A new view of hemineglect based on the response properties of parietal neurones

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SUMMARY

Lesion studies of the parietal cortex have led to a wide range of conclusions regarding the coordinate reference frame in which hemineglect is expressed. A model of spatial representation in the parietal cortex has recently been developed in which the position of an object is not encoded in a particular frame of reference, but instead involves neurones computing basis functions of sensory inputs. In this type of representation, a nonlinear sensorimotor transformation of an object is represented in a population of units having the response properties of neurones that are observed in the parietal cortex. A simulated lesion in a basis-function representation was found to replicate three of the most important aspects of hemineglect: (i) the model behaved like parietal patients in line-cancellation and line-bisection experiments; (ii) the deficit affected multiple frames of reference; and (iii) the deficit could be object-centred. These results support the basis-function hypothesis for spatial representations and provide a testable computational theory of hemineglect at the level of single cells.

1. INTRODUCTION

The representation of space in the brain is thought to involve the parietal lobes, in part because large lesions of the parietal cortex lead to hemineglect, a syndrome characterized by a lack of response to sensory stimuli that appear in the hemispace contralateral to the lesion (Heilman *et al*. 1985). In what coordinate system are objects represented in the parietal cortex? The answer to this question is not straightforward because neglect appears to affect multiple frames of reference simultaneously, and, to a first approximation, independently of the task. Here, a recent model of the response properties of neurones in the parietal cortex that can account for this observation is presented.

There is evidence that the positions of objects are represented in multiple processing systems throughout the brain, each system specialized for a particular sensorimotor transformation and using its own frame of reference (Stein 1992; Goldberg *et al*. 1990). The lateral intraparietal area (LIP), for example, appears to encode the locations of objects in oculocentric coordinates, presumably for the control of saccadic eye movements (Colby *et al*. 1995). The ventral intraparietal cortex (VIP) (Colby & Duhamel 1993) and the premotor cortex (Fogassi *et al*. 1992; Graziano *et al*. 1994), on the other hand, seem to use head-centred coordinates and might be involved in the control of hand movements towards the face.

This modular theory of spatial representations is not fully consistent with the behaviour of patients with parietal or frontal lesions. According to the modular view, the deficits should be oculocentric for eye movements and head-centred for reaching, and more generally should depend on the task. Instead, clinical studies show a more complex pattern. This point is particularly clear in an experiment by Karnath *et al*. (1993) (figure 1*a*). Subjects were asked to identify a stimulus that can appear on either side of the fixation point. In order to test whether the position of the stimuli with respect to the body affects performance, two conditions were tested: a control condition with the head held straight ahead (C1) and a second condition with head rotated 15° to the right (where right is defined with respect to the trunk) or, equivalently, with the trunk rotated 15° to the left (where left is defined with respect to the head) (see figure 1*a*, C2). In C2, both stimuli occurred further to the right of the trunk than in C1, though at the same location with respect to the head and retina. Moreover, the trunk-centred position of the left stimulus in C2 was the same as the trunk-centred position of the right stimulus in C1.

As expected, subjects with right parietal lesions performed better on the right stimulus in the control condition (C1), a result consistent with both retinotopic and trunk-centred neglect. However, to distinguish between the two frames of reference, performance should be compared across conditions. If the deficit is purely retinocentric, the results should be identical in

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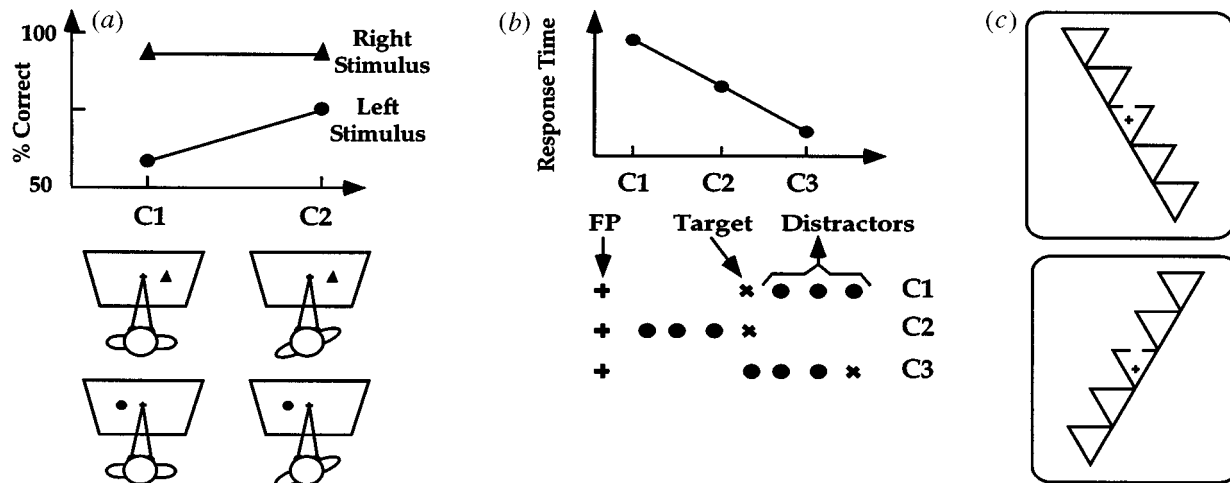*Printed in Great Britain*

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Figure 1. (*a*) Percentage of correct identification in the experiment of Karnath *et al*. (1993). In condition 1 (C1), subjects were seated with eyes, head, and trunk lined up, whereas in condition 2 (C2) the trunk was rotated by 15° to the left. The overall pattern of performance is not consistent with pure retinal or pure trunk-centred neglect and suggests a deficit affecting a mixture of these two frames of reference. (*b*) Response times for the experiment by Arguin & Bub (1993) for the three experimental conditions illustrated below the graph (FP, fixation point). The decrease from condition 1 (C1) to condition 2 (C2) is consistent with object-centred neglect, i.e. subjects are faster when the target is on the right of the distractors than when it is on the left, even though the retinal position of the target is the same. The further decrease in reaction time in condition 3 (C3) shows that the deficit is also retinotopic. (*c*) The two displays used in the experiment of Driver *et al*. (1994). Patients must detect a gap in the upper part of the central triangle. In the top display, the object made out of the triangles is perceived as rotated 60° clockwise; in the bottom display it is perceived as being rotated 60° anticlockwise. Left parietal patients detect the gap more reliably in the bottom display, i.e. when the gap is associated with the right side of the object.

both conditions because the retinotopic locations of the stimuli do not vary. On the other hand, if the deficit is purely trunk-centred, the performance on the left stimulus should improve when the head is turned right, because the stimulus now appears further towards the right of the trunk-centred hemispace. Furthermore, performance on the right stimulus in the control condition should be the same as performance on the left stimulus in the rotated condition, because they share the same trunk-centred position in both cases.

