Spatial orientation and the representation of space with parietal lobe lesions

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SUMMARY

Damage to the human parietal cortex leads to disturbances of spatial perception and of motor behaviour. Within the parietal lobe, lesions of the superior and of the inferior lobule induce quite different, characteristic deficits. Patients with inferior (predominantly right) parietal lobe lesions fail to explore the contralesional part of space by eye or limb movements (spatial neglect). In contrast, superior parietal lobe lesions lead to specific impairments of goal-directed movements (optic ataxia). The observations reported in this paper support the view of dissociated functions represented in the inferior and the superior lobule of the human parietal cortex. They suggest that a spatial reference frame for exploratory behaviour is disturbed in patients with neglect. Data from these patients' visual search argue that their failure to explore the contralesional side is due to a disturbed input transformation leading to a deviation of egocentric space representation to the ipsilesional side. Data further show that this deviation follows a rotation around the earth-vertical body axis to the ipsilesional side rather than a translation towards that side. The results are in clear contrast to explanations that assume a lateral gradient ranging from a minimum of exploration in the extreme contralesional to a maximum in the extreme ipsilesional hemispace. Moreover, the failure to orient towards and to explore the contralesional part of space appears to be distinct from those deficits observed once an object of interest has been located and releases reaching. Although patients with neglect exhibit a severe bias of exploratory movements, their hand trajectories to targets in peripersonal space may follow a straight path. This result suggests that (i) exploratory and (ii) goal-directed behaviour in space do not share the same neural control mechanisms. Neural representation of space in the inferior parietal lobule seems to serve as a matrix for spatial exploration and for orienting in space but not for visuomotor processes involved in reaching for objects. Disturbances of such processes rather appear to be prominent in patients with more superior parietal lobe lesions and optic ataxia.

1. INTRODUCTION

Parietal lobe lesions in humans lead to disturbances of spatial perception and of motor behaviour in space. Owing to the usually large extent of lesions affecting the parietal lobe, most clinical cases show a combination of these disturbances. Dissociations arguing for distinct clinical entities combined with small cortical lesions that allow a precise localization of different functions within the parietal lobe are rather rare.

The most established anatomoclinical dissociation within the parietal lobe concerns the disturbances after lesions of the superior and of the inferior lobule. Both lesion locations induce characteristic disturbances of visuospatial behaviour. Patients with inferior (predominantly right) parietal lobe lesions demonstrate a deficient response to stimuli located contralaterally to the lesion and fail to explore the contralesional part of space by eye or limb movements; this disorder is termed *spatial neglect*. Clinically, it becomes apparent by, for example, omission of objects if located contralesionally, a tendency to spontaneously turn the gaze and the body towards the ipsilesional side, or a deviation of drawings or handwriting towards the ipsilesional side on a page. In contrast, superior parietal lobe lesions lead to specific impairments of visually guided pointing and reaching for objects (Perenin 1997), termed *optic ataxia*. Typically, these patients show misreaching with either hand for objects located in the visual half-field contralateral to the lesion.

Different mechanisms of processing spatial information thus have been assumed to be represented in the human inferior and superior parietal lobule. Perenin (1997) argued that the superior part of the parietal cortex is mainly involved in 'direct coding of space for action by means of several effector-specific representations' whereas the inferior part is responsible for 'more enduring and conscious representations underlying spatial cognition and awareness'. Milner & Goodale (1995) have also argued for distinct functions of the superior and inferior parts of the parietal lobe. They suggested that the superior parietal lobe is part of the dorsal stream of visual processing, and assumed that input transformations carried out via this pathway mediated 'the control of goal-directed actions'. Lesions restricted to the superior part in humans therefore lead to disturbances of visuomotor control, such as optic ataxia. Spatial neglect was attributed to lesions of the inferior part of the parietal lobe. Milner & Goodale (1995) hypothesized that, unlike superior parietal lobe function, mechanisms evolved in the human inferior parietal or parietotemporal region deal with abstract spatial processing based on input from the ventral stream. Input transformations via the ventral stream of visual processing were supposed to permit 'the formation of perceptual and cognitive representations which embody the enduring characteristics of objects and their significance'.

The basic pathophysiological principles leading to optic ataxia and to spatial neglect, however, are still an issue of lively debate (see Halligan & Marshall 1994; Milner & Goodale 1995; Perenin 1997). Different mechanisms and possible alterations of neural representations of space have been suggested to explain the behavioural consequences in patients with parietal lobe lesions. The present paper tries to contribute to an identification of the functions represented in the parietal lobe by analysing the defective mechanisms of processing spatial information in patients with spatial neglect, i.e. in patients that predominantly suffer from lesions of the inferior part of the parietal lobe (Vallar & Perani 1986).

