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When brain damage improves perception: Neglect patients can localize motion-shifted probes better than controls

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Running title: The crucial role of attention in position shift

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Abstract

When we look at bars flashed against a moving background, we see them displaced in the direction of the upcoming motion (flash-grab illusion). It is still debated whether these motion-induced position shifts are low-level, reflexive consequences of stimulus motion, or high-level compensation engaged only when the stimulus is tracked with attention. To investigate whether attention is a causal factor for this striking illusory position shift, we evaluated the flash-grab illusion in six patients with damaged attentional networks in the right hemisphere and signs of left visual neglect and six age-matched controls. With stimuli in the top, right, and bottom visual fields, neglect patients experienced the same amount of illusion as controls. However, patients showed no significant shift when the test was presented in their left hemifield, despite having equally precise judgments. Thus, paradoxically, neglect patients perceived the position of the flash more veridically in their neglected hemifield. These results suggest that impaired attentional processes can reduce the interaction between a moving background and a superimposed stationary flash, and indicate that attention is a critical factor in generating the illusory motion-induced shifts of location.

Keywords

Attention; Motion induced position shift; Left visual neglect.

Introduction

The position of a moving object appears to healthy people to be strongly shifted in the direction of its motion (for a review of these motion-induced position shifts, see Whitney 2002; Eagleman and Sejnowski 2007). This suggests that an object's motion interacts with its position creating a mislocalization in the direction of motion. However, it is still debated whether these motion-induced position shifts are low-level, reflexive consequences of stimulus motion (e.g., Fukiage et al. 2011), or high-level compensation engaged only when the stimulus is tracked with attention (e.g., Cavanagh and Anstis 2013). Here we address this debate directly by evaluating motion-induced position illusions in parietal patients with damage to the right hemisphere attentional network and signs of left visual neglect.

Linares and Lopez-Moliner (2007) have explored the role of low-level motion in the classic motion-induced position shift, the flash-lag effect, which occurs when a flash that is aligned with a moving stimulus is perceived to lag behind it. They presented participants with a number of dot pairs whose overall structure formed a global shape. One dot of each pair moved, whereas the other flashed. When participants judged the global shape created by the field of dots, there was no mislocalization of the location of the flashed dots relative to the moving dots. This suggested that the presence of the motion itself is not sufficient to produce these predictive location shifts. Accordingly, Cavanagh and Anstis (2013) suggested that a crucial role is played by attention in producing the position shift[1]. They found that the motion-

[1] The possible explanation that the misalignment observed between the two flashed lines may simply be a product of compensatory torsional adjustments was rejected by Whitney and Cavanagh (2000). The authors presented two pairs of linear gratings moving in opposite directions, where there can be no torsional contribution. Then three flashed lines were presented in physical alignment and they still appeared misaligned consistent with the

induced position shift could be clearly seen for individual dot trajectories, but that when multiple trajectories were presented together, the individual dot trajectories could not be tracked and the position shifts were no longer observed.

Nevertheless, a number of studies claimed to find position shifts without attention, for example, for motions that reverse too rapidly or too unpredictably to be attentively tracked. Fukiage et al. (2011) used a moving stimulus randomly displacing its location at a very fast rate. The authors suggested that, given the unpredictability in direction and motion changing, it would have been impossible for observers to attentively track or to reliably attend to each motion segment. Even so, under these conditions, the motion still produced a motion-induced position shift effect (the position of the flashed stimulus appeared shifted in the direction of nearby motion, Whitney and Cavanagh 2000). Müsseler and Aschersleben (1998) used another motion-induced position shift, the Fröhlich effect, to test the attentional account. When observers are required to determine where a suddenly presented moving stimulus first appears, they usually mislocalize it in the direction of the movement (Frohlich 1923). Müsseler and Aschersleben (1998) tested the Fröhlich effect with Posner cuing (Posner 1980) and found that the position shift was larger with invalid cues than with valid cues. Although these results could be taken to suggest that the position shift is larger in the absence of attention, the authors presented a somewhat different explanation. Specifically, they argued that the perception of the moving stimulus is delayed until attention reaches it. With valid cues, attention is quickly available for the stimulus and the moving stimulus is experienced as starting soon after its actual start location. Conversely, with invalid cues, it takes longer for attention to get to the stimulus and so its perceived start location is much further along the

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direction of the nearest motion. They replicated these results also using two pairs of radial gratings rotating in opposite directions. The effect was undiminished.

trajectory. Given these various proposals, the actual role of attention in the motion-induced position shift remains unclear.

