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The automatic updating of egocentric spatial relationships and its impairment due to right posterior cortical lesions

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Abstract

The non-visual updating of body-centred spatial relationships was investigated in an experiment in which blindfolded patients had to point to previously seen targets after a body rotation in the absence of vision. Patients with lesions to the right dorsal (RD) area were impaired at updating their positions relative to non-RD patients and normal subjects: they tended to underestimate systematically the angle through which they had turned. The results are interpreted in terms of impoverished locomotor input and/or systematically biased processing or locomotor proprioception in the RD patients, which prevented accurate tracking of changes in egocentric spatial relationships. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

To remain oriented to our surroundings, we have to update our body-centred spatial relationships as they change as a result of our movement through the environment. There are several sources of information, notably vision, that play a part in allowing one to remain oriented to one's surroundings, but we can also update our changing positions relative to objects that are out of sight. One method that has been used to study this ability has been to examine performances on spatial tasks when subjects are deprived of vision, either by being blindfolded or by simply closing their eyes. The absence of vision forces the subjects to rely solely on the knowledge of spatial consequences of their actions. There have now been a considerable number of studies using this basic method that have shown that subjects can walk accurately without vision to previously seen targets that are as far as 21 m away [1–3], thus demonstrating that healthy subjects are adept at updating their changing positions non-visually, at least over the relatively short distances used in these experiments.

Work by Rieser and his colleagues [4,5] has suggested that the non-visual spatial updating demonstrated in 'blind' walking tasks of the type described above is based on the locomotor proprioceptive information that is generated by the subject's movement. It is argued that, through one's experience of moving through the environment, one is exposed to a coupling between the optical flow and proprioceptive flow that are generated by one's locomotion. Exposure to this visual-proprioceptive coupling calibrates locomotor proprioception so that, when one is momentarily deprived of visual input, one can nevertheless update one's changing spatial relationships on the basis of the incoming proprioceptive information.

Visually calibrated proprioceptive information seems, moreover, not only to update position in the absence of vision, but to do so in a relatively direct and instantaneous way. Rieser [6] asked subjects to either rotate without vision while in the centre of a cir-

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cular array of targets, or to imagine rotating. When the subjects were then asked to point to one of the targets after their actual or imagined rotation, they performed more quickly and accurately when they had performed a real rotation than when they had merely imagined rotating to a new orientation. These findings are clearly consistent with the idea that the updating that takes place during locomotion is automatic, but, as the subjects may have been making use of proprioceptive information in a voluntary and effortful way, they do not prove that updating is automatic. To test whether updating is indeed automatic Farrell and Robertson [7] and Farrell and Thomson [8] asked subjects to refrain from updating their positions while they moved without vision. The subjects were told to ignore their locomotion and to imagine that they were still in the same position in which they started. If updating only occurred as the result of effortful processing, subjects should find it relatively easy to ignore their movement to a new position and should perform better in this condition than in the updating condition; if, however, updating is automatic, they should perform worse when asked to prevent updating from taking place than when updating their positions. Both of these studies indicated that subjects found it difficult to ignore their movement to a new position, hence suggesting that the updating was automatic. Moreover, it appeared from the greater response latencies in the ignoring task that the subjects had to 'undo' updating that had already taken place to imagine themselves back in their starting positions, rather than being able to prevent the updating from occurring in the first place.

Although egocentric updating has seldom been tested directly in patient populations, there are studies in which brain-damaged subjects have performed tasks that would nevertheless seem to involve a significant updating component and that can, therefore, give some indication of the neural areas that might be involved in updating. One such task that has been used several times with neurological patients is the locomotor map test, in which the subject has, using a map, to follow a path between node points marked on the floor or walls of the room. When each of these node points are represented by identical markers, the subject, in order to remember where they are on the path, has to be able to update his/her position.

Although the findings using this task have not always been consistent, as successful performance will rely on a number of different capabilities, the weight of evidence nevertheless seems to indicate that posterior, and particularly parietal, lesions result in impaired performance. Semmes et al. [9] found that, as a whole, patients with parietal lesions (left, right, or bilateral) were impaired relative to non-brain damaged controls and patients with non-parietal lesions, although, unfortunately, no attempt was made to determine whether there were any differences in the effects of left and right parietal lesions. Hécaen et al. [10], however, found, using a similar test, that right hemisphere patients, and particularly those with posterior and parietal lesions, were more impaired than patients with left hemisphere lesions. Single case studies reported by Hécaen et al. [11] and Hublet and Demeurisse [12] have also found impaired performance on the locomotor map task in patients with lesions involving the right superior occipital area and the right parietal lobe.

On the basis of these studies, it would appear that the posterior region of the right hemisphere, and particularly the parietal lobe, might play an important part in updating egocentric spatial relationships. Such findings tie in with Milner and Goodale's [13] proposal that the dorsal cortical visual system deals with the guidance of actions, and thus encodes location egocentrically, while the ventral cortical visual system is concerned with perception and identification, and thus deals with allocentric spatial information. Thus, from this point of view, one would predict that lesions affecting the dorsal visual stream, such as posterior parietal or occipito-parietal lesions, would impair the updating of egocentric spatial relationships.

Several other workers have claimed that the posterior region of the parietal lobe is particularly important for the encoding of egocentric spatial information. Andersen [14] argues, on the basis of physiological evidence, that body-centred spatial coordinates are encoded by cells in the posterior parietal cortex. Stein [15,16] also argues for the importance of the posterior parietal cortex in encoding body-centred spatial relationships. He maintains, again on the basis of physiological studies in the monkey, that the area subserving egocentric spatial representations must be an area receiving many afferent inputs from different sensory systems, which can then be transformed to provide an egocentric spatial representation that is appropriate for whatever action that the organism is engaging in. In particular, there are extensive inputs from the proprioceptive and vestibular systems to the posterior parietal cortex, thus this area receives important information about the movement of the body that would allow it to represent changing egocentric spatial relationships.

