

On the spatial interaction of visual working memory and attention: Evidence for a global effect from memory-guided saccades

Arvid Herwig

Department of Psychology, Bielefeld University,
Bielefeld, Germany



Miriam Beisert

Max Planck Institute for Human Cognitive and Brain
Sciences, Leipzig, Germany



Werner X. Schneider

Department of Psychology & Cluster of Excellence
“Cognitive Interaction Technology”, Bielefeld University,
Bielefeld, Germany



Recent work indicates that covert visual attention and eye movements on the one hand, and covert visual attention and visual working memory on the other hand are closely interrelated. Two experiments address the question whether all three processes draw on the same spatial representations. Participants had to memorize a target location for a subsequent memory-guided saccade. During the memory interval, task-irrelevant distractors were briefly flashed on some trials either near or remote to the memory target. Results showed that the previously flashed distractors attract the saccade's landing position. However, attraction was only found, if the distractor was presented within a sector of $\pm 20^\circ$ around the target axis, but not if the distractor was presented outside this sector. This effect strongly resembles the global effect in which saccades are directed to intermediate locations between a target and a simultaneously presented neighboring distractor stimulus. It is argued that covert visual attention, eye movements, and visual working memory recruit the same spatial mechanisms that can probably be ascribed to attentional priority maps.

Keywords: memory-guided saccades, eye movements, attention, global effect, remote distractor, working memory

Citation: Herwig, A., Beisert, M., & Schneider, W. X. (2010). On the spatial interaction of visual working memory and attention: Evidence for a global effect from memory-guided saccades. *Journal of Vision*, 10(5):8, 1–10, <http://journalofvision.org/content/10/5/8>, doi:10.1167/10.5.8.

Introduction

Human vision is characterized by a consistent pattern of eye movements. Periods of fixation are interrupted by fast saccadic gaze shifts several times each second. Saccades assure that the high resolution foveal region is brought to interesting spots of the visual field for detailed visual sampling. Beside this overt form of visual attention, locations in the visual periphery can be covertly attended in the absence of eye movements (e.g., Posner, 1980). The past decades witnessed a great deal of research confirming that covert visual attention and saccadic eye movements are tightly interrelated. Prior to each saccade, perceptual processing is selectively enhanced at locations where the eyes are about to land (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995; Schneider & Deubel, 2002). Shortly before a saccade is initiated the coupling of covert and overt forms of orienting even appears to be obligatory since it is not possible to covertly attend to a location different than the saccade's destination (Deubel & Schneider,

1996). Further support for a close link between attention and eye movements can be drawn from neurophysiological studies on monkeys demonstrating that specific regions of the cortex like the frontal eye fields (FEF), the superior colliculus (SC) and lateral intraparietal cortex (LIP) are involved in both covert and overt attention (Bisley & Goldberg, 2006; Moore & Fallah, 2004; Müller, Philiastides, & Newsome, 2005; Schall, 2009).

Recently it was suggested that covert visual attention is also involved in visual working memory (e.g., Awh, Jonides, & Reuter-Lorenz, 1998). Visual working memory can be regarded as a mechanism that maintains relevant information and suppresses irrelevant information, whereas visual attention can be regarded as a bundle of mechanisms that select relevant information while irrelevant information is ignored (Olivers, 2008). Beside this overlap in definition, the memory-attention link is supported by findings from a variety of sources. There is behavioral evidence showing a processing benefit for stimuli presented at locations held in spatial working memory (Awh et al., 1998). This effect resembles the processing benefit found at attended locations (Posner, 1980). In contrast,

memory performance declines when spatial attention during the memory interval is interrupted (Awh et al., 1998). Moreover, there is a strong overlap in the neuroanatomy of visual working memory and attention related tasks (Awh et al., 1999; Kastner & Ungerleider, 2000). Other physiological work has demonstrated that monkey's LIP is not only involved in covert attention but also in maintaining spatial information in working memory (Bisley & Goldberg, 2003). One interpretation of all these findings is that covert shifts of spatial attention play a functional role in the active maintenance of information in visual working memory (attention-based rehearsal hypothesis, Awh et al., 1998; for a critical discussion see Theeuwes, Belopolsky, & Olivers, 2009).

Given this tight interdependence of covert attention and eye movements on the one hand and covert attention and visual working memory on the other hand the question arises as to whether all three processes are linked via spatial representations. To date, this issue is not well investigated. However, it has been recently shown that saccadic eye movements towards visual targets curve away not only from visible distractors (e.g., Doyle & Walker, 2001) but also from stimulus locations that are maintained in working memory (Theeuwes, Olivers, & Chizk, 2005). Importantly, this curvature of saccadic trajectories is more pronounced if the location of a previously presented stimulus has to be remembered compared to a condition in which it is task-irrelevant.

The present study was conducted to add further evidence for a link between covert attention, eye movements, and visual working memory. More specifically, we focused on the spatial interaction between all three processes by picking up a well known spatial effect of task-irrelevant stimuli on the oculomotor system. The so-called *center of gravity* or *global effect* implies that saccades are directed to intermediate locations between a target and a simultaneously presented distractor stimulus if the two stimuli are in close proximity in the visual field. Spatially averaging saccades were first reported by Coren and Hoenig (1972) and later found to be influenced by the relative visual properties of the two stimuli, such as size, luminance, or spatial frequency (Deubel, Wolf, & Hauske, 1984; Findlay, 1982; Findlay, Brogan, & Wenban-Smith, 1993).