Neuroimaging evidence based on variants of the Posner cuing task uncovered fronto-parietal networks important for the functioning of spatial attention, with hemispheric asymmetries favoring right hemisphere networks (Bourgeois et al. 2013a, 2013b; Corbetta et al. 2008; Nobre 2001). Evidence indicated the existence of a dorsal fronto-parietal network, which is bilateral and largely symmetric, and of a more ventral fronto-parietal network, which is strongly lateralized to the right hemisphere (Corbetta et al. 2008). However, recent studies have showed that, within the dorsal attentional network, only the right, and not the left superior parietal lobule carries spatial attention signals (Szczepanski et al. 2010) and that the right intraparietal sulcus generates stronger bilateral representations than its left counterpart during attentional tasks (Szczepanski et al. 2010; Sheremata et al. 2015) and during visual short-term memory tasks (Sheremata et al. 2010). Damage to right hemisphere fronto-parietal networks induces attentional deficits, with patients often disregarding information coming from the left side of space (visual neglect) (Bartolomeo 2014). In neglect patients, orienting of spatial attention to left-side objects is impaired, particularly in its exogenous, or stimulus-based aspects (Bartolomeo and Chokron 2002). Patients' attention is instead prone to be captured by right-sided stimuli (Gainotti et al. 1991; Bourgeois et al. 2015), and has problems to disengage from these stimuli to explore the left visual field (Posner et al. 1984; Rastelli et al. 2008). In contrast to the prominent exogenous deficits, endogenous, or voluntary orienting is less affected (Bartolomeo et al. 2001), and can partially compensate for clinical signs of neglect in the chronic phase (Corbetta et al. 2005). Thus, visual neglect provides a model of attention deficits potentially important to test more directly the role of attention in motion-induced position shift.

We tested the motion-induced position shift with neglect patients and age-matched controls by using the flash-grab version of motion-induced position shift (Cavanagh and Anstis 2013). In this stimulus, a background rotates and reverses direction every 660 ms. Every time the motion reverses, a bar is flashed on top of the background and it appears to be shifted in the direction of motion that follows. The effect is the strongest motion-induced position shift in the literature and quite easy to judge since the participant only needs to report the location of the flash itself. A movie (click here) gives a demonstration of this effect. Fixate the central dot for best effect. In the movie the stimulus is presented in the left visual field (one of our four conditions). The moving texture ramps up and down in contrast to show that the flashed lines are horizontal and parallel in the absence of the motion. As the moving stimulus rotates back and forth, the position of the red and green lines appear clearly transposed from their physical alignment with the fixation point. The half stimulus was used so that there would be no competing stimulus in the opposite field that might interfere with the judgments for the neglect patients.

We hypothesized that if attention plays a crucial role in producing the motion-induced position shifts, then patients with right hemisphere damage and consequent left visual neglect should show more accurate judgments of location for moving targets presented in the neglected field, i.e. they should perceive these targets at their veridical location.

Materials and methods

Participants

A total of six patients (three males) with right hemisphere damage and signs of left spatial neglect with a mean age of 64.83 years (SD, 7.93) and their age-matched healthy controls (mean age, 61.16 years; SD, 3.81) participated in the present study. The inclusion criteria for patients were: (1) impaired performance on at least one test of a systematic neglect battery of paper and pencil tests (Azouvi et al. 2002); (2) unilateral vascular damage to the right hemisphere; (3) right handedness; (4) normal visual fields, normal or corrected-to-normal visual acuity and normal color vision; and (5) ability to maintain gaze fixation and follow the instructions. The mean time of testing for the included patients was 1555.55 days since stroke onset (SD, 708.10 days). Table 1 shows the demographical and clinical data for the included patients.

------Insert Table 1 about here------

We also tested 6 healthy participants (two males), aged between 56 and 67 years old in the control group. All controls were free from (1) psychoactive pharmacological treatment likely to modify normal visual and attentional abilities, and (2) history of neurological and psychiatric disorders. Moreover, they were all able to maintain their gaze on the fixation point and to follow the instructions. Some of them were recruited through the cognitive science public website www.risc.cnrs.fr/ maintained by the CNRS (French National Centre of the Scientific Research); some of them were patients' relatives. They had normal or corrected-to-normal visual acuity and normal color vision.

All participants gave informed written consent prior to the commencement of the study. The study procedure was submitted to, and approved by the ethical committee "Ile-de-France 1", and was performed in accordance with the Declaration of Helsinki.

Apparatus

The experiment was run on an Apple Macintosh G4 computer with custom software written in C using the Vision Shell Graphics Libraries (Comtois 2003). Display was presented in a dimly lit room on a CTR monitor with 85 Hz refresh rate and resolution of 800 x 600 pixels. Adjustments were made with a computer mouse. The monitor was placed on the top of the table, in front of the participant from a distance of about 60 cm. Observers were instructed to keep their free sitting posture, to constantly stare at the fixation point, and not to move their head. The examiner ensured that fixation was maintained throughout the experiment.

Stimuli

The screen was fulfilled with a uniform, mid-grey background. A small, black fixation dot was at the screen center and a half-disk of radial sectors centered on the fixation point rotated back and forth. The half-disk had 10 dva radius (see Fig. 1), and, in separate blocks, it was placed in the left, right, top, and bottom visual field. The radial sectors had 25% contrast (Michelson) in all the conditions. The half-disk rotated 180° (degrees of rotation) every second and reversed direction every 660 ms. At each reversal, the motion stopped for 47 ms (4 frames at 85 Hz).

As to the left/right field presentation, on each reversal of direction, a horizontal line appeared for 47 ms at the 9 o'clock (for left field presentation) or at 3 o'clock (for right field presentation).

