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67 The Representation of Extrapersonal Space: A Possible Role for Bimodal, Visual-Tactile Neurons

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ABSTRACT We propose that extrapersonal space is represented in the brain by bimodal, visual-tactile neurons in inferior area 6 in the frontal lobe, area 7b in the parietal lobe, and the putamen. In each of these areas, there are cells that respond to both tactile and visual stimuli. In each area, the tactile receptive fields are arranged to form a somatotopic map. The visual receptive fields are usually adjacent to the tactile ones and extend outward from the skin about 20 cm. Thus each area contains a somatotopically organized map of the visual space that immediately surrounds the body. These three areas are monosynaptically interconnected, and may form a distributed system for representing extrapersonal visual space. For many neurons with tactile receptive fields on the arm or hand, when the arm was moved, the visual receptive field moved with it. Thus, these neurons appear to code the location of visual stimuli in arm-centered coordinates. More generally, we suggest that the bimodal cells represent near extrapersonal space in a body part–centered fashion, rather than in an exclusively head-centered or trunk-centered fashion.

A central issue in cognitive neuroscience is how the brain constructs a stable map of the world. The retinal image of an object moves every time the head or the eyes move, and yet we perceive objects as having stable positions in space. We are able to reach toward objects, saccade to targets, and avoid threatening or looming stimuli. How is the location of these nearby stimuli encoded in the brain?

We propose that in the primate, the visual space near the body—extrapersonal or peripersonal space—is encoded by a system of interconnected brain areas that includes parietal area 7b, the inferior portion of premotor area 6, and the putamen. Neurons in these areas respond to somatosensory stimuli, and have discrete receptive fields that are arranged to form a somatotopic map of the body (Robinson and Burton, 1980a; Hyvarinen, 1981; Crutcher and DeLong, 1984a; Gentilucci et al., 1988). Many of these neurons, particularly in the head and arm portions of the map, are bimodal, responding to visual as well as tactile stimuli (Graziano and Gross, 1992, 1993; Hyvarinen, 1981; Hyvarinen and Poranen, 1974; Leinonen et al., 1979; Leinonen and Nyman, 1979; Rizzolatti et al., 1981b; Robinson and Burton, 1980a, 1980b). For the bimodal neurons, the visual receptive field usually matches the location of the tactile receptive field, and is confined in depth to a region within reach of the animal's arm. Thus these neurons provide a somatotopically organized representation of the visual space near the body.

In this chapter we describe the properties of bimodal, visual-tactile neurons in the putamen, parietal area 7b, and inferior area 6, and suggest how these areas may encode the location of visual stimuli in extrapersonal space.

Neuronal response properties in three bimodal areas

We recorded from single neurons in the putamen, area 7b, and inferior area 6 in macaque monkeys anesthetized with nitrous oxide and immobilized with Pavulon. In each area, we found three types of responsive cells: somatosensory cells, visual cells, and bimodal

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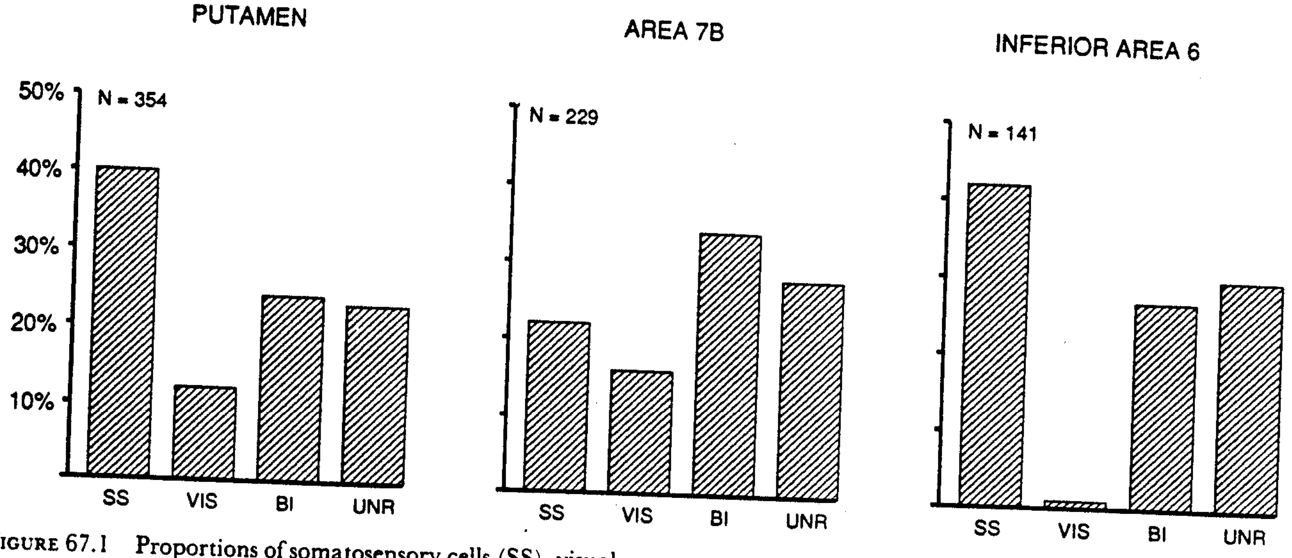