The global effect has been ascribed to an overlap between the spatial representations of target and distractor stimulus probably due to processes of distributed population coding operating within the SC (Glimcher & Sparks, 1993). Moreover, there is evidence that the global effect diminishes or even disappears with increasing saccadic latencies either within the natural variation of latencies (Ottes, Van Gisbergen, & Eggermont, 1985) or with saccades delayed by instruction (Coeffé & O'Regan, 1987; Findlay, 1983; Ottes et al., 1985). This finding has been used to suggest that the global effect might be due to the limited time available for detailed visual processing or the discrimination of target and distractor.

Importantly, the global effect heavily relies on the spatial proximity of target and distractor. Distractors that are presented farther away from the target do not affect saccadic landing positions but increase saccadic latency instead (the so called *remote distractor effect*) (Walker, Deubel, Schneider, & Findlay, 1997). Thus, the relationship between the effects of distractors on landing position and latency is reciprocal. By systematically varying the distance between target and distractor, Walker and colleagues demonstrated the critical sector that determines, whether the distractor has an effect on saccadic landing position (global effect) or latency (remote distractor effect). The global effect only occurs for distractors appearing at less than 20 deg of angular distance from the target axis. If distractors appear outside this critical region saccade amplitude is unaffected, and an increase in saccadic latency can be observed instead.

Up to now, the global effect and spatial working memory have only been studied in isolation, that is target and distractor stimuli have been presented simultaneously or in close temporal proximity. However, if spatial working memory draws on the same spatial representations as covert and overt visual attention do, a global effect should also be observed if the saccade target is no longer present, but kept in visual working memory when the distractor appears.

To address this issue, we conducted two experiments which combined a memory-guided saccade task with the presentation of distractor stimuli during the memory interval. More specifically, participants' task was to memorize the location of a peripherally flashed target while maintaining fixation and then to saccade to the memorized target location as soon as a go-signal was given (disappearance of the central fixation cross). Importantly, on some trials, a distractor stimulus was briefly flashed during the memory interval either near to the previous target location (i.e., inside the sector of $\pm 20^\circ$ around the target axis) or remote (i.e., outside the sector of $\pm 20^\circ$ around the target axis). If covert and overt visual attention and also visual working memory rely on the same spatial representations one would expect to find the memory-guided saccades shifted towards the previously presented distractor (i.e., the global effect). However, this should hold only for distractors presented near to the memory target but not for remote distractors.

Experiment 1

Method

Participants

Eight participants, aged between 23 and 29 years, took part in [Experiment 1](#). Three of the participants were female. All reported normal or corrected-to-normal vision.

Apparatus and stimuli

Participants performed the experiment in a dimly lit room and viewed the 21" display monitor running at 100 Hz from a distance of 62 cm. The screen's resolution was set to 1024×768 pixels, which corresponded to physical dimensions of 40 cm (width) \times 30 cm (height). A video-based deskmounted eye tracker (Eye Link1000, SR Research, Ontario, Canada) with a sampling rate of 1000 Hz was used for recording eye movements. The participants' head was stabilized by a chin and a forehead rest. The right eye was monitored in all participants. The central fixation stimulus consisted of a black "plus" character ($0.3^\circ \times 0.3^\circ$, line width 1 pixel). The target stimulus was a green "plus" character ($0.43^\circ \times 0.43^\circ$, line width 2 pixels). Moreover, there were four black filled possible distractor stimuli of different shapes (" Δ , O, \times , \diamond ", $0.43^\circ \times 0.43^\circ$). All stimuli were displayed on a white background.

Procedure and design

Each trial began with the presentation of the target stimulus for 500 ms. The target appeared after the participant had continuously fixated on the central fixation stimulus for at least 500 ms. The target was randomly presented at 4° or 8° to the left or right of the fixation stimulus along the horizontal axis. The following target memory interval lasted for a variable period of 1650–2150 ms. In two-thirds of the trials, 500 ms after target offset a single distractor stimulus was presented for 400 ms (see Figure 1a). For the remaining one-third of the trials, no distractor appeared. The distractor randomly varied in shape and was presented either 6° to the left or right of the fixation stimulus along the horizontal axis (see Figure 1b). Thus, if target and distractor were presented on the same side, the distractor was presented inside the

sector of $\pm 20^\circ$ around the target axis which is known to be critical for the classical global effect (Walker et al., 1997). In contrast contralateral distractors were presented outside this critical sector. The participants' task was to maintain fixation until the fixation cross disappeared, and then to make a saccade as fast and accurate as possible to the location where the target had been presented. If fixation was lost before the fixation cross disappeared, participants were reminded to maintain fixation by a visual warning message. Moreover, participants were told to ignore the irrelevant distractors. Saccades that were initiated too slowly (>600 ms) were accompanied by a short tone and a visual warning message.

The experiment consisted of one training block and six experimental blocks of 48 trials each. In contrast to the experimental blocks, no distractors were presented during training. Moreover, in the training block, the target was presented a second time 250 ms after saccade initiation to allow for a corrective saccade. Each experimental block was composed of a factorial combination of four target positions (4° vs. 8° to the left or right of fixation), three distractor conditions (absent vs. 6° left vs. 6° right), and four repetitions of each combination. Prior to each block a nine-point grid calibration procedure was applied. Training and experimental blocks were run in a single session of about 45 min.

