



Disruption of spatial memory in visual search in the left visual field in patients with hemispatial neglect

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ABSTRACT

Spatial working memory during an ongoing visual search trial was tested in both visual fields for right-brain damaged patients with contralesional spatial neglect, as well as age-matched control patients with right-hemisphere lesions but no neglect. We examined within-trial spatial memory by using a relocation search paradigm introduced by Kristjánsson (2000) (modified from Horowitz & Wolfe, 1998), in which the display items traded places every 110 ms so that the target was never to be found in the same location from one moment to the next (the relocation condition), as compared with a static condition where the display items remained in place for the whole trial duration. To equate appearance between the two conditions, all items changed orientation every 110 ms in both conditions, and were masked after each of the briefly presented visual arrays. The results showed that search was disrupted by item relocation for both patients and controls, but importantly this disruption was only seen in the right visual field for the patients, not the left, indicating that their spatial working memory in left visual space is already severely disrupted, and to a greater degree than for their right visual space, in contrast to what has been previously argued.

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1. Introduction

Hemispatial neglect is a multimodal neuropsychological disorder in which patients typically have trouble directing their attention towards the left side of space, following focal right-brain damage. Patients may fail to notice, respond to, or orient to stimuli in contralesional space, despite unimpaired primary sensory processes (Driver & Mattingley, 1998; Heilman, Watson, & Valenstein, 2003; Saevarsson, Kristjánsson, Hildebrandt, & Halsband, 2009; see e.g. Driver & Vuilleumier, 2001 for review). A neglect patient may read only the right pages of a book (Halligan & Marshall, 1998), read only the right side of single words (McManus, 2001), or repeatedly look for a particular item on his right, while seldom orienting towards his left (Husain et al., 2001).

Neglect most often follows brain damage due to stroke in the inferior parietal lobule and temporoparietal junction (Mort et al., 2003; Vallar & Perani, 1986), or in the superior temporal gyrus (Karnath, Ferber, & Himmelbach, 2001; Karnath, Fruhmann Berger, Küker, & Rorden, 2004), usually in the right hemisphere. However, a precise neuroanatomical correlate has not been identified, and despite some controversy over the most frequent site of lesions

(Bird et al., 2006; Halligan, Fink, Marshall, & Vallar, 2003; Karnath et al., 2001; Vallar, 1998), a unique critical locus is in fact unlikely to exist; rather, the disorder may essentially reflect the disruption of a distributed network for attentional orienting involving neural activity of a number of sites in the nervous system (e.g. Danckert & Ferber, 2006; Kerkhoff, 2001; Mesulam, 1999; Saevarsson et al., 2009).

1.1. Spatial working memory in neglect

The results of a few recent studies have suggested that neglect patients may suffer from a selective deficit of spatial working memory, in particular in retaining already searched spatial locations in memory, and that such a deficit may play a key role in their failure to orient to their left hemispace. Husain et al. (2001) (see also Malhotra, Mannan, Driver, & Husain (2004)) monitored the gaze of neglect patients as they had to search for “T” targets among “L’s” and to decide for each fixated target whether they had already inspected this particular item before (each search array contained several targets). The patients were required to click a response button only when they inspected a target item that they had not checked before. Critically, they very often indicated that items which they had already inspected were new, whereas such mistakes were rarely made by healthy age-matched controls.

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These results suggest that neglect patients have a deficit in retaining searched locations across saccades, in addition to their pathological bias to preferentially orient to their right side. Based on this result, Husain & colleagues suggested that the neglect syndrome has at least two major components, a bias in attention towards the right in addition to a deficit in spatial working memory, the latter being non-lateralized, affecting the whole visual field (i.e. irrespective of side). Overall, this would explain why neglect patients tend to search recursively in their right visual field but rarely orient to their left visual field. Duncan et al. (1999) have also found evidence indicating that the attentional deficit in neglect is not confined to the left visual field of the patients.

In another study, neglect patients performed a traditional paper-and-pen cancellation task (often used as a diagnostic tool of neglect), either with a pen that left a visible mark on the paper, or with a pen that left no visible mark when the patients “canceled” the item (Wojciulik, Husain, Clarke, & Driver, 2001). In the condition where the pen left no visual mark, patients tended to cancel right-sided items over and over again, unlike control participants, again suggesting that the patients have a spatial working memory deficit.

This issue was directly investigated in a study where patients were shown a sequence of items in a one-dimensional (non-lateralized) columnar array and had to remember these locations in sequence (Malhotra et al., 2005). Two tests of spatial memory were given, one in which observers had to remember the whole sequence of locations in the correct order, and another in which they were asked whether a single location probe had been part of the original sequence. Neglect patients showed impaired performance on both tasks compared with the performance of healthy controls. This result suggests that the spatial working memory deficit of these patients is not related to their lateralized deficit for left visual space, since *all* possible locations were positioned on the vertical meridian. Again this is consistent with the proposal that impaired spatial memory constitutes a distinctive component of the neglect syndrome, which is not directly connected to their impairments in attending towards the left visual field.

The findings reviewed above, suggesting a deficit in retaining searched locations in memory, converge with neurophysiological studies showing that posterior parietal cortex (which is typically damaged in neglect) is involved in remembering searched locations across saccades (Anderson et al., 1994; O’Sullivan et al., 1995). Functional imaging studies have consistently revealed that the right posterior parietal cortex is specifically activated when observers must remember the location of targets (Awh et al., 1999; Jonides et al., 1993; Owen, Doyon, Petrides, & Evans, 1996; Ruff, Kristjánsson, & Driver, 2007), with some selectivity for the contralateral visual field observed when gaze direction is dynamically shifted towards one or the other side (Merriam, Genovese, & Colby, 2003). There is also considerable evidence from neuroimaging that regions concerned with spatial working memory show a large overlap with those involved in spatial attention (Awh & Jonides, 2001; Corbetta & Shulman, 2002; Geng et al., 2006; Husain & Rorden, 2003; Kristjánsson, Vuilleumier, Schwartz, Macaluso, & Driver, 2007; Ruff et al., 2007), suggesting that damage to these sites may lead to deficits in both spatial working memory and attention.

1.2. The current study

The aim of our study was to further characterize the impairment in within-trial spatial memory for inspected location in visual search for neglect patients, by investigating their memory for target locations on either side of space during a visual search task. We compared their performance to the performance of age-matched right-brain damaged patients who showed no symptoms

of neglect. For each visual search array, observers had to decide whether an “L” target was present among a variable number of “T” distractors. The critical manipulation was that in one condition the target *traded places* with a randomly chosen distractor every 110 ms; while in the other condition all the items stayed in place but randomly *changed orientation* every 110 ms (see Fig. 1). This within-trial relocation design was originally introduced by Kristjánsson (2000), as a modification of the “random” visual search paradigm designed by Horowitz and Wolfe (1998), to test for spatial memory within trials during visual search. Horowitz and Wolfe designed this paradigm to determine whether normal observers performing a visual search task search serially and systematically through the arrays, stopping either when the target is found or when all items have been checked and a decision is made that no target is present in the array. Horowitz and Wolfe reported that relocating the items every 110 ms, did not affect the efficiency of search, as they found no effects on search slope in this condition compared to when the search items remained in place, and thus concluded that no spatial memory mechanism is at work in visual search tasks. However, with some tweaking of the experimental parameters, Kristjánsson (2000) found a cost of item relocation during search, providing evidence for the role of memory for spatial positions within single trials (see further discussion in Horowitz & Wolfe (2003), Kristjánsson (2006a), see also Hulleman (2009) for some recent evidence regarding this debate).