Neither of these hypotheses is fully consistent with the data. As expected from retinotopic neglect, subjects always performed better on the right stimulus in both conditions. However, performance on the left stimulus improved when the head was turned right (C2), although not sufficiently to match the level of performance on the right stimulus in the control condition (C1, figure 1*a*). Therefore, these results suggest a retinotopically based form of neglect modulated by trunk-centred factors. In addition, Karnath *et al*. (1991) tested patients on a similar experiment in which subjects were asked to generate a saccade towards the target. The analysis over reaction time revealed the same type of results as the one found in the identification task, thereby demonstrating that the spatial deficit is, to a first approximation, independent of the task. Several other experiments have found that neglect affects a mixture of frames of reference in a variety of tasks (Ladavas 1987; Ladavas *et al*. 1989; Calvanio *et al*. 1987; Farah *et al*. 1990; Bisiach *et al*. 1985; Behrmann & Moscovitch 1994).

An experiment by Arguin & Bub (1993) suggests that neglect can be object-centred as well. As shown in figure 1*b*, they found that reaction times were faster when a target (the 'x' in figure 1*b*) appeared on the right of a set of distractors (C2) instead of on the left side (C1), even though the target was at the same retinotopic location in both conditions. Interestingly, moving the target further to the right led to even faster reaction times (C3), showing that hemineglect is not only object-centred but retinotopic as well in this task. Several other experiments have led to similar conclusions (Bisiach *et al*. 1979; Driver & Halligan 1991; Halligan & Marshall 1994; Husain 1995; Tipper & Behrmann 1996).

Object-centred neglect is also clearly illustrated in an experiment by Driver *et al*. (1994) in which patients were asked to detect a gap in the upper part of a triangle embedded within a larger object (figure 1*c*). They reported that patients detected the gap more reliably when it was associated with the right side of the object than when it belonged to the left side, even when this gap appeared at the same retinal location across conditions (figure 1*c*).

These results strongly support the existence of spatial representations using multiple frames of reference simultaneously shared by several behaviours. A model of the parietal cortex that has similar properties has recently been developed (Pouget & Sejnowski 1995, 1997). This paper examines whether a simulated lesion of the model leads to a deficit similar to hemineglect. In the model, parietal neurones compute basis functions of sensory signals, such as visual inputs, auditory inputs, and posture signals (e.g. eye or head position). The resulting sensorimotor representation, which is here called a basis-function map, can be used for performing nonlinear transformations of the sensory inputs: the

type of transformations required for sensorimotor coordination.

The basis-function hypothesis is briefly summarized in §2 of this paper. In §3, the network architecture and the various methods used to assess the network performance in behavioural tests are described. In §4, the behaviour of a parietal patient is compared with the performance of the network model after a unilateral lesion of the basis-function representation.

2. BASIS-FUNCTION REPRESENTATION

The model of the parietal cortex is motivated by the hypothesis that spatial representations correspond to a recoding of the sensory inputs that facilitates the computation of motor commands. This perspective is consistent with the suggestion of Goodale & Milner (1990) that the dorsal pathway of the visual cortex mediates object manipulation (the 'How' pathway) as opposed to simply localizing objects as Mishkin *et al.* (1983) previously suggested (the 'Where' pathway). In general, the choice of a representation strongly constrains whether a particular computation is easy or difficult to perform. For example, addition of numbers is easy in decimal notation but difficult with Roman numerals. The same is true for spatial representations. With some representations the motor commands for grasping may be simple to perform and stable to small input errors, but in others the computation could be long and sensitive to input errors.

A set of basis functions has the property that any nonlinear function can be approximated by a linear combination of the basis functions (Poggio 1990; Poggio & Girosi 1990). Therefore, basis functions reduce the computation of nonlinear mappings to linear transformations: a simpler computation. Most sensorimotor transformations are nonlinear mappings of the sensory and posture signals into motor coordinates; hence, given a set of basis functions, the motor command can be obtained by a linear combination of these functions. In other words, if parietal neurones compute basis functions of their inputs, they recode the information in a format that simplifies the computation of subsequent motor commands.

As illustrated in figure 2(*b*), the response of parietal neurones can be described as the product of a Gaussian function of retinal location multiplied by a sigmoid function of eye position. Sets of both Gaussians and sigmoids are basis functions, and the set of all products of these two basis functions also forms basis functions over the joint space (Pouget & Sejnowski 1995, 1997). These data are therefore consistent with the idea that parietal neurones compute basis functions of their inputs and, as such, provide a representation of the sensory inputs from which motor commands can be computed by simple linear combinations (Pouget & Sejnowski 1995, 1997).