Data analysis

Saccade onsets were detected using a velocity criterion of $30^\circ/\text{s}$. Saccade latency was defined as the interval between the offset of the fixation point and the initiation of a saccade eye movement. Trials were excluded from analysis if (1) saccades were anticipatory (latency <100 ms),

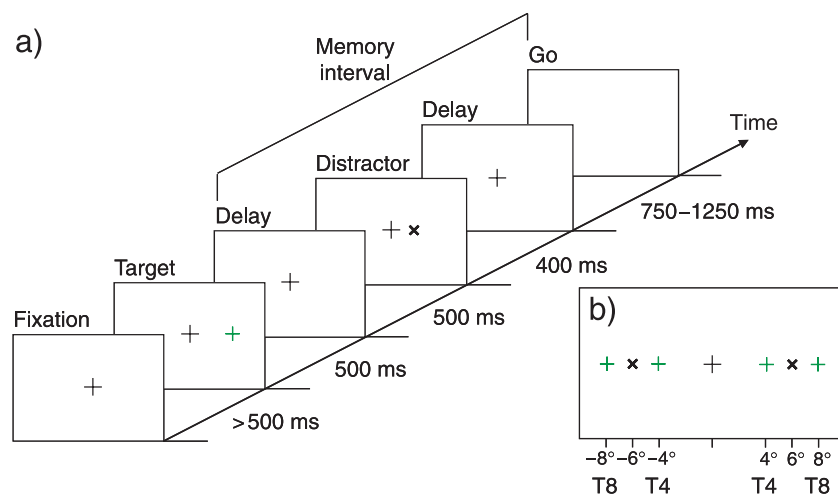


Figure 1. a) Experimental paradigm of Experiment 1. An example of an experimental trial with a distractor in the ipsilateral hemifield during the memory interval. b) Schematic representation of stimuli positions. + = potential target locations. x = potential distractor locations.

		Distractor					
		absent		ipsi		contra	
		M	SE	M	SE	M	SE
Landing position (deg)	T4	3.66	0.29	3.96	0.30	3.60	0.24
	T8	7.90	0.46	7.48	0.39	7.83	0.42
Deviation (deg)	T4			0.30	0.07	0.06	0.08
	T8			0.42	0.13	0.07	0.06
Latency (ms)	T4	249	12	235	9	241	10
	T8	245	11	229	8	233	10

Table 1. Summary of the results of [Experiment 1](#). T4 = target at 4 deg, T8 = target at 8 deg.

(2) saccadic latency was longer than 600 ms, (3) gaze deviated by more than 0.75° from the display center at the time of saccade onset, or (4) saccadic landing position (horizontal coordinate) was less than 1° in the correct direction. With these criteria, 13.6% of all trials were discarded from analysis.

Results

Saccadic landing positions and latencies were calculated as a function of target position (4° vs. 8°) and distractor condition (absent vs. 6° ipsilateral vs. 6° contralateral to the target) and are depicted in [Table 1](#). Since there was no difference for leftward and rightward saccades in landing positions and latencies, the data for the two directions

were collapsed together. The significance criterion was set to $p < .05$ for all analyses.

Landing position

For each distractor trial, the horizontal saccadic landing position was compared to the averaged mean of the horizontal landing position of all saccades in distractor absent trials which was computed separately for each target position and participant. Deviations from the mean horizontal landing position were signed so that a positive value indicated a shift towards the distractor in the distractor condition and a negative value a shift in the opposite direction.

We conducted a 2 (target position: T4 vs. T8) \times 2 (distractor position: ipsilateral vs. contralateral) repeated-measures ANOVA on the deviation values. The analysis revealed a significant main effect of distractor hemifield, $F(1,7) = 17.56$, $p < .01$, which is depicted in [Figure 2a](#). Separate tests for the ipsilateral and contralateral condition determined that the shift of 0.36° towards the ipsilateral distractor was different from zero, $t(7) = 5.27$, $p < .01$. However, no difference was found if the distractor was presented in the contralateral hemifield, $t(7) = 1.27$, $p = .24$. Furthermore, neither the main effect of target position nor the interaction of target position and distractor hemifield was significant (all $F_s < 1$).

To check whether deviations of landing positions were due to a general shift of the distribution towards the distractor (global effect) or to a part of saccades directed to the distractor position and another part directed to the target position, probability maps of the saccades' landing

