DIRECTION SPECIFIC COSTS TO SPATIAL WORKING MEMORY

FROM SACCADIC AND SPATIAL REMAPPING

by

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A thesis
presented to the University of Waterloo
in fulfilment of the
thesis requirement for the degree of
Master of Arts
in
Psychology

Waterloo, Ontario, Canada, 2007
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Abstract

Right parietal lesions often lead to neglect, in which patients fail to attend to leftward stimuli. Recent models of neglect suggest that, in addition to attentional impairments, patients demonstrate impairments of spatial remapping and/or spatial working memory (SWM). Although spatial remapping could be considered a kind of spatial memory process itself (i.e., updating remembered locations based on anticipated saccade outcomes), the two processes operate on very different time scales (milliseconds versus seconds). In the present study, the influence of saccadic and spatial remapping on SWM was examined in healthy individuals. An initial control condition, in which participants had to respond to a probe stimulus (i.e., "is the probe in the location previously occupied by the target?") following a 1500 ms delay, was contrasted with conditions in which the fixation point moved (left, right, up, or down) at the onset of the delay. In a second version of the task, participants made covert shifts of attention at delay onset requiring covert spatial, rather than saccadic, remapping. In both tasks SWM performance was best when no remapping was required. Decrements in SWM were largest overall in the spatial remapping task, whereas for both saccadic and spatial remapping, a consistent cost was observed for remapping the target array into right visual space. Results are discussed in terms of hemispheric biases in attention and differences in performance for peripersonal versus extrapersonal space.

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Introduction

One of the most common consequences of right parietal lesions is the disorder of unilateral

spatial neglect, in which patients behave as if one half of their world has simply ceased to exist

(Danckert & Ferber, 2006). Neglect is typically defined as a failure to report, respond to, or orient

towards stimuli in contralesional space (Danckert & Ferber, 2006; Heilman, Watson & Valenstein,

1993; Driver & Mattingley, 1998; Halligan, Fink, Marshall & Vallar, 2003). Neglect patients may shave

only the right side of their face or eat food from only the right half of a plate, and in general they fail to

attend or respond to stimuli or events on the left side of space. Symptom profiles of patients with neglect

tend to be extremely heterogeneous, making it difficult to construct comprehensive neurocognitive

models of the disorder. Most theories of neglect focus on the obvious impairments of spatial attention

evident in these patients, which can be broadly characterised by two interacting components. The first is

an attentional selection bias toward ipsilesional space (Kinsbourne,1993), and the second – the so-called

'disengage deficit' – represents a difficulty in reorienting attention away from ipsilesional stimuli

toward stimuli and events in contralesional space (Posner, Walker, Friedrich & Rafal, 1984).

More recent attempts to understand the neglect syndrome suggest, however, that the disorder is

not simply due to attentional impairments that favour ipsilesional stimuli. Instead, the neglect syndrome

is made up of several component deficits including spatial and non-spatial impairments that in concert

lead to impaired awareness for contralesional space (Danckert & Ferber, 2006; Ferber & Danckert,

2006; Pisella & Mattingley, 2004). In addition to attentional biases, it has been suggested that deficits in

spatial working memory (SWM) and/or spatial remapping are at the heart of the loss of awareness for

contralesional stimuli and events (Danckert & Ferber, 2006; Pisella & Mattingley, 2004).

Clinical tests used for assessing the presence or severity of neglect provide some hints that the

disorder involves more than impaired attentional orienting. For example, when performing a

cancellation task in which the patient must place a mark through targets presented on a page aligned to

their body's midline, patients typically fail to mark a substantial portion of targets to the left of midline.

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In addition to this most obvious manifestation of neglect, patients also commonly fail to cancel some targets from the right (putatively non-neglected) half of the page. Such a deficit would suggest that even for supposedly non-neglected space the patient has difficulty maintaining (or updating) an accurate representation of the spatial array. In addition, patients commonly place more than one cancellation mark through the same target, apparently treating old target locations (i.e., locations that have already been cancelled), as if they were new (Malhotra, Mannan, Driver, & Husain, 2004). These findings on more clinically based tasks are further supported by experimental research using visual search paradigms. In one such study researchers found that, for neglect patients, visual search was most impoverished for displays in left visual space (Behrmann et al., 2004). Although visual search requires the use of SWM, the previously discussed study was not designed to examine the two mechanisms independently. However, there is substantial research that indicates a SWM deficit in neglect is evident, even in tasks where search behaviour is not required (Ferber & Danckert, 2006; and Malhotra et al, 2005). Thus, the behaviours observed on clinical tests discussed above, suggest that patients' memory for a given spatial array is impaired. This deficit that has now been demonstrated in a wide variety of tasks and circumstances clearly indicates a spatial working memory deficit, relatively independent of biases in spatial attention (Ferber & Danckert, 2006; Malhotra et al., 2004; Husain et al., 2001; Wojciulik et al., 2004). In other words, these behaviours – omitting right sided targets and revisiting old locations as if they were new – cannot easily be accounted for by an attentional impairment alone favouring stimuli in right space.

Pisella and Mattingley (2004) have suggested that many of the behaviours observed in neglect could be explained by an impairment in spatial remapping during shifts of attention (both overt and covert), in addition to the commonly observed attentional deficits. In their model, internal representations of the environment, referred to as 'salience maps', must be continually updated (or 'remapped') to account for changes in the absolute and relative positions of objects. In addition, one's own actions, including eye movements or even covert shifts of spatial attention, have consequences for

those internal representations. The kind of remapping or spatial updating being referred to in Pisella and Mattingley's model reflects the process of updating internal representations as a consequence of shifts of attention, whether executed overtly (i.e., via eye movements) or covertly (e.g., via covert shifts of attention).

Initial demonstrations of saccadic remapping processes come from the monkey neurophysiology literature (Duhamel, Colby, & Goldberg, 1992a). In the classic double-step saccade task, two sequential targets for eye movements are presented and extinguished in under 200 ms (i.e., prior to the initiation of a saccade to the first target). The monkey must then anticipate the outcome of the saccade to the first target to appropriately program the saccade to the second target. Relying solely on the retinal locations of the two targets would lead to an erroneous second saccade. Neurons in the monkey lateral intraparietal region (LIP) show increased firing rates during this task, suggesting that they code for the anticipated outcome of intended actions and remap the internal representation of the spatial layout of the environment accordingly (Duhamel, Colby, & Goldberg, 1992a).

In humans, right hemisphere lesions of the kind that often lead to neglect, impair not only the initiation of contralesional saccades (Behrmann, Ghiselli-Crippa, & Dimatteo, 2001, 2002; Behrmann, Ghiselli-Crippa, Sweeney, Dimatteo, & Kass, 2002), but also the ability to perform remapping processes during the execution of saccades (Pisella & Mattingley, 2004; Vuilleumier, Sergent, Schwartz, Valenza, Girardi, Husain, & Driver, 2007). Importantly, according to Pisella and Mattingley's (2004) model of neglect, if the right hemisphere maintains a salience map for the entire visual field, then overt or covert shifts of attention to left visual space will lead to remapping deficits that affect the entire visual field, which is precisely what happens (recall the deficits observed in right, putatively non-neglected space on cancellation tasks discussed above). Duhamel and colleagues (1992b) examined performance on the double-step saccade task in a patient with a large right fronto-parietal lesion and unilateral neglect. When the first target was presented in the patient's right visual field and the second target appeared in the left visual field, the patient was able to acquire both targets accurately. This presumably reflects the

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fact that in this instance he was able to rely on left hemisphere parietal cortex to remap left visual space, based on the anticipated sensorimotor outcomes of the first saccade made to a target in right visual space. In the opposite circumstance, when the first target was presented in the left visual field and the second target appeared in the right, the patient failed to ever acquire the second target.

This result, since replicated in a larger group of patients (Heide et al., 1995), suggests that the damaged right parietal cortex was unable to accurately anticipate the outcome of a saccade made into left visual space and therefore could not remap the visual environment in such a way that the second target could be accurately acquired (Pisella & Mattingley, 2004). Given that previous work has demonstrated remapping deficits in left parietal patients (Heide et al., 1995), a saccadic remapping deficit is obviously not sufficient to demonstrate the neglect syndrome (i.e., the left parietal patients in Heide et al.'s study did not demonstrate neglect). Instead, Pisella and Mattingley (2004) suggest that such a spatial remapping deficit must be accompanied by the attentional deficits (i.e., a rightward attentional bias and a difficulty in disengaging from rightward stimuli) to demonstrate the full neglect syndrome.

More recently, it was shown that neglect patients had difficulty maintaining the spatial locations of targets in a task that required saccadic remapping over a retention interval (Vuilleumier, et al., 2007). In this study patients first identified the colour of a target (i.e., either red or green) by fixating the target (which could appear at random locations to the left and right of fixation). At delay onset the display was either blank, in which case patients were not required to maintain fixation at any specific location, or contained a letter stimulus to the far left or far right of the display, requiring the target location to be remapped due to the gaze shift. A probe appeared after a 2 second delay that could be either at the same location as the coloured target or slightly shifted to the left or right of the initial target position. Patients had to report whether or not the target had changed location by making a same/different judgement. When a gaze-shift was required to the right, thereby requiring the target location to be remapped into left, neglected space, patients demonstrated a striking cost to spatial memory. Interestingly, healthy

controls showed no cost in any of the remapping conditions (Vuilleumier et al., 2007). While the results of this study clearly show a remapping deficit for neglect patients, it is difficult to claim that this is a remapping *influence* on spatial working memory. In the no-remapping condition fixation was not restricted after the target was first identified. Presumably patients could choose to maintain fixation at the target location making this a good control for the effects of remapping (when contrasted with the conditions in which gaze is manipulated during the delay), but a poor example of spatial working memory performance. In addition, when remapping was required, it occurred in multiple stages. That is, the patient would first fixate centrally and presumably form an internal representation of the target location that must then be updated (i.e., 'remapped') when gaze was shifted there. The array must then be remapped again once gaze is shifted to the letter stimulus explicitly used to elicit remapping. Finally, the probe is sufficiently difficult to resolve in peripheral vision that it requires a gaze shift in order to make the final same/different judgement concerning its location. This would again require the internal representation to be updated or 'remapped' (Vuilleumier et al., 2007). Such multiple remapping requirements would compound performance decrements when they were in opposite directions, as was the case for the patients in this study. That is, performance was worst when a target was first identified in left neglected space, and then remapped after a rightward gaze shift and then remapped again when the probe appeared in left space (Vuilleumier et al., 2007). Thus, the methodology used in this study does not provide for an unambiguous exploration of the effects of saccadic remapping on processes of spatial working memory.

