REVIEW ■

Multiple Representations of Space in the Brain

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Lesions of the posterior parietal cortex have long been known to produce visuospatial deficits in both humans and monkeys. Yet there is no known "map" of space in the parietal cortex. The posterior parietal cortex projects to a number of other areas that are involved in specialized spatial functions. In these areas, space is represented at the level of single neurons and, in many of them, there is a topographically organized map of space. These extraparietal areas include the premotor cortex and the putamen, involved in visuomotor space, the frontal eye fields and the superior colliculus, involved in oculomotor space, the hippocampus, involved in environmental space, and the dorsolateral prefrontal cortex, involved in mnemonic space. In many of these areas, space is represented by means of a coordinate system that is fixed to a particular body part. Thus, the processing of space is not unitary but is divided among several brain areas and several coordinate systems, in addition to those in the posterior parietal cortex. The Neuroscientist 1:43–50, 1995

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At the end of World War I, Sir Gordon Holmes (1) described six brain-injured veterans with disturbances of visual and spatial orientation. Their symptoms included deficits in reaching and pointing to visual targets, avoiding obstacles, learning and remembering routes, judging distance and size, recognizing spatial relations, fixating a target, and following a moving stimulus. By contrast, their object recognition ability and other cognitive functions were essentially normal. They all had suffered bilateral penetrating missile wounds of the posterior parietal lobe. Somewhat similar observations had been made previously in both humans and monkeys (2, 3) but Holmes' careful observations and postmortem findings established the critical role of the posterior parietal cortex in visuospatial functions.

Soon afterward, J. Gerstmann (4) published an account of a patient with left parietal damage whose symptoms included right/left confusion and the inability to tell which finger was touched, indicating that the spatial functions of the posterior parietal cortex extended to the body itself. The next major development was the realization by W.R. Brain (5) (Lord Brain, the long-time editor of the journal *Brain*) that unilateral posterior parietal lesions, particularly of the right hemisphere, can produce dramatic neglect of the contralateral side of space, for example, patients often dress or shave only one side of the body, draw one side of a picture, and in general, attend to

only one-half of space, both near and far (6–9). We now know that unilateral neglect can extend to imagery and memory, as Bisiach and Luzzatti (10) demonstrated in a particularly elegant fashion. They asked their Milanese patients with right parietal lesions to imagine they were standing at one end of the Piazza del Duomo facing the cathedral and to describe, from memory, the buildings along the sides of the piazza. The patients described only the buildings on the side contralateral to the intact parietal lobe. However, when asked to imagine they were standing on the other side of the piazza with their backs to the cathedral, they then described only the opposite set of buildings. Similarly, Baxter and Warrington (11) found that parietal patients suffering from neglect of the left side of space were unable to spell the beginnings of short words, as if spelling involved reading from an imaginary screen, the left side of which was faded.

The constellation of spatial deficits after parietal lesions can vary widely from patient to patient (6–9). Particular spatial dysfunctions may occur in isolation or in different combinations. Deficits in localization may be primarily for stimuli on the body, within reach or beyond reach. Deficits in spatial memory may be primarily in short- or long-term memory. The findings that different spatial dysfunctions can occur independently indicate that there must be several different mechanisms for the processing of spatial information. Although the posterior parietal cortex can be subdivided on the basis of cytoarchitecture, anatomical connections, and single-neuron response properties (7, 12, 13), the functions of these subdivisions (Fig. 1) and their relation to the variety of
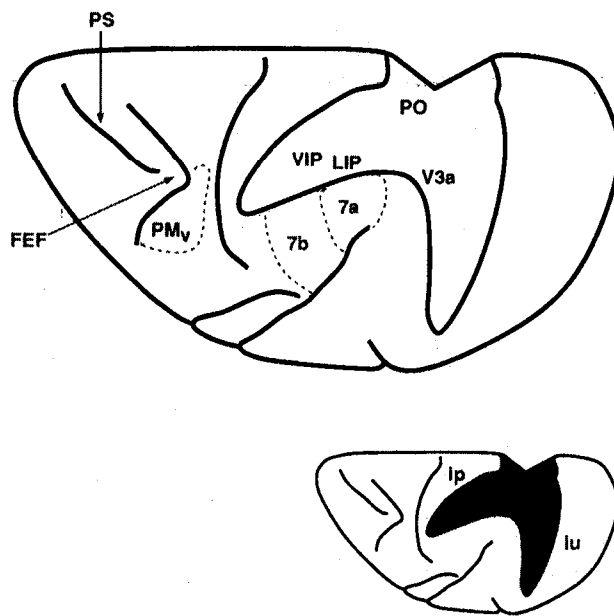
Fig. 1. Dorsal view of the left cerebral cortex of the macaque with the lunate and intraparietal sulci opened, showing some of the cortical areas involved in the processing of space. *FEF*, frontal eye fields (area 8); *LIP*, lateral intraparietal area; *PM*$_v$, ventral premotor area (ventral area 6); *PO*, parieto-occipital area; *PS*, principal sulcus; *VIP*, ventral intraparietal area. In the small brain, the shaded area shows the extent of the buried cortex in the lunate (*lu*) and intraparietal (*ip*) sulci revealed in the main figure.