2. 'DEVIATION OF EGOCENTRIC SPACE' OR 'LATERAL GRADIENT OF ATTENTION'?

One hypothesis on spatial neglect proposed an altered neural representation of body-centred space (Ventre *et al*. 1984; Karnath 1994*a*, 1997). This concept corresponds with recent neurophysiological findings supporting the assumption that the brain uses neural representations of space organized in non-retinal, body- and/or world-centred coordinates. The parietal cortex seems to provide such a representation of space by transforming the multisensory afferent input into a neural representation organized in non-retinal coordinates (Andersen 1995; Battaglini *et al*. 1997; Thier & Andersen 1997). The compensatory effects on spatial neglect that had been observed with vestibular (Rubens 1985), optokinetic (Pizzamiglio *et al*. 1990), and neck-proprioceptive stimulation (Karnath *et al.* 1993) are in accordance with the view that spatial neglect might be due to an altered representation of body-centred space. The findings demonstrate that the brain uses the input from these afferent channels to elaborate a unitary representation of egocentric space. Integration of the contributing input channels is used for spatial orientation, space exploration, and determination of the body's position in space. In neglect patients, the coordinate transformation seems to work with a systematic error that results in a deviation of the spatial reference frame to the ipsilesional side (Karnath 1994*a*, 1997).

Kinsbourne (1977, 1987) proposed an alternative theory. He assumed an attentional bias with excessive orienting towards the ipsilesional side in patients with spatial neglect, owing to an imbalance in lateral orienting tendencies. Kinsbourne argued that attention is directed along the vector resultant from the interaction of paired opponent processors that are controlled by the right and left hemispheres, respectively, each of which directs attention towards the opposite end of a visual display. An activation imbalance in neglect patients biases the vector of attentional orienting and therefore elicits ipsilesional shifts of attention and gaze. A crucial prediction of this model is that orienting is not intact within either hemispace in neglect. Rather, a lateral gradient of attention sweeps across both hemispaces, such that attention is always biased in the ipsilesional direction. The gradient is probabilistic and characterizes the probability of, for example, detecting a target. Following the gradient, the probability of detecting a target is very low on the extreme contralesional side and increases along the horizontal axis towards the ipsilesional side. According to Kinsbourne (1993), the lateral gradient applies to visual exploration and covert shifting of attention as well as to overt gaze deviation.

Within the context of their 'premotor theory', Rizzolatti *et al.* (1985; Rizzolatti & Berti 1990) also argued for a gradient of severity across the visual field in patients with neglect. They suggested that neglect results from a lesion of higher-order maps or representations of space that are responsible for the organization of motor acts in particular space sectors. The authors assumed that in patients with neglect the whole visual field is affected but with a gradient of severity ranging from a maximum in the extreme contralesional hemifield to a minimum in the extreme ipsilesional field (Rizzolatti *et al*. 1985). In addition, they assumed that lesions of those areas leading to neglect liberate competitive actions from the inhibition normally exerted by these areas (Rizzolatti & Berti 1990). The resulting abnormal activation produces additional imbalance in favour of ipsilesional space sectors.

Although based on different concepts, both Kinsbourne's and Rizzolatti's explanations assume that the left as well as the right hemispace are affected in spatial neglect, following a gradient that ranges from a maximum in the extreme contralesional hemifield to a minimum in the extreme ipsilesional field. The pattern of space exploration that follows such a *gradient* is different from the pattern that should result from a *deviated* representation of egocentric space. Studying the patients' exploratory behaviour in space thus should help to discriminate between the different hypotheses. According to the gradient model, a continuous increase of exploration along the horizontal axis is expected with a minimum on the extreme contralesional side and a maximum on the extreme ipsilesional side (figure 1*a*). In contrast, the deviation model proposes a displacement of the whole field of exploration toward the ipsilesional side. As in healthy subjects, no lateral gradient should underlie exploration of space (figure 1*b*).