Saccadic or spatial remapping processes operate on the order of milliseconds. On clinical tests of neglect, such as the cancellation tasks discussed above, the patient is given unlimited time to find the targets and still fails to cancel many left-sided targets. In addition, patients are often capable of cancelling targets to the far left of the page and returning to cancel targets on the right side of the page. They simply fail – by definition – to cancel a significant portion of left sided targets. These observations have led many authors to suggest that neglect patients suffer from impaired spatial working memory

(Husain et al., 2001; Wojciulik, Husain, Clarke, & Driver, 2001). The definition for spatial working memory (SWM) is remarkably similar to that of spatial remapping in that it involves the ability to keep in mind the locations of stimuli in space and their relation to one another. The critical difference between the two would seem to be the time scale over which they operate (milliseconds for remapping, seconds to minutes for SWM) and their relation to shifts (either overt or covert) of attention. With regard to the latter, spatial remapping processes are explicitly engaged in response to a shift of attention in any direction, whereas SWM has been shown to benefit from attentional shifts to the location of the memorized target(s) only (Awh, Jonides, & Reuter-Lorenz, 1998). Current investigations into the mechanisms behind SWM indicate that spatial information is actively maintained through focal shifts of spatial attention towards the to-be-remembered locations (Postle, Awh, Jonides, Smith, & D'Esposito, 2004; Awh & Jonides, 2001; Awh & Jonides, 1998). In this fashion, overlapping neural circuits involved in spatial attention and spatial working memory are engaged in the rehearsal of spatial information for SWM by keeping the representation of locations activated in memory.

There is mounting evidence that patients with neglect do indeed suffer from impaired spatial working memory (Husain, et al., 2001; Malhotra et al., 2005; Mannan et al., 2005; Wojciulik, Rorden, Clarke, Husain, & Driver, 2004; Ferber & Danckert, 2006). Although many of the results obtained in these studies could be at least partially accounted for by reference to a spatial remapping deficit, others offer more compelling evidence of a fundamental dysfunction of SWM, independent of any remapping problems. In one such study, SWM deficits were observed for stimuli that were vertically aligned in right visual space (Ferber & Danckert, 2006; see also Malhotra et al, 2004 and Malhotra et al, 2005). Such an arrangement ought to minimise the influence of impairments in saccadic remapping which, for neglect patients, are known to be greatest for horizontal saccades that cross the midline, or remapping that occurs entirely in left visual space (Heide et al., 1995; note that the stimuli in Ferber & Danckert's study were all within right visual space, whereas for Malhotra and colleagues stimuli were presented in central space).

The ways in which saccadic and spatial remapping may influence the efficiency of spatial working memory processes was examined in healthy individuals in two experiments. Although Vuilleumier and colleagues (2007) demonstrated clear evidence for an effect of remapping on perception of location changes in neglect patients, several key questions still need to be addressed. First, do saccadic (overt) and spatial (covert) remapping processes operate in the same manner? That is, would covert shifts of attention exert the same influence on SWM as do overt shifts? Second, are there different consequences for SWM from remapping a target array after horizontal shifts of attention (either overtly or covertly) when contrasted with remapping along the vertical meridian? In Experiment 1, I investigated the influence of saccadic remapping processes on the precision of SWM[1] performance under circumstances in which the spatial array had to be remapped as a consequence of a saccade made at the onset of the delay period. In Experiment 2, I explored the effect of covert shifts of attention on SWM accuracy using a similar paradigm in which spatial remapping was induced via a covert attentional shift made at the onset of the delay.

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[1] Memory for spatial information can be broadly categorised into two types of processes: memory for locations and route finding (De Renzi, Faglioni & Villa, 1977). Memory for locations can be further broken down into relational/categorical spatial memory, sometimes referred to as 'object-location binding', and co-ordinate spatial memory known as 'positional memory'. Object-location binding refers to the ability to keep in mind the positions of objects relative to one another (Chalfonte, Johnson, Verfaellie & Reiss, 1996), whereas positional memory is the ability to keep in mind the precise co-ordinates of objects (McNamara, Hardy & Hirtle, 1989). In the present study the SWM task reflects those processes specifically involved in positional memory.

Experiment 1

Methods

Participants

Eighteen healthy normal participants (11 females; mean age = 24 years, ±SD = 4.84; range = 20-39; 1 left handed) participated in Experiment 1. All participants had either normal or corrected to normal vision and were free from any neurological or psychiatric conditions. All participants were recruited from the University of Waterloo, and written informed consent was obtained from each participant prior to commencing the study.

Procedure

Participants were seated in front of a 15.4-inch computer screen at a distance of approximately 45 cm with their head placed in a chin rest. All stimuli were designed using E-Prime software and the task was run on a Dell Optiplex GX260 desktop computer. Each participant completed 20 practice trials and 320 experimental trials that were divided into four equal blocks to provide breaks.

At the beginning of each trial a central fixation cross was presented. After 1000 ms, five target stimuli, consisting of open circles, were presented surrounding the cross in pseudorandom locations. Participants were told that one of the five circles may or may not have a gap in it. 'Gapped circles' resembled either a "C" or a backwards "C" on an equal numbers of trials, with a gapped circle appearing on 80% of all trials. Targets for the spatial working memory task (including "gapped circles" when present) remained on the screen for 500 ms, with participants instructed to make a key press ('m' for yes and 'z' for no on a standard keyboard) to indicate whether a "gapped circle" was present among the array. Participants were then instructed to keep the location of the gapped circle in mind over a brief delay period of 1500 ms. Following the delay, during which participants made their response to the presence or absence of a gap in one of the target circles, a probe stimulus, consisting of a filled circle, appeared in any one of the five target locations. Participants had to indicate whether the probe was presented in the location previously occupied by the gapped circle (Figure 1). To introduce a saccadic

remapping component to the task, at the onset of the delay the fixation cross would shift to one of four locations: to the left, right, up, or down (Figure 1). On 20% of trials the fixation point would remain stationary, thereby not requiring any saccadic remapping of the target array. This condition acted as a control for the remapping trials. Participants were instructed to fixate the cross at all times, such that on trials in which the cross moved at the onset of the delay, participants were also to move their eyes to the new location. To ensure that the cross was fixated throughout the task, eye movements were monitored using a Canon MiniDV ZR500 camcorder.
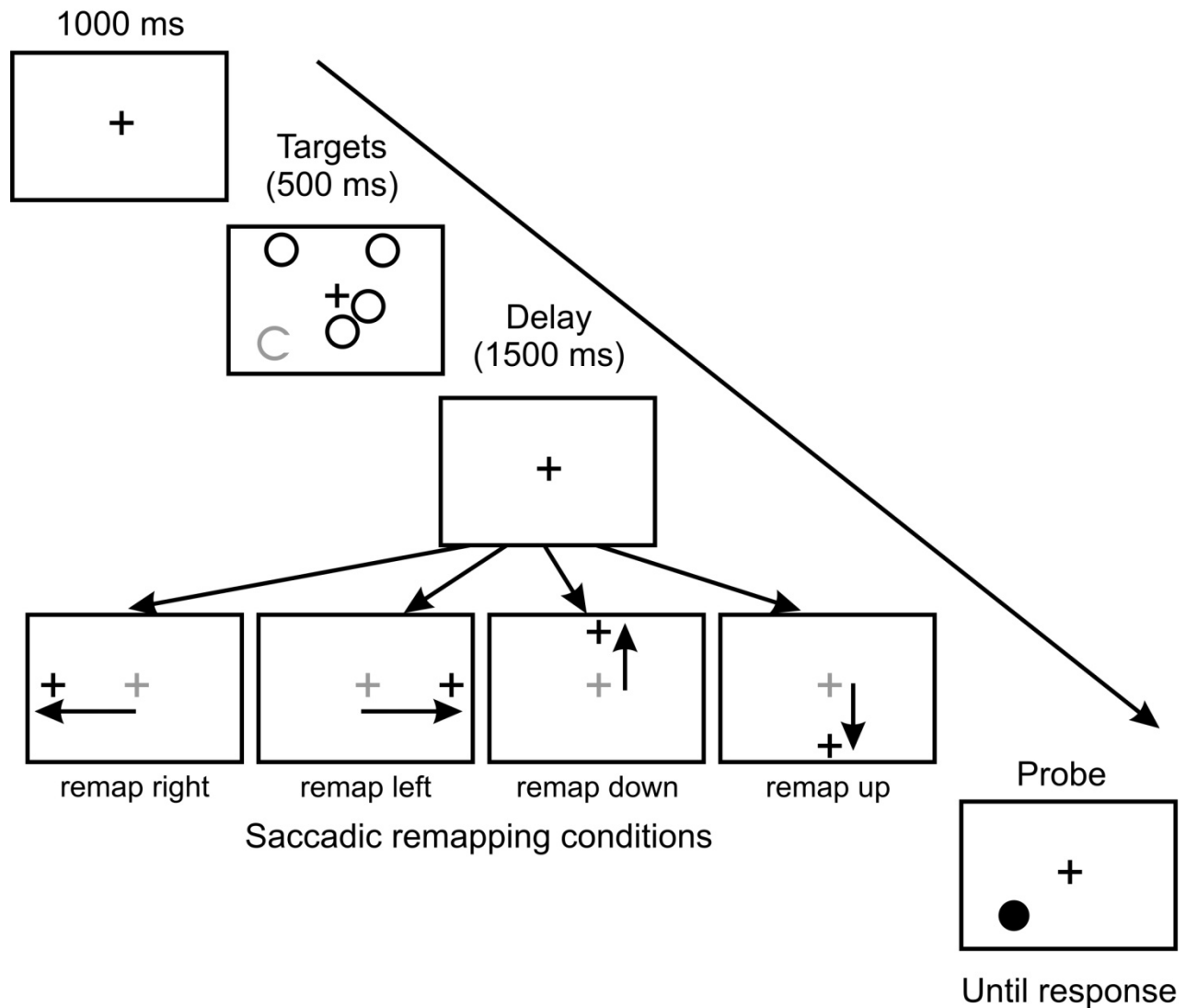
Figure 1. Time course for a single trial of Experiment 1. Participants first identified the presence of a target (a 'gapped circle' indicated in grey in the figure; note, the target was the same colour as non-targets in the actual experiment). Following a delay in which the fixation could remain static or move to one of four possible locations, subjects responded to a probe (filled circle) indicating whether it was presented in the same location as the previously detected target (in the schematic shown the correct answer would be 'yes'). Once the fixation point had shifted it remained in the new location until the end of the trial (in the schematic the fixation point at the time the probe is presented is shown as it would appear in a 'no-remapping' trial). Note that remapping of the stimulus array was in the opposite direction to the shift of the fixation such that a fixation cross moving to the left required the array to be remapped into right visual space and so on.