As to the top/bottom field presentation, on each reversal of direction, a vertical line appeared for 47 ms (coincident with the period of stopped motion) at the 12 o'clock (for top field presentation) or at 6 o'clock (for bottom field presentation). The flashed line alternated between red and green on alternating reversals and appeared at the light-dark edges of the radial sectors.

------Insert Figure 1 about here------

Procedure

The four conditions (i.e., the half-disk presented in the left, right, top, or bottom visual field) were presented in random order and in separate blocks. The red and green lines, both present in each trial, were initially at the same location and both aligned horizontally (or vertically, depending on the condition) with the fixation point (see Fig. 1a). However, due to the half-disk rotation, they may have appeared shifted away from horizontal (or vertical) in opposite directions (see Fig. 1b). Using the computer mouse and under instructions from the participants, the experimenter adjusted the locations of the red and green lines simultaneously to oppose any perceived offset until they again appeared to be superimposed, as the half-disk continued to rock back and forth (see Fig. 1c). The amount of shift required to make the lines appear superimposed was the measure of the illusion strength.

All participants were individually tested. Before starting each condition, the flashed lines were presented to the participants without the rotating half-disk on the background to explain the test and to see whether or not they could see the red and green flashed lines in the four presentation fields. They were required to say what they saw, while looking at the fixation point, and they always correctly responded to see two lines of different colors that flashed at the same location and both horizontally (or vertically) aligned. Then, the rotating half-disk was added on the background, and again, when asked to say what they saw, they gave the correct answer.

Moreover, while adjusting the location of the red and green lines, the experimenter looked at the participants to make sure they were staring at the fixation point. The four different conditions were tested at least 6 times each.

Lesion analysis

Each patient underwent a standard clinical radiological MRI assessment of the brain including T1-weighted images. Lesion masks of patients were first drawn on the native T1 images by using the MRIcron software (Rorden et al. 2007) and a graphic tablet (WACOM Intuos A6, Vancouver, Washington, USA). T1 images were normalized to a standard brain template (Montreal Neurological Institute) using rigid and elastic deformation tools provided in the software package Statistical Parametric Mapping 8 (SPM8, http://www.fil.ion.ucl.ac.uk/spm) running under Matlab 2013a (http://www.mathworks.com). Deformations were applied to the whole brain except for the voxels contained in the lesion mask in order to avoid deformation of the lesioned tissue (Brett et al. 2001; Volle et al. 2008). Finally, patients' lesions were manually segmented a second time on the normalized images. MRIcron software was used to measure the extent of the lesion and define grey matter involvement using Automated Anatomical Labeling atlas (Tzourio-Mazoyer et al. 2002). To determine whether patients' lesions encroached upon human V5/MT+ complex, which is important for the perception of movement, we created a sphere-ROI of V5/MT+ with the coordinates and the number of voxels as described in an fMRI study (Giaschi et al. 2007). Finally, we used the *tractotron* software (http://sourceforge.net/projects/tractotron/) to describe the patterns of disconnection induced by each lesion at the individual level for the following major rostrocaudal white matter tracts: the inferior fronto-occipital fasciculus, the inferior longitudinal fasciculus, the arcuate fasciculus, the three branches of the superior longitudinal fasciculus, the optic radiations and the uncinate fasciculus.

Results

Behavioral results

Fig. 2 shows the results averaged across the six neglect patients and their six matched controls. For the controls, the apparent alignment of the red and green lines was shifted by about the same amount in the direction of the rotation that followed the reversal for all locations.

------Insert Figure 2 about here------

Neglect patients showed a very similar shift compared to the controls for the top, right, and bottom locations. In fact, the differences between patients' and controls' degrees of shift in the top, right and bottom locations were not statistically significant (all $p_s > 0.5$). However, patients showed a much reduced shift when the test was presented in the left visual field (but still significantly greater than zero, $t(5)=3.8$, $p<0.05$). The difference between patients' and controls' degrees of shift in the left side visual field was significant (Mann–Whitney U test: $U = .000$, $n_1 = n_2 = 6$, $p < .005$ two-tailed). The results for each patient are presented in Table 2.

Patient	Degrees of shift in the different presentation fields			
	Left	Right	Bottom	Top
GV	7.73 (1.16)	9.00 (1.85)	11.88 (0.83)	9.65 (1.44)
AM	3.10 (2.10)	12.67 (1.02)	14.67 (0.66)	16.72 (1.44)
VS	1.20 (1.56)	15.67 (1.83)	17.67 (0.91)	20.00 (1.41)
DS	3.22 (0.86)	9.33 (0.82)	9.78 (1.23)	7.45 (1.13)
YD	2.00 (1.07)	8.67 (0.86)	9.62 (0.96)	8.71 (1.08)

DA	4.73 (1.32)	15.33 (1.40)	20.00 (1.88)	23.33 (1.54)
Average SE	1.34 (0.18)	1.29 (0.19)	1.07 (0.18)	1.34 (0.08)

Table 2. Patients' degrees of shift. Degrees of shift averaged per patient, with standard errors in brackets. The last line of the table shows the mean of the standard errors across the 6 patients in each condition. This gives a measure of the precision of the settings across the 6 repetitions of the adjustments in each condition. In brackets on this line are the standard errors of the mean across the 6 patients for these precision values.

