Oculomotor involvement in spatial working memory is task-specific

Keira Ball[1], David G. Pearson[2], Daniel. T. Smith[1*].

[1] Cognitive Neuroscience Research Unit (CNRU), Durham University.

[2] School of Psychology, University of Aberdeen.

* Correspondence should be addressed to:

Dr. Daniel T. Smith

E011 Wolfson Building

Durham University

Queen’s Campus

Stockton-On-Tees

TS176BH

(00)44 1913340436

daniel.smith2@durham.ac.uk

Abstract

Many everyday tasks, such as remembering where you parked, require the capacity to store and manipulate information about the visual and spatial properties of the world. The ability to represent, remember, and manipulate spatial information is known as visuospatial working memory (VSWM). Despite substantial interest in VSWM the mechanisms responsible for this ability remain debated. One influential idea is that VSWM depends on activity in the eye-movement (oculomotor) system. However, this has proved difficult to test because experimental paradigms that disrupt oculomotor control also interfere with other cognitive systems, such as spatial attention. Here, we present data from a novel paradigm that selectively disrupts activation in the oculomotor system. We show that the inability to make eye-movements is associated with impaired performance on the Corsi blocks task, but not on Arrow Span, Visual Patterns, Size Estimation or Digit Span tasks. It is argued that the oculomotor system is required to encode and maintain spatial locations indicted by a change in physical salience, but not non-salient spatial locations indicated by the meaning of a symbolic cue. This suggestion offers a way to reconcile the currently conflicting evidence regarding the role of the oculomotor system in spatial working memory.

Keywords: visual, spatial, working memory, eye movement, attention, saccade,

1. Introduction

Visuospatial working memory (VSWM) refers to the ability to recall and manipulate information about the visual and spatial properties of the world. For example, when buying new curtains you may have to hold the colour of a carpet in your head to ensure a good match. When returning with your new curtains you have to remember where you parked, and then the route from the store to your home. There has been considerable progress in understanding some aspects of VSWM. The architecture of VSWM is well understood (Baddeley, 2003; Repovs & Baddeley, 2006), with selective interference paradigms elegantly demonstrating the division between a visual memory that retains information about the features of an object and a spatial memory that retains information about the spatial properties of an object (Klauer & Zhao, 2004; Tresch, Sinnamon, & Seamon, 1993). However, the mechanisms responsible for encoding and retaining information in VSWM remain contentious.

An influential idea is that VSWM depends on activation of the eye-movement system, such that spatial locations are encoded as a map of the eye-movements that would be required to look at each location (Baddeley, 1986; Belopolsky & Theeuwes, 2009a, b; Postle, Idzikowski, Della Sala, Logie, & Baddeley, 2006; Tremblay, Saint-Aubin, & Jalbert, 2006). There is support for this view. For example, executing eye-movements during VSWM tasks disrupts visuospatial working memory more than other types of distractor tasks (Lawrence, Myerson, & Abrams, 2004; Pearson & Sahraie, 2003). Similarly, eye-movements to the locations of remembered stimuli are often observed during recall of spatial information (Brandt & Stark, 1997; Johansson, Holsanova, Dewhurst, & Holmqvist, 2012; Spivey & Geng (2001)

In contrast, others have argued that VSWM is reliant on covert spatial attention (the ability to attend to locations without actually looking at them), rather than plans for eye-movements. In support of the covert attention proposal, Awh and colleagues (1998) found that reaction times were faster when targets appeared at locations held in working memory, and that spatial working memory was poorer when participants were prevented from attending to these memorized locations during the retention interval (see also Awh & Jonides, 2001). Furthermore, memory performance on a task where participants were required to remember a sequence of locations indicated by the locations of numbered peripheral items was not affected when participants were required to fixate, compared to when they were free to make eye-movements, during the retention interval (Godijn & Theeuwes, 2012). However, Belopolsky and Theeuwes (2009a) were unable to find evidence that spatial attention interacted with spatial working memory performance in a match to sample task.

The key problem in evaluating these competing explanations is that making eye-movements necessarily involves a shift of covert attention (Shepherd, Findlay, & Hockey, 1986). It is also not sufficient to compare VSWM when eye-movements are made and when fixation is maintained (Godijn & Theeuwes, 2012) as participants may be covertly engaging in saccade preparation without execution.

To address this issue we utilized an experimental paradigm in which motor preparation was prevented (Craighero, Nascimben, & Fadiga, 2004; Smith, Ball, Ellison, & Schenk, 2010) and stimuli were presented beyond oculomotor range. We have previously shown that volitional attentional orienting in response to symbolic cues is unimpaired by this manipulation, whereas stimulus-driven shifts of attention triggered by peripheral cues are abolished (Smith, Rorden & Schenk 2012). Related studies of patients with oculomotor deficits have also demonstrated that attention can be covertly oriented to locations beyond the range of their eye movements. For example, Rafal, Posner, Friedman, Inhoff & Bernstien (1988) examined covert attention in patients with Progressive Supranuclear Palsy, a disease characterized by an inability to make vertical eye movements. These patients were unable to covertly attend to peripherally cued locations on the vertical midline, but were relatively unimpaired when orienting to the same locations in response to a centrally presented arrow cue. More recently, we showed that while covert attention to peripheral cues was abolished, symbolic cueing was intact in a patient with ophthalmoplegia (paralysis of the eyes) (Smith, Rorden & Jackson 2004), a result which was subsequently replicated in a larger sample of patients with Duanes Retraction Syndrome (Gabay, Henik, & Gradstein, 2010).

