# Attention and Performance XVI

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# 8 Multiple Pathways for Processing Visual Space

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## ABSTRACT

In the macaque, neurons in ventral premotor cortex and in the putamen have tactile receptive fields on the face or arms, and corresponding visual receptive fields that extend outward from the tactile fields into the space near the body. For cells with tactile receptive fields on the arm, when the arm is moved, the corresponding visual receptive fields move with it. However, when the eyes move, the visual receptive fields remain stationary, "attached" to the arm. We suggest that these "arm-centered" visual responses play a role in visuomotor guidance. We predict that other portions of the somatotopic map in premotor cortex and in the putamen contain similar receptive fields, centered on the corresponding body parts. This "body-part-centered" representation of space is only one of several ways in which space is represented in the brain.

## 8.1 INTRODUCTION

Where is space represented in the brain? A variety of sites have been implicated, including the inferior parietal lobe, the hippocampus, the superior colliculus, the frontal eye fields, and dorsolateral prefrontal cortex (Andersen 1987; Bruce 1990; Goldman-Rakic 1987; Stein and Meredith 1993; O'Keefe and Nadel 1978). Many of these areas appear to represent a specific kind of space for a specific purpose. We propose that the space near the body is represented by neurons in two interconnected brain structures: (1) ventral area 6 in the premotor region of the frontal lobes; and (2) the putamen, part of the basal ganglia.

Area 6 and the putamen have been studied extensively in monkeys (for review, see Alexander, DeLong, and Strick 1986; Wise 1985). Both areas receive topographic projections from somatosensory and motor cortex, and project back to motor cortex, directly in the case of area 6 and indirectly via the globus pallidus and the ventrolateral thalamus in the case of the putamen. Area 6 and the putamen are also directly interconnected (Kunzle 1978; Parthasarathy, Schall, and Graybiel 1992). Both areas are somatotopically organized; their neurons respond to somatosensory stimuli and have receptive fields that are arranged to form a map of the body (Crutcher and Delong 1984a; Gentilucci et al. 1988). Many cells respond during voluntary movement, and electrical stimulation in a part of the map will cause muscle contractions in the corresponding part of the body (Alexander and DeLong 1985a,b; Crutcher and DeLong 1984b; Rizzolatti et al. 1988; Weinrich and Wise 1982; Weinrich, Wise, and Mauritz 1984).

The putamen and area 6 also receive input from visual areas in the posterior parietal lobe (Cavada and Goldman-Rakic 1989, 1991; Kunzle 1978, Matelli et al. 1986; Mesulam et al. 1977; Weber and Yin 1984). About a third of the neurons in the putamen and area 6 are visually responsive, and some are bimodal, responding to both visual and somesthetic stimuli (Gentilucci et al. 1988; Graziano and Gross 1993, 1994a; Graziano, Yap, and Gross 1994; Rizzolatti et al. 1981). For these bimodal cells, the visual receptive field usually matches the location of the somatosensory field and is confined in depth to a region near the body. Thus each of the two areas contains a somatotopically organized map of the visual space that immediately surrounds the body.

In this chapter we describe the properties of bimodal, visual-tactile neurons in the putamen and area 6. We then discuss how these response properties might encode the locations of nearby objects in body-part-centered coordinates. We suggest that the function of these somatotopic visual maps is to faciliate movement within the space near the body (Graziano and Gross 1992, 1994b), that is, they are sensorimotor mechanisms. Finally, we discuss the relationship between these areas and other areas of the brain thought to be involved in the processing of visual space.

## 8.2 BIMODAL, VISUAL-TACTILE RESPONSE PROPERTIES IN THE PUTAMEN

We recorded from single neurons in the putamen of both anesthetized and awake macaque monkeys (Graziano and Gross, 1993, 1994a). Somatosensory receptive fields were plotted by stroking the skin with cotton swabs and manipulating the joints. Visual receptive fields were plotted with small objects mounted on the end of a wand and were tested quantitatively with stimuli presented by a robot. To distinguish a visual response from a tactile response, the cells were also tested with the animal's eyes covered.

### Anesthetized Recording

Of the 354 neurons studied in the putamen of anesthetized, paralyzed monkeys, 40 percent responded only to somatosensory stimuli, 12 percent responded only to visual stimuli, and 24 percent were bimodal, responding to both types of stimuli. The remaining cells did not respond under our test conditions. (See fig. 8.1).

Figure 8.2 shows a representative electrode penetration, passing vertically through the putamen. Cells in the dorsal part of the putamen had somatosensory receptive fields on the tail or legs. As the electrode moved ventrally, we encountered cells with receptive fields on the trunk, then the shoulders

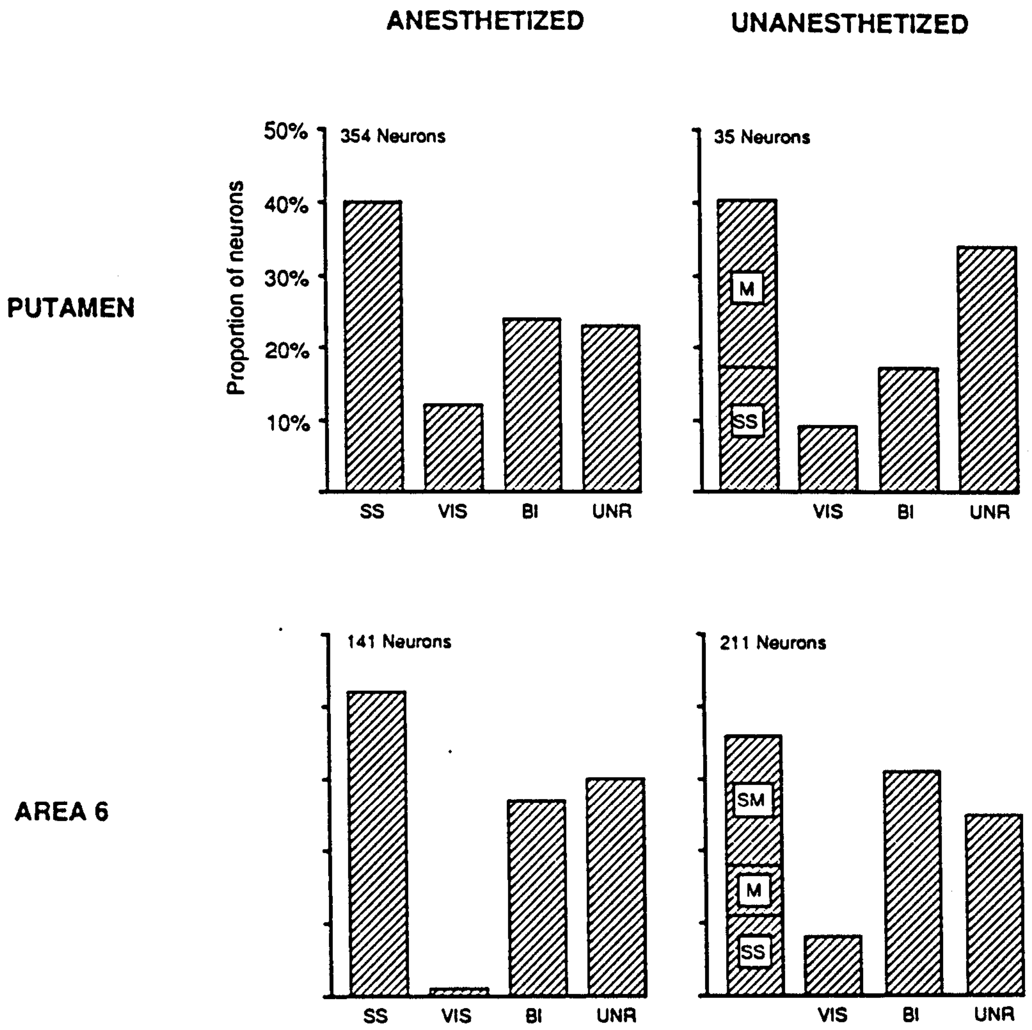

**Figure 8.1** Proportions of cell types in the putamen and area 6, in anesthetized and unanesthetized monkeys. (SS: somatosensory cells; M: motor cells; SM: somatosensory-motor cells; VIS: visual cells; BI: bimodal, visual-somatosensory cells; UNR: unresponsive cells.)

and arms, the face, and finally inside the mouth. A similar somatotopic progression was previously reported by Crutcher and Delong (1984a). However, in our experiments, we found visual and bimodal, visual-somesthetic neurons in the face and arm portions of this somatotopic map (see, for example, fig. 8.2, cells 6, 7, and 8).

