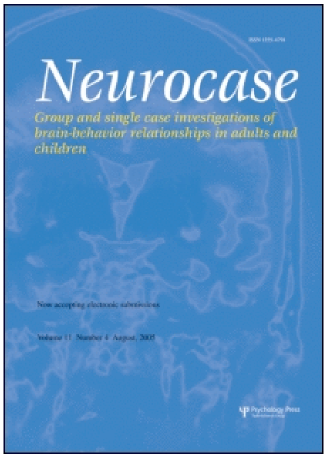

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Straight after the turn: The role of the parietal lobes in egocentric space processing

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Straight after the turn: The role of the parietal lobes in egocentric space processing

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Spatial information processing with respect to an egocentric reference frame has been shown to recruit a fronto-parietal network along the dorsal stream. The present study investigates how brain lesions in the relevant areas affect the ability to navigate through computer-simulated tunnels shown from a first person perspective. Our results suggest that parietal, but not frontal, patients are impaired in this task. They confused the direction of tunnel turns more frequently and made less accurate judgments about the location of the end position. Errors in map drawing suggest that the impairment may be linked to deficits in updating cognitive heading in the absence of corresponding perceptual information from the virtual environment.

Keywords: Virtual environment; Spatial navigation; Spatial processing; Visual flow; Parietal lobe.

INTRODUCTION

The ability to orient oneself in space is a complex process based on different spatial reference frames existing in parallel and subserving different functions (Shelton & McNamara, 2004; Woodin & Allport, 1998). Commonly, a distinction is made between an allocentric (viewpoint-independent) and an egocentric (viewpoint-dependent) reference frame, entailing different primitive parameters (Klatzky, Loomis, Beall, Chance, & Golledge 1998): An allocentric representation of space includes distances and angles between reference points in space and is used to plan a route or find detours. Egocentric space processing serves the purpose of helping the person to keep track of their own orientation within space, and to update distances and viewpoints of familiar objects along the route with respect to the person's present position and body axis (Aguirre & D'Esposito, 1999; van Asselen et al., 2006). At a higher level of processing, these two perspectives are thought to be reintegrated to form one coherent representation of space (Andersen, Snyder, Bradlet, & Xing, 1997; Bremmer, Schlack, Duhamel, Graf, & Fink, 2001).

Recent imaging studies have provided evidence that spatial representations based on different

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reference frames recruit distinct brain areas. In line with early theories of spatial navigation (O'Keefe & Nadel, 1978), activation of the ventral processing stream including hippocampal and parahippocampal areas has been found in relation to allocentric encoding of space (Brandt et al., 2005; King, Trinkler, Hartley, Vargha-Kadem, & Burgess, 2004; Maguire, Frackowiack, & Frith, 1997; Maguire et al., 2000; Mayes, Montaldi, Spencer, & Roberts, 2004; Parslow et al., 2004). Egocentric encoding of space, by contrast, has been shown to recruit a fronto-parietal network along the dorsal stream (Committeri et al., 2004; Galati et al., 2000; Vallar et al., 1999; Wilson, Woldorff, & Mangun, 2005). These separate networks have also been shown to be involved in human wayfinding in virtual environments (Ino et al., 2002; Maguire et al., 1998).

Neuropsychological evidence indicates that dorsal and ventral brain lesions affect spatial cognition selectively, with double dissociations being reported between disorders of viewpoint-centred and viewpoint-independent representations of space (Bohbot, Iaria, & Petrides, 2004; Pizzamiglio, Guariglia, & Cosentino, 1998; Vallar, 1999; van Asselen et al., 2006). Furthermore, a review of individual case studies by Aguirre and D'Esposito (1999) suggests that disorders of topographical disorientation can be grouped into subtypes according to the affected pathway: dorsal impairment leads to disorders of viewpoint-dependent processing (egocentric disorientation, heading disorientation), whereas ventral lesions result in deficits of viewpoint-independent processing (landmark agnosia, anterograde topographical disorientation).

Although neuropsychological studies suggest distinct roles for the dorsal and the ventral streams, with a necessary role for parietal structures in viewpoint-centred space processing, recent studies have questioned this dichotomy. A study by Barrash, Damasio, Adolphs, and Tranel (2000) investigated wayfinding in people with focal cortical lesions in a complex real-life environment. They found severe impairment of spatial orientation in patients with occipito-temporal lesions, but did not find a critical role of the posterior parietal cortex for route learning. Also, a functional imaging study by Mellet et al. (2000), in which subjects learned an environment from different perspectives, showed ventral activation for both egocentric and allocentric conditions. The authors argue for hippocampal areas being involved in the retrieval of topographical knowledge independent of encoding conditions. Mellet et al. (2000) also found a parieto-frontal component in both conditions, but this was attributed to the involvement of mental imagery when environmental information had to be held on-line when it was no longer visible.

Thus, whether the parietal lobe plays a necessary role in space processing, in particular with respect to egocentric encoding of spatial information, needs to be further clarified. One important point which has to be taken into account for the evaluation of the seemingly contradictory findings is recent evidence which suggests that subjects differ with respect to their preferred reference frame, and that the encoding of space may change with practice. For example, Iaria, Petrides, Dagher, Pike, and Bohbot (2003) had participants navigate through a virtual environment which allowed for both spatial (navigating between landmarks) and non-spatial strategies (counting landmarks) to be adopted. A substantial number of subjects who started out with a spatial strategy switched over to a non-spatial strategy in the course of the experiment, indicating that preferred navigation strategies may change over time. Temporal lobe patients tested on the same paradigm were impaired when using the spatial strategy; however, those who spontaneously adopted a non-spatial strategy performed as well as controls (Bohbot et al., 2004). These data suggest that presenting spatial information from an egocentric viewpoint does not necessarily affect the frame of reference which people choose to adopt for their representation of space, especially when different strategies and reference frames can lead to equally successful solutions to orient within the environment. Interpersonal differences with respect to the preferred spatial reference frames during navigation tasks could therefore provide an explanation for the inconsistent findings regarding the role of the parietal cortex in egocentric navigation. When alternative strategies can be used, some subjects may be able to build up a spatial representation from egocentrically perceived visual information (first-person perspective) in spite of a selective inability to relate spatial information to the self.