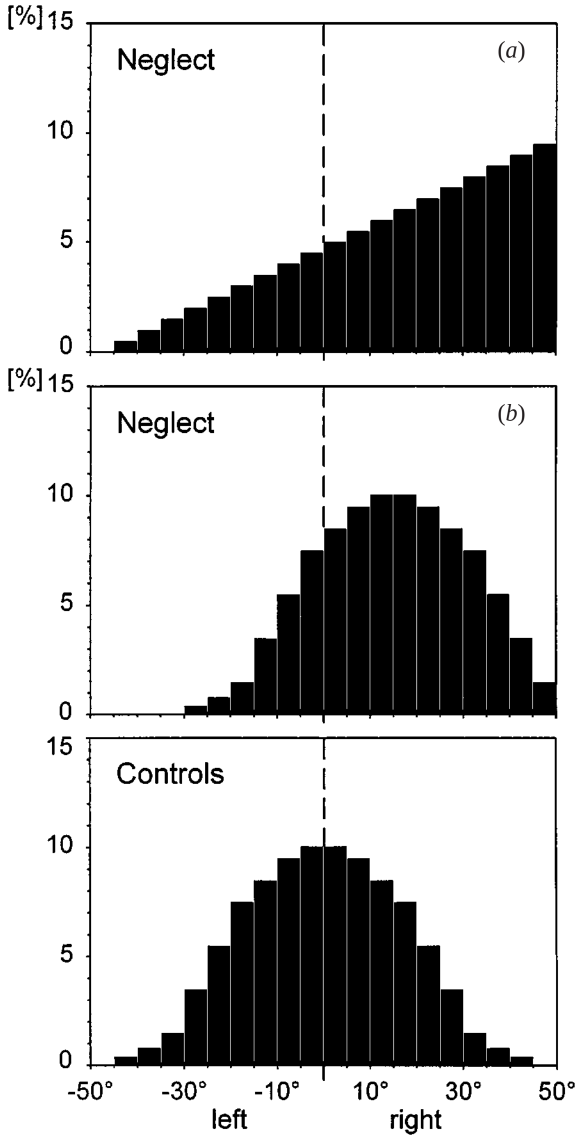

Figure 1. Expected distribution of space exploration (per cent) along the horizontal axis following two different hypotheses on spatial neglect. According to the *gradient model* (*a*), a continuous increase of exploration along the horizontal axis is expected with a minimum on the extreme contralesional side and a maximum on the extreme ipsilesional side. In contrast, the *deviation model* (*b*) proposes a displacement of the whole field of exploration toward the ipsilesional side. As in controls, no lateral gradient should underlie the patients' exploration of space.

One way to study space exploration in its natural course is by the observation of subjects' spontaneous eye movements. When humans explore space, for example in search of an object that is expected somewhere in the environment, they usually scan the scene by shifting the gaze to various locations in both hemispaces. In contrast, eye-movement recordings in right brain-damaged patients with neglect show that these patients differ from controls by predominantly fixating on the right side of presented stimuli during visual searching (Chédru *et al*. 1973; Johnston & Diller 1986), looking at different stimuli (Ishiai *et al*. 1987; Rizzo & Hurtig 1992; Jahnke *et al*. 1995; Walker *et al*. 1996), text reading (Karnath & Huber 1992) or scanning while verbally describing simple drawings (Karnath 1994*b*).

All these studies presented visual stimuli while recording exploratory eye movements. The patients' location of gaze was thus evoked by the visual characteristics of the stimuli. The spatial arrangement and individual significance of stimuli influenced patients' overt orienting of attention, the duration of fixation at different spatial locations, the amplitudes of saccades when shifting gaze from one aspect of the scene or stimulus to another, etc. In other words, subjects directed their gaze to locations that, in part, directly resulted from the experimental setup.

Such *external* ('stimulus-driven') influences on the subject's exploratory behaviour might be disturbing or even misleading when the pattern of ocular exploration should serve to identify the *internal* representation of egocentric space in these subjects. Therefore, spontaneous visual search should be investigated under a condition in which no visual stimulus can attract the subject's attention and thus influence the spatial distribution of exploration from outside. A technique that serves for this purpose is the observation of exploratory eye movements while the subject is searching for a non-existent target in complete darkness. This can be achieved by transiently presenting a spot of light in a darkened room. After extinguishing the spot, subjects are asked to search for the 'new location' of the spot, which is stated to be located 'somewhere' in the whole room. In fact, the spot is not presented and the subjects thus search in complete darkness with their eye movements being recorded at the same time. It can be assumed that the part of outer space subjects spontaneously explore under this condition is a direct function of the subject's representation of egocentric space. The subject tries to find the (non-existent) target in the 'whole room', i.e. within that part of space that is neurally represented and, of course, is reachable by moving the eyes.

With this technique, Hornak (1992) recorded eye movements in neglect patients between $+35^\circ$ and -35° of azimuth. This area of registration, however, turned out to be too narrow to plot the whole distribution of visual search in patients with neglect from the far left to the far right side. Most of the right part was not recorded and the study did not reveal how the distribution continues further towards the right. The latter, however, is critical to the determination of whether the patients' exploratory eye movements show a deviated but symmetrical distribution or whether they follow a lateral gradient across both hemispaces. According to the gradient model (figure 1*a*), one would expect a further increase of exploration, whereas the deviation model (figure 1*b*) predicts a decrease further towards the right.