The responses of a bimodal cell are shown in figure 8.3. The tactile receptive field was plotted while the animal's eyes were covered. The cell was activated by lightly touching the facial hair, and the responsive region covered most of the contralateral cheek and the area around the mouth (fig. 8.3A and B). When the animal's eyes were uncovered, the cell responded

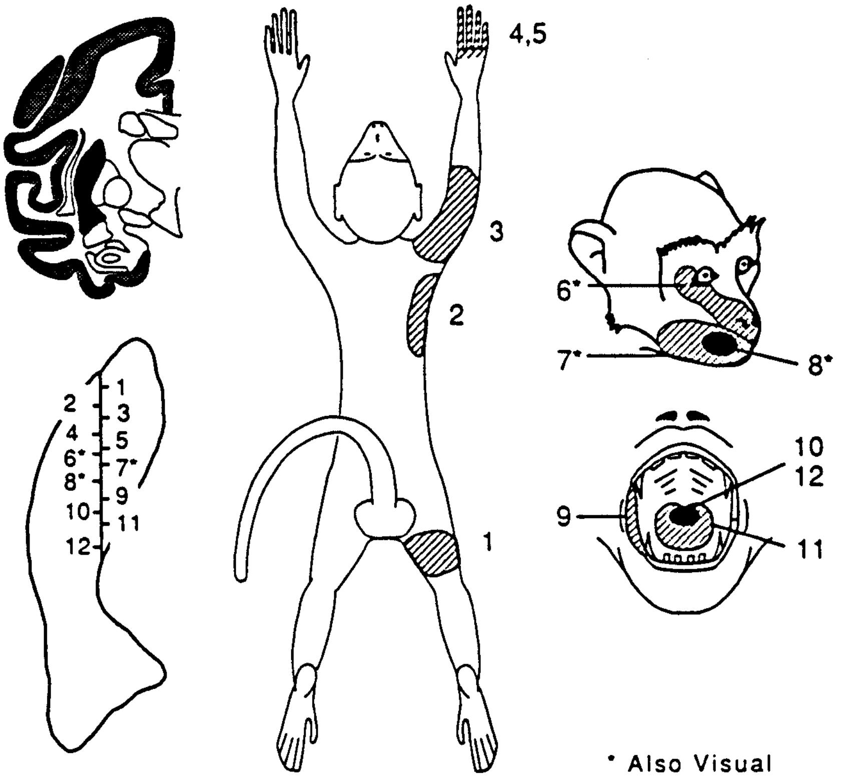

**Figure 8.2** Somatotopic organization of putamen. Left: Coronal section at anterior-posterior level 14, and enlarged view of putamen, showing location of representative electrode penetration. Receptive field locations for neurons are shown to right. Cells indicated with asterisks responded to visual as well as tactile stimuli. (Adapted from Graziano and Gross 1993).

as the stimulus approached the face without touching (fig. 8.3C). This response was not caused by inadvertent tactile stimulation, such as by air movement, since the response was eliminated by covering the eyes (fig. 8.3D). By moving the stimulus toward the tactile receptive field from various angles, we measured the extent of the visual receptive field. This responsive region differed from a classical visual receptive field because it was not only restricted in visual angle but was also limited in depth to within about 10 cm of the face.

Figure 8.4 shows several more examples of bimodal receptive fields on the face. For the cells in figure 8.4A and B, the visual receptive field extended outward about 10 cm from the face. For the cell in figure 8.4C, the visual receptive field extended out about one meter from the monkey.

Figure 8.5 shows several examples of bimodal receptive fields on the arm. The cells shown in figure 8.5A and B had tactile receptive fields on the contralateral arm and visual receptive fields in the contralateral periphery. Both cells responded to visual stimuli as far away as 1.5 m. The cell shown in

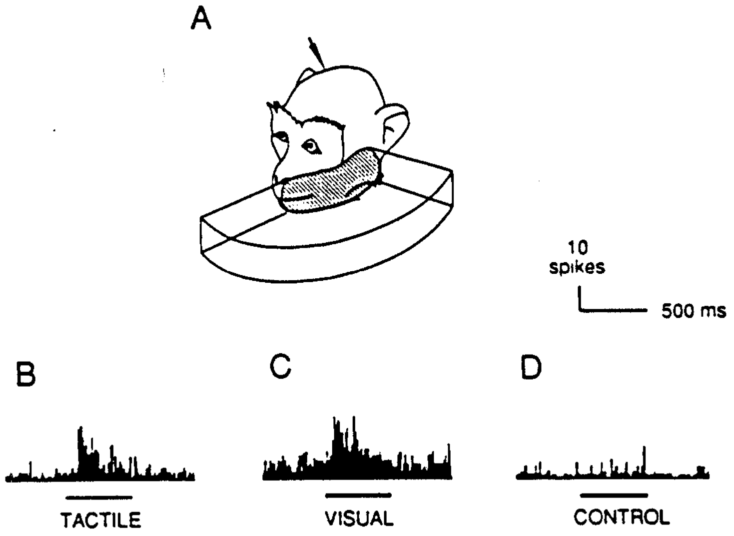

**Figure 8.3** Poststimulus time histograms, summed over 10 trials, for typical bimodal putamen cell. A. Tactile receptive field (stippled) and visual receptive field (boxed) are in register. Arrow indicates hemisphere recorded from. B. Response to cotton swab touching face while eyes are covered. C. Response to cotton swab approaching face within 10 cm while eyes are open. D. Same as C, with eyes covered. (Graziano and Gross 1993).

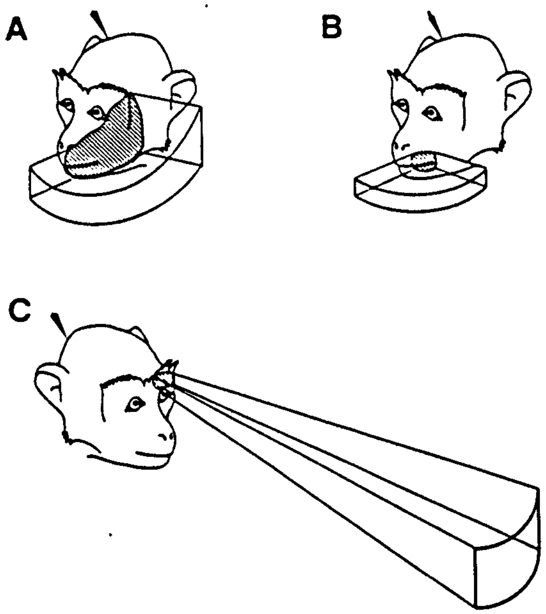

**Figure 8.4** Typical bimodal cells from putamen. In (A) and (B), visual receptive field extends about 10 cm from tactile receptive field. In (C), visual receptive field extends about 1 m from tactile receptive field. (Adapted from Graziano and Gross 1993).