It is important to emphasize that not all models of parietal cells have the properties of simplifying the computation of motor commands. For example, Goodman & Andersen (1990) as well as Mazzoni & Andersen (1995) have proposed that parietal cells simply add the retinal and eye-position signals. The
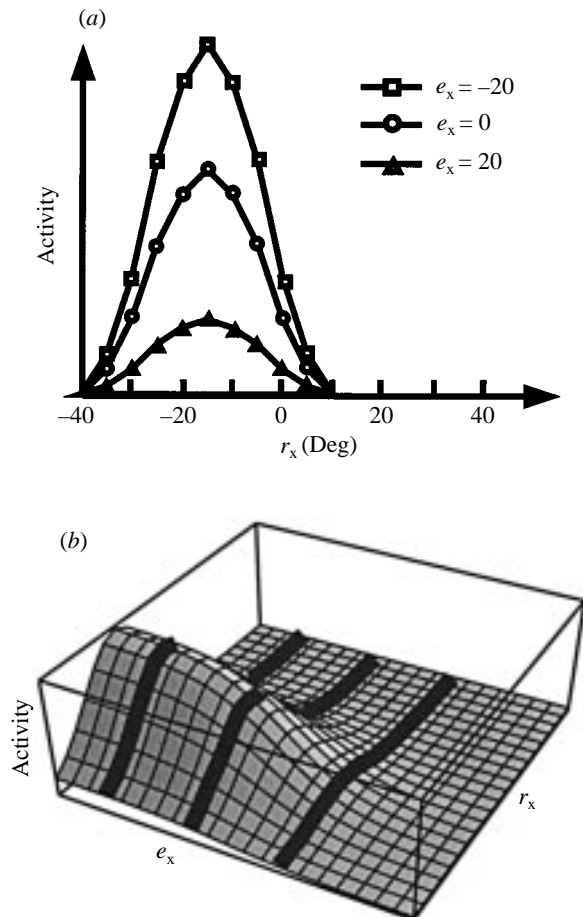

Figure 2. (*a*) Idealization of a retinotopic visual receptive field of a typical parietal neurone for three different gaze angles (e_x). Note that eye position modulates the amplitude of the response but does not affect the retinotopic position of the receptive field (adapted from Andersen *et al.* (1985)). (*b*) Three-dimensional plot showing the response function of an idealized parietal neurone for all possible eye and retinotopic positions, e_x and r_x. The plot in (*a*) was obtained by mapping the visual receptive field of this idealized parietal neurone for three different eye positions, as indicated by the bold lines.

output of this linear model does not reduce the computation of motor commands to linear combinations because linear units cannot provide a basis set. In contrast, the hidden units of the Zipser & Andersen (1988) model, or the multiplicative units used by Salinas & Abbott (1995, 1996*a*), have response properties closer to the basis-function units; the basis-function hypothesis can be seen as a formalization of these models (for a detailed discussion see Pouget & Sejnowski (1997)).

One interesting property of basis functions, particularly in the context of hemineglect, is that they represent the positions of objects in multiple frames of reference simultaneously. Thus, one can recover simultaneously the position of an object in retinocentric *and* head-centred coordinates from the response of a group of basis-function units similar to the one shown in figure 2*b* (Pouget & Sejnowski 1995, 1997). As shown in the next section, this property allows the same set of units to be used to perform multiple spatial transformations in parallel.

This approach can be extended to other sensory and posture signals and to other parts of the brain where similar gain modulations have been reported (Trotter *et al*. 1992; Field & Olson 1994; Boussaoud *et al*. 1993; Bremmer & Hoffmann 1993; Brotchie *et al*. 1995). When generalized to other posture signals, such as neck-muscle proprioception or vestibular inputs, the resulting representation encodes simultaneously the retinal, head-centred, body-centred, and world-centred coordinates of objects. The problem of the increase in the number of neurones required to integrate further frames of reference is discussed by Pouget & Sejnowski (1997).

Exploration has recently begun of the effects of a unilateral lesion of a basis-function network (Pouget & Sejnowski 1996). The next section describes the structure of this model.

3. MODEL ORGANIZATION

The model contains two distinct parts: a network for performing sensorimotor transformations, and a selection mechanism. The selection mechanism is used when there is more than one object present in the visual field at the same time.

(*a*) *Network architecture*

The network has basis-function units in the intermediate layer to perform a transformation from a visual retinotopic map input to two motor maps in head-centred and oculocentric coordinates, respectively (figure 3). The visual inputs correspond to the cells found in the early stages of visual processing and the set of units encoding eye position have properties similar to the neurones found in the intralaminar nucleus of the thalamus (Schlag-Rey & Schlag 1984). These input units project to a set of intermediate units that contribute to both output transformations. Each intermediate unit computes a Gaussian of the retinal location of the object, r_x, multiplied by a sigmoid of eye position, e_x:

$$o_{ij} = \frac{e^{-(r_x - r_{xi})^2/2\sigma^2}}{1 + e^{-\beta(e_x - e_{xj})}}.$$

Horizontal positions are considered only because the vertical axis is irrelevant for hemineglect. These units are organized in two two-dimensional maps covering all possible combinations of retinal and eye-position selectivities. The only difference between the two maps is the sign of the parameter β, which controls whether the units increase or decrease activity with eye position. The value of β was set to $8°$ for one map and $-8°$ for the other map. The indices (i,j) refer to the position of the units on the maps. Each location is characterized by a position for the peak of the retinal receptive field, r_{xi}, and the midpoint of the sigmoid of eye position, e_{xj}. These quantities are systematically varied along the two dimensions of the maps in such a way that in the upper right corner r_{xi} and e_{xj} correspond to right

retinal and right eye positions, whereas in the lower left they correspond to left retinal and left eye positions.

This type of basis function is consistent with the responses of single parietal neurones found in area 7a. The resulting population of units forms basis-function maps that encode the locations of objects in head-centred and retinotopic coordinates simultaneously.

The activities of the units in the output maps are computed by a simple linear combination of the activities of the basis-function units. Appropriate values of the weights were found by using linear regression to achieve the least mean square error (Pouget & Sejnowski 1997).

This architecture mimics the pattern of projections of the parietal area 7a, which innervate both the superior colliculus and the premotorcortex (via the ventral parietal area (VIP)) (Andersen *et al*. 1990; Colby & Duhamel 1993), where neurones have retinotopic and head-centred visual receptive fields, respectively (Graziano *et al*. 1994; Sparks 1991). Figure 3(*b*) shows a typical pattern of activity in the network when two stimuli are presented simultaneously while the eye is fixated $10°$ toward the right (only the basis-function map with positive $\beta = +8°$ is shown).

(*b*) *Hemispheric biases and lesion model*

Although the parietal cortices in both hemispheres contain neurones with all possible combinations of retinal and eye-position selectivities, most cells tend to have their retinal receptive field on the contralateral side (Andersen *et al*. 1990). Whether a similar contralateral bias exists for the eye position in the parietal cortex remains to be determined, although several authors have reported such a bias for eye-position selectivities in other parts of the brain (Schlag-Rey & Schlag 1984; Galletti & Battaglini 1989; Van Opstal *et al*. 1995).

