



# Oculomotor preparation as a rehearsal mechanism in spatial working memory



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## ARTICLE INFO

### Article history:

Received 20 December 2013

Revised 8 May 2014

Accepted 10 May 2014

### Keywords:

Visual

Spatial

Working memory

Eye movement

Attention

Saccade

## ABSTRACT

There is little consensus regarding the specific processes responsible for encoding, maintenance, and retrieval of information in visuo-spatial working memory (VSWM). One influential theory is that VSWM may involve activation of the eye-movement (oculomotor) system. In this study we experimentally prevented healthy participants from planning or executing saccadic eye-movements during the encoding, maintenance, and retrieval stages of visual and spatial working memory tasks. Participants experienced a significant reduction in spatial memory span only when oculomotor preparation was prevented during encoding or maintenance. In contrast there was no reduction when oculomotor preparation was prevented only during retrieval. These results show that (a) involvement of the oculomotor system is necessary for optimal maintenance of directly-indicated locations in spatial working memory and (b) oculomotor preparation is not necessary during retrieval from spatial working memory. We propose that this study is the first to unambiguously demonstrate that the oculomotor system contributes to the maintenance of spatial locations in working memory independently from the involvement of covert attention.

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## 1. Introduction

An essential cognitive process in human working memory is the ability to temporarily retain and manipulate information concerning the visual and spatial layout of the perceived environment. Examples include remembering the location of words in text (Le Bigot, Passerault, & Thierry, 2009), the comprehension of multimedia displays (Gyselinck, Jamet, & Dubois, 2008), and multiple-object tracking (Allen, McGeorge, Pearson, & Milne, 2006). The cognitive systems responsible for the temporary retention and manipulation of visual and spatial material are collectively referred to as *visuo-spatial working memory* (VSWM). Over the last three decades there have been considerable theoretical and methodological advances in our understanding of

VSWM, but there also remains an on-going debate concerning its precise structure and function (McAfoose & Baune, 2009; Pearson, 2007). Evidence from studies using selective interference paradigms suggest VSWM can be dissociated from verbal working memory (Baddeley, 2003; Repovs & Baddeley, 2006), with a further division made between a visual component focused on retaining object features and a spatial component focused on retaining object properties (Klauer & Zhao, 2004). Evidence suggests both visual and spatial memory can be selectively disrupted by specific concurrent interference tasks (Logie, 2011). For example, exposure to dynamic visual noise disrupts vividness of mental imagery (Baddeley & Andrade, 2000), but not memory for spatial location (Pearson & Sahraie, 2003). Conversely, exposure to tones played from different locations disrupts memory for spatial location, but not vividness of mental imagery (Smyth & Scholey, 1994). Other interference-based studies conducted by Logie and Marchetti (1991), Morris (1989),

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and Tresch, Sinnamon, and Seamon (1993) have shown concurrent spatial tasks interfere with spatial memory to a significantly greater extent than tasks involving the retention of color, static patterns, or form information in visual memory.

However, despite growing insight into the structure of VSWM, there remains little consensus regarding the specific processes responsible for the encoding, maintenance, and retrieval of visual and spatial information in working memory. In particular, the nature of the mechanism responsible for *rehearsal* in VSWM (i.e., maintaining activation of encoded visuo-spatial stimuli prior to retrieval) remains contentious.

One influential theory is that VSWM may involve activation of the eye-movement system (Baddeley, 1986; Belopolsky & Theeuwes, 2009a, 2009b; Postle, Idzikowski, Della Sala, Logie, & Baddeley, 2006; Tremblay, Saint-Aubin, & Jalbert, 2006). Specifically, it is argued that spatial locations are encoded as the goals of potential eye-movements, rehearsed by covertly planning saccades to the to-be-remembered locations, and recalled using saccade plans that guide selection of correct locations during retrieval. Some evidence in favor of this position comes from a series of studies by Pearson and Sahraie (2003), who found saccades executed during a retention interval disrupted spatial memory (as measured by the Corsi Blocks task) to a significantly greater extent than other types of distracter task. Eye-movements to the locations of remembered stimuli have also been reported as often occurring during the recall of spatial information (e.g., Brandt & Stark, 1997; Johansson, Holsanova, Dewhurst, & Holmqvist, 2012; Spivey & Geng, 2001). Further support comes from neuropsychological studies that have demonstrated links between the Frontal Eye Field (FEF) and spatial working memory performance (e.g., Cabeza & Nyberg, 2000; Campana, Cowey, Casco, Oudsen, & Walsh, 2007; Gaymard, Ploner, Rivaud-Pechoux, & Pierrot-Deseilligny, 1999), while experiments in non-human primates suggest activation in oculomotor regions such as FEF signals the location of memorized targets even after they have disappeared (Bruce & Goldberg, 1985; Sommer & Wurtz, 2001).

However, an alternative to the eye-movement theory is that VSWM relies on shifts in *covert spatial attention* (i.e., the ability to shift attention to locations without executing any overt eye movement). For example, Awh and Jonides (2001) and Awh, Jonides, and Reuter-Lorenz (1998) found reaction times were faster when targets appeared at locations held in working memory, and that participants' spatial working memory was disrupted when they were prevented from attending to memorized locations during a retention interval. Furthermore, Godijn and Theeuwes (2012) report that memory for a sequence of locations indicated by numbered peripheral items is unaffected by requiring participants to maintain fixation, in comparison to a condition in which they are free to execute overt eye movements during a retention interval. Conversely, however, Belopolsky and Theeuwes have reported being unable to find evidence that spatial attention interacts with spatial working memory during performance of a match to sample task (2009a).

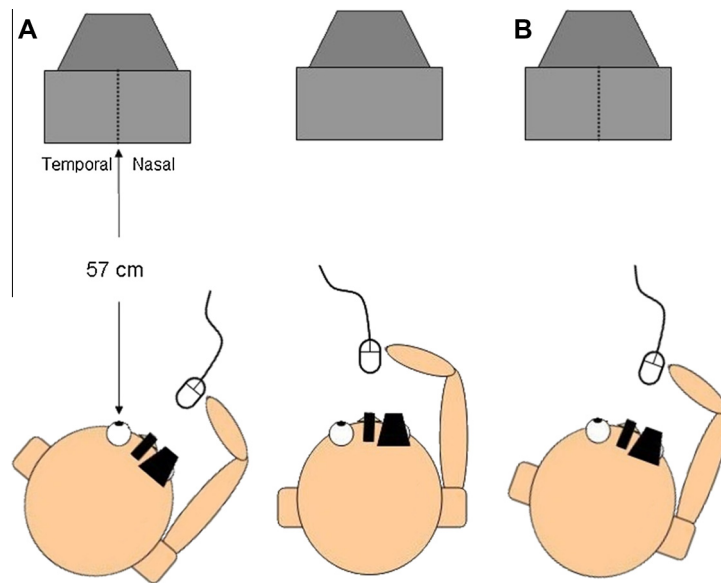
We argue that there are several reasons why previous studies in the literature may have struggled to differentiate

between eye-movement and attention-based mechanisms in VSWM. One major problem has been the apparent lack of any experimental paradigm that can reliably decouple attentional processes from oculomotor control processes in VSWM. This arises because executing an eye-movement necessarily involves a participant also producing a comparable shift of covert attention (Shepherd, Findlay, & Hockey, 1986). Equally, we argue it is insufficient to investigate oculomotor involvement in VSWM by comparing conditions in which participants move their eyes to conditions where their gaze remains fixated (e.g., Godijn & Theeuwes, 2012), as participants may still engage in saccade preparation even without subsequent execution.