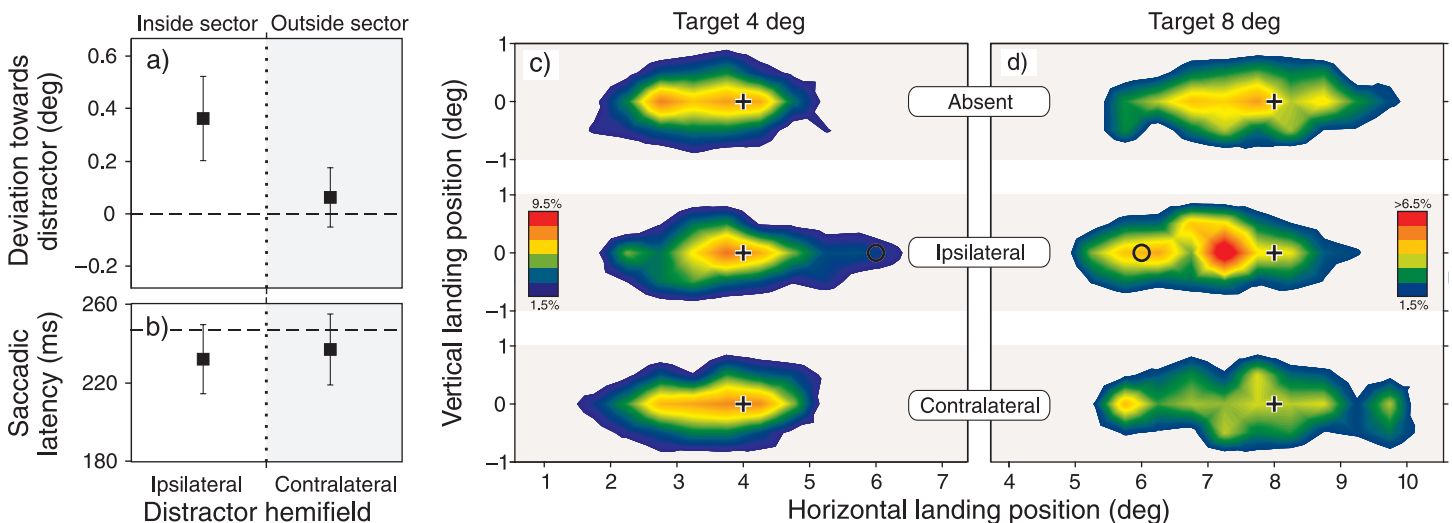


Figure 2. a) Deviation towards the distractor and b) saccadic latency in [Experiment 1](#) as a function of distractor position. Conditions displayed on a white background are inside (on a shaded background outside) the classical global effect sector of $\pm 20^\circ$ around the target axis. The horizontal dashed lines mark the distractor absent control conditions. Error bars represent the 95% confidence interval of the difference between the respective distractor condition and the control condition. c–d) Probability maps of the saccades' landing positions for targets at 4° (panel c) and 8° (panel d) as a function of distractor condition (absent vs. 6° ipsilateral vs. 6° contralateral, from top to bottom) pooled for all 8 participants. The “+” marks the target position, the circle marks the distractor position.

positions were plotted separately for the different conditions and are depicted in [Figure 2c](#) and [2d](#). Indeed, presenting a distractor during the memory interval in the ipsilateral hemifield resulted in a general shift of the distribution towards the distractor. There was no indication for an enhanced probability to direct the saccades to the exact distractor location.

Latency

Latencies of memory guided saccades in the distractor absent control condition were at least descriptively a bit longer (247 ms) than latencies in the distractor present conditions (234 ms), possibly attributable to warning signal effects (Walker, Kentridge, & Findlay, 1995). However, the 2 (target position) \times 2 (distractor position) repeated-measures ANOVA on saccadic latencies revealed no significant effects.

Discussion

[Experiment 1](#) provided evidence that the landing position of memory-guided saccades is deviated towards task-irrelevant stimuli that briefly occur during the retention interval. Importantly, deviation effects were observed only for distractors presented in the ipsilateral hemifield of the memorized target, whereas contralateral distractors did not affect saccadic landing position. The results thus support the assumption that distractors appearing near memorized target locations can affect the spatial representation of these targets in working memory. On a descriptive basis, this effect resembles the global effect which is observed when a distractor occurs simultaneously with a saccade target at less than 20 deg of angular distance from the target axis.

However, before proposing a direct link between the present findings and the classical global effect, two aspects should be taken into account. First, in [Experiment 1](#), the distractor always appeared at 6° on the horizontal axis either ipsi- or contralateral to the memorized target location. Thus, there were only two possible distractor locations. Although this layout corresponded to the inside/outside sector difference of the classical global effect sector, it allowed no direct test whether spatial effects in the present paradigm were restricted to the narrow window of $\pm 20^\circ$ around the target axis. Second, the ipsilateral distractor was always presented at an intermediate position between the two possible target locations (4° and 8°). It thus might be the case that its appearance triggered a process of averaging between these target locations in the course of the experiment and did not in itself attract visual attention.

We therefore conducted a second experiment in which we systematically varied the distance between target and

distractor to directly test for sector effects. Moreover, the possibility of averaging between possible target locations was negated by reducing the predictability of distractor appearance in time and space, as well as by using only one target position in each hemifield.

Experiment 2

Method

Participants

Eight new participants, aged between 19 and 26 years, took part in [Experiment 2](#). Six of the participants were female. All reported normal or corrected-to-normal vision.

Apparatus and stimuli

In contrast to [Experiment 1](#), participants viewed a 19" display monitor from a distance of 71 cm. The screen's resolution of 1024 \times 768 pixels corresponded to physical dimensions of 36 cm (width) \times 27 cm (height). A video-based tower mounted eye tracker (Eye Link1000, SR Research, Ontario, Canada) with a sampling rate of 1000 Hz was used for recording eye movements. Stimuli were the same as in [Experiment 1](#) with the exception that only one distractor shape ("×") was used in [Experiment 2](#).

Procedure and design

The procedure was identical to [Experiment 1](#), except that the target was now randomly presented at 8° to the left or right of the fixation stimulus. Furthermore, in two-thirds of the trials, 400–600 ms (randomly chosen) after target offset a single distractor stimulus was presented for 400 ms. The distractor was presented either 6° or 10° to the left or right of the fixation stimulus, either on the axis of 0° (i.e. the horizontal axis), $\pm 10^\circ$ or $\pm 30^\circ$ from horizontal (see [Figure 3](#)). [Experiment 2](#) was run in two single sessions of about 55 min, each consisting of one training block of 36 trials and four experimental blocks of 72 trials. Each experimental block was composed of a factorial combination of two target positions (8° to the left vs. right of fixation), three distractor hemifield conditions (absent vs. ipsilateral vs. contralateral), two distractor eccentricity conditions (6° vs. 10°), three distractor axis conditions (0° vs. $\pm 10^\circ$ vs. $\pm 30^\circ$), and two repetitions of each combination.

Data analysis

Using the same criteria as in [Experiment 1](#), 9.4% of all trials were discarded from analysis.

