature-based memory-driven attentional capture: Visual working memory content affects visual attention. *Journal of Experimental Psychology: Human Perception & Performance, 32*, 1243–1265.

Olivers, C. N. L. (2008). Interactions between visual working memory and visual attention. *Frontiers in Bioscience, 13*, 1182–1191.

Olivers, C.N.L. (in press). What drives memory-driven attentional capture? The effects of memory type, display type, and search type. *Journal of Experimental Psychology: Human Perception & Performance.*

Paré, M., & Wurtz, R. H. (1997). Monkey posterior parietal cortex neurons antidromically activated from superior colliculus. *Journal of Neurophysiology, 78*, 3493–3497.

Peelen, M. V., Heslenfeld, D. J., & Theeuwes, J. (2004). Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *Neuroimage, 22*, 822–830.

Pierrot-Deseilligny, C., Rivaud, S., Gaymard, B., & Agid, Y. (1991). Cortical control of memory-guided saccades in man. *Experimental Brain Research, 83*, 607–617.

Posner, M. I. (1980). Orienting of attention, the VIIth Sir Frederic Bartlett lecture. *Quarterly Journal of Experimental Psychology, 32*, 3–25.

Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance X: Control of language processes* (pp. 531–556). Hillsdale, NJ: Lawrence Erlbaum.

Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience, 139*(1), 23–38.

Rafal, R. D., Calabresi, P. A., Brennan, C. W., & Sciolto, T. K. (1989). Saccade preparation inhibits reorienting to recently attended locations. *Journal of Experimental Psychology-Human Perception and Performance, 15*(4), 673–685.

Repovs, G., & Baddeley, A. (2006). The multi-component model of working memory: Explorations in experimental cognitive psychology. *Neuroscience, 139*(1), 5–21.

Riggio, L., & Kirsner, K. (1997). The relationship between central cues and peripheral cues in covert visual orientation. *Perception and Psychophysics, 59*(6), 885–899.

Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia, 25*, 31–40.

Schmidt, B. K., Vogel, E. K., Woodman, G. F., & Luck, S. J. (2002). Voluntary and automatic attentional control of visual working memory. *Perception & Psychophysics, 64*(5), 754–763.

Schreij, D., Owens, C., & Theeuwes, J. (2008). Abrupt onsets capture attention independent of top-down control settings. *Perception & Psychophysics, 70*(2), 208–218.

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.

Smyth, M. M., & Scholey, K. A. (1994). Interference in immediate spatial memory. *Memory & Cognition, 22*, 1–13.

Theeuwes, J. (1989). Effects of location and form cuing on the allocation of attention in the visual field. *Acta Psychologica, 72*, 177–192.

Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Perception & Psychophysics, 50*, 184–193.

Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics, 51*, 599–606.

Theeuwes, J. (1994). Stimulus-driven capture and attentional set: Selective search for color and visual abrupt onsets. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 799–806.

Theeuwes, J. (1995). Temporal and spatial characteristics of preattentive and attentive processing. *Visual Cognition, 2*(2/3), 221–233.

Theeuwes, J., & Godijn, R. (2004). Inhibition of return and oculomotor interference. *Vision Research, 44*, 1485–1492.

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., Kramer, A. F., Hahn, S., & Irwin, D. E. (1998). Our eyes do not always go where we want them to go: Capture of eyes by new objects. *Psychological Science, 9*, 379–385.

Theeuwes, J., Kramer, A. F., Hahn, S., Irwin, D. E., & Zelinsky, G. J. (1999). Influence of attentional capture on oculomotor control. *Journal of Experimental Pscyhology: human Perception and Performance, 25*(6), 1595–1608.

Theeuwes, J., & Van der Burg, E. (2007). The role of spatial and non-spatial information in visual selection. *Journal of Experimental Psychology: Human Perception and Performance, 33*, 1335–1351.

Theeuwes, J., & Van der Burg, E. (2008). The role of cueing in attentional capture. *Visual Cognition, 16*(2), 232–247.

Theeuwes, J., Van der Stigchel, S., & Olivers, C. N. L. (2006). Spatial working memory and inhibition of return. *Psychonomic Bulletin & Review, 13*(4), 608–613.

Tremblay, S., Saint-Aubin, J., & Jalbert, A. (2006). Rehearsal in serial memory for visuo–spatial information: Evidence from eye movements. *Psychonomic Review & Bulletin, 13*, 452–457.

Van der Stigchel, S., Meeter, M., & Theeuwes, J. (2006). Eye movement trajectories and what they tell us. *Neuroscience & Biobehavioral Reviews, 30*, 666–679.

Van der Stigchel, S., Merten, H., Meeter, M., & Theeuwes, J. (2007). The effects of a task-irrelevant visual event on spatial working memory. *Psychonomic Bulletin & Review, 14*, 1066–1071.

Vogel, E. K., Woodman, G. F., & Luck, S. J. (2001). Storage of features, conjunctions, and objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance, 27*, 92–114.

Woodman, G. F., & Luck, S. J. (2007). Do the contents of visual working memory automatically influence attentional selection during visual search? *Journal of Experimental Psychology: Human Perception and Performance, 33*, 363–377.

Walker, R., Deubel, H., Schneider, W. X., & Findlay, J. M. (1997). Effect of remote distractors on saccade programming: Evidence for an extended fixation zone. *Journal of Neurophysiology, 78*(2), 1108–1119.

Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 121–134.

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