FIGURE 67.1 Proportions of somatosensory cells (SS), visual cells (VIS), bimodal cells (BI), and unresponsive cells (UNR) in the putamen, area 7b, and area 6.

cells. The bimodal cells responded both to visual and to somatosensory stimuli. In this section, we describe the properties of these cells for each of the three brain areas.

PUTAMEN We studied 354 putamen neurons, of which 40% were somatosensory, 12% were visual, 24% were bimodal, and 23% were unresponsive (figure 67.1).

Somtosensory cells Somatosensory responses were studied using manual palpation, manipulation of joints, gentle pressure, and stroking with cotton swabs. Receptive fields were plotted by repeated presentation of the most effective of these stimuli. Neurons were somatotopically organized in a manner similar to that described by Crutcher and DeLong (1984a). On vertical electrode penetrations, the first cells encountered had receptive fields on the tail or the legs. As the electrode moved ventrally, cells had receptive fields on the trunk, then the shoulders and arms, then the face, and finally inside the mouth. Figure 67.2 shows a representative penetration.

Bimodal cells In addition to somatosensory neurons, we found bimodal, visual-somesthetic neurons in the face and arm region of the somatotopic map (eg, figure 67.2, cells 6, 7, and 8). Most bimodal cells (86%) responded to light cutaneous stimulation. Sixty-six percent had somatosensory receptive fields on the face, 29% had receptive fields on the arm, and 5% had receptive fields that encompassed the entire body.

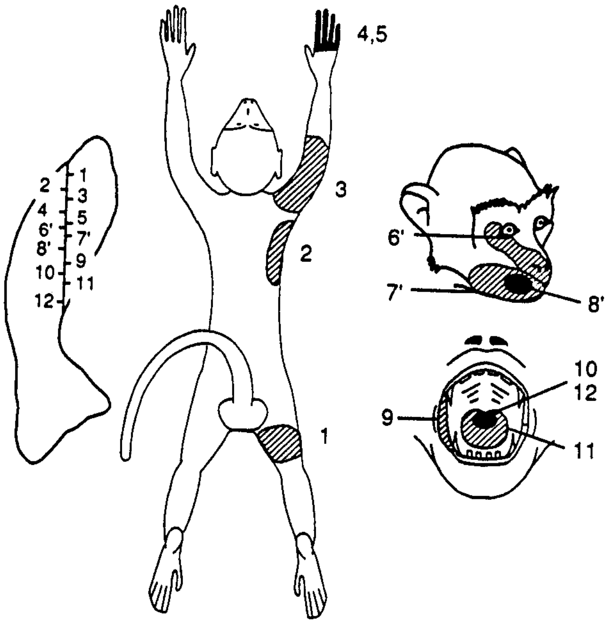

FIGURE 67.2 Somatotopic organization of the putamen. A representative electrode penetration is shown on a coronal section through the putamen, at AP level 14. Receptive field locations for the neurons are shown to the right. Cells indicated with single quotes (eg, 6') responded to visual as well as tactile stimuli.

We tested bimodal cells with moving bars of light on a tangent screen. Since cells often appeared to be selective for the depth of the visual stimulus, the screen was placed at various distances from the animal and the lenses were changed to adjust the animal's plane of focus. Many cells did not respond to these projected light stimuli, and only responded to stimuli moving near the animal's face or hands. Cells that preferred small stimuli particularly close to the skin were tested with a cotton swab. The stimulus was moved slowly toward and away from the animal to determine the maximum distance for which a response could be obtained. The dimensions of the responsive region were determined by approaching the animal from various angles.

A typical example of a bimodal cell is shown in figure 67.3. The tactile receptive field was plotted while the animal's eyes were covered. The cell was activated by a light touch to the facial hairs, and the responsive region covered most of the contralateral cheek and the area around the mouth (A and B). However, when the animal's eyes were uncovered, the response began before the stimulus had touched the face. A cotton swab was moved toward the tactile receptive field, and the cell began responding when the stimulus was within about 10 cm of the face (C). We know that this response was not caused by inadvertent tactile stimulation, such as by air movement, because it was eliminated when the eyes were covered (D).