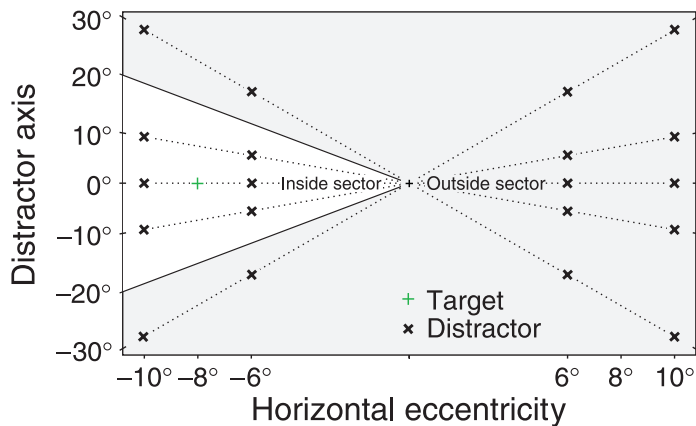


Figure 3. Schematic representation of stimuli positions used in Experiment 2 which are located either inside (white area) or outside (shaded area) the classical global effect sector of $\pm 20^\circ$ around the target axis. To simplify matters, the right target position at $+8^\circ$ is not displayed in the illustration.

Results

Landing position

Because distractor positions were manipulated in horizontal as well as vertical direction in Experiment 2, the procedure for computing deviations towards distractors used in Experiment 1 had to be extended. This was done following Van der Stigchel, Merten, Meeter, and Theeuwes (2007) in two steps. We first computed the vectors between the mean landing position of trials without distractor and trials with distractor separately for each distractor position and participant. In a second step, the component reflecting the target-distractor direction of these vectors was computed and signed so that a positive value indicated a deviation towards the distractor and a negative value a deviation away from the distractor (see Figure 4).¹

We conducted a 2 (distractor hemifield) \times 2 (distractor eccentricity) \times 3 (distractor axis) repeated-measures ANOVA on the deviation values. The analysis revealed a significant main effect of distractor hemifield, $F(1,7) = 14.51$, $p < .01$, indicating a deviation of $+0.24^\circ$ towards ipsilateral distractors and no deviation towards contralateral distractors (deviation = -0.06°). Moreover, there was a significant main effect of distractor axis, $F(2,14) = 7.70$, $p < .01$, indicating pronounced deviation for distractors on the axis of 0° and $\pm 10^\circ$ (deviation = $+0.18^\circ$ and $+0.12^\circ$, respectively) but not on the axis of $\pm 30^\circ$ (deviation = -0.02°). More importantly, the main effect of distractor hemifield strongly depended on the distractor axis as indicated by the significant interaction of distractor hemifield and axis, $F(2,14) = 9.16$, $p < .01$. As can be seen in Figure 5a, saccadic landing position deviated only towards ipsilateral distractors that were presented on the axis of 0° and $\pm 10^\circ$ (deviation = $+0.39^\circ$ and $+0.31^\circ$, respectively). However, ipsilateral distractors on the axis of $\pm 30^\circ$ from horizontal as well as all contralateral distractors did not

attract saccadic landing position. Thus, only distractors inside the classical global effect sector of $\pm 20^\circ$ around the target axis affected saccadic landing position, whereas distractors outside this sector did not. Additionally, distractor hemifield interacted with distractor eccentricity, $F(1,7) = 6.47$, $p < .05$, which was due to a pronounced effect of distractor hemifield for distractors at horizontal eccentricity of 10° compared to 6° . Neither the main effect of distractor eccentricity nor any other interaction was significant (all F s < 2 , p s $> .18$).

Latency

Once again, memory-guided saccades in the distractor absent control condition were initiated a bit slower (215 ms) than saccades in the distractor present conditions (207 ms). The 2 (distractor hemifield) \times 2 (distractor eccentricity) \times 3 (distractor axis) repeated-measures ANOVA on saccadic latencies yielded a significant interaction of distractor hemifield and axis, $F(2,14) = 9.13$, $p < .01$, indicating an effect of distractor axis for ipsilateral presented distractors but not for contralateral presented distractors (see Figure 5b). Separate tests of the ipsilateral distractors showed that saccadic latencies for distractors on the axis of $\pm 30^\circ$ were 13 ms longer than for distractors on the axis of 0° , $t(7) = 2.89$, $p < .05$, as well as 10 ms longer than for distractors on the axis of $\pm 10^\circ$, $t(7) = 2.56$, $p < .05$. Thus, latency was increased when ipsilateral distractors appeared outside the $\pm 20^\circ$ sector around the target axis. No further effect reached significance.

Discussion

Experiment 2 perfectly replicated and extended the finding of Experiment 1. Once again, the landing position of memory-guided saccades was deviated towards task-irrelevant stimuli that briefly occurred during the retention interval. More specifically, deviation effects were only found for distractors presented within $\pm 20^\circ$ of the target

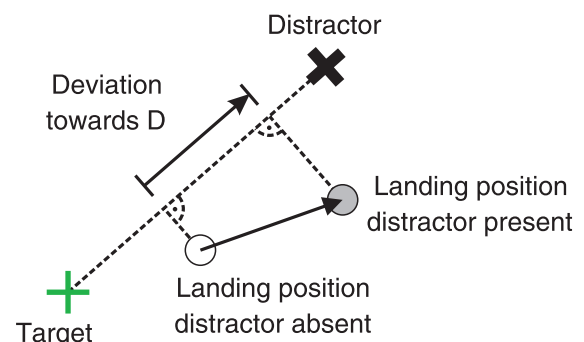


Figure 4. Procedure for determine deviation towards the distractor used in Experiment 2.

