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VISION, MOVEMENT, AND THE MONKEY BRAIN

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INTRODUCTION

We find it effortless to reach toward or avoid nearby objects. However, the spatial and visuo-motor computations must be quite complicated, especially since our eyes, head, limbs, body, and the objects themselves may be continually changing positions. How does the brain construct a representation of the visual space surrounding the body, and how does this representation guide movement?

Figure 1 shows some of the brain areas in the Macaque monkey through which information from the retina might reach the motor system (e.g., Desimone and Ungerleider, 1989; Felleman and Van Essen, 1991; Goodale *et al.*, 1994; Kandel *et al.*, 1991; Wise *et al.*, 1985). Inputs from the eye pass through the lateral geniculate nucleus to primary visual cortex (V1). Information about spatial location and movement is further processed by extrastriate visual areas in the so-called dorsal stream. Areas V3A and PO are thought to be involved in analyzing stimulus location, and areas MT, MST and STP are thought to be involved in analyzing stimulus motion. These areas in turn project to several subdivisions of the posterior parietal cortex, shown in black in Figure 1.

The posterior parietal cortex receives much more than just visual input. It also receives tactile, joint, efference-copy, auditory, and vestibular information (for review see Andersen, 1987; Stein, 1991). Because of its multimodal nature, this cortical region is ideally suited to process the space surrounding the body. Indeed, lesions to the posterior parietal cortex in both humans and monkeys produce devastating visuo-spatial and visuo-motor impairments (for review, see De Renzi, 1982; Robertson and Marshall, 1993).

Posterior parietal cortex projects to a variety of areas involved in the further processing of visual space and visuo-motor coordination. These areas include the hippocampus, the lateral prefrontal cortex, the frontal eye fields, the supplementary eye fields, the superior colliculus, the ventral premotor cortex, the supplementary motor area, and the striatum (Bruce, 1990; Goldman-Rakic *et al.*, 1990; Graziano and Gross, 1993; O'Keefe and Nadel, 1978; Schall, 1991; Stein and Meredith, 1993; Tehovnik and Lee, 1993; Wise, 1985). Some of these areas, in turn, modulate the activity of motor structures such as primary motor cortex, the red nucleus, the spinal cord, and eye movement generators in the brain stem (e.g.,

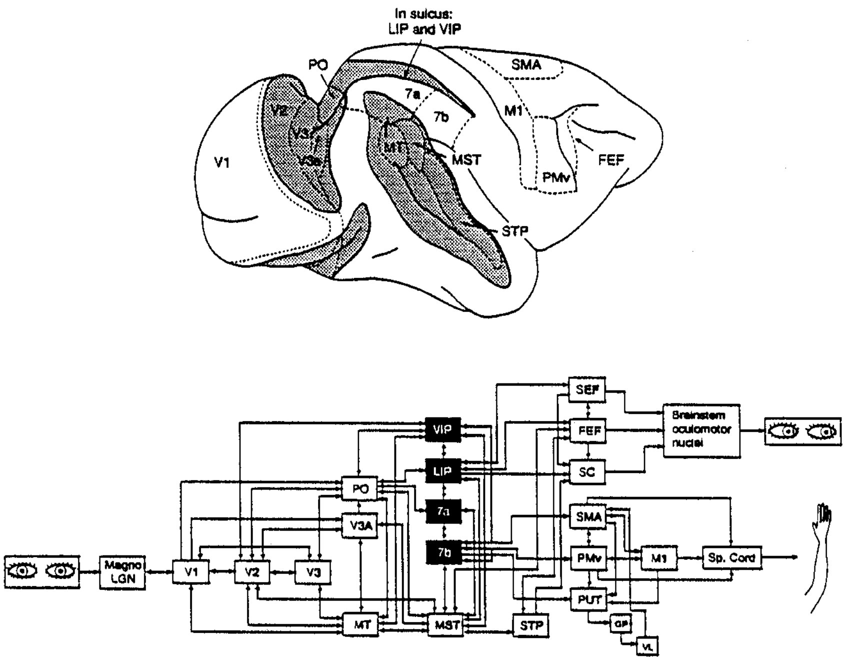

Figure 1 Top. Lateral view of macaque cerebral cortex showing some of the cortical areas involved in the representation of visual space and visuomotor coordination. Major posterior sulci have been "opened up" to show the buried cortex in grey. Bottom. Some of the neuronal pathways by which visual information entering the eye might guide movement of the eyes and limbs. Areas shown in black are in the posterior parietal lobe. SEF, supplementary eye fields; FEF, frontal eye fields; SC, superior colliculus; SMA, supplementary motor area; PMv, ventral premotor cortex; PUT, putamen; GP, globus pallidus; VL, ventrolateral thalamus; STP, superior temporal polysensory area.

