



Direction specific costs to spatial working memory from saccadic and spatial remapping

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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, we examined the influence of saccadic and covert spatial remapping on SWM in healthy individuals. An initial control condition in which subjects 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 with the largest decrements in SWM being observed in the covert spatial remapping task. For both saccadic and covert 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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1. Introduction

One of the most common consequences of right parietal lesions is the disorder of unilateral 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; Driver & Mattingley, 1998; Halligan, Fink, Marshall & Vallar, 2003; Heilman, Watson & Valenstein, 1993). Symptom profiles of neglect patients tend to be heterogeneous, making it difficult to construct neurocognitive models of the disorder. Most theories of neglect focus on the obvious impairments of spatial attention, which can be broadly characterised by two interacting components; an attentional selection bias towards ipsilesional space (Kinsbourne, 1993), and the so-called 'disengage deficit', defined as a difficulty in reorienting attention from ipsilesional towards contralesional stimuli (Posner, Walker, Friedrich & Rafal, 1984).

More recent attempts to understand the neglect syndrome suggest that the disorder is not simply due to attentional impairments that favour ipsilesional stimuli. Instead, the neglect syndrome is made up of component deficits including spatial and non-spatial impairments that in concert lead to impaired awareness for contralesional space (Danckert & Ferber, 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 space (Danckert & Ferber, 2006; Pisella & Mattingley, 2004).

Clinical tests used to assess the presence and severity of neglect, provide some hints that the disorder involves more than impaired attentional orienting. For example, when performing cancellation tasks, in which patients must place a mark through targets aligned to their body's midline, patients typically fail to mark a substantial portion of targets to the left of midline. In addition, 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. Furthermore, patients commonly place more than one cancellation mark through the same target, treating old locations (i.e., locations already cancelled), as if they were new (Malhotra, Mannan, Driver, & Husain, 2004). These findings on

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clinical tasks are further supported by experiments using visual search paradigms (e.g., Behrmann, Ebert, & Black, 2004; Husain et al., 2001). In addition, there is mounting evidence that indicates a SWM deficit in neglect is evident, even in tasks where search behaviour is *not* required (Ferber & Danckert, 2006; Malhotra et al., 2005). Given the fact that deficits in SWM have now been shown to be present in right visual space, with relatively uncomplicated displays (i.e., minimal distractor stimuli), it is reasonable to suggest that impaired SWM is relatively independent of biases in spatial attention (Ferber & Danckert, 2006; Husain et al., 2001; Malhotra, Mannan, Driver, & Husain, 2004; Wojciulik, Husain, Clark & Driver, 2001). In other words, these behaviours observed on clinical and experimental tests of spatial working memory cannot easily be accounted for by an attentional impairment alone.

Pisella and Mattingley (2004) have suggested that many of the behaviours observed in neglect could be explained by impairments to *spatial remapping* during overt and covert shifts of attention, in addition to the commonly observed attentional deficits. In their model, internal representations of the environment, referred to as 'salience maps', are continually updated (or 'remapped') to account for changes in the absolute and relative positions of objects. In addition, one's own actions (e.g., eye movements or covert shifts of attention), have consequences for those internal representations. Initial demonstrations of saccadic remapping processes come from 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 initiating the saccade to the first target). The monkey must then anticipate the outcome of the first saccade 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). An important distinction must be made here between pre-saccadic remapping processes (discussed above) and memory-based remapping processes (Colby, Duhamel & Goldberg, 1995). On the one hand pre-saccadic remapping processes are used to account for the anticipated outcome of intended saccades, while on the other a memory trace of a previously encoded stimulus location is used to update internal representations of the external world (i.e., memory-based remapping; Colby et al., 1995). These distinct types of remapping processes are likely to operate on very different timescales – milliseconds for pre-saccadic remapping and seconds to minutes for memory-based remapping processes. There is some evidence that in non-human primates similar neural regions may be involved in both types of remapping. Duhamel, Colby, and Goldberg (1992a) found evidence of memory-based remapping mechanisms in area LIP—the same region shown to be involved in pre-saccadic remapping. In this instance a stimulus was briefly presented for 50 ms well outside the receptive field of the monkey's neuron, as the monkey fixated. Neurons in area LIP showed increased firing rates when a subsequent saccade then brought the receptive field of the recorded neuron to the location of the previously shown stimulus (which was no longer present in the display; Duhamel, Colby, & Goldberg, 1992a). Since the stimulus had been removed from the screen prior to saccade onset, the authors argue that this neuronal response reflects the use of a memory trace (Duhamel, Colby, & Goldberg, 1992a; Colby, Duhamel, & Goldberg, 1995).

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 (Heide, Blankenburg, Zimmermann & Kompf, 1995; Vuilleumier et al., 2007). Importantly, according to Pisella and Mattingley (2004), if the right hemisphere maintains a salience map for the entire visual field, then 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, Goldberg, Fitzgibbon, Sirigu, and Grafman (1992b) examined performance on the double-step saccade task in a patient with unilateral neglect resulting from a right frontoparietal lesion. When the first target was in ipsilesional space and the second target appeared contralesionally, the patient acquired both targets accurately. This presumably reflects the fact that he could rely on left parietal cortex to accurately anticipate the outcome of the first saccade made to right space. In the opposite circumstance, when the first target was presented contralesionally and the second target appeared in ipsilesional space, the patient never acquired the second target.

