



# No functional role of attention-based rehearsal in maintenance of spatial working memory representations

Artem V. Belopolsky\*, Jan Theeuwes

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

## ARTICLE INFO

### Article history:

Received 15 July 2008

Received in revised form 18 December 2008

Accepted 14 January 2009

Available online 23 February 2009

### PsycINFO classification:

2346

### Keywords:

Working memory

Attention-based rehearsal

Oculomotor suppression

Inhibition of return

## ABSTRACT

The present study systematically examined the role of attention in maintenance of spatial representations in working memory as proposed by the attention-based rehearsal hypothesis [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]. Three main issues were examined. First, Experiments 1–3 demonstrated that inhibition and not facilitation of visual processing is often observed at the memorized location during the retention interval. This inhibition was caused by keeping a location in memory and not by the exogenous nature of the memory cue. Second, Experiment 4 showed that inhibition of the memorized location does not lead to any significant impairment in memory accuracy. Finally, Experiment 5 connected current results to the previous findings and demonstrated facilitation of processing at the memorized location. Importantly, facilitation of processing did not lead to more accurate memory performance. The present results challenge the functional role of attention in maintenance of spatial working memory representations.

© 2009 Elsevier B.V. All rights reserved.

## 1. Introduction

The visual system provides us with information about what is where in the environment, but this information can change very rapidly. In order to be able to carry out goal-driven behavior there is a need to keep the information that is no longer present available for online access and manipulation. Visuospatial working memory (VSWM) is a system that is thought to subserve the temporary storage of spatial information (Baddeley, 1986).

In recent years, the mechanisms underlying visuospatial working memory have been a topic of considerable interest. The most prominent view is the attention-based rehearsal hypothesis (Awh, Vogel, & Oh, 2006), according to which the maintenance of spatial information in working memory is accomplished through a sustained shift of spatial attention to a memorized location. It was demonstrated that keeping a location in memory resulted in enhancement of visual processing at that location measured at both behavioral and neural levels. Analogous to allocating spatial attention, maintaining location in memory resulted in faster behavioral responses and amplified neural activity in early contralateral visual areas (Awh, Anllo-Vento, & Hillyard, 2000; Awh et al., 1999; Jha, 2002). In addition, both visuospatial working memory and spatial attention tasks have shown to activate a similar network of frontal and parietal brain areas (Corbetta, Kincade, & Shulman, 2002). Most importantly, the functional role of attention in

maintenance of spatial representations in memory is suggested by the fact that memory performance is impaired when attention is shifted away from the memorized location (Awh, Jonides, & Reuter-Lorenz, 1998).

However, several recent studies (Krishna, Steenrod, Bisley, Sirotnin, & Goldberg, 2006; Ostendorf, Finke, & Ploner, 2004) have reported inhibition of visual processing when participants had to keep a location of a future saccade in memory (i.e., the memory-guided saccade task). These studies showed that both humans (Ostendorf et al., 2004) and monkeys (Krishna et al., 2006) were slower in discriminating visual choice probes at the goal of the memory-guided saccade than at other locations. Some researchers interpreted these inhibitory effects as being caused simply by the exogenous nature of the memory cue (Krishna et al., 2006; Theeuwes, Van der Stigchel, & Olivers, 2006). Since the memory cue was always an abrupt onset, after long delays it could have produced inhibition of return (IOR, Posner & Cohen, 1984). IOR is an inhibitory effect, specific to the exogenous attention and refers to both a phenomenon and a mechanism by which attention is biased from returning to the previously attended locations (Posner & Cohen, 1984). The net inhibition of the memorized location was explained by IOR triggered by the abrupt onset of the memory cue overshadowing endogenous attention allocated to the memorized location. In fact, recent research has shown the co-existence of endogenous attention and IOR at the same location (Berger, Henik, & Rafal, 2005; Berlucchi, Chelazzi, & Tassinari, 2000; Lupianez et al., 2004).

Other researchers (Ostendorf et al., 2004), however, have shown that the inhibition of visual processing at the memorized location

\* Corresponding author. Tel.: +31 20 598 8807; fax: +31 20 598 8971.

E-mail address: [A.Belopolsky@psy.vu.nl](mailto:A.Belopolsky@psy.vu.nl) (A.V. Belopolsky).

was not simply due to the abrupt onset of the memory cue. Inhibition of the cued location was greater and persisted longer when the location was maintained in memory as the goal of the memory-guided saccade, instead of being ignored (Ostendorf et al., 2004). Furthermore, the accuracy of memory representation seemed to be dependent on the strength of this inhibitory effect, suggesting that maintaining a location in spatial memory results in inhibition of a memorized location. Ostendorf and colleagues attributed the presence of inhibition of visual processing at the memorized location to the nature of the task used, since in the memory-guided saccade task participants need to memorize a location of a future saccade target, suppression of a saccade to the remembered location is required throughout the retention interval (see also Rafal, Calabresi, Brennan, & Sciolto, 1989). Direct evidence that saccade programs are suppressed when the probability of their execution is low has recently been obtained (Belopolsky & Theeuwes, submitted for publication; Belopolsky & Theeuwes, 2009). Indeed, studies that have shown enhancement of visual processing at the memorized location during the retention interval typically did not require saccades to be made to the memorized location (Awh et al., 1998; Awh et al., 2000; Jha, 2002).

The purpose of the present study was to systematically investigate the relationship between enhancement of processing attributed to the attention-based rehearsal and inhibition at the memorized location. In order to address this question, we used a “delayed match to sample” task closely modeled after Awh et al. (1998) (see Fig. 1). In this task participants have to maintain a loca-

tion in memory and then match it to the location of a memory probe presented at the end of a retention interval. Importantly, in this task participants never had to prepare a saccade: throughout the whole trial they were instructed to maintain fixation, which was verified with an eye-tracker. In the present study, three main issues were examined. First, Experiments 1–3 examined possible sources of the inhibitory processing, i.e., whether the inhibition of the memorized location is due to the exogenous nature of the memory cue or to the process of keeping a location in memory. Second, Experiment 4 examined the functional role of sustaining attention at the memorized location in accurate memory maintenance. Finally, Experiment 5 was aimed to make a connection to the previous findings of facilitation of processing at the memorized location by examining the role of probability with which discrimination probes occur at the memorized location on the direction of attentional effects.

## 2. Experiment 1

The goal of Experiment 1 was to examine the contribution of inhibition of return produced by the abrupt onset memory cue in the standard delayed match to sample task. The magnitude of the inhibitory contribution to the overall enhancement of visual processing in the retention interval was never examined in the original study by Awh et al. (1998). Clearly, the time-course of IOR should have overlapped with the time-course of the sustained attentional shift, but perhaps spatial working memory counteracted IOR and led to net facilitation of processing at the memorized location.

To measure processing at the memorized location, a discrimination probe was presented on every trial during the retention interval, but coincided with the memorized location only in 25% of the trials. We expected a net facilitation effect (as in Awh et al., 1998) since facilitation that is due to attentional rehearsal should be greater than IOR triggered by the exogenous memory cue. To estimate the amount of inhibition caused by the exogenous cue, we also included a no-memory condition, which was identical to the memory condition, except that participants did not have to keep the cued location in memory.

### 2.1. Method

#### 2.1.1. Participants

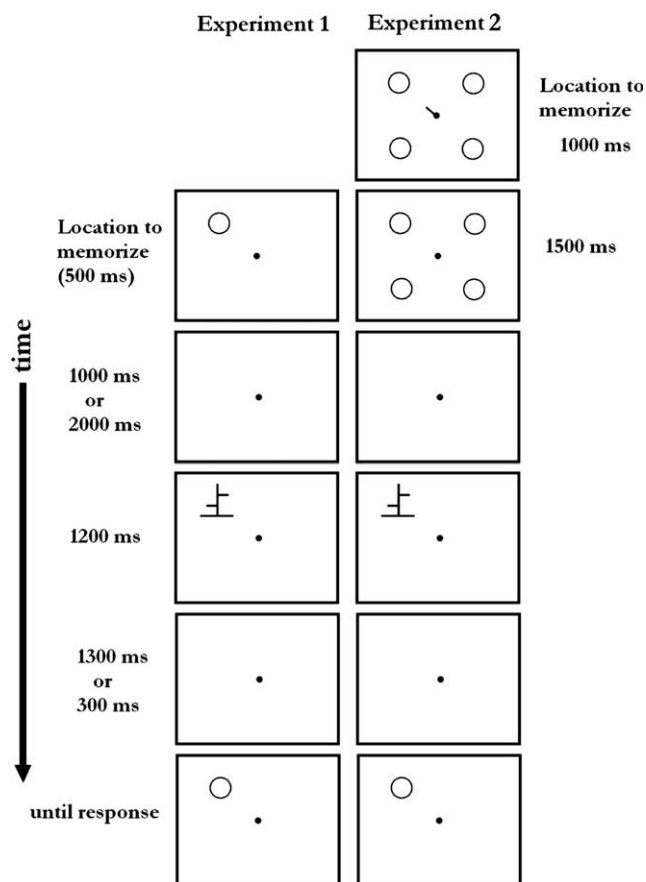
Twenty-four volunteers from the Vrije Universiteit Amsterdam were paid to participate in a 1 h session. Their age varied between 18 and 27, with a mean age of 21. They all had normal or corrected to normal visual acuity and normal color vision. Twelve participants were randomly assigned to the memory condition and the other twelve were assigned to the no-memory condition.