The role of the parietal cortex in mediating egocentric spatial awareness in humans has been investigated extensively by Karnath and his colleagues [17–19]. They have argued that one of the fundamental factors underlying the syndrome of unilateral neglect, which is most commonly associated with lesions to the right posterior parietal cortex, is that the patients' egocentric representation of space has been biased to one side (to the right) so that items on the left are ignored.

Karnath [19], for example, asked neglect patients to aim a laser pointer in the direction that they felt to be directly in front of them. The direction in which these patients pointed erred systematically to the ipsilesional side, which was not the case in either normal or brain-damaged controls, thus supporting the view that the neglect patients had a skewed egocentric spatial representation. Karnath [18] then went on to demonstrate the importance of vestibular and proprioceptive information in egocentric spatial encoding. The neglect patients were subjected to caloric stimulation and stimulation of the neck proprioceptors, which, when carried out on the left side, ameliorated the extent of the neglect. Thus, the production of similar proprioceptive and vestibular feedback to that which would be generated by turning to the left partially corrected the symptoms.

The evidence provided by Rieser and his colleagues for the importance of locomotor proprioceptive information in non-spatial updating has already been described, and is clearly consistent with the arguments of Stein and Karnath on the influence of proprioceptive and vestibular information on egocentric spatial awareness. If, then, egocentric spatial awareness depends in large part on proprioceptive input to the right dorsal (RD) area, and posterior parietal cortex in particular, one would also expect that the proprioceptively based updating described by Rieser would also be dealt with by the right dorsal area. It follows from this that patients with RD lesions should be impaired on non-visual updating tasks. Deprived of vision, they should be unable to make use of the incoming locomotor proprioceptive information to update their positions automatically. Patients with lesions to other areas, however, should be unimpaired in their ability to update their positions in the absence of vision. In addition, one would perhaps also predict that RD patients should perform better than normal on the ignoring task used to demonstrate the automaticity of updating [7,8], in which they have to imagine that they have not moved when, in fact, they have moved. As the automatic updating mechanism should be damaged in such patients, it should be easier for them to ignore their movement to a new position and to imagine that they are still facing in their original direction. The present experiment set out to test these predictions by asking patients with RD lesions and patients with right anterior parietal lesions and left parietal (anterior and posterior) lesions to rotate without vision while in the centre of a previously seen circular array of targets. In one condition, they were asked to update their positions and to point to a named target from their new orientation. In another condition, they rotated without vision but were asked to ignore this movement and to point to the named target as if they were still in their original position.

2. Method

2.1. Patients

2.1.1. Right dorsal patients

2.1.1.1. Patient MN. Patient MN was a 51 year old male who had suffered a stroke affecting the right posterior parietal lobe 4 years previous to testing. He had

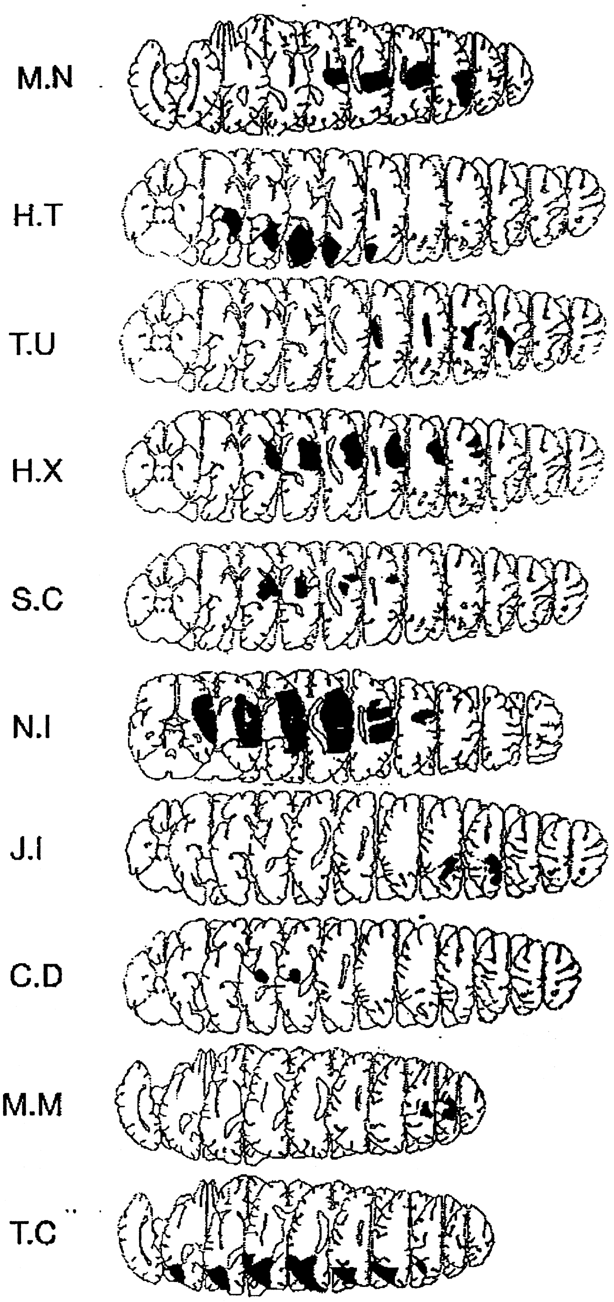

Fig. 1. Illustrations of the lesioned areas in the ten patients tested. Presented first are the two right dorsal patients (NM and HT) followed by the four other right hemisphere patients and then the four left hemisphere patients.

since returned to work and lived independently. Fig. 1 shows the region affected by his lesion. There was, in particular, damage to the inferior parietal lobule of the right hemisphere (Brodmann areas 39 and 40).