If the neglect patients do indeed have a deficit in retaining searched locations across the visual field, we should expect to see little disruption of search with the relocation procedure, and this should not vary depending upon the visual field of the target. But if memory for spatial locations is differentially impaired for the contralesional and ipsilesional visual fields, we should observe differences in the costs of relocation across the two visual fields. On the other hand, we should expect the search of the control patients to be similarly affected in both visual fields by the relocation procedure.

2. Methods

2.1. Observers

We examined eight patients with focal right-hemispheric lesions from stroke (see Table 1 and Fig. 2 for clinical details on the patients). Four patients had visuospatial neglect (three males, one female, age range 56–80 year-old, mean 69.8), while four other patients had no neglect and served as age matched, brain-damaged controls (two males, two females, age range 66–78 year-old, mean 72.8). Neglect was diagnosed by standard clinical tests including Mesulam shape cancellation (Mesulam, 1985), Albert line cancellation (Albert, 1973), a star cancellation test from the Behavioral Inattention Test (Wilson, Cockburn, & Halligan, 1987), and a bisection task on lines of various length (Schenkenberg, Bradford, & Ajax, 1980). All patients had intact visual fields on both sides, as tested with clinical confrontation, with normal or corrected to normal visual acuity. All were right-handed and had no other neurological or psychiatric disease. They gave their written informed consent to participate in the study. A brief neuropsychological assessment of neglect (see results in Table 1) was administered on the same day as the current experimental investigations. Table 1 clearly shows that the neglect group had strong neglect symptoms as measured by standard tests, while the age-matched right-brain-damaged controls showed no indication at all of neglect. The brain lesions were identified by MRI scans in all patients, and rendered on a standard normalized brain template using MRIcro software (Rorden & Brett, 2000) according to standard procedures (e.g. see Grandjean, Sander, Lucas, Scherer,

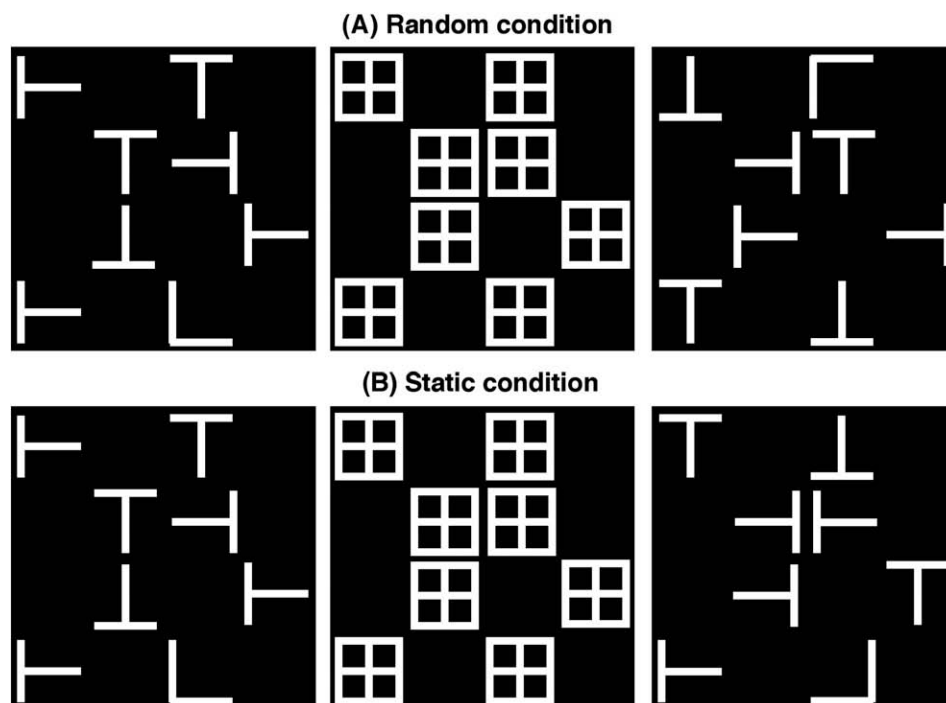


Fig. 1. The two conditions of the experiment. Panel A shows the “random” condition where the “L” target could appear in a new location following a refresh (occurring every 110 ms; the display items were presented for 83 ms and the mask for 27 ms). Panel B shows the “static” condition where the target stayed in the same place throughout a given trial. The distractors and target also randomly changed orientation in both conditions, in order to create a similar dynamic appearance for both search types. Orthogonally to these two conditions, target location was either within the left or within the right visual field.

Table 1
Clinical characteristics of the patients.

Patient	Sex, age	Months post-stroke onset	Albert cancellation (total misses)	Mesulam cancellation (total misses)	Star cancellation (total misses)	Line bisection (% left deviation)
<i>Neglect group</i>						
1	m, 56	20	0	17	8	8.6
2	f, 80	2	0	29	5	2.4
3	m, 75	4	4	12	8	4.2
4	m, 68	1	1	9	6	6.1
<i>Control group</i>						
1	m, 66	3	0	0	0	0.5
2	f, 78	1	0	1	0	−0.2
3	m, 78	12	0	0	0	0.3
4	f, 69	2	5	0	0	0.6

& Vuilleumier, 2008; Lucas & Vuilleumier, 2008). Fig. 2A and B shows the lesion overlap separately for the two groups. The lesion overlap between the two groups (lesions for control patients subtracted from the lesions for the neglect patients) is then illustrated in Fig. 2C, showing more common involvement of the right inferior parietal regions in the neglect patients than the control patients, as expected from their clinical symptoms.

2.2. Stimuli and procedure

The observers searched for a white “L” target among white “T”s on a black background, in a 2×2 design in which we manipulated the visual field in which the target could appear (right or left) and whether the target item stayed in the same location throughout a trial or was randomly relocated. The observers were unaware of on which trials the target was confined to the left side and in which cases to the right. When the items were relocated, they always fell on positions previously occupied by another item (a “T” distractor). The display items were thus confined to as many locations as the

set-size on each trial (in contrast to the methods used by Horowitz & Wolfe, 1998). The stimulus display was programmed in C and presented on a Macintosh Laptop.

In the random (relocation) condition the L-targets and T-distractors were relocated every 110 ms, whereas in the static condition, the L-targets and T-distractors all remained in the same position, with a 27 ms local mask presented between each change in the search array under both conditions. Importantly, the display items changed orientation randomly (the items could be oriented 0° , 90° , 180° or 270° away from vertical) every 110 ms, *independently* of condition (relocation or static). The visual appearance of the display was thus kept constant across all conditions despite the target relocation. This was done to equate visual changes between the “relocation” and “static” conditions¹. The mask consisted of a “+” surrounded by a square (see Fig. 1) and thus contained all possible individual features of the L’s and T’s at any of the four

¹ Failure to do this may have introduced some confounds in the original Horowitz and Wolfe (1998) paradigm, as discussed in Kristjánsson (2000).