In the model, the two basis-function maps are divided into two sets of two maps, one set for each hemisphere (again, the two maps in each hemisphere correspond to two possible values for the parameter β). Units are distributed across each hemisphere to create neuronal gradients. These neuronal gradients induce contralateral activity gradients, such that there is more activity overall in the left maps than in the right maps when an object appears on the right of the retina and the eyes are turned to the right, with the opposite being true in the right maps.

Several types of neuronal gradient can lead to these activity gradients. The gradients used for the simulations presented here affected only the maps with positive β; that is, maps with units whose activity increases as the eyes turn to the right. In both the right and the left map, the number of units for a given pair of (r_{xi}, e_{xi}) values increased for contralateral values of eye and retinal location, as indicated in figure 4; this increase is consistent with the experimental observation that hemispheres over-represent contralateral positions.

A right parietal lesion was modelled by removing the right parietal maps and studying the network behaviour produced by the left maps alone. The effect
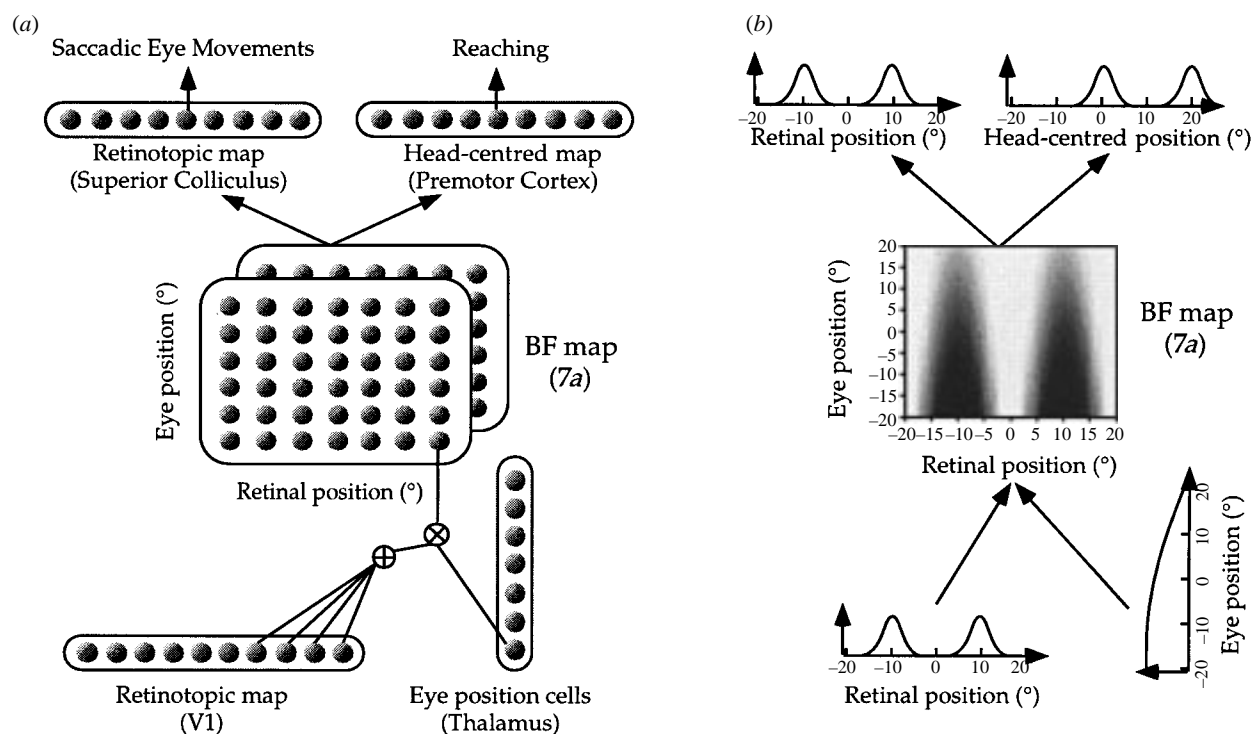
Figure 3. (*a*) Network architecture. Each unit in the intermediate layers is a basis-function unit with a Gaussian retinal receptive field modulated by a sigmoid function of eye position. This type of modulation is characteristic of the response of parietal neurones. (*b*) Pattern of activity for two visual stimuli presented at $+10°$ and $-10°$ on the retina with the eye pointing at $+10°$.

of the lesion is therefore to induce a neuronal gradient such that there is more activity in the network for right retinal and right eye positions.

The exact profile of the neuronal gradient across the basis-function maps did not matter as long as it induced a monotonically increasing activity gradient as objects were moved further to the right of the retina and the eyes fixated further to the right. The results presented in this chapter were obtained with linear neuronal gradients.

(*c*) *Selection model*

The selection mechanism in the model was adapted from Burgess (1995), and was inspired by the visual search theory of Treisman & Gelade (1980) and the saliency map mechanism proposed by Koch & Ullman (1985). It was used to model the behaviour of patients when presented with several stimuli simultaneously, and it operates on what is here called the *saliency value* associated with each stimulus.

The simultaneous presentation of multiple stimuli induced multiple hills of activity in the network (see, for example, the pattern of activity shown in figure 1*b* for two visual stimuli). The stimulus saliency, s_i, is defined as the sum of the activities of all the basis-function units whose receptive field is centred exactly on the retinal position of the stimulus (it is the sum of activities along the dotted line shown on the basis-function map in figure 3*b*). The index i varies from 1 to n, where n is the number of stimuli in view at a given time. This method is mathematically equivalent to

looking at the profile of activity in the output map of the superior colliculus and defining the saliency of the stimulus as the peak value of activity. Consequently, one need only consider the profiles of activity in the colliculus output map to determine the network's behaviour. Qualitatively similar values could also be obtained by looking at the profile of activation in the head-centred map.