By approaching the tactile receptive field from various angles, we determined the three-dimensional responsive region, which we called the visual receptive field. This responsive region differed from a classical receptive field because it was not only restricted in visual angle, it was also confined in depth. As shown in figure 67.3A, the visual receptive field as thus defined was a solid angle centered at the tactile receptive field and extending out approximately 10 cm. The response was weak and erratic toward the edges of the visual receptive field. The response was better to a stimulus moving toward the face than to a stimulus moving away.

Figure 67.4 shows several more examples of bimodal cells with tactile receptive fields on the face. As in the previous example, these cells responded to touching of the facial hair. They also responded to visual stimuli moving toward the tactile receptive field. For the cells shown in A and B, the visual receptive field extended outward about 10 cm from the tactile receptive field. The cells shown in C, D, and E differed slightly from this basic pattern. The cell in C had a bilateral tactile receptive field, but a contralateral visual receptive

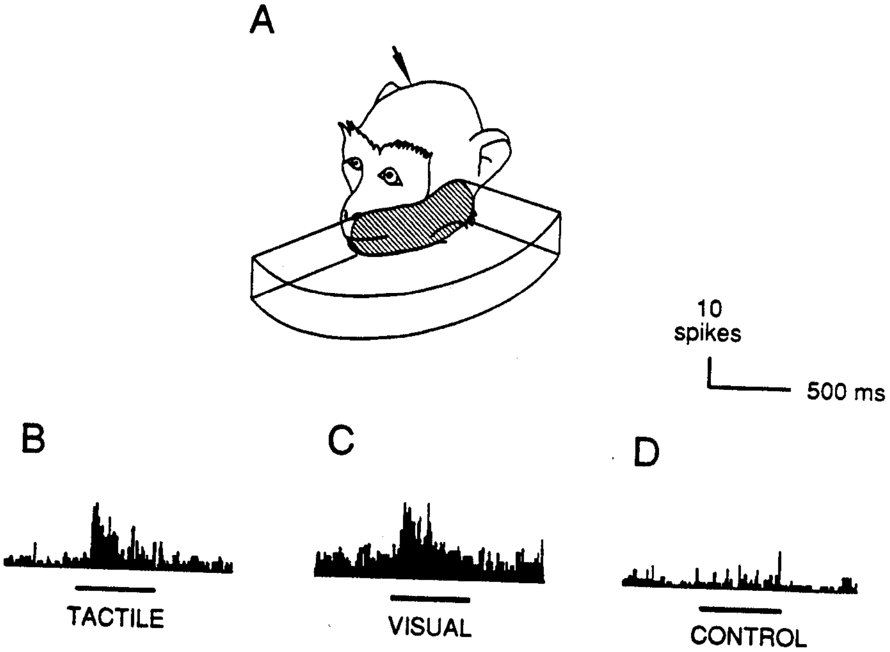

FIGURE 67.3 Poststimulus time histograms, summed over 10 trials, for a typical bimodal putamen cell. (A) The tactile receptive field (stippled) and the visual receptive field (boxed) are in register. The arrow indicates the hemisphere recorded from. (B) Response to a cotton swab touching the face while the eyes are covered. (C) Response to a cotton swab approaching the face within 10 cm while the eyes are open. (D) Same as C, with the eyes covered.