#### 2.1.2. Apparatus

A Pentium II computer with a 21" color monitor generated the stimuli and controlled the timing of the events. Eye movements were recorded by means of an Eyelink II tracker with a 500 Hz temporal resolution and a 0.2° spatial resolution.

#### 2.1.3. Stimuli, design, procedure

The experiment was closely modeled after Awh et al. (1998). The stimuli were presented in dark gray (2.8 cd/m<sup>2</sup>) on a light gray background (19.5 cd/m<sup>2</sup>). The sequence of events in the memory condition is illustrated in Fig. 1. The trial began with participants fixating the dot (0.3° in diameter) in the center of the screen and pressing a spacebar to start. After 500 ms an exogenous memory cue appeared for 500 ms. To remove any identity information from the memory cue, instead of letters, we used an unfilled circle (1.35°



**Fig. 1.** Examples of the displays used in Experiment 1 (exogenous memory cue, left panel) and Experiment 2 (endogenous memory cue, right panel). In the no-memory condition of Experiment 1, the displays were identical to the memory condition, but since the location of the cue did not need to be memorized, the last panel was omitted. In both experiments the letter-like choice probe occurred at the cued location on 25% of the trials.

in diameter, two pixels wide) as the memory cue and the memory probe. Participants had to memorize the exact location of the cue for 3500 ms (5000 ms was used in the original study). To prevent verbal coding of locations, we reduced the number of possible memory cue locations by eliminating the locations on and close to the cardinal axes (from 108 to 48 possible locations). The memory cue was equally likely to appear at any of the 48 possible locations on circumferences of three imaginary concentric circles with radii of 4°, 4.8° and 5.5° of visual angle from the fixation (the inner, middle and outer circles, respectively). Only 16 locations at the angles of 30°, 40°, 50° and 60° were chosen per circle, resulting in a total of 12 possible locations per quadrant of the screen (top left, top right, bottom left, bottom right).

In order to increase the number of trials, we used two choice probe delays (1000 and 2000 ms), instead of three delays (1500, 2500 and 3500 ms) used by Awh et al. (1998). During the retention interval, a letter-like choice probe ( $1.6 \times 1.6^\circ$ , four pixels wide) was presented for 1200 ms. Participants had to be fast and accurate in determining which one of the two letter-like stimuli was presented by pressing either “v” or “m” on the keyboard. Just as in the original study, the choice probe could appear at the same potential locations as the memory cue, but matched the location of the memory cue only on 25% of trials, thus precluding participants from strategically orienting to the cue for the benefit of discrimination task. When the choice probe location did not match the memory cue location, the choice probe was presented at the same eccentricity as the memory cue (i.e. on the same circle and equivalent position), but in a different quadrant. This was done to make sure that reaction times to the choice probes matching the location of the memory cue at each distance could be compared to choice probes mismatches at the same eccentricity.

At the end of the retention interval, a memory probe (physically identical to the memory cue) was presented with equal probability either at the same memorized location or at a different location (randomly chosen to be 0.7°, 1.1° or 1.5° away from the memorized location). Participants had to indicate whether the memory probe appeared at the memorized location by pressing “m” key or at a different location by pressing “v” key. The memory probe stayed on the screen until the response was made.

Participants were seated 75 cm from a computer screen with their head positioned on a chin rest. They were told to keep their eyes on the fixation dot throughout each trial. To familiarize participants with the task, they first received a block of 48 trials with memory task alone (no choice probe was presented). It was followed by another practice block of a dual-task (48 trials), in which participants were instructed to give the highest priority to the memory task. Practice blocks were followed by six experimental dual-task blocks (48 trials each), the total of 288 trials. The 288 dual-task trials consisted of 72 trials on which the choice probe location matched the memory cue location (24 on each circle) and 216 on which it did not (72 on each circle). After each block, participants received feedback about their average memory accuracy and response time to the choice probe. On each trial, participants also received auditory feedback for errors in memory recognition or choice probe discrimination, as well as when they made eye movements.

The no-memory condition was very similar to the memory condition, except that participants were not instructed to memorize the cue. As a result, the memory probe display was omitted. The first practice memory block was also discarded.

## 2.2. Results

### 2.2.1. Discarded data

Trials in which participants made eye movements greater than 1° of visual angle from the central fixation were discarded from

further analyses. In the memory condition, on average, participants made saccades in the direction of the cue on 5.2% of all trials and saccades to the choice probe on 6.2% of the trials. In the no-memory condition, on average, participants made saccades in the direction of the cue on 2.7% of all trials and saccades to the choice probe on 8.8% of the trials. Trials in which participants responded to the choice probe faster than 150 ms or slower than 950 ms in the no-memory condition (1000 ms in the memory condition) were excluded from the analysis. This led to a loss of 3% of the trials. One participant was replaced because of a large number of errors in choice probe discrimination (>10%).

### 2.2.2. Memory performance

On average, participants were quite accurate in the memory task (74%). There were no significant differences in spatial memory performance across conditions. Participants were slightly more accurate when the choice probe location matched the memory cue location (75% vs. 73%), but this difference was not significant ( $t < 1$ ). Memory performance improved as the distance between the memory probe and the memorized location increased (42%, 69% and 87%, for the 0.7°, 1.1° and 1.5° displacements, respectively,  $F(2, 22) = 155.95, p < .001$ ).

### 2.2.3. Choice probe responses

The mean correct RTs to the choice probe in the memory and no-memory conditions are presented in Fig. 2. Contrary to our expectations, both memory and no-memory conditions showed inhibition of the cued location, albeit with a different time-course.

To examine whether the time-course of inhibition was different depending on whether the location of the cue had to be memorized, we compared the two conditions in a mixed-effects ANOVA. The condition was the between-subject factor, while choice probe delay and choice probe location were within subject factors. There was a significant effect of choice probe location ( $F(1, 22) = 6.70, p < .05$ ), with participants responding faster at the uncued than at cued locations. Participants responded faster with a long choice delay than with a short delay ( $F(1, 22) = 22.03, p < .001$ ). The three-way interaction was also significant ( $F(1, 22) = 4.61, p < .05$ ), suggesting that IOR was different across conditions and across delays. Posthoc analyses showed that for 1000 ms delay between the cue and the choice probe, IOR was significantly greater in the no-memory condition than in the memory condition (27 ms vs. 5 ms, respectively;  $F(1, 22) = 4.73, p < .05$ ). However, the magnitude of IOR was not different at 2000 ms delay (−0.2 ms vs. 6 ms, respectively;  $F(1, 22) = 0.42, p = .52$ ). On average, participants made very few errors in discriminating the choice probe shape (3.2%). ANOVA on the error rates showed no significant main effects or interactions.

Planned comparisons were used to examine the net effect of spatial working memory on processing at the memorized location. In the memory condition, a two-way repeated ANOVA on correct RT to the choice probe (choice probe delay and choice probe location as factors) showed a main effect of choice probe location ( $F(1, 11) = 8.01, p < .05$ ). Contrary to the results of Awh et al. (1998), participants were slower to respond to the choice probe appearing at the memorized location than at the other locations. The interaction between the choice probe location and choice probe delay was not significant ( $F < 1$ ).

## 2.3. Discussion

The present results indicate that participants were slower in discriminating the choice probe when it appeared at the location kept in memory than at other locations throughout the retention interval. Although our task was closely modeled after the experiment of Awh et al. (1998), we failed to replicate their results showing