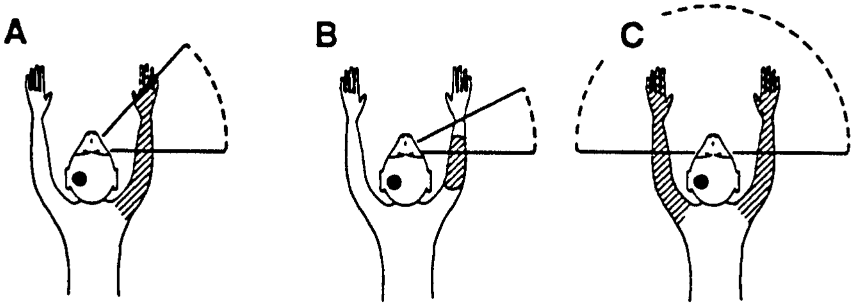

**Figure 8.5** Bimodal cells from putamen with tactile receptive fields on arm. Lines indicate angle subtended by visual receptive fields in horizontal plane. Dashed lines indicate that receptive fields extend farther than 1 m. Stippling shows tactile fields, and black dots on head show hemisphere recorded from. (Adapted from Graziano and Gross 1993).

figure 8.5C responded to touching both arms, and the visual receptive field was bilateral. Again, the cell responded to stimuli as far away as 1.5 m.

How would the cell behave if the arm were moved to a new location? Would the tactile and visual receptive fields become dissociated, or would one receptive field shift in order to remain in register with the other? Figure 8.6 shows the result for two cells. The cell shown in figure 8.6A responded to visual stimuli only when the arm was propped forward in the monkey's field of view. When the arm was tucked back, thus placing the tactile receptive field out of sight, the cell no longer responded to visual stimuli presented anywhere in the visual field. The tactile response, however, was equally good for both arm positions. The cell shown in figure 8.6B had a particularly close match between the tactile and visual receptive field; when the arm was moved to different locations within the animal's sight, the visual receptive field also moved to follow the location of the hand. Of 25 bimodal cells with tactile receptive fields on the arm or hand, 5 had visual responses that depended on the position of the arm.

## Unanesthetized Recording

Previous studies of single neuron activity in the putamen used awake monkeys sitting in a chair (e.g., Alexander 1987; Crutcher and Delong, 1984a,b, Kimura et al. 1992; Liles 1985; Schultz and Romo 1988). Under these conditions, bimodal cells with visual receptive fields near the body were not observed. One possible reason for this oversight is that stimuli moving close to the head or arms would have made the monkey flinch, and any associated neuronal discharge might have been interpreted as motor or somatosensory in nature, rather than visual.

In order to clarify this discrepancy between our results and the previous ones, we recorded in the putamen of an awake monkey whose head was fixed by a head bolt and whose arms were restrained in padded arm rests. Eye position was measured with a scleral search coil, and EMG was measured

**A**

**B**

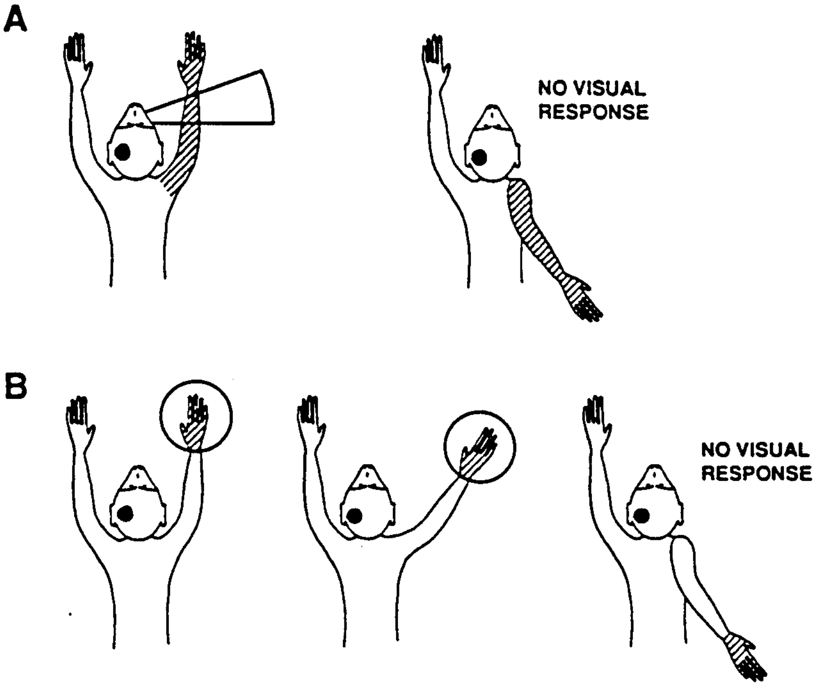

**Figure 8.6** Effects of arm movement on some bimodal arm cells in putamen. These cells responded visually only when arm was within the monkey's field of view (left), but did not respond when arm was moved out of view (right). For cell shown in B, visual receptive field moved as hand moved. (Graziano and Gross 1993).

through surface electrodes pasted over various muscles of the upper and lower arm. The animal was trained to fixate a spot of light during presentation of visual stimuli, which consisted of small objects mounted on the end of a wand and brought near the face, shoulders, arms, or hands at various speeds. After several weeks, the animal became habituated to the presentation of these stimuli and sat quietly, fixating the light.

Although our sample size in this control animal was small (35 neurons), we were able to demonstrate that bimodal neurons with corresponding visual and tactile receptive fields do exist in the awake preparation. For example, the neuron shown in figure 8.7 had a tactile receptive field on the contralateral arm and responded to visual stimuli within about 10 cm of the arm. The rasters and histogram in figure 8.7B show the response as the visual stimulus was moved toward the tactile receptive field. A record of the EMG during one trial is also shown. There was no change in EMG activity during the presentation of the stimulus, that is, this particular cell had a pure sensory response, not associated with voluntary movement.

Figure 8.1 shows the relative proportions of somatosensory, visual, and bimodal cells that we found in the awake animal. These proportions are similar to those found in the anesthetized preparation, except that in the

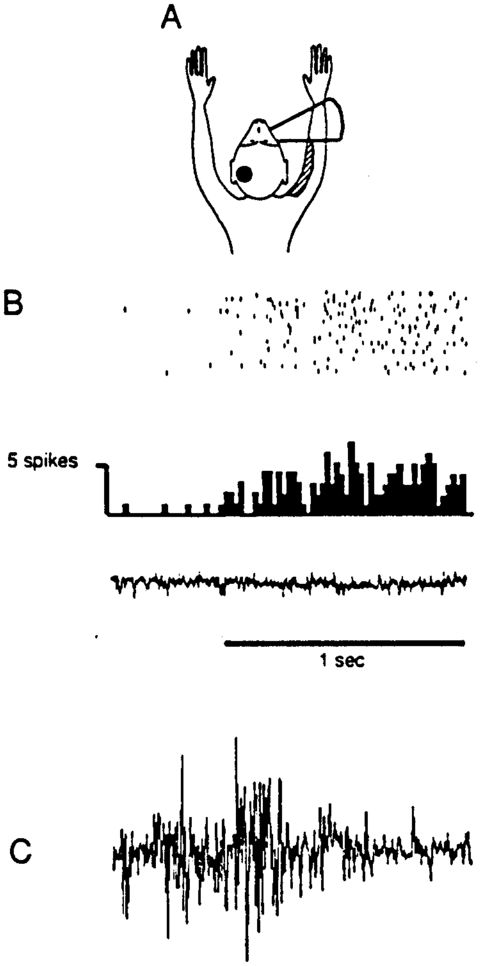

**Figure 8.7** Bimodal neuron recorded from putamen of awake, fixating monkey. A. Visual receptive field was confined within 10 cm of tactile receptive field. B. Neuronal response, based on 20 trials, as visual stimulus approached tactile receptive field. Time bar indicates stimulus duration. EMG trace (palmaris longus muscle), taken from one of 20 trials, shows that arm was stationary during stimulus presentation. C. EMG trace while animal touched grape presented near its fingers. (Graziano and Gross 1994a).

awake animal 23 percent of the neurons fired in relation to active reaching movements of the arm. The relevance of this motor-related activity will be discussed in a later section.