The same problem characterizes a recent study by Behrmann *et al*. (1997). In light, these authors recorded eye movements during visual search in an array of randomly presented letters that had a horizontal extent of only $\pm 25^\circ$. Their study also could not determine the distribution of eye movements beyond these narrow boundaries, in particular beyond +25° further towards the right. Nevertheless, the studies by both Hornak and Behrmann *et al.* found a distribution with a single peak at about 15–18° on the right side with clearly decreasing frequencies toward the left of this maximum, and at least a tendency for a decrease (i.e. as far as the area of registration could follow eye movements) towards the right of this maximum also.

Our own studies (Karnath & Fetter 1995; Karnath *et al.* 1996) recorded exploratory eye movements up to ±50°, which permitted the observation and plotting of the whole distribution of visual search along the horizontal axis. Interestingly, the visual search of neglect patients showed no skewed distribution of ocular exploration with a maximum on the ipsilesional right side and a minimum on the contralesional left. Rather, exploratory eye movements showed a symmetrical, bell-shaped distribution with a maximum around 15° right of the body's midsagittal plane, in clear contrast to the prediction of the gradient model but in full accordance with the deviation model.

To strengthen this conclusion, we aimed to record exploratory eye movements in a larger group of neglect patients and over a longer period of time per subject than in the previous studies. In contrast to the short intervals of registration used in these studies, a dense scan pattern should be obtained in each subject to plot a more stable distribution of exploratory eye movements along the horizontal axis. A comparison was made of three groups of patients.

Five patients with neglect were examined (median age = 56 years). All five patients suffered from right-sided parietal-lobe lesions. Clinical and demographic variables of three of the five patients were as previously described (Karnath *et al.* 1996). The additional two patients with neglect suffered an infarct 8 and 12 days before the examination. Computed tomography (CT) scans showed a small hypodense area located in the right parietal cortex in one case and a hypodensity extending from the right temporal cortex to the parieto-occipital junction in the other case. Five patients with unilateral right brain damage but no neglect (RH-group) served as a control group (median age = 59 years). In three of the patients, the lesions were due to infarcts affecting the fronto-temporal region. One patient suffered a basal-ganglia haemorrhage and one a temporal lesion due to surgery of a grade IV glioma. The median time since lesion was 11 days. None of the patients with or without neglect had oculomotor palsies or visual-field defects. As an additional control group (NBD-group), five neurological patients without brain damage were examined (median age = 53 years).

Subjects were seated in a spherical cabin with a fixed head and body position and, as described above, were asked to search for the location of a (non-existent) spot, which was stated to be located 'somewhere' in the darkened room. Eye movements were recorded within the next 30–40 s. Subsequently, the laser spot was presented at a random location to feign the existence of a real target. The procedure was repeated three times so that the whole duration of registration was between 1.5 and 2 min per subject with a sampling rate of 100 Hz.

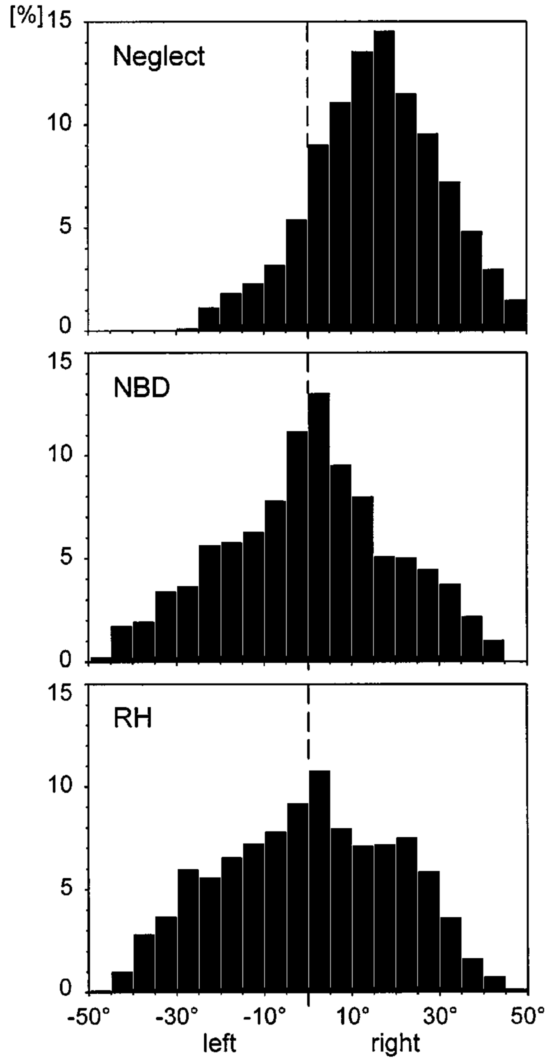

Figure 2. Distribution of ocular space exploration (per cent) along the horizontal axis in a group of five patients with neglect, in six non-brain-damaged neurological patients (NBD) and in a group of five patients with unilateral right hemispheric lesions but without neglect (RH); 0° = position of subjects' midsagittal body plane.