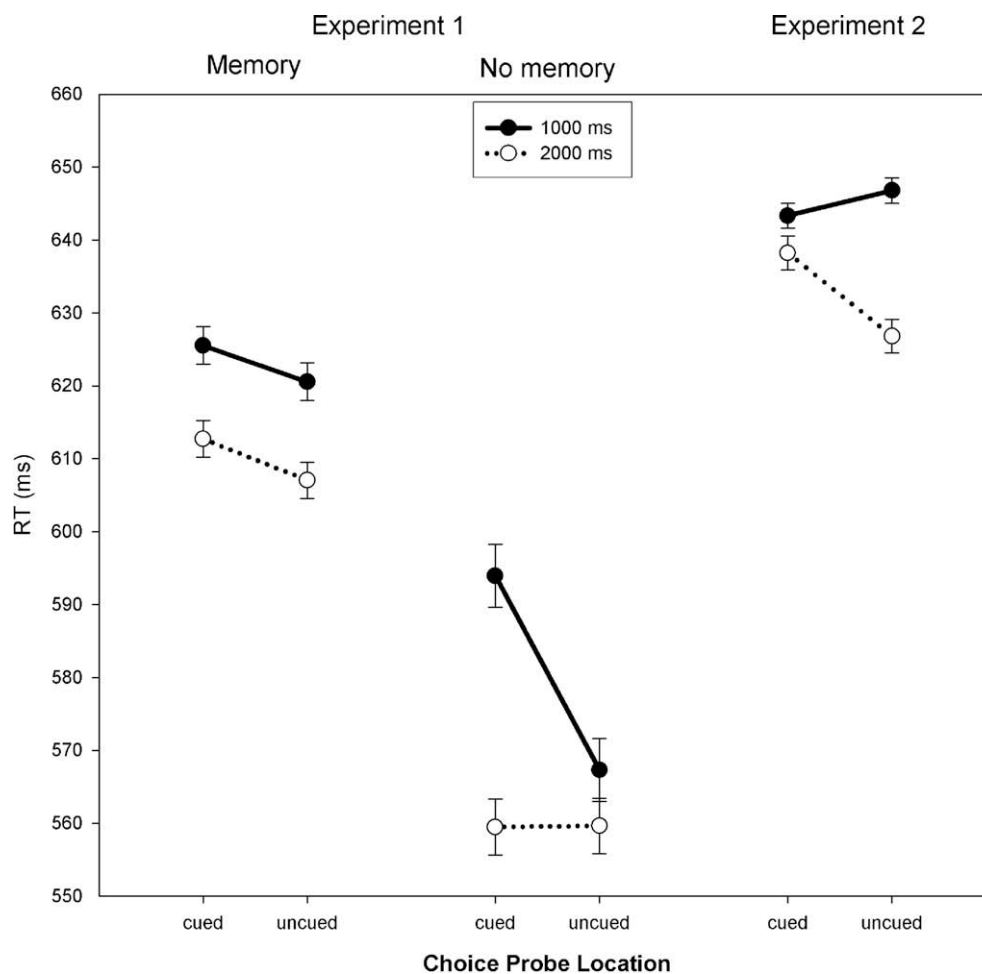


Fig. 2. Mean correct reaction times in Experiments 1 and 2 as a function of choice probe location and delay.

facilitation of visual processing at the memorized location throughout the retention interval. Comparison to the no-memory condition showed that early in the retention interval this inhibition was partially caused by inhibition of return produced by the exogenous memory cue. Thus, spatial memory facilitated visual processing early in the retention interval and countered inhibition of return caused by the exogenous memory cue. Memorizing the location of the cue reduced IOR from 27 ms to 5 ms, suggesting that spatial attention was maintained at the memorized location up to 1000 ms after the cue offset. However, at the later stage (2000 ms) of the retention interval, no facilitation was found at the memorized location, even though IOR caused by the cue had subsided. It appears that attention was not maintained at the memorized location the whole time during the retention interval; however, no decrease in memory performance was found at the longer delays.

Clearly, unlike the inhibitory effects in the memory-guided saccade tasks (Krishna et al., 2006; Ostendorf et al., 2004), the inhibition in our task could not be attributed to explicit saccade inhibition, since in our task no eye movements were required. However, it is still not clear whether the presence of the exogenous memory cue is a prerequisite for the inhibitory effect in the memory task or it is caused merely by the act of keeping a location in memory. This was explored in Experiment 2.

### 3. Experiment 2

Experiment 2 examined whether the act of keeping a location in memory alone is responsible for inhibition of the memorized loca-

tion found in Experiment 1. As mentioned above, IOR is observed only with exogenous cues (Klein, 2000). In the present experiment, we cued the memorized location endogenously (see Fig. 1, panel 2). If inhibition of memorized location is caused by keeping a location in memory, it should also be observed in the present experiment. If, as suggested by the attention-based rehearsal hypothesis, attention is maintained at the memorized location, then it should no longer be hindered by IOR, and facilitation of processing at the memorized location should be observed throughout the retention interval.

#### 3.1. Method

##### 3.1.1. Participants

Eleven students from the Vrije Universiteit Amsterdam were paid to participate in a 1 h session. Their age varied between 18 and 31, with a mean age of 22. They all had normal or corrected to normal visual acuity and normal color vision.

##### 3.1.2. Stimuli, design, procedure

The setup of Experiment 2 was very similar to Experiment 1. However, instead of a single memory cue, participants were presented with four equidistant location cues and a central arrow cue (1° in length, three pixels wide) indicated the location that they were to hold in working memory (see Fig. 1). The arrow cue was turned off after 1000 ms, but the circles remained on the screen for another 1500 ms. The rest of the trial was identical to the memory condition of Experiment 1.

### 3.2. Results

#### 3.2.1. Discarded data

Trials on which participants made eye movements greater than 1° of visual angle from the central fixation were discarded from further analyses. On average, participants made saccades in the direction of the memory cue on 9.9% of all trials and saccades to the choice probe on 9.7% of the trials. Trials in which participants responded to the choice probe faster than 150 ms or slower than 1000 ms were excluded from the analysis. This led to a loss of 4% of the trials.

#### 3.2.2. Memory performance

On average, participants were quite accurate in the memory task (73%). There were no significant differences in spatial memory performance across conditions. Participants were slightly more accurate when the choice probe location matched the memory cue location (74% vs. 72%), but this difference was not significant ( $t < 1$ ). Memory performance improved as the distance between the memory probe and the memorized location increased (37%, 66% and 81%, for the 0.7°, 1.1° and 1.5° displacements, respectively,  $F(2, 20) = 67.46, p < .001$ ).

#### 3.2.3. Choice probe responses

The mean correct RTs to the choice probe are presented in the right panel of Fig. 2. To examine whether spatial working memory enhances processing at the memorized locations, we conducted a two-way repeated measures analysis of variance (ANOVA) on correct RT to the choice probe with choice probe delay (1000 or 2000 ms) and choice probe location (same as the memory cue or different) as factors. There was no main effect of choice probe location ( $F(1, 10) = 1.21, p = .3$ ) or choice probe delay ( $F(1, 10) = 2.90, p = .12$ ). Importantly, the interaction between the choice probe location and choice probe delay was significant ( $F(1, 10) = 16.24, p < .005$ ). While participants were not significantly faster to respond to the choice probe appearing at the memorized location at 1000 ms ( $t(10) = 1.0, p = .34$ ), they were slower to respond to it at 2000 ms ( $t(10) = 2.47, p < .05$ ). Participants made very few errors in discriminating the choice probe shape (3%). ANOVA on error rates showed no significant main effects or interaction.

### 3.3. Discussion

The present results indicate that keeping a location in memory was responsible for inhibition of processing at the memorized location. Although the memorized location was cued endogenously, inhibition was found at the longer delays during the retention interval. This result is inconsistent with the attention-based rehearsal hypothesis, which postulates that attention has to be maintained at the memorized location throughout the retention interval. Similar to Experiment 1, inhibition was not present at the early delay; however, a trend for facilitation of processing was observed instead. Perhaps, attention plays a role in encoding the location in memory, but is not necessary for maintenance of spatial information in working memory.

One could argue that there are important differences between the task used in Experiments 1 and 2 and the findings reported by Awh et al. (1998) that could account for the discrepancy in the results. First of all, we might have not used enough locations for presenting memory targets. In our experiments there were 48 possible locations, while 108 locations were used in the original study. Although 48 locations should be sufficient to prevent verbal coding (for example, only six possible locations were used by Jha, 2002), perhaps subjects did in fact stop active rehearsal of the memory location during the final part of the trial because they

have learned all the possible locations. Second, when the intervening choice probe did not appear at the memorized location, it was always presented at the same eccentricity as the memory cue (i.e., on the same circle and equivalent position, but in a different quadrant). This means that the four possible positions of the choice stimulus were always defined by a perfect rectangle that had the memorized location at one vertex. If this predictive relationship were noticed, subjects would have had direct motivation to attend the imaginary rectangle that defined the possible positions of the choice stimulus, and this could have had an effect on the degree to which a sharp focus was maintained on rehearsing the memory position throughout the delay period. These discrepancies in design were eliminated in Experiment 3.

## 4. Experiment 3

Experiment 3 replicated Experiment 2 in using endogenous cueing of memory location, but used exactly the same number of possible memory locations and the same procedure for creating a more random-looking distribution of possible non-matching choice probe locations as was used by Awh et al. (1998). The rest of their design was also replicated, except that allocation of attention was also measured earlier in the retention interval (500 ms instead of 1500 ms). If differences in design were responsible for inhibition found in the previous experiments, then in the present experiment facilitation of processing at the memorized location should be found during the whole retention interval.

### 4.1. Method

#### 4.1.1. Participants

Fifteen students from the Vrije Universiteit Amsterdam were paid to participate in a 1 h session. Their age varied between 17 and 24, with a mean age of 21. They all had normal or corrected to normal visual acuity and normal color vision.

#### 4.1.2. Stimuli, design, procedure

As in Experiment 2, the endogenous memory cue was used, but the rest of the experiment (except for an earlier choice probe delay) was an exact replication of Experiment 1 of Awh et al. (1998). There were 108 possible memory cue locations, with 36 equally spaced locations (each 0.5° in diameter) on each of the three imaginary circles. As in Experiment 2, all possible locations on the circle were presented at once and a central arrow cue pointed directly at the location to be kept in memory (see Fig. 3).