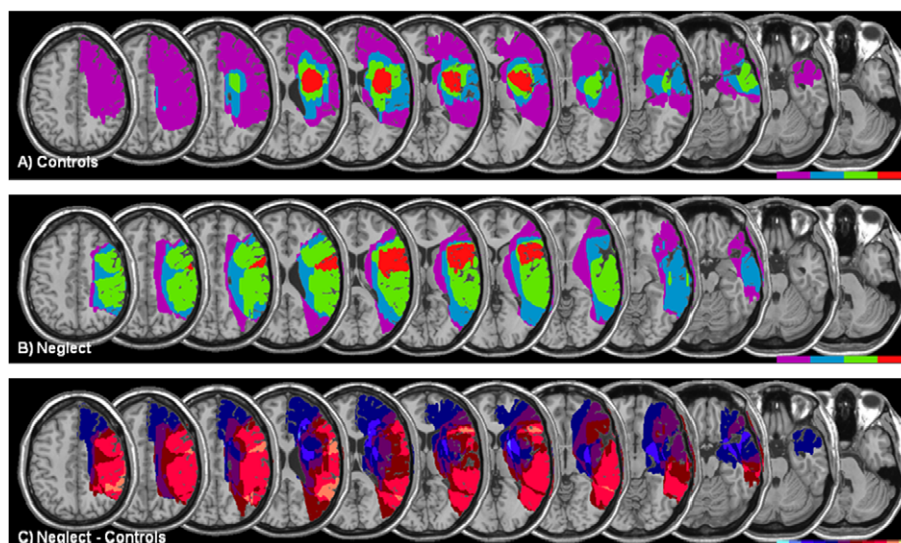


Fig. 2. Brain lesion sites in our two groups of patients. The overlap of damage is shown (A) for patients with neglect and (B) for patients without neglect. The color scales for A and B show the degree of overlap, with the rightmost color on the scale denoting the largest degree of overlap. (C) Lesions differentially associated with neglect are highlighted by subtracting lesions for the control patients from those for the neglect patients, showing more common damage in inferior parietal cortex when neglect symptoms were present.

orientations. The target was confined to the left or right visual field on any given trial in both conditions, to test memory performance in the different visual fields.

There were 4, 8, 12, or 16 items on the screen on each trial. On 50% of the trials one of the items was an “L” target among “T” distractors (a target-present) trial, while on the other 50% of trials there were only “T” distractors on the screen. There were 64 possible locations and the display items were dispersed randomly among those (i.e. a number of locations equal to the set-size was randomly picked for each trial). The observers were never informed of any differences between the conditions. They were only told to indicate by key press whether an “L” oriented in any of the four possible ways was present on the screen.

Observers performed the static and relocation conditions in separate blocks of 64 trials, with a short self-terminated pause every 16 trials. Static and relocation blocks alternated in an A–B–B–A order, with the first block type counterbalanced across participants. Each observer performed 3 or 4 blocks of each type (in total, 192–256 trials), depending on individual willingness or fatigue. All stimuli were presented on a laptop screen (17-in.), at a viewing distance of approximately 50 cm. At this distance each display item subtended approximately 1.5° of visual angle. Before starting, patients were shown the whole visual display with static examples without any time limitations. They were explicitly told that targets could appear on either side of the fixation, and encouraged to explore the whole display (on the computer screen). Responses, dependent upon whether the observers thought that the target was present or not, were made by pressing one of two keys on a numerical pad connected to the laptop and held in front of the patient (aligned with their trunk midline).

3. Results

Mean RTs and accuracy rates were calculated for each search condition and each visual field, for both groups of observers. Overall, the presence or absence of targets was correctly reported on 89.6% of trials by the neglect patients and 90.2% of trials by the age-matched, right-brain-damaged controls (although the pattern of errors differed slightly between groups, see below, and in Table 3).

3.1. Response times

The RTs for correct target detection as a function of condition under the 2×2 design are shown in Fig. 3A for the neglect patients, and Fig. 3B for the control patients. Overall, the relocation condition resulted in increased response times, both in terms of search rate and intercept. A 4 (set size) $\times 2$ (relocation versus static) $\times 2$ (visual field) repeated measures ANOVA was performed separately on target-present and target-absent trials and separately for neglect patients and control patients.

For the neglect patients, the ANOVA on the response times for the target-present trials revealed a main effect of set-size ($F_{(3,9)} = 12.6$, $p = .001$) and of condition ($F_{(1,3)} = 20.8$, $p = .02$), while the main effect of visual field showed only a non-significant trend ($F_{(1,3)} = 6.3$; $p = .087$). Most importantly, however, there was a significant interaction between visual field and condition ($F_{(1,3)} = 11.17$, $p = .044$) which indicated that relocating the target had a larger effect on performance in the right visual field than the left. In other words, changing the locations of visual items within trials has a larger cost for visual search performance in the right visual field, indicating that spatial memory on the left is already quite disrupted for the patients, and affected only to a limited degree by the relocation procedure (see further analysis below).

The interaction between set-size and condition was also significant ($F_{(3,9)} = 3.86$, $p = .05$), which is consistent with increasing costs of relocating items across the screen within a trial when the number of locations in the display increases, as previously observed by Kristjánsson (2000). However, the interaction between set-size and visual field was not significant ($F_{(3,9)} = 1.4$, $p = .23$), nor was the 3-way interaction ($F_{(3,9)} = 1.90$, $p = .20$). Hence, the left–right asymmetry of relocation costs was generally independent of the display set-size.

The ANOVA for the target-absent trials in neglect patients showed a significant effect of set-size only ($F_{(3,9)} = 4.86$; $p = .02$), while neither condition ($F_{(1,3)} = 0.57$; $p = .47$) nor side ($F_{(1,3)} = 2.46$; $p = .21$) had a significant effect, nor any of the interactions (set-size by condition: $F_{(3,9)} = 1.64$, $p = .24$; set-size by visual field: $F_{(3,9)} = 1.35$, $p = .32$; visual field by condition: $F_{(1,3)} = 1.11$; $p = .37$; set-size by visual field by condition: $F_{(3,9)} = 0.58$, $p = .64$).