## 8.3 BIMODAL, VISUAL-TACTILE RESPONSE PROPERTIES IN VENTRAL AREA 6

The bimodal, visual-tactile cells we discovered in the putamen are similar to neurons described by Rizzolatti and colleagues in ventral area 6 (Gentilucci

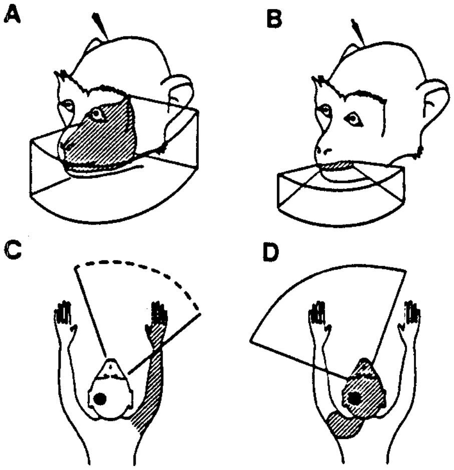

**Figure 8.8** Typical bimodal cells from ventral area 6. Visual and tactile receptive fields correspond spatially, just as for neurons in putamen (see fig. 8.4).

et al. 1988; Rizzolatti et al. 1981). In order to compare the two areas directly, we recorded from area 6 in both anesthetized and awake monkeys, using the same procedures that we used to study the putamen (Graziano and Gross 1994a; Graziano, Yap, and Gross 1994).

## Anesthetized Recording

We found somatosensory cells (42 percent), visual cells (27 percent), and bimodal cells (30 percent) in ventral area 6 of anesthetized, paralyzed monkeys. These proportions are similar to those found in the putamen (see fig. 8.1). The somatosensory receptive fields were somatotopically organized in a manner consistent with previous reports (Gentilucci et al. 1988). When electrode penetrations were made in the lateral part of ventral area 6, the tactile receptive fields were located on the face, and when electrode penetrations were made in the medial part, the tactile receptive fields were located on the arm. We found bimodal, visual-somesthetic neurons throughout the entire region, also in agreement with previous reports (Gentilucci et al. 1988; Rizzolatti et al. 1981).

Figure 8.8 shows the receptive fields of several representative bimodal neurons. The response properties are strikingly similar to those in the putamen. The cells shown in figure 8.8A–B had tactile receptive fields on the contralateral side of the face and matching visual receptive fields within about 10 cm of the face. For the cell in figure 8.8C, the tactile receptive field covered the contralateral arm and the visual receptive field extended outward beyond one meter. For the cell in figure 8.8D, the tactile receptive field covered both the face and a portion of the shoulder. This cell was unusual in that it responded to stimulation of the ipsilateral but not the contralateral

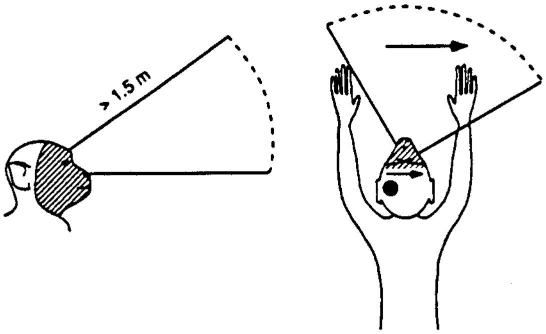

**Figure 8.9** Example of bimodal cell from area 6. Both visual and tactile response preferred rightward motion. (Adapted from Graziano and Gross 1994a).

shoulder. The visual receptive field also extended farther into the ipsilateral periphery.

Figure 8.9 shows the results from a cell with a directionally selective tactile response; it preferred stimuli that moved across the skin from left to right. The visual response matched the location of the tactile response and was also directionally selective, again from left to right.

For bimodal neurons with tactile responses on the arm, we tested the effect of placing the arm in different locations. Figure 8.10 shows the result for one neuron. When the arm was bent backward (fig. 8.10A), the visual response began 45° in the contralateral field and extended to the edge of the monkey's sight. When the arm was positioned out to the side (fig. 8.10B), the visual response began closer to the midline, at 30°. When the arm was bent forward (fig. 8.10C), the visual response began 20° in the ipsilateral field and no longer extended to the edge of the contralateral field. Finally, with the hand roughly centered at the nose (fig. 8.10D), the visual response extended 70° into the ipsilateral field.

In total, 12 bimodal neurons with tactile receptive fields on the arm were tested by placing the arm in different positions, and for 8 of these the visual receptive field moved with the arm. A related phenomenon was noted earlier by Rizzolatti and colleagues (Fogassi et al. 1992; Gentilucci et al. 1983), who studied ventral area 6 in awake monkeys trained to fixate. They found that for many cells, the visual receptive field remained stationary in space, even when the monkey's eyes moved; they interpreted their results as indicating that the visual receptive fields were anchored to the head, encoding the locations of visual stimuli in "head-centered" space. In fact, their data show only that the receptive fields were not anchored to the eye. By contrast, our results indicate that at least some visual receptive fields are anchored to the arm, encoding the locations of stimuli in "arm-centered" space. As described in the next section, we recorded from awake behaving monkeys in order to test the effect of both eye and arm position in the same neurons.

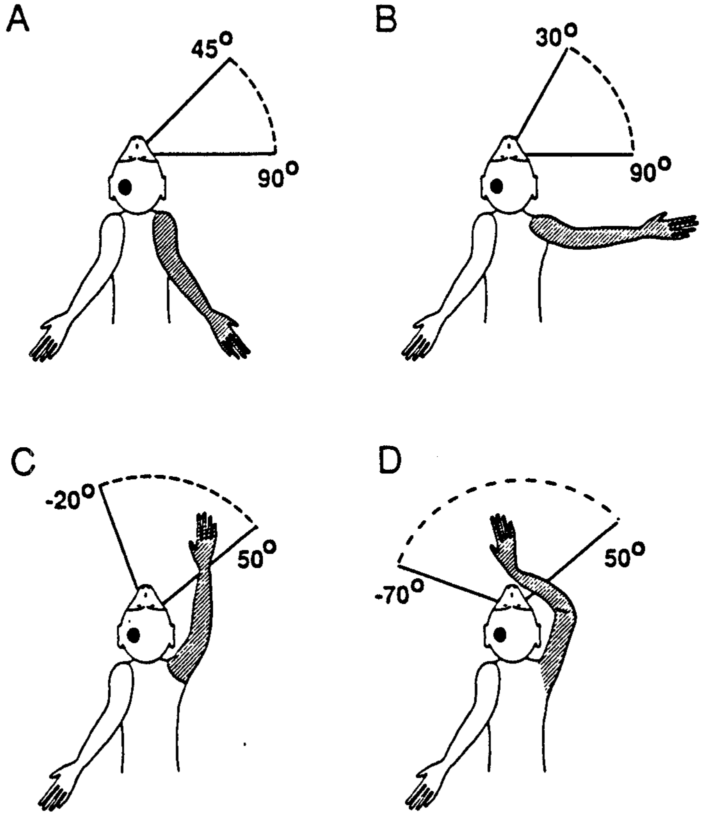

Figure 8.10 Example of bimodal cell from ventral area 6 for which visual receptive field moved as arm moved. (Adapted from Graziano and Gross 1994a).

## Unanesthetized Recording

The proportions of cell types that we found in area 6 of awake, behaving monkeys were similar to the proportions found in the anesthetized animal (see fig. 8.1): 39 percent of the neurons were somatosensory, motor, both; 10 percent were visual; and 25 percent were bimodal.

Figure 8.11 (left) shows the experimental paradigm that we used to test the effect of eye and arm position on the visual response. Each trial began with illumination of one of three lights, A, B, or C, spaced 20° apart along the horizontal meridian. The monkey was required to fixate the light and maintain fixation throughout the trial for a juice reward. During fixation, a 10 cm diameter white ball mounted on a robot was advanced toward the monkey at 14.5 cm/sec along one of the four trajectories shown. The 3 eye positions and 4 stimulus positions yielded 12 conditions, which were presented in an interleaved fashion. The effect of arm position was studied by running a block of trials while the arm was in one position, and then strapping the arm into to a new position and running a second block.