This result, since replicated in a larger group of patients (Heide, Blankenburg, Zimmermann & Kompf, 1995), suggests that the damaged right parietal cortex was unable to accurately anticipate the outcome of a saccade made into left space (Pisella & Mattingley, 2004). Given that previous work has demonstrated similar remapping deficits in left parietal patients (Heide, Blankenburg, Zimmermann & Kompf, 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 disengage deficit) to demonstrate the full neglect syndrome. In addition, Pisella and Mattingley (2004) suggest that it is not only the initial saccade direction that determines the nature of errors on the double-step saccade task. They suggest that remapping deficits will also be observed following rightward (ipsilesional) saccades when the second target location was *initially* presented in left, contralesional space. This highlights a theoretical suggestion that remapping deficits in neglect should be greatest when memory-based remapping processes are invoked (see Colby et al., 1995 for the distinction between pre-saccadic and memory-based remapping).

More recently, it has been shown that neglect patients had difficulty performing a perceptual discrimination task following saccadic remapping (Vuilleumier et al., 2007). In this study patients first identified the colour of a target (i.e., either red or green) by fixating it (targets appeared randomly 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 right of the display requiring the target location to be remapped due to the gaze shift. A probe appeared after a 2 s 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 reported whether or not the target location changed by making a same/different judgement. When a rightward gaze-shift was required, requiring the target location to be remapped into left, neglected space, patients demonstrated a striking cost to spatial memory. At first glance this result appears to be in opposition to the double-step saccade results discussed above in which the patient failed to acquire the second target only after the initial saccade was made into *left* visual space (Duhamel, Goldberg, Fitzgibbon, Sirigu, & Grafman, 1992b; see also Heide, Blankenburg, Zimmermann & Kompf, 1995). As mentioned above, however, remapping deficits will not only be determined by

the initial saccade direction but also by the initial location of the second target for a saccade (Heide, Blankenburg, Zimmermann & Kompf, 1995; Pisella & Mattingley, 2004). Vuilleumier et al. (2007) do not report separately the results from the various manipulations of initial and subsequent target locations making it difficult to directly contrast their results with previous work discussed above. One possibility for resolving the apparent difference in results would suggest that saccadic remapping and SWM deficits in neglect have opposing spatial consequences. Alternatively, previous remapping deficits have been shown by explicitly examining saccade metrics (Heide, Blankenburg, Zimmermann & Kompf, 1995) while Vuilleumier et al. (2007) referred to a perceptual location judgement in order to examine the presence of remapping deficits. Such differences in methodology may have led to the distinct differences in results, a possibility that obviously requires further investigation.

In addition, while the results of the Vuilleumier et al. (2007) study clearly shows a remapping deficit for neglect patients it is difficult to claim that this is a remapping *influence* on spatial working memory. First, 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 relatively facile spatial working memory task. That is, retaining the target location in mind over a delay in this condition would be trivial if fixation was maintained at the initial target location. This would then inflate the performance in the no-remapping condition. The very difficult same/different judgement required by patients (the probe when not in the same location as the target was only *slightly* shifted, as opposed to appearing in a totally distinct location) may lead to perceptual discrimination difficulties that are known to be greater in left than right space for neglect patients. Together, these factors would inflate findings for performance following a right gaze shift in which the perceptual discrimination now has to occur in left space. Second, when remapping was required it occurred in multiple stages. That is, patients first fixate centrally and form internal representations of the target location that are updated (i.e., 'remapped') when gaze is shifted there. The array must then be remapped again once gaze is shifted to the letter stimulus which was explicitly used to engage remapping processes. Finally, the probe is sufficiently difficult to resolve in peripheral vision that it requires yet another gaze shift in order to make the final same/different judgement concerning 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 to the letter stimulus 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 remapping on spatial working memory.

As mentioned above, many authors suggest that an important component deficit of neglect is impaired spatial working memory (Husain et al., 2001; Wojciulik, Husain, Clark & 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 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, remapping processes are explicitly engaged in response to an overt or covert shift in attention in *any* direction, whereas SWM has been shown to ben-

efit from attentional shifts to the location of the to-be-remembered targets only (Awh, Jonides, & Reuter-Lorenz, 1998). That is, spatial information may be actively maintained through focal shifts of spatial attention towards the to-be-remembered locations (Awh & Jonides, 1998; Awh & Jonides, 2001; Postle, Awh, Jonides, Smith, & D'Esposito, 2004). Overlapping neural circuits involved in spatial attention and SWM are thereby engaged in the rehearsal of spatial information for SWM by keeping the representation of locations activated in memory (Awh & Jonides, 2001). Although many of the SWM deficits demonstrated in neglect 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 remapping problems. In one study, SWM deficits were observed for stimuli that were vertically aligned in right visual space (Ferber & Danckert, 2006; see also Malhotra, Mannan, Driver & Husain, 2004; Malhotra et al., 2005). Such an arrangement minimises the influence of impairments in saccadic remapping which, for neglect patients, are greatest for horizontal saccades that cross the midline, or remapping that occurs entirely in left space (Heide, Blankenburg, Zimmermann & Kompf, 1995; note, the stimuli in Ferber & Danckert's study were all within right space, whereas for Malhotra and colleagues stimuli were in central space). Thus it is still unclear how these distinct processes might interact even in the healthy brain. Although Vuilleumier et al. (2007) demonstrated clear evidence for an effect of remapping on perceptual discrimination of location changes in neglect patients we feel that several key questions still need to be addressed (note this study also failed to show any effect of remapping in healthy controls). First, do saccadic (overt) and spatial (covert) remapping processes operate in the same manner? Second, are there different consequences for SWM from remapping a target array after horizontal shifts of attention when contrasted with remapping along the vertical meridian?