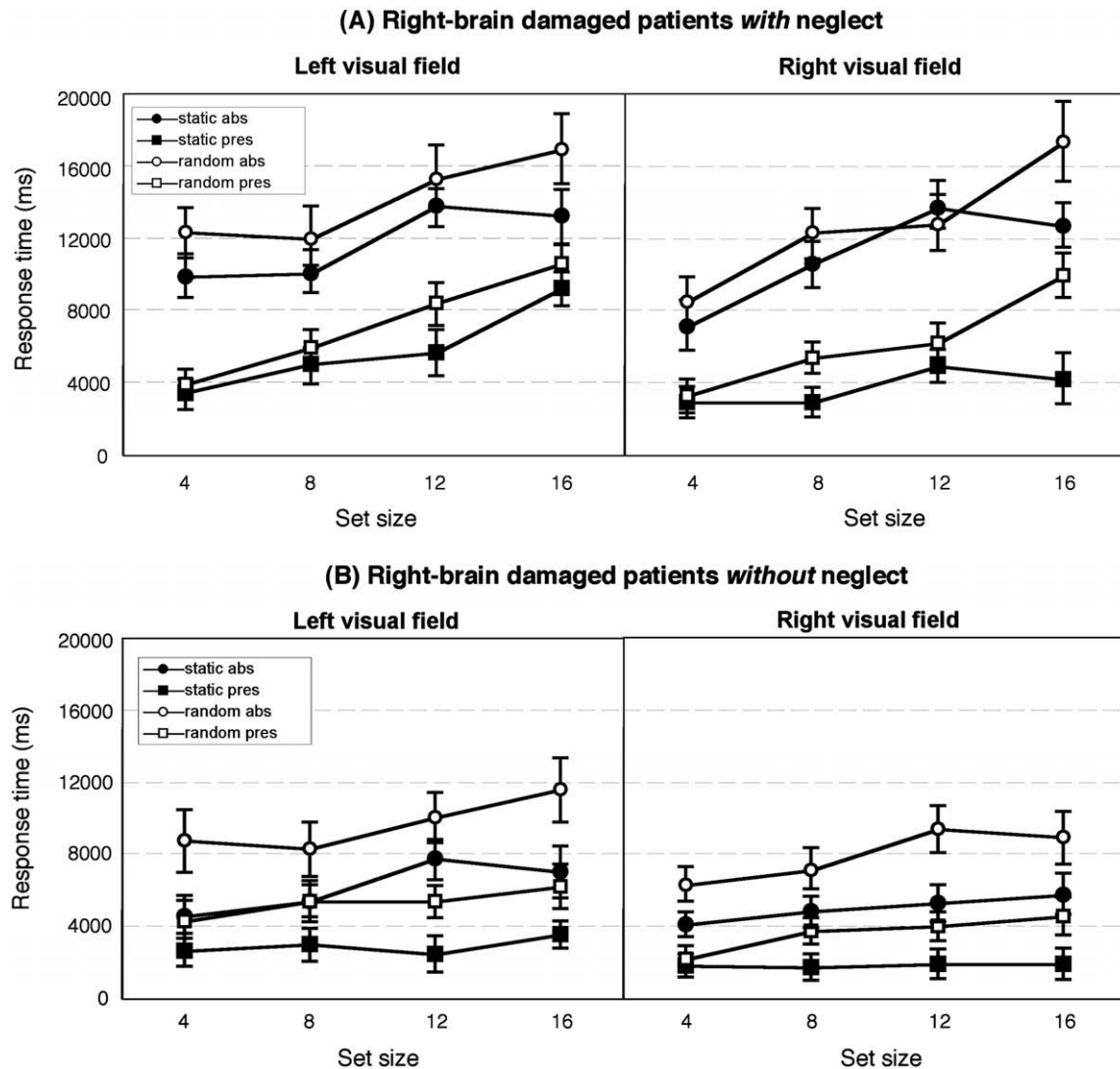


Fig. 3. Search performance for the two groups of patients as a function of condition. The relocation (or random) condition is shown in white, while the static condition is shown in black. Squares denote target-present trials, while circles denote target-absent trials. Performance in the left visual field is shown on the left and performance in the right visual field is shown on the right. Panel A shows performance for neglect patients, and panel B for the control patients (with right hemisphere damage, but no neglect). The error bars show the standard error of the mean for each experimental condition.

In sum, this indicates that our manipulations had little effect on performance on the target-absent trials for the patients. The decision that no target is present is hard to make for dynamic displays like the one we use and may, to a considerable extent, be a decision criterion issue rather than an issue of spatial working memory (see Chun & Wolfe, 1996; Horowitz & Wolfe, 1998; Kristjánsson, 2000 for further discussion of this).

For the target-present trials for the age-matched, neurologically damaged controls who did not suffer from neglect, there was a significant effect of set-size ($F_{(3,9)} = 12.55, p = .001$) and of condition ($F_{(1,3)} = 27.89; p < 0.001$), but not of visual field ($F_{(1,3)} = 4.28; p = .13$) which is not surprising given that these individuals had no attentional biases to either visual field. The interaction term between set-size and condition showed a marginally significant trend ($F_{(3,9)} = 2.97, p = .089$) which indicates that the effect of relocation might be slightly weaker for controls than the neglect patients, although there was a clear hint of a significant cost in the data. Moreover, note that such an effect was found for the neglect patients in the right visual field and overall this indicates that the relocation did indeed have a deleterious effect upon performance. The effect may be found to be marginal in the neglect

patients because of the low number of observers. In any case, the ANOVAs showed that the 3-way interaction of group by set-size by condition was far from significant, ($F_{(3,9)} = 0.25, p = .86$), showing that the trend found for the control patients indeed reflected a small but consistent effect of set-size by condition, generally similar to that found for the neglect patients and healthy observers (Kristjánsson, 2000). Other interaction terms were not significant (set-size by visual field: $F_{(3,9)} = 1.28, p = .17$; condition by visual field: $F_{(1,3)} = 0.25, p = .86$).

For the target-absent trials for the controls there was a significant effect of relocation condition ($F_{(1,3)} = 10.05, p = .11$) and of set-size ($F_{(3,9)} = 7.75; p = .007$) as well as an almost significant effect of visual field ($F_{(1,3)} = 10.05; p = .051$). The reason for this trend of visual field in this condition is unclear, but note that it did not show up for the target-present trials in the same group and might possibly reflect a compensatory strategy when targets are not found (see e.g. Barton & Black, 1998; Kerkhoff & Bucher, 2008). None of the interactions turned out to be significant (set-size by visual field: $F_{(3,9)} = 1.64, p = .25$; set-size by condition: $F_{(3,9)} = 1.22, p = .36$; condition by visual field: $F_{(1,3)} = 0.51, p = .51$; the 3-way interaction $F_{(3,9)} = 1.32, p = .33$). Note that the contrast

for the condition by visual field interaction, which was significant for the neglect patients was far from significant for the right-brain damaged controls showing no signs of neglect.

Overall the most notable result is the significant interaction between visual field of target and relocation condition that was *selectively* found for the neglect patients (there was no hint of such an interaction for the controls). This interaction shows that relocating the distractors every 110 ms disrupted performance only in the RVF for the patients, but caused no performance decrements in their contralesional LVF (see further confirmation of this below and in Section 3.2). This in turn suggests that any spatial working memory deficit is more pronounced for the left than right visual field for patients suffering from (left) hemispatial neglect, such that searched locations were not retained, or tagged as already inspected, within a trial even in the static condition when the target was not randomly relocated.

These results were confirmed by a direct comparison between groups, using a new ANOVA on RTs for target-present trials from both groups, with the same within-subject factors as above plus the between-subject factor of group (neglect patients versus right-brain-damaged controls with no neglect). All main effects (relocation condition, side, set-size) were significant (all F s > 10.4, all p 's < 0.018) except for the effect of group ($F_{(1,6)} = 2.07$, $p = .20$). There were also significant interactions of set-size by task condition ($F_{(3,18)} = 6.38$, $p = .023$) and set-size by group ($F_{(3,18)} = 7.07$, $p = .022$). Much more critically, a triple interaction of group by task condition by side was also found ($F_{(1,6)} = 12.97$, $p = .011$) again confirming (with high reliability) that there was a large difference in the effects of relocation as a function of visual field across the two groups. The quadruple (4-way) interaction was not significant ($F = 1.01$). A similar analysis for the target-absent trials showed no significant effects except for a main effect of set-size ($F_{(3,18)} = 9.24$, $p = .001$).

3.2. Slopes of set-size versus response times

In order to further cement that there was indeed a difference between the effects of relocation between the two hemifields for the neglect patients, we calculated the slopes of set-size versus response times for the target-present trials, yielding a number that shows the increase in search time (in ms) with each added item to the set size. Horowitz and Wolfe (1998) argued that if relocating items within a trial affects the search, an effect should be found upon the slopes since they indicate how many more items must be checked when items are relocated, versus when they stay in place. While this putative importance of slopes of set-size versus response times for determining whether spatial memory plays a role in search requires the assumption that observers perform serial self-terminating search (e.g. Neisser, 1967; Tresiman & Gelade, 1980) and need not apply under other conceptions of the visual search process (Bundesen & Habekost, 2008; Eckstein, 1998; Palmer, 1995; Sternberg, 1975; see discussion in Kristjánsson, 2000), we reasoned that finding a difference in slope between the hemifields would further cement our argument of a visual-field difference for patients and not controls. Note that because of the problem of decision criteria for terminating search on target-absent trials (as discussed in the previous section) we performed this analysis of slopes on the target-present trials only (as was done by Horowitz & Wolfe, 1998).

The slopes for the eight patients are shown in Table 2. We performed two separate 2×2 ANOVAs on the slopes for the two groups of patients with the factors visual field (LVF versus RVF) and condition (relocation versus static). For the neglect patients the effect of condition was significant ($F_{(1,3)} = 36.84$; $p = .009$) while no main effect of visual field upon the slopes was seen ($F_{(1,3)} = 2.25$; $p = .227$). Importantly, however, there was a significant interaction

Table 2

Slopes of set-size versus response times for the target-present trials (ms per added item) for the two groups of patients as a function of visual field.