The retention interval was increased to 5000 ms, during which a choice probe (1 × 1°) was presented for 1000 ms. The choice probe was equally likely to occur 500, 2500, or 3500 ms after the offset of the location cues. The choice probe appeared at the memorized location on 25% of all trials. When the choice probe appeared at a different location, it appeared either at 4.8°, 6.6°, or 8.2° away from the memorized location (on the inner, middle and outer circles, respectively). At the end of the retention interval, a memory probe (physically identical to a single location cue) was presented with equal probability either at the same memorized location or at a different location (randomly chosen to be 0.7°, 2° or 2.7° away from the memorized location). The memory probe was identical to a single location cue.

Participants first received a block of 24 trials with memory task alone (no choice probe was presented). It was followed by another practice block of a dual-task (24 trials), in which participants were instructed to give the highest priority to the memory task. Practice blocks were followed by eight experimental dual-task blocks (36 trials each), the total of 288 trials. The 288 dual-task trials consisted of 72 trials on which the choice probe location matched

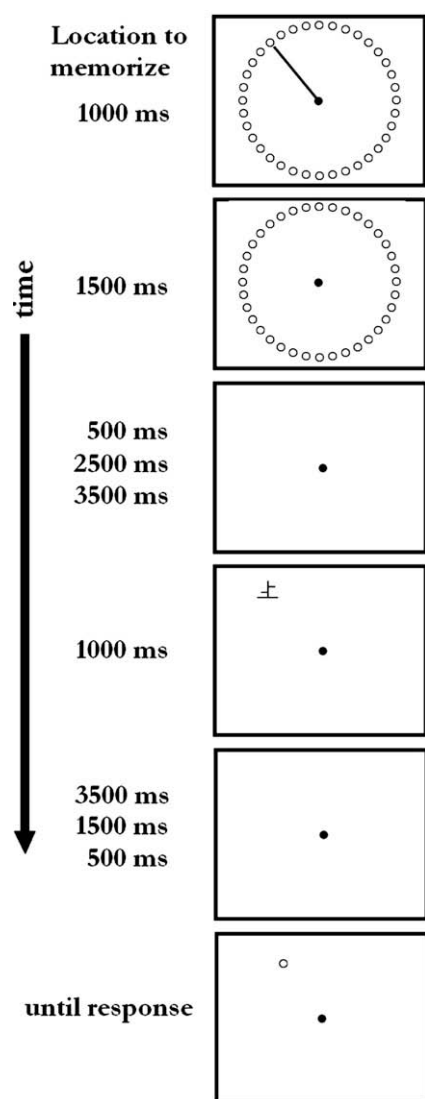


Fig. 3. Examples of the displays used in Experiment 3, in which there were 108 possible locations for the endogenous memory cue.

the memory cue location (24 for each delay, 8 per circle) and 216 on which it did not (72 for each delay, 24 per circle).

## 4.2. Results

### 4.2.1. Discarded data

Trials on which participants made eye movements greater than  $1^\circ$  of visual angle from the central fixation were discarded from further analyses. On average, participants made saccades in the direction of the memory cue on 4% of all trials and saccades to the choice probe on 6% of the trials. Trials in which participants responded to the choice probe faster than 150 ms or slower than 950 ms were excluded from the analysis. This led to a loss of 5% of the trials.

### 4.2.2. Memory performance

On average, participants were quite accurate in the memory task (80%). There were no significant differences in spatial memory performance across conditions. Participants were not more accurate when the choice probe location matched the memory cue location (80% vs. 79%,  $t < 1$ ). Memory performance improved as the distance between the memory probe and the memorized loca-

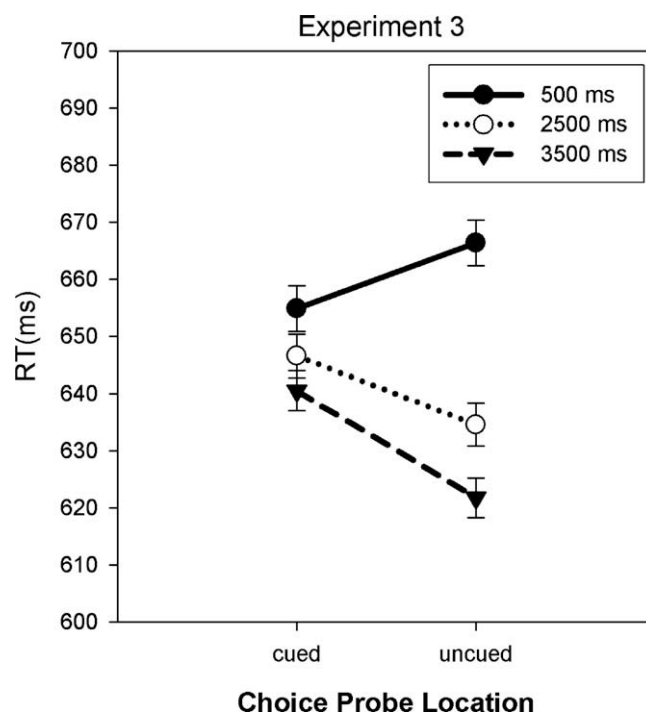


Fig. 4. Mean correct reaction times in Experiment 3 as a function of choice probe location and delay.

tion increased (33%, 88% and 94%, for the  $0.7^\circ$ ,  $2^\circ$  and  $2.7^\circ$  displacements, respectively,  $F(2, 28) = 237.27$ ,  $p < .001$ ).

### 4.2.3. Choice probe responses

The mean correct RTs to the choice probe are presented in Fig. 4. To examine whether spatial working memory enhances processing at the memorized locations, we conducted a two-way repeated measures analysis of variance (ANOVA) on correct RT to the choice probe with choice probe delay (500, 2500, or 3500 ms) and choice probe location (same as the memory cue or different) as factors.

Participants responded faster when the choice probe delay was longer ( $F(2, 28) = 19.56$ ,  $p < .001$ ). There was no main effect of choice probe location ( $F(1, 14) = 1.89$ ,  $p = .19$ ). Importantly, the interaction between the choice probe location and choice probe delay was significant ( $F(2, 28) = 4.80$ ,  $p < .05$ ), suggesting that inhibition of memorized location emerged later in the retention interval. Posthoc comparisons showed that while participants were not significantly faster to respond to the choice probe appearing at the memorized location at 500 ms ( $t(14) = 1.44$ ,  $p = .17$ ), they tended to respond to it slower at 2500 ms ( $t(14) = 1.59$ ,  $p = .14$ ) and significantly slower at 3500 ms ( $t(14) = 2.69$ ,  $p < .05$ ). Participants made very few errors in discriminating the choice probe shape (6%). ANOVA on error rates showed no significant main effects or interaction.

## 4.3. Discussion

The present results are clear. Even though we used the exact design of Awh et al. (1998), inhibition of processing was found at the memorized location at the later stages of the retention interval. As in Experiment 2, no significant facilitation of processing was found at the earlier stage of the retention interval even though the processing at the memorized location was probed even earlier (500 ms)<sup>1</sup>. Altogether the results of Experiments 1–3 suggest that attention is not maintained at the memorized location throughout

<sup>1</sup> We expect that shortening of the choice probe delay would eventually lead to finding facilitation of visual processing at the memorized location.

the retention interval. It appears that attention is allocated to the memorized location only very early in the retention interval (before 500 ms). Importantly, maintaining a location in memory produces long-lasting inhibition of processing at that location.

However, from the experiments conducted so far it is not clear whether the lack of attention at the memorized location had significant consequences for maintenance of memory representations. As mentioned in the introduction, Awh et al. (1998) have also found that memory accuracy was significantly worse when attention was directed away from the memorized location. One could argue that finding evidence that attention is not oriented during a specific part of the delay period does not rule out the possibility that there were real costs to this lack of focused attention at the memory location. Following this logic, if memory is supported by spatial attention in the current experiments, then the apparent absence of attentional orienting in the later part of the delay period should lead to worse performance than in a condition where attention is maintained at the memorized location during that period. Note, however, that in Experiments 1–3 memory performance was uniformly high, independently of whether the probes were presented early or late in the retention interval. Experiment 4 examined the functional role of attention for the accurate memory performance in detail.