In Experiment 1, we investigated the influence of saccadic remapping processes on the precision of SWM¹ 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, we 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. If the right hemisphere is indeed dominant for both remapping and SWM processes – as the neglect literature would suggest – then we would expect that remapping the target array into right visual space will have a greater impact on SWM than does remapping into left visual space. We did not have explicit hypotheses concerning remapping into upper and lower visual space.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Eighteen healthy normal participants (11 females; mean age = 24 years, \pm S.D. = 4.84; range = 20–39; 1 left handed) participated in Experiment 1. All participants had normal or corrected to normal vision and were free from any neurological

¹ Memory for spatial information can be broadly categorized 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 our SWM task reflects those processes specifically involved in positional memory.

or psychiatric condition. All participants were recruited from the University of Waterloo and written informed consent was obtained from each participant prior to commencing the study.

2.1.2. Procedure

Participants were seated in front of a 15.4-in. 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 divided into four blocks to provide breaks. Each trial began with central fixation followed 1 s later by five target stimuli consisting of open circles surrounding the cross in pseudorandom locations. Participants were told that one of the 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") 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, 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 (Fig. 1). To introduce a saccadic remapping component to the task, at the onset of the delay the fixation cross could shift to one of four locations: to the left, right, up, or down (Fig. 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.

Several important aspects of the stimulus array warrant further discussion. First, targets could appear in locations that formed two concentric circles around fixation. The outer rim of the first circle was 5° from fixation; the rim of the second circle was 15° from fixation. This allowed us to present 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, we 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. Initial target detection allowed us to examine whether there were any differences in perceptual capacity for detecting targets according to their location (i.e., left or right of fixation and close to or distant from fixation) that may later influence SWM performance. In other words, would the perceptual capacity with which targets could initially be identified influence the subsequent ability to encode those locations for later SWM performance? 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. In addition, on half of the trials in which the fixation point moved at the onset of the delay period 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°. The five circle stimuli appeared in various arrangements out of a possible sixteen locations, with the constraint that at least 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. Each