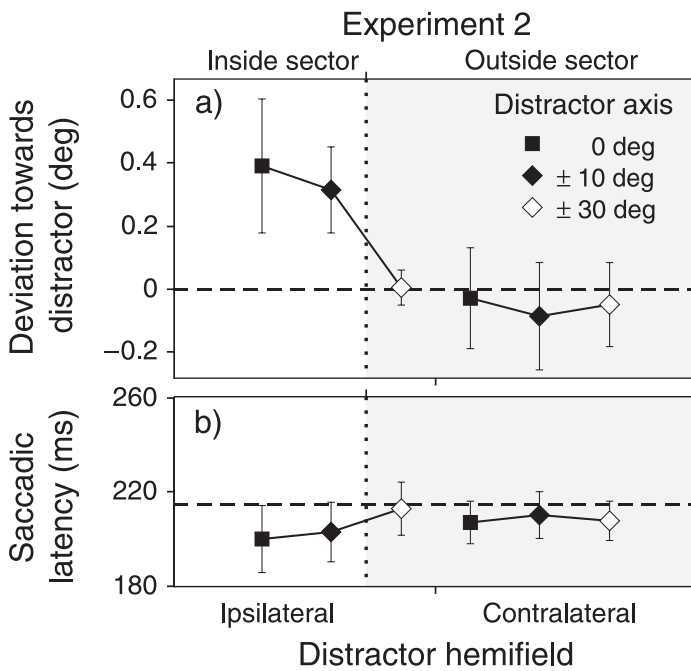


Figure 5. a) Deviation towards the distractor and b) saccadic latency in [Experiment 2](#) as a function of distractor position. Conditions displayed on a white background are inside—on a shaded background outside—the classical global effect sector of $\pm 20^\circ$ around the target axis. The horizontal dashed lines mark the distractor absent control condition. Error bars represent the 95% confidence interval of the difference between the respective distractor condition and the control condition.

axis. The spatial resolution of this effect thus strongly resembles the classical global effect in which target and distractor are simultaneously presented.

Additionally, [Experiment 2](#) revealed an effect of distractor position on saccadic latencies. Ipsilateral distractors that were flashed outside $\pm 20^\circ$ of the target axis led to an increase in saccadic latency. Thus the results indicate a reciprocal relationship between modulation of landing position and latency that is to some extent comparable to the distinction between the classical global and remote distractor effect. Distractors presented within $\pm 20^\circ$ of the target axis modulated landing position but did not increase latency. Distractors presented outside $\pm 20^\circ$ of the target axis had no effect on landing position but increased latency. However, in contrast to the classical remote distractor effect, an increase of saccadic latencies seems to be restricted to distractors presented outside the sector in the ipsilateral hemifield.

General discussion

The present study clearly shows that irrelevant stimuli that are briefly presented during the retention interval of a

memory guided saccade attract the saccadic landing position. Importantly, attraction effects were observed only for distractors presented inside a narrow sector of $\pm 20^\circ$ around the target axis. This effect strongly resembles the classical global effect that is found when the saccade target and the distractor occur simultaneously. The same spatial effect on saccadic eye movements can thus be observed regardless of whether a stimulus is directly received from the retina or kept in visual working memory. It thus can be assumed that spatial working memory draws on the same spatial representations as covert visual attention and saccade control do.

Given the finding that the classical global effect diminishes or even disappears with increasing saccadic latencies (Coeffé & O'Regan, 1987; Findlay, 1983; Ottes et al., 1985), it has been suggested that it might be due to the limited time available for detailed visual processing or the discrimination of target and distractor. For instance, it has been suggested that the global effect is due to a short-lived exogenous attentional signal with low spatial resolution that can be displaced by a time-consuming process feeding a high-resolution signal from the visual system to the oculomotor signal (Findlay, 2009; Findlay & Blythe, 2009). However, in the present experimental paradigm there was plenty of time both after target and distractor presentation to counteract the low-resolution signal and to complete discrimination of target and distractor. The fact that a global effect can be found even in a situation in which there were relaxed time constraints and in which participants were told to completely ignore the irrelevant distractors strongly suggests that it is not possible to encapsulate the target location during the memory interval against neighboring onset distractors. Evidently, maintaining a target location for a memory-guided saccade implies to maintain the fused distractor, too.

Up to now, most models of oculomotor distractor effects are based on a competitive integration mechanism of goal-related and stimulus-driven signals (Godijn & Theeuwes, 2002; Trappenberg, Dorris, Munoz, & Klein, 2001). These models share the assumption that competitive integration occurs on a common winner-take-all map with a retinotopic organization which may be found in the intermediate layers of the SC. In the case of neighboring stimuli, when two nearby locations are activated, competitive integration might lead to *cooperation* of both signals, i.e. the formation of a single activation peak somewhere between the two stimulus locations resulting in the global effect (Glimcher & Sparks, 1993). In contrast, *competition* between signals may arise when two remote locations are activated. Via lateral inhibition, remote distractors might thus slow down the speed at which a threshold for saccade initiation is reached (Godijn & Theeuwes, 2002). To account for distractor effects, competitive integration models assume temporal overlap of the neural activity representing target and distractor location. However, in the present experiments, target, distractor, and saccadic go signal were all separated in time. Yet, a number of

studies show sustained neural activity during the retention interval of memory guided saccades at SC neurons representing the target location (Kojima, Matsumura, Togawa, & Hikosaka, 1996; Pare & Wurtz, 2001). This neural memory activity in SC is probably generated by input from higher areas like DLPFC, FEF, and LIP (Johnston & Everling, 2008). It is thus tempting to extend recent competitive integration models by including a memory component.

In contrast to the remote distractor effect that is found when the saccade target and the distractor occur simultaneously, effects on saccadic latency in the present paradigm were restricted to ipsilateral distractors outside the sector. This result firstly suggests that participants maintain a memory trace for task-irrelevant remote distractors in the ipsilateral hemifield that slows the speed at which a threshold for saccade initiation is reached. Moreover, remote distractors in the ipsilateral field seem to be stronger competitors than distractors in the contralateral field. This observation is consistent with findings in a partial report task showing that target identification was disturbed slightly more by ipsilateral than contralateral distractors (Finke et al., 2005).