In order to investigate the role of the parietal lobe in the representation of egocentrically perceived spatial information, research has to focus on virtual navigation tasks which can only be solved by integrating spatial information from a first-person perspective. One type of spatial cue which cannot be interpreted within an allocentric reference frame is virtual motion, that is, accelerational and rotational cues of the subject's own progression in space, which constitute physical phenomena that can only be interpreted with respect to the self. Extraction of spatial information from this type of cue is thought to be achieved through path integration, which describes the process of using sensed motion to update one's own current position and body orientation relative to a starting point (Klatzky et al., 1998; Loomis et al., 1993; Loomis, Klatzky, & Golledge, 2001). In a study by Gramann, Müller, Eick, and Schönebeck (2005) it was tested whether virtual motion in absence of other visual or proprioceptive spatial cues provides sufficient information for healthy subjects to build up a representation of space through path integration. Participants were progressing through a virtual tunnel, in which motion was created through the visual flow of the tunnel walls. The subject had no influence on direction or speed of motion; these parameters were set by the experimenter. Once the end position of the tunnel passage was reached, subjects had to indicate the position of the starting point relative to the endpoint. It was found that, despite the input being presented from an egocentric perspective, subjects showed stable preferences for answering within either an egocentric or an allocentric reference frame. Also these spatial preferences were reflected in specific cortical activations distinguishing between subjects answering in different reference systems (Gramann, Müller, Schönebeck, & Debus, 2006). Computation of an egocentric reference frame was accompanied by dominant activity in a parietal-premotor network, with additional activity in frontal areas. Computation of an allocentric reference frame was associated with prevailing activity within an occipito-temporal network, confirming right-temporal structures to play a crucial role for an allocentric representation of space. The findings support the idea that the tunnel environment, despite its limited spatial cues, is sufficient for healthy subjects to build up relatively rich spatial representations. It is important to note that, in the tunnel paradigm, encoding has to take place from an egocentric viewpoint, independently of the preferred reference frame that subjects might switch to for a more permanent representation. Therefore, if the parietal lobe plays a necessary role in the representation of space from an egocentric perspective, patients with parietal lesions should be impaired in this type of task, both in comparison to healthy subjects and to neurological patients with other focal lesions.

In the present study, patients and healthy subjects performed a virtual tunnel task adapted from Gramann et al.'s study. During the tunnel passage, spatial input consisted of sparse visual-flow information reflecting translational and rotational changes without self-locomotion. All information was presented from a first-person perspective only (see Figure 1 and examples of the tunnel task at http://www.sccn.ucsd.edu/~klaus/tunnel.html). Subjects were instructed to keep track of their momentary position relative to the origin of the path, which could only be achieved by computing spatial relations among reference points. Subjects had no influence on pace of motion or the direction of tunnel bends. Given that reference points were no longer visible at the end of the passage, the task could only be solved on the basis of an internal spatial representation. More detailed descriptions of the tunnel task are reported in Gramann et al. (2005).

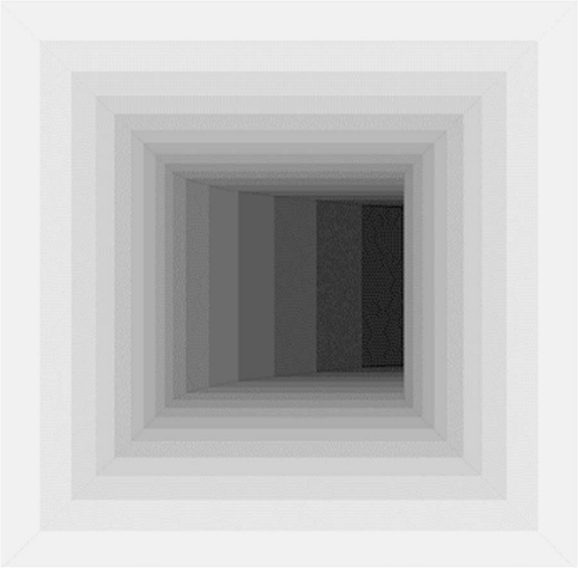

Figure 1. View into a tunnel with a turn to the right.

For further elaboration of the relationship between navigational abilities and general visuo-spatial skills, a number of neuropsychological tests were administered to assess functions typically associated with the parietal lobe. These included tests of mental rotation and visuo-spatial short-term memory.

GENERAL METHOD

Subjects

A group of four parietal-lobe patients (three males and one female, three left-hemisphere lesions (LH) and one right-hemisphere lesions (RH)), mean age = 66.0, *SD* = 9.38) participated in the present study along with four patients with frontal lesions (all male, two LH and two RH, mean age = 58.5, *SD* = 17.8) and 10 healthy control subjects (eight male, two female, mean age = 63.2, *SD* = 6.5). Two other patients were tested, but were excluded from analysis due to a lack of specificity of their lesions. All subjects had normal or corrected-to-normal vision and all were right-handed, except for one left-parietal patient who was left-handed (based on self-report). All patients were a minimum of 2 years post lesion and had stable deficits. The clinical deficits along with reports on background neuropsychological tests are listed in Appendix 1. The two groups of patients did not differ in terms of their performance on background tests linked to IQ and executive function (see Appendix 1). Transcriptions of MRI scans for the patients are presented in Appendix 2. All subjects gave informed consent to participate in the study and all experiments were carried out in accordance with the code of ethics of the World Medical Association (Helsinki II).

Task, materials and procedure

Subjects underwent neuropsychological testing on mental rotation skills and spatial short-term memory. Every subject then performed two different versions of the tunnel task as described below.

Neuropsychological tests

Mental Rotation Test (MR). A canonical letter/mirror letter task was used to assess mental rotation skills (for similar previous studies, see e.g., Alivisatos & Petrides, 1996). The test was programmed in house using E-Prime V1.0. Each trial showed a static display of three white squares of 60 × 60 mm, each containing a single letter R. The top square contained the target letter, which was a canonical or a mirror image letter rotated on the picture plane. Rotations between 0 and 330 in steps of 30 yielded two sets of 12 stimuli.