Several important aspects of the stimulus array warrant further discussion. First, targets could appear in locations that formed two concentric circles around the fixation point (Figure 2). The outer rim of the first circle was 5° from fixation; the rim of the second circle was 15° from fixation. This allowed for the presentation of targets (i.e., gapped circles) in locations close to, or more distant from fixation. This factor was crucial once the saccadic remapping component was added to the task. In short, I wanted to be sure that any influence of saccadic remapping on the efficiency of SWM was not due solely to any effects of the initial eccentricity of targets. By requiring participants to detect a gapped circle in the initial target array, it provided the option to examine whether there were any differences in perceptual capacity for detecting targets according to their distance from fixation that would later influence their SWM performance. In other words, did participants encode target locations more efficiently when they were close to fixation? So on half of the trials in which a gapped circle appeared, it would appear close to fixation, whereas on the other half of trials it would appear further away from fixation (Figure 2). In addition, on half of the trials in which the fixation point moved at the onset of the delay period (see below), the physical location of the gapped circle would now be close to fixation (i.e., after initially being further away from fixation), whereas on the other half of trials the opposite circumstance would arise (i.e., a gapped circle that was initially close to fixation would now be further away from fixation). Once again, this ensured that any possible influence of eccentricity was effectively counterbalanced across trials.

All individual circle stimuli (i.e., open targets, gapped circles, and filled circle probes) subtended a visual angle of 3.25^{o}. The five circle stimuli appeared in various arrangements out of a possible sixteen locations, with the constraint that one stimulus occupied a location in 3 of the 4 quadrants surrounding fixation, and two stimuli occupied a location in the fourth quadrant of the screen (Figure 2). Each visual quadrant contained two stimuli on an equal number of trials. The cross was presented in all five 'shift' fixation positions (centre, left, right, up, or down) an equal number of times (64 trials per condition). When the fixation cross was moved, the visual angle of the displacement was 20° in the horizontal

dimension and 13.75° in the vertical dimension (Figure 2). Probes appeared in the same location as the

previously presented "gapped circle" (the target) on 50% of trials.
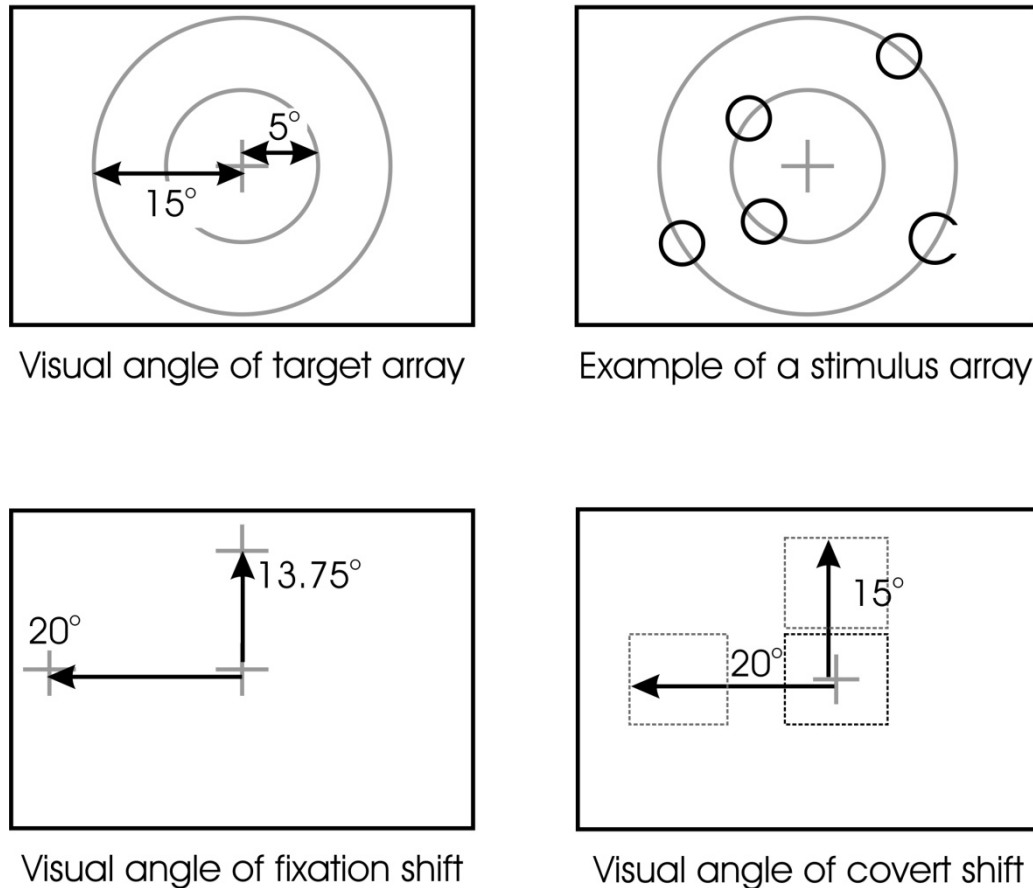
Figure 2. Schematic representations of the visual angles involved in stimulus displays for Experiments 1 and 2. The upper panel shows the arrangement of potential target and distractor stimuli being placed around two concentric circles (not visually present in the display) with a radius of 5 and 15 degrees of visual angle. An example target array is presented to the right. The lower panels represent the degree of visual angle for the shift in fixation (for Experiment 1 represented on the left) and the shift in the target reference frame (for Experiment 2 represented on the right).

Data Analysis

First, the accuracy with which gapped circles were detected was examined according to their location in the target array (prior to any SWM component of the task). These data were explored using a repeated measures ANOVA with two factors: distance from fixation (near vs far) and visual quadrant of the display (upper left, upper right, lower right and lower left). Responses to the probe stimulus were then examined as an index of SWM performance (i.e., "was the probe in the same location as the previously detected 'gapped circle'?"; Figure 1). This was done via an accuracy score in which the proportion of false alarms (i.e., saying a probe was in the location of a target when in fact it wasn't) were subtracted from the proportion of hits (i.e., correctly indicating that the probe was in the same location as the target). Accuracy scores for each individual were calculated in this manner, with group mean accuracy scores compared across the different conditions (i.e., no remapping, remapping up, down, left, or right) via repeated measures ANOVA. A' was also calculated, which provided an index of sensitivity. As the results from this measure were identical to the results obtained from the accuracy scores, we are reporting only the accuracy scores here.

Results

All participants had no difficulty following the movement of the cross in the remapping trials with all participants moving their eyes to refixate the new location and maintaining fixation there until the end of the trial.

Gapped circle detection

Although repeated measures ANOVA revealed a significant interaction between the factors of distance from fixation and visual quadrant of the display ($F(7, 119) = 3.96$, $p < .01$), post-hoc t-tests contrasting near and far target detection in each quadrant separately (with Bonferroni correction for the number of comparisons made setting alpha at 0.0125) found no significant differences. There was a

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slight trend for target detection to be superior for near versus far targets in all conditions, although this was only significant at the far less conservative alpha level of p<0.05 for the upper right and upper left quadrants (Table 1). It is important to note here that target detection was uniformly high in all locations across the display. In addition, SWM performance was only analysed for those trials in which the target had been accurately detected.

Table 1. Mean hit % (±SD) for detection of a gapped circle close to (near) and further away from (far) fixation.