Patient	Static		Relocation	
	LVF	RVF	LVF	RVF
<i>Neglect group</i>				
1	908.63	193.88	1107.48	709.15
2	371.98	202.40	504.80	405.13
3	220.28	82.10	282.68	535.08
4	302.18	93.63	363.40	423.98
<i>Control group</i>				
1	95.70	85.43	257.60	187.75
2	103.88	−101.03	325.55	347.73
3	−45.10	11.35	150.35	110.78
4	45.50	58.13	217.03	92.25

Table 3

Error rates (in percentages) in each condition for each group. Standard errors are given in parentheses.

Condition	LVF	RVF
<i>Control patients</i>		
Target present		
Static	6.25 (4.6)	10.41 (6.9)
Relocation	12.5 (5.9)	5 (2.9)
Target absent		
Static	12.2 (4.7)	16.67 (7.8)
Relocation	2.5 (2.9)	12.5 (6.7)
<i>Neglect patients</i>		
Target present		
Static	10.42 (5.4)	4.17 (3.9)
Relocation	22.92 (7.3)	8.33 (5.3)
Target absent		
Static	6.25 (4.4)	8.33 (6.1)
Relocation	16.67 (6.7)	6.25 (5.1)

between the effects of visual field and condition upon the slope ($F_{(1,3)} = 13.43$; $p = .035$). For the control patients the effect of condition was also significant ($F_{(1,3)} = 11.56$; $p = 0.42$) while the effect of visual field was not ($F_{(1,3)} = 4.67$, $p = .12$). In stark contrast to what was found for the neglect patients, there was *no hint* of an interaction between the effects of visual field and condition upon the slopes ($F_{(1,3)} = 0.04$; $p = .855$). This difference in the interaction terms for the two groups shows that the effect of relocation as a function of visual field is quite different depending on whether the patients have a diagnosis of neglect or not.

Our results show slopes for both visual fields for the neglect patients. On the surface one might think that this is in stark contrast to the findings of Husain et al. (2001) in that they claim that neglect patients suffer from a deficit in memory for locations already checked in search. Let us note in this context that it is somewhat naïve to assume that a slope difference indicates spatial memory in attentional operation. This is only valid if one assumes that observers perform a serial self-terminating search (see our discussion of this issue above).

3.3. Error rates

Table 3 shows the mean rates of misses on target-present trials and false alarms on target-absent trials. As expected, misses were generally more frequent for neglect patients than controls (11.45% versus 8.54%), with a greater disadvantage for the contralesional left visual field relative to the ipsilesional right side in neglect patients (16.67% versus 6.25%, respectively) but not in controls

(9.38% versus 7.71%). The rate of false alarms on target-absent trials was roughly similar between the two groups (neglect: 9.38%, controls: 10.96%).

We performed a 4 (set size) $\times 2$ (relocation versus static) $\times 2$ (visual field) repeated measures ANOVA on the percentage of errors made on target-present and target-absent trials, separately for neglect patients and controls. For the neglect patients, for misses on target-present trials, all main effects and interactions were significant (all F 's > 9.4 , all p 's $< .05$). The same results were found for the percentage of false alarms made on target-absent trials in these patients (all F 's > 8.38 , all p 's $< .05$), except for the factor of task condition which produced only a marginal main effect ($F_{(1,3)} = 8.22$, $p = .064$). In contrast, a similar $4 \times 2 \times 2$ ANOVA on the percentage of errors for the control patients showed no significant main effect or interaction for either target-present or target-absent trials.

Finally, we directly compared the two groups by using an ANOVA on error rates with the same within-subject factors as above plus the between-subject factor of group (neglect patients versus control patients). For misses on target-present trials, this analysis showed a significant interaction of group with side ($F_{(1,6)} = 109$, $p < .001$), as well as a triple interaction of group by task condition by set size ($F_{(3,18)} = 41.5$, $p < .001$), and a quadruple (4-way) interaction of group by task condition by set size by side ($F_{(3,18)} = 7.07$, $p < .031$). This result calls for some follow-up tests, since the 4-way interaction may be indicative of a speed accuracy trade-off, which might partly account for the differences in RT between the left and right hemifields for the patients. Direct t -tests on the error rates did not reveal any reliable differences between the two hemifields, however (for the control patients: static condition: $t_{(3)} = 1.12$, $p = .34$; relocation condition: $t_{(3)} = 1.59$; $p = .21$). For the neglect patients a comparable analysis revealed no significant effect for the static condition ($t_{(3)} = .987$; $p = .39$) nor for the relocation condition ($t_{(3)} = 1.89$; $p = .149$). Finally let us note that our analyses of the error rates are low-powered, because of the relatively low number of participants, so this issue may warrant further study in future.

For false alarms on target-absent trials, the ANOVA showed only a triple interaction of group by task condition by set size ($F_{(3,18)} = 20.95$, $p = .004$). There was no significant main effect of group in either case. Furthermore, the four way interaction was not significant showing that there was no hint of a difference in search strategies between the two groups (such as a possible speed-accuracy trade-off).

In sum, these results for error rates indicate that the two groups differed mainly in terms of their misses on target-present trials, with a differential impact of relocation condition as a function of set size and visual field seen for the neglect patients but not the control patients.

4. Discussion

Our results indicate that relocating targets within trials of a visual search task has a significant detrimental effect on search performance in the right visual field but not to the same degree in the left visual field for neglect patients, whereas such asymmetry is not seen for right-brain-damaged controls without neglect whose performance is affected in both visual fields to a similar extent with relocation. This indicates that spatial memory for locations during visual search is impaired in the affected visual field of neglect patients, even when targets are not relocated, but also shows that this does not apply to the same degree to the right visual field of the patients.

More broadly, the results also replicate the results of Kristjánsson (2000), since there was a significant interaction between

set-size and condition for target-present trials (although it was only marginally significant for the controls, most likely due to our small sample). This result shows that the effect of set-size differs according to whether the items are relocated within trials, or not, indicating that some form of spatial memory for the searched locations is disrupted by the relocation procedure. This interaction was not seen for the target-absent trials. How observers terminate a search and decide that a target is absent may be a matter of decision criteria (Chun & Wolfe, 1996), particularly in a paradigm where the search items constantly change orientation or even trade places. This result suggests that relocating items in visual search slows the detection of targets considerably, suggesting that some form of spatial memory for previously searched locations is at work during visual search tasks of this sort. This is consistent with other behavioral findings suggesting that some spatial memory component is likely to be involved in visual search, as already argued by Kristjánsson (2000) (see also Von Mühlenen, Müller, & Müller, 2003). Note, however, that Horowitz and Wolfe (2003) found little effects of relocation upon search slopes, using a search paradigm similar to the one used here, but in that study the search items traded places every 500 ms instead of every 110 ms, clearly a critical difference between the two procedures.

Our results show significant slopes of response time as a function of set-size for both visual fields in the relocation condition for the neglect patients. On the surface one might think that this is in contrast to the findings of Husain et al. (2001) in that they claim that neglect patients suffer from a deficit in memory. We have two things to say about this – firstly it is somewhat naïve to assume that a slope difference unequivocally indicates spatial memory in attentional operation. This is only valid if one assumes that observers perform a serial self-terminating search, as we discuss above. Also, a set-size effect may come about through other channels, for e.g. crowding can increase uncertainty about a decision, especially as it interacts with random relocation.

4.1. Spatial memory in hemispatial neglect

In our introduction, we reviewed neuropsychological results indicating that spatial working memory (SWM) might be impaired for neglect patients. However, those previous results have usually been taken to imply that this spatial working memory deficit is non-lateralized, and that the deficit applies to the whole visual field (e.g. see Husain et al., 2001). But our new results here suggest, on the other hand, that any such deficit is more pronounced for the left visual field.