As it may be seen from the standard errors of the mean in Table 2, patients were equally precise at localizing the flashed target appearing in all four locations. The accuracy of patients' judgment (mean of standard errors of judgments across patients, 1.34 degrees ± 0.18) at the left location demonstrated that patients were responding to the target in the neglected field with little or no deficit in terms of precision compared to the other locations. Despite this maintained precision, the bias from the illusion was diminished at the left-sided location. The precision of the judgments of the control participants was similar (mean of standard errors of judgments across controls over al 4 locations, 0.79 degrees ± 0.11).

Anatomical results

Table 3 and Fig. 3 summarize the anatomical location of the brain lesions. In three patients (VS, YD, DA), the lesions mostly involved the frontal and temporal cortices. Patient AM had damage to the parietal and temporal cortices. In two patients (GV and DS), lesions extended to the occipital lobe, with additional fronto-parietal (GV) or fronto-temporo-parietal (DS) involvement. There was no overlap between the lesions and the V5/MT+ ROI and in any of the patients. Concerning the long-range white matter fasciculi, all patients had fronto-parietal disconnection involving the superior longitudinal fasciculus, as typically observed in neglect patients (Bartolomeo 2006; Bartolomeo et al. 2007). There was additional damage to the inferior longitudinal fasciculus in all patients except AM, to the inferior fronto-occipital fasciculus in four patients, and to the uncinate fasciculus in four patients (see Table 3).

Patient name	Lesion volume	Grey matter lesion sites	White matter lesion sites
GV	43.66	PrCe/PsCe, SFg, MFg, IFo, IFg pars triangularis, Ro, I, SOg, MOg, SPg, IPg, SMg, angular g, Caudate, Pu, Pa, MTg	Arcuate, IFOF, ILF, Optic Radiations, SLF I-III, Uncinate
AM	25.55	PrCe/PsCe, Ro, SPg, IPg, SMg, STg	Arcuate, SLF I-III
VS	23.72	PrCe/PsCe, IFo, IFg pars triangularis, Ro, I, H, SMg, Caudate, Pu, Pa, Th, He, STg, STp, MTg	Arcuate, ILF, Optic Radiations, SLF I-III, Uncinate
DS	171.35	PrCe gyrus, SFg, MFg, Ro, I, MCg, calcarine sulcus, cuneus, lingual gyrus, SOg, MOg, IOg, Fg, PsCe, SPg, IPg, SMg, angular gyrus, precuneus, paracentral gyrus, He, STg, MTg, ITg	Arcuate, IFOF, ILF, Optic Radiations, SLF I-III
YD	29.99	PrCe, orbitofrontal cortex, MFg, IFo, IFG pars triangularis, IOFg, Ro, I, A, SMg, Caudate, Pu, Pa, He, STg, STp	Arcuate, IFOF, ILF, SLF I-III, Uncinate
DA	43.47	Orbitofrontal cortex, SMg, Ro, I, PHg, A, Pu, Pa, Caudate, He, STg, STp, MTg, MTp, Itg, Fusiform g	Arcuate, IFOF, ILF, SLF II-III, Uncinate

Table 3. Anatomical descriptions of patients' right hemispheric lesions.

IFg, inferior frontal gyrus; IFo, inferior frontal operculum; IOFg, inferior orbitofrontal gyrus; MOFg, middle orbitofrontal gyrus; MFg, middle frontal gyrus; SFg, superior frontal gyrus;

PrCe, precentral gyrus; PsCe, postcentral gyrus; Ro, rolandic operculum; IPg, inferior parietal gyrus; ITg, inferior temporal gyrus; MTg, middle temporal gyrus; STg, superior temporal gyrus; STp, superior temporal pole; IOg, inferior occipital gyrus, MOg, middle occipital gyrus; SOg, superior occipital gyrus; Th, thalamus; H, hippocampus; PHg, parahippocampal gyrus; He, Heschl gyrus; A, amygdala; I, insula; CN, caudate nucleus; Pu, putamen; Pa, pallidum; SMg, supramarginal gyrus; SLF, superior longitudinal fasciculus; IFOF, inferior fronto-occipital fasciculus; ILF, inferior longitudinal fasciculus.

------Insert Figure 3 about here------

Discussion

Since the seminal case descriptions by Broca and Wernicke in the XIX century, performance deficits induced by brain lesions have been used to infer the corresponding normal cognitive abilities. Here we report that brain damage can induce a paradoxical "improvement" in perception. Patients with right hemisphere lesions and signs of left visual neglect demonstrated a striking reduction of motion-induced position shift in their left, neglected visual field. However, these same patients did show the standard illusion at all the other tested locations (top, right, and bottom). Thus, impaired attention in these patients paradoxically led to a "more veridical" perception of the target position in the neglected space.