symptoms after parietal lesions are still unclear in both humans and monkeys.

Parietal Neurons and Space

How do parietal neurons carry information about space? As Sir Gordon Holmes (1) pointed out, in order to calculate the spatial location of an object, it is not enough to know where the visual image falls on the retina. It is also necessary to know where the eyes are pointing and how the head is angled. Andersen and his colleagues (14, 15) found neurons in parietal areas 7a and LIP (Fig. 1) that combine exactly these three signals. The firing rate of these neurons is a function of the position of the stimulus on the retina, the position of the eyes in the orbit, and the angle of the head on the trunk. These neurons carry enough information to specify the location of the stimulus with respect to the head and the trunk. However, this spatial information is not present in the firing pattern of a single neuron. Rather, it is represented by the pattern of firing of a population of such neurons. (More recently, it has been found that the visual responses in other areas, e.g., V1, V3A, and PO, are also a function of both the site of the retinal stimulus and the position of the eyes [16-18].)

In addition to the posterior parietal cortex, there are a number of other brain areas that, on the basis of lesion and single-neuron recording experiments, are known to be involved in the processing of spatial information.

These areas, shown in Figure 2, all receive direct projections from the posterior parietal cortex. In them, space is represented explicitly at the level of single neurons. Indeed, in many of these areas, the neurons are topographically arranged, forming a map of space, unlike in the posterior parietal cortex. These extraparietal areas and their specialized spatial functions are discussed in the following sections. Emphasis is on two areas relatively recently implicated in visuospatial functions, namely, the premotor cortex and the putamen.

Premotor Cortex and the Putamen: Visuomotor Space

In the macaque, the ventral portion of the premotor cortex (area 6) contains neurons that respond to somatosensory stimuli such as light touch. Their tactile receptive fields are arranged to form a crude map of the body surface (19). As first shown by Rizzolatti and his colleagues (20), many of these cells also respond to visual stimuli in the space adjacent to their tactile receptive fields, i.e., they are bimodal, sensitive to both vision and touch (21) (Fig. 3). When the eyes move, the visual receptive fields of these bimodal cells do not move with the eyes; rather, they remain in register with the tactile receptive fields (22, 23) (Fig. 4). That is, unlike most visual cells, their receptive fields are not in retinocentric coordinates. Furthermore, for the majority of cells with tactile receptive fields on the face, when the head moves, the visual receptive fields also move, again staying in register with the tactile fields (24). Similarly, for the majority of cells with tactile receptive fields on the hands or arms, when the arm moves, the visual fields move with the arm, remaining attached to the tactile fields (22, 25) (Figs. 4 and 5). Thus, these premotor cells represent the visual space near the face in "head-centered" coordinates and the space near the arm in "arm-centered" coordinates. (A few neurons in various parietal areas have also been reported to have visual receptive fields that do not move when the eyes move, but whether they are anchored to the head, arm, another body part, or some external landmark is still unclear [18, 26, 27].)

In the putamen, there is also a somatotopic map of the body, which has a more fine-grained topographic organization than that in the ventral premotor cortex (28). Furthermore, as in the premotor cortex, the putamen contains many bimodal visuotactile cells that have visual receptive fields that are immediately adjacent to the tactile fields on the head or arms (29). Again, as in the premotor cortex, the visual receptive fields on the arm move as the arm moves: They code the adjacent space in an arm-centered coordinate system. However, the visual fields on the face have not yet been tested with head movement.