2.1.1.2. Patient HT. Patient HT was a 64 year old male who had suffered a stroke 1 year prior to testing. Fig. 1 shows that the area primarily affected by the lesion was the occipito-temporal region of the right hemisphere. The most extensively damaged areas are the superior interior parts of Brodmann areas 19 and, particularly, 18 (cuneate gyrus). Although the parietal cortex was not damaged directly in this patient, the lesion extended into the white matter underlying the parietal lobe and thus it is likely that projections to the posterior parietal cortex would have been affected.

2.1.2. Non-RD patients

Four patients with left parietal lesions (anterior and posterior) and four patients with right anterior parietal lesions were tested. Their details are given in Table 1 and their lesions illustrated in Fig. 1.

In addition to the testing of the above patients, a preliminary experiment was done with 10 normal subjects (five male, five female, mean age: 53.7 years, SD: 11.9 years) from the MRC Cognition and Brain Sciences Unit subject panel.

2.2. Apparatus and layout of experimental space

The experiment was carried out in a room in which a 2.5 × 2.5 m space had been cleared. Seven common household objects with one syllable names were used as targets, and these also served to define the seven possible subject orientations. They were placed on wooden plinths 1 m high that were spaced at 51.5° intervals to form a circle with a diameter of 2 m. The subject sat in a rotatable chair directly over the centre of this circle and pointed to the targets with a hand-held pointer. While pointing the subjects wore a blindfold and listened through headphones to white noise played by a tape recorder attached to the back of the chair. The volume of the white noise was loud enough to mask any background sounds that could have acted as localisation cues but still permitted the experimenter to be heard when giving instructions.

2.3. Design

Patients performed the pointing task under the three following conditions:

1. Updating: after viewing the targets, the subjects rotated without vision to face another direction and had to point to the true position of the named target from this new orientation.
2. Ignoring: after blindfolding, the subject rotated to face a new direction, but had to try to ignore this rotation and to imagine that s/he was still facing the initial direction. The subject thus had to point to the targets *as if* s/he were pointing to them from the starting position.
3. Control: in this condition the subjects rotated in one direction and then in the opposite direction so that they ended up facing in their original direction. The subject then pointed to the true location of the target. The inclusion of this condition is of crucial importance to the interpretation of the results. Without this condition, impaired responses in the other conditions could simply be interpreted as the result of deficits such as optic ataxia, neglect, or simply an inability to encode the target layout in memory. By having the patients point to the targets under conditions that did not require the updating of position or the ignoring of locomotion, we could, on the basis of accurate performance in this task, rule out the above explanations of impaired performance in the other conditions.

In all of the conditions the subjects rotated once through each of the eight rotation magnitudes. The

Table 1
Background information on the eight patients with lesions not involving the right dorsal area

Patient	Sex	Age	Years post	Aetiology	Lesion location	Brodmann areas
Right						
TU	F	53	4 months	Hemorrhage	Subcortical	White matter, underlying areas 4, 5, 6, 23, 40
HX	M	46	5	Infarct	Temporo–parietal	2, 3, 4, 6, 22, 41, 42, 44
SC	M	56	4	Infarct	Temporo–parietal	2, 3, 6, 22
NI	M	54	3	Infarct	Temporo–parietal	2, 3, 4, 6, 9, 21, 22, 40, 41, 42, 45
Left						
JI	F	46	4	Tumour	Parietal	1, 2, 4, 5, 7
CD	F	53	3	Hemorrhage	Subcortical (parieto–temporal area)	White matter, underlying areas 3, 22, 41, 42
MM	M	51	4	Tumour	Parietal	2, 4, 5
TC	M	41	3	Infarct	Parieto–temporal	7, 19, 22, 37, 39, 40

direction of rotation (clockwise or anticlockwise) and the order of presentation of the three conditions were randomised. As not all of the permutations of the different possible starting points, rotation sizes, and target objects could be performed, the same trials were used in all three conditions. Thus, the amount of rotation that had to be updated or ignored was the same in each condition, as were and the target objects and correct responses. Any differences between the conditions, therefore, could not be due to some responses being intrinsically more difficult or time consuming than others, or to particular targets being remembered more easily than others.

2.4. Procedure

The subjects were seated in a rotating chair in the centre of the circular array of target objects. They were told the names of the objects and instructed to look at them and to try to remember where they were. The subjects were then tested on their memory for the target positions by pointing with their eyes closed at each of the target objects while facing each of the seven possible directions. After each practice trial the subjects were allowed to look to see how accurate the response was. It was emphasised to the subjects that they should try to point directly at the target, not just in the correct general direction. At the end of this practice period all the subjects were able to point correctly to each of the target objects, i.e. were closer to the correct target than to any other target. All subjects said that they were confident that they knew the layout of the targets and none said that they wished any additional practice trials.

For the experimental trials the subjects were fitted with the blindfold and the headphones. In the updating condition, the subject looked at the targets while facing the object defining the starting orientation and then was blindfolded. The experimenter then touched the subject on one shoulder and the subject then started to rotate around towards the side on which s/he had been touched (e.g. if touched on the right shoulder, the subject would rotate in a clockwise direction). When the subject had reached the new orientation, the experimenter told him/her to stop and then named the target to which the subject had to point and simultaneously started a stopwatch. During rotation, the experimenter stood directly behind the subject's chair and grasped the back of it when the subject was instructed to stop. In this way the experimenter was able to prevent the subject rotating past the required stopping orientation. When the target was named, the subject pointed to it and the experimenter stopped the stopwatch as soon as the subject had pointed to the target. The subjects were instructed to point as quickly and as accurately as possible and, to facilitate accurate timing of the responses, to point in a single decisive movement. They were also instructed not to make any subsequent corrections to their responses, but to keep the pointer in position.