The spatial distribution of the subjects' exploratory eye movements is illustrated in figure 2. The average percentage of exploration time is presented in discrete five-degree sectors along the horizontal axis. The control groups showed a symmetrical, bell-shaped distribution of exploratory eye movements along the horizontal axis. They explored space with eye movements leading up to *ca.* 45° to the left and to the right of their sagittal midplane. The ocular exploration of patients with neglect was also symmetrical and bell-shaped but—compared with both control groups—deviated towards the right. The maximum of exploration lay between +10° and +20° right of the body's sagittal midplane in neglect patients, whereas it lay around 0° in both control groups.

The results permit the conclusion that neglect patients' exploratory eye movements during visual search in the dark show a bell-shaped distribution with a clear maximum around 15° right of the objective position of the body's midsagittal plane. Ocular exploration decreases symmetrically toward the left *as well as* towards the right side of this maximum. This finding clearly argues against a lateral gradient underlying the bias of space exploration in patients with neglect. The patients did not orient their gaze toward the extreme right and spent most of the time searching at that location in space. The maximum of exploration rather lay 'only' 15° right of the peak obtained in controls. Spontaneous visual search clearly decreased towards more eccentric positions on the right.

3. 'ROTATION' OR 'TRANSLATION' OF THE EGOCENTRIC FRAME?

The above findings argue for a deviation of egocentric space representation underlying neglect patients' exploration of space. However, they leave open the actual *gestalt* of the deviated representation. Different hypotheses have been put forward (see figure 3*a*). One suggestion has been a *rotation* of the whole egocentric reference frame around the earth-vertical body axis toward the ipsilesional side (Ventre *et al.* 1984; Karnath *et al.* 1993); another has been a *translation* of the whole reference system towards the side of the lesion (Vallar *et al.* 1995).

To distinguish between both hypotheses, neglect patients' perception of subjective body orientation was measured at two different distances away from the subject's body. In complete darkness, a red light-emitting diode (LED) was randomly presented either on the left or on the right side of the patient's midsagittal body plane. (The area of LED presentation ranged from −40° to −20° on the left or from +20° to +40° on the right side of the midsagittal plane.) The LED could be moved on two parallel, horizontal guide rails located 120 cm and 300 cm from the subjects (see figure 3*b*). Subjects sat upright in an armchair; head and body axes were aligned. The subjects' task was to verbally direct the LED to the position that they felt lay exactly 'straight ahead' of their bodies' midsagittal plane. These 'straight ahead' adjustments were conducted at each distance, i.e. 120 cm and 300 cm from the subjects (see figure 3*b*), in an alternating order. Sixteen trials of 'straight ahead' adjustment were conducted, eight at each distance. The 'straight ahead' position was determined for both distances by averaging the respective eight position judgements.

A comparison was made of three groups of patients. Four patients with neglect were examined (median age = 58 years). All patients suffered from right hemispheric lesions documented by CT and/or magnetic resonance imaging (MRI) scans. In three of the patients, the lesions were due to infarcts affecting the frontoparietal region in two cases and the temporoparietal region in one case. The fourth patient suffered a temporoparietal lesion due to surgery of a grade IV glioma. Time since lesions ranged between 7 and 135 days (median = 12 days). None of the patients had