Each angle of rotation was shown five times for canonical and mirror images, respectively, resulting in a total number of 120 trials which were presented in random order. At the bottom of the display a picture of a canonical letter R was presented next to a picture of a mirror image of a letter R (‘R’ rotated around its vertical axis). The subjects’ task was to decide whether the target letter, if rotated back to the upright position, would match the picture at the bottom left (canonical R) or the bottom right (mirror R) and to press the left or the right mouse button accordingly. Subjects were instructed to respond as quickly and as accurately as possible.

Corsi Block-Tapping Task. This test assesses the ability to keep spatial information in working memory over a very short period of time. Nine wooden cubes (50 × 50 × 50 mm), mounted on a white wooden board, were used in the present study. Visible only to the examiner, the digits 1–9 were written on one side of the cubes. The procedures as well as the block sequences were adapted from van Zandvoort, Postma, Kappelle, and de Haan (2000). The experimenter started with a sequence of three cubes, and, following two different sequences of the same length being repeated in the correct order by the subject, increased the sequence by one cube. This procedure was continued until the participant failed twice to reproduce a sequence of a certain length.

Tunnel task

Start-end vector response format. The experimental stimuli were adapted from previous studies (Gramann et al., 2005). Subjects were presented with tunnel passages ending up at eccentricities of 20 or 60 to the left and right, respectively, relative to the starting point. All tunnels consisted of four segments, with the turn taking place in the second segment. In addition, four-segment tunnels without turn were included ending up at 0 eccentricity. Tunnels for each eccentricity were repeated six times in a pseudo-randomized order, resulting in 30 trials altogether. Figure 2A illustrates the five possible end positions from a bird’s eye view.

Each trial started with an asterisk which stayed on the screen for 500 ms, followed by a static display of the tunnel entrance for another 500 ms. Then the tunnel movement started. Each segment took about three seconds to traverse, resulting in a presentation time of about 12 s for each tunnel. Having traversed the four segments, the tunnel movement ended with a display of the last frame for 500 ms. Subsequently, the tunnel display disappeared and the response arrow was presented. This display was made up of a three-dimensional arrow which was presented in the display centre aligned with the sagittal axis of the navigator, with the arrowhead pointing towards the subject within the

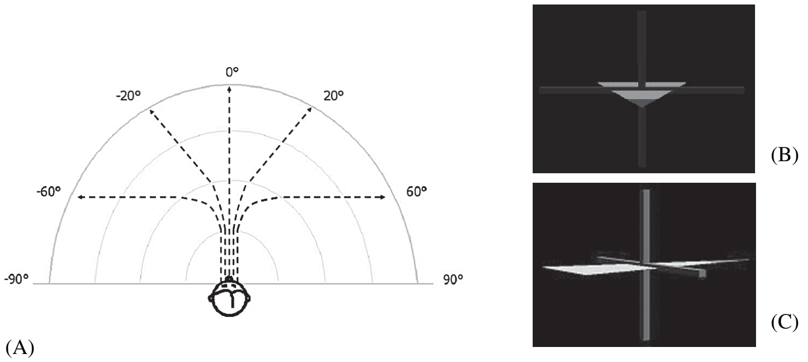

Figure 2. Depiction of the five different possible passages through the tunnel in the start-end vector task (A), followed by examples of the start-end vector answer format. (B) Depicts the arrow in the default setting; (C) displays the correct angular adjustment for a 60 turn to the right.

simulated space (i.e., the subject saw a lengthened view of the arrow's tail side, see Figure 2B). By pressing the left or right mouse button, the arrowhead was rotated and the subjects' task was to set the arrow so that it pointed into the direction of the tunnel's end point as seen from the starting point (see Figure 2C). When the subjectively correct angular setting was reached, the subject confirmed the setting by pressing the middle mouse button, and the next trial started after a short interval. Subjects were instructed to watch the tunnels carefully and, for their answer, to take into account the direction as well as the angle of turn. Importantly, this answer format differs from the one used in the Gramann et al. (2005) study in that the end point has to be indicated relative to the starting point rather than the starting point relative to the endpoint. As in the starting position the egocentric and allocentric axis are aligned, this answer format does not allow for a distinction between an allocentric and an egocentric strategy. However, this task served the purpose of determining in how far patients differed from controls in their ability to keep track of the direction of turn and to make fine-grained distinctions between different angles of turn.

Map drawing response format. The vector-response format provides information on the accuracy of the represented angular relation of the endpoint relative to the starting position, but not on the represented path layout of the outbound path. Therefore, an additional answer format was included where subjects were asked to draw a bird's eye-view map of the tunnel on a sheet of paper. In this part of the study, the subjects were shown 10 tunnels consisting of two segments and 10 tunnels consisting of four segments each, all with a 90 bend in the second segment, ending up at an eccentricity of 60 for the four segment tunnels and 20 for the two segment tunnels. Half the turns were bending towards the left and half towards the right. This resulted in four different conditions, each of which was presented five times, yielding a total of 20 trials presented in a pseudo-randomized order. In this part of the study shorter tunnels were introduced to directly contrast map drawing performance for tunnels including straight segments after the turn vs. tunnels having no additional translation after heading changes. This allows for a direct comparison of the represented spatial information based on allocentric and egocentric reference frames since additional straight segments after the turn differ with respect to the cognitive heading based on an allocentric or an egocentric reference frame. In order to keep the number of conditions reasonable only one turn angle was realized. The parameters for the tunnel presentation were the same as described above for the start-end vector task. However, after the tunnel ended, a static display of a white cross appeared on the screen and the subjects were asked to make their drawing. When the subjects indicated that they had finished, the experimenter started the next trial. Subjects were told that tunnels may differ in length and were asked to include this information in their drawings.

The experiment was carried out in a single session for the control subjects and in two sessions for the patients. Instructions were given verbally before each individual task. All tasks (apart from the Corsi Block-Tapping Task) were presented on a 17″ computer screen (1024 × 768 pixel screen resolution; 70-Hz refresh rate). The Corsi Block-Tapping task was conducted placed on a tabletop between the subject and the experimenter.

RESULTS

Neuropsychological tests

MR accuracy

This score refers to the relative number of correct answers regarding the orientation of the target letter, which were arc-sine transformed. A 3 × 2 × 6 ANOVA was conducted with 'lesion site' (none/frontal/parietal) as a between-subject factor and 'letter orientation' (canonical/reversed) and 'rotation angle' as within-subject factors. For the factor 'rotation angle', the 12 possible angles were collapsed into six scores, with corresponding values towards the left or the right side being incorporated into a single score (e.g., 90 and 240 were collapsed into a score describing a 90 rotation from the upright position). The 0 condition was excluded from analysis.