An additional limitation of previous studies is that many studies have adopted a selective interference paradigm in which participants are required to produce eye-movements during the rehearsal period of a spatial working memory task (e.g., Guerard, Tremblay, & Saint-Aubin, 2009; Pearson & Sahraie, 2003; Postle et al., 2006). One drawback of this technique is that it only permits investigation of *retention* processes within VSWM, as the execution of incongruent eye-movements during encoding and retrieval stages of a memory task leads to direct concurrent interference with sensory processing of stimuli. A further weakness of dual-task paradigms that require participants to actively produce responses such as eye-movements is that it can become difficult to distinguish selective interference effects from more general attentional interference that results from overall task difficulty (for related discussion, see Pearson & Sawyer, 2011).

One paradigm that addresses these limitations is the *abducted-eye paradigm*, in which oculomotor preparation is prevented by presenting stimuli to a region of participants' visual field that lies beyond their oculomotor range (Craighero, Nascimben, & Fadiga, 2004; Smith, Ball, Ellison, & Schenk, 2010). Crucially, this paradigm allows the role of the oculomotor system in spatial working memory to be examined independently from any confounding effect of saccade preparation on covert attention. Support for this position derives from studies of patients suffering oculomotor deficits which have demonstrated that attention can be covertly oriented to locations that lie beyond the possible range of their eye movements (Gabay, Henik, & Gradstein, 2010; Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988; Smith, Rorden, & Jackson, 2004). Following from this, Smith et al. have previously shown that stimulus-driven shifts of attention are abolished by placing participants in an eye-abducted position, while their volitional attentional orienting remains unimpaired (Smith, Rorden, & Schenk, 2012; Smith, Ball, & Ellison, 2014).

Recently we have used a version of the abducted-eye paradigm to explore oculomotor involvement in spatial working memory (Ball, Pearson, & Smith, 2013). Participants were required to fixate the center of a display while the other eye was patched, and their head and body were then rotated until there was an angle of 40° between their trunk midline and the center of gaze (Fig. 1A). This manipulation meant that while participants could still see everything in the display, they were physically unable to make eye-movements further into the temporal hemifield. While participants were required to maintain central fixation in



**Fig. 1.** Illustration of the experimental setup. Panel A shows the Abducted 40 position and the Frontal position. In Experiment 1 participants began in the abducted position and translated to the frontal position after stimulus presentation. In Experiment 2 participants began in the frontal position and translated to the abduction position during rehearsal and retrieval. In Experiment 3 participants were in the frontal position for encoding and rehearsal then translated to the abducted position for retrieval. Panel B shows the Abducted 20 position. The non-preferred eye was patched, Eye Position was monitored with EOG and head position was monitored using a laser attached to the head.

all conditions, eye-movements into the nasal hemifield remained physically possible even in the eye-abducted position. During the study memoranda were presented wholly in the nasal hemifield or the temporal hemifield. Using this paradigm the oculomotor account of VSWM made a clear prediction: Eye-abduction should only disrupt spatial memory if memoranda were presented in the *temporal* hemifield, as this was the only condition in which saccadic preparation was rendered physically impossible.

The results of Ball et al. (2013) clearly showed eye-abduction was associated with impaired performance on the Corsi Blocks task (De Renzi, Faglioni, & Previdi, 1977), but not with performance of the Visual Patterns task (Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999), the Arrow Span task (Shah & Miyake, 1996), a size comparison task (Thompson et al., 2006), or a visually-presented digit span task (Dempster & Zinkgraf, 1982). Critically, in terms of supporting the oculomotor hypothesis, we found that eye-abduction only impaired Corsi performance when memoranda were presented in the temporal hemifield (when saccadic eye movements were physically impossible), but not when presented in the nasal hemifield (when eye movements remained possible even with central fixation).<sup>1</sup>

<sup>1</sup> A reviewer suggested that microsaccades around the central fixation may have rehearsed spatial information in the nasal hemifield. While we acknowledge such microsaccades might have gone undetected in our paradigm, we do not regard them as a plausible candidate for rehearsal in comparison to saccade plans. Previous studies have shown that the rate and direction of microsaccades are only weakly related to attention shifts and the layout of target locations (Hermens & Walker, 2010). Microsaccades also generate no interference during spatial working memory tasks (Gaunt & Bridgeman, 2012), and the direction of microsaccades are unrelated to the location of spatial memoranda maintained in working memory (Gaunt & Bridgeman, 2014)

On the basis of these findings we concluded that spatial working memory (but not visual or verbal memory) is critically dependent on activity in the eye-movement system, consistent with the claims advanced by an oculomotor account of VSWM. However, this involvement appeared task-specific; namely, that the oculomotor system contributes when memorized locations are *directly* indicated by a change in visual salience (as with Corsi Blocks), but not when memorized locations are *indirectly* indicated by the meaning of symbolic cues (as occurs with Arrow Span). This pattern of results is consistent with the earlier finding that stimulus-driven shifts of attention triggered by peripheral cues are abolished by eye-abduction, while volitional attentional orienting made in response to symbolic cues remains unimpaired (Smith et al., 2012).

### 1.1. The present study

A key element of the method used by Ball et al. (2013) is that eye-abduction was applied through-out the encoding, retention, and retrieval of memoranda. Therefore, while an overall selective impairment of Corsi performance was observed, it could not be established from the data whether this disruption occurred during the encoding, maintenance, or retrieval stages of the task. This is an important limitation, as our claim the oculomotor system acts as a rehearsal mechanism for salient spatial locations assumes eye-abduction restricts the *retention* of memoranda presented to the abducted temporal hemifield. However, the data presented in Ball et al. (2013) cannot rule out the possibility that eye-abduction impaired only the *retrieval* stage of the Corsi task, in which participants moved a mouse in order to select the memorized locations on a screen. The present study aimed to directly address

this issue, and establish the specific contribution made by the oculomotor system to encoding, maintenance, and retrieval processes in spatial working memory.

We report three experiments that have examined the effect of eye-abduction on the encoding (Experiment 1), maintenance (Experiment 2), and retrieval (Experiment 3) of memoranda in spatial and visual working memory. Spatial memory was assessed using the Corsi Blocks task (De Renzi et al., 1977) and visual memory using the Visual Patterns task (Della Sala et al., 1999). Unlike selective interference paradigms that require participants to actively produce responses such as eye-movements, eye-abduction is a passive manipulation that can be selectively applied to the encoding and retrieval stages of a memory task. If the oculomotor system does contribute to encoding, maintenance, and/or retrieval in spatial working memory, a clear prediction follows that eye-abduction should only disrupt performance when memoranda are presented in the temporal hemifield; i.e., where the planning and executing of eye movements is physically impossible. Following the findings of Ball et al. (2013), no effect of eye-abduction on visual working memory performance was expected at any stage.