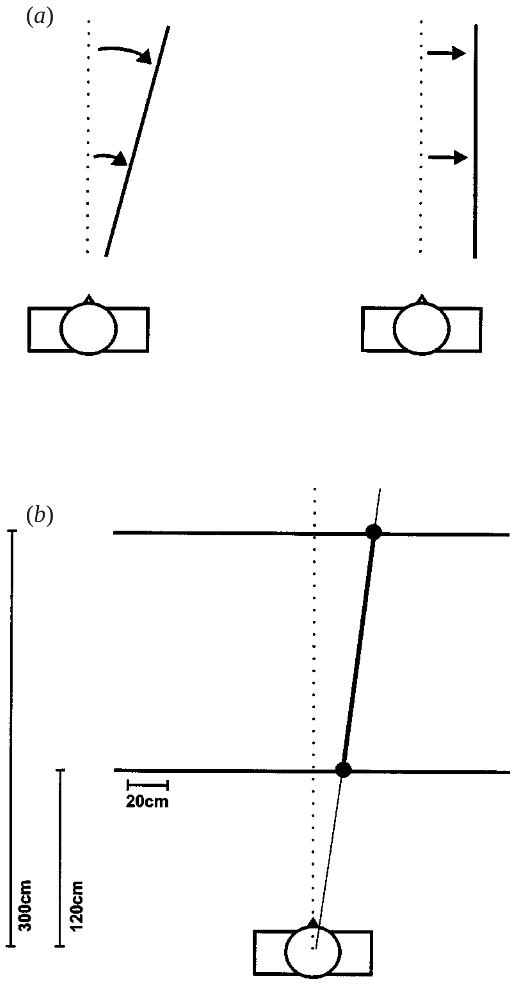

Figure 3. (*a*) Models of disturbed neural representation of space in spatial neglect leading to a *rotation* (left) of the whole egocentric reference frame around the earth-vertical body axis to the ipsilesional side or to a *translation* (right) of the reference system towards the side of the lesion. The subject's body orientation is illustrated as seen from above; the body is represented by a rectangle, the head by a circle. The dotted line represents the body's physical midsagittal plane in the front half-space. The bold line illustrates the subjectively perceived orientation of the body's midsagittal plane according to the two different hypotheses. (*b*) Obtained perception of subjective body orientation in four patients with neglect. The subjects' task was to direct an LED to the position that they felt lay exactly 'straight ahead' of their bodies' midsagittal plane. To distinguish between the rotation and translation hypotheses, the LED was presented at two different distances by using two parallel guide rails located 120 cm and 300 cm from the subjects at eye level. Filled circles indicate average 'straight ahead' judgements measured at the two spatial distances away from the patient's body. The bold line connecting the circles illustrates the subjectively perceived orientation of the body's midsagittal plane. Its orientation was determined by graphically connecting the two 'straight ahead' positions obtained at the two different spatial distances from the body. The resulting line was then graphically elongated up to the level of the subjects' physical body position.

visual-field defects as assessed by Goldmann perimetry. Neuropsychological examination included confrontation testing, copying, line bisection, letter cancellation, picture comparison, and the backing-tray task. At the time the experiment was conducted, two patients showed severe and two patients moderate left-sided neglect. Five right brain-damaged patients without neglect or hemianopia, aged from 26 to 71 years (median = 59 years), served as a control group (RBD-group). One patient suffered from a grade II oligoastrocytoma in the right basal ganglia and thalamus. Two patients had a temporal and one other a temporoparietal lesion due to surgery on a grade IV glioma. One patient sustained an infarct in the right parieto-occipital region. Median time since lesion was 7.5 weeks. As an additional control group (NC-group), five neurological patients without brain damage aged from 52 to 76 years (median = 60 years) were examined.

Subjective 'straight ahead' judgements of the control groups were close to the objective position of the midsagittal plane at both distances from the subjects at eye level. The RBD-group directed the LED to an average position of −2.5 cm (s.d. 5.0); the NC-group to an average position of +2.0 cm (s.d. 8.3). Significantly different from controls, neglect patients perceived their bodies as being oriented toward the ipsilesional side. Figure 3*b* shows that this egocentric deviation of body representation was clearly due to a rotation around the earth-vertical body axis to the ipsilesional side rather than a translation of the reference system to that side; the ipsilesional displacement of LED position increased linearly with the distance from the subjects.

To explore also any possible distortions of perceived space in the vertical dimension, the same procedure of determining 'straight ahead' perception was carried out at two further elevations, 30 cm above and 30 cm below the individual eye level of the subject. (The order of measuring the 'straight ahead' position at the three spatial levels was randomized between the subjects.) Subjective 'straight ahead' judgements of the controls again were closely scattered around the objective body position. Elevation and distance had no significant effect on their judgements; no relevant differences were observed in a comparison of the judgements at the three different elevations and in the two different distances from the subjects' bodies. The RBD-group directed the LED to a position of −3.2 cm (s.d. 7.2) averaged over all six spatial positions; the NC-group directed it to an average position of +0.4 cm (s.d. 7.9) in all six positions.

Figure 4 demonstrates the results revealed for the patients with neglect at the three elevations. In contrast to controls, neglect patients showed a marked disparity of subjective and objective body orientation. At all three elevations this egocentric deviation of body representation was due to a rotation around the earth-vertical body axis to the ipsilesional right side rather than to a translation of the reference system to that side.