Alexander *et al.*, 1986; Georgopoulos, 1991; Kandel *et al.*, 1991; Wise, 1985). Thus, light falling on the retina can eventually result in motor behavior.

When we look at an object, its image is projected through the cornea and lens and evokes neuronal activity on a localized part of the retina. Already, the location of the stimulus is partly encoded; that is, the firing of retinal ganglion cells can signal the location of the stimulus on the retina, in what are called "retinocentric" coordinates. However, if we reach toward that object, we must control the joints and muscles of the arm using a set of motor coordinates. How does the visuomotor system outlined in Figure 1 transform retinocentric coordinates into motor coordinates? The answer would seem to lie primarily in posterior parietal cortex and structures efferent to it. In this paper we discuss some of these areas and how they represent visual and visuo-motor space. Emphasis is on the parietal cortex and on two areas recently implicated in visuo-spatial functions, namely, the putamen (part of the basal ganglia) and premotor cortex.

POSTERIOR PARIETAL CORTEX

As described above, visuo-spatial and visuo-motor functions are severely impaired by lesions to the posterior parietal cortex, in humans and monkeys. The subjects show deficits in reaching and pointing to visual targets, avoiding obstacles, learning and remembering routes, judging distance and size, recognizing spatial relations, fixating a target, following a moving stimulus, localizing a touch on the body, and attending to the contralateral side of space (e.g., Balint, 1909; Brain, 1941; De Renzi. 1982; Holmes, 1918; Robertson and Marshall, 1993). Other cognitive functions, such as object recognition ability, can be essentially normal, depending on whether the lesion is restricted to the parietal lobe or spreads to other areas. How are these spatial functions represented by neurons in parietal cortex?

The first puzzle uncovered by single neuron recording in the parietal lobe was that there is no topographic map of space (for review, see Andersen, 1987; Pouget *et al.*, 1993; Stein, 1991). There is not even a map of the retina such as can be found in lower-order visual areas. Instead there are a multiplicity of non-topographically organized areas, each of which has slightly different response properties (Colby and Duhamel, 1991). The second puzzle was that the activity of any one neuron did not seem to correlate with the location of a visual stimulus in space. How, then, can the posterior parietal cortex encode visual space?

The first set of experiments to suggest a possible code for visual space in the parietal cortex were carried out by Andersen and his colleagues (Andersen *et al.*, 1985, 1993). They studied the visual receptive fields of neurons in posterior parietal area 7a and found that when the eye moved, the visual receptive fields also moved, anchored to the retina. That is, the neurons encoded the locations of visual stimuli in retinal coordinates. In addition to this visual information, neurons in area 7a also carried proprioceptive information about the position of the eyes. For one class of neurons, the firing rate was directly proportional to the angle of the eyes. For a second class of neurons, the angle of the eyes had an indirect effect, gating the ability of the neuron to respond to visual stimuli. These neurons became relatively unresponsive when the eyes were angled one direction, but were highly visually responsive when the eyes were angled the opposite direction. A similar modulation by eye position has since been reported for a number of other visual areas, including LIP, PO, V3a, V1 and the lateral geniculate nucleus (Andersen *et al.*, 1990; Galletti and Battaglini, 1989; Galletti *et al.*, 1993; Lal and Friedlander, 1989; Trotter *et al.*, 1992). Further studies of area 7a and the adjacent LIP showed that some neurons are also modulated by the angle of the neck on the body, and some by vestibular input during rotations of the head

(Andersen *et al.*, 1993; Brotchie *et al.*, 1995). There is evidence that neurons in 7a may also be modulated by the position of the arm (MacKay, 1992).

Thus the spatial code in the parietal cortex may consist of retinocentric receptive fields that are modulated by kinesthetic input about the position of parts of the body. It has been suggested that the information carried by these neurons could be used to reconstruct the locations of visual stimuli with respect to the head, the trunk, and even with respect to the external world (Andersen *et al.*, 1993).