Interestingly, task-irrelevant distractors attracted memory-guided saccades in the present experiment, whereas a previous experiment showed that saccadic trajectories curve away from locations kept in memory (Theeuwes et al., 2005). Thus, combining a spatial memory task with an eye movement can result in attraction effects as well as repulsion effects. Although the two experiments differ in a variety of parameters, including different measurements of saccades (i.e., landing positions vs. trajectories) and different functions of the involved stimuli (i.e., task-irrelevant vs. relevant), there is one more crucial difference which might be responsible for the diverging results. In the study by Theeuwes et al. (2005), the location of the memory stimulus was outside the 20 deg of angular distance from the target axis that is known to be critical for observing the global effect (Walker et al., 1997). For non-target stimuli presented outside this critical region there is no overlap between the spatial representations of target and non-target stimulus. This, in turn, might be a requirement for specific inhibition of one location (e.g., the location of the memory stimulus) which is thought to underlie the repulsion effect.

Interestingly, a recent study by Van der Stigchel et al. (2007) provides converging evidence for an influence of task-irrelevant visual events on visual working memory. Comparable to the present findings, task-irrelevant stimuli that were flashed near the memorized target location on some trials during a memory interval had an attraction effect on the memory judgment. However, there were two crucial differences to the present experiments. First, no oculomotor effects were tested in the study by Van der Stigchel and colleagues because judgments were indicated by an unspeeded mouse click. Second, the experiment was therefore not designed to test for sector effects. The

present experiments thus extend the recent finding by showing effects directly on the oculomotor system and by elucidating the decisive role of the global effect sector on these effects.

The current finding provides evidence for a close link between covert attention, eye movements and visual working memory. A framework for the link between covert attention and eye movements is provided by the Visual Attention Model (VAM) proposed by Schneider (1995). VAM argues that targets for perception and targets for action (i.e., the selection of a saccade target) are selected by one and the same mechanism of visual attention. Recently, it has been suggested that such a common selection mechanism might be implemented in attentional priority maps for covert and overt attention (Fecteau & Munoz, 2006). Importantly, attentional priority maps are thought to combine both the representations of objects' bottom-up distinctiveness (i.e., salience) and their relevance to observers in a topographical map of space. Since an object's salience and relevance are known to affect perception and the oculomotor system in comparable ways, these defining characteristics make attentional priority maps a feasible candidate to underlie selection for perception and selection for action. On the other hand, covert shifts of spatial attention have been suggested to play a functional role in the active maintenance of information in visual working memory (Awh, Armstrong, & Moore, 2006). Thus, one might assume that the target location for a memory guided saccade is maintained via the attentional priority map as well. This idea would fit well to the suggestion that LIP might be a suitable candidate for hosting such an attentional priority map (Ipatá, Gee, Bisley, & Goldberg, 2009) since LIP is also involved in maintaining spatial information in working memory (Bisley & Goldberg, 2003).

In summary, the present experiment showed that task-irrelevant distractors which are presented during the retention interval of a memory-guided saccade attract saccadic landing position. Thus, a global effect occurs even when saccade target and distractor are separated in time. To account for the present finding, it is hypothesized that VAM and the concept of attentional priority maps need to be extended by including visual working memory. If covert and overt forms of orienting can be ascribed to attentional priority maps, and if information is kept in visual working memory via covert visual attention (Awh et al., 2006), then attentional priority maps might be best characterized as the "neurocomputational space" where memory, perception and motor control meet.

Acknowledgments

This research was supported by a publication fund of Bielefeld University and by grants of the Cluster of Excellence Cognitive Interaction Technology (CITEC)

and resources of the Max-Planck-Institute for Human Cognitive and Brain Sciences. We would like to thank the anonymous reviewers for helpful comments on an earlier version of this article.

Commercial relationships: none.

Corresponding author: Arvid Herwig.

Email: arvid.herwig@uni-bielefeld.de.

Address: Department of Psychology, Bielefeld University, P.O. Box 100131, D-33501 Bielefeld, Germany.

Footnote

¹Since the target-distractor direction was always horizontal in [Experiment 1](#), the calculation of deviations from the mean horizontal landing position used in [Experiment 1](#) is a special case of the more general computation procedure used in [Experiment 2](#).