There are other results which suggest that an impaired representation of contralesional space in neglect patients might produce an asymmetrical impact on their maintenance of locations in memory over short time intervals, and thus affect contralesional/left-side visual stimuli more than ipsilesional/right-side stimuli (see Pisella & Mattingley, 2004; Pouget & Driver, 2000). In a recent study, Vuilleumier et al. (2007) reported results suggesting that neglect patients may suffer from losses in gaze-centric representations for locations in their left visual field. They found that gaze shifts to the right of a fixated visual target had a disastrous effect upon subsequent spatial memory for the targets' location, which was now shifted to the left of the new gaze direction. Specifically, patients had to encode a single target location, presented either on the right or left side of the visual display, and then to retain it in memory for 2–3 s, during which they could shift gaze to their right, to their left, or maintained gaze at the same location. The neglect patients showed a dramatic loss of memory for target location after shifting gaze to the right, but importantly *not* when they shifted their gaze to the left. This deficit was present even when the target initially appeared in the right visual field. This indicates that the patients have severe problems with retaining locations in their left

hemifield in memory; a deficit which does not apply to stimuli in their right hemifield. Such a deficit should obviously have disastrous consequences for performance in a relocation search paradigm such as the one used here, where gaze had presumably to shift from item to item, and would thus impair spatial memory in particular for the left visual field. These results of Vuilleumier et al. (2007) are therefore quite consistent with the results presented here in that the spatial memory deficit for previously fixated locations is lateralized. It is much more pronounced for the left than the right visual field.

Husain et al. (2001) (Malhotra et al., 2004; Mannan et al., 2005) have, as mentioned in the introduction, argued that neglect may reflect a bias to the right as well as a selective, *non-lateralized*, memory deficit for spatial locations. While the current results do not necessarily cast serious doubt upon this proposal, they indicate that such a deficit may be much more lateralized than these authors have previously argued, and can thus have an asymmetrical impact on memory for locations in contralesional space.

Of even more interest would be to find patients suffering from one deficit (i.e. a lateral bias of attention or a spatial memory deficit) but not the other. Finding such a double dissociation would strongly support this conjecture. It would also be of great interest if some anatomical specificity could be revealed for each deficit, although likely overlaps in the neural mechanisms devoted to these different components of spatial behavior may make such a neurological dissociation hard to find (e.g. Corbetta & Shulman, 2002; Kristjánsson et al., 2007). Neurons in posterior parietal cortex do not only respond to visual stimuli presented at specific locations in the contralateral visual field but also to the location of a target held in memory when this remembered target would fall on the neuron's receptive field (Colby, Berman, Heiser, & Saunders, 2005; Duhamel, Colby, & Goldberg, 1992). Accordingly, Pisella, Berberovic, and Mattingley (2004) have reported that spatial working memory deficits were most pronounced for patients suffering from lesions affecting the parietal cortex. In contrast, Pisella et al. found no impairment of SWM for patients with lesions that left the parietal cortex intact, while the patients still showed other symptoms of neglect. On the other hand, neglect may arise after lesions in a variety of brain regions, including not only parietal but also frontal or subcortical areas (Damasio, Damasio, & Chui, 1980; Driver, Vuilleumier, & Husain, 2004; Husain & Kennard, 1997; Maguire & Ogden, 2002). Hence, such patients with lesions outside the parietal lobe might potentially show biases in spatial attention or search behavior in the absence of spatial memory deficits. In the present study, lesion overlap analysis (see Fig. 2C) indicated that, as expected, inferior parietal cortex was more often damaged in the patients with neglect than in those without neglect, but the small sample examined here does not allow us to draw strong conclusions regarding behavioral-anatomical correlations. Nevertheless, a recent study combining factorial analysis and lesion mapping in a large cohort of patients provided further evidence for a crucial role for parietal damage in inducing spatial memory deficits associated with neglect (Verdon, Schwartz, Lovblad, Hauert, & Vuilleumier, in press).

Spatial memory deficits for contralesional stimuli in neglect patients have also been found with tests of priming effects in visual search. Kristjánsson, Vuilleumier, Malhotra, Husain, and Driver (2005) tested priming for repeated features and position in a visual search task with pop-out targets (adapted from Bravo & Nakayama, 1992). Priming for various features (as well as target location) has been observed across successive trials in numerous search studies (Fecteau, 2007; Goolsby & Suzuki, 2001; Hillstrom, 2000; Kristjánsson, 2006b; Kristjánsson, Ingvarsdóttir, & Teitsdóttir, 2008; Maljkovic & Martini, 2005; Maljkovic & Nakayama, 1994; Maljkovic & Nakayama, 1996; Sigurdardóttir, Kristjánsson, & Driver, 2008; see Kristjánsson & Campana, 2010 for review). For the neglect patients,

Kristjánsson et al. found a difference in priming of color and position in that color priming proceeded *without* explicit awareness of the target, whereas explicit awareness of the target appeared to be necessary for position priming to occur. This result is consistent with the proposal that hemispatial neglect involves memory deficits on the left that are specific to position. Whether priming from repeated position may also play a role in retaining locations across the visual field during search is at present somewhat speculative, however. Interestingly, Saevarsson, Jóelsdóttir, Hjaltason, and Kristjánsson (2008) have recently found that priming of context (or distractor sets, in other words, see e.g. Geyer, Müller, & Krummenacher, 2006; Kristjánsson & Driver, 2008; Kristjánsson, Wang, & Nakayama, 2002; Lamy, Antebi, Aviani, & Carmel, 2008; Wang, Kristjánsson, & Nakayama, 2005) in visual search is, for the most part, intact in neglect patients. However, note that in the latter task, no explicit memory for *particular* spatial locations was required, but the intact memory representation must retain the distractor set identity, while particular locations are irrelevant since the distractors are randomly dispersed on the screen on each trial. Moreover, implicit memory for distractor context during search has been shown to depend on medial temporal lobe structures (hippocampus) that are typically spared in most neglect patients (Chun & Phelps, 1999) although this was observed for longer-term learning of spatial relations within a visual search display. Note also that Finke et al. (2009) have reported that inhibition effects from changed distractors in visual search may be disrupted for a subset of neglect patients.

Therefore, along with the latter result of Saevarsson et al. (2008), our current results indicate that the deficit of neglect patients is indeed specific to *spatial* working memory since the repetition of distractor sets in the neglected visual field may lead to priming whereas repetition of absolute position does not lead to priming. Note, however, that this argument rests on the assumption that the mechanisms involved in spatial priming are related to the same spatial mechanisms as those underlying spatial working memory, which currently remains a plausible conjecture, rather than established fact.

Finally, Battelli, Cavanagh, Martini, and Barton (2003) reported that neglect patients also seem to have a deficit for temporal judgments across the visual field. They found that when a single target flickers from dark to bright at the same frequency as five distractors, while the brightness transitions were out of phase with the distractors, right parietal patients require much slower rates of polarity change than normal observers or left parietal patients to perform the task accurately. Such a deficit could also be a contributing factor to the pattern of results here, since the changes in our paradigm occur rapidly, or every 110 ms (~9 Hz) and the temporal order judgment thresholds for the patients in the Battelli et al. study were in the range of 1–2 Hz, which is likely add to the difficulty of the task for the patients, if they have such a deficit in temporal processing.