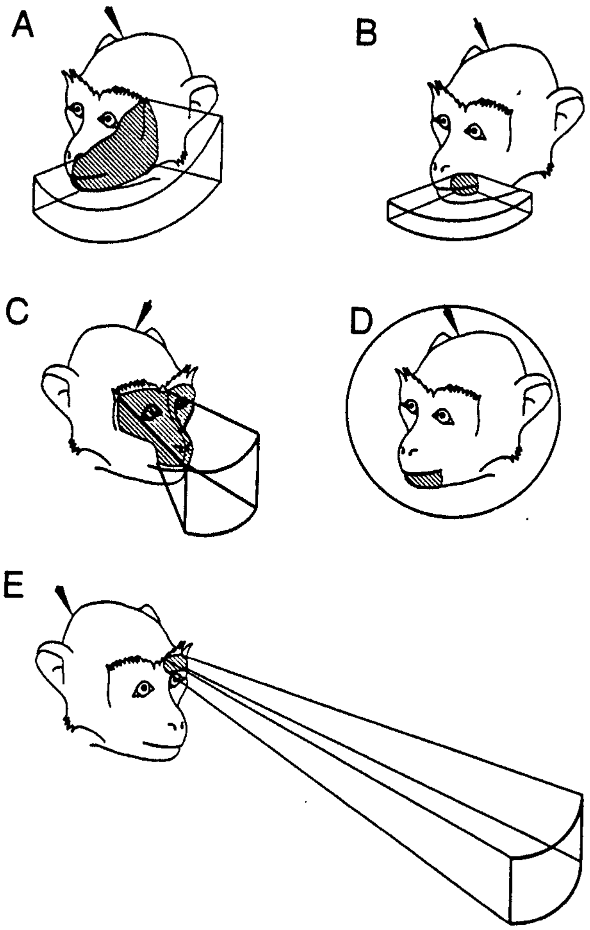

FIGURE 67.4 (A and B) Typical bimodal cells from the putamen, in that the visual and tactile receptive fields correspond and the visual receptive field extends about 10 cm from the face. (C–E) Atypical bimodal cells, because in (C) the tactile receptive field is bilateral and the visual receptive field is contralateral; in (D) the tactile receptive field is confined to the lower jaw but the visual receptive field extends from the face in all directions; and in (E) the visual receptive field extends about 100 cm from the face.

field. Stimuli moving toward the ipsilateral side of the face did not activate the cell, even though touching the ipsilateral side of the face did. The cell in figure 67.4D had a small bilateral tactile receptive field covering the chin, and a visual receptive field covering the entire visual field but extending outward only about 10 cm from the face. Approaching any part of the face, even the upper face, caused a visual response. The cell in E had a tactile receptive field on the contralateral brow, and a visual receptive field that extended out about one meter from the monkey.

Figure 67.5 shows several examples of bimodal cells with tactile receptive fields on the arm. The cells shown in A 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 67.5C responded to touching of both arms, and the visual receptive field was bilateral. Again, the cell responded to stimuli as far away as 1.5 m.

We were able to characterize the visual receptive field for 48 bimodal cells. Of these, 77% responded best or only to visual stimuli within 20 cm of the skin, while 23% responded to stimuli at greater distances. Cells with tactile receptive fields on the arm generally responded to more distant stimuli than cells with tactile receptive fields on the face.

As illustrated above, for most bimodal cells the location of the tactile receptive field matched the location of the visual receptive field. However, for bimodal cells with tactile receptive fields on the arm, what happens when the arm is moved to a new location? Do the tactile and visual receptive fields become dissociated, or does one receptive field shift in order to remain in register with the other? Figure 67.6 shows the result for two cells. The cell shown in A responded to visual stimuli only when the arm was propped forward into 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 67.6B had a particularly close match between the tactile and visual receptive fields; the visual receptive field extended 5 cm from the hand. 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. When the hand was placed out of sight, the cell did not respond at all to visual stimuli. Of 25 bimodal cells with tactile receptive fields on the arm, 5 had visual responses that were gated by the position of the arm in this fashion.

Bimodal cells or cells with visual receptive fields near the body have not been reported previously for the putamen. This may be because other groups studying single-unit activity in the putamen used awake animals sitting in chairs (DeLong, 1973; Liles, 1983; Crutcher and DeLong, 1984a, 1984b; Liles, 1985; Liles and Updyke, 1985; Alexander, 1987; Schultz and Romo, 1988). Under these conditions, stimuli moving close to the head or arms would be likely to elicit movements, and any associated neuronal discharges might have

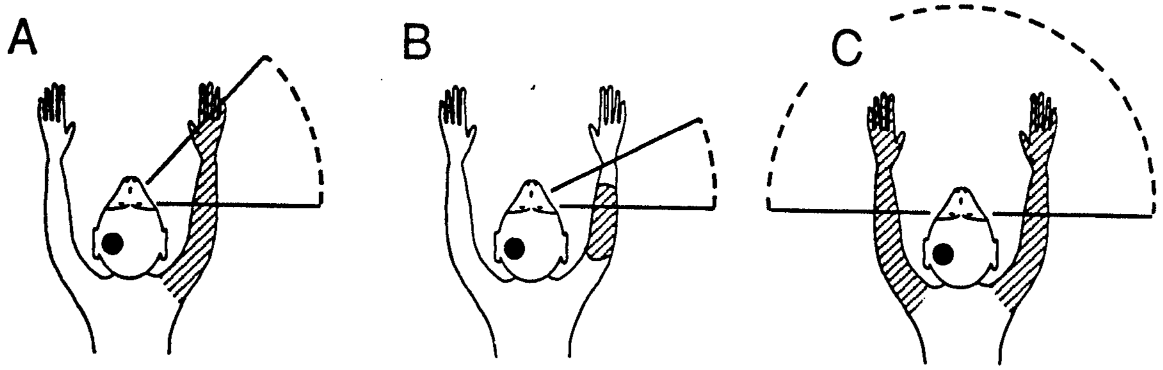

FIGURE 67.5 Bimodal cells from the putamen with tactile receptive fields on the arm. The lines indicate the angles subtended by the visual receptive fields in the horizontal plane. The dashed lines indicate that the receptive fields extend farther than one meter. The stippling shows the tactile receptive fields, and the black circles on the head show the hemisphere recorded from.