In the current version of the paradigm the participant fixated the centre of the display with one eye (the other was patched). The head and body were then rotated such that there was an angle of 40° between the trunk midline and the center of gaze (Fig. 1A). Participants could see everything in the display, but they were physically unable to make eye-movements further into the temporal hemispace. Eye-movements into the nasal hemispace were physically possible but not permitted as in all conditions participants were required to maintain central fixation. Memoranda were presented wholly in the nasal hemifield or temporal hemifield. In a control condition memory span was assessed with the eye in the center of its orbit (Fig. 1B). VSWM was assessed using four tasks: the Corsi Blocks Task (De Renzi, Faglioni, & Previdi, 1977), the Visual Patterns Task (Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999; Della Salla, Gray, Baddeley, & Wilson, 1975), the Arrow Span Task (Shah & Miyake, 1996), and a size comparison task (Thompson, Hamilton, Gray, Quinn, Mackin, Young, & Ferrier, 2006). A Digit Span task (Dempster & Zinkgraf, 1982) assessed phonological memory. The oculomotor account of VSWM makes a clear prediction: Eye-abduction should disrupt spatial memory when memoranda appear in the temporal hemispace. In contrast, phonological and visual memory should be unaffected by eye-abduction.

2. Method

2.1 Participants

Twenty four participants from Durham University participated in exchange for credits in the department participant pool. Participants were assigned to one of two groups. Group 1 performed the Corsi Blocks task, the Visual Patterns task and the Digit Span task. Group 2 performed the Arrow Span task, the Size Estimation task and the Digit span task. There were 12 participants in each group (Group 1: 4 male, age range 18 to 36 years, mean age 22.6, SD = 5.6, 8 were right eyed; Group 2: 3 male, age range 18 to 31 years, mean age 21.3, SD = 4.5, 6 were right eyed). 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 those who wore contact lenses were tested.

2.2 Procedure

Stimuli were presented on a 20-inch monitor (1024 by 768 resolution, refresh rate 100 Hz) using E-prime (Psychology Software Tools Inc., Pittsburgh, PA, USA). The viewing distance was 57cm with the centre of the screen at eye level. The head was supported by a chin rest. Participants sat in a chair attached to a rotating base that was marked with plus and minus

40° enabling the experimenter to accurately rotate the chair in either direction. A handle was attached to the back of the chair to allow efficient movement. Likewise, the chin rest could be rotated to +/- 40°. Participants used their dominant eye and their non-dominant eye was patched. Eye-dominance was assessed using a confrontation technique: 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 left eye was dominant, the right eye was patched and the participant was rotated to the right.

For all tasks participants were required to fixate on a central spot (0.3° visual angle) during the whole trial. Eye-movements were recorded to ensure compliance. Trials where participants made an eye-movement were discarded and repeated. Participants did not receive feedback about whether they had responded correctly. Memory span was assessed three times in each of the four conditions (Frontal Nasal, Frontal Temporal, Abducted Nasal, Abducted Temporal, Fig.1). The tasks were blocked such that all 12 spans were taken before the next task was started. The order of tasks was counterbalanced between participants, as was the order of field of presentation and eye position within tasks. The only constraint was that participants did not complete two conditions of the same eye positions in a row.

Fig.1.

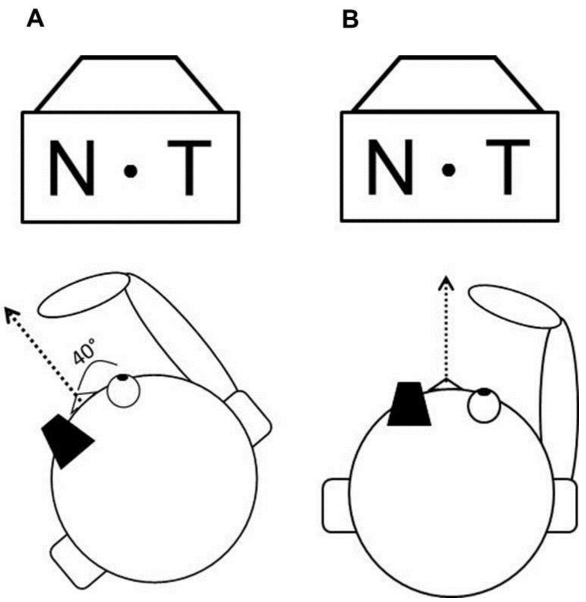

Figure 1. Schematic of the experimental set up. Participants performed the task monocularly with the preferred eye. The non-preferred eye was patched. T= temporal hemifield, N= nasal hemifield. In the Eye abducted condition the head and torso were rotated away from the vertical midline by an angle of 40° (Panel A). A laser pointer was attached to the centre of the head to allow the experimenter to monitor head position. Eye position was monitored using EOG. In the Eye frontal condition the eye was in the centre of its orbit (Panel B).

2.3 Tasks

2.3.1 Spatial memory: Corsi Blocks

Nine boxes, arranged in a 3 x 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 second 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 250ms luminance change at a placeholder. There was a 250ms delay between consecutive items in a sequence. After presentation of the final item, the placeholder array disappeared and participants maintained fixation for 3000 ms. The array then reappeared and participants were required to click the squares in the order they flashed. Each placeholder measured 2.2° x 2.2° visual angle and the array of locations measured 7.2° visual angle in height and width. The center of the array was 4.4° from fixation.