	Visual quadrant of target			
	Upper right	Lower right	Upper left	Lower left
Target location	Experiment 1			
Near	.998 (.01)	1.0	.995 (.02)	.991 (.02)
Far	.984 (.03)	.995 (.01)	.976 (.03)	.981 (.03)
p-value	.028	.083	.021	.165
	Experiment 2			
Near	.987 (.02)	.983 (.02)	.968 (.03)	.981 (.03)
Far	.992 (.02)	.979 (.02)	.975 (.04)	.973 (.03)
p-value	.436	.521	.579	.410

α = .05/4 = .0125

SWM Analysis

First, SWM in the 'no remapping' condition was analysed to ensure that there were no inherent biases in spatial memory relative to the particular location of the target to be remembered. Repeated measures ANOVA with the factor of target quadrant (upper right, lower right, lower left, upper left) showed a trend towards a significant effect of quadrant on spatial memory ($F(3, 51) = 2.60$, $p = .06$). To examine the possibility of significant effects further, performance for each quadrant was contrasted with one another. Alpha was set at 0.0083 to correct for the number of comparisons made (i.e., 0.05/6;

Bonferroni correction). The results of this analysis revealed no significant effects, indicating that there

was no bias for spatial memory to be more efficient in any particular region of space in this task when

no remapping was required (Table 2).

Table 2. Comparison of hits, false alarms, and mean accuracy (±SE) for probe detection between the
four display quadrants for the no remapping condition in Experiment 1

Quadrant comparison	Hits	False Alarms	Mean Accuracy scores
Upper right	.981 (.01)	.100 (.04)	.882 (.04)
Lower right	.951 (.02)	.204 (.06)	.748 (.07)
p-value			.041
Upper left	.944 (.02)	.079 (.04)	.865 (.04)
Lower left	.929 (.03)	.111 (.04)	.818 (.06)
p-value			.312
Upper right	.981 (.01)	.100 (.04)	.882 (.04)
Upper left	.944 (.02)	.079 (.04)	.865 (.04)
p-value			.726
Lower right	.951 (.02)	.204 (.06)	.748 (.07)
Lower left	.929 (.03)	.111 (.04)	.818 (.06)
p-value			.228

$\alpha = .05/6 = .0083$

Note: Two comparisons are not shown in this table – upper right vs. lower left and upper left vs. lower
right, as these were not considered meaningful. If these are removed from consideration when setting the
alpha level, significance would still be set at 0.0125 ($\alpha = .05/4 = .0125$) rendering all comparisons non-
significant.

Then, the complete data set was analyzed to determine the effects of saccadic remapping on

SWM. It is important to note here that the direction of remapping was opposite to that of the direction in

which the cross was shifted. For example, if the fixation cross was shifted to the left, then the initially

encoded target array would have to be remapped into right visual space. A one-way ANOVA with the

five different levels of remapping (no remapping, remap left, right, down, or up) revealed a significant

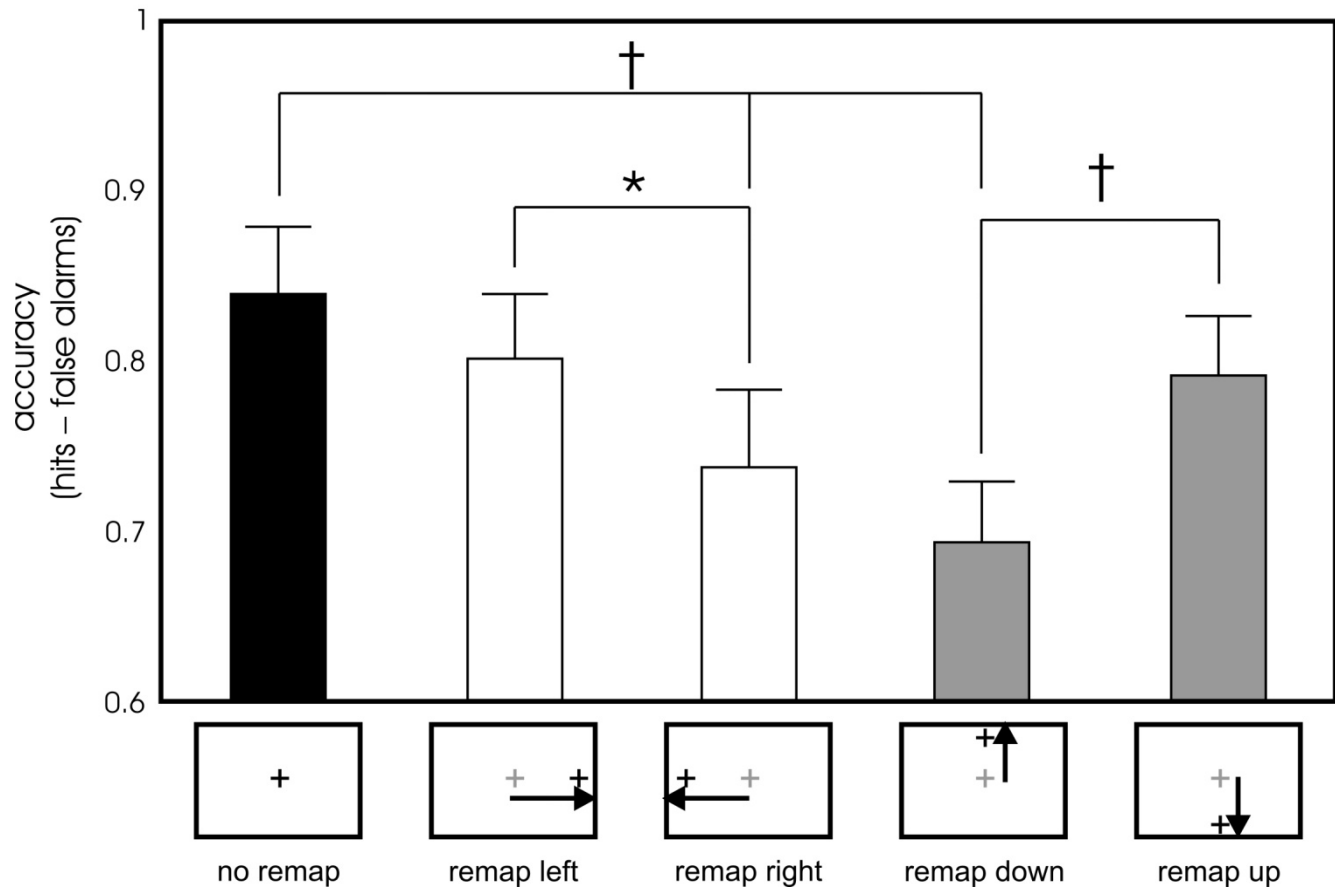effect for remapping direction ($F_{(4, 68)} = 8.72$, $p < .001$; Figure 3).

Figure 3. SWM performance for Experiment 1 – Saccadic remapping. Performance is measured as an accuracy score (% hits – % false alarms) and compared across five conditions: no remapping (black bar), leftward vs. rightward remapping (white bars), downward vs. upward remapping (grey bars). Error bars represent the standard error for each condition. † represents $p < .01$ and * represents $p < .05$.

Planned comparisons contrasted performance in the left remapping condition with performance in the

right remapping condition and, similarly, contrasted performance in the upward remapping condition

with performance in the downward remapping condition. Results showed a significant difference for

accuracy between left and right remapping ($t(17) = -2.48$, $p < .05$), with rightward remapping being

associated with inferior performance. As well, a significant difference between the downward and

upward remapping conditions (t(17) = 3.98, p< .01) was found, with downward remapping being associated with inferior performance by comparison (Figure 3).

Each remapping condition was then explicitly contrasted to the no-shift condition to determine whether the specific remapping direction led to a cost in SWM performance. Alpha was set at 0.0125 to correct for the number of comparisons made (i.e., 0.05/4; Bonferroni correction). This analysis revealed significant cost for rightward (t(17) = -3.04, p < .01) and downward remapping (t(17) = -5.13, p < .001). At a less conservative alpha level there was a slight trend towards a cost to SWM for leftward remapping (t(17) = -1.85, p = .08), while upward remapping did not lead to any significant cost (t(17) = -1.61, p = .13). These costs are represented graphically in Figure 4 by way of a difference score such that accuracy in the particular remapping condition of interest was subtracted from accuracy in the no remapping condition. A difference score approaching zero would indicate no significant cost to SWM performance in the remapping condition relative to the no remapping condition (Figure 4).
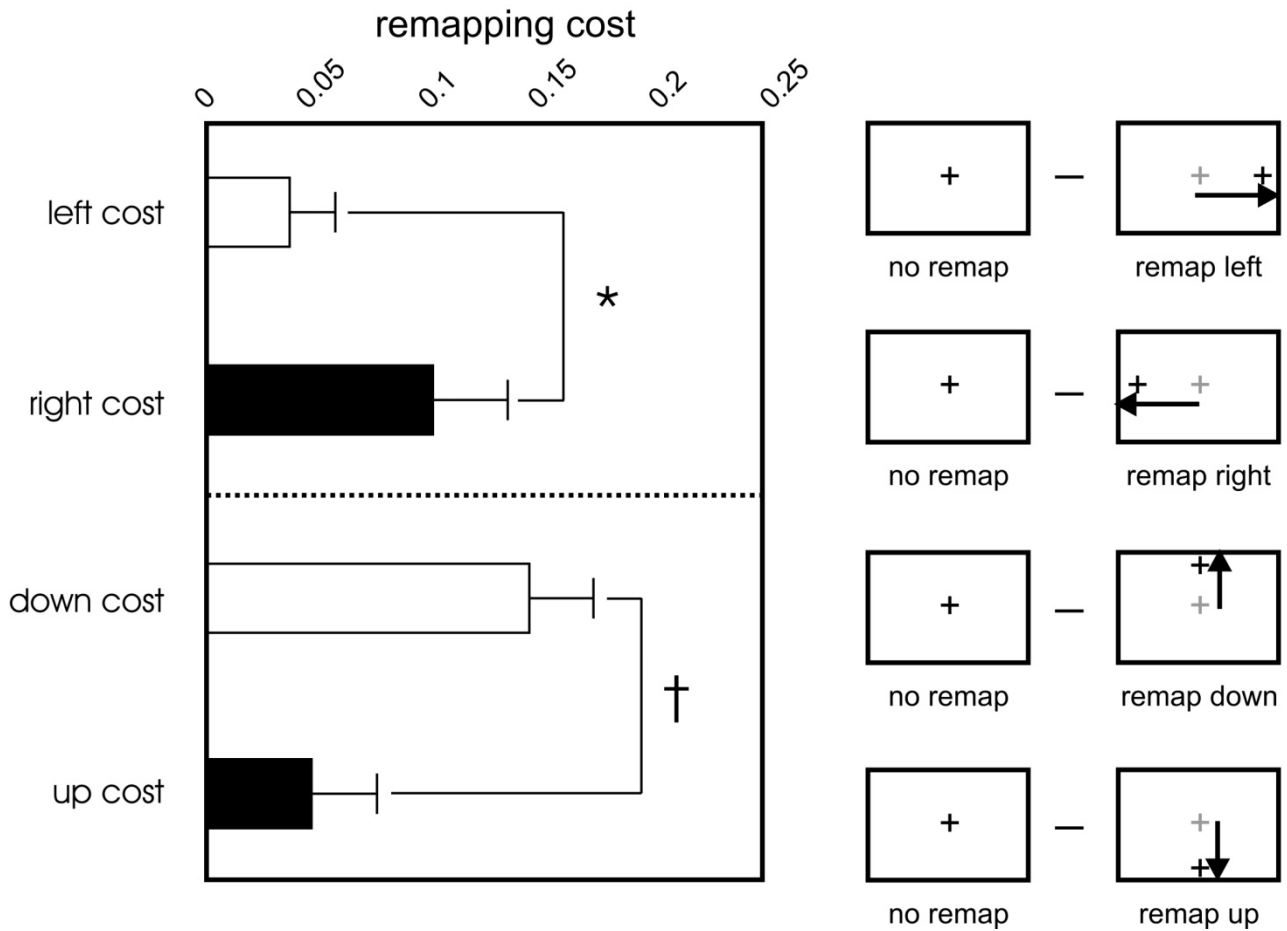
Figure 4. Remapping cost of Experiment 1 expressed as differences scores for SWM accuracy comparing remapping to specific directions (left, right, down, up) with no remapping. A difference score greater than zero signifies a cost to SWM for remapping in that direction. Error bars represent the standard error. A schematic outlining the method used to calculate the difference scores is shown to the right. * represents $p < .05$ and † represents $p < .01$.