There were significant main effects of rotation angle, ($F(2, 75) = 8.06$, $p = .002$) and of lesion site ($F(2, 15) = 4.51$, $p = .029$). A *post-hoc* Tukey–HSD test was significant for the difference between control and parietal subjects ($p = .023$), with the parietal group exhibiting a higher number of errors.

MR reaction times

Reaction times for the correct trials were analyzed according to group and condition as well as rotation angle. A 3 × 2 × 6 ANOVA showed a main effect of rotation angle ($F(2.32, 75) = 6.94$, $p = .002$), with larger rotation angles resulting in longer response times. There was a tendency for a main effect of lesion site ($F(2, 15) = 3.02$, $p = .079$). In addition, there was a significant interaction between angle and lesion site ($F(4, 75) = 3.45$, $p = .019$). Figure 3 illustrates the mean values per group and rotation angle. Both patients showed stronger effects of angle than the controls. When the controls were removed from the analysis there was an effect of rotation angle ($F(3.503, 30) = 3.40$, $p = .031$) but no effect of lesion group ($F(1, 6) = .090$, $p = .774$) and no interaction ($F(3.503, 30) = 1.381$, $p = .276$).

Corsi Block-Tapping Task

A 'total score' was computed for each subject, which consisted of the Block Span (i.e., the number of blocks in the highest correctly repeated sequence) multiplied by the number of correctly repeated sequences until the testing procedure was stopped. This score takes into account the performance on the two trials of equal sequence length, thus providing a more reliable measure of visuo-spatial working memory performance than the Block Span alone (Kessels et al., 2000). Mean scores were at 42.7 (SD = 8.1) for the control group, 42.0 (SD = 13.37) for the frontal group and 31.5 (SD = 23.57) for the parietal patient group.

A univariate ANOVA on the total score with 'lesion site' as between-subject factor showed no significant effects.

Tunnel task

Start-end vector task

Side errors. This measure refers to the relative number of trials on which the side of the end position within the virtual environment (left vs. right) was indicated incorrectly. Again, an arc-sine transformation was applied to normalize the distribution of the data, which were then analyzed separately for the ipsilesional and the contralesional side; control subjects were pseudo-randomly assigned to the left- and the right-hemisphere group, respectively, according to the ratio between RH and LH lesions in the patient groups. Trials on which the arrow had been moved by less than 50 to either side from the default position were interpreted as slips and excluded from analysis. This value corresponds to two SD below the mean arrow setting across subjects. Figure 4 depicts the mean percentage of side errors as a function of 'lesion site' and 'direction of turn' (ipsilesional/contralesional). A 3 × 2 ANCOVA was performed with 'lesion site' as between-subject factor and 'direction of turn' as within-subject factor. An overall accuracy score from the mental rotation test and the Corsi Block Tapping Task score were entered as covariates. Neither of the covariates influenced performance significantly, therefore ANOVA results are reported. The results showed a main effect of lesion site ($F(2, 15) = 11.04$, $p = .001$). There was also a main effect of 'direction of turn' ($F(1, 15) = 6.17$, $p = .025$), with more errors made on the ipsi- than on the contralesional side. A *post-hoc* Tukey–HSD test revealed a significant difference between the control group and the parietal patients ($p = .005$), and between the control group and the frontal patients ($p = .005$).

Angular fit. One criterion for a correct spatial representation is that the subject should be sensitive to varying eccentricities of the end position within

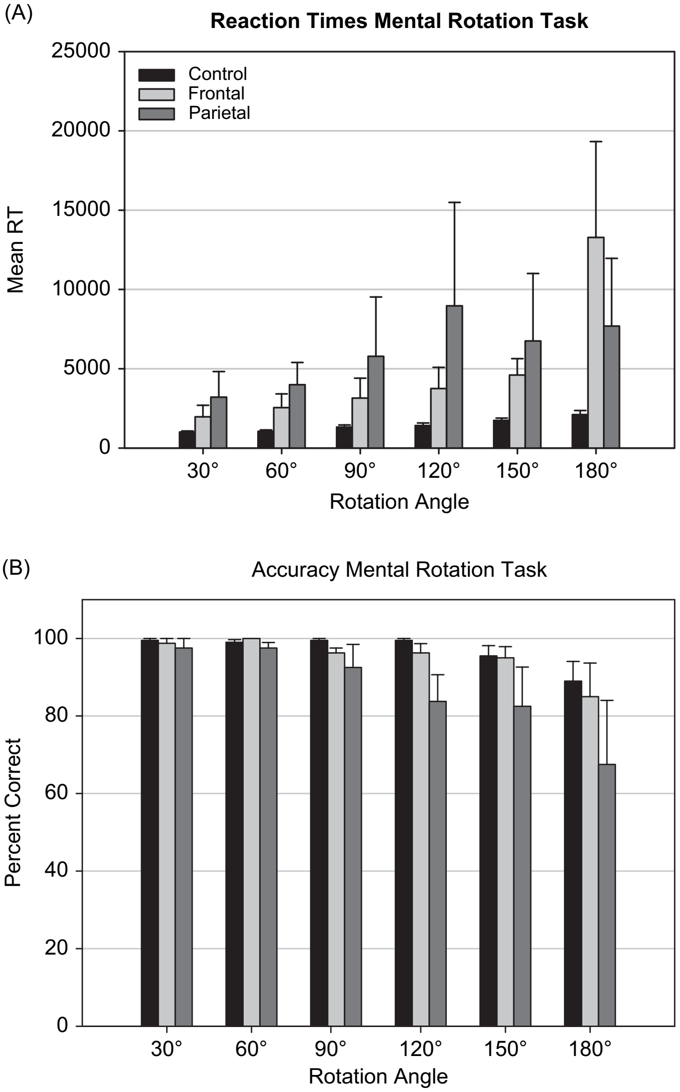

Figure 3. Mean reaction times (A) and accuracy (B) for the mental rotation task; error bars indicate ±1 *SE*.

the virtual environment. If subjects vary their angular settings according to the eccentricity of end position, the results should follow a linear function from high negative values for the most eccentric positions to the left to high positive values for a the most eccentric positions to the right. This would be reflected in a high correlation between the real angular value of the end position and the response. A linear regression was calculated on the angular settings as a function of end position (with trials on which side errors or slips had occurred being excluded from the analysis).