When the subject had pointed, a plumb line was dropped from the end of the pointer to floor and a marker placed at this location. This procedure only took about 3 or 4 seconds, and the subjects were able to keep the pointer in position for this short period. The subjects were not allowed to see how well they had done during the experimental trials, and the presence of decoy markers on the floor from the start meant that the subjects were unable to use the markers to gauge the accuracy of their responses. The subject was then rotated to the starting orientation for the next trial.

In the ignoring condition the subject rotated to a new orientation, as described above, but was told beforehand to try to ignore this rotation and imagine that s/he was still facing in his/her initial direction. After rotating the subject was instructed: 'point to the [*insert name of target object*] as if still facing the [*insert name of original orientation object*].' In the control condition the subject, after being blindfolded, was touched on the shoulder and started to rotate towards that side. When s/he had rotated through half of the angle used in the corresponding trial in the other conditions, the experimenter touched him/her on the other shoulder and s/he rotated back in the opposite direction and was told to stop once the initial orientation had been regained. The subject then pointed to the target named by the experimenter.

During all trials the subjects and patients rotated at their own preferred velocity. It has been demonstrated [2] that non-visual updating is most accurate when subjects are allowed to move at their own normal speed of locomotion, and that imposing, for example, a faster than normal speed on the subjects' locomotion leads to increased errors in positional updating.

3. Results

A preliminary study was done with normal subjects. One-way repeated measures analysis of variance (ANOVA) revealed that there was a significant effect of condition on absolute angular pointing error ($F(3, 27) = 6.61$, $P < 0.02$). Post-hoc comparisons using Tukey's HSD procedure showed that errors were significantly greater in the ignoring condition than in the control condition ($P < 0.01$) (see Fig. 2A). There was, however, no difference between the control condition and the updating condition, and the updating and ignoring conditions did not differ significantly from one another in terms of error.

There was also a significant effect of condition on overall mean response latency ($F(3, 27) = 35.19$, $P < 0.01$). Post-hoc pairwise comparisons indicated that there were significantly longer response latencies in the ignoring condition than in the updating and control conditions ($P < 0.01$). There were, however, no significant differences between the control and updating conditions (see Fig. 2B).

The results obtained corroborate other work on the updating of egocentric spatial relationships [6–8,20] in that they suggest that spatial updating is automatic, at least in the sense that it seems to occur without volitional control. The extent to which the seemingly involuntary nature of spatial updating is, consistent with the classical definition of an automatic process, accompanied by a relatively small demand on cognitive processing resources remains to be seen. It should be noted, however, that several authors [2,21–23] have suggested that updating does require the use of cognitive resources in the form of working memory or path integration mechanisms. One can therefore only conclude that spatial updating is automatic in one of the senses used by Norman and Shallice [24]: the process occurs in the absence of a deliberate intention on the part of the subject. According to this interpretation, it is only when the subjects are asked to prevent the updating from taking place that a deliberate intention seems to be required, and, as the present results demonstrate, subjects find it difficult to override spatial updating in this way.

The relatively long response latencies in the ignoring condition suggest that, to respond in accordance with their original (pre-rotation) orientations, the subjects had to engage in supplementary processing that was not required when responding in accordance with their actual orientations. The linear increase in response latency with increasing rotation magnitude in the ignoring condition suggests that this supplementary processing is likely to have taken the form of a mental rotation of the body-centred reference frame from the post-rotation orientation back into alignment with the original orientation (see Fig. 3A; ‘0’ rotation corresponds to no rotation; ‘7’ corresponds to a complete 360° rotation through all seven target orientations). The greater the angle through which the subject has rotated, the greater is the angular disparity between pre- and post-rotation orientations, and, hence, more time is required to rotate the reference frame back to the starting orientation. Thus, in the ignoring condition the subjects did not appear to be able to simply discount their movement to the new orientation, but could only imagine themselves still to be in the original orientation by undoing by mental rotation the automatic updating that had already taken place. This pattern of responses provides further support for the proposal that the subjects updated their positions automatically.

Non-visual spatial updating would have to rely on proprioceptive and vestibular information and, as was described in the introduction, there is evidence that visually-calibrated locomotor proprioceptive information may be of particular importance in the sort of task used in the present experiment. The linear increase in error size with increasing rotation magnitude (see Fig. 3B) is consistent with the idea that updating was based in large part on visually calibrated proprioception. As such a calibration would not be

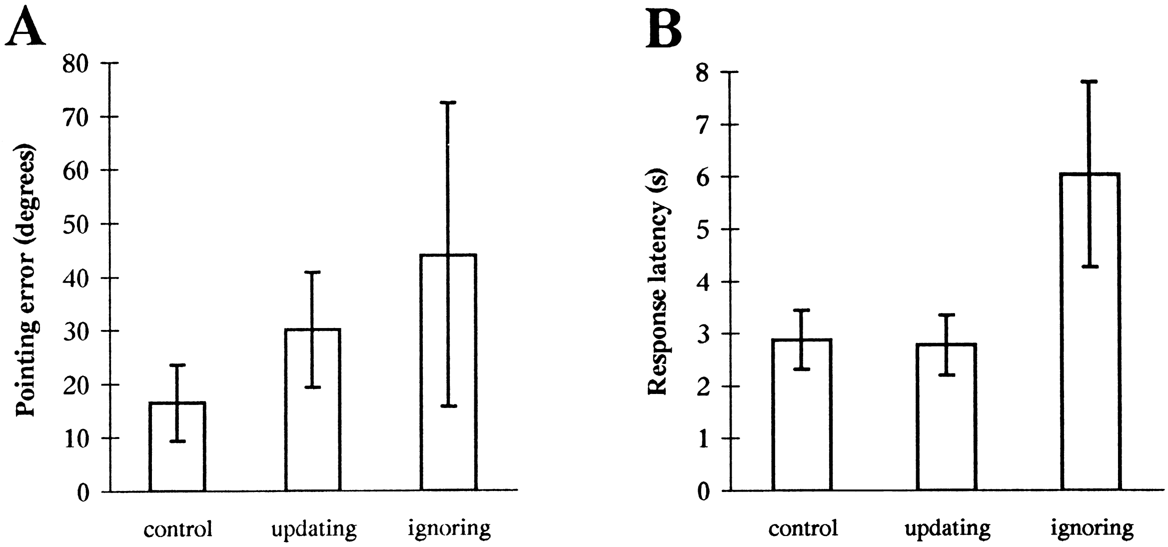

Fig. 2. (A) Mean angular errors and SDs for normal subjects in the control, updating, and ignoring conditions. (B) Mean response latencies and SDs for normal subjects in the control, updating, and ignoring conditions.