## 2. Experiment 1: Effect of 40° and 20° eye-abduction on encoding in visual and spatial working memory

Experiment 1 examined the extent to which eye-abduction disrupts memory span when applied only during the encoding stage for visual and spatial memoranda. This was accomplished by having participants encode memoranda in an eye-abducted position at the beginning of each trial, then immediately following presentation their trunk and head were rotated such that their eye was placed in a non-abducted frontal position. This was a passive manipulation in which the experimenter rotated the participant's chair while they maintained fixation, and did not require any active generation of saccadic eye movements by participants.

The procedure followed that previously described by Ball et al. (2013) with one important addition. Because the encoding manipulation required that participants head and trunk be rotated mid-way in a trial in conjunction with simultaneous counter-rotation of the eye to maintain fixation, this raised the possibility that the rotation in itself could cause disruption independent of any effect of eye-abduction. To control for this possibility we created an additional control condition in which participants encoded memoranda with their eyes rotated 20° to the left or right, immediately after which their head and trunk were rotated to a frontal position. Critically, while this condition still required counter-rotation of the eye and head and trunk rotation mid-way through each trial as occurred for 40° abducted trials, participants in the 20° abducted position were still able to physically move their eyes into the temporal hemifield and engage in oculomotor preparation. If the oculomotor system does contribute to the encoding of memoranda in spatial working memory, then disruption of Corsi performance should only be observed during the 40° abduction condition when memoranda are presented in participants' temporal hemifield.

### 2.1. Method

#### 2.1.1. Participants

Fourteen participants took part in this experiment (5 male, mean age 20.8,  $SD = 3.0$ , 12 were right eyed). Participants were from Durham University and received course credit for taking part. Ethical approval was obtained from the Psychology Research Ethics Committee at Durham University, and participants gave informed consent. All participants had normal or corrected-to-normal vision. In the case of corrected vision, only people who wore contact lenses could be tested.

#### 2.1.2. Apparatus

The experiment was run on an IBM compatible personal computer with a 20-inch monitor (1024 by 768 resolution, refresh rate 100 Hz) and was programmed using E-prime (Psychology Software Tools Inc., Pittsburgh, PA, USA). The viewing distance was 57 cm and the center of the screen was at eye level, with a chin rest being used to ensure that this was maintained. Participants sat in a chair with a handle attached to the back to allow efficient movement between the frontal and abducted positions. The chair was attached to a rotating base on which plus and minus 40° and 20° were marked enabling the experimenter to accurately rotate the chair in either direction. Likewise, the chin rest could be rotated to  $\pm 40^\circ$  and  $\pm 20^\circ$ . The experiment was completed in a dark room.

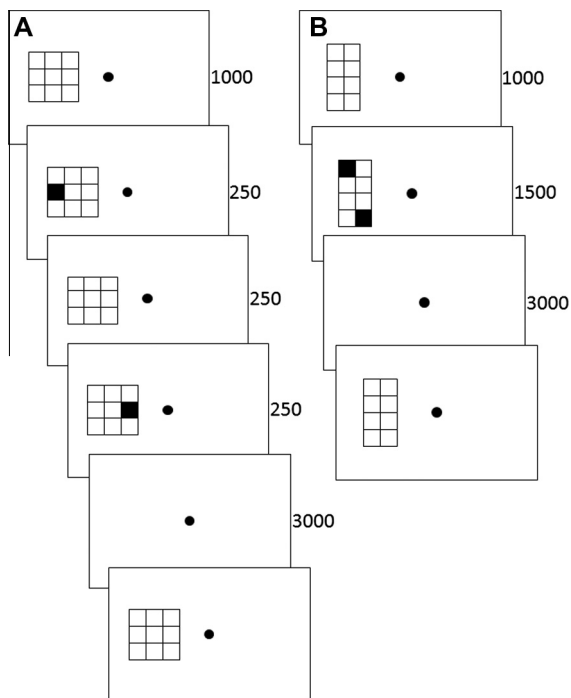
#### 2.1.3. Procedure

Participants used their dominant eye and their non-dominant eye was patched. Participants sat two meters away from the experimenter, extended their arms and brought their hands together in front of their eyes, leaving only a small gap through which they could see the experimenter's nose. The eye that the experimenter could see through this gap was recorded as the participant's dominant eye. If the right eye was dominant, the left eye was patched and the participant was rotated to the left. Stimuli were presented on either side of a central fixation spot. In the case of the right eye being dominant, as shown in Fig. 1A, the temporal hemifield was the right side of the screen. There were six conditions: Frontal Temporal, Frontal Nasal, Abducted 20° Temporal, Abducted 20° Nasal, Abducted 40° Temporal, Abducted 40° Nasal. In the abducted conditions participants started each trial with their bodies and heads turned 20° or 40° to either the left or right. After the presentation of the stimuli they were rotated back to the front. This meant that participants encoded the stimuli in the abducted position but rehearsed it and recalled it in the frontal position. In the frontal condition participants faced forwards for the duration of the trial, thus the eye was in the center of its orbit throughout. In all conditions participants were required to fixate on a central spot (0.3° visual angle) for the whole trial. Participants completed two tasks: the visual patterns task as a measure of visual memory; and the Corsi Blocks task as a measure of spatial memory. For each task, memory span was assessed four times in each condition across two testing sessions, with each session lasting approximately 1 h 45 min. In one session participants completed half the

frontal spans (2 Frontal Temporal spans and 2 Frontal Nasal spans) and all the Abducted 40° spans (8 spans) per task, and in the other session they completed the remaining half of the Frontal spans and the Abducted 20° spans. The order of the two sessions was counterbalanced. Each session was divided into 4 blocks, two for each task, with each block containing 6 spans (two abducted nasal, two abducted temporal, one frontal nasal, and one frontal temporal per block). The order of tasks was counterbalanced across participants, as was the field of presentation (Temporal, Nasal) and Eye Position (Frontal, Abducted) within blocks. Participants completed three frontal and three abducted practice trials for each task.

#### 2.1.4. Spatial memory – Corsi Block task

Nine boxes, arranged in a 3 × 3 grid, were presented (Fig. 2A). A sequence of boxes flashed (starting with three boxes, up to a maximum of nine boxes, and each box could only flash once per sequence). After a 3 s retention interval participants had to reproduce the sequence by clicking in the boxes in the correct order. At trial onset the fixation spot and placeholders were presented for 1000 ms. Memoranda were indicated by a 250 ms luminance change at a placeholder. There was a 250 ms delay between consecutive items in a sequence. After presentation of the final item, the placeholder array disappeared and participants maintained fixation for 4000 ms. The array then reappeared and participants were required to click the squares in the order they flashed. Each placeholder measured 2.2° × 2.2° visual angle and the array of locations measured 7.2° visual angle in height and width. The center of



**Fig. 2.** An example of the sequence of events and presentation times during the Corsi Blocks task (A) and the Visual Patterns task (B). Times are in milliseconds. The response screens were displayed until the response was completed.

the array was 4.4° from fixation. In the abducted condition, immediately after the offset of the grid, and on hearing a beep, the experimenter rotated participants to the front. The grid was then represented and participants were required to click in the boxes in the order they flashed.