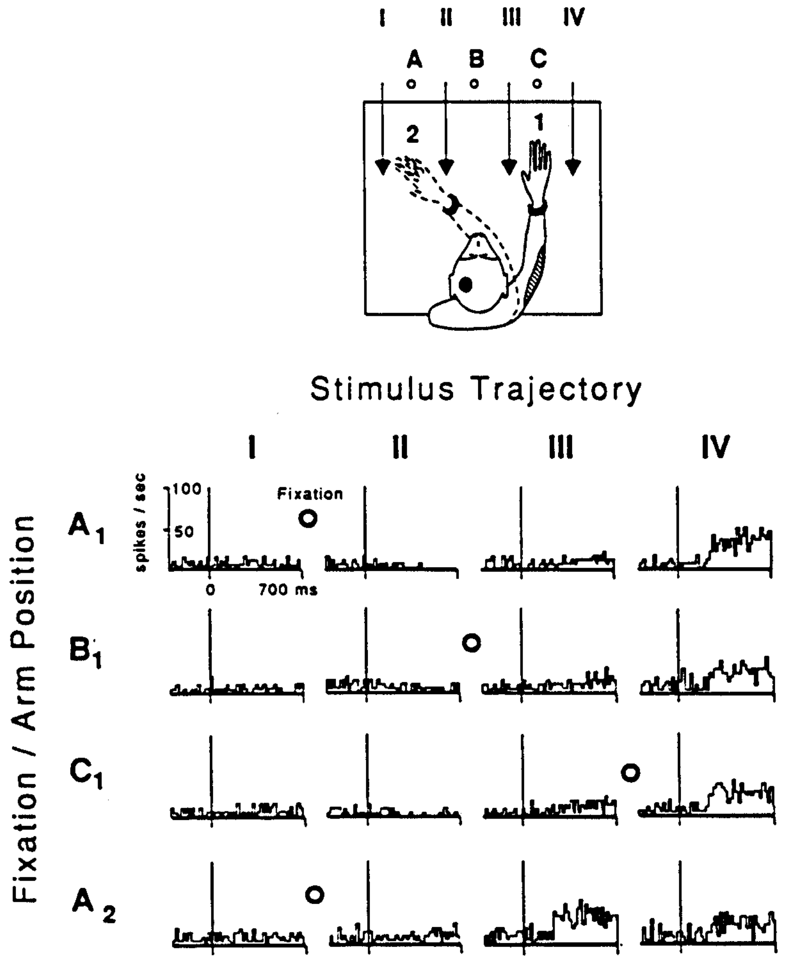

**Figure 8.11** Upper: Experimental paradigm for studying area 6 in awake preparation. On each trial animal fixated one of three lights 20° apart (A, B, or C), and stimulus was advanced along one of four trajectories (I–IV). Arm was fixed in one of two positions (1 or 2). Stippling shows tactile receptive field of cell illustrated beneath. Lower: Histograms of neuronal activity, summed over 10 trials, as function of eye position (A, B, C), stimulus position (I–IV), and arm position (on right in $A_1$, and $B_1$, and $C_1$, on left in $A_2$). Vertical lines indicate stimulus onset. Circles indicate location of fixation light. When arm was fixed in position 1, neuron responded best to stimulus trajectory IV, whether eye looked to left ($A_1$), to center ($B_1$), or to right ($C_1$). However, when arm was fixed in position 2 ($A_2$), neuron responded best to stimulus trajectory III, that is, visual receptive field moved toward left with tactile receptive field. (Graziano, Yap, and Gross 1994).

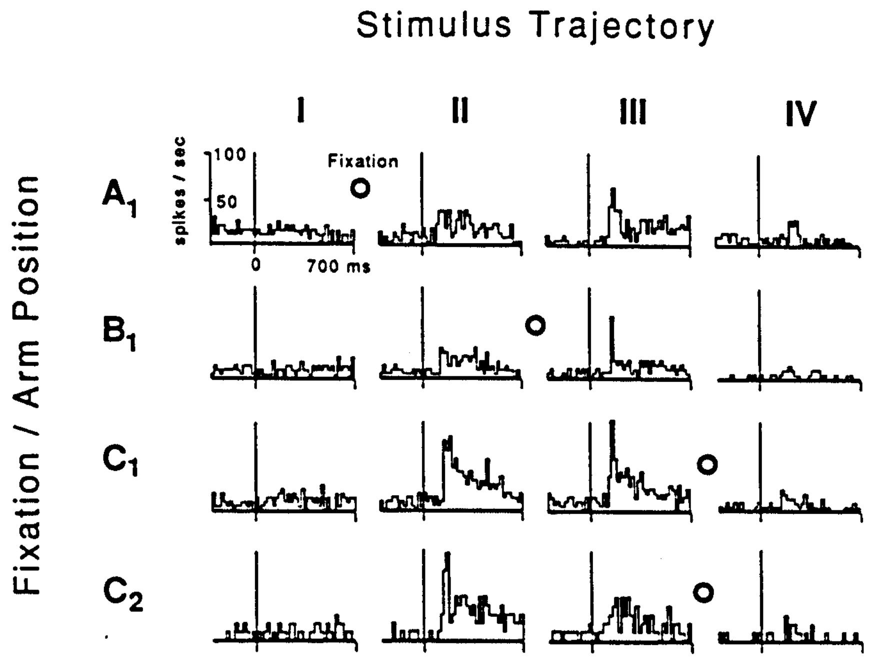

**Figure 8.12** Response of bimodal neuron from area 6 with tactile receptive field on eyebrows. Visual response was best when stimulus was near midline (trajectories II and III), matching location of tactile receptive field. Visual receptive field remained at same location in space, whether eyes looked to left ($A_1$), center ($B_1$), or right ($C_1$). However, magnitude of the response varied with eye position. When arm was moved toward left ($C_2$), visual receptive field still did not move, presumably because it was anchored to tactile field on head. (See also caption to fig. 8.11). (Graziano, Yap, and Gross 1994).

Figure 8.11 (right) shows the result for one neuron. This cell had a tactile receptive field on the contralateral arm. $A_1$, $B_1$, and $C_1$ show the visual response when the arm was held to the right. The cell gave a significant visual response only when the stimulus was presented on the far right, near the arm. The visual response remained at the same location in the right-hand periphery, whether the eyes were fixating 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. The arm was then bent toward the left, and the cell was retested. As shown in $A_2$, the visual response moved with the arm. ($B_2$ and $C_2$, not shown, were similar to $A_2$).

Responses from a second neuron are shown in figure 8.12. This cell had a bilateral tactile receptive field on the eyebrow. The corresponding visual receptive field did not move when the eyes moved. This spatial invariance is particularly striking because the fovea fell to the left of the receptive field when the monkey fixated light A, and fell to the right of the receptive field when the monkey fixated light C. Although the location of the response was independent of eye position, the magnitude of the response was greatest when the eyes were fixating to the right. Similar modulation by gaze has

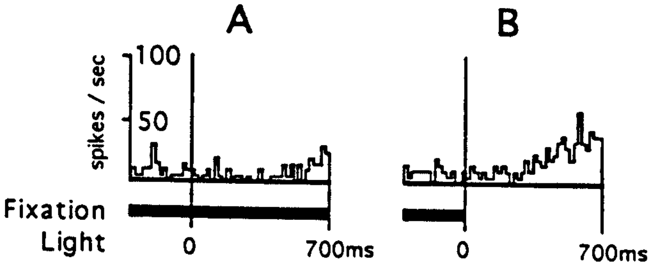

**Figure 8.13** Response of bimodal area 6 neuron to stimulus at position III (see fig. 8.11) while monkey fixated central light. A. When fixation light was on continuously through trial, there was little or no response. B. When fixation light was extinguished at stimulus onset but monkey was still required to fixate until the end of trial, cell responded vigorously.

been reported for neurons in several regions of the parietal lobe, including area 7a (Andersen, Essick, and Siegel 1985) area LIP (Andersen et al. 1990), area PO (Galletti, Battaglini, and Fattori 1993), and area V3a (Galletti and Battaglini 1989).