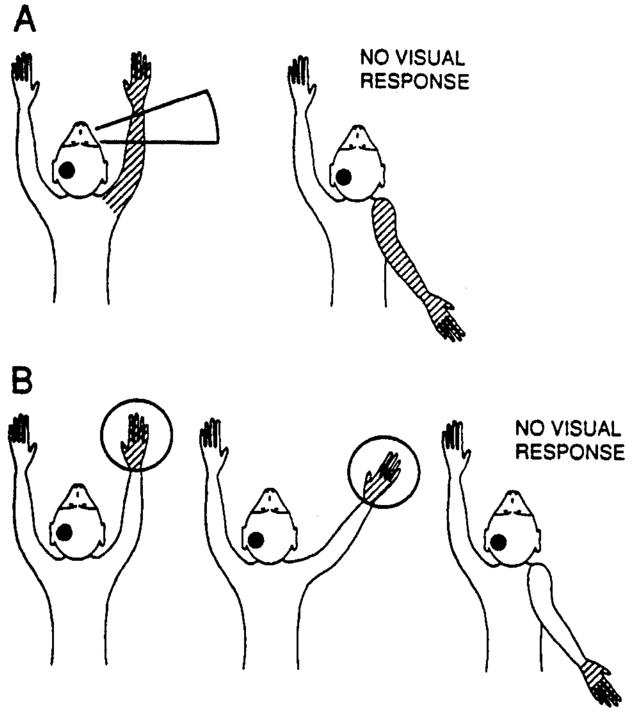

FIGURE 67.6 Two examples of a special type of bimodal arm cell from the putamen. These cells responded visually when the arm was within the monkey's field of view (left), but did not respond when the arm was moved out of view (right). For the cell shown in (B), the visual receptive field moved as the hand moved.

been interpreted as motor or somatosensory responses rather than visual ones.

Visual cells In addition to somatosensory cells and bimodal cells, we also found cells that responded only to visual stimuli. Figure 67.7 shows the response of a visual cell, which was located within the face portion of the somatotopic map. As was the case for many of the bimodal cells, this cell responded to visual stimuli moving toward the face within about 50 cm, but not to stimuli moving away.

PARIETAL AREA 7B We studied 229 neurons in area 7b, of which 22% were somatosensory, 16% were visual, 34% were bimodal, and 28% were unresponsive (see figure 67.1).

Somatosensory cells The somatotopic organization in area 7b is crude, with considerable overlap between the representations of different body parts (Hyvarinen, 1981). However, like Hyvarinen, we found that the representation of the face is generally more anterior than the representation of the arm.

Bimodal cells We found a high proportion of bimodal neurons in area 7b, in agreement with previous reports (Hyvarinen, 1981; Hyvarinen and Poranen, 1974; Leinonen et al., 1979; Leinonen and Nyman, 1979; Robinson and Burton, 1980a, 1980b). As was the case for the putamen, most of these neurons (65%) responded to light cutaneous stimulation. Bimodal cells had somatosensory receptive fields on the face (13%), the arm (48%), both the face and the arm (33%), the chest (2%), and the whole upper body (4%). We obtained visual receptive field plots for 50 bimodal cells. Of these, 42% preferred stimuli out to 20 cm from the animal, 42% preferred stimuli out to one meter, and 16% responded well to stimuli at greater distances.

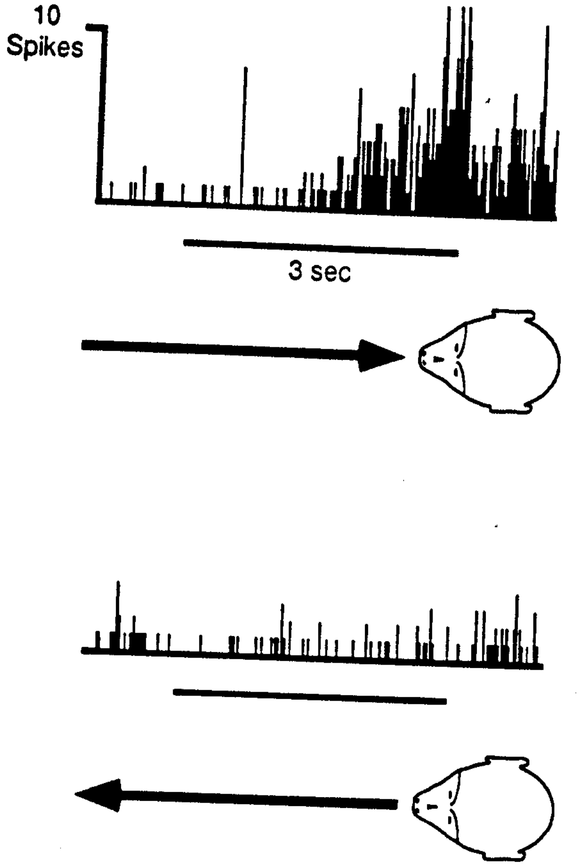

FIGURE 67.7 Response of a visual putamen cell to a sphere 5 cm in diameter moving on a track at 23.3 cm/s toward or away from the face. Far point, 78 cm; near point, 8 cm; duration, 3 s; based on 9 trials with an intertrial interval of 15 s.