2.3.2. Spatial memory: Arrow span

A sequence of arrows was presented (sequences started with three arrows up to a maximum of eight). After a 3 second retention interval participants had to reproduce the sequence by clicking in the locations indicated by the arrows. Trials began with the presentation of a central fixation spot for 500 ms. Each arrow was presented for 1000ms with a 250ms interval between arrows (arrow length 3.3°, arrow tips 0.8° wide). Following the final arrow of the sequence the array disappeared and a fixation spot was presented for 3000 ms. After this delay participants were presented with an array of eight boxes (2.2° x 2.2°) arranged in a hollow square configuration for 500ms. The center of the array was 4.5 ° from fixation

Participants were required to recall the locations indicated by the arrows in the correct sequence. Responses were made by mouse-clicking the box that had been indicated by the arrow. Each orientation could only be presented once within a sequence. Figure 2C illustrates the sequence of events.

2.3.3. The visual patterns task

Participants were presented with matrices in which half of the squares were white and the other half were black and they had to reproduce the pattern after the retention interval (Fig. 2B). Patterns started with 8 squares and increased by two squares each time up to a maximum of 20 squares. At trial onset a fixation spot and an empty grid were presented for 1000 ms. This grid was replaced with a matrix in which half of the squares were black, presented for 1500 ms. Following the offset of the matrix a fixation spot was presented for 3000 ms. An empty grid was then presented. Participants were required to click in the squares that were previously black, and when clicked, the square went black. Each square measured 2.1° of visual angle. 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. The center of the array was 4.15° from fixation.

2.3.4. Visual memory – size estimation

Participants were required to compare the size of two squares (Fig 2D). The percentage size difference (in pixels) between the two squares decreased as participants moved through the levels. The six levels of difficulty were 30% difference between the two squares, 20%, 15%, 10%, 5%, and 3%. There were three sizes of starting squares that participants could be presented with: 100 x 100 pixels (3.6° of visual angle), 150 x 150 pixels (5.4° of visual angle), and 200 x 200 pixels (7.2° of visual angle). For each of these squares, the second square could be smaller, the same, or bigger, thus creating nine possible combinations of stimuli. For example, if first presented with a square 150 x 150, and the difference was 30%, the second square could be 195 or 105 pixels (or 150 pixels if the second square was the same size). The biggest square was 260 x 260 and measured 9.4° visual angle. For each level, participants were presented with four trials, randomly selected from the nine possible trials. Participants were required to get at least three of the four trials correct in order to progress to the next level where the percentage difference in size between the two squares would be reduced. Span was taken as the percentage change at which participants were correct on at least three out of the four trials.

In the case of left side presentation, the square was right aligned 1.1° degrees of visual angle from the central fixation spot. Had the squares been centralised, participants would be able to tell if the shading was in the same place or not and it would not be a size estimation task but memory for the location of the start of the shading. Likewise, squares presented on the right side were left aligned 1.1° from fixation.

Participants were presented with a central fixation spot for 500 ms. The first square was then presented for 1000 ms. This was followed by the fixation spot for 3000 ms. The second box was then presented for 1000 ms. Participants then had to decide if the second square was bigger, smaller, or the same size as the first square. Participants made their response by using a mouse to click in one of three boxes presented on the screen (response boxes were 5.3° in width and 2.9° visual angle in height).

2.3.5. Verbal memory

Verbal memory was assessed using a digit span task, whereby participants were presented with random strings of digits (containing a minimum of 3 digits and a maximum of 9, with each digit only presented once) at the rate of one per second. Each trial started with the central fixation spot presented for 500ms. This spot remained on the screen throughout the trial and participants were required to keep fixation on this at all times. Each digit was presented for 1000 ms with 500 ms between each item in the sequence. After the final digit the fixation spot remained on screen for 3000 ms. A prompt then appeared instructing participants to verbally report the digits in the correct order. Digits measured 0.6° of visual angle in height and 0.5° of visual angle in width (Courier New, bold) and were located 2.0° of visual angle either side of the fixation spot.