Condition $C_2$ (fig. 8.12) shows the result for the same neuron when the arm was bent toward the left. The visual receptive field still did not move, that is, as expected, when the tactile receptive field is not on the arm, the visual receptive field does not move with the arm.

Many cells gave a more robust visual response when the animal was not fixating on a light. An example is shown in figure 8.13. When the monkey was required to fixate continuously on a spot of light throughout the entire trial, there was no significant response to the visual stimulus (fig. 8.13A). However, when the fixation light was extinguished at stimulus onset but the monkey was still required to fixate until the end of the trial, the cell gave a significant visual response (fig. 8.13B). Richmond, Wurtz, and Sato (1983) described a similar "blink" effect for visual neurons in IT cortex; they suggested that the fixation light modifies the attentional state of the animal, which in turn modulates the responses of the neurons. Perhaps a similar attentional modulation occurs for area 6 neurons.

The act of fixation itself also contributes to the suppression the response, as illustrated in figure 8.14 for one neuron. In this experiment, the fixation light was never illuminated during stimulus presentation. In conditions A–C, the fixation light was briefly flashed at the beginning of the trial, and the animal was required to fixate throughout the trial. In $A_1$, when the eyes looked to the left, the visual response was best at stimulus position III, near the arm. This peak response remained at the same location even when the eyes looked to the center ($B_1$) and to the right ($C_1$), that is, the visual receptive field did not move with the eyes. The cell had a tactile receptive field on the arm, and when the arm was bent toward the left, the visual response moved with it (C2).

Because the visual receptive field for this cell was independent of the position of the eyes, it was not necessary for the animal to fixate in order for

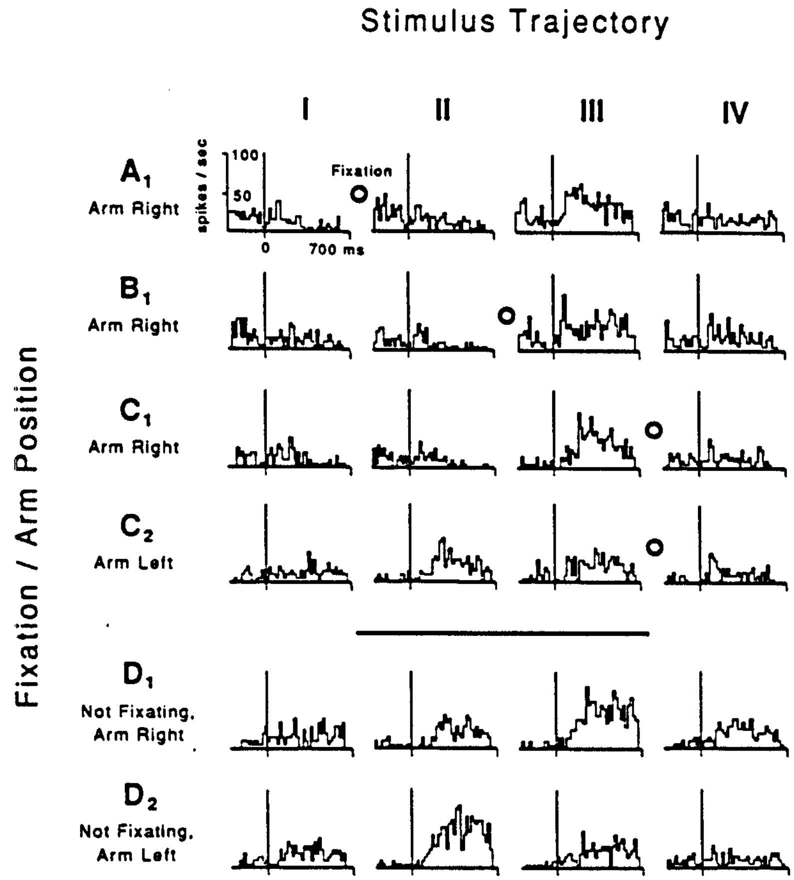

**Figure 8.14** Response of bimodal neuron from area 6 with tactile receptive field on arm. In A–C, fixation light was extinguished at stimulus onset but monkey was still required to fixate until end of trial. Visual receptive field remained at same location in space, whether eyes looked to left ($A_1$), center ($B_1$), or right ($C_1$). However, when arm was bent toward left ($C_2$), visual response also moved toward left. In $D_1$ and $D_2$, fixation light was never illuminated and monkey was not required to fixate; response improved.

us to plot the receptive field. In $D_1$ and $D_2$, the fixation light was never illuminated and the animal was not required to fixate at all; the stimuli were presented automatically, regardless of the monkey's behavior. The cell gave a much stronger visual response, and the movement of the visual receptive field with the arm became more clear; the peak response moved leftward, from position III to position II. Perhaps the highly artificial situation of a long, continuous fixation interferes with the animal's allocation of attention and thus obscures the response properties of these neurons.

In total, 33 cells were tested by varying the position of the eye (fig. 8.15). For 32 cells (97 percent), the visual receptive field remained at the same location in space, despite the 40° shift in eye position. Only one cell, with a tactile response on the chin, had a visual receptive field that was not anchored

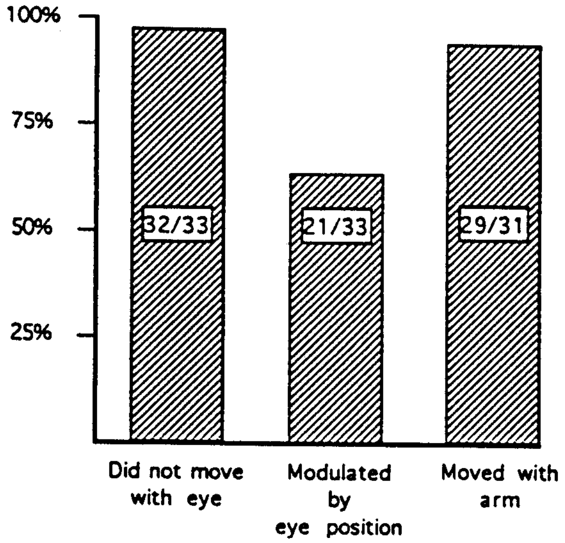

**Figure 8.15** Proportions of cell types in area 6, studied in awake preparation. For 32 of 33 cells, visual receptive field did not move with eye. For 21 of 33 cells, visual response magnitude was significantly modulated by eye position. For 29 of 31 cells with tactile receptive fields on arm, visual receptive field moved with arm.

to its tactile receptive field and that moved with the eye. For 21 cells (64 percent), the magnitude of the response was significantly modulated by eye position.

Thirty-one "arm" bimodal cells were tested by varying the position of the arm. For 29 cells (94 percent), the visual receptive field moved with the arm. Twenty-two of the 29 were tested with multiple eye positions, and in all cases the visual receptive field remained near the arm, independent of the position of the eyes.

## 8.4 REPRESENTATION OF VISUAL SPACE IN BODY-PART-CENTERED COORDINATES

In most visual areas of the brain, the receptive fields are "retinocentric," that is, when the eyes move, the visual receptive fields also move. Although cells of this type can measure the coordinates of a stimulus on the retina, some investigators have suggested that a retinocentric coordinate system is too unstable for representing visual space because it shifts every time the eyes move (Fogassi et al. 1992; Galletti, Battaglini, and Fattori 1993; Schlag et al. 1980; Andersen, Essick, and Siegel 1985). Instead, a slightly more stable coordinate frame attached to the head or trunk might better serve visuospatial function. Accordingly, various groups have looked for nonretinocentric visual receptive fields, that is, receptive fields which do not move with the eye. Such cells have been found by Wiersma (1966) in the crayfish, by

Schlag et al. (1980) in the thalamus of the cat, by Pigarev and Rodionova (1988) in parietal cortex of the cat, by Galletti, Battaglini, and Fattori (1993) in area PO of the monkey parietal cortex, and by Fogassi et al. (1992) in monkey area 6. In some cases these nonretinocentric visual receptive fields were interpreted as forming the long-sought head- or trunk-centered coordinate system, providing a "stable" map of space. However, the results do not support such a conclusion because the head and trunk were not rotated during the experiments; instead, these results show only that the visual receptive fields were not fixed to the retina.