Galletti *et al.* (1993) proposed a different solution for the role of posterior parietal cortex in spatial cognition. They studied visually responsive cells in area PO, in the parieto-occipital sulcus, and found that for a small percentage of cells, the visual receptive fields did not move when the eyes moved. Instead, these receptive fields remained anchored to one location in space. The firing of one of these cells would therefore signal the presence of a stimulus at that particular spatial location. The investigators concluded that these visual receptive fields must be fixed with respect to the head, coding space in head-centered coordinates. However, they did not test the crucial prediction of their idea: namely, that their putative head-centered receptive fields would move when the head was rotated. Thus, although these receptive fields did not move with the eyes and therefore were not in a coordinate system centered on the retina, they might have been in a coordinate system centered on the chest, the arm, the leg, or some external landmark. There is no evidence that they were centered on the head.

Duhamel *et al.* (1992) have proposed yet another function for posterior parietal cortex. In their view, parietal cortex, particularly area LIP, does not encode external space at all. Instead, it encodes the locations of visual images on the retina, and helps to guide movements of the eye. The proprioceptive, efferent-copy, and vestibular information present in parietal cortex, according to this view, is used to predict how the visual image will shift across the retina as a result of head and eye movements.

What is most striking about these different experiments and viewpoints is that there is no obvious, single code for space in the parietal cortex. All of these studies show that the parietal areas *contain enough information* to encode space, but whether objects are located in a coordinate frame centered on the eye, the head, the chest, or the external world, and whether that coordinate frame is represented in a distributed fashion across many neurons, or represented by means of individual spatial receptive fields, is still in dispute. We suggest that the reason for this ambiguity is that the posterior parietal cortex is an intermediate stage in the processing of space, for which there is no single coordinate system, and for which visual space has not yet been represented in the form of spatial receptive fields arranged in a topographic map (Gross and Graziano, 1995). On this view, projections from parietal cortex distribute an implicit, partially processed spatial information to other areas, which construct their own, special purpose maps, variously gaze-centered, head centered, trunk-centered, or world-centered. The following sections describe two of these target areas, the putamen and the ventral premotor cortex. Unlike posterior parietal cortex, each of these areas contains a topographic map of visual-motor space.

PUTAMEN

The putamen is a large subcortical structure in the forebrain, part of the basal ganglia, and thought to be involved in the control of movement (for review, see Alexander *et al.*, 1986). Somatosensory and motor cortex project to the putamen in a topographic fashion (Jones *et al.* 1977; Kemp and Powell 1970; Kunzle 1978; Liles and Updyke 1985). The putamen then projects to the globus pallidus, which in turn projects to the ventro-lateral thalamus, which projects back to motor areas in the cortex, especially to the supplementary motor area (SMA) (see Figure 1). Crutcher and Delong (1984a,b) recorded from single neurons in the putamen and found a somatotopic map of the body. The hind limbs are represented dorsally, the trunk and forelimbs are represented in the middle, and the face is represented ventrally. Most putamen neurons respond to joint movement or deep muscle pressure, and many will respond only when the animal makes a voluntary movement (Alexander 1987; Crutcher and DeLong 1984b; Kimura *et al.*, 1992; Liles 1985; Schultz and Romo 1988). Electrical stimulation of the putamen causes movement of the corresponding body part (Alexander and DeLong 1985a,b). Because of these anatomical and physiological properties, the putamen has been considered largely a somatomotor structure (eg, Alexander *et al.* 1986).

As shown in Figure 1, the putamen also receives direct projections from parietal area 7b, which contains visually responsive neurons. (Weber and Yin 1984; Cavada and Goldman-Rakic 1991; Hyvarinen 1981; Hyvarinen and Poranen 1974; Leinonen *et al.* 1979; Leinonen and Nyman 1979; Robinson and Burton 1980a,b). Are there visual neurons in the putamen? We recorded from the putamen both in anesthetized and awake macaque monkeys, and found that about 30% of the neurons in the face and arm region of the somatotopic map responded to visual stimuli (Graziano and Gross, 1993; Graziano and Gross, 1995). Visual and tactile responses were usually combined in a single neuron, and for these bimodal neurons, the location of the visual receptive field usually matched the location of the tactile receptive field.