References

- Awh, E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection: Links, causes and implications for spatial attention. *Trends in Cognitive Sciences*, *10*, 124–130. [[PubMed](#)]
- Awh, E., Jonides, J., & Reuter-Lorenz, P. A. (1998). Rehearsal in spatial working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 780–790. [[PubMed](#)]
- 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*, 433–437.
- Bisley, J. W., & Goldberg, M. E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science*, *299*, 81–86. [[PubMed](#)]
- Bisley, J. W., & Goldberg, M. E. (2006). Neural correlates of attention and distractibility in the lateral intraparietal area. *Journal of Neurophysiology*, *95*, 1696–1717. [[PubMed](#)]
- Coëffé, C., & O'Regan, J. K. (1987). Reducing the influence of non-target stimuli on saccade accuracy: Predictability and latency effects. *Vision Research*, *27*, 227–240. [[PubMed](#)]
- Coren, S., & Hoenig, P. (1972). Effect of non-target stimuli upon length of voluntary saccades. *Perceptual and Motor Skills*, *34*, 499–508. [[PubMed](#)]
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*, 1827–1837. [[PubMed](#)]
- Deubel, H., Wolf, W., & Hauske, M. (1984). The evaluation of the oculomotor error signal. In A. G. Gale & F. W. Johnson (Eds.), *Theoretical and applied aspects of oculomotor research* (pp. 55–62). Amsterdam: Elsevier.
- Doyle, M., & Walker, R. (2001). Curved saccade trajectories: Voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research*, *139*, 333–344. [[PubMed](#)]
- Fecteau, J. H., & Munoz, D. P. (2006). Saliency, relevance, and firing: A priority map for target selection. *Trends in Cognitive Sciences*, *10*, 382–390. [[PubMed](#)]
- Findlay, J. M. (1982). Global processing for saccadic eye movements. *Vision Research*, *22*, 1033–1045. [[PubMed](#)]
- Findlay, J. M. (1983). Visual information processing for saccadic eye movements. In A. Hein & M. Jeannerod (Eds.), *Spatially oriented behaviour* (pp. 281–303). New York: Springer.
- Findlay, J. M. (2009). Saccadic eye movement programming: Sensory and attentional factors. *Psychological Research*, *73*, 127–135. [[PubMed](#)]
- Findlay, J. M., & Blythe, H. I. (2009). Saccade target selection: Do distractors affect saccade accuracy? *Vision Research*, *49*, 1267–1274. [[PubMed](#)]
- Findlay, J. M., Brogan, D., & Wenban-Smith, M. (1993). The spatial signal for saccadic eye movements emphasizes visual boundaries. *Perception & Psychophysics*, *53*, 633–641. [[PubMed](#)]
- Finke, K., Bublak, P., Krummenacher, J., Kyllingsbaek, S., Müller, H. J., & Schneider, W. X. (2005). Usability of a theory of visual attention (TVA) for the parameter-based measurement of attention I: Evidence from normal subjects. *Journal of the International Neuropsychological Society*, *11*, 832–842. [[PubMed](#)]
- Glimcher, P. W., & Sparks, D. L. (1993). Representation of averaging saccades in the superior colliculus of the monkey. *Experimental Brain Research*, *95*, 429–435. [[PubMed](#)]
- Godijn, R., & Theeuwes, J. (2002). Programming of exogenous and endogenous saccades: Evidence for a competitive integration model. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 1039–1054. [[PubMed](#)]
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual-attention in saccadic eye-movements. *Perception & Psychophysics*, *57*, 787–795. [[PubMed](#)]

- Ipata, A. E., Gee, A. L., Bisley, J. W., & Goldberg, M. E. (2009). Neurons in the lateral intraparietal area create a priority map by the combination of disparate signals. *Experimental Brain Research*, *192*, 479–488. [[PubMed](#)]
- Johnston, K., & Everling, S. (2008). Neurophysiology and neuroanatomy of reflexive and voluntary saccades in non-human primates. *Brain and Cognition*, *68*, 271–283. [[PubMed](#)]
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, *23*, 315–341. [[PubMed](#)]
- Kojima, J., Matsumura, M., Togawa, M., & Hikosaka, O. (1996). Tonic activity during visuo-oculomotor behavior in the monkey superior colliculus. *Neuroscience Research*, *26*, 17–28. [[PubMed](#)]
- Kowler, E., Anderson, E., Doshier, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*, 1897–1916. [[PubMed](#)]
- Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, *91*, 152–162. [[PubMed](#)]
- Müller, J. R., Philiastides, M. G., & Newsome, W. T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Science*, *102*, 524–529. [[PubMed](#)]
- Olivers, C. N. L. (2008). Interactions between visual working memory and visual attention. *Frontiers in Bioscience*, *13*, 1182–1191. [[PubMed](#)]
- Ottes, F. P., Van Gisbergen, J. A., & Eggermont, J. J. (1985). Latency dependence of colour-based target vs. nontarget discrimination by the saccadic system. *Vision Research*, *25*, 849–862. [[PubMed](#)]
- Pare, M., & Wurtz, R. H. (2001). Progression in neuronal processing for saccadic eye movements from parietal cortex area lip to superior colliculus. *Journal of Neurophysiology*, *85*, 2545–2562. [[PubMed](#)] [[Article](#)]
- Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, *3*, 3–25. [[PubMed](#)]
- Schall, J. D. (2009). Frontal eye fields. In L. R. Squire (Ed.), *Encyclopedia of neuroscience* (vol. 4, pp. 367–374). Oxford: Academic Press.
- Schneider, W. X. (1995). VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action. *Visual Cognition*, *2*, 331–375.
- Schneider, W. X., & Deubel, H. (2002). Selection-for-perception and selection-for-spatial-motor-action are coupled by visual attention: A review of recent findings and new evidence from stimulus-driven saccade control. In W. Prinz & B. Hommel (Eds), *Attention and performance XIX: Common mechanisms in perception and action* (pp. 609–627). Oxford: Oxford University Press.
- Theeuwes, J., Belopolsky, A., & Olivers, C. N. L. (2009). Interactions between working memory, attention and eye movements. *Acta Psychologica*, *132*, 106–114. [[PubMed](#)]
- Theeuwes, J., Olivers, C. N. L., & Chizk, C. L. (2005). Remembering a location makes the eyes curve away. *Psychological Science*, *16*, 196–199. [[PubMed](#)]
- Trappenberg, T. P., Dorris, M. D., Munoz, D. P., & Klein, R. M. (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience*, *13*, 256–271. [[PubMed](#)]
- 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. [[PubMed](#)] [[Article](#)]
- Walker, R., Deubel, H., Schneider, W. X., & Findlay, J. M. (1997). The effect of remote distractors on saccade programming: Evidence for an extended fixation zone. *Journal of Neurophysiology*, *78*, 1108–1119. [[PubMed](#)]
- Walker, R., Kentridge, R. W., & Findlay, J. M. (1995). Independent contributions of the orienting of attention, fixation offset and bilateral stimulation on human saccadic latencies. *Experimental Brain Research*, *103*, 294–310. [[PubMed](#)]