This significant reduction of the flash grab effect for left-sided targets in brain-damaged patients provides causal evidence about the origin of motion-induced shifts in location, and strongly supports the claim that the shifts are generated only for attended stimuli (Cavanagh and Anstis 2013). If the effect were generated simply by the reflexive, preattentive motion responses (Fukiage et al. 2011), then neglect patients should have reported the illusion even in their neglected field. Indeed, in contrast with the present results, neglect patients can normally manifest other illusory visual effects in their neglected field when these illusions are based on low-level, perhaps preattentive, perceptual mechanisms (Mattingley et al. 1995; Ro and Rafal 1996; Vallar et al. 2000; Sedda et al. 2013).

Patients' judgments at the left location were accurate and consistent, demonstrating that patients, who had mild to moderate signs of left neglect, were actually responding to left-sided targets despite their neglect. To prevent the occurrence of non-specific phenomena due to symptom fluctuations in acute patients, we recruited patients in the chronic phase of their stroke. Although some spontaneous recovery occurs in the first weeks after a stroke (e.g., Ringman et al. 2004), it is well known that left visual neglect may persist chronically and remain severe in a substantial proportion of patients (e.g., Farne et al. 2004, Lunven et al. 2015). We do not have data for the Flash Grab in patients tested just after stroke but the illusion strength could not be much weaker; on the other hand, more acute and severe patients might find themselves unable to detect the left-sided targets in order to perform the test. It is thus possible that the Flash Grab test offers a more sensitive measure of neglect than the much more extensive standard battery of clinical tests. Note, moreover, that even patients who have clinically recovered from neglect still show residual deficits of attention on more stringent tests, such as response time tests (Bartolomeo 1997, 2000; Bonato 2012). These residual deficits have been interpreted as a chronic persistence of a rightward bias/leftward deficit of exogenous attention (Bartolomeo 1997, 2000), whereas the use of recovered endogenous components of attention may permit the clinical compensation of neglect in the chronic phase (Bartolomeo and Chokron 2002; Corbetta et al. 2005). Interestingly, exogenous attention appears to be crucial to integrate distinct visual features in a single percept (Briand and Klein 1987). It is therefore likely that spared endogenous capabilities allowed patients to attend to the known locations of the flashes and adjust them with relative precision. However, exogenous deficits could have decreased the strength of selection of the motion near the flash, reducing the effect of the motion on the flash location. In a similar way, neglect patients typically deviate rightwards the perceived position of the center of horizontal lines, even after having accurately detected the left endpoint of the line (Urbanski and Bartolomeo 2008).

The observed reduction of flash grab effect in the left visual field was unlikely to result from visual field defects, which were an exclusion criterion (see Materials and methods); moreover, patients had comparable precision of performance in the two visual fields. As regards to the upper and lower positions where half of the stimulus was in the affected (left, neglected) visual field for the patients, we were surprised that the shift was unaffected compared to the presentation that was entirely in the right field. We have no explanation other than to restate the data: even half of the moving texture presented in the unaffected right field is sufficient to displace the test flash.

The observed pattern of performance was unlikely to depend on a unilateral deficit of perceived movement. Patients' lesions did not encroach upon the human homologue of V5/MT+ complex, that integrates local-motion information along complex trajectories, including translation, rotation and radial motion (for a review see Morrone et al. 2000). Furthermore, patients' informal comments suggest that they did perceive the background motion itself. Battelli et al. (2001) showed that patients with parietal lesions did register motion direction in the neglected field (they recognized motion-defined shape), but were incapable of tracking the motion of individual targets. This distinction between low-level, reflexive motion responses (intact in the neglected field) and exogenous tracking of a moving target is a critical one for the motion-induced position shift. Cavanagh and Anstis (2013) claimed that the motion-induced shift was seen only when targets were individually tracked – when the stimulus motion was clearly seen but not tracked, no shift was reported. The absence of tracking of the background would then lead to an absence of the predictive shift in the neglected field, compared to the other tested locations.

Although we report improved localization in the left visual field of neglect patients, a number of other studies have found, instead, increased localization errors in similar patients. Halligan and Marshall (1991) observed a patient with severe left neglect, due to lesion of the right temporo-parietal region, who showed systematic deflections in her judgment of target positions. The authors suggested that these distortions were consequent to a rightward compression of the 'left space'. However, subsequent evidence strongly suggested an attentional origin of the mislocalization, because errors were nullified when no attention-grabbing distractors were present on the right side of the target (Bartolomeo et al. 2004). In any case, our tests of location were always orthogonal to the radial axis, so up vs. down for the left visual field, and these judgments would be immune to compression towards the fovea. Furthermore, there were no competing distractors in the right visual field. Milner and Harvey (1995) found that patients with right hemisphere damage and left visual neglect underestimated the size of forms presented on their left side. According to the researchers, such patients failed to generate accurate representations of the shapes of patterns seen in their left hemifield, an effect which should not have influenced the simple judgment of bar location in our study. Finally, neglect patients may have impaired re-positioning and combination of the different details present in the visual scene, producing a distortion of the underlying representations when making eye movements (Pisella and Mattingley 2004). Our procedures did not involve any eye movements and should not have triggered these distortions. Husain et al. (1997) observed that the attentional blink (i.e., the significant loss of attention occurring soon after having processed a target for identification purposes) may be significantly more protracted and more severe in neglect patients than in controls with the stimulus presented at the center of the computer monitor. The authors suggested a deficit in temporal processing as a possible root for this phenomenon. This mechanism is unlikely to account for the present results, because impaired temporal processing should have altered the judgment of bar location in all the visual fields in our patients.