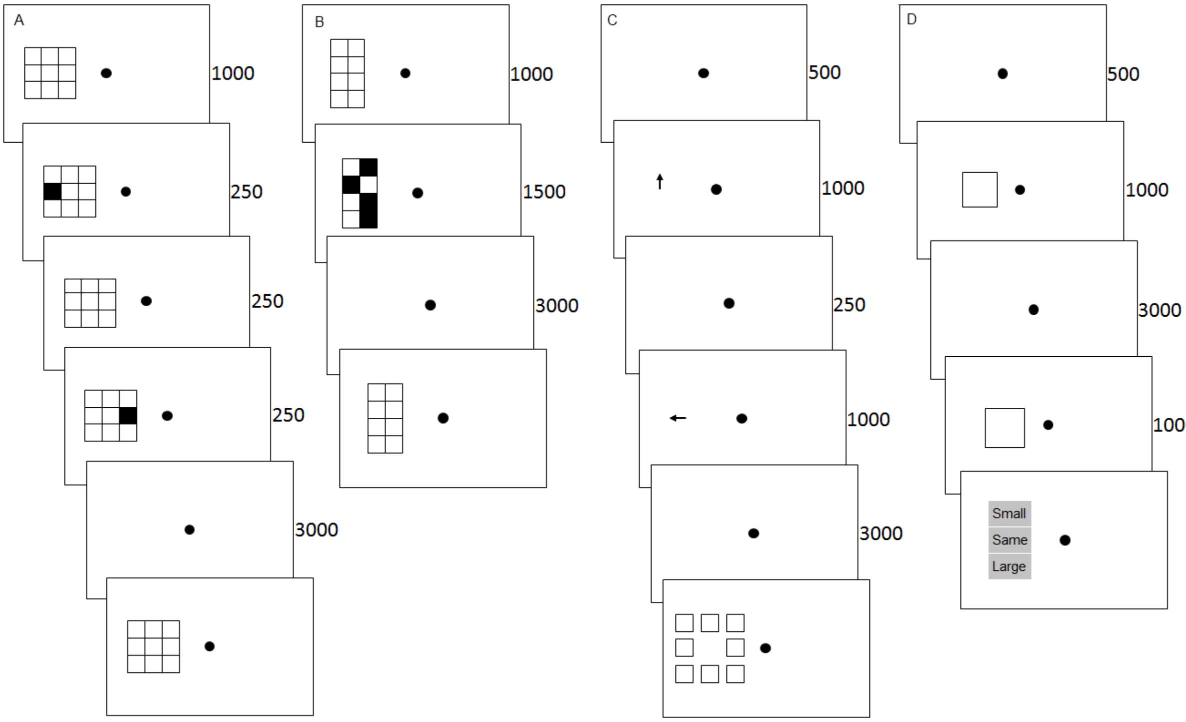

Figure 2. The sequence of events and presentation times during the Corsi Blocks task (A), the Visual Patterns task (B), the Arrow Span task (C), and the Size Estimation task with a 15%

difference between the objects (D). Times are in milliseconds. The response screens were displayed until the response was completed. The digit span task is not shown.

2.4 Eye-movement recording

Electro-oculographic eye-movement data were recorded throughout the trials using a Biopac MP150 acquisition unit and Acqknowledge 4.2 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: two electrodes 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.

3. Results

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 was applied, or where noted in the test. Span for each condition was taken three times and averaged. Each task was analysed separately using 2 (Eye Position: Frontal, Abducted) x 2 (Side of Presentation: Nasal, Temporal) repeated measures ANOVAs.

3.1. Eye Movements

Eye movement data were analysed online by the experimenter. Trials where the participant broke fixation or made a head movement were repeated immediately (4.12% of spatial trials, 2.69% visual, and 1.87% verbal).

3.2. Corsi Blocks Task

ANOVA revealed a significant main effect of Side of Presentation ($F_{(1,11)} = 5.18$; $p = .044$, $\eta^2 = 0.32$) and a significant interaction between Eye Position and Side of Presentation ($F_{(1,11)} = 13.36$; $p < 0.01$, $\eta^2 = 0.55$). Planned comparisons (paired samples t-tests) revealed that memory span was significantly lower for stimuli in the Temporal hemispace compared to the Nasal hemispace in the eye-abducted condition ($M = 3.91$, $SE = 0.31$ vs. $M = 4.51$, $SE = 0.30$; $t_{(11)} = 8.68$; $p < 0.01$, $d = 0.58$). In contrast, in the Frontal condition memory spans were equivalent in the Temporal and Nasal hemifields ($M = 4.43$, $SE = 0.35$ vs. $M = 4.37$, $SE = 0.35$; $p = .791$). See Figure 3 for an illustration of these results.

3.3. Arrow Span Task

There were no significant main effects. The interaction between Side of Presentation (Temporal, Nasal) and Eye Position (Frontal, Abducted) was not statistically significant ($F_{(1,11)} = 0.019$; $p = 0.892$).

3.4. Visual Patterns Task

There were no significant main effects. The interaction between Side of Presentation (Temporal, Nasal) and Eye Position (Frontal, Abducted) was not statistically significant ($F_{(1,11)} = 0.063$; $p = 0.807$).

3.5. Size Estimation Task

There were no significant main effects. The interaction between Side of Presentation (Temporal, Nasal) and Eye Position (Frontal, Abducted) was not statistically significant ($F_{(1,11)} = 0.972$; $p = 0.356$).

3.6. Digit Span Task

Data from the digit span task were collapsed across Groups 1 and 2. Mean spans and standard deviations are shown in Table 1. There was a non-significant trend toward a main effect of Side of Presentation ($F_{(1,11)} = 3.1$; $p = 0.088$), such that digit spans were longer in the Temporal hemispace (6.26 items) than in the Nasal hemispace (6.07 items). However, the interaction between Side of Presentation (Temporal, Nasal) and Eye Position (Frontal, Abducted) was not statistically significant ($F_{(1,23)} = 2.76$; $p = 0.110$).

Table 1
Mean digit span collapsed across groups 1 & 2. Standard deviations are shown in brackets.