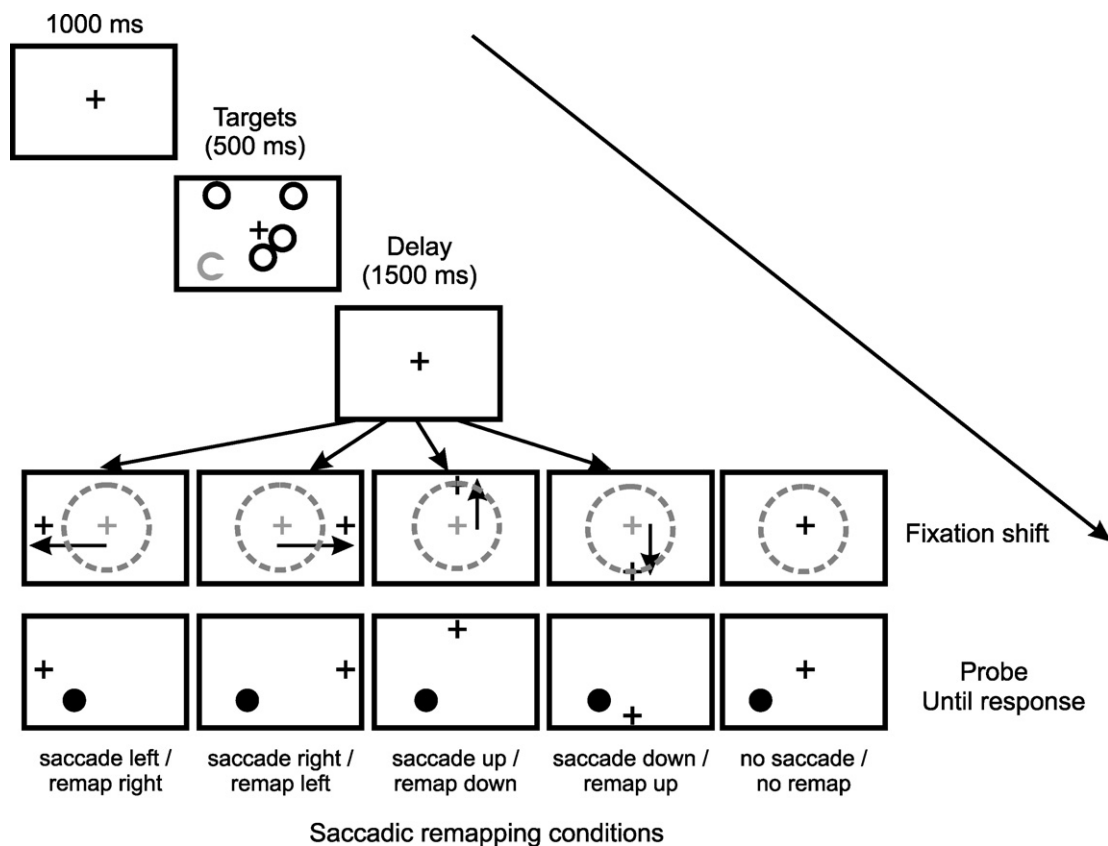


Fig. 1. Time course for a single trial of Experiment 1—saccadic remapping. Participants first identified the presence of a target (a 'gapped circle' indicated in grey in the figure; note, the target was the same colour as non-targets in the actual experiment). Following a delay in which the fixation 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. The five possible remapping conditions (saccade left/remap right; saccade right/remap left; saccade up/remap down; saccade down/remap up; and no remapping) and their associated relative probe locations are shown in the bottom two rows of the schematic. 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. This is indicated by the dashed grey circle which highlights the physical area in which a probe could appear. Note that the *physical* locations of targets and probes never changed in this experiment. What changed was the fixation point such that a rightward saccade now meant that all possible probe locations were to the left of fixation leading to what we are referring to as 'leftward remapping' (and vice versa for a leftward saccade). An upward saccade would mean that all possible probe locations now fall below fixation leading to what we refer to as 'downward remapping' (and vice versa for a downward saccade). This differs from Experiment 2 in which the entire target array had to be remapped with respect to the shift in the reference frame (see Fig. 3).

visual quadrant contained two stimuli on an equal number of trials. The cross was presented in all five 'shift' fixation positions (no-shift, 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. Probes appeared in the same location as the previously presented "gapped circle" (the target) on 50% of trials. Finally, it is important to note, that in this experiment the precise physical locations of targets and probes did not change. That is, it was the saccade made at the onset of the delay that induced the need for the target array to be remapped. Therefore, a leftward saccade now meant that all possible probe locations appeared to the right of fixation (and vice versa) for rightward saccades, while an upward saccade meant that all possible probe locations now appeared below the fixation point in the lower visual field (and vice versa for a downward saccade; see Fig. 1). Subjects were explicitly informed of this component of the task prior to commencing the experiment. This aspect of the current experiment will become important when contrasting the results with our covert remapping task in which subjects were explicitly informed that they must remap the entire target array into the shifted reference frame (Fig. 3). In this instance target and probe locations *do* shift with the shift in the reference frame such that a rightward shift in the reference frame requires the target array to be remapped into right visual space as fixation is constantly maintained in the centre of the screen.

2.1.3. Data analysis

We first examined the accuracy with which gapped circles were detected 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 versus 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'?; Fig. 1). We did this 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 was not) 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. We also calculated *A'*, which provided an index of sensitivity. As the results from this measure were identical to the results obtained from the accuracy scores, for the sake of simplicity we are reporting only the accuracy scores here.

2.2. Results

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

2.2.1. 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 is a 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.

2.2.2. SWM analysis

We first analysed SWM in the 'no remapping' condition 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 this further, accuracy within each quadrant was contrasted with accuracy in all other quadrants with alpha set at 0.0083 to correct for the number of comparisons made (i.e., 0.05/6). The results of this analysis revealed no significant

Table 1

Mean hit % (\pm S.D.) for detection of a gapped circle close to (near) and further away from (far) fixation

Target location	Visual quadrant of target			
	Upper right	Lower right	Upper left	Lower left
Experiment 1				
Near	.998 (.01)	1.0	.995 (.02)	.991 (.01)
Far	.984 (.03)	.995 (.01)	.976 (.03)	.981 (.03)
p-Value	.028	.083	.021	.165
Overall (whole display)	.990 (.01)			
Experiment 2				
Near	.989 (.02)	.983 (.02)	.968 (.03)	.981 (.03)
Far	.992 (.02)	.979 (.02)	.975 (.04)	.973 (.03)
p-Value	.436	.521	.579	.410
Overall (whole display)	.980 (.01)			

$\alpha = .05/4 = .0125$.

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). In fact, only the comparison between the upper and lower right quadrants neared significance, with performance slightly better in the upper right quadrant. If anything then, SWM should be best when targets are remapped into right upper space. As we will demonstrate below, this was clearly not the case.

We then analysed the complete data set 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 ($F(4, 68) = 8.72, p < .001$; Fig. 2).

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 condi-

Table 2

Comparison of hits, false alarms, and mean accuracy (\pm S.E.) for probe detection between the four display quadrants for the no remapping condition in Experiment 1

Quadrant comparison	Hits	False alarms	Mean accuracy scores	<i>A'</i>
Upper right	.981 (.01)	.100 (.04)	.881 (.04)	.969 (.01)
Lower right	.951 (.02)	.204 (.06)	.747 (.07)	.915 (.03)
<i>p</i> -Value			.041	.045
Upper left	.944 (.02)	.079 (.04)	.865 (.04)	.964 (.01)
Lower left	.929 (.03)	.111 (.04)	.818 (.06)	.943 (.02)
<i>p</i> -Value			.312	.187
Upper right	.981 (.01)	.100 (.04)	.881 (.04)	.969 (.01)
Upper left	.944 (.02)	.079 (.04)	.865 (.04)	.964 (.01)
<i>p</i> -Value			.726	.684
Lower right	.951 (.02)	.204 (.06)	.747 (.07)	.915 (.03)
Lower left	.929 (.03)	.111 (.04)	.818 (.06)	.943 (.02)
<i>p</i> -Value			.228	.224
Overall (whole display)	.950 (.01)	.111 (.04)	.839 (.04)	.955 (.01)

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

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.