Converging evidence on the role of attention in producing motion-induced position shifts comes from psychophysical studies in normal participants. Shim and Cavanagh (2005) have observed that, independently of the low-level motion system, attentive tracking of a moving target may modulate the perception of positions of stationary objects. Watanabe et al. (2003) found that movements of visible and hidden targets might distort the perceived location of flashed stimuli and suggested the crucial involvement of a high-level representation of 'objects in motion'. Altogether, this evidence suggests that attention is responsible for the integration of briefly flashed targets with their moving background that causes the motion-induced position shift for the target.

In conclusion, the study presented here suggests that impaired attentional processes can reduce the interaction between a moving background and a superimposed stationary flash, rendering the perceived position of the flash more veridical. Our neglect patients showed more accurate localization in the left field than did the controls. On the basis of the close relationship between the effects of attention and object motion on position judgments, we suggest that attention to the continuous motion of the background may be a key mechanism producing the position shift illusion.

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Figure Captions

Table 1. Demographical and clinical characteristics of patients. Patients' performances on visuo-spatial tests.

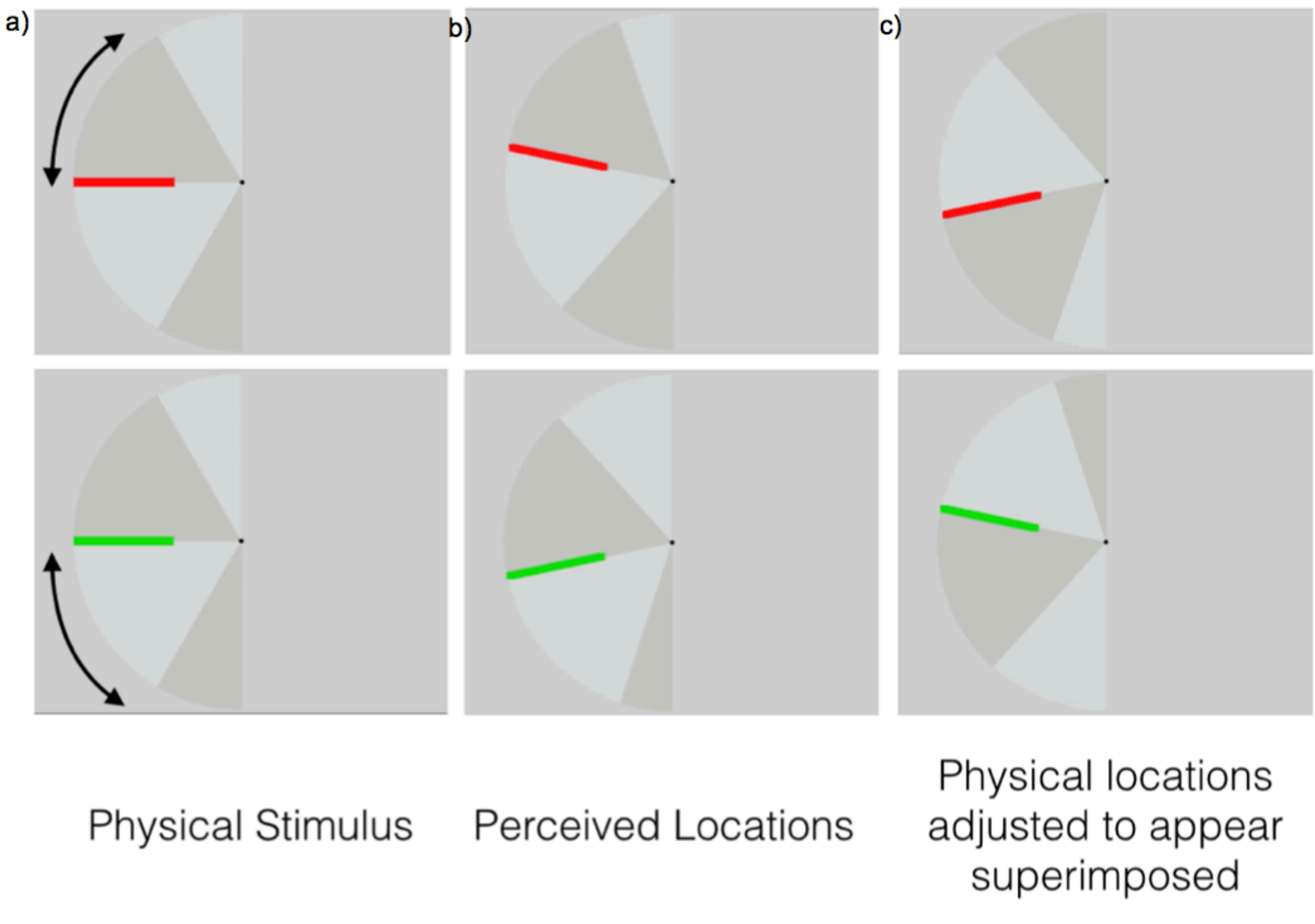
I, ischemic; H, hemorrhagic. Scores for landscape drawing indicate the number of omitted left-sided details. Asterisks denote pathological performance.