At the first time-step, the stimulus with the highest saliency is selected by a winner-takes-all process, and its corresponding saliency is set to zero to implement inhibition of return. At the next time-step, the second highest stimulus is selected and inhibited, while the previously selected item is allowed to recover slowly. These operations are repeated for the duration of the trial. This procedure ensures that the most salient items are not selected twice in a row, but because of the recovery process, the stimuli with the highest saliencies might be selected again if displayed for long enough.

In this model of selection, the probability of selecting an item is proportional to two factors: the absolute saliency associated with the item, and the saliency relative to that of competing items.

(*d*) *Evaluating network performance*

This model was used to simulate several experiments in which patient performance was evaluated according to reaction time or percentage of correct responses.

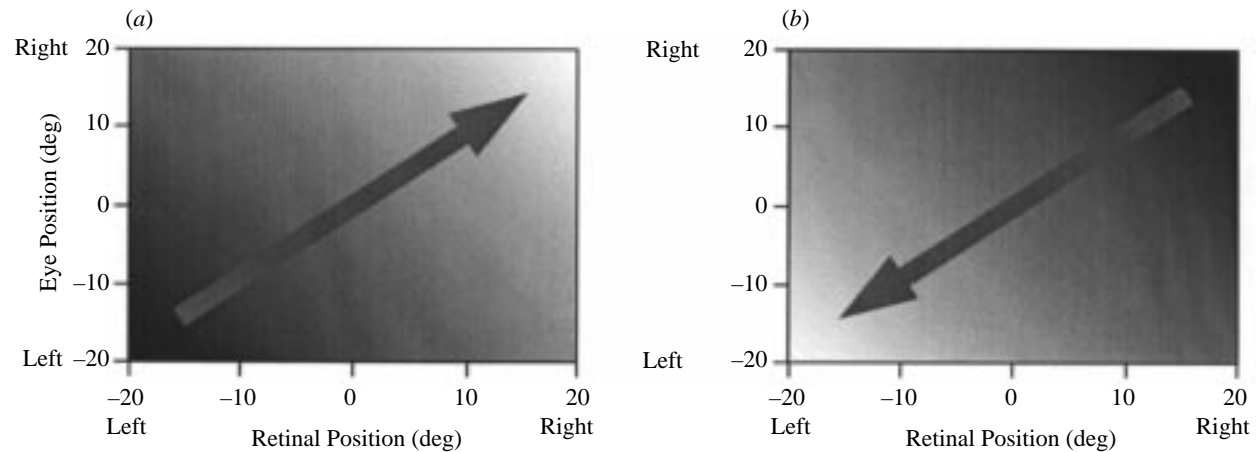In reaction-time experiments, it was assumed that processing involves two sequential steps: target

Figure 4. Neuronal gradients in left and right basis-function maps for which the parameter β is positive: the activities of the units increase with eye position. The right map contains more neurones for left retinal and left eye positions, whereas the left map has the opposite gradient.

selection and target processing. Target-selection time was assumed to be proportional to the number of iterations, n, required by the selection network to select the stimulus by using the mechanism described above. Each iteration was arbitrarily chosen to be 50 ms long. This term matters only when more than one stimulus is present, so that distractors could delay the detection of the target by winning the competition.

The time (RT) for target processing (that is to say, target recognition, target naming, etc.) was assumed to be inversely proportional to stimulus saliency, s_i:

$$RT = 100 + 50n + \frac{500}{1000s_i}.$$

The percentage of correct responses to a stimulus was determined by a sigmoid function of the stimulus saliency:

$$p = \frac{0.5}{1 + e^{-(s_i - s_0)/t}} + 0.5,$$

where s_0 and t are constants.

This model for evaluating performance is based on signal-detection theory, where signal and noise are normally distributed with equal variance (Green & Swets 1966). This is equivalent to assuming that the rate of correct detection (hit rate) is the integral of the probability distribution of the signal from the decision threshold to infinity.

In line-bisection experiments, subjects were asked to judge the midpoint of a line segment. In the network model, the midpoint, m, was estimated by computing the centre of mass of the activity induced by the line in the basis-function map:

$$m = \frac{\sum_{\text{allunits}} a_i r_{xi}}{\sum_{\text{allunits}} a_i},$$

where r_{xi} is the retinal position of the peak of the visual receptive field of unit i.

4. RESULTS

All the results given here were obtained from the lesioned model, in which the right basis-function maps have been removed. For control tasks on the normal network, see Pouget & Sejnowski (1997).

(*a*) *Line cancellation*

The network was first tested on the line cancellation test, in which patients were asked to cross out short line segments uniformly spread over a page. To simulate this test, the display shown in figure 5*a* was presented and the selection mechanism was run to determine which lines were selected by the network. As illustrated in figure 5*a*, the network crossed out only the lines located in the right half of the display, mimicking the behaviour of left-neglect patients in the same task (Heilman *et al*. 1985). The rightward gradient introduced by the lesion makes the right lines more salient than the left lines. As a result, the rightmost lines always won the competition, preventing the network from selecting the left lines. The probability that the line was crossed out as a function of its position in the display is shown in figure 5*a*, where position is defined with respect to the frame of the display. A sharp jump in the probability function was found such that lines to the right of this break have a probability near to unity of being selected, whereas lines to the left of the break have a probability close to zero (figure 5*b*).