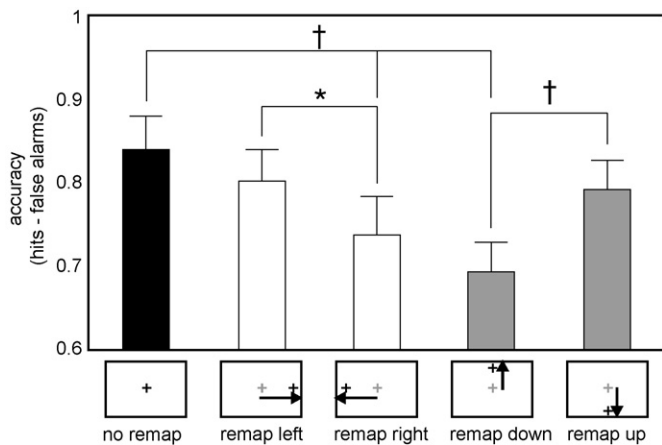


Fig. 2. SWM performance for Experiment 1—saccadic remapping. Performance is measured as an accuracy score (%hits – % false alarms) and compared across five conditions: no remapping (black bar), leftward vs. rightward remapping (white bars), downward vs. upward remapping (grey bars). Error bars represent the standard error for each condition. Symbol (†) represents a significant difference between the conditions indicated at $p < .01$ and (*) represents $p < .05$.

tion. Results showed a significant difference for accuracy between left and right remapping ($t(17) = -2.48, p < .05$), with rightward remapping being associated with a greater cost to SWM.² As well, we found a significant difference between the downward and upward remapping conditions ($t(17) = 3.98, p < .01$), with downward remapping incurring a greater cost to SWM than upward remapping (Fig. 2).

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 a significant cost for rightward ($t(17) = -3.04, p < .01$) and downward remapping ($t(17) = -5.13, p < .001$) only. 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 Fig. 5 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 (Fig. 5).

The results of the first experiment indicated that remapping the target array into right or lower visual space 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 (Fig. 2). 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 (Hellige & Michimata, 1989; Kessels, Kappelle, de Haan, & Postma, 2002; Kosslyn et al., 1989). 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 pro-

cessing of the kind involved in 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 the neural representation of 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 specialised for such things as visual search and visual memory (1998; Previc & Intraub, 1997). In the current study, remapping to upper space was relatively unaffected, compatible with Previc's notion that extrapersonal space (operationalised here as upper visual space) demonstrates superior visual search and memory. We will explore these hypotheses further in the discussion.

3. Experiment 2

We now turn our attention to the possibility that the interactions observed between saccadic remapping and SWM are unique to the execution of a saccade. In other words, would we observe similar deficits to SWM performance 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 (Friedrich et al., 1998; Posner et al., 1984; 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 regions activated by covert shifts of attention (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.

3.1. Methods

3.1.1. Participants

Eighteen healthy normal subjects (11 females; mean age = 20.67 years, \pm S.D. = 2.11; range = 18–25; 1 left handed) participated in Experiment 2. All participants had 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.

3.1.2. 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 (Fig. 3). To induce covert spatial remapping of the target array, we first required participants 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 (Fig. 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 (Fig. 3).

It was not possible to equate all aspects of the displays used in the two experiments. Critically, we felt that it was 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. To do this, we had to reduce the physical size of the target stimuli as they appeared on the computer screen and then back project the stimuli onto a rear projection screen measuring 125 cm \times 125 cm using an InFocus LP130 projector. The projected on screen display measured 125 cm \times 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 blocks separated by breaks.

² Note the cost to SWM for rightward remapping was equivalent regardless of whether the target initially appeared in the upper or lower region of the display.