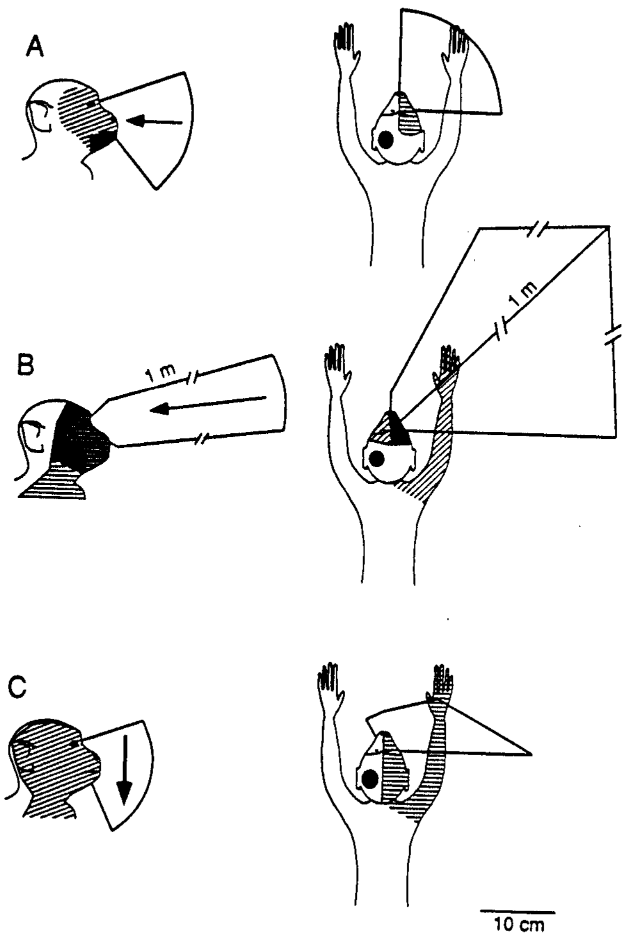

FIGURE 67.8 Three examples of bimodal cells from area 7b. The lines indicate the angles subtended by the visual receptive fields in both the horizontal and vertical planes. Arrows indicate directional selectivity. All lines are drawn to the scale shown at bottom, except for the broken lines in B, which are as labeled. The stippling indicates the tactile receptive fields; the darker stippling indicates regions of strongest response. The black circles on the head indicate the hemisphere recorded from.

Figure 67.8 shows several examples of bimodal responses. The cell shown in A had a tactile receptive field on the contralateral side of the face. It responded best to touching the jaw, and more weakly to touching the cheek or eyebrow. It also responded to visual stimuli within about 15 cm of the face. The visual receptive field was contralateral and mostly in the lower visual field, thus matching the tactile receptive field. The cell only responded to visual stimuli moving inward toward the face, never to stimuli moving outward. The cell shown in B had a large tactile receptive field on the face and the contralateral arm. It also responded to contralateral visual stimuli within about one meter of the animal. Again, the cell responded only to inward motion toward the face, never to outward motion. The cell shown in C also had a contralateral tactile receptive field on the face and the arm. It responded best to visual stimuli in a region within about 20 cm of the animal; however, it also responded weakly to more distant stimuli, as far away as 2 m. This cell responded to visual stimuli moving in any direction within the receptive field, but responded best to downward motion.

Thirty bimodal neurons with tactile receptive fields on the arm were further tested, by moving the arm to different locations. Unlike in the putamen, in all 30 cases the visual response was independent of the position of the arm. Even when the arm was placed entirely out of the animal's view, the visual receptive field remained unchanged. There is a previous report of visual responses in area 7b that change as the arm moves (Leinonen et al., 1979), however no further information, such as receptive field plots, is provided. These results suggest that such cells may be found in area 7b as well as in the putamen, but perhaps in much smaller numbers.

INFERIOR PREMOTOR AREA 6 We recorded from 141 neurons in inferior area 6, of which 42% were somatosensory, 1% were visual, 27% were bimodal, and 30% were unresponsive (see figure 67.1).