	Eye Frontal		Eye Abducted	
	Temporal	Nasal	Temporal	Nasal
Digit Span	6.28 (1.7)	5.92 (1.39)	6.10 (1.46)	6.15 (1.4)

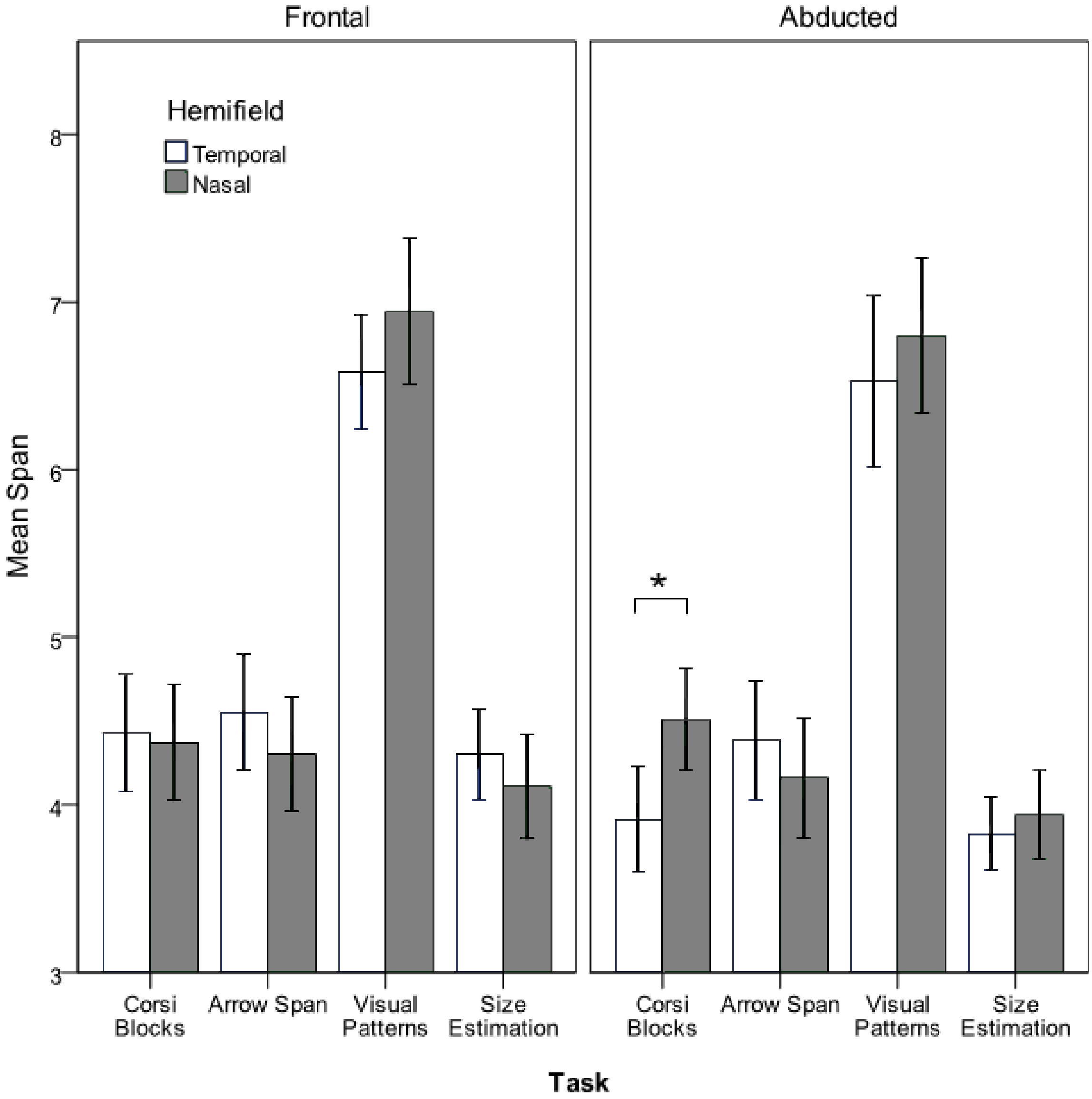

Figure 3: Mean memory span on the different visuospatial working memory tasks. Eye abduction led to significantly reduced memory span in the Temporal hemifield for the Corsi

Blocks Task. No other task was affected by Eye Abduction. *$p < 0.01$. Error bars show +/-1 SEM.

4. Discussion

Spatial span was reduced when stimuli were presented at locations that could not be encoded as the goal of an eye-movement, but only for the Corsi blocks task (Fig. 3). On first inspection, the finding that disrupting oculomotor preparation by eye-abduction interfered with memory span on the Corsi blocks task but not visual patterns, size estimation or digit span tasks appears to be consistent with the view that spatial, but not visual working memory is critically dependent on activity in the eye-movement system (Baddeley, 1986; Lawrence et al., 2004; Postle et al., 2006). However, it was also found that performance on the arrow span task was unaffected by eye-abduction. This result was somewhat surprising, given that the arrow span task is typically regarded as a measure of spatial working memory (Shah & Miyake, 1996).