#### 2.1.5. Visual memory – visual patterns task

Participants were presented with matrices in which half of the squares were white and the other half were black (Fig. 2B). Participants were required to reproduce the pattern in an empty grid. Patterns started with 8 squares (2 × 4 grid) in which 4 squares were black, and increased by two squares each time up to a maximum of 20 squares (10 black). Patterns were randomly generated by E-prime. The grid could not be more than 3 squares wide. Each square measured 2.1° of visual angle, and the grid extended to a maximum width of 7.3° visual angle from fixation and a maximum height of 9.1° visual angle above and below the fixation spot. Participants completed three trials at each level and were required to get at least two out of three trials correct in order to progress to the next level, where two additional squares were added to the matrix. Visual span was taken as the highest number of black squares that participants could correctly recall. At the start of each trial participants were presented with the fixation spot and the empty grid for 1000 ms. The matrix to-be-remembered was then presented for 1500 ms. At the offset of the pattern a beep sounded, instructing the experimenter to rotate the participants back to the front in the abducted conditions. The fixation spot remained present for 4000 ms before an empty grid was presented. Participants were required to click the squares that were previously shaded. Once clicked, the square went black.

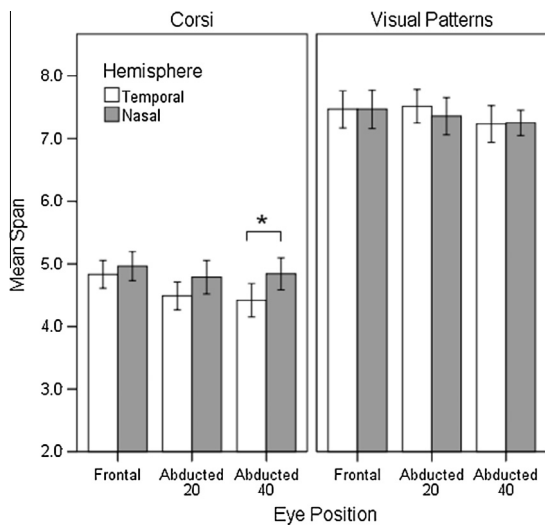
#### 2.1.6. Eye movement recording

Electro-oculographic eye movement data were recorded throughout the trials using an MP35 acquisition unit and BSL Pro 3.7 software (Biopac Systems Inc., CA, USA). Three shielded 4 mm AgCl electrodes were attached to the participants' skin using adhesive disks, and electrode gel was used to improve recording conductance. Only horizontal eye movements were measured: the two electrodes that measured the horizontal movements were placed adjacent to the temporal canthus of each eye, and the ground electrode was placed in the center of the participant's forehead. The data was sampled at a rate of 1000 Hz. The data were analyzed online by the experimenter and if participants did not keep fixation the trial was discarded and repeated.

## 2.2. Results

The results are presented in Fig. 3. All data were tested for normality using the Shapiro–Wilk statistic; the data were normal unless otherwise stated. Inferential statistics used a significance level of  $p < .05$ , except when multiple comparisons were performed, where a Bonferonni correction of  $p < .016$  was applied. For both tasks less than 1% of trials were redone because participants failed to keep fixation (CBT: 0.58%; Visual Patterns: 0.56%). Analyses are





**Fig. 3.** The effect of eye abduction during encoding on memory span (Experiment 1). Corsi span was significantly lower in the Temporal hemisphere in the Abducted 40 condition ( $p < 0.016$ ). Eye abduction had no effect on Pattern span. Error bars show  $\pm 1$  SEM.

concerned with the mean span for each condition. A  $2 \times 2 \times 3$  repeated measures ANOVA with the factors Task (Visual, Spatial), Side of Presentation (Temporal, Nasal), and Eye Position (Frontal, Abducted 20, Abducted 40) was performed. A significant main effect of Task was found,  $F_{(1,13)} = 235.68$ ;  $p = .00$ , with memory span being higher in the visual patterns task ( $M = 7.38$ ,  $SE = .26$ ) compared to the Corsi Blocks task ( $M = 4.72$ ;  $SE = .22$ ); therefore, the two tasks are analyzed separately. The only statistically significant result was the interaction between Task and Side of Presentation,  $F_{(1,13)} = 6.27$ ;  $p = .026$ .

### 2.2.1. Visual patterns

A  $2 \times 3$  repeated measures ANOVA with the factors Side of Presentation (Temporal, Nasal), and Eye Position (Frontal, Abducted 20, Abducted 40) revealed no significant main effects (Side of Presentation:  $p = .625$ ; Eye Position:  $p = .280$ ). The interaction was also not statistically significant ( $p = .682$ ,  $\eta^2 = 0.2$ ).

### 2.2.2. Corsi Blocks

The same  $2 \times 3$  repeated measures ANOVA was performed for Corsi spans. While the main effect of Eye Position was not statistically significant ( $p = .145$ ,  $\eta^2 = 0.14$ ), the main effect of Side of Presentation was,  $F_{(1,13)} = 11.56$ ;  $p = .005$ ,  $\eta^2 = 0.47$  with span being higher in the nasal conditions ( $M = 4.86$ ,  $SE = .22$ ) compared to the temporal conditions ( $M = 4.58$ ,  $SE = .23$ ). The interaction was not significant ( $p = .393$ ,  $\eta^2 = 0.069$ ).

Bonferroni-corrected planned comparisons (paired samples  $t$ -tests; corrected alpha level  $p < .016$ ) revealed that Corsi span in the temporal hemifield was significantly impaired compared to span in the nasal hemifield, but only in the Abducted 40 condition  $t_{(13)} = 2.84$ ;  $p = .014$ ,  $d = .78$ ; span reduced by  $.42$  ( $SE = .15$ ). There was a trend in the same direction in the Abducted 20 condition that did not approach significance when corrected for multiple com-

parisons ( $t_{(13)} = 2.12$ ;  $p = .053$ ;  $d = .59$ ). There was no difference in performance in the Frontal condition condition  $t_{(13)} = .89$ ;  $p = .39$ ,  $d = .23$ ).

### 2.3. Discussion

Memory span on the Corsi Blocks task was significantly reduced only when presented locations could not be encoded as the goal of saccadic eye movements; i.e., when memoranda were presented in the temporal hemifield in the  $40^\circ$  eye-abducted condition. Consistent with the previous findings of Ball et al. (2013), there were no observed effects of eye-abduction on Visual Pattern span in any of the conditions. On first inspection the results appear consistent with the hypothesis that the eye-movement system contributes to encoding of spatial locations in working memory. Specifically, when a location is directly indicated by a change in visual salience participants encode this location as the goal of a potential eye-movement. Because this is rendered impossible when locations are presented in the temporal hemifield with  $40^\circ$  eye-abduction, participants' spatial span is significantly reduced. Overall this finding is supportive of the view that spatial working memory is critically dependent on activity within the eye-movement system (Baddeley, 1986; Pearson & Sahraie, 2003; Postle et al., 2006).