Somatosensory cells Neurons in inferior area 6 were somatotopically organized in a manner similar to that described in previous reports (Gentilucci et al., 1988). When electrode penetrations were made in the lateral part of inferior 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.

Bimodal cells A high proportion of neurons in inferior area 6 were bimodal, in agreement with previous reports (Rizzolatti et al., 1981b). As in the putamen and in area 7b, most of these (79%) responded to light cutaneous stimulation. Bimodal cells had somatosensory receptive fields on the face (24%), the arm (34%), both the face and the arm (29%), the chest (2%), the face and the chest (2%), and the whole upper body (8%). Of cells with sufficiently clearly plotted visual receptive fields, 39% preferred stimuli within 20 cm of the animal, 22% preferred stimuli within 1 m, and 39% responded well to stimuli at greater distances.

Figure 67.9 shows two examples of bimodal neurons with tactile receptive fields on the face. The cell shown in A had a receptive field on both sides of the face and on the ipsilateral shoulder. It responded to visual stimuli within one meter of the animal, and preferred stimuli within 30 cm. The visual receptive field was bilateral and extended farther into the ipsilateral side, thus matching the tactile receptive field. For the cell shown in B, the tactile response was directional. 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, from left to right.

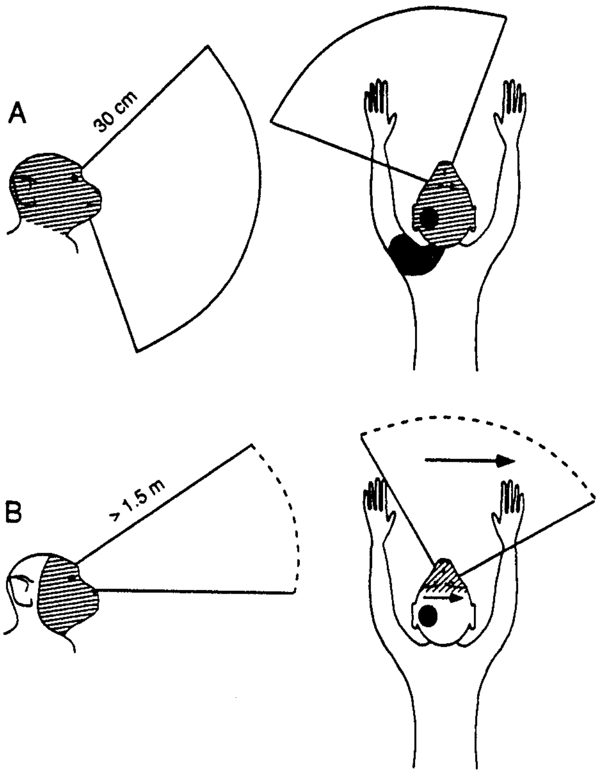

FIGURE 67.9 Two examples of bimodal cells from inferior area 6. For the cell in (B), both the visual and tactile responses preferred rightward motion.

Figure 67.10 shows a bimodal cell with a tactile receptive field on the contralateral arm. The visual receptive field was confined to the lower visual field, and the response was strongest on the contralateral side, thus matching the location of the tactile receptive field. However, when the arm was bent back, placing the tactile receptive field out of the animal's field of view, the cell no longer responded to visual stimuli. There are two possible ways that arm position might affect the response of the cell: through proprioceptive feedback or through visual feedback. We tested these alternatives by placing an opaque shield between the face and the arm, thus blocking any visual feedback from the arm. As illustrated in figure 67.10C, when the arm was bent forward, even though it was blocked from view, the cell responded to visual stimuli. When the arm was bent back (figure 67.10D), the visual response disappeared. Therefore, the visual response for this neuron was modulated by proprioceptive feedback about the position of the arm.

Figure 67.11 shows another example of a bimodal neuron with a tactile receptive field on the arm. This neuron responded to visual stimuli at least 2 m from the animal, and preferred movement from left to right.