Discussion

The results of the first experiment indicated that remapping the target array into right visual space or lower visual space, as a consequence of a saccade in the opposite direction, led to a significant cost in terms of SWM performance. This was true when these two conditions were compared with either the no remapping condition, or the condition that required remapping of the target array into the opposite visual hemifield. In other words, the greatest cost to SWM was observed for remapping the

target array into right or lower visual space (Figures 3 and 4). It may be the case that the observed decrements to SWM performance from rightward remapping arose as a consequence of mechanisms related to hemispheric dominance for spatial processing. That is, the right hemisphere has been shown to be more proficient at processing exact metric spatial information when compared to the left hemisphere (Kosslyn et al., 1989; Hellige & Michimata, 1989; Kessels et al., 2002). If one considers that rightward remapping may rely on left hemisphere neural systems (Kinsbourne, 1993), it is possible that remapping right space is less efficient than the opposite condition in which right hemisphere structures specialised for spatial processing of the kind involved by saccadic remapping perform the task more efficiently. In contrast, the performance decrements to SWM observed for downward remapping may result from different mechanisms entirely. Previc's model of how the brain processes three-dimensional space (1998) suggests that neural systems involved in processing different regions of space are also specialised for performing specific tasks within those regions of space. Specifically, he argues that far (extrapersonal) space is specialized for such things as visual search and visual memory (1998; Previc & Intraub, 1997). In the current study, remapping to upper space was relatively unaffected, which is compatible with Previc's notion that extrapersonal space (operationalized here as upper visual space) demonstrates superior visual search and memory. These hypotheses will be explored further in the general discussion.

Experiment 2

There still remains the possibility that the interactions observed between saccadic remapping and SWM are unique to the execution of a saccade. In other words, would similar deficits to SWM performance be observed if the remapping required was performed covertly, in the absence of any movement of the eyes? Pisella and Mattingley (2004) first made the suggestion that spatial remapping, independent of the execution of an eye movement, may be critically impaired in neglect patients. Indeed, a great deal of research has demonstrated specific covert orienting deficits as a consequence of parietal injury (Poser et al., 1984; Friedrich et al., 1998; see Losier & Klein, 2001 for review). In addition, a great deal of human neuroimaging research has demonstrated overlapping neural circuitry for overt and covert shifts of attention (see Corbetta, 1998 for review). Importantly, these networks rarely (if ever) completely overlap, suggesting that there are distinct neural networks invoked when covert shifts of attention are made (see Corbetta, 1998 and Corbetta & Shulman, 2002 for review). It is important, therefore, to examine whether or not similar influences on SWM will be observed when the target array must be remapped covertly.

Methods

Participants

Eighteen healthy normal participants (11 females; mean age = 20.67 years, ±SD = 2.11; range = 18-25; 1 left handed) participated in Experiment 2. All participants had either normal or corrected to normal vision and were free from any neurological or psychiatric condition. All participants were recruited from the University of Waterloo, and written informed consent was obtained prior to commencing the experiment.

Procedure

In Experiment 2, participants completed a similar SWM task to the one used in Experiment 1, with a few notable exceptions. Most critically, rather than moving the fixation point at the onset of the delay, thus requiring *saccadic* remapping to take place, participants were instead required to make covert shifts of attention at delay onset that would require *spatial* remapping of target locations (Figure 5). To induce covert spatial remapping of the target array, participants were first required to maintain central fixation throughout a trial. Targets were then presented within a square reference frame which on some trials was shifted up, down, left, or right at the onset of the delay (Figure 5). Participants were instructed to make judgments concerning a probe stimulus presented inside the shifted reference frame, thus requiring them to have covertly remapped the entire target array into the new location occupied by the reference frame (Figure 5).
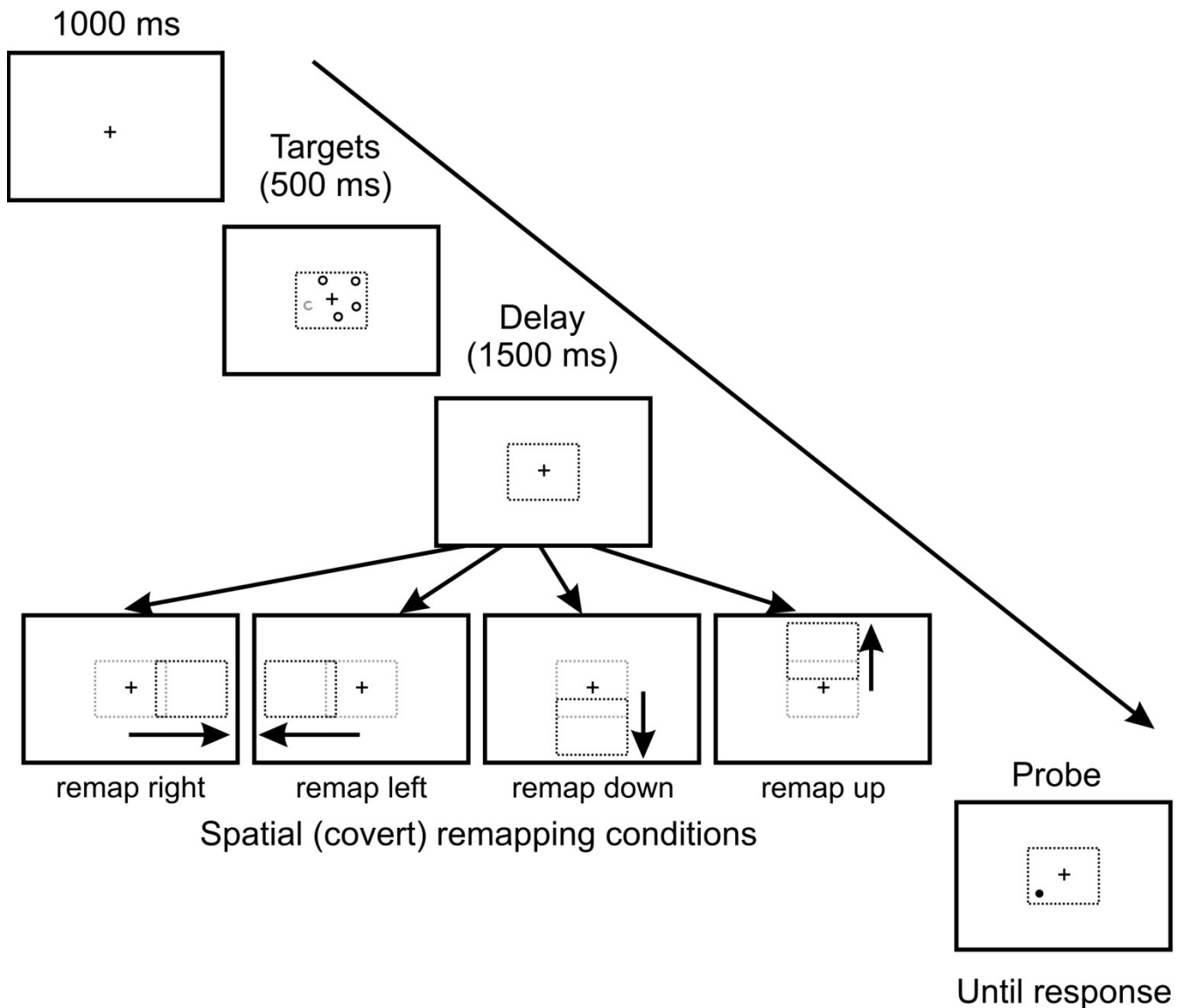
Figure 5. The time course for a single trial of Experiment 2. In addition to the control condition where the target reference box remains static during the delay period, the four possible spatial remapping conditions are also shown. This manipulation of the box landmark was maintained throughout the remainder of the trial. Remapping of the stimulus array was in the same direction as the box shift. Participants had to identify the presence or absence of a 'gapped circle' (the target) upon initial presentation. Following that, participants had to make a judgment as to whether the probe occupied the same location as the previously presented target relative to the box. Note that in the schematic, the probe location is indicated as it would appear for a trial in which no remapping was required.