However, closer comparison between the Abducted  $40^\circ$  Temporal and the Abducted  $20^\circ$  temporal conditions reveals some ambiguity in this interpretation. Although not significant, there was a trend for span on the Corsi task to be lower in the Temporal Abducted  $20^\circ$  condition in comparison to the Temporal Frontal condition. This implies that the rotation of participants' head and trunk and counter-rotation of their eye immediately following encoding of spatial memoranda may itself have acted as a source of interference. One possibility is that changes in head and body position following stimuli presentation may interfere with head and/or body-centered frame of references in which locations are encoded. However, a series of studies by Bernardis and Shallice have shown that changes in head-position during both encoding and retrieval do not interfere with memory span on the Corsi Blocks task (Bernardis & Shallice, 2011). Nonetheless, there remains a possibility that participants may have encoded locations in the form of a combined eye-head movement that could be compromised by an Abducted  $20^\circ$  condition (Land, 2004; Land, Furneaux, & Gilchrist, 2002).

An alternative explanation is that a head and truck rotation combined with eye fixation immediately following encoding in the Abducted  $20^\circ$  condition acts as a general distracter. Rudkin, Pearson, and Logie (2007) have shown performance of the Corsi Blocks task involves attention-based executive resources to a significantly greater extent than performance of the Visual Patterns test. This can be attributed to the increased complexity of encoding serial-sequential spatial locations in comparison to simultaneous presentation of a visual pattern (Helstrup, 1999; Kemps, 2001; Rudkin et al., 2007). Although in the present study placing participants in an eye-abducted position was a passive manipulation carried out by the experimenter, requiring only that they maintain fixation, the movement may still have been distracting enough to affect the construc-

tion of mental path configurations derived from sequential presentation of spatial locations (Berch, Krikorian, & Huha, 1998; Parmentier, Elford, & Maybery, 2005).

If the trend for lower span in the Abducted 20° condition is specifically linked to demands imposed by the initial encoding of spatial memoranda, then it should not be observed when the abduction occurs only during the maintenance and retrieval periods of spatial memory. This issue is addressed further in Experiments 2 and 3.

### 3. Experiment 2: Effect of 40° and 20° eye-abduction on maintenance and retrieval in visual and spatial working memory

The focus of Experiment 2 was to examine the effect of eye-abduction on the maintenance of visual and spatial memoranda in working memory. While establishing the procedure we initially considered applying the eye-abduction position only during the retention interval of the visual and spatial memory tasks. This would have required participants' encoding memoranda in the Frontal Eye Position, then being rotated to either the 40° or 20° Abducted position for the retention interval, and finally being rotated back to a Frontal Eye Position for memory retrieval. However, a consequence of this procedure was that participants in Experiment 2 would be exposed to two head and trunk rotations per trial, in comparison to only one rotation per trial in Experiment 1 (eye-abduction during encoding) and Experiment 3 (eye-abduction during retrieval). This procedure would therefore prevent direct comparisons across the three experiments, particularly considering the non-significant trend observed in Experiment 1 for lower Corsi span even with the 20° Eye-Abducted condition following a single rotation.

In response to this concern we decided in Experiment 2 to apply eye-abduction to both maintenance and retrieval stages of the memory tasks. This was accomplished by having participants encode memoranda in the non-abducted Frontal position at the beginning of each trial, then immediately following presentation their trunk and head were rotated to either the 40° and 20° Abducted position for the remaining maintenance and retrieval stages of the trial. This ensured Experiment 2 remained comparable with the design of Experiments 1 and 3, as the procedure was a direct reversal of how eye-abduction had previously been applied in Experiment 1. Furthermore, comparison between Experiment 2 (eye-abduction during maintenance and retrieval) and Experiment 3 (eye-abduction during retrieval only) would enable the effect of abduction specifically on maintenance to be established without introducing any disparity in the number of head and trunk rotations per trial.

#### 3.1. Method

##### 3.1.1. Participants

14 Participants took part in this experiment (5 male, mean age 21.7,  $SD = 2.4$ , 10 were right eyed).

##### 3.1.2. Trial procedure

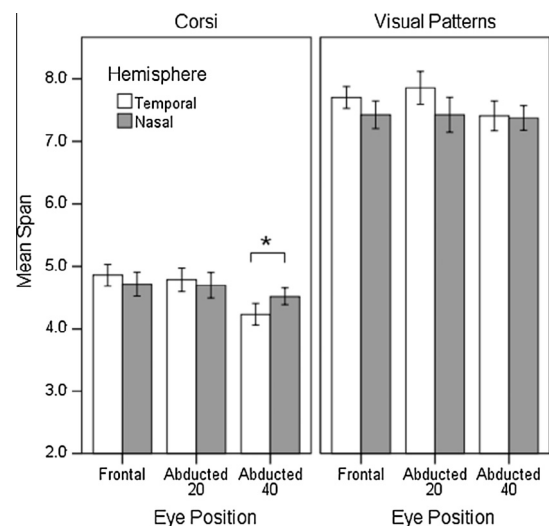
For both the visual patterns and Corsi Blocks tasks the trial procedure was the same as Experiment 1 with one exception. In the abducted conditions participants started in the frontal position. At the offset of the stimuli, a beep sounded instructing the experimenter to put participants in the abducted position by rotating the chair and chin rest. At the end of the 4000 ms rehearsal period participants had to reproduce the pattern in the case of the visual patterns task or recall the sequence in the Corsi Blocks task. This meant that in the abducted conditions participants encoded the stimuli normally but rehearsed and retrieved the information in the abducted position.

#### 3.2. Results

The results are presented in Fig. 4. 1.15% of CBT trials and 0.79% of visual pattern trials were redone because participants failed to keep fixation. A  $2 \times 2 \times 3$  repeated measures ANOVA with the factors Task (Visual, Spatial), Side of Presentation (Temporal, Nasal), and Eye Position (Frontal, Abducted 20, Abducted 40) was performed. A significant main effect of Task was found,  $F_{(1,13)} = 351.15$ ;  $p < .000$ , with memory span being higher in the visual patterns task ( $M = 7.53$ ,  $SE = .17$ ) compared to the Corsi Blocks task ( $M = 4.63$ ;  $SE = .15$ ); therefore, the two tasks are analyzed separately. The main effect of Eye Position was significant,  $F_{(2,26)} = 3.73$ ;  $p = .038$ , as was the interaction between Side of Presentation and Eye Position,  $F_{(2,26)} = 3.44$ ;  $p = .047$ .

##### 3.2.1. Visual patterns

A  $2 \times 3$  repeated measures ANOVA with the factors Side of Presentation (Temporal, Nasal), and Eye Position (Frontal, Abducted 20, Abducted 40) revealed no significant



**Fig. 4.** The effect of eye abduction during rehearsal on memory span (Experiment 2). Corsi span was significantly lower in the Temporal hemisphere in the Abducted 40 condition ( $p < 0.016$ ). In the Abducted 20 condition the difference between nasal and temporal hemisphere was not significant. Eye abduction had no effect on Pattern span. Error bars show  $\pm 1$  SEM.

main effects (Side of Presentation:  $p = .134$ ,  $\eta^2 = 0.16$ ; Eye Position:  $p = .401$ ,  $\eta^2 = 0.07$ ). The interaction between these factors was not statistically significant ( $p = .414$ ,  $\eta^2 = 0.06$ ).