The arm-centered neurons in the ventral premotor cortex and the putamen would be useful for hand–eye coordination, such as guiding the arm toward or away
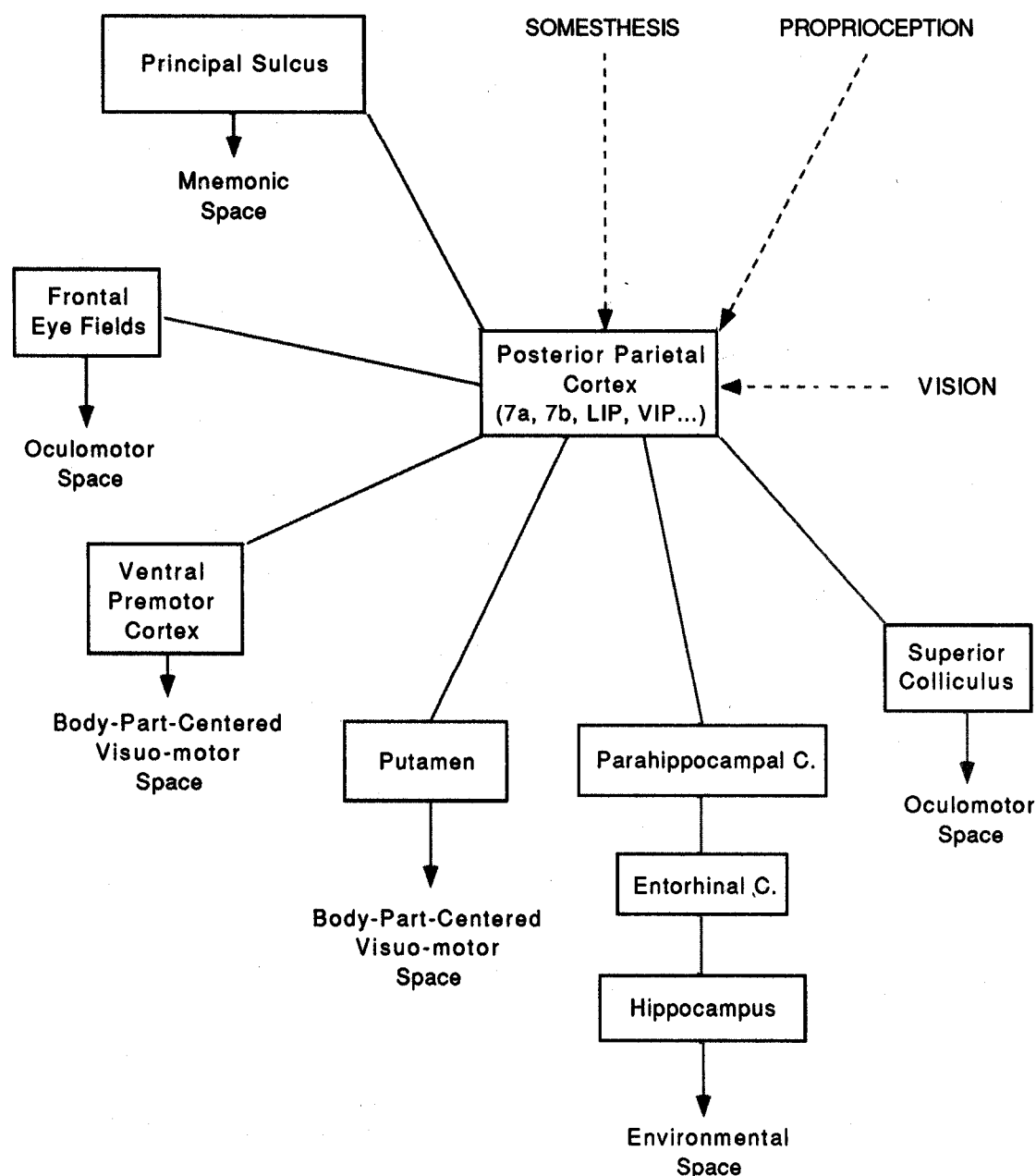
SOMESTHESIS   PROPRIOCEPTION

Principal Sulcus

Mnemonic
Space

Frontal
Eye Fields

Posterior Parietal
Cortex
(7a, 7b, LIP, VIP...)

VISION

Oculomotor
Space

Ventral
Premotor
Cortex

Superior
Colliculus

Body-Part-Centered
Visuo-motor
Space

Putamen

Parahippocampal C.

Oculomotor
Space

Body-Part-Centered
Visuo-motor
Space

Entorhinal C.