The Arrow span and Corsi tasks differ in a fundamental way. Specifically, the arrow span task uses a symbolic cue to indicate the to-be-remembered location, whereas in the Corsi task the memory locations are indicated using a peripheral visual transient at the to-be-remembered location. This difference is important because several lines of evidence from studies on spatial attention suggest that the oculomotor system is critically involved in attentional orienting in response to peripheral cues (known exogenous attention), but not required for attentional orienting in response to symbolic cues. In the introduction we described several examples of neuropsychological dissociations between symbolic cueing and the oculomotor system, such that patients with defective oculomotor control were still able to covertly orient attention in response to symbolic cues (Gabay et al., 2010; Rafal et al., 1988;

Smith et al., 2004). Similarly, our previous work using the eye-abduction technique offers more direct evidence that endogenous attention shifts can occur independently of the ability to make eye-movements (Smith et al., 2012), in that numeric cues elicited covert endogenous shifts of attention to locations in the temporal hemispace that could not become the goal of a saccadic eye movement. In related work, Klein and colleagues conducted a series of dual-task studies in which the primary task was to covertly orient attention in response to a symbolic cue and the secondary task was to make a saccadic eye-movement. Consistent with the idea that symbolic cueing and oculomotor control can be dissociated, Klein et al., found that a covert shift of attention triggered by a symbolic cue did not facilitate a subsequent saccadic eye-movement (Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1994). Similarly, Belopolsky & Theeuwes (2009b) report that covert attention to items in working memory is associated with inhibition of the oculomotor system, and argue that maintaining attention at a spatial location must therefore be independent of the preparation of movements to that location (see also Belopolsky & Theeuwes, 2012). A more detailed review of the behavioural and neuropsychological evidence relating to the role of the eye-movement system is covert attention can be found in Smith & Schenk (2012). Together, these studies suggest that the oculomotor system has a highly specific function in spatial attention: It mediates orienting to sudden peripheral events, but not endogenous orienting or maintenance of attention in response to a symbolic cue. The current experiment suggests that this functional dissociation with respect to the role of the eye-movement system in different modes of spatial attention extends to the role of the eye-movement system in spatial working memory.

The finding that disrupting oculomotor preparation has a specific effect on memory span in the Corsi blocks task has important implications for the understanding of the mechanisms mediating visuospatial working memory. There has been a lively debate concerning the mechanism underlying VSWM, with some authors arguing for an oculomotor mechanism (e.g. Lawrence et al., 2004; Pearson & Sahraie, 2003) and others arguing for a higher-level attentional mechanism (e.g. Awh, Vogel, & Oh, 2006). The implicit assumption in this debate is that spatial memory relies on a single mechanism. However, our results suggest that this assumption may not be correct. Rather, it may be that spatial memory tasks that require the processing of symbolic cues utilize an attentional encoding/rehearsal mechanism, whereas tasks that do not require this processing (i.e. where the memoranda are directly signaled by a salient peripheral transient) utilize a lower-level oculomotor mechanism. Consistent with this suggestion, the studies which argue for the primacy of the oculomotor system typically use tasks in which the locations of multiple spatial locations are indicated by peripheral visual transients (Group 1 of this study; Lawrence et al., 2004; Pearson & Sahraie, 2003; Smyth & Scholey, 1994; Tremblay et al., 2006), whereas those that argue for independence of oculomotor and spatial memory systems use tasks in which the location of memoranda are indicated using some form of symbolic cueing system (Group 2 of this study; Godijn & Theeuwes, 2012).

Our findings can also be considered within the context of the “looking at nothing” phenomenon reported in the literature, in which participants are observed to make regular eye movements to empty regions of space previously occupied by relevant visual stimuli (Altmann, 2004; Richardson & Spivey, 2000). It has been argued that this phenomenon provides evidence 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 et al., 2004). However, it is notable that previous studies have typically failed to find any association between regular shifts of gaze and improved memory accuracy (Richardson & Spivey, 2000; Hoover & Richardson, 2008). Along similar lines, a recent study by Martarelli and Mast (2013) manipulated eye-position during pictorial recall and found no increase in memory accuracy when participants look at areas where stimuli had previously appeared, in comparison to when looking at non-corresponding areas of the screen.

Our present findings show that accuracy for spatial memory is significantly reduced when participants are unable to make saccades to peripherally cued locations, in contrast to conditions where their gaze is fixated but oculomotor preparation to salient locations remains possible. Considering that participants can covertly prepare saccades without subsequent execution, the functional importance of actual overt eye movements in spatial memory may well be limited. Pearson and Sahraie (2003) found no difference in Corsi span when participants were free to move their eyes compared to when participants' gaze remained fixated. A similar finding has been reported regarding spatial memory for the location of simultaneously presented digits (Godijn & Theeuwes, 2012). A considerable advantage of the eye abduction paradigm we have used in the current study is that it allows for oculomotor involvement in spatial working memory to be examined independently from overt movement of the eyes.

We have argued that impaired memory for peripherally cued locations that cannot become the goal of a saccadic eye-movement is evidence for an oculomotor theory of spatial working memory. However, it may be argued that given that VSWM performance is not completely abolished in the abducted temporal condition, but rather it is reduced on average by 0.6 of an item (*SE* .07, range 0.33 to 1.00 item reduction) relative to the abducted nasal condition, our conclusion that VSWM is dependent on the eye-movement system is too strong. However, a reduction in spatial span, as opposed to an abolishment, is comparable with the findings from verbal working memory. Articulatory suppression, where participants are required to utter an irrelevant word or sound which prevents rehearsal, does not result in participants being able to recall no words/digits but rather a significant reduction in verbal span (Baddeley, Thomson, & Buchanan, 1975; Murray, 1967). Reductions in verbal recall with articulatory suppression are taken as evidence of articulatory rehearsal processes within the phonological loop of the working memory model (Baddeley, 2003). Our current findings demonstrate that Corsi span is significantly enhanced when participants have the ability to plan saccades to the to-be-remembered locations. In contrast, when eye-abduction prevents locations being encoded as the goal of eye-movements this capacity is lost, and participants are forced instead to rely on less effective visual-based strategies (Rudkin, Pearson, & Logie, 2007; Parmentier, Elford, & Maybery, 2005). Thus, we argue that for optimal VSWM for a sequence of peripherally cued locations the oculomotor system is necessary.