5. Conclusions

In sum, we found that relocating items within a trial in a visual search task disrupted visual search for right-brain damage patients without neglect, as previously found for healthy observers, whereas patients with left neglect showed this disruption only within their right visual field, but not their left. This asymmetry suggests that searched locations in the left visual field were not retained in memory in the neglect patients, even when targets were not relocated but remained at the same position throughout the whole trial. We conclude that left hemispatial neglect is associated with a selective deficit in spatial working memory that affects the left visual field to a larger extent than the right visual field, such that little further disruption occurs in memory for left visual stimuli following their relocation.

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References

- Albert, M. L. (1973). A simple test of visual neglect. *Neurology*, 23, 658–664.
- Anderson, T. J., Jenkins, I. H., Brooks, D. J., Hawken, M. B., Frackowiak, R. S., & Kennard, C. (1994). Cortical control of saccades and fixation in man. A PET study. *Brain*, 117, 1073–1084.
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and working memory. *Trends in Cognitive Sciences*, 5, 119–126.
- Awh, E., Jonides, J., Smith, E. E., Buxton, R. B., Frank, L. R., Love, T., et al. (1999). Rehearsal in spatial working memory: Evidence from neuroimaging. *Psychological Science*, 10, 437–443.
- Barton, J. J. S., & Black, S. E. (1998). Line bisection in hemianopia. *Journal of Neurology, Neurosurgery & Psychiatry*, 64, 660–662.
- Battelli, L., Cavanagh, P., Martini, P., & Barton, J. J. S. (2003). Bilateral deficit of transient visual attention in right parietal patients. *Brain*, 126, 2164–2174.
- Bird, C. M., Malhotra, P., Parton, A., Coulthard, E., Rushworth, M. F., & Husain, M. (2006). Visual neglect after right posterior cerebral artery infarction. *Journal of Neurology, Neurosurgery & Psychiatry*, 77, 1008–1012.
- Bravo, M., & Nakayama, K. (1992). The role of attention in different visual search tasks. *Perception and Psychophysics*, 51, 465–472.
- Bundesen, C., & Habekost, T. (2008). *Principles of visual attention*. Oxford: Oxford University Press.
- Chun, M. M., & Phelps, E. A. (1999). Memory deficits for implicit contextual information in amnesic subjects with hippocampal damage. *Nature Neuroscience*, 2, 844–847.
- Chun, M. M., & Wolfe, J. M. (1996). Just say no: How are visual searches terminated when there is no target present? *Cognitive Psychology*, 30, 39–78.
- Colby, C. L., Berman, R. A., Heiser, L. M., & Saunders, R. C. (2005). Corollary discharge and spatial updating: When the brain is split, is space still unified? *Progress in Brain Research*, 149, 187–205.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3, 201–215.
- Damasio, A. R., Damasio, H., & Chui, H. C. (1980). Neglect following damage to frontal lobe or basal ganglia. *Neuropsychologia*, 18, 123–132.
- Danckert, J., & Ferber, S. (2006). Revisiting unilateral neglect. *Neuropsychologia*, 44, 987–1006.
- Driver, J., & Mattingley, J. (1998). Parietal neglect and visual awareness. *Nature Neuroscience*, 1, 17–22.
- Driver, J., & Vuilleumier, P. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, 79, 39–88.
- Driver, J., Vuilleumier, P., & Husain, M. (2004). Spatial neglect and extinction. In M. Gazzaniga (Ed.), *The new cognitive neurosciences* (3rd ed., pp. 589–606). Cambridge, MA: MIT Press.
- Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, 255, 90–92.
- Duncan, J., Bundesen, C., Olson, A., Humphreys, G., Chavda, S., & Shibuya, H. (1999). Systematic analysis of deficits in visual attention. *Journal of Experimental Psychology: General*, 128, 450–478.
- Eckstein, M. P. (1998). The lower visual search efficiency for conjunctions is due to noise and not serial attentional processing. *Psychological Science*, 9, 111–118.
- Fecteau, J. H. (2007). Priming of pop-out depends upon the current goals of the observer. *Journal of Vision*, 7(6), 1–11.
- Finke, K., Bucher, L., Kerkhoff, G., Keller, I., von Rosen, F., Geyer, T., et al. (2009). Inhibitory and facilitatory location priming in patients with left-sided visual hemi-neglect. *Psychological Research*, 73, 177–185.
- Geng, J. J., Eger, E., Ruff, C., Kristjánsson, Á., Rotstein, P., & Driver, J. (2006). On-line attentional selection from competing stimuli in opposite visual fields: Effects on human visual cortex and control processes. *Journal of Neurophysiology*, 96, 2601–2612.
- Geyer, T., Müller, H. J., & Krummenacher, J. (2006). Cross-trial priming in visual search for singleton conjunction targets: Role of repeated target and distractor features. *Perception & Psychophysics*, 68, 736–749.
- Goolsby, B. A., & Suzuki, S. (2001). Understanding priming of color – singleton search: Roles of attention at encoding and “retrieval”. *Perception & Psychophysics*, 63, 929–944.
- Grandjean, D., Sander, D., Lucas, N., Scherer, K. R., & Vuilleumier, P. (2008). Effects of emotional prosody on auditory extinction for voices in patients with spatial neglect. *Neuropsychologia*, 46, 487–496.
- Halligan, P. W., Fink, G. R., Marshall, J. C., & Vallar, G. (2003). Spatial cognition: Evidence from visual neglect. *Trends in Cognitive Sciences*, 7, 125–133.
- Halligan, P. W., & Marshall, J. C. (1998). Neglect of awareness. *Consciousness & Cognition*, 7, 356–380.
- Heilman, K. M., Watson, R. T., & Valenstein, E. (2003). Neglect and related disorders. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (4th ed., pp. 279–336). New York: Oxford University Press.
- Hillstrom, A. P. (2000). Repetition effects in visual search. *Perception & Psychophysics*, 62, 800–817.
- Horowitz, T. S., & Wolfe, J. M. (1998). Visual search has no memory. *Nature*, 394, 575–577.
- Horowitz, T. S., & Wolfe, J. M. (2003). Memory for rejected distractors in visual search? *Visual Cognition*, 10, 257–298.
- Hulleman, J. (2009). No need for inhibitory tagging of locations in visual search. *Psychonomic Bulletin & Review*, 16, 116–120.
- Husain, M., & Kennard, C. (1997). Distractor-dependent frontal neglect. *Neuropsychologia*, 35, 829–841.
- Husain, M., Mannan, S., Hodgson, T., Wojciulik, E., Driver, J., & Kennard, C. (2001). Impaired spatial working memory across saccades contributes to abnormal search in parietal neglect. *Brain*, 124, 941–952.
- Husain, M., & Rorden, C. (2003). Non-spatially lateralized mechanisms in hemispatial neglect. *Nature Reviews Neuroscience*, 4, 26–36.
- Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S., & Mintun, M. A. (1993). Spatial working memory in humans as revealed by PET. *Nature*, 363, 623–625.
- Karnath, H., Ferber, S., & Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature*, 411, 951–953.
- Karnath, H. O., Fruhmann Berger, M., Küker, W., & Rorden, C. (2004). The anatomy of spatial neglect based on voxelwise statistical analysis: A study of 140 patients. *Cerebral Cortex*, 14, 1164–1172.
- Kerkhoff, G. (2001). Spatial hemineglect in humans. *Progress in Neurobiology*, 63, 1–27.
- Kerkhoff, G., & Bucher, L. (2008). Line bisection as an early method to assess homonymous hemianopia. *Cortex*, 44, 200–205.
- Kristjánsson, Á. (2000). In search of remembrance. Evidence for memory in visual search. *Psychological Science*, 11, 328–332.
- Kristjánsson, Á. (2006a). Rapid learning in attention shifts – A review. *Visual Cognition*, 13, 324–362.
- Kristjánsson, Á. (2006b). Simultaneous priming along multiple dimensions in visual search task. *Vision Research*, 46, 2554–2570.
- Kristjánsson, Á., & Campana, G. (2010). Where perception meets memory: A review of priming in visual search. *Attention, Perception & Psychophysics*, 72, 5–18.
- Kristjánsson, Á., & Driver, J. (2008). Priming in visual search: Separating the effects of target repetition, distractor repetition and role-reversal. *Vision Research*, 48, 1217–1232.
- Kristjánsson, Á., Ingvarsdóttir, Á., & Teitssdóttir, U. D. (2008). Object- and feature-based priming in visual search. *Psychonomic Bulletin & Review*, 15, 378–384.
- Kristjánsson, Á., Vuilleumier, P., Malhotra, P., Husain, M., & Driver, J. (2005). Priming of color and position during visual search in unilateral spatial neglect. *Journal of Cognitive Neuroscience*, 17, 859–873.
- Kristjánsson, Á., Vuilleumier, P., Schwartz, S., Macaluso, E., & Driver, J. (2007). Neural basis for priming of pop-out revealed with fMRI. *Cerebral Cortex*, 17, 1612–1624.
- Kristjánsson, Á., Wang, D., & Nakayama, K. (2002). The role of priming in conjunctive visual search. *Cognition*, 85, 37–52.
- Lamy, D., Antebi, C., Aviani, N., & Carmel, T. (2008). Priming of pop-out provides reliable measures of target activation and distractor inhibition in selective attention. *Vision Research*, 48, 30–41.
- Lucas, N., & Vuilleumier, P. (2008). Effects of emotional and non-emotional cues on visual search in neglect patients: Evidence for distinct sources of attentional guidance. *Neuropsychologia*, 46, 1401–1414.
- Maguire, A. M., & Ogdan, J. A. (2002). MRI brain scan analyses and neuropsychological profiles of nine patients with persisting unilateral neglect. *Neuropsychologia*, 40, 879–887.
- Malhotra, P., Jager, H. R., Parton, A., Greenwood, R., Playford, D. T., Brown, M. M., et al. (2005). Spatial working memory capacity in unilateral neglect. *Brain*, 128, 424–435.
- Malhotra, P., Mannan, S., Driver, J., & Husain, M. (2004). Impaired spatial working memory: One component of the visual neglect syndrome? *Cortex*, 40, 667–676.
- Maljkovic, V., & Martini, P. (2005). Implicit short-term memory and event frequency effects in visual search. *Vision Research*, 45, 2831–2846.
- Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, 22, 657–672.
- Maljkovic, V., & Nakayama, K. (1996). Priming of pop-out: II. Role of position. *Perception & Psychophysics*, 58, 977–991.
- Mannan, S. K., Mort, D. J., Hodgson, T. L., Driver, J., Kennard, C., & Husain, M. (2005). Revisiting previously searched locations in visual neglect: Role of right parietal and frontal lesions in misjudging old locations as new. *Journal of Cognitive Neuroscience*, 17, 340–354.
- McManus, I. C. (2001). Charles Dickens: A neglected diagnosis. *Lancet*, 358, 2158–2168.
- Merriam, E. P., Genovese, C. R., & Colby, C. L. (2003). Spatial updating in human parietal cortex. *Neuron*, 39, 361–373.
- Mesulam, M. M. (1985). *Principles of behavioral neurology*. Philadelphia: F.A. Davis.