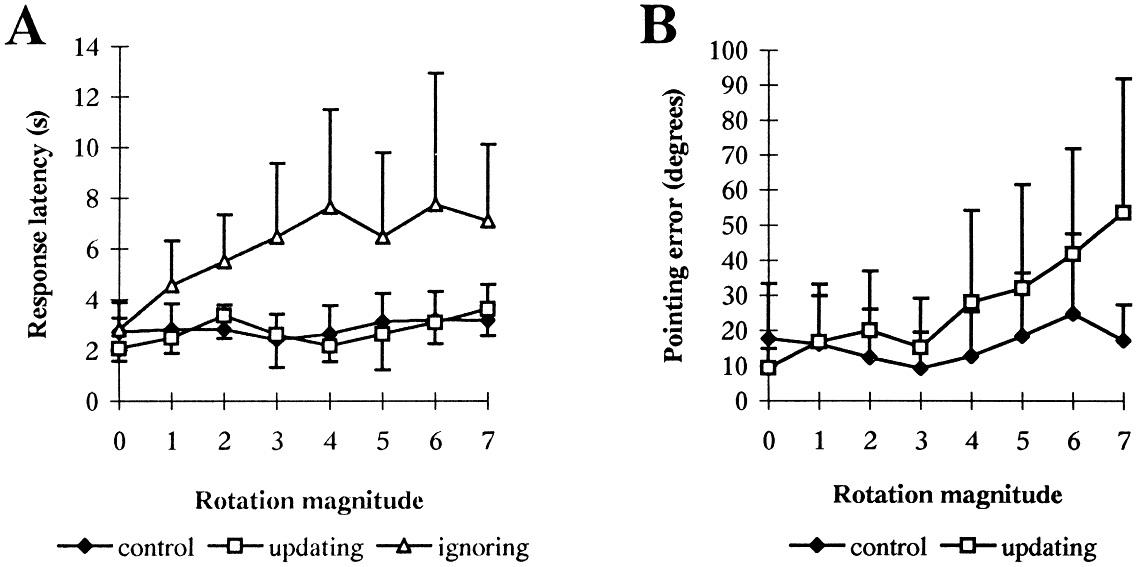

Fig. 3. (A) Mean response latencies and SDs for normal subjects in the control, updating, and ignoring conditions as a function of rotation magnitude. The figures on the abscissa represent the number of target positions passed on the rotation. 0 therefore corresponds to no rotation and 7 to a complete revolution. (B) Mean angular errors and SDs for normal subjects in the control, updating, and ignoring conditions as a function of rotation magnitude.

exact, error would accumulate as the distance over which updating took place became greater. This result accords with studies in which subjects had to walk without vision to previously seen targets [1,2], which have also found a linear increase in error as the subjects have to update their positions non-visually over increasing distances.

The overall accuracy of the performances of the two RD patients was markedly worse than that of the two non-RD groups (see Fig. 4A). In both cases the median error score was more that two standard deviations greater than the errors of the non-RD patients. They were also more than two standard deviations greater than the errors of the normal subjects. None of the non-RD had an median error that was more than two SDs above that of the normal subjects. The RD patients, nevertheless, performed the control task as well as the non-RD patients. The ignoring condition

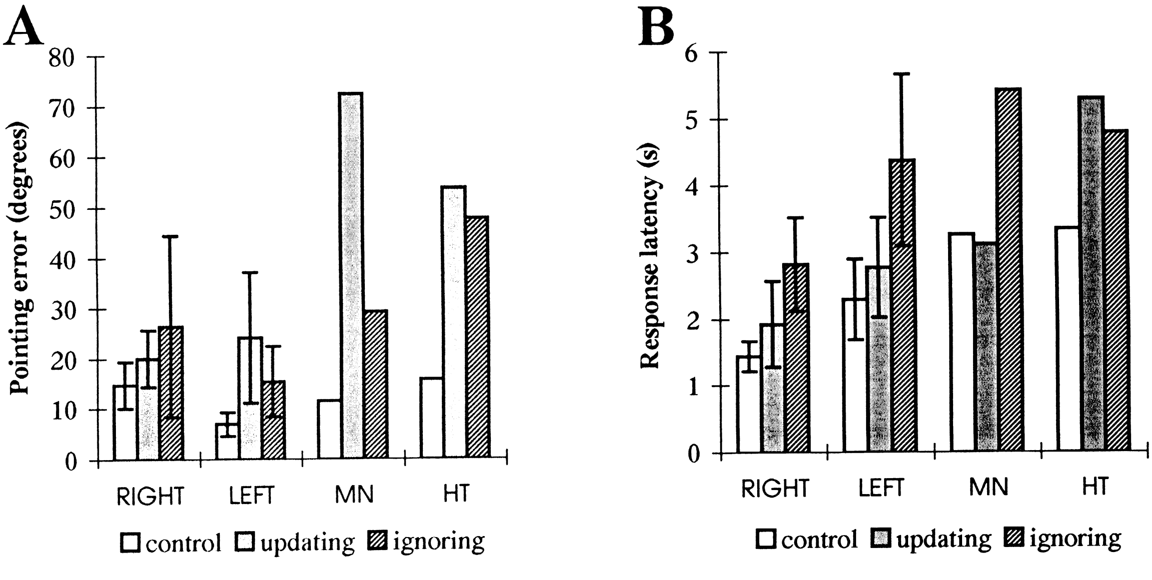

Fig. 4. (A) Average median angular errors and SDs in each of the three rotation conditions for the right hemisphere, left hemisphere and right dorsal patients. (B): Average median response latencies and SDs in each of the three rotation conditions for the right hemisphere, left hemisphere and right dorsal patients.