Hippocampus

Environmental
Space

Fig. 2. Brain areas involved in the processing of information about space. Somesthetic, proprioceptive, and visual information are brought together in various areas of the posterior parietal cortex, which project to extraparietal structures for further, more specialized, processing of spatial information. All the connections shown are monosynaptic. Not shown are the interconnections among the different targets of the parietal cortex, such as between ventral area 6 and the putamen and between the frontal eye fields and the superior colliculus.

from visual targets. Indeed, a high proportion of the neurons in both areas are active during voluntary movement (30). In the premotor cortex, cells that are active during movements of the arm are spatially tuned, responding best when the arm reaches into a particular region of space, the cell's "motor field" (31). When the arm is shifted to a different location, this motor field also shifts, rotating, on average, by the same angle that the shoulder has rotated. That is, the motor response fields are in arm-centered coordinates, just as are the

visual receptive fields. Thus, the arm-centered bimodal neurons of the ventral premotor region and the putamen appear to be part of a visuomotor control system, encoding the location of the target in the same coordinate system as is used to control the arm.

In a similar fashion, the head-centered visual receptive fields in the premotor cortex, attached to tactile receptive fields on the face, may be useful for visuomotor coordination, such as in biting food or enemies, flinching from approaching objects, heading soccer
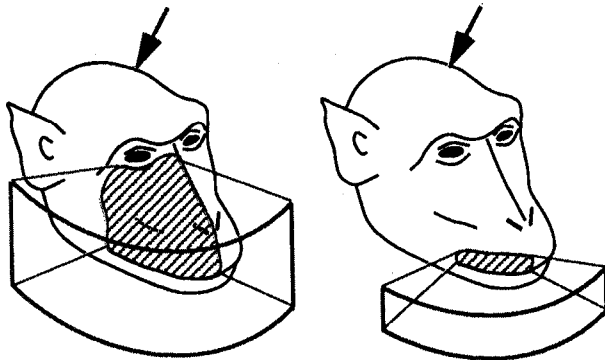
Fig. 3. Typical bimodal receptive fields of ventral premotor (area 6) neurons. The tactile receptive field (*striped*) and the visual receptive field (*boxed*) are in register (21, 22). The *arrow* indicates the hemisphere in which the recording was made. Virtually identical receptive fields were also found in the putamen (23).

balls, or kissing accurately. Indeed, it would be useful to have neurons with body-part-centered visual receptive fields fixed to each part of the body surface for the purpose of hitting, grasping, or avoiding visual stimuli in the space near that body part.

The somesthetic and visual information required to construct these maps of near extrapersonal space is presumably provided to the premotor cortex and the putamen by the projections from the posterior parietal lobe, particularly from area 7b and area VIP (32, 33). Both 7b and VIP contain bimodal, visuotactile neurons with visual fields in close association with the tactile fields, just as are found in the ventral premotor cortex and the putamen (21, 34, 35). Together, these areas form a distributed system for representing the space near the body. Malfunctions of this system must be the basis of the reaching and other visuomotor deficits that follow lesions of the posterior parietal cortex, diseases of the basal ganglia (8, 36), and damage to the premotor cortex (37).

Frontal Eye Fields, Superior Colliculus, and LIP: Oculomotor Space

The frontal eye fields and the deep layers of the superior colliculus are crucial for the control of saccadic eye movements. Each is topographically organized, presumably to help locate targets for saccades (38, 39). Another area that is involved in guiding saccadic eye movements is LIP, which lies in the posterior parietal cortex (Fig. 1) and is a major source of input for both the frontal eye fields and the superior colliculus (32, 40–42). The oculomotor disorders that follow parietal lesions in both humans and monkeys are presumably due to the deafferentation of the saccadic mechanisms in the frontal eye fields and the colliculus as well as damage to oculomotor areas, such as LIP, in the posterior parietal cortex itself.