#### 5. Experiment 4

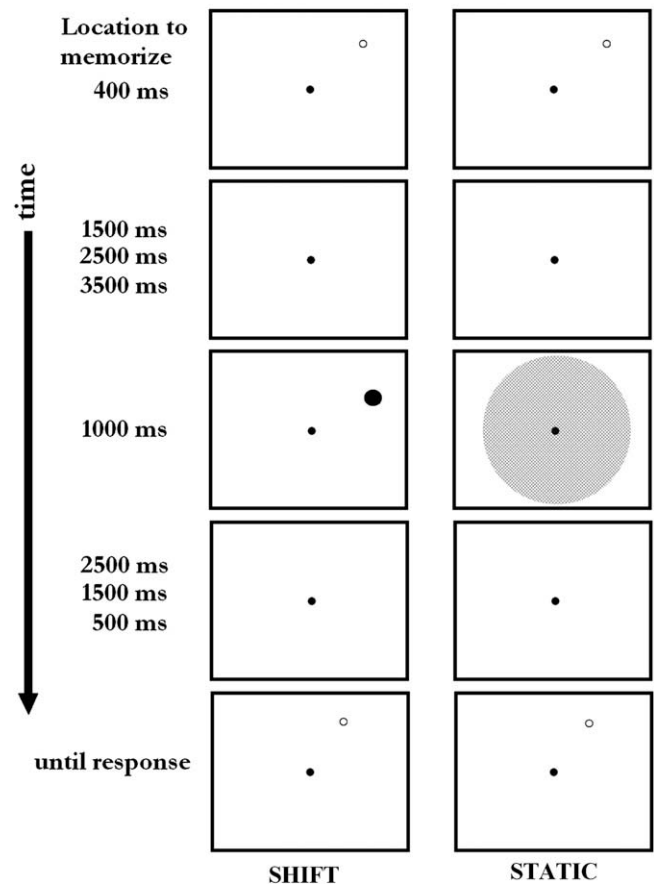
The goal of this experiment was to examine whether sustained attention shifts are necessary for maintaining locations in working memory. The experiment was modeled closely after Experiment 3 of Awh et al. (1998). In one condition, participants had to shift their attention away from the memorized location during the retention interval in order to detect a small color probe. In another condition a large color probe was presented and shifts of attention were not necessary for color discrimination. Since attention could not be maintained at the memorized location during shifts of attention, this should lead to significant impairments in memory performance in the condition which required such shifts. However, if attention is not crucial for maintenance of spatial information, then no significant impairments should be found. In the original study, small color probes were presented at randomly selected locations, which made it impossible to determine whether the processing at the memorized location was enhanced or inhibited. In the present experiment the color probes were presented either close or far from the memorized location. If the memorized location is inhibited, then the probes falling close to the memorized location should be discriminated slower than probes falling at the far locations.

##### 5.1. Participants

Eight students from the Vrije Universiteit Amsterdam were paid to participate in two sessions (2.5 h total). Their age varied between 18 and 33, with a mean age of 23. They all had normal or corrected to normal visual acuity and normal color vision.

##### 5.2. Stimuli, design, procedure

As in the previous experiments, participants needed to memorize the location of the memory cue and to respond to the choice probe. The possible memory locations and choice probe locations were the same as in Experiment 3. The exogenous memory cue (unfilled circle of  $0.5^\circ$ ) was presented for 400 ms and the choice probe was equally likely to occur 1500, 2500 or 3500 ms after the offset of the memory cue (Fig. 5). In the shifting-attention condition, the choice probe was a small color circle ( $1^\circ$ ), which could be either blue (CIE: 0.158/0.082) and purple (CIE: 0.363/0.199) or red (CIE: 0.590/0.337) and pink (CIE: 0.270/0.140). Importantly,



**Fig. 5.** Examples of the displays used in Experiment 4. In the shift-attention condition participants had to discriminate the color of a small choice probe during the retention interval. The probe could appear either near or far from the memorized location. In the static-attention condition participants had to discriminate the color of a large choice probe.

the small circle was equally likely to occur either near ( $\pm 20^\circ$ ) or far ( $\pm 90^\circ$ ) from the memorized location (clockwise and counter-clockwise), but never at the memorized location. In the static-attention condition, the choice probe was a large color circle ( $8.6^\circ$ ), which could be either two different shades of blue (CIE: 0.151/0.068 or CIE: 0.156/0.071) or two different shades of red (CIE: 0.612/0.345 or CIE: 0.577/0.314). There were also two control conditions: the shifting-control and the static-control. They were identical to their experimental counterparts, except that no responses to the choice probes were required.

Attention and control conditions had different color pairs to prevent participants from responding in the control conditions to the color previously responded to in the attention condition. Four participants received blue and purple stimuli in the shifting-attention condition, shades of blue stimuli in the static-attention condition, red and pink in the shifting-control condition and shades of red in the static-control condition. The color pairs were exchanged between the attention and control conditions for the other four participants.

Attention and control conditions were run in two separate sessions. The order of the sessions and the order of shifting and static conditions were counterbalanced across participants. In the experimental session, before each attention condition, responses to the choice probes were practiced in four blocks (36 trials each) with only choice probe presented (i.e. shifting-alone or static-alone). The discrimination of colors was designed to be easier for the shifting-alone task than for the static-alone task. Therefore, if a greater decrement in the memory task is found in the shifting-attention

than in the static-attention condition, it could not be explained by a difference in the general task difficulty between these tasks. In addition, a response deadline based on 1.5 times the mean reaction time in practice blocks was imposed for the attention conditions (a tone sounded during the dual-task when the deadline was not met or when participants made a mistake). The deadline was used to encourage participants to allocate similar amount of resources in the dual-task conditions as in the single task. This was important in order to observe the possible decrements in memory performance in the dual-task. One block of memory-alone practice and a dual-task practice block followed the first set of practice-alone blocks. The second set of practice-alone blocks was directly followed by one dual-task practice block. Dual-task practice blocks were followed by four dual-task blocks (36 trials each) of the respective attention condition. In the shifting-attention condition, the 144 dual-task trials consisted of 72 trials on which the choice probe location occurred near the memory cue location (24 for each delay, 8 per circle) and 216 on which it occurred far from the memory cue location (72 for each delay, 24 per circle). The control session started with one block of memory-alone practice. Before each control condition, one control practice block was presented. Each control condition consisted of four blocks of 36 trials. All practice blocks in the experiment (except practice-alone blocks) consisted of 24 trials.

Participants were told that the choice probe task was the primary task and instructed to match their performance in the dual-task trials to the practice-alone trials. They were also told to be as accurate as possible in the memory task. On each trial, participants also received auditory feedback for errors in memory recognition or choice probe discrimination, as well as when they made eye movements.

### 5.3. Results

#### 5.3.1. Discarded data

Trials on which participants made eye movements greater than 1° of visual angle from the central fixation were discarded from further analyses. In both shifting- and static-attention conditions, on average, participants made saccades in the direction of the memory cue on 1.5% of all trials and saccades to the choice probe on 2% of the trials. Trials in which participants responded to the choice probe faster than 150 ms or slower than 950 ms were excluded from the analysis. This led to a loss of 4% of the trials.

#### 5.3.2. Memory performance

Two-way repeated measures ANOVA with probe (shift or static) and task (single or dual) showed no significant main effects or interaction (all  $F_s < 1$ ). There was no difference in memory accuracy across shifting-attention and static-attention conditions ( $t(7) = 0.12$ ,  $p = .90$ , both 78%). Therefore, contrary to the attention-based rehearsal hypothesis, shifting attention away from the memorized location during the retention interval did not impair the memory performance. It is possible, however, that in the shifting-attention condition, probe discrimination was possible without shifting of attention in the cases when the probe occurred near the memorized location. To test for this possibility, the memory performance was calculated separately for the near and far intervening small probes. There was no difference between the memory accuracy when the probe occurred near or far from the memorized location (77% vs. 79%, respectively,  $t(7) = 0.7$ ,  $p = .5$ ). Furthermore, the memory accuracy in both near small probe condition and far small probe condition was not different from the memory performance in the static-attention condition (78%;  $t(7) = 0.27$ ,  $p = .79$ ;  $t(7) = 0.66$ ,  $p = .53$ , respectively).

In addition, discrimination of the small color probe led only to 1% decline in memory accuracy, relative to the shifting-control

condition (79%,  $t < 1$ ). Discrimination of the large color probe led to 2% decline in memory accuracy, relative to the static-control condition (80%,  $t = 1.42$ ,  $p = .19$ ).

#### 5.3.3. Choice probe responses

During practice, participants were faster discriminating the small color probes (547 ms) than the large color probes (587 ms,  $t(7) = 2.7$ ,  $p < .05$ ), indicating that our manipulation to make the discrimination of the large color probes more difficult was successful. There was no difference in accuracy between these two conditions (93% and 90%, respectively,  $t(7) = 1.63$ ,  $p = .15$ ). Color discrimination performance was also not significantly different between the small color probes (91%) and the large color probes (93%) when participants had to carry out a concurrent memory task during the experiment ( $t(7) = 2.29$ ,  $p = .06$ ).

The mean correct RTs to the choice probe in the shifting-attention condition are presented in Fig. 6. To examine whether spatial working memory enhances processing at the memorized locations, we conducted a two-way repeated measures analysis of variance (ANOVA) on correct RT to the choice probe with probe delay (1500, 2500, or 3500 ms) and choice probe location (near or far to the memory cue) as factors. Participants responded faster when the choice probe delay was longer ( $F(2, 14) = 12.31$ ,  $p < .005$ ). Importantly, participants responded slower when choice probes were presented near the memorized location compared to when they were presented far away ( $F(1, 7) = 8.71$ ,  $p < .05$ ). The interaction between probe location and probe delay was not significant ( $F < 1$ ). As mentioned above, participants were quite accurate in responding to the probe in the shifting-attention condition (91%). No main effects or interactions were significant ( $F < 1$ ).