also gave rise to relatively high levels of error, especially in patient HT. His median error, however, was within two SDs of both the other right parietal patients' mean and the normal subjects' mean. Thus, the updating condition is only one under which one can confidently conclude that the RD patients were impaired.

Patient MN's response latencies were not markedly greater than those of the non-RD patients' in any of the conditions (see Fig. 4B). Patient HT's median response latency in the updating condition was, however, more that two SDs greater than that of any of the other groups. This patient, therefore, seemed to be selectively impaired on the updating task, both in terms of accuracy and in terms of latency; patient MN was selectively impaired on the updating task only in terms of accuracy.

Investigation of the effect of rotation magnitude on errors and latencies showed that under the control condition no linear or curvilinear trend was present in the error scores of patient HT (see Fig. 5A). Patient MN's errors, however, showed a significant linear increase with rotation magnitude ($r^2 = 0.614$, $F(1,6) = 9.54$, $P = 0.021$), and the errors of the non-RD patients showed a significant curvilinear relationship with rotation magnitude ($r^2 = 0.727$, $F(2,5) = 6.66$, $P = 0.039$). Examination of Fig. 5A shows, however, that for the non-RD patients, although the curvilinear trend was reliable, it was nevertheless not very marked. The errors of MN, however, show a marked increase at the larger rotation magnitudes.

In the updating condition (see Fig. 5B), like the normal subjects, both the non-RD patients and MN showed a linear increase in error with increasing rotation magnitude (MN: $r^2 = 0.609$, $F(1,6) = 9.34$, $P = 0.022$; non-RD: $r^2 = 0.895$, $F(1,6) = 51.12$, $P < 0.001$). The rate of increase, however, was much more marked for MN than it was for the non-RD patients. Patient HT's errors showed no significant linear or curvilinear relationships with rotation magnitude, although he did seem to perform particularly poorly at the higher rotation magnitudes, with the exception of the maximum (360°) rotation, in which the pre- and post-rotation orientations were identical. There were no significant relationships between error and rotation magnitude in the ignoring condition (see Fig. 5C), although HT again produced particularly large errors at the higher rotation magnitudes (again with the exception of the 360° rotation).

The response latencies in the control condition showed no significant relationships with rotation magnitude (see Fig. 6A). The only trend that was significant in the updating condition was a linear increase in response latency with increasing rotation magnitude in the non-RD patients ($r^2 = 0.860$, $F(1,6) = 36.73$, $P = 0.001$). Examination of Fig. 6B, however, reveals that, although this trend was reliable, it was characterised by a relatively flat curve. In the

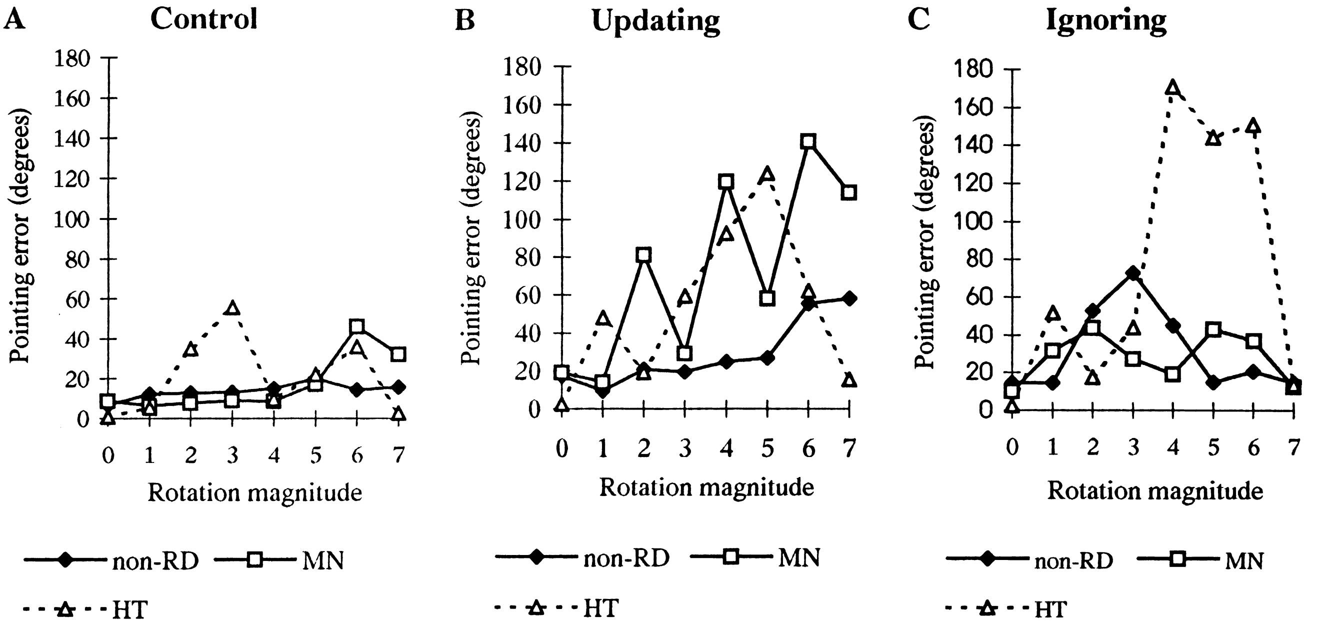

Fig. 5. (A) Angular errors for the non-right dorsal (RD) patients and the two RD patients (MN and HT) in the control condition as a function of rotation magnitude. The figures on the abscissa represent the number of target positions passed on the rotation. 0 therefore corresponds to no rotation and 7 to a complete revolution. (B) Angular errors for the non-right dorsal (RD) patients and the two RD patients (MN and HT) in the updating condition as a function of rotation magnitude. (C) Angular errors for the non-right dorsal (RD) patients and the two RD patients (MN and HT) in the ignoring condition as a function of rotation magnitude.