Our results in the putamen and area 6 suggest an entirely different interpretation. For many bimodal cells with tactile receptive fields on the arm or hand, the visual receptive fields remain anchored to the arm, moving as the arm moves. These visual receptive fields are not retinocentric, head-centered, or trunk-centered. They are "arm-centered," that is, they encode the location of the stimulus with respect to the arm. We predict that bimodal cells associated with other body parts will behave in a similar fashion. For example, if the tactile receptive field is on the face, then the visual receptive field will be head-centered, moving as the head is rotated.[1] Area 6 and the putamen, according to this view, represent visual space by means of multiple coordinate frames attached to multiple parts of the body.

What function might such a "body-part-centered" representation of space serve? Arm-centered neurons would be useful for hand-eye coordination, such as guiding the arm toward or away from visual targets. Indeed, a high proportion of the neurons in both the putamen and area 6 are active during voluntary movement (e.g., Alexander 1987; Crutcher and DeLong 1984b; Gentilucci et al. 1988; Rizzolatti et al. 1988; Weinrich, Wise, and Mauritz 1984). In area 6, cells that are active during movements of the arm are spatially tuned, responding best when the arm reaches into a particular region of space. When the arm is shifted to a different location, this motor field also shifts, rotating by the same angle that the shoulder has rotated (Caminiti, Johnson, and Urbano 1990); that is, just as for the visual receptive fields, the motor response fields are arm-centered. These neurons would appear to form a sensory-motor interface, encoding the location of the target in the same coordinate system used to control the arm.

Head-centered visual receptive fields would also be useful for visuomotor coordination, such as for reaching with the mouth toward food or enemies, flinching from approaching objects, heading soccer balls, or kissing accurately. Indeed, it would be useful to have a visual coordinate frame 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. We hypothesize that area 6 and the putamen provide exactly this type of visual map. In support of this view, lesions to area 6 impair the ability to localize visual stimuli that are within reaching distance but leave intact the ability to localize more distant stimuli (Rizzolatti, Matelli, and Pavesi 1983).

## 8.5 MULTIPLE MAPS OF SPACE BEYOND PARIETAL CORTEX

On the basis of anatomical and lesion studies in monkeys and humans, Ungerleider and Mishkin (1982) proposed that visual space is processed by a sequence of cortical areas, beginning with striate cortex, continuing through areas in the dorsal part of the occipital lobe, and culminating in posterior parietal cortex (see fig. 8.16). The general idea of this "dorsal stream" has been confirmed in many subsequent anatomical, physiological, and neuropsychological experiments (for review, see Desimone and Ungerleider 1989; Merigan and Maunsell 1993).

Nevertheless, exactly how space is represented in the parietal cortex remains obscure. Most posterior parietal areas (e.g., 7a, 7b, LIP, and VIP; see fig. 8.16) have little or no topographic organization. Because visual receptive fields in parietal cortex move with the eye, Duhamel, Colby, and Goldberg (1992) speculate that parietal neurons represent space in retinocentric coordinates. However, Andersen and colleagues have shown that for neurons in LIP and 7a, the magnitude of the visual response is modulated by proprioceptive input about the position of the eye and the rotation of the head (Andersen, Essick, and Siegel 1985; Andersen et al. 1990; Brotchie and Andersen 1991).

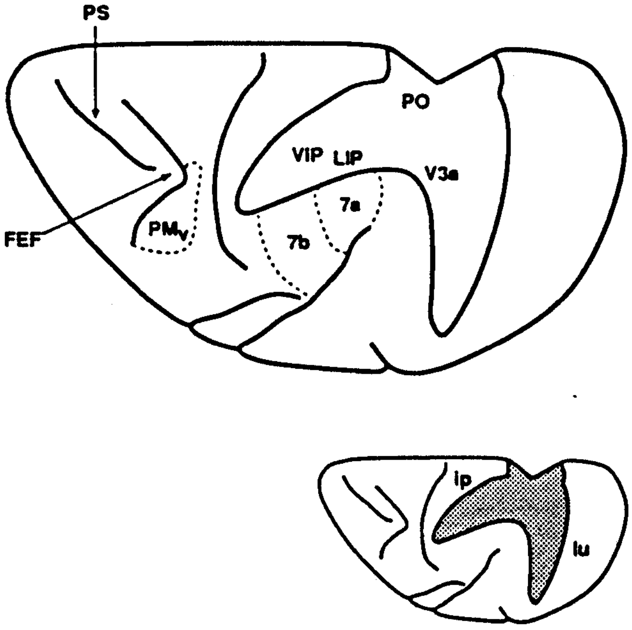

Figure 8.16 Dorsal view of left cerebral cortex of macaque with lunate and intraparietal sulci opened, showing some of the cortical areas involved in processing of space: FEF, frontal eye fields (area 8); LIP, lateral intraparietal area; PMv, ventral premotor area (ventral area 6); PO, parieto-occipital area; PS, principal sulcus; VIP, ventral intraparietal area. In small brain, shaded area shows extent of buried cortex in lunate (lu) and intraparietal (ip) sulci revealed in main figure.

They suggest that a population of these neurons forms a distributed code for a coordinate system centered on the head or maybe the trunk (Zipser and Andersen 1988). Some authors have even concluded that there is no coordinate frame and no map of space anywhere in the brain but instead a "distributed system of rules" to represent space in a way that is not explicit (Stein 1992).

One reason for this confusion is the persistent belief that the posterior parietal cortex is the end point of spatial processing. This is unlikely, since posterior parietal cortex projects to a variety of other brain structures also known to process visual space (see fig. 8.17). In our view, parietal cortex is an

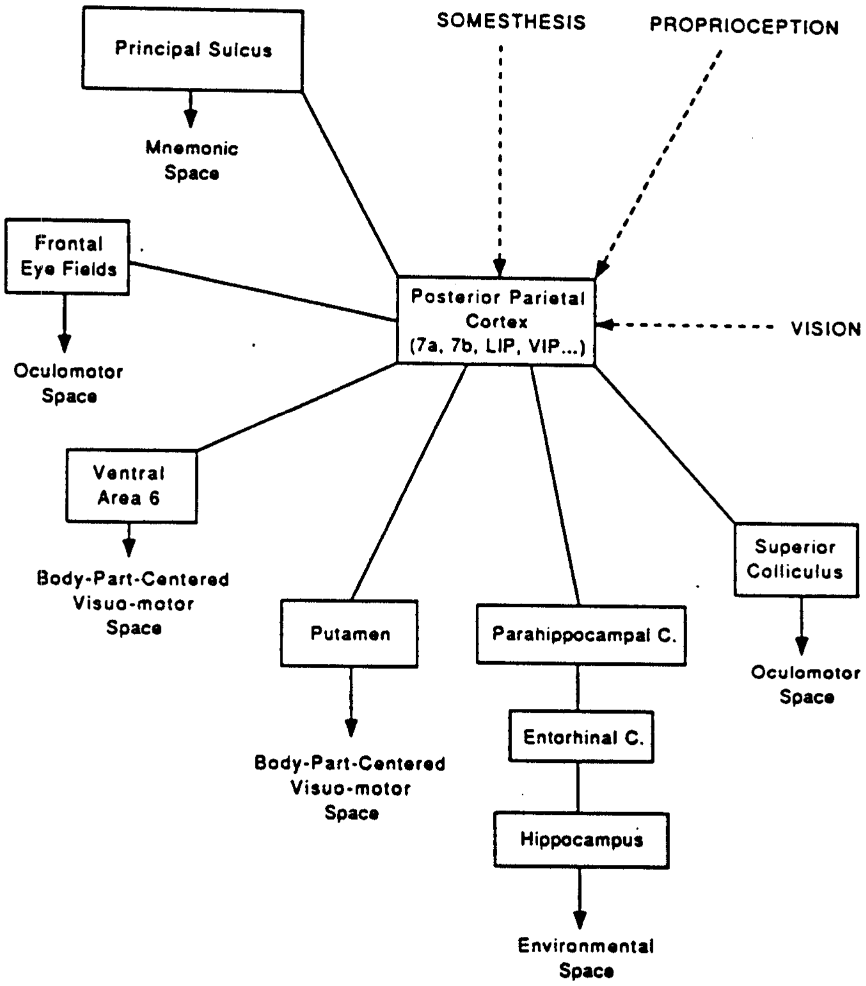

**Figure 8.17** Somesthetic, proprioceptive, and visual information are brought together in various areas of posterior parietal cortex, which project to extraparietal structures for further, more specialized, processing of spatial information. All connections shown are monosynaptic. Not shown are interconnections among different targets of parietal cortex such as between ventral area 6 and putamen and between frontal eye fields and superior colliculus.