A typical example of a bimodal cell is shown in Figure 2. The tactile receptive field, located on the cheek, was plotted while the animal's eyes were covered. When the eyes were uncovered, the cell responded to visual stimuli placed within about 10 cm of the cheek. We termed this type of neuron a "face+visual" cell. We also found bimodal cells with tactile responses on the arm and the hand, that is, "arm+visual" cells.

The bimodal neurons in the putamen can encode the locations of visual stimuli within reaching distance of the body. Since the visual receptive fields are generally large, each one provides only relatively crude information about stimulus location.

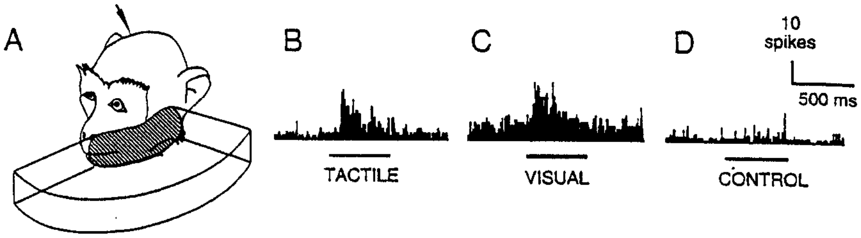

Figure 2 Peri-stimulus time histograms, summed over 10 trials, for a typical bimodal putamen cell. A. The tactile receptive field (stippled) and the visual receptive field (boxed) are in register. The arrow indicates the hemisphere recorded from. B. Response to touching the face with the eyes covered. C. Response to a stimulus approaching the face within 10 cm with the eyes open. Background activity increased when the eyes were uncovered, even before the stimulus (underline) was presented. D. Same as C but with the eyes covered (Graziano and Gross, 1993).

However, a population of overlapping receptive fields could localize stimuli precisely. Even the distance from the animal to the stimulus could be encoded precisely, since different cells have receptive fields that extend to different depths. Why should the putamen contain such a map of visual space? The putamen is a motor structure, and a high proportion of its neurons respond during voluntary movement (e.g., Alexander, 1987; Crutcher and Delong, 1984a). One possibility, therefore, is that these bimodal cells function to locate visual stimuli for the purpose of making movements toward or away from them.

VENTRAL PREMOTOR CORTEX

The ventral premotor cortex (PMv) is thought to be involved in sensory-motor integration (Wise, 1985). Its neurons respond to somatosensory stimuli and are also active during voluntary movement (e.g., Caminiti *et al.*, 1990; Gentilucci *et al.*, 1988; Rizzolatti *et al.*, 1988; Wise, 1985). The lateral part of PMv contains a somatosensory and motor representation of the face, and the medial part contains a representation of the arms (Gentilucci *et al.*, 1988; Rizzolatti *et al.*, 1988). As first shown by Rizzolatti *et al.* (1981) and subsequently corroborated by our own studies (Graziano, Yap and Gross, 1994), many of the somatosensory cells in PMv also respond to visual stimuli. That is, the neurons are bimodal. As for the case of neurons in the putamen, the bimodal neurons in PMv have matching visual and tactile receptive fields. The most likely source for this visual input is parietal area 7b, which projects densely to PMv (Cavada and Goldman-Rakic, 1989; Matelli *et al.*, 1986; Parthasarathy, 1992).

Fogassi, Rizzolatti and colleagues (1992) found that the visual receptive fields

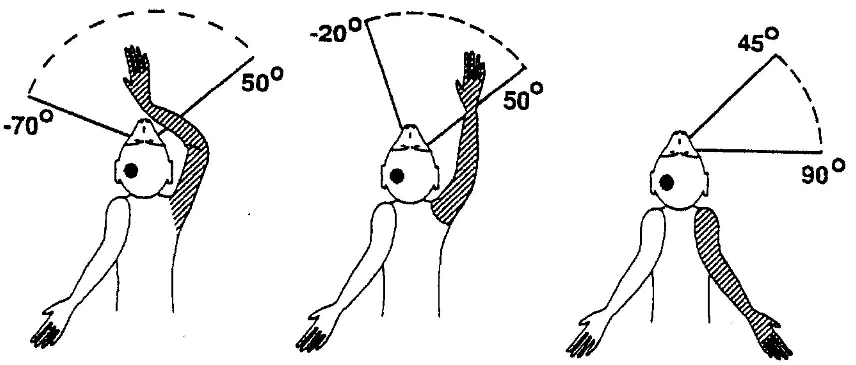

Figure 3 Tactile receptive field (shaded) and visual receptive field (solid lines) for a bimodal cell in PMv of an anesthetized monkey. When the arm was moved to different locations, the visual receptive field moved with it, remaining in approximate register with the tactile field on the arm. The black dot indicates the hemisphere recorded from (Graziano, Yap and Gross, 1994).

