Two basic properties of space representation in the brain: evidence from unilateral neglect

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SUMMARY It is argued, on the grounds of earlier findings, that the neural substrate of egocentric space representation has analogue (non-symbolic) topo-topical properties. It is then argued from fresh evidence that space representation appears to be anchored to the sagittal midplane of the trunk and to the line of sight. A tentative reduction of the suggested properties of space representation to the neuro-physiological level is briefly outlined.

The behaviour of complex organisms with reference to their environment—particularly those implying predictive abilities—have led to the assumption of inner models for outside reality, that is of representations of states of affairs in the world. Though space and time, as relational properties, could be viewed as intrinsic to and inseparable from any such model, the terms "space representation" and "time representation" should not give rise to ambiguities once their sui generis status has been accepted. The issue of space representation is still a controversial issue in cognitive science, and studies of unilateral neglect may contribute to the evaluation of competing hypotheses and to their refinement.

Unlike propositional models, analogue models for representation assume a relation of physical—as opposed to logical—correspondence between the representation and the object being represented. They do not seem to enjoy wide popularity. This may be partly due to the fact that on a simplistic level of interpretation such models suggest a relation of strict isomorphism between neural representations and the represented domain, which in most cases is manifestly false (for example, in the case of neural representation of colours and tunes). It can also be attributed in part to current approaches to mental processes which decline any involvement with the brain hardware.1 There is nonetheless evidence suggesting that the structure of egocentric space representation is organised in conformity with a definite topological principle.

A topological model of egocentric space representation implies that there are circumscribed brain areas in which lesions would result in a representational loss limited to definite regions of this space. In fact this is what might be inferred from the behaviour of patients showing neglect for the left half of personal and peri-personal space after injury to the opposite half of the brain, usually, though not necessarily, involving the parietal lobe near its junction with the temporal and occipital lobes.2-4

The notion of a topo-topic space representation raises the question of its bodily reference system. It is first necessary to qualify the rather loosely conceived egocentre of peri-personal space with reference to a body which has spatial extent and is composed of several jointed segments each of which, to complicate matters further, may individually come into prominence during the course of different spatial activities. One possible way to answer this question is to ascertain how in a tactile exploration task the cleavage between the attended and the unattended space in patients with unilateral neglect is related to the sagittal midplane of the trunk and the line of sight.

Materials and methods

Subjects in the experiment were 15 right-handed adult patients (8 male, 7 female). Criteria for inclusion were clinical and instrumental (CT scan) evidence of a circumscribed cortical and/or subcortical lesion confined to the right hemisphere and evidence of left hemi-space neglect in a cancellation task. Details about this task, as well as a rationale for confining the investigation to right brain-damaged patients can be found in Bisiach et al.5 All patients of the present group had vascular lesions located in the posterior regions of the right hemisphere, with one
exception (patient FS who had subcortical softening involving the right frontal lobe, the head of caudate nucleus, the lenticular nucleus, the internal capsule and possibly the white matter beneath the lower third of the post-central gyrus).

A wooden apparatus for blind tactual exploration was devised, with 37 adjacent hexagonal cells grouped to form a larger hexagon with 220 mm sides (fig). The inside breadth of the cell walls was 30 mm and their height 40 mm. A peg 40 mm high and 5 mm wide was loosely fixed in a hole in the bottom of each cell so that its upper extremity lay 10 mm below the top of the wall. The apparatus was mounted on a circular platform with radius 270 mm, and was surmounted by an aluminium circle of the same radius. Over this a white cloth was spread to hide the apparatus.

The subject's task was to draw all the pegs out of their holes, leaving them on the bottom of the corresponding cell. The task was performed with the right hand, which was passively led by the examiner over the cell in the centre of the apparatus before starting.