This finding contrasts with the conclusions (not necessarily with the results) drawn from a recent study that used an auditory localization task to determine the subjective midsagittal plane (Vallar *et al.* 1995). The authors found a displacement to the ipsilesional right in the front half-space but also in the back half-space. They interpreted their results in favour of a *translation* of the whole egocentric coordinate system to the patients' ipsilesional side. Their results, together with those reported here, could indicate that the egocentric reference frame is affected differentially in neglect patients, in that it is rotated in the front half-space and translated in the back half-space or, alternatively, in that it is rotated to the ipsilesional side in both the front and the back half-spaces.

However, it is more plausible that the findings of Vallar and co-workers had an origin different from a distortion of space representation. A 'prior entry' advantage for ipsilesional inputs, as has recently been found in patients with parietal lesions and extinction (Rorden *et al.* 1997), could readily explain the

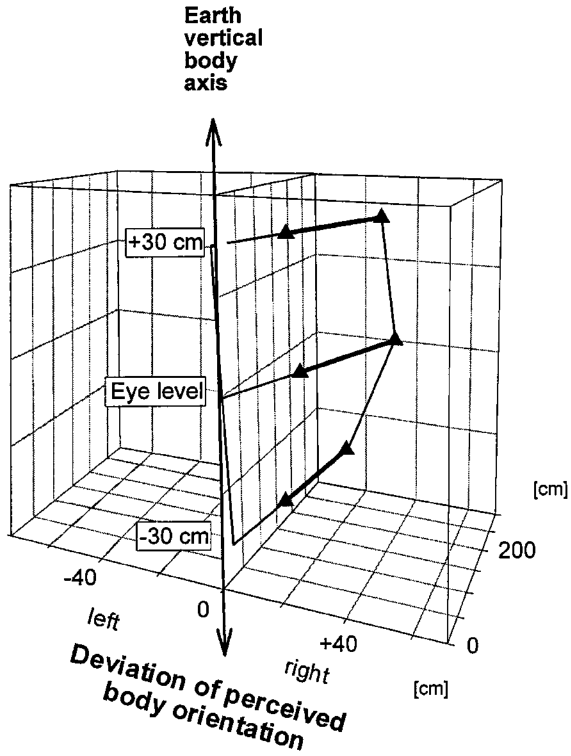

Figure 4. Neglect patients' perception of subjective body orientation in 3D space. The vertical plane in the centre represents the patients' physical midsagittal plane in the front half-space. Filled triangles indicate average 'straight ahead' judgements measured at two spatial distances (120 cm and 300 cm) away from the subject's body. The three bold lines connecting the triangles illustrate the subjectively perceived orientation of the body's midsagittal plane in three-dimensional space as determined at three different elevations (eye level, 30 cm above and 30 cm below eye level). The orientations of the bold lines were determined by graphically connecting the two 'straight ahead' positions obtained at the two different spatial distances from the body. The resulting lines were elongated up to the level of the subjects' physical body position. The average orientations obtained in the patients with neglect are illustrated.

observations in that study. Because one of the most important cues for auditory localization is given by internaural time difference, any pathological 'prior entry' for inputs to the ipsilesional ear could produce the auditory mislocation in both the front and the back half-space.

A further possible explanation of the results of Vallar *et al*. (1995) is the normal influence of eye position on auditory lateralization (Lewald & Ehrenstein 1996). When the subjects of Vallar *et al*. had to decide whether the position of the sound source was to the left or to the right of their sagittal midplane, eye position was not restricted. Subjects were free to move their eyes during the experiment. However, various studies (references see above) have shown that spontaneous gaze direction in neglect patients is not balanced in both hemispaces but rather demonstrates a characteristic deviation toward the ipsilesional side. This spontaneous bias of eye position could well account for the 'translated' subjective auditory median plane to the ipsilesional side found by Vallar and co-workers in their patients with neglect. As was demonstrated by Lewald & Ehrenstein (1996) in healthy subjects, the subjective auditory median plane shifts with the spatial direction of gaze position. Thus, a spontaneous bias of eye position toward the ipsilesional side in patients with neglect would *physiologically* lead to a shift of their auditory median plane in the same direction (as it is the case in healthy subjects with their gaze directed to that side).

4. DOES THE IPSILESIONAL DEVIATION LEAD TO A BIAS OF GOAL-DIRECTED ARM MOVEMENTS?

To study this question, reaching for targets was investigated in patients with acute spatial neglect (Karnath *et al*. 1997). The question was whether or not patients who show a severe bias of space exploration toward the ipsilesional side, demonstrate a comparable bias in goal-directed arm movements in pointing to targets in peripersonal space. By means of an optoelectronic three-dimensional camera system, the study examined unrestrained, three-dimensional arm movements during pointing to targets positioned either in the centre or in the left and right hemispace. Spatial hand kinematics of five consecutively admitted patients with acute neglect were compared with those of five patients with right hemispheric lesions without neglect and of six non-brain-damaged subjects. Subjects sat in front of a table and performed unrestricted pointing movements with their right hand to three LEDs that lit up in a random order. The LEDs were positioned in front of the subjects at eye level and arranged in a straight line. The central LED was aligned to each subject's sagittal body midplane; the two other LEDs were located in the left and the right hemispace.