It should also be noted that although eye-abduction disrupted oculomotor control, it remains possible that participants encoded spatial locations in the temporal hemispace as some other form of action (e.g. a combined eye-head movement). So, while our results clearly argue for the importance of the oculomotor system in the Corsi Blocks task, the failure to observe effects of eye-abduction on the other tasks should not be taken as unequivocal evidence that other forms of VSWM are independent of action control.

Our findings cannot be explained by a generalized disruptive effect of eye-abduction as performance in the abducted nasal condition was no different than its frontal counterpart ($t(11) = -.570$; $p = .580$), and the main effect of Eye Position was not statistically significant.

Similarly, the observation of reduced spatial span in the abducted temporal condition cannot be explained by differences in the quality of the sensory information across the four conditions for three reasons. Firstly, participants were required to fixate on the centre of the screen throughout all trials, so memoranda were equidistant from the fovea in different conditions (trials where fixation was not kept were repeated). Secondly, previous findings show that eye-abduction does not reduce visual acuity (Craighero et al., 2004). Finally, there was no deficit of verbal or visual working memory for stimuli presented in the temporal hemifield, arguing against an explanation that the spatial deficit we observe in the abducted temporal condition is because of reduced visual acuity in this condition.

To summarise, it has been shown that disrupting oculomotor preparation produces a significant impairment of spatial working memory that is specific to the Corsi blocks task. We have argued that the oculomotor system plays an important role in spatial working memory, but only under conditions where the memorized locations are directly indicated by a change in visual salience. When the memorized locations are indicated by the meaning of a symbolic cue spatial working memory is mediated by attention, not the oculomotor system. This hypothesis accounts for the existing empirical data and offers a way of resolving the debate regarding the role of the eye-movement system in spatial working memory.

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). We thank Mr. Andrew Long for mechanical assistance.

References

Altmann, G.T. (2004). Language-mediated eye movements in the absence of a visual world: The 'blank screen paradigm'. *Cognition, 93(2),* B79-B87.

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

Awh, E., Jonides, J., & Reuter-Lorenz, P. A. (1998). Rehearsal in spatial working memory. [Article]. *Journal of Experimental Psychology-Human Perception and Performance, 24*(3), 780-790. doi: 10.1037//0096-1523.24.3.780

Awh, E., Vogel, E. K., & Oh, S. H. (2006). Interactions between attention and working memory. *Neuroscience, 139*(1), 201-208.

Baddeley, A. (1986). *Working Memory*. New York: Oxford University Press.

Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience, 4*(10), 829-839. doi: Doi 10.1038/Nrn1201

Baddeley, A., Thomson, N., & Buchanan, M. (1975). Word length and the structure of short-term memory. *Journal of Verbal Learning and Verbal Behavior, 14*(6), 575-589. doi: 10.1016/s0022-5371(75)80045-4

Belopolsky, A. V., & Theeuwes, J. (2009)a. No functional role of attention-based rehearsal in maintenance of spatial working memory representations. [Article]. *Acta Psychologica, 132*(2), 124-135. doi: 10.1016/j.actpsy.2009.01.002

Belopolsky, A. V., & Theeuwes, J. (2009)b. Inhibition of saccadic eye movements to locations in spatial working memory. [Article]. *Attention Perception & Psychophysics, 71*(3), 620-631.

Brandt, S. A., & Stark, L. W. (1997). Spontaneous eye movements during visual imagery reflect the content of the visual scene. *Journal of Cognitive Neuroscience, 9*(1), 27-38. doi: 10.1162/jocn.1997.9.1.27

Craighero, L., Nascimben, M., & Fadiga, L. (2004). Eye position affects orienting of visuospatial attention. *Current Biology, 14*(4), 331-333.

De Renzi, E., Faglioni, P., & Previdi, P. (1977). SPATIAL MEMORY AND HEMISPHERIC LOCUS OF LESION. [Article]. *Cortex, 13*(4), 424-433.

Della Sala, S., Gray, C., Baddeley, A., Allamano, N., & Wilson, L. (1999). Pattern span: a tool for unwelding visuo-spatial memory. [Article]. *Neuropsychologia, 37*(10), 1189-1199.

Della Salla, S., Gray, C., Baddeley, A., & Wilson, L. (1975). *Visual Patterns Test: A test of short-term visual recall*. Bury-St-Edmonds: Thames Valley Test Company.

Dempster, F. N., & Zinkgraf, S. A. (1982). Individual-Differences in Digit Span and Chunking. *Intelligence, 6*(2), 201-213.

Ferreira, F., Apel, J., & Henderson, J.M. (2008). Taking a new look at looking at nothing. *Trends in Cognitive Sciences, 12(11),* 405-410.

Gabay, S., Henik, A., & Gradstein, L. (2010). Ocular motor ability and covert attention in patients with Duane Retraction Syndrome. *Neuropsychologia, 48*(10), 3102-310

Godijn, R., & Theeuwes, J. (2012). Overt is no better than covert when rehearsing visuo-spatial information in working memory. *Memory & Cognition, 40*(1), 52-61. doi: 10.3758/s13421-011-0132-x

Hoover, M.A., & Richardson, D.C. (2008). When facts go down the rabbit hold: Contrasting features and objecthood as indexes to memory. *Cognition, 108,* 533-542.