### 3.2.2. Corsi Blocks

The  $2 \times 3$  repeated measures ANOVA with the factors Side of Presentation (Temporal, Nasal), and Eye Position (Frontal, Abducted 20, Abducted 40) revealed a non-significant main effect of Side of Presentation ( $p = .831$ ,  $\eta^2 = 0.004$ ), and a significant main effect of Eye Position,  $F_{(2,26)} = 8.90$ ;  $p = .001$ ,  $\eta^2 = 0.41$ . Span was lowest in the Abducted 40 conditions ( $M = 4.38$ ,  $SE = .15$ ) compared to the Abducted 20 ( $M = 4.74$ ,  $SE = .18$ ) and Frontal conditions ( $M = 4.79$ ,  $SE = .17$ ). The interaction between Side of Presentation and Eye Position approached statistical significance ( $p = .052$ ,  $\eta^2 = 0.20$ ).

Bonferroni-corrected planned comparisons (paired samples  $t$ -tests) revealed that Corsi span in the temporal hemispace was significantly impaired compared to span in the nasal hemispace, but only in the Abducted 40 condition  $t_{(13)} = 2.83$ ;  $p = .014$ ,  $d = .83$ ; reduction of .29 ( $SE = .13$ ). There was no difference in spatial span in the frontal condition (Frontal Nasal:  $M = 4.71$ ,  $SE = .19$ ; Frontal Temporal:  $M = 4.86$ ,  $SE = .17$ ;  $t_{(13)} = -1.02$ ;  $p = .328$ ). Likewise, there was no difference between the two Abducted 20 conditions (Abducted 20 Nasal:  $M = 4.70$ ,  $SE = .20$ ; Abducted 20 Temporal:  $M = 4.79$ ,  $SE = .19$ ;  $p = .567$ ;  $t_{(13)} = -0.59$ ;  $p = .57$ ).

### 3.3. Discussion

Memory span on the Corsi Blocks task was found to be significantly reduced only when memoranda were presented in the temporal hemifield in the 40° eye-abducted condition. Conversely, there was no effect of eye-abduction on Visual Pattern span in any condition. In comparison to Experiment 1, there was also no longer any trend for lower memory span to be observed on the Corsi task in the 20° eye-abducted condition. These results establish that disruption of spatial memory occurred only when participants' ability to engage in oculomotor preparation during the maintenance and retrieval stages of the Corsi task was rendered physically impossible. The results also clarify that the observed non-significant trend in Experiment 1 for spatial span to be lower in the 20° eye-abducted condition was specifically associated with the encoding of memoranda, and does not reflect a more general disruption that affects the maintenance and retrieval of presented spatial locations. Critically, the passive manipulation of participants' head and trunk position took place at the same point in all trials in both Experiments 1 and 2, i.e., immediately following presentation of the visual and spatial memoranda. The only difference was that participants in Experiment 1 were moved from an abducted to a non-abducted eye-position, while in Experiment 2 the opposite rotation occurred.

Overall, Experiment 2 offers strong support for the oculomotor account of VSWM, and the findings are consistent with the view that rehearsal of directly-indicated spatial locations in working memory is critically dependent on activity in the eye-movement system. However, as with

the results reported by Ball et al. (2013), it remains possible that the disruptive effect of 40° eye-abduction on spatial memory is restricted only to the retrieval stage of the Corsi task, and is not associated with the maintenance of encoded locations. This possibility was directly examined in Experiment 3.

## 4. Experiment 3: Effect of 40° and 20° eye-abduction on retrieval in visual and spatial working memory

### 4.1. Method

#### 4.1.1. Participants

14 participants took part (6 male, mean age 30.1,  $SD = 11.1$ , 6 were right eyed).

#### 4.1.2. Trial procedure

The design was the same as that of Experiments 1 and 2 with the following exception. In the abducted conditions participants started each trial in the frontal condition and at the end of the retention interval they were rotated either 20° or 40° to the left or right (depending on eye dominance). This meant that participants encoded and rehearsed the stimuli normally but retrieved the stimuli in the abducted position.

For both tasks, after 2500 ms into the retention interval a beep sounded instructing the experimenter to rotate participants. The total duration between the end of the stimulus presentation and recall was 4000 ms, the same as Experiments 1 and 2. This allowed sufficient time to move the participants. At the end of the 4000 ms rehearsal period participants had to reproduce the pattern in the case of the visual patterns task or recall the sequence in the Corsi Blocks task

### 4.2. Results

The results are presented in Fig. 5. 0.83% of CBT trials and 0.68% of visual pattern trials were redone because participants failed to keep fixation. A  $2 \times 2 \times 3$  repeated measures ANOVA with the factors Task (Visual, Spatial), Side of Presentation (Temporal, Nasal), and Eye Position (Frontal, Abducted 20, Abducted 40) was performed. A significant main effect of Task was found,  $F_{(1,13)} = 129.35$ ;  $p = .000$ , with memory span being higher in the visual patterns task ( $M = 7.33$ ,  $SE = .30$ ) compared to the Corsi Blocks task ( $M = 4.70$ ;  $SE = .24$ ); therefore, the two tasks are analyzed separately.

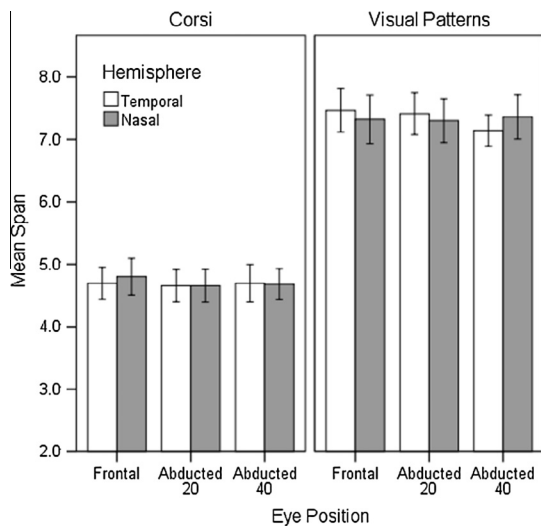
#### 4.2.1. Visual patterns

A  $2 \times 3$  repeated measures ANOVA with the factors Side of Presentation (Temporal, Nasal), and Eye Position (Frontal, Abducted 20, Abducted 40) revealed no significant main effects (Side of Presentation:  $p = .944$ ,  $\eta^2 = 0.00$ ; Eye Position:  $p = .666$ ,  $\eta^2 = 0.031$ ). The interaction was also not statistically significant ( $p = .408$ ,  $\eta^2 = 0.067$ ).