of most PMv cells did not move when the monkey moved its eyes. Rather, the receptive fields seemed to be stationary in space. On this basis the investigators suggested that the receptive fields were fixed to the head, or possibly the trunk, and therefore coded space in head- or trunk-centered coordinates rather than in coordinates centered on the retina. However, this idea remained untested because the investigators did not study the effect of head and trunk movement. Head-centered visual receptive fields should move when the head is rotated, and trunk-centered receptive fields should move with the trunk.

We tested PMv cells while manipulating the positions of various body parts including the arm, the head, and the eyes (Graziano, Yap and Gross, 1994). Figure 3 shows an example of a cell studied in an anesthetized monkey whose eyes were focused straight ahead. The tactile receptive field covered the contralateral arm. When the arm was placed in different locations, the visual receptive field also changed location, remaining in rough register with the arm. Clearly, this visual receptive field was not fixed to one site on the retina; that is, it was not retinocentric. But it was also not head- or trunk-centered, as had been proposed by Rizzolatti and colleagues. Instead, it was arm-centered, encoding the locations of visual stimuli with respect to the arm.

Figure 4 (left) shows the paradigm that we used to test the effect of eye position and arm position in awake monkeys (Graziano, Yap and Gross, 1994). The visual receptive field was plotted by means of a ping-pong ball that was mounted on a robot arm and advanced toward the monkey along various trajectories. In general, PMv cells responded vigorously as the ping-pong ball entered their visual receptive fields. The effect of eye position was studied by requiring the monkey

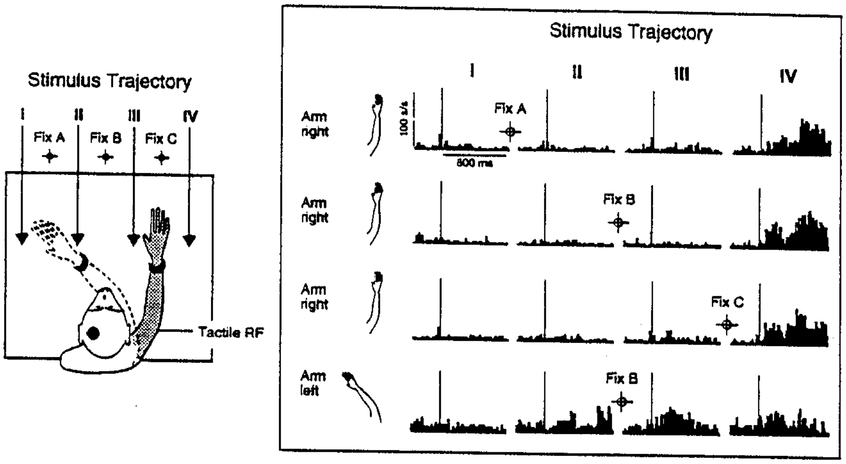

Figure 4 Left. Experimental paradigm for testing cells with receptive fields on the arm. On each trial the animal fixated one of three lights 20° apart (A, B or C) and the stimulus was advanced along one of four trajectories (I-IV). The arm contralateral to the recording electrode was either fixed straight ahead or bent leftward across the chest. The stippling shows the tactile receptive field of the cell illustrated on the right. Right. Histograms of neuronal activity, summed over 10 trials, as a function of eye position (A, B, C), stimulus position (I-IV) and arm position (right or left). The vertical lines indicate stimulus onset. When the arm was fixed to the right, the neuron responded best to the right most stimulus trajectory (IV), whether the eye looked to the left (A), to the center (B), or to the right (C). When the arm was bent leftward across the chest, the visual receptive field also extended across the chest.

to fixate on one of three lights, A, B or C, spaced 20° apart along the horizontal meridian. The effect of arm position was studied by testing the cell while the arm was strapped in one position, and then strapping the arm into a new position and testing the cell again.