It was not possible to equate all aspects of the displays used in the two experiments. Critically, it seemed most important to equate the distance shifted by the fixation cross in Experiment 1 with the distance shifted by the reference frame in Experiment 2 (Figure 2). To do this, the physical size of the target stimuli had to be reduced as they appeared on the computer screen. Then, the stimuli were back projected onto a rear projection screen measuring 125 cm by 125 cm using an InFocus LP130 projector. The projected on-screen display measured 125 cm by 93 cm. Participants sat in front of the screen at a viewing distance of 168 cm, with their head positioned in a chin rest. As with Experiment 1, each participant completed 20 practice trials and 320 experimental trials with intermixed conditions. The task was again divided into four equal blocks separated by breaks.

For the back projected display in Experiment 2, the fixation cross subtended a visual angle of 0.5^o and the width of the box subtended a visual angle of 8.5^o. All circle stimuli subtended a visual angle of 1.1^o. Despite this reduction in visual angle of the target size from Experiment 1 to Experiment 2, no participants reported any difficulty in detecting the gapped circle targets. As will become clear below, the accuracy of target detection was very similar across the two experiments. Once again, the stimuli locations were arranged in two "rings" around the fixation cross with an inner ring creating a visual angle of 1.7^o from central fixation and the outer ring creating a visual angle 3.2^o from central fixation. The visual angle between the centrally presented cross and the outer edge of the displaced box was 20° in the horizontal dimension and 15° in the vertical dimension (Figure 2). Thus, the shift of fixation in Experiment 1 and the shift of reference frame in Experiment 2 were roughly equivalent in terms of degrees of visual angle despite the overall reduction in size for the other stimuli used in the second experiment. Data were analysed in the same manner as in Experiment 1.

Results

Gapped circle detection

Again, I wanted to ensure that participants were able to detect the target (a gapped circle) to-be-remembered equally well when it was presented in the different regions of the display. One subject had to be removed from this analysis because of a data recording failure. The mean hit percentages per quadrant can be seen in Table 1. Repeated measures ANOVA with factors of distance from fixation (near vs far) and visual quadrant (upper right, lower right, lower left, upper left) showed no significant main effects or interactions, indicating that participants did not demonstrate any differences in their ability to detect the gapped circle as a function of either the proximity to fixation or the visual quadrant in which the target appeared.

SWM Analysis

As in Experiment 1, I first wanted to ensure that there were no inherent biases in spatial memory when no remapping was required. Repeated measures ANOVA with the factor of target location within the box (upper right, lower right, lower left, upper left) revealed no significant effect of location on spatial memory, $F(3, 51) = 1.38$, $p = .261$. This indicates that there was no inherent bias for spatial memory in any quadrant of the visual display when no remapping was required.

Spatial working memory performance was then analyzed to determine the effects of covert spatial remapping. Unlike Experiment 1, the direction of remapping was the same as the direction in which the box was shifted at the onset of the delay, such that when the box was shifted to the left, the target array had to be remapped into left visual space (Figure 5). A one-way repeated measures ANOVA with remapping direction as the within subjects factor (left, right, up, down, or no remapping) revealed a significant effect for remapping direction ($F(4, 68) = 15.53$, $p < .001$). The no remapping condition had the highest mean accuracy; all other conditions had substantially lower mean accuracy scores (Figure 6).
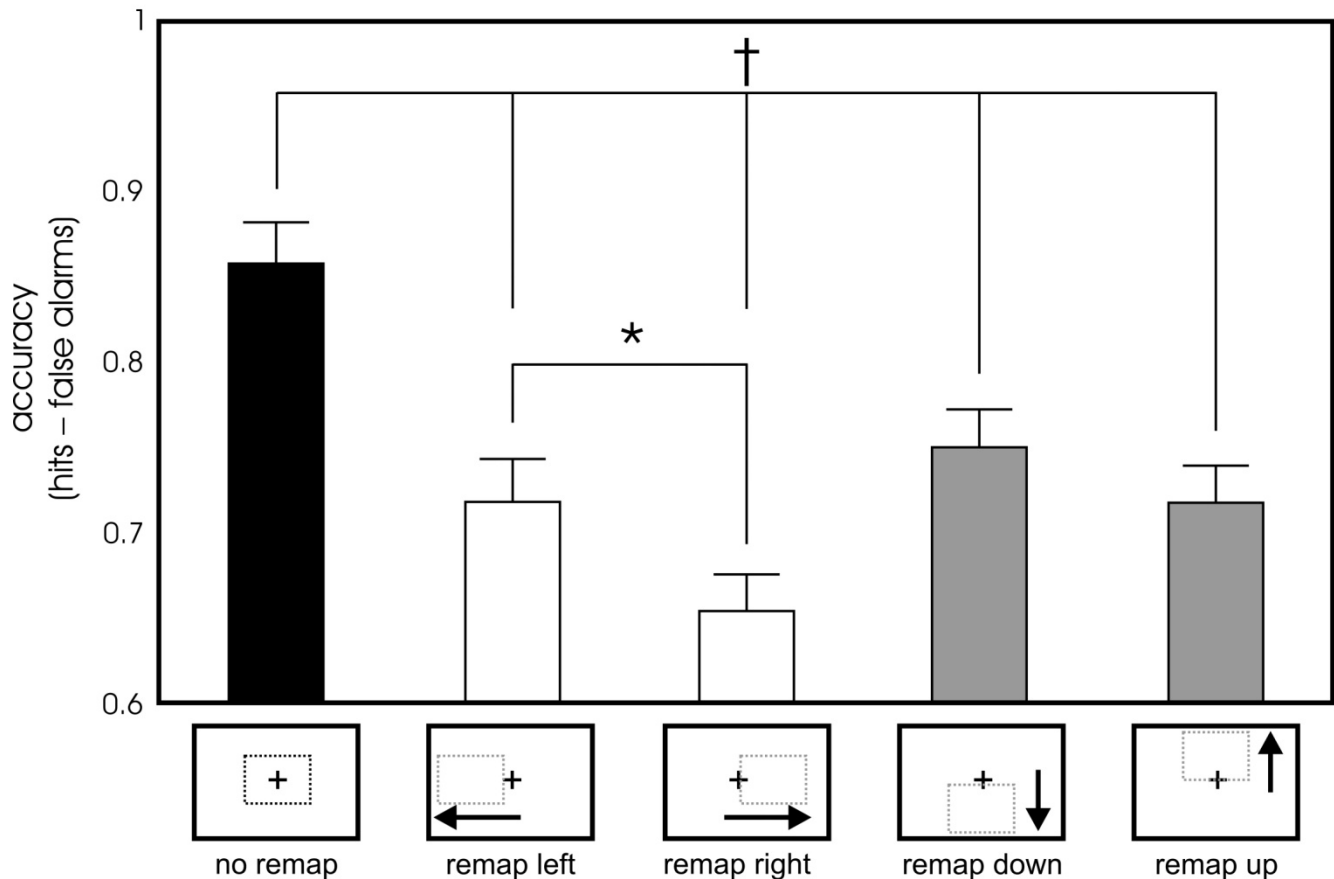
Figure 6. SWM performance for Experiment 2 – Spatial remapping. Performance is measured as an accuracy score (% hits – % false alarms) and compared across five conditions: no remapping (black bar), leftward vs. rightward remapping (white bars) and downward vs. upward remapping (grey bars). Error bars represent the standard error for each condition. † represents $p < .01$ and * represents $p < .05$.

Again, planned comparisons were run to compare performance in the left and right remapping conditions and the down and up remapping conditions separately. Results showed a significant difference for accuracy between left and right remapping, ($t(17) = 2.43$, $p < .05$) but no significant difference between the downward and upward remapping conditions, although there was a trend toward upward remapping having a greater cost ($t(17) = 1.80$, $p = .09$; Figure 6). Each remapping condition was then contrasted with the no-remapping condition to examine whether covertly remapping the target array led to a cost in SWM accuracy for each direction of movement separately. Four post hoc comparisons