All patients were able to point to these targets. In light as well as in darkness, i.e. with or without visual feedback about actual hand position, terminal accuracy of pointing did not differ between patients with neglect and controls along the horizontal, vertical and anterior–posterior axis. Even more interestingly, no characteristic differences were found between the three groups of subjects when actual finger positions *during* the pointing movements were compared by plotting them on a straight-line hand path between start and target. In particular, the patients with neglect showed no direction-specific deviation of their trajectories toward the ipsilesional, right side. Goal-directed arm movements to single targets in peripersonal space thus seem to be unaffected by the deviated egocentric representation of space that underlies the severe bias of ocular space exploration in these patients.

5. CONCLUSIONS

The observations reported in this paper suggest an altered representation of space associated with the clinical manifestation of 'spatial neglect'. The distribution of the patients' exploratory eye movements during visual search in the dark clearly argues against a lateral gradient (Kinsbourne 1993, Rizzolatti *et al*. 1985) underlying the bias of space exploration in these patients. They rather favour a disturbed input transformation that leads to an ipsilesional deviation of egocentric space representation. The ipsilesional deviation causes the patients' contralesional neglect when orienting in space or searching in the surround. Figure 5 presents a sketch of the consequences following from this model of altered space representation. It considers that the egocentric deviation is due to a rotation around the earth-vertical body axis to the ipsilesional side rather than a translation to that side.

The kinematic analysis of goal-directed arm movements in patients with acute neglect supports the view of dissociated functions in the human superior and inferior parietal lobule. It demonstrates that patients with neglect, showing a severe bias of space exploration toward the ipsilesional side, do not exhibit a comparable bias of their hand trajectories when pointing to targets in peripersonal space. The failure to orient toward and to explore the contralesional part of space appear to be distinct from those deficits observed once an object of interest has been located and releases reaching.

The findings argue that (i) exploratory and (ii) goal-directed behaviour do not share the same neural control mechanism. They suggest that neural representation of egocentric space in the inferior parietal lobule serves as a matrix for spatial exploration and for orienting in space but not for visuomotor processes involved in reaching for objects. Disturbances of such processes rather seem to be characteristic for patients with more superior parietal lobe lesions and optic ataxia.

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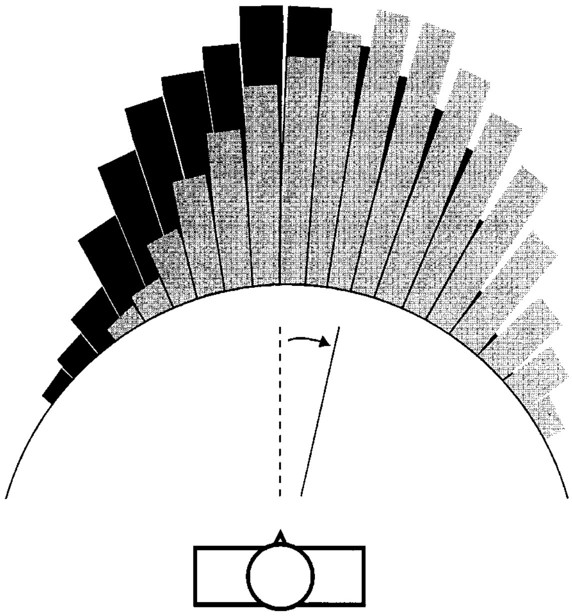

Figure 5. Sketch of the ipsilesional (rightward) deviation of egocentric space representation in patients with spatial neglect. The subject's body orientation is illustrated as seen from above; the body is represented by a rectangle, the head by a circle. The dashed line symbolizes the egocentric coordinate system (horizontal dimension) in healthy subjects; the black histogram their ocular exploration of space (per cent) along the horizontal dimension. The continuous line symbolizes the egocentric coordinate system (horizontal dimension) in patients with neglect. It is rotated around the earth-vertical body axis toward the ipsilesional, right side. The grey histogram showes the patients' ocular exploration of space along the horizontal dimension. It is suggested that such an ipsilesional deviation of egocentric space representation underlies the bias of space exploration in these patients and their contralesional neglect when orienting in space or searching in the surround.

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