In a univariate ANCOVA with the slope of this linear function as the dependent variable, lesion site as the between-subject factor and MR accuracy score and Corsi total score as covariates, there was no significant effect of lesion site. However, the influence of the MR accuracy score was significant ($F(1, 13) = 6.44$, $p = .025$). For the explained variance (R^2), a Kruskal–Wallis test was calculated because patients showed less explained variance than controls leading to unequal distributions of variance. This revealed a main effect of lesion site ($\chi^2(2) = 8.33$, $p = .016$). A *post-hoc* Mann–Whitney *U*-test showed that a linear function explained less of the variability of the angular settings for parietal patients than for the control group ($U = 2.0$, $p = .008$).

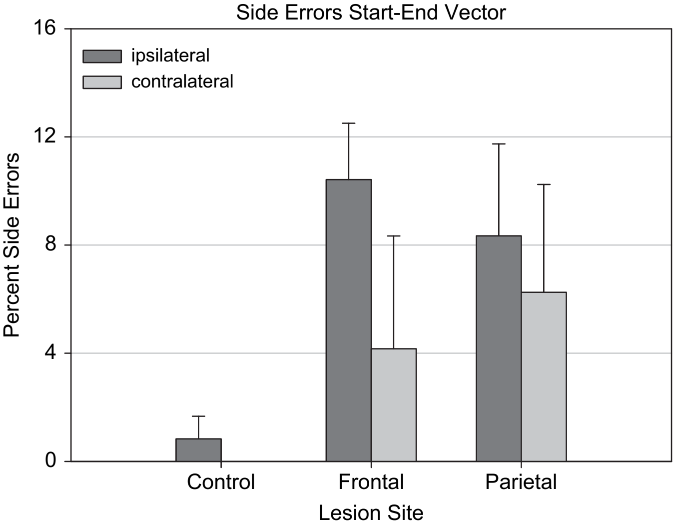

Figure 4. The mean percentage of side errors for control, frontal and parietal group, separately for ipsilesional and contralesional turns. Error bars indicate ±1 *SE*. Note that the data of the control subjects was randomly divided into a right- and a left-hemisphere group; however, no side errors were made by control subjects on their 'contralesional' side-hence, the bar is missing.

Relative error. This measure describes the signed deviation of the angular setting in degrees from the correct value. A negative value describes an underestimation, a positive value an overestimation. A $3 \times 2 \times 2$ ANCOVA was conducted with 'lesion site' as a between-subject factor and 'eccentricity of end position' (60 /20) and 'direction of turn' (ipsi-/contralesional) as within-subject factors. The overall accuracy score from the mental rotation test and the Corsi Block Tapping Task score were used as covariates. Trials on which side errors or slips had occurred were excluded from the analysis. The mean values per subject group and condition are depicted in Figure 5.

The MR accuracy score had a significant influence on the number of side errors made ($F(1, 13) = 6.44$, $p = .025$). While the main effect of lesion site was not significant, there was a reliable interaction between lesion site and direction of turn ($F(2, 13) = 5.90$, $p = .015$). While healthy controls demonstrated a tendency towards the middle with underestimations of high eccentric end positions and overestimations of

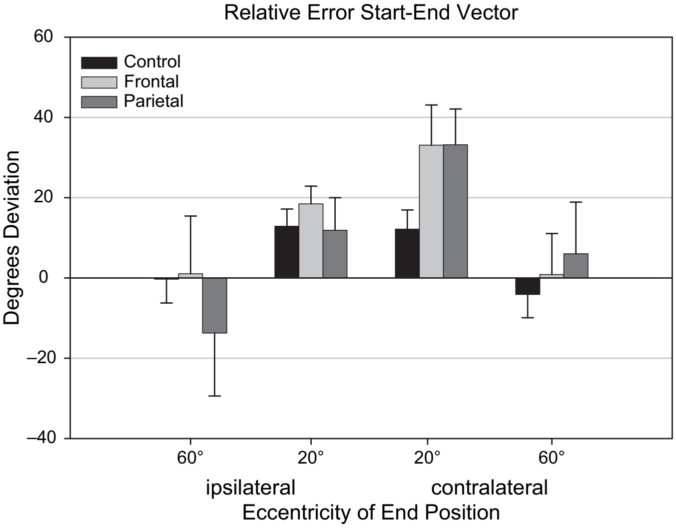

Figure 5. The mean relative errors, shown separately for each eccentricity, side and subject group. Error bars depict ±1 *SE*.

end positions of lower eccentricity, this was not observed for the two patient groups. Frontal patients revealed a general overestimation of all end positions which was most pronounced for 20 and fairly accurate for the most eccentric end positions of 60 . In contrast, parietal patients revealed an overestimation for less eccentric end positions and for 60 for contralateral turns, but a strong underestimation for 60 turns to the ipsilesional side.

Tunnel drawing task

Complete data sets of tunnel drawings were obtained from five control subjects only. All other control subjects only gave samples of two four-segment tunnels bending to the left and right, respectively. Figure 6 shows overlay plots of tunnel drawings for all subjects by direction of turn and tunnel length. Two independent raters scored the tunnel drawings according to two criteria (disagreement between the raters occurred for less than 1% of trials; such trials were excluded from further analysis). Pictures were as a first step rated with respect to the percentage of side errors per condition, i.e., pictures in which the side of the endpoint in relation to the starting point was indicated incorrectly. A ceiling effect on side errors in the control group