In all three areas, the movements of the eye are guided by visual receptive fields that are fixed to the

eyeball, just as movements of the arm may be guided by receptive fields in the premotor cortex and the putamen that are fixed to the arm. As shown by Duhamel et al. (41) in area LIP, this correspondence between the position of the receptive fields and of the eye is unu-
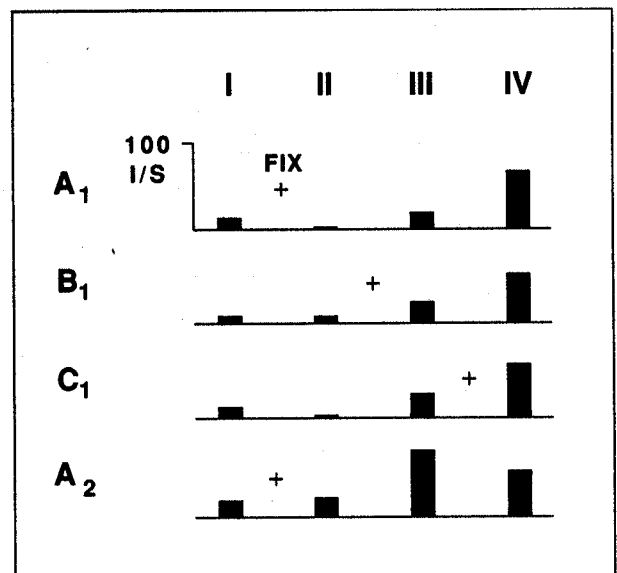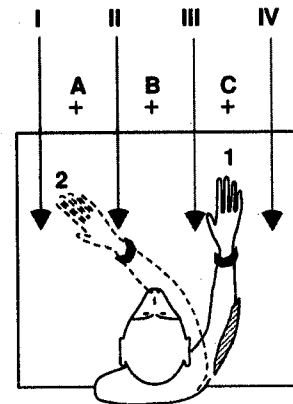

Fig. 4. *Top*, experimental paradigm for studying the effect of hand and eye position on the visual responses of neurons in the ventral premotor cortex of the awake monkey. On each trial, the animal fixated one of three lights 20 degrees apart (*A*, *B*, or *C*) and the stimulus was advanced along one of four trajectories (*I-IV*). The arm was fixed in one of two positions (*1* or *2*). The *striped area* shows the tactile receptive field of the cell whose responses are illustrated below. *Bottom*, histograms of neuronal activity in impulses per sec (*I/S*), summed over 10 trials, as a function of eye position (*A*, *B*, *C*), stimulus position (*I-IV*), and arm position (on the right in A_1, B_1, and C_1, and on the left in A_2). *FIX* indicates the location of the fixation light. When the arm was on the right, the neuron responded best to the right-most stimulus trajectory (*IV*), whether the eye looked to the left (as in A_1), to the center (as in B_1), or to the right (as in C_1). However, when the arm was placed to the left (A_2), the neuron responded best to stimulus trajectory *III*; that is, the visual receptive field moved toward the left with the tactile receptive field (22).
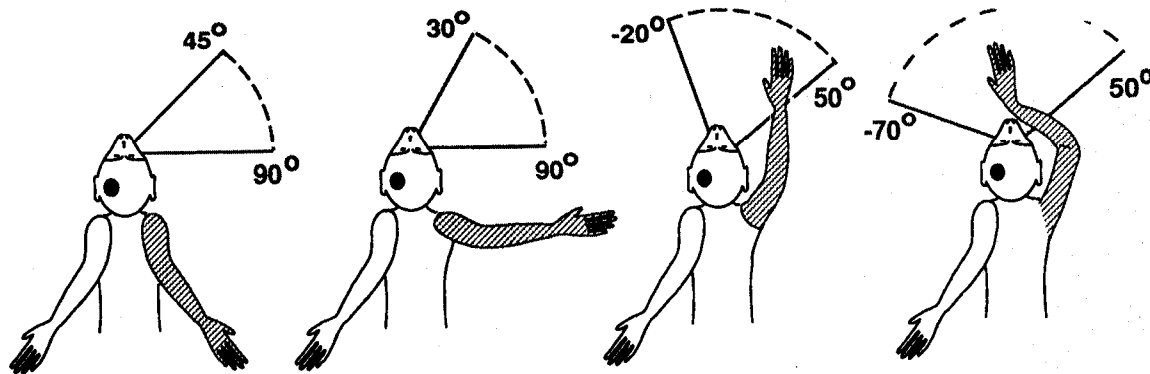
Fig. 5. Effect of arm position on the location of the visual receptive field of a bimodal cell in the ventral premotor cortex of an anesthetized monkey with immobilized eyes. The *black dot* indicates the hemisphere in which the recording was made. The tactile receptive field is *striped*. The lateral borders of the visual receptive field are shown in *solid lines*, and their deviation from the midline is indicated in *degrees*. As the arm was moved to the left (ipsilateral to the recording site), the visual receptive field also moved leftward into the ipsilateral field. That is, the visual receptive field moved across the retina and thereby remained in register with the tactile receptive field (22).

sually close; for many LIP neurons, the visual receptive field moves simultaneously with the eye. This is in contrast to the typical visual neuron that responds with considerable latency after an eye movement brings a visual stimulus into its receptive field. Some LIP receptive fields actually move before the eye moves, thereby anticipating the saccade. Both these properties of LIP neurons are examples of reafference or corollary discharge: The signal to the oculomotor system sends a parallel command to adjust receptive field position for the simultaneous or upcoming eye movement.