There were four conditions. In condition (a) the apparatus was placed in front of the subject so that the longitudinal axes of the head and of the exploring hand lay in the sagittal midplane of the trunk, while the eyes looked straight ahead. In condition (b) the apparatus was displaced to the right so that the exploring arm was at an angle of 60° to the sagittal midplane of the trunk, while the head and eyes were kept at 0°. In condition (c) the apparatus remained displaced as in (b) but head and eyes were in line with the exploring arm at an angle of 60° with respect to the sagittal midplane of the trunk. Finally, in condition (d) the apparatus was returned to its original position, while head and eyes were kept at an angle of 60°. In each condition, the axis of the exploring arm placed in the starting position was collinear with one of the minor diameters of the large hexagon. Further conditions, mirror-symmetrical to (b), (c) and (d), implying a leftward displacement of the line of sight and/or of the axis of the exploring arm were not included as they were impossible for some patients with left-sided neglect. For all subjects the four conditions were run in the order from (a) to (d) and after each condition, as soon as the subject had declared that he had completed his exploration, the unexplored cells were counted (that is the cells in which the peg had not been dislodged from its hole). It should be noted that the honeycomb pattern of the apparatus was such as to equate tactual cues along the axes of 0° and 60°, and that the height of the edge of the cells prevented a sweeping search of the pegs by the hand.

We registered for each condition the omissions in the two halves of the display lying on either side of the large hexagon's minor diameter which was aligned to the axis of the exploring arm in the starting position, and these scores were entered into the statistical analysis. The three cells lying astride the bisecting diameter were disregarded. An ANOVA was carried out on the left-right difference of omissions in the four experimental conditions, according to a randomised blocks, 2 × 2 factorial design. The factorial structure of the experimental design derives from the fact that two sources can be hypothesised for left-right differences of omissions, that is the contribution of the trunk's sagittal midplane and that of the direction of gaze: in fact, they may be expected to give rise to left-right differences whenever their axis coincides with the midline of the display (that is with the axis of the exploring hand) and not when the display lies entirely to the left or the right side with respect to their axes. On this assumption, both contributions to left-right differences are effective in conditions (a), none of them in condition (b), only the direction of gaze in condition (c), and only the sagittal midplane of the trunk in condition (d).

Results

Although the patients' hands had been passively placed over the cell in the centre of the apparatus prior to each exploration, even this cell was neglected on some occasions and the patient started from a cell located nearby.

Table 1 shows the performance of our patients in the four experimental conditions. The statistical analysis is reported in table 2. It appears that both the sagittal midplane of the trunk and the line of sight contribute significantly to the gradient of left-right omissions, and that their effects do not interact.

A slight positive, nonsignificant correlation ($r$ =

| Table 1 Mean number of omissions in the left and right halves of the display |
|-----------------------------|-----|-----|-----|-----|
| Condition:                  | a   | b   | c   | d   |
| Left half                   | 10-600 | 5-733 | 6-267 | 9-466 |
| Right half                  | 4-733 | 5-733 | 4-467 | 6-133 |
| Difference                  | 5-867 | 0-000 | 1-800 | 3-333 |
| Total                       | 15-333 | 11-466 | 10-734 | 15-599 |
Source of variability | Sum of squares | df  | F      | p       |
<table>
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<tbody>
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<td>Trunk's midplane</td>
<td>205-350</td>
<td>1</td>
<td>4-571</td>
<td>0.05</td>
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<tr>
<td>Error</td>
<td>628-900</td>
<td>14</td>
<td></td>
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<tr>
<td>Line of sight</td>
<td>70-417</td>
<td>1</td>
<td>7-050</td>
<td>&lt;0.02</td>
</tr>
<tr>
<td>Error</td>
<td>139-833</td>
<td>14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interaction</td>
<td>2-017</td>
<td>1</td>
<td>&lt;0-1</td>
<td>ns</td>
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<tr>
<td>Error</td>
<td>290-233</td>
<td>14</td>
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0.24) was found between the amount of left-side neglect in conditions (b) and (d). This runs contrary to the hypothesis that the two factors affecting our patients’ performance—the trunk’s sagittal midplane and line of sight—concern two different populations. In fact, if we had sampled from two different populations, one characterised by its tendency to show neglect related to the trunk’s sagittal midplane and the other by neglect related to the line of sight, a negative correlation would have resulted between the scores of conditions (b) and (d). Only two patients showed neglect in condition (d)—related to the trunk’s sagittal midplane—and no neglect in condition (b) (LA: right parietal infarction; ZT: haematoma of the right thalamus). One patient (FS, the only frontal patient—see above) showed neglect in condition (b)—related to the line of sight—and no neglect in condition (d).