were run with alpha set to .0125 to correct for the number of comparisons made (i.e., 0.05/4; Bonferroni correction). Leftward and rightward remapping both led to significant costs to performance (t(17) = -4.34, p < .001 for leftward remapping and t(17) = -8.41, p < .001 for rightward remapping). Remapping to upper and lower visual space also resulted in significant costs to SWM performance (t(17) = -6.33, p < .001 for upward remapping and t(17) = -3.92, p < .001 for downward remapping). These costs are represented graphically in Figure 7 as difference scores calculated in the same manner as in Experiment 1.
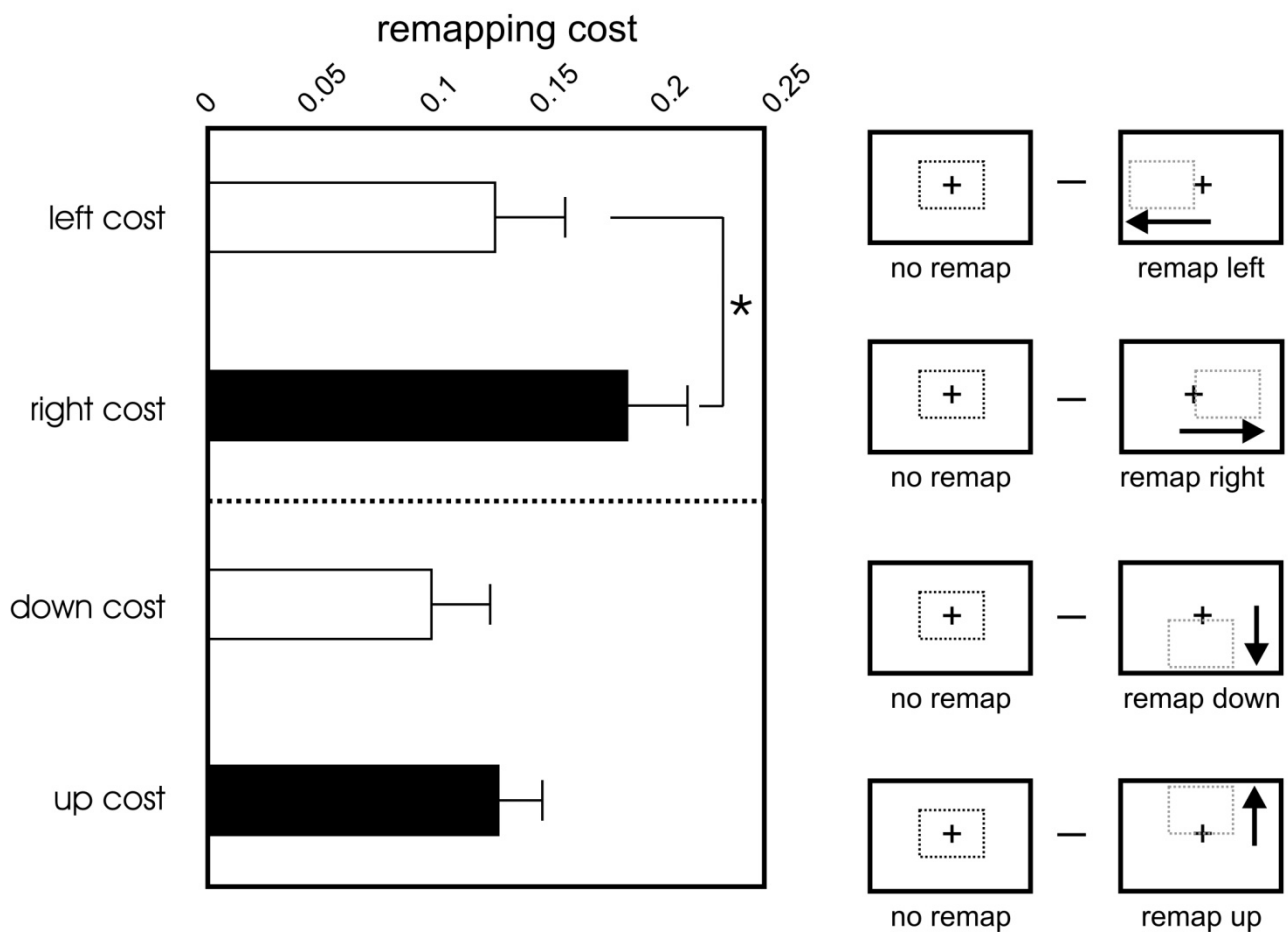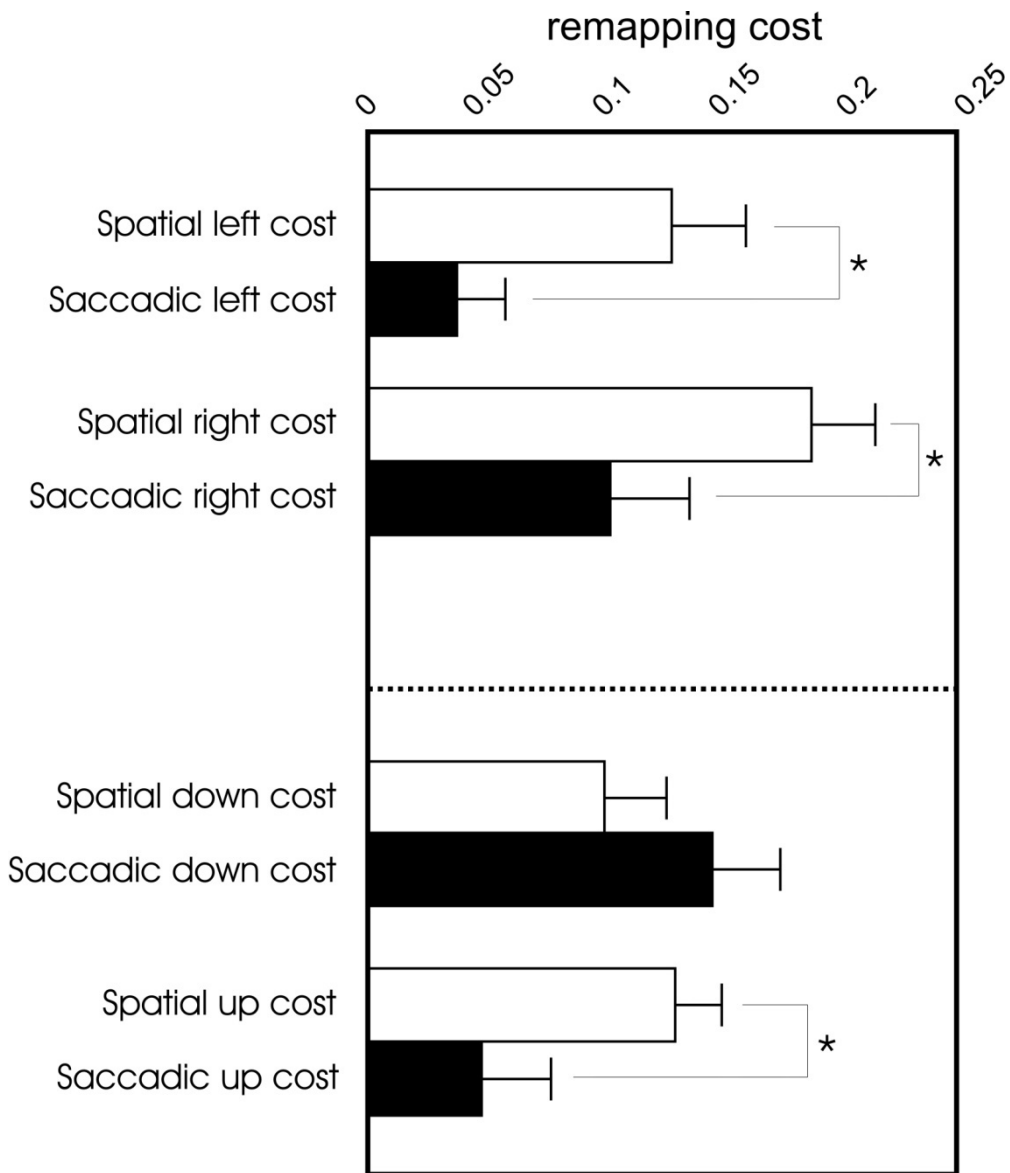

Figure 7. Remapping cost of Experiment 2 expressed as differences scores for SWM accuracy comparing remapping to specific directions (left, right, down, up) with no remapping at all. Error bars represent the standard error. * represents p < .05.

Finally, I wanted to compare the effects of remapping on SWM across Experiments 1 and 2. To do this, the differences scores from each individual in the two experiments were subjected to a between-subjects ANOVA, with the fixed factor being experiment number (1 or 2). A significant difference was found between Experiments 1 and 2 for the cost of leftward remapping ($F(1, 34) = 7.11$, $p < .05$), and rightward remapping ($F(1, 34) = 5.86$, $p < .05$). Also, a significant difference was found for the cost of upward remapping ($F(1, 34) = 6.19$, $p < .05$), but no difference in the cost associated with downward remapping across the two experiments ($F(1, 34) = 0.99$, $p = .33$) (Figure 8; also see Figures 4 and 7 for comparison).

Figure 8. Comparison of the remapping cost for Experiments 1 and 2. Costs are expressed as differences scores for SWM accuracy contrasting remapping to specific directions (left, right, down, up) for spatial and saccadic remapping. Error bars represent the standard error. * represents $p < .05$.

Discussion

The results of Experiment 2 indicated that covertly remapping the target array in any direction

had a negative impact on SWM accuracy compared with the no remapping condition. In addition,

rightward remapping was associated with a greater cost to SWM compared to leftward remapping.

Finally, there was a slight trend for upward remapping to have a greater cost than downward remapping. The decrements to SWM demonstrated in the horizontal dimension can once again be accounted for by hemispheric dominance for spatial processing. Remapping rightward may rely on the left hemisphere, which is not as proficient at processing spatial information as the right hemisphere (Kinsbourne, 1993).

The pattern of costs associated with saccadic remapping in upper and lower visual space was not observed for covert remapping. Several previous studies have shown that attention is superior in the lower visual field (He, Cavanagh, & Intrilligator, 1996) which also seemed to be the case here with a trend towards a greater cost for SWM when remapping towards upper visual space. That saccadic remapping produces the opposite pattern of performance suggests that the execution of an eye movement improves memory performance only for the upper visual field.