- Mesulam, M. M. (1999). Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 354, 1325–1346.
- Mort, D. J., Malhotra, P., Mannan, S. K., Rorden, C., Pambakian, A., Kennard, C., et al. (2003). The anatomy of visual neglect. *Brain*, 126, 1986–1997.
- Neisser, U. (1967). *Cognitive Psychology*. New York: Appleton Century Crofts.
- O'Sullivan, E. P., Jenkins, I. H., Henderson, L., Kennard, C., & Brooks, D. J. (1995). The functional anatomy of remembered saccades: A PET study. *Neuro Report*, 13, 2141–2144.
- Owen, A. M., Doyon, J., Petrides, M., & Evans, A. C. (1996). Planning and spatial working memory: A positron emission tomography study in humans. *European Journal of Neuroscience*, 8, 353–364.
- Palmer, J. (1995). Attention in visual search: Distinguishing four causes of a set-size effect. *Current Directions in Psychological Science*, 4, 118–123.
- Pisella, L., Berberovic, N., & Mattingley, J. B. (2004). Impaired memory for location but not for color or shape in visual neglect: A comparison of parietal and non-parietal lesions. *Cortex*, 40, 379–390.
- Pisella, L., & Mattingley, J. B. (2004). The contribution of spatial remapping impairments to unilateral visual neglect. *Neuroscience & Biobehavioral Reviews*, 28, 181–200.
- Pouget, A., & Driver, J. (2000). Relating unilateral neglect to the neural coding of space. *Current Opinion in Neurobiology*, 10, 242–249.
- Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioral Neurology*, 12, 191–200.
- Ruff, C. C., Kristjánsson, Á., & Driver, J. (2007). Readout from iconic memory involves similar neural processes as selective spatial attention. *Psychological Science*, 18, 901–909.
- Saevarsson, S., Jóelsdóttir, S., Hjaltason, H., & Kristjánsson, Á. (2008). Repetition of distractor sets improves visual search performance in hemispatial neglect. *Neuropsychologia*, 46, 1161–1169.
- Saevarsson, S., Kristjánsson, Á., Hildebrandt, H., & Halsband, U. (2009). Prism adaptation improves visual search in hemispatial neglect. *Neuropsychologia*, 47, 717–725.
- Schenkenberg, T., Bradford, D. C., & Ajax, E. T. (1980). Line bisection and unilateral visual neglect in patients with neurologic impairment. *Neurology*, 30, 509–517.
- Sigurdardóttir, H. M., Kristjánsson, Á., & Driver, J. (2008). Repetition streaks increase perceptual sensitivity in brief visual search displays. *Visual Cognition*, 16, 643–658.
- Sternberg, S. (1975). Memory scanning: New findings and current controversies. *Quarterly Journal of Experimental Psychology*, 27, 1–32.
- Treisman, A., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12, 97–136.
- Vallar, G. (1998). Spatial hemineglect in humans. *Trends in Cognitive Sciences*, 2, 87–97.
- Vallar, G., & Perani, D. (1986). The anatomy of unilateral neglect after right-hemisphere stroke lesions. A clinical/CT-scan correlation study in man. *Neuropsychologia*, 24, 609–622.
- Verdon, V., Schwartz, S., Lovblad, K.-O., Hauert, C.-A., & Vuilleumier, P. (in press). Neuroanatomy of hemispatial neglect and its functional components: A study using voxel-based lesion symptom mapping. *Brain*.
- Von Mühlenen, A., Müller, H. J., & Müller, D. (2003). Sit and wait strategies in dynamic visual search. *Psychological Science*, 14, 309–314.
- Vuilleumier, P., Sergent, C., Schwartz, S., Valenza, N., Girardi, M., Husain, M., et al. (2007). Impaired perceptual memory of locations across gaze-shifts in patients with unilateral spatial neglect. *Journal of Cognitive Neuroscience*, 19, 1388–1406.
- Wang, D., Kristjánsson, Á., & Nakayama, K. (2005). Efficient visual search without top-down or bottom-up guidance. *Perception & Psychophysics*, 67, 239–253.
- Wilson, B. A., Cockburn, J., & Halligan, P. W. (1987). *Behavioural inattention test*. Titchfield, UK: Thames Valley Test Company.
- Wojciulik, E., Husain, M., Clarke, K., & Driver, J. (2001). Spatial working memory deficit in unilateral neglect. *Neuropsychologia*, 39, 390–396.