The sharp jump in the probability of selection stands in contrast to the smooth and monotonic profile of the neuronal gradient. Whereas the sharp boundary in the pattern of line crossing may suggest that the model 'sees' only one-half of the display, the linear profile of the neuronal gradient shows that this is not the case. The sharp jump is mainly a consequence of the dynamics of the selection process: because right bars are associated with higher saliencies, they consistently win the competition, to the detriment of left bars. Consequently, the network starts by selecting the bar which is furthest to the right and, owing to inhibition of return, moves its way towards the left. Eventually,
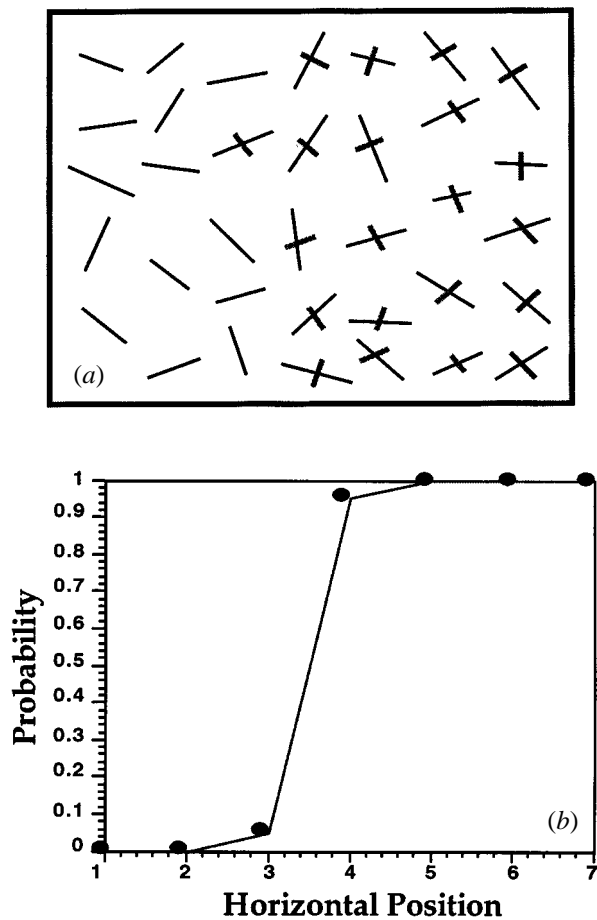
Figure 5. Line cancellation task. (*a*) The network failed to cross out the line segments on the left side of the page, as in right parietal patients. (*b*) Probability of crossing a line as a function of its horizontal position in the display. The probability of crossing a bar on the left side of the display is zero, as if the neuronal gradient introduced by the lesion were a step function. The gradient, however, is smooth; the sudden change in behaviour in the centre of the display is the result of the dynamics of the selection mechanism.

however, previously inhibited items recover and win the competition again, preventing the network from selecting the leftmost bars. The point at which the network stops selecting bars towards the left depends on the exact recovery rate and the total number of items displayed.

The pattern of line crossing by the network is not due to a deficit in the selection mechanism, but rather is the result of a selection mechanism operating on a lesioned spatial representation. The network had difficulty detecting stimuli on the left side of space not because it was unable to orient toward that side of space—it would orient to the left if only one stimulus were presented in the left hemifield—but because the bias in the representation favoured the rightmost bars in the competition.

(*b*) *Line bisection*

In the line-bisection task, the network estimated the midpoint of the line to be slightly to the right of the

actual midpoint (figure 6*a*), as reported in patients with left neglect (Heilman *et al.* 1985). In contrast, the performance of an intact network was perfect (not shown).

The error does not occur because the lesioned network does not 'see' the left side of the line. On the contrary, the whole line is represented in the lesioned network, but owing to the neuronal gradient, more neurones respond to the right side of the line than to the left side. As a result, the centre-of-mass calculation used to estimate the middle of the line leads to a rightward error.

Increasing the length of the line leads to a proportional increase in the error, a result consistent with what has been observed in patients (figure 6*b*). The constant of proportionality between the error and the length of the line varies from patient to patient (Burnett-Stuart *et al.* 1991). A similar variation was found in the present study when the severity of the lesion in the model was varied by changing the slope of the neuronal gradient. Lesions with large slope led to larger constant of proportionality. Finally, the effect of line orientation was tested: the error followed a cosine function of orientation (figure 6*c*). The phase of this cosine function depended on the orientation of the neuronal gradient along the retina. A perfectly horizontal gradient led to a phase of zero (i.e. the maximum error is obtained for a horizontal line) but oblique retinal gradients led to a non-zero phase. A similar cosine relation with variation in the phase across subjects has been reported in patients (Burnett-Stuart *et al.* 1991).

Thus, as assessed by the line cancellation (§4*a*) and line bisection tests (§4*b*), a lesioned network exhibited a behaviour consistent with the neglect syndrome observed in humans after unilateral parietal lesions.

(*c*) *Mixture of frames of reference*

The frame of reference of neglect in the model was examined next. Because Karnath *et al.* (1993) manipulated head position, their experiment was simulated in this study by using a basis-function map that integrated visual inputs with head position, rather than with eye position. In figure 7*b*, the pattern of activity obtained in the retinotopic output layer of the network is shown in the various experimental conditions. In both conditions, head straight ahead (broken lines) or turned to the side (solid lines), the right stimulus is associated with more activity than is the left stimulus. This is a consequence of the larger number of cells in the basis-function map for rightward position. In addition, the activity for the left stimulus increased when the head was turned to the right. This effect is related to the larger number of cells in the basis-function maps tuned to right head positions.