In addition to their visual responses, neurons in the frontal eye fields, colliculus, and LIP also respond to localized auditory stimuli, presumably to help guide saccadic eye movements to sound sources (43–45). These spatial auditory receptive fields are anchored to the eyeball, shifting as the animal looks in different locations (46).

All three eye movement areas also contain cells that continue to fire after a visual stimulus is extinguished, especially if the monkey is required to remember the location of the stimulus (39, 41, 47). These cells appear to be maintaining a memory trace of stimulus location. Figure 6 shows one paradigm used to study these cells (48). In T_1, the monkey fixates a small spot (shown by the plus sign) and another stimulus is flashed at the point indicated by the asterisk. The neuron does not respond, because the stimulus is outside of the receptive field (whose location is shown by the circle). In T_2, the monkey is required to fixate a new location and consequently the receptive field of the cell moves with the eye. In its new location, the receptive field is now aligned with the remembered location, and, therefore, the neuron responds. No visual stimulus has actually entered the receptive field of the cell; rather the cell is activated by the "memory" of the stimulus. Presumably, this memory activation results from a combination

of inputs from other visual neurons and information about the previous position of the eye.

In summary, neurons involved in programming saccadic eye movements have receptive fields that are anchored to the eye. Even the auditory and memory fields are eye centered, just like the visual ones. In other words, these brain areas, like the putamen and premotor cortex, use body-part-centered coordinate systems; the body part in this case being the eyeball. A general principle of sensory-motor control appears to be that a sensory stimulus is located by means of a coordinate system that is anchored to the relevant body part.

The Hippocampus: Environmental Space

At least in rats, the hippocampus is critical for learning to navigate through a complex spatial environment (49). Furthermore, many hippocampal neurons have
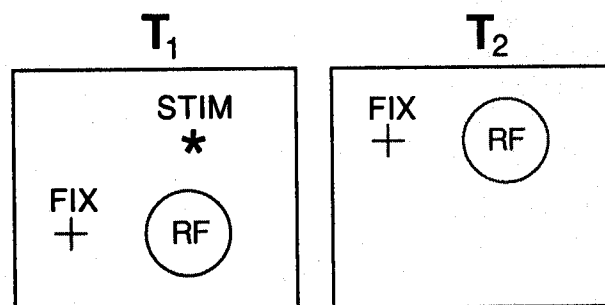

Fig. 6. Experimental paradigm used to study cells that are activated by the memory of a stimulus. T_1, condition at the start of the trial. *FIX* indicates the fixation point; *RF* indicates the visual receptive field of a cell; *STIM* indicates the site at which a stimulus is flashed. As the stimulus is outside the receptive field, the cell does not respond. T_2, the fixation point is now moved to a new locus such that the site of the previously flashed stimulus falls within the receptive field of the cell. If the cell has "mnemonic" properties, it will now fire, although no stimulus falls within the receptive field (48).

remarkable spatial properties, originally discovered by O'Keefe (50); each neuron responds only when the animal is in a particular small region of his environment, the "place field" of the cell. These neurons encode the location of the animal in coordinates of the external world. Ensembles of simultaneously recorded hippocampal cells provide a more accurate representation of space than do individual cells (51). In the monkey, there are hippocampal neurons that have visual receptive fields that appear fixed in space and do not move, even when the animal is moved to a new vantage point in the room. These receptive fields seem to encode the locations of visual stimuli in the external environment (52, 53). In humans, the hippocampus may also have spatial functions (54).

The posterior parietal cortex is the most likely source for the hippocampus's information about space. Parietal areas 7a and LIP project to the parahippocampal cortex, which projects to the entorhinal cortex, which in turn projects to the hippocampus (55, 56). Along this pathway, spatial information in eye and body coordinates is transformed into a coordinate frame that is now based on the external environment. The route-finding difficulties that follow posterior parietal lesions in both humans and monkeys may be due, at least in part, to the deafferentation of the spatial mechanisms of the hippocampus.