#### 4.2.2. Corsi Blocks

The same repeated measures ANOVA was performed for Corsi spans. The main effect of Side of Presentation was not





**Fig. 5.** The effect of eye abduction during retrieval on memory span (Experiment 3). Eye abduction had no effect on Corsi or Pattern span. Error bars show  $\pm 1$  SEM.

statistically significant ( $p = .702$ ,  $\eta^2 = 0.012$ ), and likewise, the main effect of Eye Position ( $p = .862$ ,  $\eta^2 = 0.011$ ). The interaction between Side of Presentation and Eye Position was also not significant ( $p = .759$ ,  $\eta^2 = 0.021$ ). Planned comparisons (paired samples  $t$ -tests) showed no difference in span in the two frontal conditions (Frontal Nasal:  $M = 4.80$ ,  $SE = .29$ ; Frontal Temporal:  $M = 4.70$ ,  $SE = .26$ ;  $t_{(13)} = 0.74$ ;  $p = .474$ ), the two Abducted 20 conditions (Abducted 20 Nasal:  $M = 4.66$ ,  $SE = .26$ ; Abducted 20 Temporal:  $M = 4.66$ ,  $SE = .26$ ;  $t_{(13)} = 0.00$ ;  $p = 1$ ) or the two Abducted 40 conditions (Abducted 40 Nasal:  $M = 4.68$ ,  $SE = .25$ ; Abducted 40 Temporal:  $M = 4.70$ ,  $SE = .30$ ;  $t_{(13)} = 0.111$ ;  $p = .913$ ).

To establish that Corsi span was impaired only during the maintenance stage of the task but not during retrieval, Experiments 2 and 3 were directly compared using a post hoc repeated measures ANOVA with a between-participants factor. A  $2 \times 2 \times 2$  ANOVA was conducted with Eye Position (Frontal, Abducted 40), Side of Presentation (Temporal, Nasal), and Processing Stage (Maintenance and Retrieval, Retrieval only) specified as factors. The three-way interaction was significant ( $F(1,26) = 4.48$ ;  $p = 0.044$ ;  $\eta^2 = 0.147$ ) with Corsi span significantly reduced in the Abducted 40 Temporal condition only when there was a task requirement to rehearse spatial memoranda (Experiment 2), but not during retrieval alone (Experiment 3).

#### 4.3. Discussion

There was found to be no effect of 40° or 20° eye-abduction on memory span when participants were in the abducted position only during the retrieval stage of the Corsi Blocks task. As in previous experiments, performance on the Visual Patterns test was also unaffected. These results enable us to discount the possibility that placing participants in a 40° abducted Eye Position may have interfered with the element of retrieval in the Corsi task in

which participants moved a mouse in order to select the memorized locations on a screen. Experiment 3 also clearly demonstrates that involvement of the oculomotor system is *not* a critical component in the retrieval of directly-indicated spatial locations in working memory, provided that participants are able to encode and maintain the locations under circumstances in which oculomotor preparation remains physically possible.

The absence of any effect of eye-abduction in Experiment 3 (where abduction was applied only during retrieval) also strengthens our interpretation of Experiment 2 (where abduction was applied during both maintenance and retrieval). Spatial span in Experiment 2 was only significantly reduced when memoranda were presented to the temporal hemifield and participants were abducted 40° during the maintenance and retrieval stages. In contrast, there was no disruption of spatial span at all for temporally presented stimuli when participants were abducted 40° only during retrieval. On this basis we conclude the disruptive effect of eye-abduction observed in Experiment 2 is specific to the *maintenance* of memoranda in spatial working memory, i.e., participants were unable to effectively rehearse directly-indicated spatial locations when eye-movements to the hemifield where the locations were presented were rendered physically impossible.

#### 5. General discussion

The aim of the present study was to establish the extent of oculomotor involvement during the encoding, maintenance, and retrieval of visual and spatial memoranda in working memory. This was accomplished across three experiments in which we used an abducted-eye paradigm to restrict participants' ability to engage in oculomotor preparation at different stages of spatial and visual memory tasks. In all three experiments it was predicted that if performance was critically dependent on the eye-movement system, then a reduction in span should only occur when memoranda were presented in the temporal hemifield of the 40° eye-abducted condition. This is because this was the *only* condition in which it was physically impossible for participants to plan or execute saccadic eye-movements to spatial locations in the temporal hemifield. In contrast no significant reduction in span was expected in the Temporal 20° Abducted condition, as in this condition participants were still able to plan saccades to spatial locations presented within the temporal hemifield.

In Experiment 1 eye-abduction was applied only during the encoding of memoranda in visual and spatial memory. Spatial span was significantly reduced in the Temporal 40° Abducted condition, which is consistent with oculomotor involvement during spatial encoding. However, there was also a trend for lower span in the Temporal 20° Abducted condition. Although this trend was not significant, we feel it is evident enough in the data to require us to be more guarded in our interpretation of Experiment 1. If there is oculomotor involvement during the maintenance of spatial locations in working memory (as demonstrated in Experiment 2), it can be expected that participants would first need to encode the locations as the goal of potential eye-

movements. The reduction in Corsi span in the Temporal 40° Abducted condition in Experiment 1 is fully consistent with this. However, we acknowledge that encoding during the Corsi Blocks task will also engage nonspatial executive processes (Berch et al., 1998; Parmentier et al., 2005; Pearson, 2007; Rudkin et al., 2007) that could be disrupted by eye rotation or head and torso movements required to place the participant in either the 20° or 40° eye-abducted condition.

In Experiment 2 (eye abduction during retention and retrieval) the only significant reduction in spatial span was observed when memoranda were presented in the Temporal 40° Abducted condition, with no comparable drop or trend in the 20° Abducted condition. Considering the further absence of any effect of abduction in Experiment 3 (abduction during retrieval only), we argue these results offer strong support for oculomotor involvement during the maintenance of directly-indicated spatial locations in working memory. As outlined in the introduction, previous studies have struggled to reliably decouple attentional processes from oculomotor control processes in VSWM. We propose the present study is the first to unambiguously demonstrate that the oculomotor system contributes to the maintenance of spatial locations in working memory independently from any involvement of covert attention. This claim rests on the decoupling of oculomotor processes and attention that occurs when participants are placed in a 40° Abducted position and spatial memoranda are presented wholly in the temporal hemifield. Critically, participants can still see everything in the display and can covertly shift their attention within the abducted hemifield, but are they physically unable to make any further eye-movements. It is only in this condition that spatial memory span is significantly reduced. This reduction cannot be explained by differences in the quality of sensory information between conditions, as previous studies have shown that eye-abduction does not reduce visual acuity (Ball et al., 2013; Craighero et al., 2004).

Given that our interpretation of these data rests on the decoupling of endogenous attention and saccade control, it is worth noting that there is substantial behavioral and neuropsychological evidence for this dissociation. For example, neuropsychological evidence supporting separation between the oculomotor system and attentional control comes from reported cases of patients with defective oculomotor control who are still able to covertly orient their attention (Gabay et al., 2010; Rafal et al., 1988; Smith et al., 2004). Smith et al. (2012) have also previously shown using an eye-abduction paradigm that numeric cues elicit covert endogenous shifts of attention to locations in the temporal hemispace even when they cannot become the goal of saccadic eye movements. In healthy participants, a series of studies by Klein and colleagues have shown that covert shifts of attention triggered by symbolic cues do not facilitate subsequent saccadic eye-movements (Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1992). Furthermore, Belopolsky and Theeuwes (2009b, 2012) have argued that endogenous attention associated with maintaining attention at a spatial location is independent from the preparation of an eye-movement to the same location. A comprehensive discus-

sion of the evidence for a dissociation between endogenous attention and saccade control can be found in Smith and Schenk (2012).