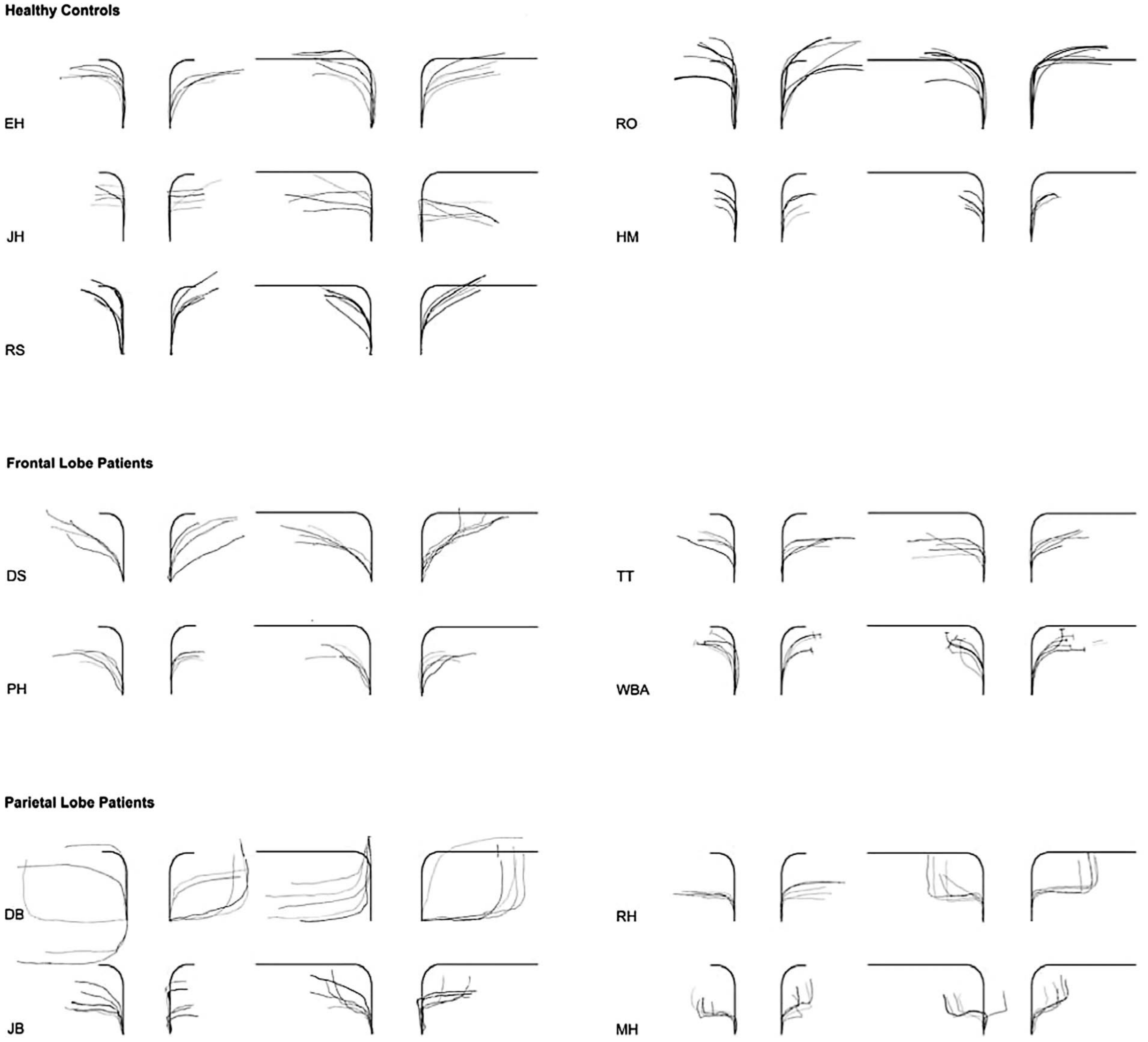

Figure 6. Overlay plots of tunnel drawings for right bends separately for long and short tunnels and per subject. Red line shows ideal drawing. To view this figure in colour, please visit the online version of this issue.

put the equal variance assumption between groups into question; hence Kruskal–Wallis tests for three independent samples were calculated to investigate possible between-group differences separately for tunnels bending to the ipsilesional and the contralesional side. This did not yield any significant results.

Drawings were also rated for the tunnel shape, and scores calculated per length and direction of turn. A rating of one point was awarded for each tunnel drawing which indicated a straight first segment, followed by one clear change of direction. Tunnels drawn in circular shapes right from the beginning did not receive a score, nor did drawings including more than one curve. Figure 7 indicates mean scores of each group and condition. However, both tunnels with and without straight segments following the curve were counted as correct, since the raters could not always tell the exact endpoint of the curve. In the control group, none of the tunnels were drawn incorrectly according to either of these criteria, whether the drawings were made by subjects with complete or with incomplete data sets. This indicates that the task was easy for healthy subjects, and that the five complete sets were representative for the sample as a whole. In the following, we therefore only included the participants of the control group for whom we had complete datasets available.

Because of the ceiling effect in the control group a Kruskal–Wallis test for three independent samples was calculated. There was a significant effect of lesion in the long tunnels presented ipsilaterally ($\chi^2(2) = 6.34$, $p = .042$), and a tendency for such an effect on the contralesional side ($\chi^2(2)=5.39$, $p = .069$). No significant effects were found for the short tunnels.

Post-hoc Mann–Whitney *U*-tests revealed significant differences between the control and the parietal patient group for ipsilateral long tunnels ($U = 2.50$, $p = .029$) and for contralateral long tunnels ($U = 2.50$, $p = .028$). There were no significant differences between the control group and the frontal lobe patient group, or between the two patient groups.

As an additional measure of tunnel drawing accuracy, we calculated the ratio between width and height of the picture drawn. We computed one sample *t*-tests in which the scores of each subject group were compared against the real ratio of the tunnel, which was 1.6 for the long tunnels and 0.5 for the short tunnels. While the distribution of the control group did not differ significantly from ideal score in the long tunnels ($T(4) = -1.41$, $p = .23$), there was a tendency for such a difference in the frontal patient group ($T(3) = -2.66$, $p = .076$), and a significant difference in the parietal patient group ($T(3) = -3.99$, $p = .028$).

For the short tunnels, we found a tendency for a difference in the control group ($T(4) = 2.24$, $p = .089$), and significant differences for the frontal patients ($T(3) = 3.61$, $p = .037$) and for the parietal patients ($T(3) = 3.20$, $p = .049$).