Figure 4 (right) shows the result for a neuron with a tactile receptive field on the contralateral arm. The visual response remained at the same location near the arm, whether the eyes fixated on light A, light B, or light C. That is, even a 40° shift in eye position failed to change the location of the visual receptive field. However, when the arm was bent toward the left, the visual response moved with the arm. Therefore, this visual receptive field was centered on the arm, not on the retina. Most of the arm+visual cells tested (70%) showed a significant movement of the visual receptive field with the arm.

For cells with a tactile response on the face, such as the one illustrated in Figure 5, we tested the effect of rotating the head to the right or the left by 15 degrees, and found that in most cases (95%) the visual receptive fields moved with the head. By contrast, when we placed the arm in different locations or

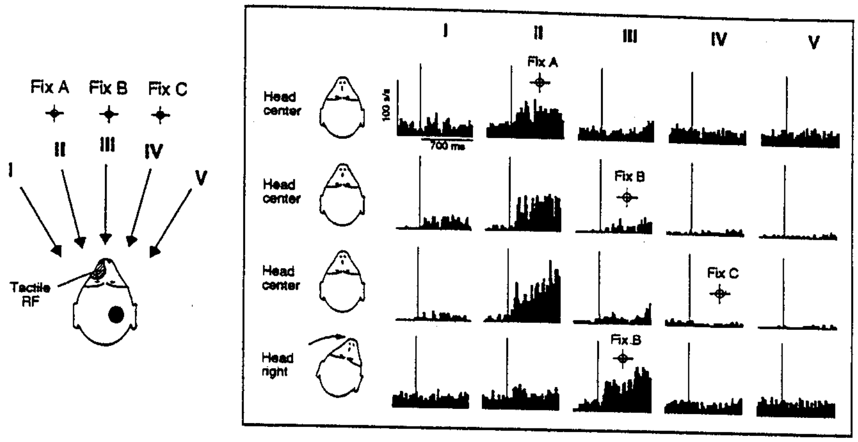

Figure 5 Left. Experimental paradigm for testing cells with receptive fields on the face. On each trial the animal fixated one of three lights 15° apart (A, B or C) and the stimulus was advanced along one of five trajectories (I-V). The head was fixed in one of three positions 15° apart. The stippling shows the tactile receptive field of the cell whose responses are illustrated on the right. Right. Histograms of neuronal activity, summed over 10 trials, as a function of eye position (A, B, C), stimulus position (I-V) and head position. When the head was straight, the neuron responded best to the stimulus II, whether the eye looked to the left (A), to the center (B), or to the right (C). However, when the head was fixed to the right, the neuron responded best to stimulus trajectory III. That is, the visual receptive field moved with the head.

required the animal to look in different directions, the visual receptive fields remained stationary, fixed with respect to the head. Therefore, these receptive fields associated with the head are indeed in head-centered coordinates.

Based on these results we propose that PMv and possibly the putamen use more than one visual coordinate system. Cells related to the arm use arm-centered coordinates, locating visual stimuli with respect to the arm; and cells related to the face use head-centered coordinates, locating stimuli with respect to the head. Perhaps portions of dorsal premotor cortex represent space around the legs in leg-centered coordinates. What function might such a "body-part-centered" representation of space serve? Arm-centered neurons would be useful for hand-eye coordination, guiding the arm toward or away from visual targets. Indeed, a high proportion of neurons in the putamen and PMv are active during reaching (e.g., Alexander *et al.*, 1987; Wise *et al.*, 1985). In PMv, the cells are spatially tuned, responding best when the arm reaches into a particular region of space (Caminiti *et al.*, 1990). When the starting position of the arm is changed, this motor field also moves, maintaining the same spatial relationship with the arm. That is, just

MULTIPLE BRAIN AREAS FOR THE REPRESENTATION OF SPACE

In summary, posterior parietal cortex is where vision, touch, proprioception, vestibular sensation, and efference-copy come together for the first time. It is the hub of a system for the processing of spatial information. This system includes not only several regions within parietal cortex such as areas 7a, 7b, LIP, and VIP and possibly PO, but also a widespread network of other cortical and subcortical areas, including ventral premotor cortex, the putamen, the frontal eye fields, the superior colliculus, the hippocampus (O'Keefe and Nadel, 1978) and the principal sulcus (Goldman-Rakic *et al.*, 1990). These areas are specialized for a variety of different spatial functions such as visuomotor guidance of limb and eye 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 lobe.

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