#### 5.3.4. Discussion

The present findings clearly demonstrate that memory performance was not impaired when participants were required to shift their attention away from the memorized location during the retention interval. The memory accuracy was not affected whether participants had to shift attention near or far from the memorized

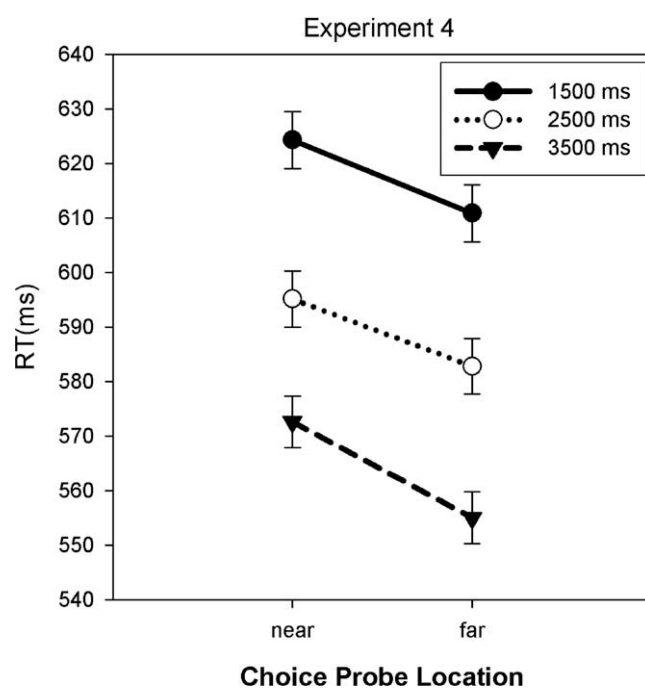


Fig. 6. Mean correct reaction times in the shift-attention condition of Experiment 4 as a function of choice probe location (near or far from the memorized location) and delay.

location or not to shift their attention at all. In addition, maintenance of a spatial location in working memory was also not affected compared to the respective control conditions, in which no intervening task had to be performed during the retention interval. Altogether these results suggest that maintenance of spatial information in working memory can occur without a sustained shift of attention at the memorized location.

The present results contrast results of the analogous experiment of Awh and colleagues (Experiment 3, 1998), who showed that shifts of attention drastically interfered with the maintenance of spatial working memory (memory accuracy impairment of 12%). One possibility is that the color probe discrimination task in our experiment was not working in the same manner since it did not produce any dual-task costs in memory accuracy in either small or large color probe conditions, while it did produce such costs in the experiment of Awh and colleagues. However, a more obvious reason for such a discrepancy from our results is that in the experiment of Awh and colleagues participants were making a lot of eye movements (p. 787, Awh et al., 1998). Importantly, participants made more eye movements in the experimental dual-task conditions (shifting-attention – 25% and static-attention – 24%) than in the control single-task conditions (shifting-control – 17% and static-control – 16%). Several previous studies (Baddeley & Lieberman, 1980; Lawrence, Myerson, & Abrams, 2004; Lawrence, Myerson, Oonk, & Abrams, 2001) have shown that eye movements made during the retention period significantly interfere with spatial working memory, much more than the shifts of spatial attention. This may explain the large dual-task cost in working memory performance in the experiments of Awh and colleagues, but not in our experiment, in which eye movements were closely monitored.

The design of our experiment also allowed examining the nature of attentional processing at the memorized location. Consistent to the Experiments 1–3, inhibition of the memorized location was revealed throughout the retention interval, since the probes that fell close to memorized location were discriminated slower than the probes presented far from the memorized location. The presence of inhibition during the retention interval suggests its potential importance for memory maintenance.

Alternatively, finding inhibition of processing near the memorized location is also consistent with findings, showing that spatial attention is characterized by enhanced sensory processing at the focus of attention, but that this focus is surrounded by a suppressive region. (for example, Hopf et al., 2006). This explanation cannot be directly ruled out in Experiment 4, since the probes never occurred at the memorized location. However, based on Experiments 1–3 (see also Experiment 5B) in the present paper that used a very similar design but probed the memorized location, we can conclude that inhibition can also be observed at the memorized location.

In Experiments 1–4, we have consistently found inhibition of processing at the memorized location, while the previous studies that used similar paradigms have reported facilitation (Awh et al., 1999; Jha, 2002). How can such discrepancies in results be explained? One possibility is that maintenance of attention at the memorized location was in fact disrupted by intervening and frequently occurring probe discrimination task. The probe task occurred on every trial and the probe could appear at the memorized location only 25% of the time. Therefore, participants could have learned that the probe is highly unlikely to appear at the memorized location and stopped attention rehearsal (without any significant memory impairment). This hypothesis was examined in Experiment 5.

## 6. Experiment 5

Experiment 5 examined the influence of frequency of the intervening attentional shifts during the retention interval on processing at the memorized location. Again, we replicated the task used

in Experiment 1 of Awh et al. (1998). However, we increased the probability of the choice probe occurring at the memorized location to 50% (as was used in Jha, 2002). This manipulation should have increased attentional rehearsal on every trial, since attention did not need to be withdrawn from the memorized location on every trial. In addition, in Experiment 5A, the probe occurred on every trial, while in Experiment 5B, the probe occurred only on half of the trials. The latter manipulation made the necessity of shifting attention away from the memorized location even more unpredictable. If the probability of shifting attention away from the memorized location affects the maintenance of attention at the memorized location, then in the present experiment attentional rehearsal should not be stopped as frequently as in the previous experiments. Since overall probability of shifting attention away from the memorized location was lower in Experiment 5B than in Experiment 5A, larger facilitation effects were expected in the former experiment. Note that according to the attention-based rehearsal hypothesis, attention is allocated to the memorized location in service of the memory task and should not be affected by the probability manipulation without an accompanying drop in memory accuracy.

### 6.1. Method

#### 6.1.1. Participants

Twenty-two volunteers from the Vrije Universiteit Amsterdam were paid to participate in a 1 h session. Their age varied between 18 and 27, with a mean age of 21. They all had normal or corrected to normal visual acuity and normal color vision. Eight participants were randomly assigned to Experiment 5A and the other fourteen were assigned to Experiment 5B. Three participants in Experiment 5B had to be replaced due to large number of errors in the probe discrimination task (>14%).

#### 6.1.2. Stimuli, design, procedure

The experiment was very similar to Experiment 3, except that as in the original experiment by Awh et al. (1998), an exogenous memory cue was used and choice probe delays were 1500, 2500 and 3500 ms. In addition, the memory task was made slightly more difficult, with the non-matching memory probe presented closer (0.5°, 1.2° or 2°) to the memorized location. In both experiments, the choice probe occurred at the memorized location with 50% probability. In Experiment 5A, the choice probe was presented on every trial, while in Experiment 5B its presentation was less predictable, since it occurred only on half of the trials.

### 6.2. Results

#### 6.2.1. Discarded data

Trials on which participants made eye movements greater than 1° of visual angle from the central fixation were discarded from further analyses. In Experiment 5A, on average, participants made saccades in the direction of the memory cue on 16% of all trials and saccades to the choice probe stimulus on 3% of the trials. In Experiment 5B, on average, participants made saccades in the direction of the memory cue on 8% of all trials and saccades to the choice probe on 2% of the trials. Trials in which participants responded to the choice probe faster than 150 ms or slower than 950 ms were excluded from the analysis. This led to a loss of 3.5% of the trials.