Discussion

In the situation created by our experiment the boundary of the neglect area seems to be influenced both by the sagittal midplane of the trunk and by the line of sight. Thus, besides the analogue property of space representation in the brain suggested by previous observations, the results of the present investigation seem to reveal another basic property of this representation: namely, its double anchorage, as it were, to the sagittal midplane of the trunk and to the line of sight. In one way this conclusion is consistent with the findings of Heilman and Valenstein. These authors asked patients with left neglect to bisect lines lying to the left or to the right of their trunk’s sagittal midplane. They found rightward displacement of the subjective midpoint definitely greater in the first condition. On the other hand, this conclusion is in accordance with the phenomenon of displacement of acoustical localisation produced by shifts of gaze and the phenomenon of visuo-spatial discrepancies induced by prisms.

Merzenich and Kaas have recently reviewed the principles of organisation of sensory-perceptual systems in mammals. Some of their conclusions are relevant here. They point out that in the cortex there are a number of topographic maps of sensory surfaces for each sensory system. In the macaque, for example, there are probably ten or more maps of the retina. Sensory maps occupy most of the cortex caudal to the central sulcus in monkeys, and there is proportionately little non-topographically organised cortex. In their paper they claim that it is simpler to hypothesise that this neural mechanism subserves representation as well as perception. This is clearly a defence of an analogue structure of representations, which matches the clinical evidence for a topological structure of egocentric space representation in man, even though the latter might differ in some organisational aspects from that of the monkey, as Ettlinger has suggested. A possible neuro-physiological correlate of clinico-anatomical data supporting an analogue model for space representation may be extracted from the characteristics of the neural system of the inferior parietal lobule in primates. According to Mountcastle this system is involved in the construction of a neural model of the space surrounding the individual, and the activity of most neurons in this area is related to events in contralateral hemisphere.

Data obtained by recording single neuron activity from the inferior parietal lobule are also potentially relevant to the question of the orientation of space representation with reference to the individual’s body. Cells have been described in area PG of monkeys, the firing of which is conditioned by foveation of interesting stimuli in particular oculomotor states. Since head fixation was necessary in these experiments, it was not possible to learn whether the oculomotor state was itself one of the conditions concomitantly sufficient for the occurrence of neuronal discharge, or whether the locus of the stimulus in the egocentric space—with respect to a reference system which is to be defined—played the effective role. In other words, if the firing of a neuron were found to be contingent upon a particular location of the light-stimulus and to remain unaltered throughout the different oculomotor arrangements which are caused by foveation of the stimulus in different head positions, it would be possible to conclude that the effective spatial condition for the firing is the location of the target with respect to the animal’s trunk. This argument applies, seemingly, to “saccade neurons” as well, and more precisely to those which fire just before and during saccades to targets with specific spatial parameters.

Schlag et al have found cells in the thalamic internal medullary lamina of the cat which respond to visual stimuli having a definite location on a tangent screen, “no matter where the eyes were fixed”. The firing of these cells was “unperturbed by
the abrupt changes in the retinal position of the stimulus produced by changes of fixations." More recently, Gentilucci et al. have found cells in the premotor area of a macaque, which fired when a visual stimulus approached the mouth in a definite region of peri-personal space; this occurred independently of the direction of gaze, that is to say independently of the retinal co-ordinates of the proximal stimulus.

The firing of these cells seems therefore to require a computation performed on two variables—eye position and focus of retinal stimulation—to ensure spatial selectivity in a co-ordinate system referred to the head or to the trunk. The possibility of a higher order spatial coding independent of head position is suggested by Schlag et al. on the grounds of vestibular projections to the internal medullary lamina found by Magnin and Kennedy.

It seems plausible to hypothesise that the neural mechanisms which map perceptual space into different reference frames subserve an equally articulated differentiation of representational space, such that space representation may be related to more than one co-ordinate system, as suggested by the results of our investigation. Since the field to be explored by our patients was not under visual control, the exploration was not data driven but governed by representational hypotheses. One component of the two-fold co-ordinate system to which the neglect gradient may be referred—the trunk’s sagittal midplane—seems quite unequivocal. The other is more ambiguous, since head-position and eye-position have not been studied separately. The influence of the line of sight might therefore refer either to the retinal co-ordinates or to the head’s sagittal midplane, though the first alternative seems more likely. This double anchorage of space representation does not seem to be an artefact due to the presence, in our sample, of patients with two differing kinds of neglect, one related to the trunk and the other to the line of sight; rather, it seems to reflect a versatility of space representation. In the present case it might be suggested that setting the field of exploration astride different critical axes involves shifts in the orientation of the represented space, which become apparent in patients suffering from unilateral neglect owing to the observable shifts of a pathological marker.

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References