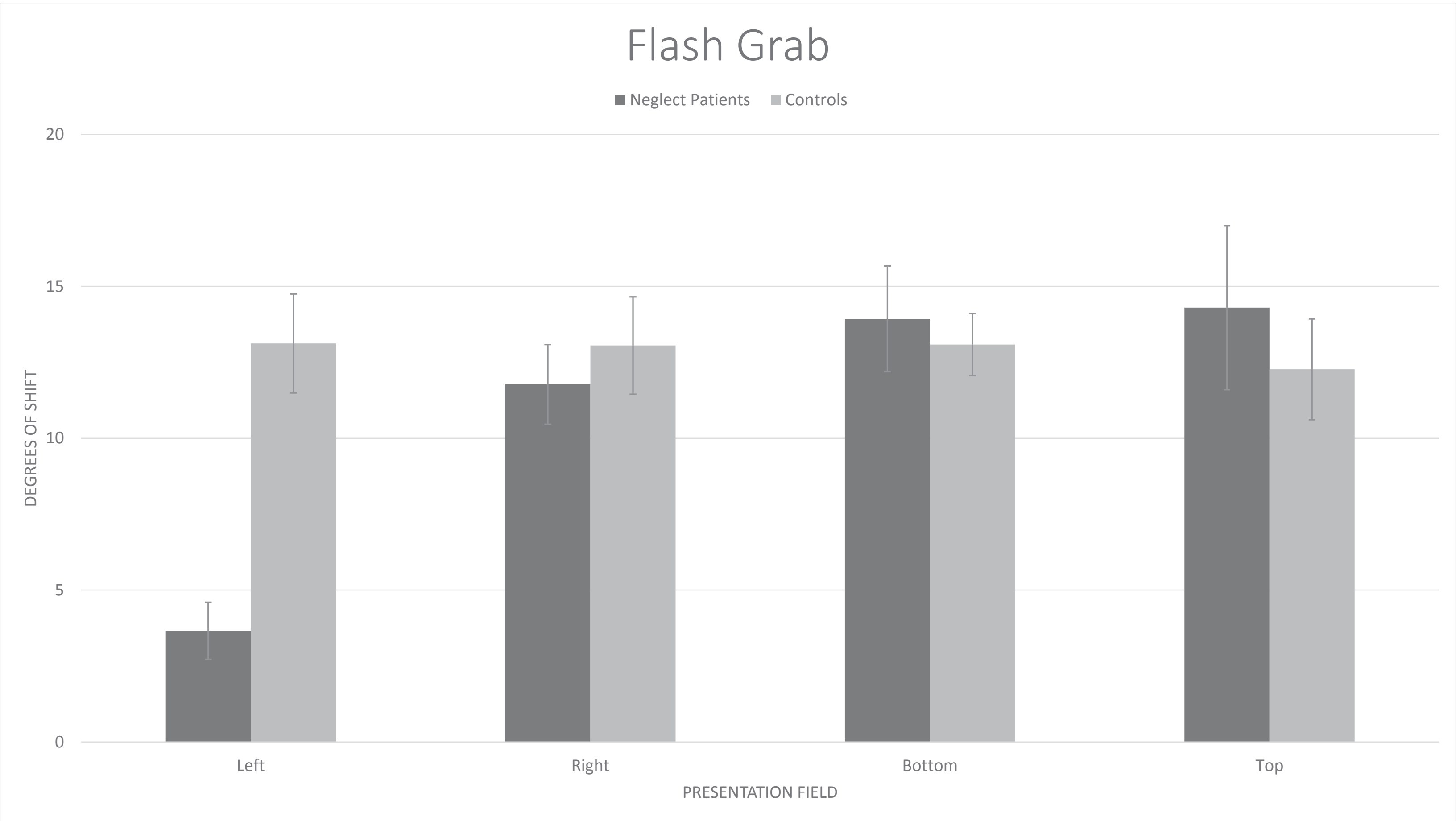
Figure 1. An example of the task with the motion background and test flashes presented in the left visual field. a) The background sectors rotated back and forth through 180° and a test bar was flashed at each reversal of direction (see Movie). b) The red bar was flashed as the background started to move up and it appeared to be displaced upward along with that motion. The green bar was flashed as the motion reversed and moved downward, and it appeared shifted downward. c) The participant was asked which bar, red or green, appeared on top and the experimenter adjusted the physical locations of the flashes until the participant reported that they appeared superimposed. This adjustment procedure was repeated at least 6 times for each of the 4 conditions (left, right, top, and bottom locations).

Figure 2. Participants' results. The graph shows the results averaged across the two groups of participants, i.e. neglect patients and controls. Data are represented as mean. Error bars represent ±1.0 standard errors of the mean.

Figure 3. Right hemispheric lesions. Reconstruction of brain lesions (in red) for each of the neglect patients, in transverse sections (with MNI z coordinates) and sagittal sections.The coordinates of V5/MT+ (as described by Giaschi et al. 2007) are represented in blue. No overlap of lesions with V5/MT+ is found in any of the patients.