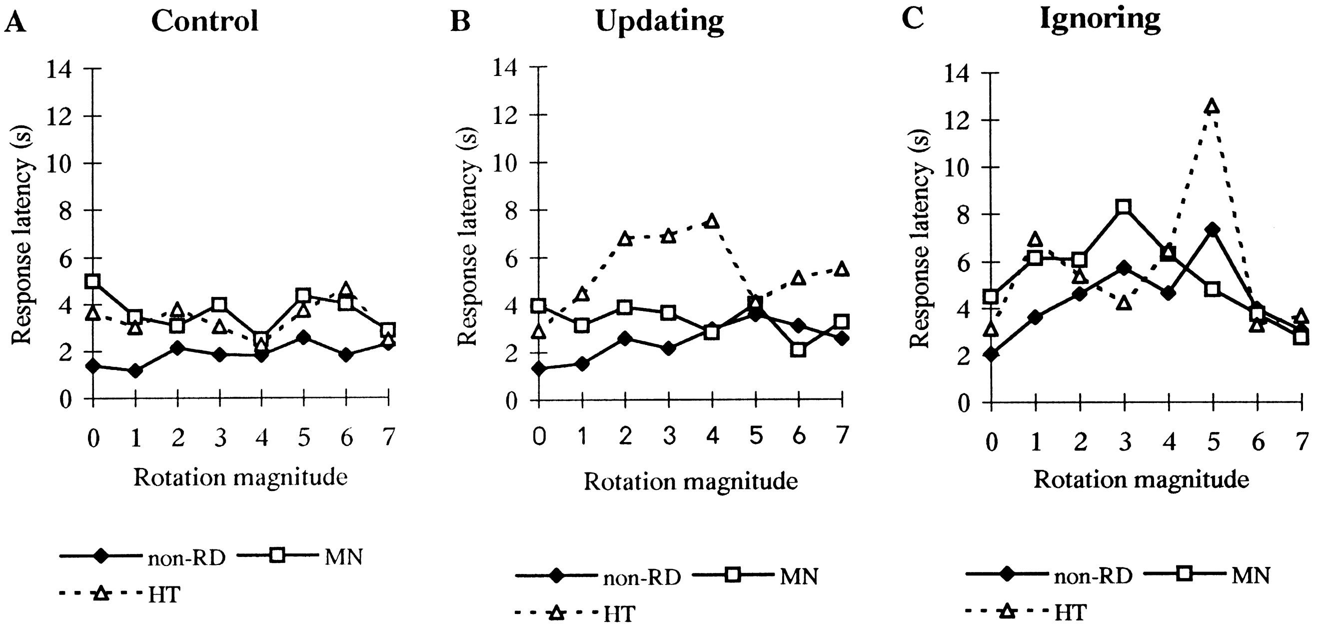

Fig. 6. (A) Response latencies for the non-right dorsal (RD) patients and the two RD patients (MN and HT) in the control condition as a function of rotation magnitude. The figures on the abscissa represent the number of target positions passed on the rotation. 0 therefore corresponds to no rotation and 7 to a complete revolution. (B) Response latencies for the non-right dorsal (RD) patients and the two RD patients (MN and HT) in the updating condition as a function of rotation magnitude. (C) Response latencies for the non-right dorsal (RD) patients and the two RD patients (MN and HT) in the ignoring condition as a function of rotation magnitude.

ignoring condition (see Fig. 6C), there were significant curvilinear relationships between the response latencies of the non-RD patients and rotation magnitude ($r^2 = 0.710$, $F(2,5) = 6.11$, $P = 0.045$) and between MN's response latencies and rotation magnitude ($r^2 = 0.823$, $F(2,5) = 11.59$, $P = 0.013$). Thus, response latency increased with increasing magnitude in both clockwise and anticlockwise directions between the post-rotation heading and the pre-rotation heading, in accordance with which the subjects had to perform. The response latencies of HT showed no significant trends.

As well as examining the absolute size of the errors made by the patients, we also examined the constant (i.e. signed) errors that they made to see if their was any directional bias in their responses. Given that both the pointing responses of the patients and the bearings of the targets were measured in a clockwise direction from a fixed origin, an overestimate of the bearing of the target after clockwise rotation would correspond to an underestimation of the rotation angle: the subject's response would indicate that the angular distance between him/herself and the target was larger than it actually was. The opposite is true after anti-clockwise rotation, i.e. an underestimate of the target's bearing would correspond to an underestimate of the rotation angle. Both of the RD patients showed, in the updating condition, a marked tendency to underestimate the size of the angle through which they had rotated (see Fig. 7). This pattern was observed regardless of the direction of rotation. The same extent of directional bias was not seen in the non-RD patients, although one did of the left parietal patients did consistently