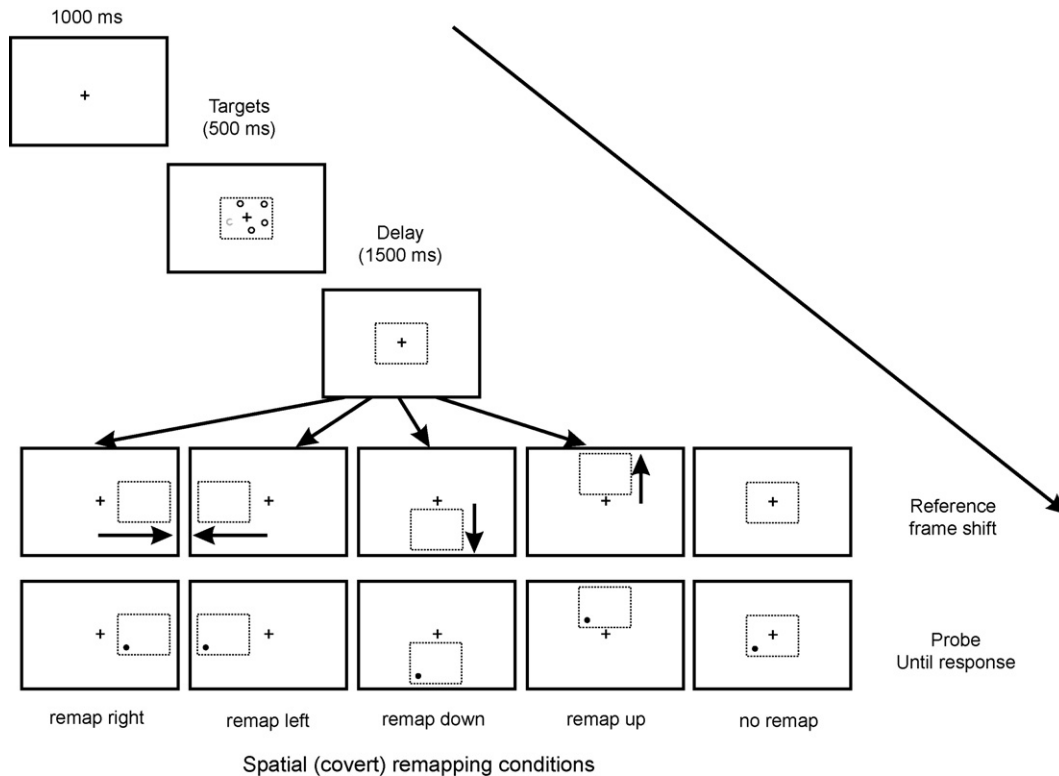


Fig. 3. Time course for a single trial of Experiment 2—spatial remapping. In addition to the control condition where the target reference box does not move during the delay period, the four possible spatial remapping conditions are also shown. This manipulation of the box landmark was maintained throughout 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. All possible remapping conditions and their associated probe locations are shown in the bottom two rows of the schematic. Note, that in contrast to Experiment 1, subjects were instructed to judge whether the probe appeared in the previous location occupied by the target *with respect to the new location of the shifted reference frame*. Thus, probe locations could only appear within the shifted reference frame (indicated by the dashed line) such that a leftward shift in the reference frame required the array to be remapped into left space relative to central fixation (which was maintained throughout).

For the back projected display in Experiment 2, the fixation cross subtended a visual angle of 0.5° and the width of the box subtended a visual angle of 8.5° . All circle stimuli subtended a visual angle of 1.1° . Despite this reduction in visual angle of the target size from Experiment 1 to Experiment 2, no subjects 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 stimulus locations were arranged in two "rings" around the fixation cross with an inner ring creating a visual angle of 1.7° from central fixation and the outer ring creating a visual angle of 3.2° 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. 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. Finally, what is important to re-emphasise here is the equivalence of a rightward saccade in Experiment 1 leading to remapping the target array into left space and a leftward shift in the reference frame here leading to a similar remapping requirement into left space (and all other combinations). In Experiment 1, the physical locations of targets and probes on the screen did not change. Thus, a rightward saccade required participants to remap the target array into left visual space (and vice versa for a leftward saccade). In Experiment 2, we instructed subjects to consider that the shift in the reference frame indicated that the entire target array had also been shifted in the same direction and to the same magnitude. Thus, after a shift in the reference frame participants were required to remap the target array to the new location with respect to their fixation which was constantly held at the centre of the screen. Therefore, a leftward shift in the reference frame, with all possible probe locations now appearing within the new location of the reference frame, required a leftward remapping processing in order to perform the task appropriately. Data were analysed in the same manner as in Experiment 1.

3.2. Results

3.2.1. Gapped circle detection

We again 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 target detection percentages per quadrant can be seen in Table 1. Repeated measures ANOVA with factors of distance from fixation (near versus 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.

3.2.2. SWM analysis

As in Experiment 1, we 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 ($F(3, 51) = 1.38, p = .261$).

We then analysed SWM performance 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 (Fig. 4). 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 (Fig. 4).

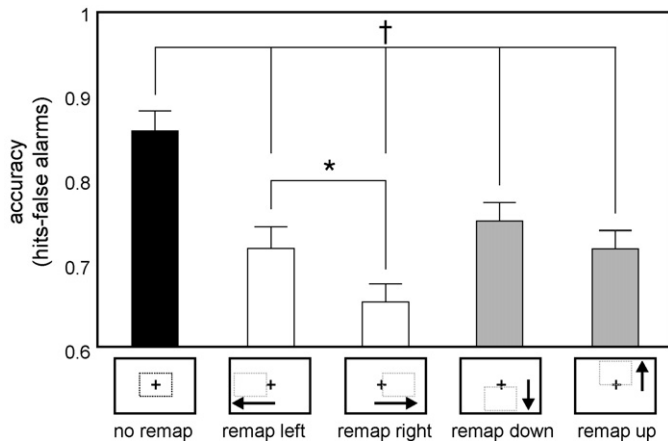


Fig. 4. SWM performance for Experiment 2—spatial remapping. Performance is measured as an accuracy score (%hits – % false alarms) and compared across five conditions: no remapping (black bar), leftward vs. rightward remapping (white bars) and downward vs. upward remapping (grey bars). Error bars represent the standard error for each condition. Symbol (†) represents a significant difference between the conditions indicated at $p < .01$ and (*) represents a significant difference at $p < .05$.