A 3 × 2 × 2 ANCOVA with tunnel length and direction of turn as within-subject factors and lesion site as a between-subject factor as well as MR accuracy and Corsi total score as covariates

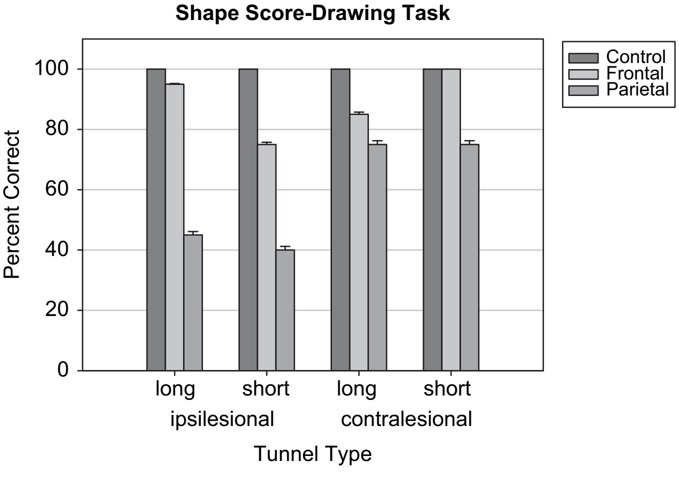

Figure 7. Tunnel drawing task: mean scores for correctness of shape per lesion group. Error bars depict ±1 *SE*.

was also calculated to test for significant between-group effects. However, this yielded no significant results.

DISCUSSION

The aim of the present study was to investigate whether parietal and frontal lobe lesions selectively affect performance in a virtual navigation task which relies entirely on information presented from a first person perspective. A number of measures were taken to evaluate performance in two answer formats; these measures were also analyzed with respect to covariation with two standard tasks of cognitive performance, a mental rotation task and the Corsi Block-Tapping Task. While some impairment could be observed in both patient subgroups, our data clearly suggest a distinct contribution of the parietal lobe to space processing from an egocentric viewpoint.

In the start-end vector response format, when the number of side errors was compared, both parietal lobe and frontal lobe patients performed worse than the control group. As we did not find significant group differences in spatial working memory performance, it seems unlikely that memory problems can account for this finding. Interestingly, we did find a hemispheric effect on error rates, suggesting that lateralized attentional deficits may have impaired task performance. Counterintuitively, this increase of errors affected the ipsilesional rather than the contralesional side. A plausible explanation can be derived from the stimulus material: As can be seen in Figure 1, the width and number of sub-segments at each tunnel and the edges at the bottom and top of the wall bend provide spatial cues. However, during the turn, the inner side of the bend narrows so that spatial information can more easily be retrieved from the outer tunnel wall located on the opposite side of the turn. Thus, a turn to the right (ispilesional for right-hemispheric patients) will provide relevant information on rotational changes in the left hemifield relative to the navigator's sagittal axis. Therefore contralateral attentional deficits should lead to more side errors for ipsilesional turns.

Additionally, the use of the answer format might be difficult for the patients in that a coordination of mouse presses with movement of the arrow in both visual hemifields on the screen is required. In the present group of parietal patients there was no evidence of spatial neglect, though one individual (RH) showed some evidence of object-based neglect in reading tasks (Appendix 1); hence it is difficult to ascribe these results to spatial neglect. Nevertheless, previous work with these patients has indicated spatial biases in visual selection when stimuli are presented relatively briefly (e.g., see Riddoch, Humphreys, Edwards, Baker, & Willson, 2003, for data on JB and RH). These spatial biases, when there is competing information on the ipsi- and contralesional sides, could have been a contributory factor in the errors that arose as a function of the direction of the tunnel's bend.

While it could be argued that making a right/left distinction only involves very basic navigation skills, and could in theory be solved just by verbal memorization of directional information, the fine adjustment of the arrow requires building up a more detailed representation of virtual space. Our results indicate that the parietal-lobe patient group, but not the frontal-lobe patient group, was impaired here relative to healthy subjects of the same age. Only in the parietal-patient group, the angular settings did not exhibit a linear increase as an effect of eccentricity, as would have been expected from previous results in a healthy sample (Gramann et al., 2005). Accuracy in the fine adjustments of the arrow and slope of linear fit covaried with the mental rotation score. Also, in line with imaging studies reporting increased activation of the posterior and inferior parietal lobes during mental rotation (Alivisatos & Petrides, 1996; de Lange, Hagoort, & Toni, 2005; Harris et al., 2000), we found the parietal patient group to be most severely impaired in the mental rotation task (at least in terms of errors) as well as the angular fit of their arrow settings.

Our findings therefore support the notion that object-based transformations and transformations of egocentric perspective draw on the same cognitive resources which have generally been associated with parietal-lobe function (Bremmer et al., 2001; Harris et al., 2000). Again, no effect of visuo-spatial working memory capacity on the fine adjustment of arrow settings was found, indicating that task performance cannot be explained by a selective impairment to memorize directional information.

To get a clearer impression of the type of mistakes leading to misjudgments of rotation angles, we included the map drawing answer format. Subjects reported to find map drawing more intuitive than the 3D arrow response format and made their directional choices more quickly. The low side-error scores in this task might be a result of this answer format being easier to handle for patients, and support our assumption that the observed difficulties do not relate to impairment in interpreting visual flow as such. The major difficulties of parietal-lobe patients in the map drawing response format concerned the shape of the tunnel drawing, and in particular the orientation of the straight segments after the tunnel had bent. All of the parietal lobe patients tested were clearly impaired here. Patient DB aligned the last tunnel segment in the drawing with his real present axis of view. Keeping the overall shape of the tunnel correct, this meant that he had to adjust the direction of the initial tunnel segment. Importantly, all of the remaining parietal lobe patients resorted to an identical strategy: they often included an additional turn into their drawing occurring directly after the real bend, resulting in the last straight segments of the drawing to again be aligned with the first straight segment. Interestingly, this type of error was more frequent for long than for short tunnels, supporting the hypothesis that the presence of a translation after rotational changes in particular led to confusion in parietal patients. Out of 10 long tunnels per subject, this kind of mistake occurred in 10 of MH's drawings, nine of RH's drawings, and four of JB's drawings. Only MH made the same error in all 10 of his short tunnels; the other patients drew one-bend tunnels when there was no straight segment following the turn. This type of mistake never occurred in healthy subjects, and was rare in frontal patients. Of the frontal group, two subjects did not show any general shape errors. The remaining two also showed a pattern of aligning the first and last segments, but it occurred less frequently and in both long and short tunnels. DS drew two bends in two long and three short tunnels, and JQ in four long tunnels.