early stage of spatial processing; it is where vision, touch, and proprioception come together for the first time. Projections from parietal cortex then distribute this implicit, partially processed spatial information to other areas, which construct their own, special purpose maps, variously head-centered, eye-centered, arm-centered, or allocentric. Some of these areas are shown in figure 8.17, and discussed below.

### Area 6 and Putamen

As described above, the putamen and area 6 contain maps of the space near the body. At least in the arm area, the visual receptive fields are body-part-centered, and could contribute to sensorimotor coordination. The somesthetic and visual information required to construct these maps is presumably provided to area 6 and the putamen through the monosynaptic projections from the parietal lobe, specifically from area 7b (Cavada and Goldman-Rakic 1989, 1991; Kunzle 1978; Matelli et al. 1986; Mesulam et al. 1977; Weber and Yin 1984). Area 7b itself contains bimodal, visual-tactile neurons (Hyvarinen 1981; Robinson and Burton 1980a,b), but the response properties are different from in the putamen and area 6, and consistent with it being an earlier processing stage in this hierarchy of bimodal areas. Specifically, the somatotopic organization in area 7b is much more crude, if indeed it exists at all, and the visual receptive fields near the arm do not appear to move when the arm is moved (Graziano and Gross 1994a).

Bimodal, visual-tactile responses have also been found in parietal area VIP (Colby, Duhamel, and Goldberg 1993; Duhamel, Colby, and Goldberg 1991), which projects to area 7b and possibly directly to area 6 and the putamen (Jones and Powell 1970; Mesulam et al. 1977; Cavada and Goldman-Rakic 1989, 1991). Therefore, VIP may be another source for the properties we have seen in the putamen and area 6.

### Frontal Eye Fields and Superior Colliculus

Saccadic eye movements are controlled by several interconnected brain areas including the frontal eye fields, the deep layers of the superior colliculus and parietal area LIP (Andersen et al. 1990; Bruce 1990; Sparks 1991). These three areas appear to be arranged hierarchically, with LIP as an earlier processing stage, supplying information to the other two areas (Andersen, Asanuma, and Cowan 1985; Cavada and Goldman-Rakic 1989; Felleman and Van Essen 1991; Lynch, Graybiel, and Lobeck 1985). The superior colliculus and the frontal eye fields each contain a topographic map of space, but area LIP apparently does not.

In all three areas, the movements of the eye are guided by receptive fields that are fixed to the eyeball, just as movements of the arm may be guided by receptive fields in area 6 and the putamen that are fixed to the arm. In LIP and the frontal eye fields, this correspondence between the position of the receptive fields and of the eye is unusually close; for many neurons, the visual receptive field actively follows the eye, instead of lagging behind by the expected visual latency of approximately 70 ms (Duhamel, Colby, and Goldberg 1992).

In addition to their visual responses, neurons in all three areas also respond to auditory stimuli, presumably to guide saccadic eye movements to sound sources. Just as for the visual receptive fields, these auditory receptive fields are also anchored to the eyeball, shifting as the animal looks in different locations (Jay and Sparks 1984; Mazzoni et al. 1993; Russo and Bruce 1989; Stricanne et al. 1994).

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 (Bruce and Goldberg 1985; Gnadt and Andersen 1988; Mays and Sparks 1980a,b). These cells could help to guide the eyes toward remembered targets. In one memory paradigm, the visual stimulus is flashed briefly outside the receptive field of the cell, and therefore does not elicit a response. The monkey is then 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 encompasses the remembered location of the stimulus, and therefore the neuron responds. No visual stimulus has actually entered the receptive field of the cell; rather, the cell is activated when a remembered stimulus falls within its "memory" field.

In summary, neurons involved in programming saccadic eye movements have receptive fields that are anchored to the eye. Not just visual, but even auditory and memory fields are eye-centered. Therefore, these brain areas, like the putamen and area 6, use body-part-centered coordinate systems; the body part in this case is the eyeball. We suggest that a general principle of sensorimotor control is that the sensory stimulus is located by means of a coordinate system that is anchored to the relevant body part.

### Hippocampus

Numerous functions have been ascribed to the hippocampus (e.g., Eichenbaum and Otto 1992; O'Keefe and Nadel 1978; Zola-Morgan and Squire 1993). At least in rats, the hippocampus is critical for learning to navigate through a complex spatial environment (O'Keefe and Nadel 1978; Nadel 1991). Lesions to the hippocampus impair the rat's ability to learn mazes (e.g., Morris, Garrud, and Rawlins 1982; Olton, Walker, and Gage 1978). Furthermore, hippocampal neurons have remarkable spatial properties; each neuron responds only when the animal is in a particular small region of his environment, the "place field" of the cell (O'Keefe and Nadel 1978). These neurons encode the allocentric or external location of the animal. In the monkey, hippocampal neurons appear to encode the allocentric locations of visual stimuli (Feigenbaum and Rolls 1991; Ono et al. 1991; Rolls et al. 1989).

Parietal areas 7a and LIP project to the parahippocampal cortex, which projects to the entorhinal cortex, which in turn projects to the hippocampus (Jones and Powell 1970; Seltzer and Pandya 1976; Suzuki and Amaral 1994). Presumably, the allocentric spatial properties in the hippocampus are generated at least in part from information supplied by the parietal cortex along this pathway.

### Principal Sulcus

Ever since the lesion studies of Jacobsen (1936), the dorsolateral prefrontal cortex, area 46, has been known to play a role in short-term spatial memory. Recently, Funahashi, Bruce, and Goldman-Rakic (1989, 1990, 1993) have shown that the region around the principal sulcus, within area 46, 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." Furthermore, these memory fields are organized topographically, such that lesions to 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 (Andersen, Asanuma, and Cowan 1985; Cavada and Goldman-Rakic 1989), from which it presumably gets the spatial information necessary to construct its mnemonic map (Goldman-Rakic 1987).

### Parietal Cortex

In summary, the parietal lobe is the hub and information source for several areas that are specialized for a variety of visuospatial functions. Each area contains its own, specially tailored map of space. This scheme of how spatial processing is organized in the brain suggests an answer to one of the long-standing questions about parietal function. Lesions to parietal cortex produce a vast array of spatial deficits, many of which are not dissociable by smaller lesions (for review, see Critchley 1953; DeRenzi 1982; Ratcliff 1991). Humans with parietal damage have difficulty reaching and saccading accurately, estimating distances, remembering routes, reading maps, and navigating through a room full of obstacles. They sometimes show neglect of an entire half of space; they may even confuse the locations of tactile stimuli, such as in finger agnosia, the inability to know which finger has been touched. Perhaps the reason for this diversity of dysfunction is that parietal lesions deafferent a large number of spatial maps located in different brain areas and serving different purposes.

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## NOTE

1. We have recently confirmed our hypothesis and found that about 95 percent of bimodal cells with a tactile response on the face have head-centered visual receptive fields that move when the head is rotated but do not move with the eye or the arm.

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