Again, we ran planned comparisons 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 towards upward remapping inducing a greater cost to SWM ($t(17) = 1.80$,

$p = .09$; Fig. 4). We then contrasted each remapping condition 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 Fig. 5 as difference scores calculated in the same manner as in Experiment 1.

Finally, we wanted to compare the effects of remapping on SWM across Experiments 1 and 2. To do this, we subjected the difference scores from each individual in the two experiments to a between-subjects ANOVA, with the fixed factor being experiment number (1 or 2). We found a significant difference between Experiments 1 and 2 for the cost of leftward remapping ($F(1, 34) = 7.11$, $p < .05$), and rightward remapping ($F(1, 34) = 5.86$, $p < .05$). We also found a significant difference 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 ($F(1, 34) = 0.99$, $p = .33$; Fig. 5).

The results of Experiment 2 indicate 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, as was the case in the saccadic

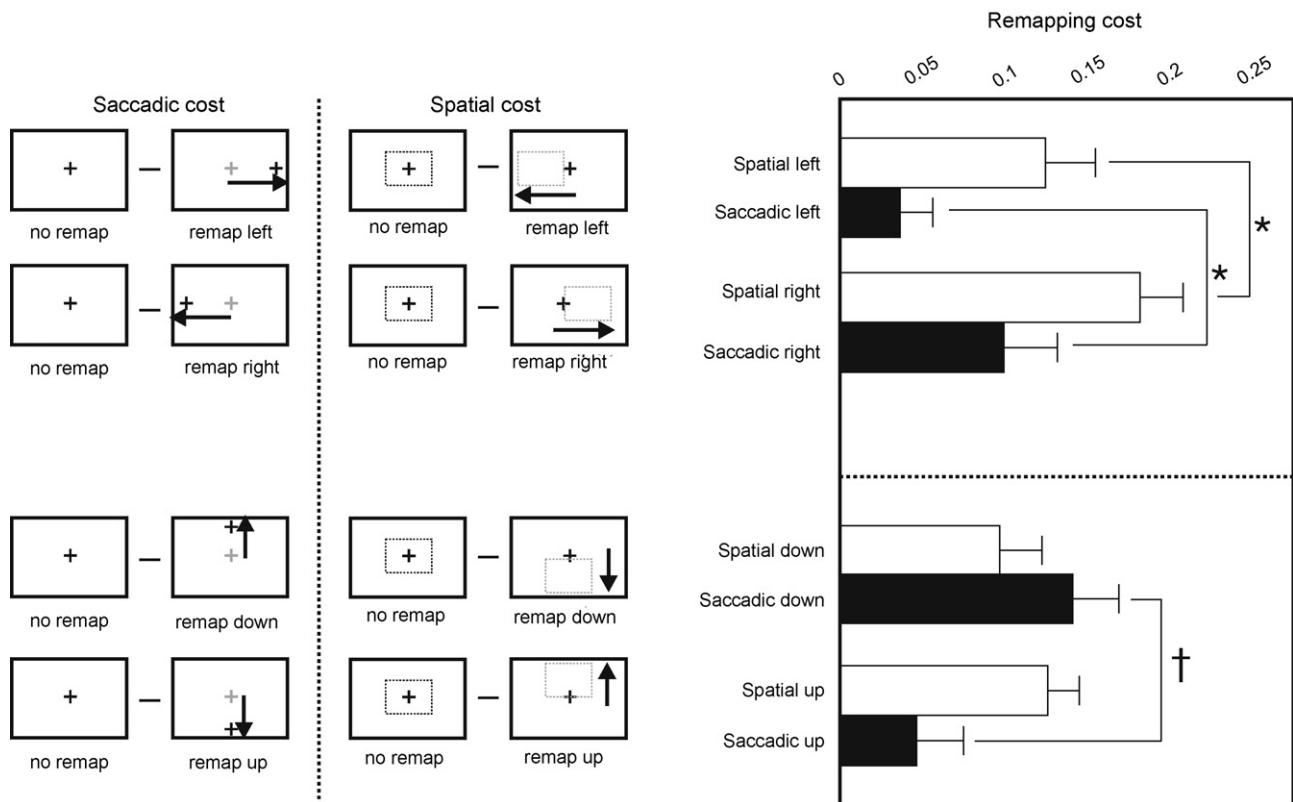


Fig. 5. Comparison of the effects of remapping across the two experiments (results from Experiment 1 are referred to as 'saccadic' and are presented in black bars, while results from Experiment 2 are referred to as 'spatial' and are shown in white bars). A schematic for the method of calculating each cost is represented to the right of the data. Symbol (*) represents a significant difference between the conditions indicated at $p < .05$ and (†) represents a significant difference at $p < .01$.

remapping version of the task in Experiment 1. Finally, there was a slight trend for upward remapping to have a greater cost than downward remapping.