One possible explanation for this finding is that the additional drawing of a turn might not be an error due to the characteristics of the computed spatial representation. Rather the patients might start to draw, then realize that the start-endpoint relationship does not reflect the impression during the tunnel movement and try to correct the image by adding an additional line. The fact that for the long tunnels, the height–width ratio was lower in the patient groups in comparison to the ideal value, but not for the control subjects, makes this interpretation unlikely. Also the fact that for short tunnels, all groups deviated from the ideal ratio indicates that getting this ratio right is a difficult task across subject groups and is unlikely to affect drawing to a major extent unless explicitly required. However, between-group differences were not significant here due to the high amount of within-group variability.

A more likely explanation for the observed pattern might be derived from the fact that a spatial representation of the traversed tunnel space requires that subjects interpret information about translational and rotational changes as they move within the tunnel. In the present task, visual information is available only from an egocentric perspective. This poses the difficulty that all straight segments lead into the depth of the screen in front of which the observer is seated, i.e., straight segments before and after the bend provide identical perceptual input, that is, the perceived heading is the same. Only the second segment, in which the visual flow indicates the turn, provides perceptual information about directional changes. Subjects have to continue tracking these visual orientation changes during the straight segments following the turn to determine their position in virtual space and to successfully solve the task. This has to be done by computing and maintaining a cognitive heading in the absence of concordant visual information.

Impairment of mental rotation skills likely contributes to this deficit. The idea that lesions of the posterior parietal lobe result in an inability to keep track of one's heading in space is in line with Aguirre and D'Esposito's (1999) account of topographical disorders, suggesting that posterior parietal lesions relate to a variant of topographical disorientation rooted in the egocentric domain. It is also in line with studies in non-human primates suggesting that the parietal cortex plays an important role in the integration of body-referenced and world-referenced encoding of space (Bremmer et al., 2001; Snyder, Grieve, Brotchie, & Andersen, 1998), thus serving as an integration zone for different types of spatial representation.

As only the end position is indicated in the start-end vector response format, no information is conveyed on the subjects' cognitive heading at different stages of traversing the tunnel. Whether difficulties in the updating of heading may have contributed to the observed inability of parietal patients to make fine-grained arrow settings therefore has to remain uncertain at this stage. However, as tunnel navigation in both response formats places equal demands at the encoding stage, this seems highly likely. Future studies should use a different response format such as the analogous movement of a joystick to receive information on the perceived direction of motion of the subject and ruling out any possible memory artefacts.

It is interesting to note that, despite the problems in solving the tunnel task, the parietal patients did not report severe wayfinding impairments in their everyday life. Given that subjects have been shown to be able to build up a variety of spatial representations from identical input (Gramann et al., 2005; Ruddle, Payne, & Jones, 1997; Wolbers, Weiller, & Büchel, 2004), it is likely that, in normal environments with a greater variety of spatial cues available, the patients resort to alternative strategies which are better suited to their individual remaining navigation skills. Therefore, the issue of the preferred spatial cues deserves further attention: determining the spatial strategies patients with focal lesions resort to might provide additional information on preserved orientation abilities and possibilities to compensate for selective problems of spatial representation.

Taken together, the results of the present study support our hypothesis of a necessary role of the parietal lobe in processing information presented from an egocentric perspective. Parietal patients proved to be less able to make fine-grained distinctions between different angles of turn than frontal patients and age-matched control subjects. Analyses of the types of error made in the drawings indicated that the main problem may consist in connecting present and previous positions in the environment to form a coherent representation, a task which has to be achieved by integrating information about one's own heading throughout the tunnel passage. These findings shed light on the problems in spatial navigation which may occur as a result of injury to the parietal lobes. Varying and extending the types of information provided in spatial tasks will be a necessary step towards a more detailed understanding of how the brain integrates different aspects of spatial information into a whole.

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APPENDIX 1

Lesion information for individual patients

Patient	*Sex/Age/ Handedness*	*Lesion site*	*Clinical deficit*	*Aetiology*	*Years post lesion*	*NART IQ equivalent*	*Brixton test (raw score)*
Frontal							
DS	M/70/R	Left inferior, middle and superior frontal gyri	Right hemiplegia, aphasia	Stroke	14	105	20
WBA	M/58/R	Right inferior and middle frontal gyri, right superior temporal gyrus	Aphasia	Stroke	3	115	26
PH	M/33/R	Left medial and superior temporal, left inferior and middle frontal gyri	Right hemiplegia, aphasia	Stroke	5	80	12
TT	M/68/R	Right middle frontal gyrus	Impaired working memory and dual task performance	Stroke	5	112	21
Parietal							
DB	M/68/R	Left parietal inferior (angular gyrus), superior, and middle temporal gyri	Aphasia	Stroke	6	95	20
JB	F/58/R	Right inferior parietal/ temporo-parietal junction	Right hemiplegia	Stroke	2	105	20
MH	M/50/R	Left angular and supramarginal gyri, lentiform nucleus	Right extinction, optic ataxia	Anoxia	10	104	34
RH	M/70/L	Left inferior parietal (angular and supramarginal gyrus) and superior temporal gyrus	Right neglect on reading single words- no evidence of spatial neglect on standard tests (e.g., star cancellation); aphasia	Stroke	8	85	32

#The NART (Nelson & Willison, 1991) is a reading test that provides an IQ-related score. In patients PH and RH, performance on this test was hampered by the presence of a significant reading deficit (respectively deep and neglect dyslexia), which lowered their scores. PH was a law graduate and RH a former successfully self-employed plumber.

*The Brixton test of executive function (Burgess & Shallice, 1997) provides a measure of non-verbal executive function. A raw score above 26 indicates a clinical abnormality. The two patient groups did not differ in terms of either their estimated IQ ($t < 1.0$) or their performance on the Brixton test (t(80 = 1.61, $p = .15$).

APPENDIX 2

Lesion reconstructions from MRI scans for the patients. Lesions have been drawn onto standard slides from Gado, Hanaway, and Frank (1979). The whole brain (bottom) shows the 10 slices used. Only slices 3–8 are depicted here. Left of the slice represents the left hemisphere