Patient	Sex/age/education	Onset of illness (days)	Aetiology	Bells cancellation (left, right hits, max = 15/15)	Letter cancellation (left/right hits, max = 30/30	Line cancellation (left/right hits, max = 30/30	Line bisection (mm of rightward deviation for 200 mm lines)	Landscape drawing score	Reading (left/right hits = 61/55)
GV	M/51/11	1889	I	14/14	23/28*	28/26	8*	6	61/55
AM	F/75/9	2118	H	5/13*	20/21*	29/30	7*	6	61/55
VS	F/62/12	1485	H	14/15	28/30	30/30	5	5*	59/55*
DS	M/69/8	1883	I	14/15	27/29	29/30	5	5*	61/55
YD	F/57/9	1786	H	11/13	29/30	28/30	12*	5*	61/55
DA	M/67/9	172	I	13/15	28/30	30/30	10*	6	60/55*


a)
b)
c)
Physical Stimulus
Perceived Locations
Physical locations adjusted to appear superimposed



Flash Grab
Neglect Patients
Controls
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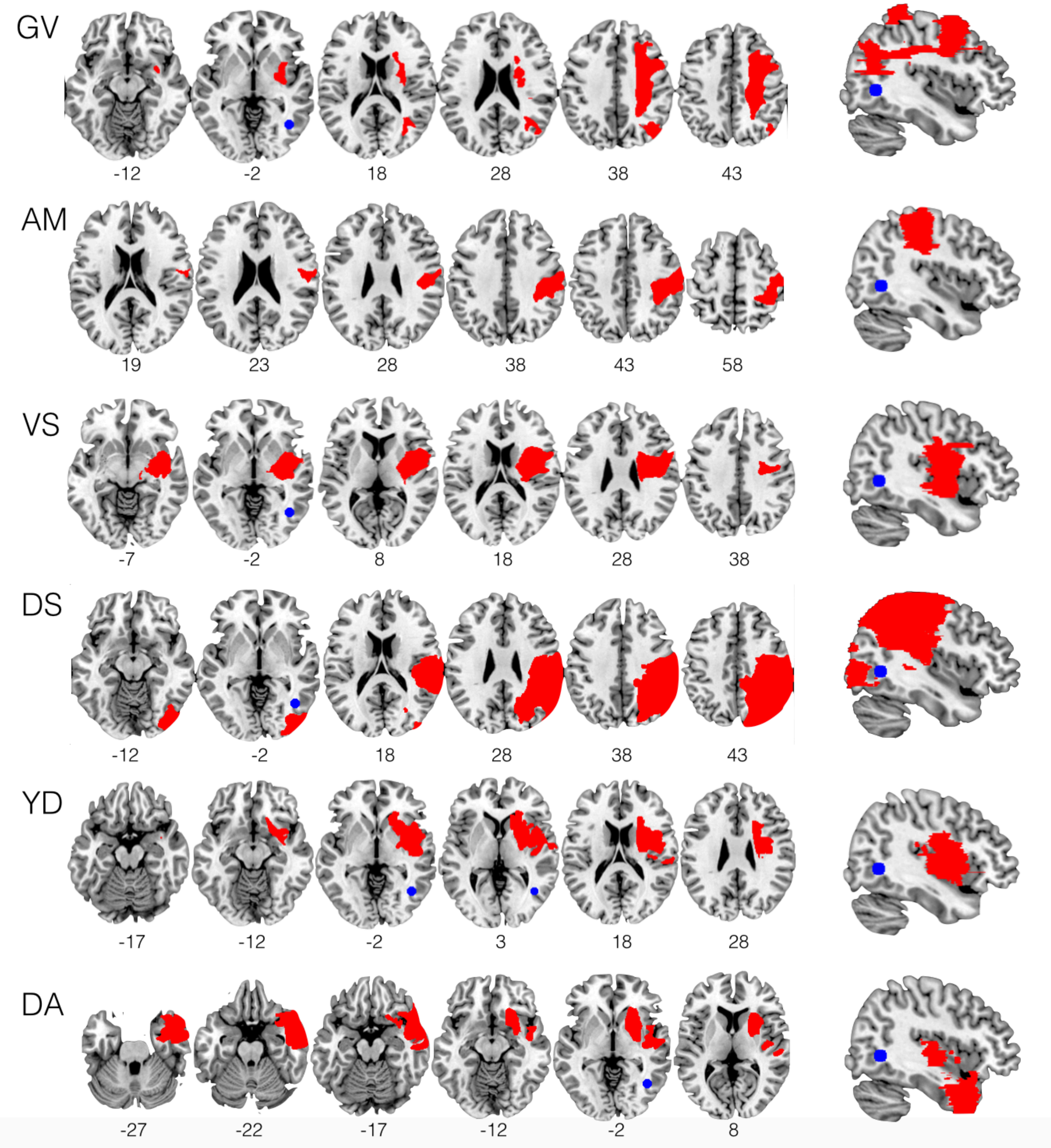
DEGREES OF SHIFT
Left
Right
Bottom
Top
PRESENTATION FIELD


GV
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