Because network performance is proportional to activity strength, the overall pattern of performance was found to be similar to that reported in human patients (figure 1*a*): the right stimulus was better processed than was the left stimulus, and performance on the left stimulus increased when the head was rotated towards the right, although not sufficiently to
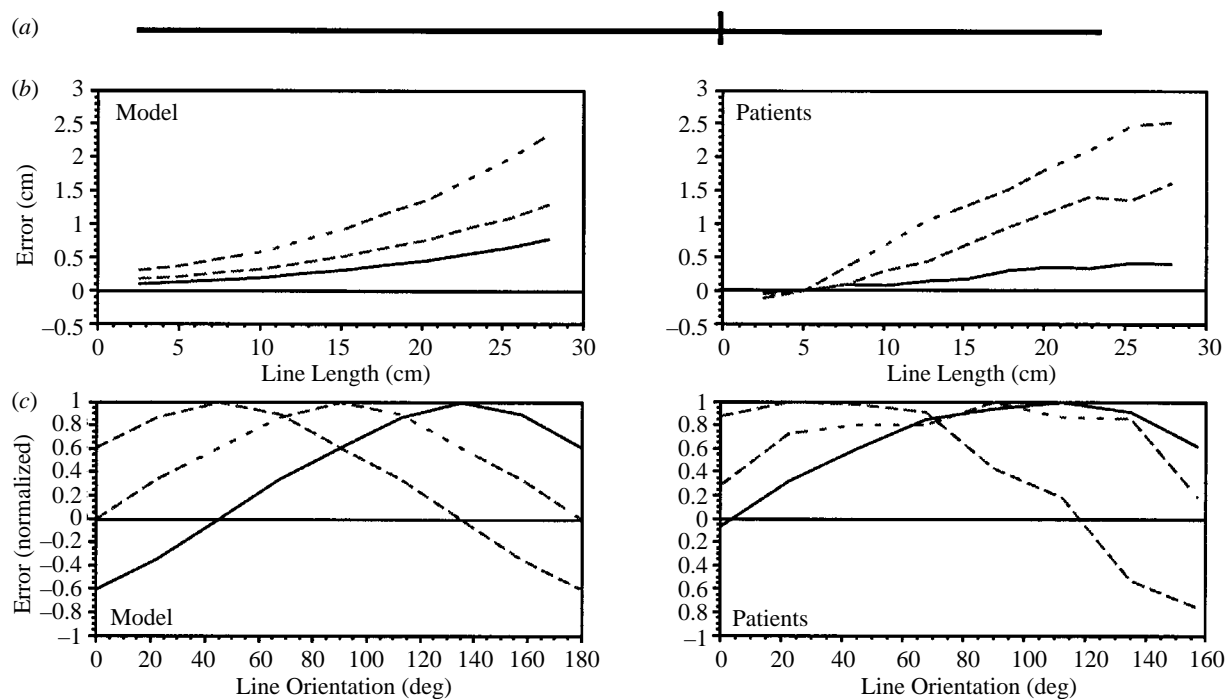
Figure 6. Line bisection task. (*a*) Network behaviour. The midpoint is estimated too far to the right, owing to the over-representation of the right side of space. (*b*) Error as a function of line length. As in patients, the error in the model is proportional to the length of the line. (*c*) Error as a function of line orientation. The curves follow a cosine function for both the model and the patients.

match the performance on the right stimulus in condition 1. Therefore, as in humans, neglect in the model was neither retinocentric nor trunk-centred alone, but both at the same time.

Similar principles can be used to account for the behaviour of patients in many other experiments that involve frames of reference (Ladavas 1987; Ladavas *et al*. 1989; Calvanio *et al*. 1987; Farah *et al*. 1990; Bisiach *et al*. 1985; Behrmann & Moscovitch 1994).

(*d*) *Object-centred effect*

The network's reaction times in simulations of the experiments of Arguin & Bub (1993) followed the same trends reported in human patients (figure 1*b*). Figure 7*b* illustrates the patterns of activity in the retinotopic output layer of the network for the three conditions in those experiments. Although the absolute levels of activity associated with the target (solid lines) in conditions 1 and 2 were the same, the activity of the distractors (broken lines) differed in the two conditions. In condition 1, they had relatively higher activity and thereby strongly delayed the detection of the target by the selection mechanism. In condition 2, the distractors were less active than the target and did not delay target processing as much as they did in condition 1. The reaction time decreased even more in condition 3 because the absolute activity associated with the target was higher. Therefore, the network exhibited retinocentric and object-centred neglect, with the same pattern observed in parietal patients (Arguin & Bub 1993).

The object-centred effect might not have been expected: there was no *explicit* object-centred representation in the model. An explicit object-centred representation would be a picture-like representation of the object, much like the retinotopic map in V1, but normalized for size, translation and rotation. If it exists and if it is mapped onto the cortex in such a way that each side of the object is represented on the contralateral hemisphere, then lesions should automatically induce object-centred neglect.

The results presented here, however, demonstrate that object-based neglect does not necessarily imply that an explicit object-based representation has been lesioned in neglect patients. The form of neglect found in the experiment of Arguin & Bub (1993) could be a consequence of *relative* neglect: the apparent object-based effect could be explained by the relative saliency of the subparts of the object.

Relative saliency, however, cannot explain the results obtained by Driver *et al*. (1994) in the experiment depicted in figure 1*c*. In this case, explicit object-centred representations would provide a natural explanation for the behaviour of the patients. There exists, however, an alternative explanation for these results.

The view of an object rotated around an axis perpendicular to the frontoparallel plane can indicate that either the object *or the viewer* is rotated (Li & Matin 1995; Matin & Li 1995). In the latter case, the image is used as a cue to infer the orientation of the head in space. For instance, seeing the horizon tilted is more likely to be the result of the viewer being tilted (flight simulators on computers rely heavily on this
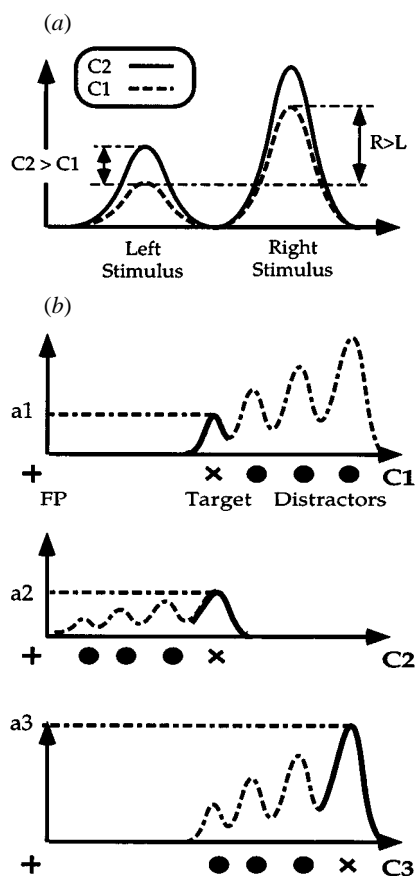
Figure 7. Activity patterns in the retinotopic output layer when simulating the experiments by (*a*) Karnath *et al.* (1993) and (*b*) Arguin & Bub (1993). (*a*) Performance on the left stimulus improved from condition 1 (C1) to condition 2 (C2) because the stimulus saliency increased across conditions. This increase in saliency, however, is not sufficient to match the saliency of the right stimulus in condition 1. (*b*) Reaction time between conditions 1 and 2 decreased, owing to the change in the relative saliency of the target with respect to the distractors, even though the absolute saliency of the target was the same in these two conditions (a1 = a2). FP, fixation point; C3, condition 3.

illusion). It would therefore make sense for the cortex to integrate general orientation cues in the image with vestibular inputs, the main cue for the determination of the head orientation in space. The right hemisphere in this case would favour vestibular rotation to the *right* and image rotation to the *left*.