### 6.3. Experiment 5A

#### 6.3.1. Memory performance

On average, participants were quite accurate in the memory task (71%). There were no significant differences in spatial memory performance across conditions. There was a trend for participants

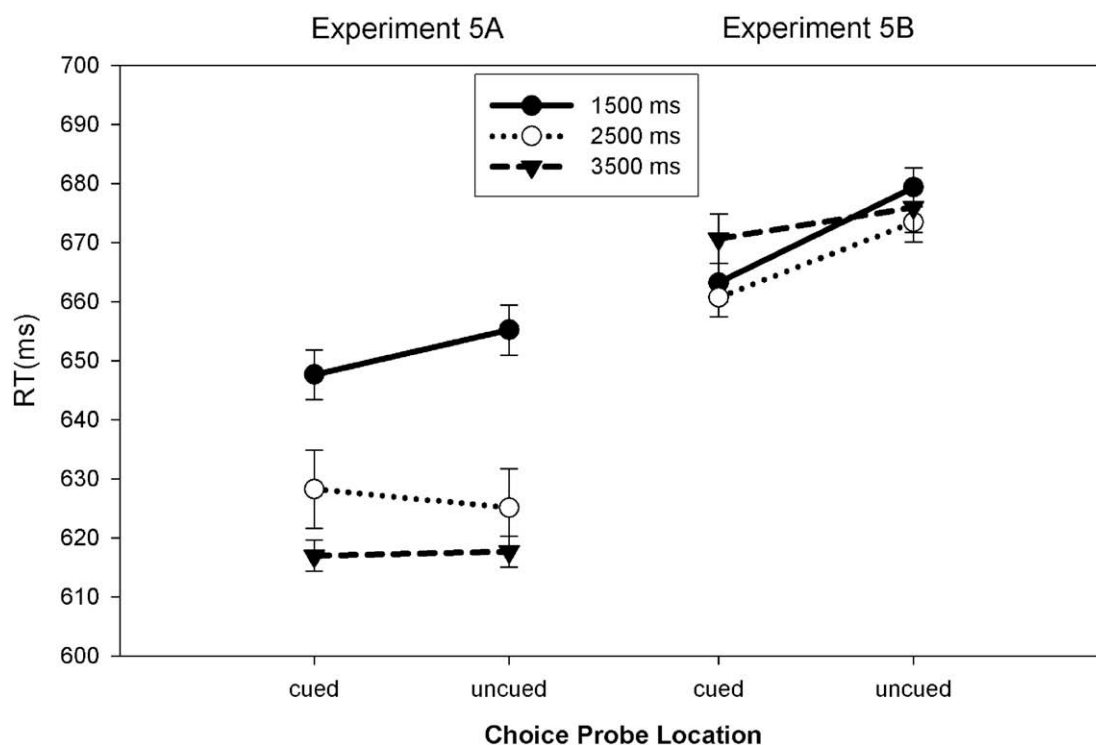


Fig. 7. Mean correct reaction times in Experiment 5 as a function of choice probe location and delay.

to be more accurate when the choice probe location matched the memory cue location (74% vs. 68%); however, it was not significant ( $t(7) = 1.5, p = .19$ ). Memory performance improved as the distance between the memory probe and the memorized location increased (34%, 64% and 86%, for the 0.5°, 1.2° and 2° displacements, respectively,  $F(2, 14) = 74.32, p < .001$ ).

#### 6.3.2. Choice probe responses

The mean correct RTs to the choice probe are presented in the left panel of Fig. 7. To examine whether spatial working memory enhances processing at the memorized locations, we conducted a two-way repeated measures analysis of variance (ANOVA) on correct RT to the choice probe with choice probe delay (1500, 2500, or 3500 ms) and choice probe location (same as the memory cue or different) as factors. Participants responded faster when the choice probe delay was longer ( $F(2, 14) = 7.18, p < .01$ ). The effect of choice probe location and the interaction was not significant ( $F < 1$ ). Participants made very few errors in discriminating the choice probe shape (5%). ANOVA on error rates showed no significant main effects or interaction.

#### 6.4. Experiment 5B

##### 6.4.1. Memory performance

On average, participants were quite accurate in the memory task (72%). There were no significant differences in spatial memory performance across conditions. There was a trend for participants to be more accurate when the choice probe location matched the memory cue location (73% vs. 71%); however, it was not significant ( $t(13) = 1.0, p = .32$ ). Memory performance improved as the distance between the memory probe and the memorized location increased (35%, 74% and 91%, for the 0.5°, 1.2° and 2° displacements, respectively,  $F(2, 26) = 292.17, p < .001$ ).

##### 6.4.2. Choice probe responses

The mean correct RTs to the choice probe are presented in the right panel of Fig. 7. To examine whether spatial working memory

enhances processing at the memorized locations, we conducted a two-way repeated measures analysis of variance (ANOVA) on correct RT to the choice probe with choice probe delay (1500, 2500, or 3500 ms) and choice probe location (same as the memory cue or different) as factors. There was only a main effect of choice probe location, indicating that participants responded faster when the choice probe occurred at the memorized location ( $F(1, 13) = 5.92, p < .05$ ). The effect of probe delay and the interaction was not significant ( $F < 1$ ).<sup>2</sup> Participants made very few errors in discriminating the choice probe shape (8%). ANOVA on error rates showed no significant main effects or interaction.

##### 6.4.3. Discussion

The present results clearly indicate that allocating attention to the memorized location is affected by the probability of shifting attention away from the memorized location. When the choice probe was presented on every trial in Experiment 5A, neither facilitation nor inhibition of processing was observed during the retention interval. This suggests that attention was maintained at the memorized location on some trials and was withdrawn from it on other trials. However, when the necessity to shift attention away from the memorized location was made even more unpredictable in Experiment 5B, facilitation of processing was found throughout the retention interval. Note that unpredictability of the choice probe in Experiment 5B was also reflected in the absence of the effect of the choice probe delay. This effect was present in all previous experiments. Importantly, there was no difference in memory performance between Experiment 5A and 5B (71 and 72% for Experiment 5A and 5B, respectively,  $F < 1$ ), suggesting that facilitation of processing at the memorized location is not accompanied by improvement in memory performance.

<sup>2</sup> In all experiments in the paper, the pattern and magnitude of probe discrimination results did not change significantly when trials with incorrect memory responses were removed from the analysis. Despite a reduction in the number of trials, all inhibitory effects were still significant. The facilitation effect in Experiment 5B was marginally significant ( $F(1, 13) = 3.20, p = .1$ ).

## 7. General discussion

The findings reported here provide new insights into mechanisms involved in maintenance of spatial working memory. From the results it is clear that spatial working memory is not supported by a sustained facilitation mechanism, as suggested by the attention-based rehearsal hypothesis (Awh et al., 1998). Despite replicating the design of previous studies, we have consistently demonstrated inhibition of processing at the memorized location, which is similar to the findings from studies using memory-guided saccade tasks (Krishna et al., 2006; Ostendorf et al., 2004). These studies have proposed that the inhibitory processing was caused either by explicit preparation and inhibition of saccade towards the memorized location (Ostendorf et al., 2004; Rafal et al., 1989) or by IOR elicited by the exogenous memory cue (Krishna et al., 2006). Importantly, in our series of experiments, we have demonstrated that neither mechanism could be responsible for the inhibitory effect. First, in all of our experiments, participants were instructed to maintain fixation and never had to plan or execute saccades. Second, in Experiments 1–3, we demonstrated that keeping a location in memory triggered a shift of attention to the memorized location. Early in the retention interval, this attentional shift reduced IOR elicited by the exogenous memory cue in Experiment 1 and was probably responsible for a trend for facilitation of processing found in Experiments 2 and 3. However, at the later stages of the retention interval, even when memory location was cued in endogenous way (Experiments 2 and 3), we have consistently found inhibition of visual processing at the memorized location. Finding inhibition and not facilitation of processing at the memorized location is inconsistent with the first tenet of the attention-based rehearsal hypothesis.

Experiment 4 examined the second tenet of the attention-based rehearsal hypothesis concerning causal relationship between sustained attentional shift and successful memory maintenance. It was demonstrated that lack of attention at the memorized location does not result in a significant deficit in memory maintenance. When participants were required to shift their attention away from the memorized location during memory maintenance, memory performance was not impaired relatively to when such shifts were not required. Importantly, simultaneous measurement of processing at the memorized location indicated that it was inhibited throughout the most of the retention interval. Perhaps, inhibition reflects an operation of a mechanism for maintenance of the memory representation and the presence of attention reported in some of previous studies reflects an epiphenomenon produced by aspects of task design or strategies of the observer.

Experiment 5 demonstrated that sustained facilitation effects can be obtained under certain task conditions. In particular, predictability of the intervening task during the retention interval seemed to play a crucial role. When the intervening task was made unpredictable by presenting the choice probe only on half of the trials, facilitation of processing was obtained throughout the retention interval. Note that in the original study (Awh et al., 1998), facilitation of processing was observed even when the choice probe was presented on every trial. However, in the present study when the choice occurred on every trial, we have consistently found inhibition of processing at the memorized location even when all of the design aspects of the original study (Awh et al., 1998) were replicated.

The finding of facilitation of processing in Experiment 5 can shed light on why facilitation of processing was reported in the previous studies that used electrophysiological methods (Awh et al., 2000; Jha, 2002). In these studies, there was no intervening task, and event-related potentials (ERPs) were time-locked either to changes in the background (Awh et al., 2000) or to an

irrelevant and unpredictable probe (Jha, 2002). Critically, Experiment 5 showed that facilitation of processing did not result in any increase in memory accuracy, which would be expected if attention was functionally involved in maintenance of memory representations.

Taken together, the present experiments suggest that spatial working memory requires a shift of attention to the memorized location and initial maintenance of attention at that location, perhaps for encoding its coordinates into working memory. If the probability that attention is drawn away during the retention interval is low, then attention would remain focused at the memorized location “by default”. If such probability is high then attention is withdrawn from the memorized location without any negative consequence for memory performance.