Dorsolateral Prefrontal Cortex: Short-Term Mnemonic Space

In the monkey, the dorsolateral prefrontal cortex, specifically the area of the principal sulcus, has long been known to play a role in short-term spatial memory. As originally shown by Lashley's student Jacobsen, lesions of this area produce a severe impairment in spatial delayed response. In this task, the monkey is required to remember, for a few seconds, which of two cups was baited with a raisin (57, 58). Recently, Funahashi et al. (59, 60) have shown that the region of the principal sulcus contains a map of mnemonic space. Neurons in this region respond when the monkey holds the location of a visual target in working memory. Each neuron is sensitive to a particular region of space, its "memory field" (Fig. 7). Furthermore, these memory fields are organized topographically, such that subtotal lesions in the region of the principal sulcus will produce selective scotomas—holes in the monkey's spatial working memory. The principal sulcus receives a dense projection from parietal area 7a, from which it presumably gets the spatial information necessary to construct its mnemonic map (32).

Posterior Parietal Cortex as the Control Center for Visuospatial Functions

In summary, the posterior parietal cortex is where vision, touch, and proprioception come together for the first time. It is the hub of a system for the processing
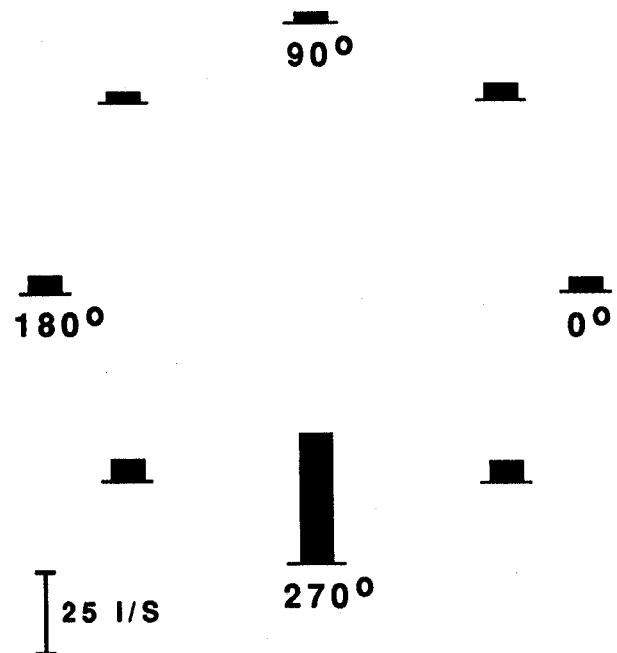

Fig. 7. Mnemonic coding of visual space by a dorsolateral prefrontal neuron. The monkey was trained to perform an oculomotor delayed-response task. After the monkey fixated a central spot, a target was presented for 0.5 seconds at one of eight peripheral locations arranged in a circle and located 13 degrees away from the fixation spot. The animal was required to continue to fixate through a 3-second delay period. At the end of the delay, the animal was signaled to make a saccade to the position where the target had been presented seconds before; that is, the animal was required to remember the location of the target and then to saccade to that remembered location. The *bar graphs* show the mean neuron discharge rate in impulses per second (I/S) during the delay period at each of the eight target locations. This neuron responded only when the target had been presented at 270 degrees (59).

of spatial information. This system includes not only several regions within the parietal cortex, such as areas 7a, 7b, LIP, and VIP and possibly PO, but, as described above, a widespread network of other cortical and subcortical areas, including the ventral premotor cortex, the putamen, the frontal eye fields, the superior colliculus, the hippocampus, and the principal sulcus. These areas are specialized for a variety of different spatial functions, such as visuomotor guidance of limb, eye, and head movements, navigating in the external environment, and holding recent memory about the location of objects in space. They appear to carry on, in specialized fashions, the processing of information about space that is begun in the parietal cortex.

This formulation of how spatial information is organized in the brain helps explain the range and variety of visuospatial deficits after posterior parietal lesions, described at the beginning of this article. Parietal lesions not only directly disrupt the several parietal areas concerned with somatic and visual space, but they also cut off the critical inputs to a widespread system of spatial

mechanisms underlying the perception and memory of space and the visual guidance of behavior.

Acknowledgements

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