4. Discussion

The results of the second experiment demonstrated a more consistent cost to SWM during covert shifts of attention in that all directions of remapping led to a significant decrement to SWM performance (Figs. 2, 4 and 5). Additionally, the between experiment analysis suggests that spatial remapping led to greater costs for SWM than did saccadic remapping (Fig. 5). While the change in absolute stimulus size may have partially influenced this result it seems more likely that covert remapping is more difficult than is overt remapping for several reasons. First, the ability to detect the gapped circle target prior to any remapping requirement was not significantly different across the two experiments (Table 1). Second, previous research has already demonstrated that directing spatial attention towards a to-be-remembered location improves SWM (Awh & Jonides, 1998; Awh & Jonides, 2001). The requirement to covertly remap the entire display in the current experiment would often have been at odds with the normal desire to covertly attend the to-be-remembered location thus making this task more difficult. What is important to emphasise here is that the observed decrements to SWM were specific to particular directions of remapping. In other words, the overall increase in difficulty for covertly remapping a stimulus array did not eliminate direction specific costs. This argument also holds for the criticism that the task used here has no built-in control for the fact that any observed effects of remapping on SWM could simply reflect an increase in complexity from the no-remapping to the remapping conditions. Such an effect of task complexity would not be expected to lead to the *direction-specific* effects observed here.

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. In both instances this cost likely reflects the fact that rightward remapping relies on left hemisphere processing which is less specialised for spatial behaviours of this kind. 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 (Figs. 2, 4 and 5). There was a slight trend towards a greater cost for upward remapping in the covert spatial remapping version of the task which 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 the no-remapping condition, 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. As mentioned briefly above, this is unlikely to be due to the smaller visual angles subtended by the targets in Experiment 2 as target detection in the initial stages of a trial was uniformly high and not different from the detection rates in Experiment 1. In addition, the effects observed here are unlikely to be due to an inability to properly *rehearse* target locations in SWM. Although Awh, Jonides, and Reuter-Lorenz (1998) have shown that *preventing* attention from being directed towards a to-be-remembered target location impaired SWM performance, 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 location of the target. It was the requirement 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).

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 along the horizontal axis. 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,³ SWM was worse than in conditions in which leftward remapping was required (Figs. 2 and 4). 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 (Corbetta & Shulman, 2002; Heilman & Van Den Abell, 1979, 1980). Right hemisphere mechanisms have also been shown to be more efficient for attentional tasks in general (Mesulam, 1981). Furthermore, as initially suggested by Pisella and Mattingley (2004), 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 (Hellige & Michimata, 1989; Kessels, Kappelle, de Haan, & Postma, 2002; Kosslyn et al., 1989). 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, Kapur, Moscovitch, Winocur and Houle (1995) indicated that the right inferior parietal lobule was more involved in a spatial location matching task than in an object identity matching task (see also Köhler, Moscovitch, Winocur, Houle, & McIntosh, 1998).

Horizontal remapping resulted in the same effects on SWM whether it was performed overtly or covertly. 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. 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. One possible explanation for this dissociation comes from Previc's theory of the neural representation of three-dimensional 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 the 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

³ We are not suggesting here that these two conditions reflect some common underlying physiological process. Indeed, remapping covertly or overtly may involve somewhat distinct neural networks or mechanisms. What is equivalent across these two conditions is the region of space to which the target array had to be remapped. The schematics in Fig. 5 are intended to make this comparison clear.

and action in near (peripersonal) space (Butler, Eskes, & Vandorpe, 2004; Danckert & Goodale, 2001, 2003; Goodale & Milner, 1992; Previc, 1990; Weiss et al., 2000). 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 Intrilligato (1996) found that attentional resolution was greater in the lower visual field during a task in which the random motion of multiple targets had to be tracked. In addition, Danckert and Goodale (2001) have shown that a more robust speed-accuracy trade-off is observed for visually guided movements executed in the lower 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 when contrasted with circumstances in which the display is covertly remapped into upper visual space. There was only a slight trend to this effect in Experiment 2 and the opposite effect (i.e., greater cost for downward remapping) in Experiment 1. Further research will be needed to examine this dissociation carefully.

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 we are 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 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 for remapping into lower visual space (Fig. 2). The contrasting effects of overt and covert remapping in the vertical axis may 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. Further research is required to determine whether more robust differences in covert and overt remapping in the vertical axis can be demonstrated, 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 (see also Vuilleumier et al., 2007). The current data set would also suggest that separable deficits in SWM (i.e., Ferber & Danckert, 2006) and spatial remapping (i.e., Heide, Blankenburg, Zimmermann & Kompf, 1995; Vuilleumier et al., 2007) will interact in neglect patients to further impair their ability to maintain an accurate representation of left visual space. In addition, one influential 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, Riggio, Dascola, & Umiltà, 1987). In the present study, the greater costs to SWM seen when covert remapping is required in any direction (Fig. 5) suggests 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 (Butler, Eskes, & Vandorpe, 2004; Guariglia & Antonucci, 1992; Halligan & Marshall, 1991, 1995; see also Berti & Frassinetti, 2000). 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 (Mort et al., 2003) and the superior temporal gyrus (Karnath, Ferber & Himmelbach, 2001) – 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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