Importantly, our results showed that location information was not lost when attention was withdrawn from the memorized location. Instead, visual processing at that location was inhibited. What can be the source of this inhibition? In a recent study (Belopolsky & Theeuwes, submitted for publication), we showed that the oculomotor system is typically activated when attention has to be maintained at a certain location. However, when the probability of making an eye movement to that location is very low the oculomotor program is suppressed, while the visual processing is still enhanced. Similarly, another recent study (Belopolsky & Theeuwes, 2009) demonstrated that saccades to the memorized location were inhibited in a delayed match to sample task, in which participants were never instructed to make a saccade in response to the memory cue and the intervening saccade task occurred unpredictably (as in Experiment 5B). Such inhibition of an implicit saccade program could be the source of inhibition of visual processing of the memorized location observed in the present set of experiments.

A similar idea of oculomotor suppression was proposed by Berlucchi et al. (2000), Tassinari, Aglioti, Chelazzi, Marzi, and Berlucchi (1987) as an explanation for the phenomenon of IOR. They suggested that RT inhibition at the exogenously cued location (e.g. IOR) is caused by “suppression of a natural ocular reaction toward a lateralized cue in order to maintain fixation” (Berlucchi, 2006). Instruction to memorize a location might also require suppression of a natural tendency to make an eye movement to that location, especially if saccade towards that location is never required or at least not required on the majority of trials. Endogenous attention that can be allocated to the memorized location in some situations (as in Experiment 5B) might overshadow the inhibitory effect and result in an overall facilitation of processing. Such co-existence of endogenous and exogenous attention has been proposed in studies that showed that endogenous attention cannot override IOR caused by an exogenous cue (Berger et al., 2005; Berlucchi et al., 2000; Lupianez et al., 2004). It appears that keeping a location in memory is also capable of engaging the memorized location in the oculomotor system, but this location is inhibited if the probability of executing the saccade program is low.

In fact, recent studies by Theeuwes, Olivers, and Chizk (2005), Theeuwes et al. (2006) demonstrated a close link between spatial working memory and the oculomotor system. They showed that keeping a location in memory causes saccade trajectories to deviate away from that location, just like saccades deviate from the visually presented stimuli that need to be ignored (Sheliga, Riggio, & Rizzolatti, 1994). It was proposed that spatial working memory entailed sustained endogenous activation in the oculomotor system that had to be inhibited in order for an eye movement in a different direction to be made. Given a tight coupling between attention and eye movements (Hoffman & Subramaniam, 1995), it is quite feasible that when participants keep a location in space active in working memory, the act of directing spatial attention to

that location results in oculomotor activity. In other words, the oculomotor system is used to code and maintain location information in memory (Theeuwes et al., 2005).

From the present results, it appears that keeping a location in working memory is accompanied by either facilitation or inhibition of visual processing depending on the task demands. 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. One could assume that both attentional and oculomotor codes could be used for maintenance of working memory representations and the choice of the most appropriate code to use depends on the context of the memory task. Such an assumption is viable, although it represents a less parsimonious solution comparing to the assumption of a general coding mechanism responsible for the maintenance of spatial working memory representations. In all of the experiments reported here eye movements were discouraged and participants should have been inclined to use the attentional code. Nevertheless, we have found no significant impairments in memory accuracy when attention was withdrawn from the memorized location, providing evidence against the use of attentional code in the working memory maintenance.

Although from the present results it is clear that inhibition of processing at the memorized location and IOR caused by exogenous orienting of attention are separate phenomena, they might share a similar mechanism, stemming from inhibition of the oculomotor system (Berlucchi, 2006). Interestingly, a close link between spatial working memory and IOR has been suggested by a few researchers (Castel, Pratt, & Craik, 2003; Klein, 2000). IOR has been obtained with multiple sequentially cued locations, as well as at multiple previously examined locations during overt and covert visual search (for review see Klein, 2000). Such maintenance of inhibition at multiple locations has been proposed to involve a spatial working memory component. Even more convincingly, a recent study (Castel et al., 2003) showed that IOR was eliminated when a spatial working memory load was introduced at the fixation, but was still present with non-spatial working memory secondary tasks. Such selective disruption suggested that IOR was also relying on spatial working memory resources (Baddeley, 1986).

To summarize, the results of the present study contradict the attention-based rehearsal hypothesis, which postulates that maintenance of spatial working memory is based entirely on a sustained attentional shift. Keeping a location in memory often resulted in inhibition of processing at the memorized location without a significant impairment in memory accuracy. Even when the previously reported finding of facilitation of processing at the memorized location was replicated, no benefit in memory performance was observed. The results suggest that attention is not necessary for maintenance of information in spatial working memory. We propose that spatial information is maintained in the oculomotor system, which could be either activated or inhibited based on the probability of executing an eye movement to the memorized location.

## Acknowledgements

We thank Guido Peek for his help in data collection. This research was funded by Grants from Human Frontier Science Program (HSFP-RGP39/2005) to Jan Theeuwes.

## References

- Awh, E., Anllo-Vento, L., & Hillyard, S. A. (2000). The role of spatial selective attention in working memory for locations: Evidence from event-related potentials. *Journal of Cognitive Neuroscience*, *12*(5), 840–847.
- Awh, E., Jonides, J., & 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., Vogel, E. K., & Oh, S. H. (2006). Interactions between attention and working memory. *Neuroscience*, *139*(1), 201–208.
- Baddeley, A. D. (1986). *Working memory*. Cambridge, MA: MIT Press.
- Baddeley, A. D., & Lieberman, K. (1980). Spatial working memory. In R. S. Nickerson (Ed.), *Attention and performance* (Vol. VIII, pp. 521–539). Hillsdale, NJ: Lawrence Erlbaum Associates Inc.
- Belopolsky, A. V., & Theeuwes, J. (2009). Inhibition of saccadic eye movements to locations in spatial working memory. *Attention, Perception and Psychophysics*, *71*, 620–631.
- Belopolsky, A. V., & Theeuwes, J. (submitted for publication). When are attention and saccade preparation dissociated?
- Berger, A., Henik, A., & Rafal, R. (2005). Competition between endogenous and exogenous orienting of visual attention. *Journal of Experimental Psychology – General*, *134*(2), 207–221.
- Berlucchi, G. (2006). Inhibition of return: A phenomenon in search of a mechanism and a better name. *Cognitive Neuropsychology*, *23*(7), 1065–1074.
- Berlucchi, G., Chelazzi, L., & Tassinari, G. (2000). Volitional covert orienting to a peripheral cue does not suppress cue-induced inhibition of return. *Journal of Cognitive Neuroscience*, *12*(4), 648–663.
- Castel, A. D., Pratt, J., & Craik, F. I. M. (2003). The role of spatial working memory in inhibition of return: Evidence from divided attention tasks. *Perception and Psychophysics*, *65*(6), 970–981.
- Corbetta, M., Kincade, J. M., & Shulman, G. L. (2002). Neural systems for visual orienting and their relationships to spatial working memory. *Journal of Cognitive Neuroscience*, *14*(3), 508–523.
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception and Psychophysics*, *37*(6), 787–795.
- Hopf, J. M., Boehler, C. N., Luck, S. J., Tsotsos, J. K., Heinze, H., & Schoenfeld, M. A. (2006). Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(4), 1053–1058.
- 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.
- Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, *4*(4), 138–147.
- Krishna, B. S., Steenrod, S. C., Bisley, J. W., Sirotin, Y. B., & Goldberg, M. E. (2006). Reaction times of manual responses to a visual stimulus at the goal of a planned memory-guided saccade in the monkey. *Experimental Brain Research*, *173*(1), 102–114.
- Lawrence, B. M., Myerson, J., & Abrams, R. A. (2004). Interference with spatial working memory: An eye movement is more than a shift of attention. *Psychonomic Bulletin and Review*, *11*(3), 488–494.
- Lawrence, B. M., Myerson, J., Oonk, H. M., & Abrams, R. A. (2001). The effects of eye and limb movements on working memory. *Memory*, *9*(4–6), 433–444.
- Lupianez, J., Decaix, C., Sieroff, E., Chokron, S., Milliken, B., & Bartolomeo, P. (2004). Independent effects of endogenous and exogenous spatial cueing: Inhibition of return at endogenously attended target locations. *Experimental Brain Research*, *159*(4), 447–457.
- Ostendorf, F., Finke, C., & Ploner, C. J. (2004). Inhibition of visual discrimination during a memory-guided saccade task. *Journal of Neurophysiology*, *92*(1), 660–664.
- 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.
- 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.
- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research*, *98*, 507–522.
- Tassinari, G., Aglioti, S., Chelazzi, L., Marzi, C. A., & Berlucchi, G. (1987). Distribution in the visual-field of the costs of voluntarily allocated attention and of the inhibitory aftereffects of covert orienting. *Neuropsychologia*, *25*(1A), 55–71.
- Theeuwes, J., Olivers, C. N. L., & Chizk, C. L. (2005). Remembering a location makes the eyes curve away. *Psychological Science*, *16*(3), 196–199.
- Theeuwes, J., Van der Stigchel, S., & Olivers, C. N. L. (2006). Spatial working memory and inhibition of return. *Psychonomic Bulletin and Review*, *13*(4), 608–613.