We have previously argued that oculomotor involvement in spatial working memory is task-specific (Ball et al., 2013). While eye-abduction reduces performance on the Corsi Blocks task (where locations are directly indicated), it has no effect on Arrow Span (where locations are symbolically indicated by the direction of an arrow; Shah & Miyake, 1996). We therefore do not claim that the oculomotor system will contribute to encoding and maintenance during all forms of spatial memory task. Instead, we argue the oculomotor system contributes to optimal spatial memory during encoding and maintenance specifically when the to-be-remembered locations are directly indicated by a change in visual salience, but *not* when memorized locations are indirectly indicated by the meaning of symbolic cues. This interpretation of the role of oculomotor involvement in working memory is consistent with previous findings that have demonstrated the oculomotor system mediates orienting to sudden peripheral events, but not endogenous orienting or maintenance of attention in response to symbolic cues (Smith et al., 2012). Furthermore, it also provides a means to reconcile apparently conflicting theories of spatial rehearsal in working memory that have attributed maintenance either to oculomotor processes (e.g., Pearson & Sahraie, 2003; Postle et al., 2006) or to higher-level attentional processes (e.g., Awh, Vogel, & Oh, 2006). We argue that spatial memory tasks in which memoranda are directly signaled by a change in visual salience involve a critical contribution from the oculomotor system during the encoding and maintenance of to-be-remembered location, while spatial memory tasks in which locations are indirectly signaled by the meaning of symbolic cues predominantly utilize higher-level attentional processes for encoding and rehearsal.

The results of Experiment 3 clearly demonstrate that although the oculomotor system contributes to the encoding and maintenance of spatial locations in working memory, there is no evidence that the ability to plan and execute eye-movements to the memorized locations is necessary for subsequent accurate retrieval. This result can be related to so-called “looking at nothing” debate in the literature, which has focused on the experimental observation that participants frequently make regular eye-movements to empty regions of space that were previously occupied by salient visual stimuli (e.g., Altmann, 2004; Richardson & Spivey, 2000). This has been interpreted as demonstrating that eye-movements form part of integrated mental representations that include visual and semantic properties of encoded stimuli (Ferreira, Apel, & Henderson, 2008; Richardson, Altmann, Spivey, & Hoover, 2009; Spivey, Richardson, & Fitneva, 2004). However, while these regular eye-movements appear to have functional importance, they are not typically associated with any actual improvement in memory accuracy (Hoover & Richardson, 2008; Richardson & Spivey, 2000).

An influential theory in this field is “scanpath theory” (Norton & Stark, 1971), which proposed that reinstatement of the sequence of eye-movements made during encoding

of a visual stimulus plays a causal role in its subsequent successful recognition. A hard interpretation of this theory entails that recapitulation of eye-movements made during encoding of visual scenes facilitates successful recall. However, a recent study by [Martarelli and Mast \(2013\)](#) manipulated eye-position during pictorial recall and found that there was no increase in memory accuracy when participants looked at areas where stimuli had previously appeared, in comparison to when they looked at non-corresponding areas of screen. Similarly, [Foulsham and Kingstone \(2013\)](#) have recently reported a series of experiments in which participants' fixations were constrained during encoding and recognition of images in order to manipulate scanpath similarity. Although scanpath similarity was a predictor of recognition accuracy, there was no recognition advantage when participants re-viewed their own fixations of a scene versus someone else's, or for retaining serial order of fixations between encoding and recognition. Foulsham and Kingstone conclude that while congruency in eye-movements between encoding and retrieval is beneficial for scene recognition, there is no evidence to suggest recapitulation of the exact scanpath at encoding is necessary for accurate recall.

Our own results are broadly in line with these recent findings, as there is no evidence from Experiment 3 in the present study that the ability to engage in saccade preparation to memorized locations is necessary for their accurate recall. Thus, while the rehearsal of directly salient locations in the oculomotor system allows for optimal spatial memory at recall, we regard this as a contributing mnemonic mechanism that operates in conjunction with visually-based strategies such as mental path construction or visual imagery ([Parmentier et al., 2005](#); [Rudkin et al., 2007](#)). Critically, we have previously shown that eye-abduction only reduces, rather than abolishes, spatial memory even when applied across all encoding, maintenance, and retrieval stages of a trial ([Ball et al., 2013](#)). Therefore, clearly the involvement of oculomotor encoding and rehearsal *enhances* spatial memory for a sequence of visually-salient locations rather than critically enables it. However, this position is not dissimilar to that observed when articulatory suppression is used to prevent subvocal rehearsal of words and digits during verbal working memory ([Baddeley, Thomson, & Buchanan, 1975](#); [Murray, 1967](#)), where verbal memory span is significantly reduced but not abolished ([Baddeley, 2003](#)).

Both the findings of [Ball et al. \(2013\)](#) and our current study also demonstrate that manipulating participants' gaze through central fixation does not in itself prevent the oculomotor system from contributing to the encoding and maintenance of spatial material. This has implications for previous studies that have attempted to investigate the functional role of eye-movements during cognitive tasks by comparing central fixation and free eye-movement conditions (e.g., [Godijn & Theeuwes, 2012](#); [Pearson & Sahraie, 2003](#)). We argue that the absence or constraint of overt eye-movements during a task cannot be taken as indicative of the absence of any underlying oculomotor involvement in task performance. Again, this has some parallels with the operation of subvocal rehearsal as a maintenance process during verbal working memory: while some people

may overtly mutter under their breath or speak out loud while rehearsing a sequence of unfamiliar verbal material, in the majority of cases the rehearsal process is covert rather than explicit ([Baddeley, 2003](#)).

In summary, previous studies of VSWM have struggled to reliably decouple the involvement of attentional processes from oculomotor control processes. We propose the present study is the first to unambiguously demonstrate that the oculomotor system contributes to the maintenance of spatial locations in working memory independently from any involvement of covert attention. Across three experiments using an abducted-eye paradigm we have shown that preventing oculomotor preparation during the encoding and maintenance of visually-salient locations in working memory significantly impairs spatial span, but it has no effect if prevented only during recall. We argue these findings provide strong support for the theoretical view that the oculomotor system plays an important role during spatial working memory. Specifically, we conclude that oculomotor involvement is necessary for participants to optimally maintain a sequence of locations that have been directly indicated by a change in visual salience.

## Acknowledgments

This work was supported by the Economic and Social Research Council (RES-000-22-4457). Data are archived in the ESRC Data Store ([oai:store.ac.uk:archive:635](http://oai:store.ac.uk:archive:635)). We thank Mr. Andrew Long for mechanical assistance.

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