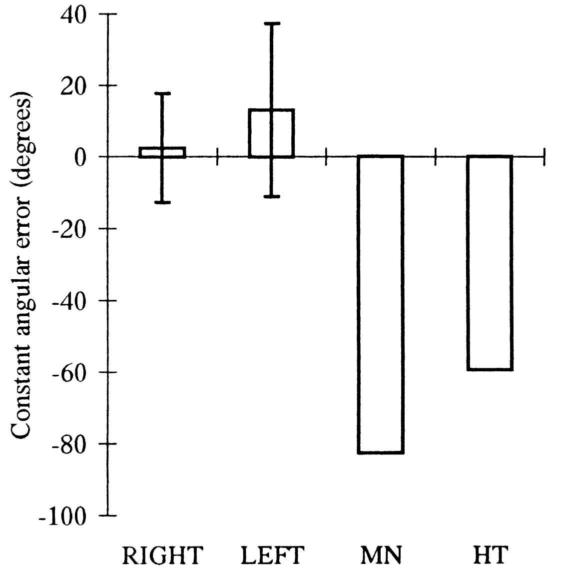

Fig. 7. Constant (signed) angular errors and SDs for the right hemisphere, left hemisphere, and right dorsal patients (MN and HT) in the udpating condition. Negative scores correspond to an underestimation of the angle through which the subject has been rotated; positive scores to an overestimation.

overestimate the size of the angle through which she had been rotated.

4. Discussion

The results obtained are supportive of the view that the RD area plays an important role in the updating of body-centred spatial relationships. In terms of overall accuracy, the two RD patients were the only ones to produce errors that were more than two SDs above the mean of the normal subjects tested. Both of these patients, however, were not impaired in the control condition or in the ignoring condition. The selective nature of the impairment is consistent with the idea that the RD area is particularly important for the updating of egocentric spatial relationships, rather than, for example, spatial memory per se.

The pattern of response latencies was not as clear as that for the error scores. The response latencies of MN were not markedly longer in any condition than those of the non-RD patients. Patient HT, however, did take longer than the other groups to respond in the updating condition, although his response latencies in the control and ignoring conditions were not abnormally long.

The response latencies of the non-RD patients in the ignoring condition show a slightly different pattern to those of the normal subjects. Instead of a linear increase in response latency with increasing rotation magnitude, they take the form of an inverted U-shaped curve. Such a pattern is, nevertheless, interpretable in terms of 'undoing' automatic spatial updating: it may be the case that, while the normal subjects chose to imagine themselves back at the start by mentally rotating their frame of reference back in the opposite direction to that in which they had rotated, the non-RD patients chose to take the 'shortest' route back to the original orientation. Thus, if they had rotated though more than 180°, the shortest route would be to mentally continue their rotation in the same direction rather than mentally rotating back in the opposite direction. It is likely that the different patterns in the normal subjects and the non-RD patients reflect a difference in the strategy that was chosen by the participants rather than a genuine difference between normal subjects and patients, as Farrell and Robertson [7] have shown that the inverted U-shape curve can also be found in non brain damaged subjects.

The results from the normal subjects were interpreted in terms of the automaticity of spatial updating. It was thought that, if the RD was important in such updating, lesions in this area would not only impair performances in the updating condition, but would perhaps also enhance performances in the ignoring condition. Although the first prediction has been confirmed, the second has not. The inability of the RD patients to ignore their movement more easily than the other groups, although impaired at updating their positions, is explicable in terms of their systematic tendency to underestimate the angle through which they had rotated. No such large directional biases were seen in the normal subjects or in the other patients, although one left parietal patient tended to overestimate the distance through which she had turned, albeit to a lesser extent than the underestimations of the RD patients. The tendency of the RD patients to underestimate the angle through which they had turned is interesting in the light of the findings reported by Blouin et al. [25], in which passively rotated normal subjects tended systematically to underestimate the angle through which they had turned. In this latter study the subjects were deprived of locomotor proprioceptive information, and it may be the case that impoverished proprioceptive feedback or an inability to process it in the case of the RD patients in the present study may have played an important role in the underestimations that they produced.

It is therefore likely that the RD patients were not completely deprived of proprioceptive input, although it may have been impoverished and/or processed in a systematically biased way. In the case of MN, a weak input may nevertheless have allowed him to distinguish between large and small rotations so that he would have been aware of the relative distance that he had moved from his initial orientation. An ability to appreciate the relative size of rotations would account for the inverted U-shape pattern of his response latencies in the ignoring condition. When, however, MN's appreciation of the absolute distance through which he had moved was tested in the updating condition, his errors were large.

In the case of HT, the systematic tendency to underestimate the angle through which he had rotated again suggests an impoverished proprioceptive input and/or systematically biased processing rather than a complete absence of proprioceptive input, which one would expect to produce an erratic performance, with errors in both directions tending to cancel one another out. It may therefore be the case that HT received enough proprioceptive input to indicate that he had moved from his original position while not being sufficient to allow him to update his position accurately. Such an explanation may account for the impaired updating along with an inability to simply ignore the fact that he had moved.

The results reported in this paper are supportive of the idea that normal healthy subjects can update their changing spatial relationships in the absence of vision. Moreover, such updating takes place automatically in that they cannot simply ignore their movement to a new orientation. It would appear, on the basis of the patient data, that the right dorsal area may play a particularly important role in such updating, as the only patients in whom this process was impaired were those with damage to this region. Though one cannot argue that the present results conclusively prove the importance of the RD area in spatial updating, they are clearly consistent with such an interpretation. The present findings also fit in with previous work reported by Stein [15] and Karnath and his colleagues [17–19] as well as with several cases in the literature on spatial impairments resulting from brain damage (see Farrell [26] for review).

In particular, the two RD patients appeared, in general, to underestimate the angle through which they had turned. In the light of Rieser and his colleagues' [4,5] proposal that non-spatial updating is based on locomotor proprioceptive information, such a finding can be interpreted in terms of damaged proprioceptive connections to the RD resulting in reception of impoverished proprioceptive information or a systematically distorted processing of the proprioceptive input.

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