Therefore, after a right lesion, a head rotation to the right *or* an object rotation to the left would reduce neglect in the same way that head rotation to the right (this time along an axis perpendicular to the coronal plane) improves subjects' performance in the experiment of Karnath *et al.* (1993) (figure 1*a*). There is already evidence that head rotation improves neglect (Ladavas 1987; Farah *et al.* 1990). The experiments by Driver *et al.* (1994) can be interpreted as evidence that rotating an object to the left can have the same effect, assuming that the triangle display illustrated in figure 1*c* engages the neural mechanisms responsible for the determination of the head orientation in space. Note that not all visual stimuli

may have such cues; this could explain why Farah *et al.* (1990) and Behrmann & Moscovitch (1994) have failed to find object-centred neglect when using images such as a rotated rabbit.

It is therefore possible to reconcile the results of Driver *et al.* (1994) with the basis-function approach without invoking explicit object-centred representations. Further research is needed to determine which interpretation is valid.

(i) *Object-centred representation at the single-cell level*

Explicit object-centred representations at the neuronal level appear to be supported by the recent work of Olson & Gettner (1995). They trained monkeys to perform saccades to a particular side of an object (right or left, depending on a visual cue) regardless of its position in space, and subsequently recorded the activity of cells if the supplementary eye field to characterize the neural representation involved in the task.

Olson & Gettner found that some cells responded selectively before eye movements directed to a particular side of an object, a response consistent with an explicit object-centred representation. However, *all* the cells recorded by Olson & Gettner can be interpreted as having an oculocentric motor field—they have bell-shaped tuning to the direction of the next saccadic eye movement, where direction is defined with respect to the fixation point—which is gain-modulated by the side of the object (C. R. Olson, personal communication). In a few cases, the modulation could be so strong that a cell fires when the eye movement is directed to one side of the object but not when it is directed to the other side, even if the direction of the saccade is kept constant across these conditions. Nevertheless, the directional tuning is preserved for saccades directed to the side of the object for which the cell responds, a result consistent with the gain-modulation hypothesis. Therefore, object-centred representations may not fundamentally differ from other spatial representations. In all cases, the response of neurones can be interpreted as being a basis function of the input signals. Nonetheless, whether explicit object-centred representations exist remains an empirical issue. There is no incompatibility between the basis-function approach and explicit representations.

5. DISCUSSION

The model of the parietal cortex presented here was originally developed by considering the response properties of parietal neurones and the computational constraints inherent in sensorimotor transformations. It was not designed to model neglect, so its ability to account for a wide range of deficits is additional evidence in favour of the basis-function hypothesis.

As has been shown in this paper, the model presented here captures three essential aspects of the neglect syndrome: (i) it reproduces the pattern of line crossing of parietal patients in line cancellation and line bisection experiments; (ii) the deficit coexists in multiple frames of reference simultaneously; and (iii) the model accounts for some of the object-based effects. These

results rely in part on the existence of monotonic gradients along the retinal and eye-position axis of the basis-function map. The retinal gradient is supported by recordings from single neurones in the parietal cortex (Andersen *et al*. 1990), but gradients for the postural signals remain to be demonstrated. The retinal-gradient hypothesis is also at the heart of Kinsbourne's theory of hemineglect (Kinsbourne 1987) and some models of neglect dyslexia and line bisection are based on a similar idea (Mozer & Behrmann 1990; Mozer *et al*. 1996).

The basis-function approach can account for many studies beyond the ones considered here by using similar computational principles. It can reproduce, in particular, the behaviour of patients in line-bisection experiments (Halligan & Marshall 1989; Burnett-Stuart *et al*. 1991; Bisiach *et al*. 1994) and a variety of experiments dealing with frames of reference, whether in retinotopic, trunk-centred (Bisiach *et al*. 1985; Moscovitch & Behrmann 1994), environment-centred (i.e. with respect to gravity) (Ladavas 1987; Farah *et al*. 1990), or object-centred coordinates (Driver & Halligan 1991; Halligan & Marshall 1994; Husain 1995). It is also possible to account for the inability of parietal patients to imagine the contralesional side of a visual scene if visual imagery uses a basis-function map as its 'projection screen' (Bisiach & Luzzatti 1978).

In addition, a model with a basis-function map integrating sensory signals with vestibular inputs would also exhibit a temporary recovery after strong vestibular stimulation, as reported in humans after caloric stimulation of the inner ear. The explanation would be identical to that for the performance improvement on left targets observed by Karnath *et al*. (1993) when subjects turn their heads to the right (figures 1*a* and 7*a*).

The results presented in this paper have been obtained without using explicit representations of the various Cartesian frames of reference (except for the retinotopy of the basis-function map). It is precisely because the lesion affected non-Cartesian representations that the model was able to reproduce these results. The lesion affects the functional space in which the basis functions are defined, which shares common dimensions with Cartesian spaces, but cannot be reduced to them. Hence, a basis-function map integrating retinal location and head position is retinotopic, but not solely retinotopic. Consequently, any attempt to determine the Cartesian space in which hemineglect operates is bound to lead to inconclusive results in which Cartesian frames of reference appear to be mixed.

Finally, recent neurophysiological data and theoretical models are raising the possibility that attention plays a role in spatial perception analogous to that of posture signals. Hence, Connor *et al*. (1996) have found that the position of attention in space can modulate the visual response of V4 neurones just as eye position modulates parietal neurones. Salinas & Abbott (1996*b*), as well as Riesenhubber & Dayan (1997), have pointed out that a population of such neurones provides a basis-function representation in which one of the available frames of reference is centred on attention.

If attentional modulation is distributed in such a way that each hemisphere responds preferentially when attention is oriented toward the contralateral side, one would predict that neglect can be influenced by the position of attention in the same way that it is modulated by postural signals. To our knowledge, this conjecture has not been tested on parietal patients but this would certainly be a subject worth investigating.

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