General Discussion

The results of the second experiment demonstrated a more reliable cost to SWM during covert shifts of attention, in that the decrement was observed for all directions of remapping (Figures 3, 4, 6 and 7). Additionally, the between experiment analysis suggests that spatial remapping led to greater costs for SWM than did saccadic remapping (Figure 8). Despite this, there remained some similarities in the nature of the decrements to SWM caused by the need to remap the target array. When subjects were required to remap the array into right visual space, in both the saccadic and spatial remapping tasks, there was a significant cost to SWM relative to both the no remapping and leftward remapping conditions. Along the vertical dimension, remapping the target array into lower visual space led to equivalent costs to SWM in both the saccadic and spatial remapping tasks (Figures 4 and 7). Although there was no significant difference in the spatial remapping task between upward and downward remapping conditions, there was a trend toward a greater cost for upward remapping. This was in stark contrast to the findings for saccadic remapping, which revealed a significantly greater cost to SWM for *downward* compared to upward remapping. Finally, whereas saccadic remapping did not induce any cost for leftward or upward remapping conditions relative to no remapping, the same was not true for spatial remapping. Thus, spatial remapping seems to pose a greater difficulty in terms of accurately maintaining the remapped target locations over a brief delay. It should be noted that it is not believed that these effects were due to an inability to properly rehearse target locations in SWM. Although Awh, Jonides, & Reuter-Lorenz (1998) found that preventing attention from being directed to the memorized target locations impaired SWM performance by reducing rehearsal ability, this was unlikely to confound the results of the present study. In both experiments, participants were fully able to covertly attend to, and thus rehearse, the spatial locations of the targets. However, they were then required to *remap* the target array, which ultimately impaired SWM efficiency. Furthermore, inhibited spatial rehearsal cannot explain the differential effects to SWM accuracy for remapping to different regions of space (e.g. greater cost to remapping into right compared to left space).

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What is clear from the two experiments presented here is that there are distinct influences of remapping processes on the efficiency of SWM, despite the fact that the two processes normally operate on very different time scales. The most consistent effect across the two experiments occurred for remapping in the horizontal direction. That is, when participants had to remap the target array into right visual space with either a leftward saccade or a rightward shift of covert attention, SWM was worse than in conditions in which leftward remapping was required (Figures 3 & 6). This result may reflect the fact that the right hemisphere is specialised for spatial processes across a broad range of cognitive functions. For instance, it has been demonstrated in a wide variety of paradigms that the right hemisphere controls attention for both left and right space, whereas the left hemisphere controls attention only for right space (Heilman & Van Den Abell, 1979, 1980; Corbetta & Shulman, 2003). Right hemisphere mechanisms have also been shown to be more effective in the execution of attentional tasks in general (Mesulam, 1981). Furthermore, and perhaps more relevant to the current study, the right hemisphere dominance for spatial cognition extends beyond the realm of attentional control. A great deal of research has shown that the right hemisphere is more proficient at processing exact metric spatial information (i.e., positional or location memory) compared to the left hemisphere (Kosslyn et al., 1989; Hellige & Michimata, 1989; Kessels et al., 2002). Recently, Vuilleumier et al. (2007) demonstrated that right hemisphere patients with neglect were impaired on a perceptual memory task (i.e., detecting slight variations in position of a target) when they had to remap the target array into left space after a right gaze-shift. In addition, a PET study by Köhler and colleagues (1995) indicated that the right inferior parietal lobule was more involved in a spatial location matching task than in an object identity matching task. Studies such as this one have suggested that each hemisphere is specialized for the processing of different types of information, with the right hemisphere demonstrating superiority for spatial processing (Kosslyn et al., 1989; Hellige & Michimata, 1989; Köhler et al., 1995, 1998; Kessels et al., 2002), and the left hemisphere demonstrating a clear preference for language functions including auditory working memory capacity (Wise et al., 2001).

Our results demonstrate that remapping into right space led to a larger performance decrement for SWM than did leftward remapping. One possibility is that remapping the target array into right space relies more heavily on the left hemisphere, which in turn is not as efficient for either attentional processing or positional memory (Corbetta & Shulman, 2003; Kessels et al., 2002; Köhler et al., 1998). Importantly, it is not merely the side of *initial* target presentation driving the asymmetry in spatial processing; when no remapping was required, there were no inherent biases in SWM performance evident. In addition, spatial or covert remapping in any direction, regardless of original target position, was shown to have a detrimental effect on SWM accuracy. It was simply that remapping into right space led to a greater cost to SWM than did remapping into left space (which led to no significant cost when saccadic remapping was required). These results strongly suggest that the effects we found on SWM accuracy in the horizontal dimension were due to an interaction between mechanisms of spatial remapping and SWM, which demonstrate biases that are driven by the right hemisphere's dominance for spatial processing.

Horizontal remapping resulted in the same effects on SWM whether it was performed overtly or covertly (i.e. SWM cost for rightward remapping only). However, remapping the target array in the vertical dimension led to differential costs to SWM, depending on the nature of the remapping task. Specifically, when the target array had to be remapped overtly, a decrement to SWM was only observed for downward remapping compared to upward remapping. Conversely, covert remapping of the array led to an observable cost for both directions of remapping with a slight trend for upward remapping to have a greater cost compared to downward remapping. Of the eighteen participants, twelve showed this direction of effect with lower accuracy scores for upward remapping.

One possible explanation for this dissociation could be found in Previc's theory of the three-dimensional representation of space (1990, 1998). Broadly speaking, Previc suggests that the neural systems devoted to processing events in peripersonal and extrapersonal space have been adapted to processing specific kinds of information relevant to different task demands typically associated with

each region of space. In short, he suggests that the ventral visual stream – which runs from primary visual cortex (area V1) to inferotemporal cortex – is involved in attending to far (extrapersonal) space and is specialised for such things as visual search and visual memory. In contrast, the dorsal visual stream – which runs from V1 to posterior parietal cortex – is principally involved in the control of attention and action in near (peripersonal) space (Previc, 1990; Danckert & Goodale, 2001, 2003; Goodale & Milner, 1992; Weiss et al., 2000; Butler, Eskes, & Vandorpe, 2004).

Several different lines of research have suggested that both visuomotor control and the efficiency with which attention is deployed is more proficient in lower visual space, which can be taken as a rough analogue of peripersonal space (i.e., space that is close to the body). For example, He, Cavanagh and Intrilligator (1996) found that attentional resolution was greater in the lower visual field during a covert visual attention task. In addition, Danckert and Goodale (2001) have shown that a more robust speed-accuracy trade-off is observed for visually guided movements that are executed in the lower as compared to the upper visual field. So when covert attention is employed to remap the display to the lower visual field, one might expect there to be a lower cost than when covertly remapping the display into upper visual space. In contrast, Previc's theory would suggest that visual search, and by extension the execution of saccades in a visual search type paradigm, should be more efficient in extrapersonal space, or that region of space that is beyond arms reach (Previc, 1990, 1998; note that here I am using the upper visual field as a rough analogue of far, extrapersonal space).

Indeed, previous research has demonstrated that saccadic reaction times are shorter for saccades executed to targets appearing in upper versus lower visual space (Sheliga, Craighero, Riggio, & Rizzolatti, 1997). In addition, when asked to reproduce (via drawing) a previously viewed scene, healthy participants included greater detail in the upper portions of the scene, even expanding the upper region of their reproduction relative to the actual scene presented (Previc & Murphy, 1997). What this work suggests is that the execution of eye movements, and subsequent visual memory for scenes, is more efficient in upper versus lower visual space. This kind of anisotropy in visual processing may be

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responsible for the findings in Experiment 1 in which there was no appreciable cost for saccadic remapping into upper visual space, but a substantial cost was observed for remapping into lower visual space (Figure 3).

The contrasting effects of overt and covert remapping in the vertical axis suggest that different mechanisms are at play here, as opposed to the common mechanism that is likely to be responsible for the effects of remapping along the horizontal axis. Interestingly, vertical biases in performance were not evident during the static conditions when no remapping was required. According to Previc's model (1998), biases should be evident even in cases in which no remapping is required. The current results suggest that although there are no inherent biases in pure positional memory, biases will become evident when an additional requirement to remap the to-be-remembered target array is included in the task. Further research is required to determine whether the dissociable differences in covert and overt remapping in the vertical axis are robust, and whether they represent distinct biases in the three-dimensional perception of space for covert and overt mechanisms of attention, as suggested above.

The current findings have considerable implications for research on neglect. The consistent effects of remapping along the horizontal axis provide some support for Pisella and Mattingley's (2004) model which suggests a remapping deficit as the cornerstone of the neglect syndrome. The current data set would also suggest that separable deficits in SWM (i.e., Ferber & Danckert, 2006) and spatial remapping (i.e., Heidi et al., 1995) will interact in neglect patients to further impair their ability to maintain an accurate representation of left visual space. In addition, one theory of visual attention would suggest that covert shifts of attention precede the execution of eye movements (i.e., the premotor theory of attention; e.g., Rizzolatti et al., 1987). In the present study, the greater costs to SWM seen when covert remapping is required in any direction suggest that any requirement to execute covert spatial remapping may lead to greater impairment in neglect patients than does overt spatial remapping (i.e., via saccades). This hypothesis would of course require further investigation with neglect patients using the paradigm developed here.

Finally, in addition to lateral biases in spatial processing, neglect patients have also demonstrated performance gradients for the near-far dimension in peripersonal and extrapersonal space (Chatterjee, Thompson, & Ricci 1999; Mark & Heilman, 1997). Several studies have found that neglect of contralesional space is more severe in peripersonal than in extrapersonal space, where it is often not demonstrated at all (Halligan & Marshall, 1991; Guariglia & Antonucci, 1992; Halligan & Marshall, 1995; see also Berti & Frassinetti, 2000; Butler et al., 2004). The demonstration here that both overt and covert remapping into lower visual space led to a cost to SWM is consistent with what is known of peripersonal neglect. That is, the current data suggest that processes of remapping generally lead to poorer SWM when the to-be-remembered stimuli must be remapped into the lower visual field. Demonstrations of more severe neglect symptoms in peripersonal space may suggest that the regions commonly damaged in neglect patients – including the inferior parietal cortex and the superior temporal gyrus – may well be responsible for maintaining and updating representations of this region of space. Further research in patients with dissociable deficits in peripersonal and extrapersonal space will be needed to determine whether remapping impairments are worse for patients with predominantly peripersonal neglect.

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