Johansson, R., Holsanova, J., Dewhurst, R., & Holmqvist, K. (2012). Eye movements during scene recollection have a functional role, but they are not reinstatements of those produced during encoding. *Journal of Experimental Psychology: Human Perception and Performance, 38*(5), 1289-1314. doi: 10.1037/a0026585

Klauer, K. C., & Zhao, Z. M. (2004). Double dissociations in visual and spatial short-term memory. *Journal of Experimental Psychology-General, 133*(3), 355-381. doi: Doi 10.1037/0096-3445.133.3.355

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 & Review, 11*(3), 488-494. doi: 10.3758/bf03196600

Martarelli, C.S., & Mast, F.W. (2013). Eye movements during long-term pictorial recall. *Psychological Research, 77,* 303-309.

Murray, D. J. (1967). Role of Speech Responses in Short-Term Memory. *Canadian Journal of Psychology, 21*(3), 263-263.

Parmentier, F.B., Elford, G., & Maybery, M. (2005). Transitional information in spatial serial memory: path characteristics affect recall performance. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31(3)*, 412-427.

Pearson, D. G., & Sahraie, A. (2003). Oculomotor control and the maintenance of spatially and temporally distributed events in visuo-spatial working memory. [Article]. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology, 56*(7), 1089-1111. doi: 10.1080/02724980343000044

Postle, B. R., Idzikowski, C., Della Sala, S., Logie, R. H., & Baddeley, A. D. (2006). The selective disruption of spatial working memory by eye movements. [Article]. *Quarterly Journal of Experimental Psychology, 59*(1), 100-120. doi: 10.1080/17470210500151410

Rafal, R. D., Posner, M. I., Friedman, J. H., Inhoff, A. W., & Bernstein, E. (1988). Orienting of Visual-Attention in Progressive Supranuclear Palsy. *Brain, 111*, 267-280

Repovs, G., & Baddeley, A. (2006). The multi-component model of working memory: Explorations in experimental cognitive psychology. [Review]. *Neuroscience, 139*(1), 5-21. doi: 10.1016/j.neuroscience.2005.12.061

Richardson, D.C., Altmann, G.T.M., Spivey, M.J., & Hoover, M.A. (2009). Much ado about eye movements to nothing: A response to Ferreira et al.: Taking a new look at looking at nothing. *Trends in Cognitive Sciences, 13(6),* 235-236.

Richardson, D.C., & Spivey, M.J. (2000). Representation, space and Hollywood squares: Looking at things that aren't there anymore. *Cognition, 76(3),* 269-295.

Rudkin, S.J., Pearson, D.G., & Logie, R.H. (2007). Executive processes in visual and spatial working memory tasks. *Quarterly Journal of Experimental Psychology, 60(1),* 79-100.

Shah, P., & Miyake, A. (1996). The separability of working memory resources for spatial thinking and language processing: An individual differences approach. [Proceedings Paper]. *Journal of Experimental Psychology-General, 125*(1), 4-27.

Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The Relationship between Eye-Movements and Spatial Attention. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology, 38*(3), 475-491.

Smith, D. T., Ball, K., Ellison, A., & Schenk, T. (2010). Deficits of reflexive attention induced by abduction of the eye. *Neuropsychologia*, *48*, 1269-1276.

Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. *Current Biology, 14*(9), 792-795.

Smith, D. T., Rorden, C., & Schenk, T. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. [Journal Article]. *Journal of Experimental Psychology-Human Perception and Performance, 38*(6), 1438-1447. doi: 10.1037/a0027794

Smith, D. T., & Schenk, T. (2012). The Premotor theory of attention: Time to move on? *Neuropsychologia, 50*(6), 1104-1114.

Smyth, M. M., & Scholey, K. A. (1994). CHARACTERISTICS OF SPATIAL MEMORY SPAN - IS THERE AN ANALOGY TO THE WORD-LENGTH EFFECT, BASED ON MOVEMENT TIME. [Article]. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology, 47*(1), 91-117.

Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: eye movements to absent objects. *Psychological Research-Psychologische Forschung, 65*(4), 235-241. doi: 10.1007/s004260100059

Spivey, M.J. et al. (2004). Thinking outside the brain: oculomotor indexes to visual and linguistic information. In J.M. Henderson and F. Ferreira. (Eds), *The Interface of Language, Vision and Action: Eye Movements and the Visual World,* pp. 161-190, Hove: The Psychology Press.

Thompson, J.M., Hamilton, C.J., Gray, J.M., Quinn, J.G., Mackin, P., Young, A.H., & Ferrier, I.N. (2006). Executive and visuospatial sketchpad resources in euthymic bipolar disorder: implications for visuospatial working memory architecture. *Memory, 14(4),* 437-451.

Tremblay, S., Saint-Aubin, J., & Jalbert, A. (2006). Rehearsal in serial memory for visual-spatial information: Evidence from eye movements. *Psychonomic Bulletin & Review, 13*(3), 452-457. doi: 10.3758/bf03193869

Tresch, M. C., Sinnamon, H. M., & Seamon, J. G. (1993). Double dissociation of spatial and object visual memory: evidence from selective interference in intact human subjects. *Neuropsychologia, 31*(3), 211-219.