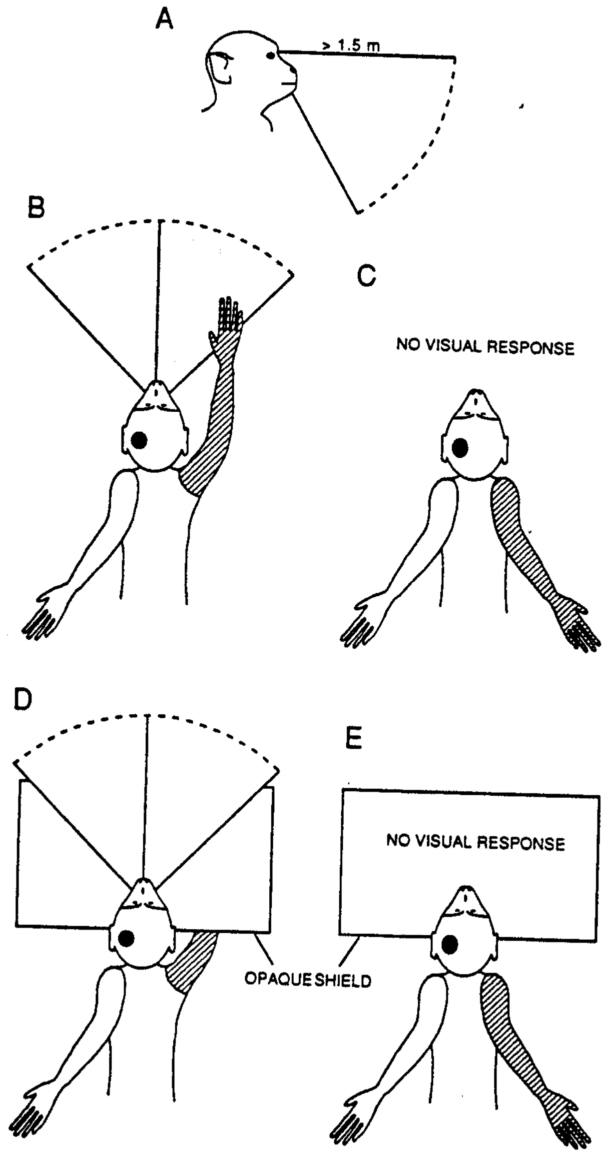

FIGURE 67.10 An example of a cell from inferior area 6, for which the visual response depended on arm position. (A and B) The visual receptive field was lower field and bilateral, but the response was best contralateral. The tactile receptive field was on the contralateral arm. (C) When the arm was placed out of sight, the visual response disappeared. (D and E) The visual response depended on arm position even when the arm was blocked from view with an opaque shield.

When the arm was bent backward (as in A), the visual response began 45° into the contralateral field and continued to the edge of sight. When the arm was positioned out to the side (as in B), the visual response began closer to the midline, at 30°. When the arm was bent forward (C), the visual response began 20° into the ipsilateral field, and no longer extended to the edge of the contralateral field. Finally, with the hand roughly centered at the nose (D), the visual response began as far as 70° in the ipsilateral field.

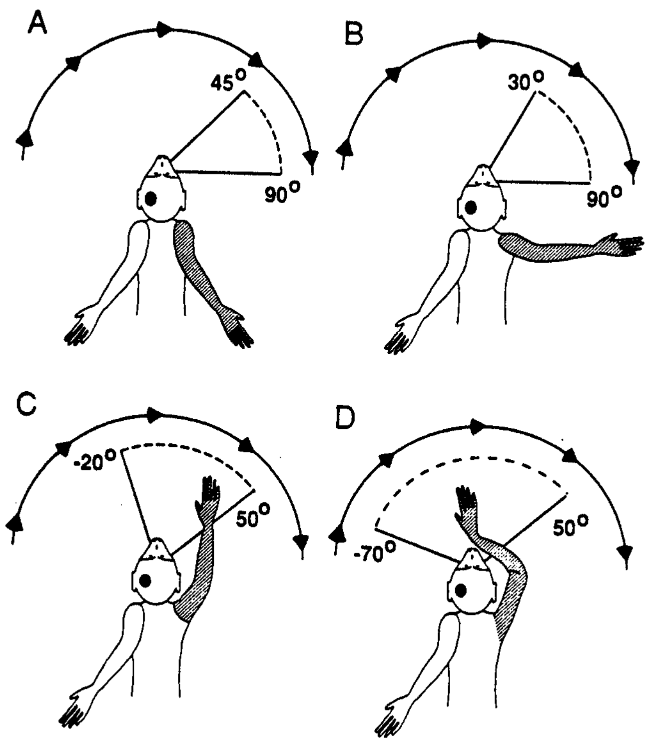

FIGURE 67.11 An example of a cell from inferior area 6 for which the visual receptive field moved as the arm moved. The stimulus was swept in an arc from left to right, in the cell's preferred direction of motion.

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. That is, the visual receptive field remained attached to the tactile receptive field. This phenomenon was noted earlier by Rizzolatti and colleagues (personal communication), who studied inferior area 6 in awake monkeys trained to fixate. They also found that for many cells, the visual receptive field remained fixed to the tactile receptive field even when the monkey's eyes moved to a new location (Fogassi et al., 1992; Gentilucci et al., 1983). That is, whether the arm is moved as in our experiment, or the retina is moved as in the experiments by Gentilucci et al. and by Fogassi et al., the visual receptive field adjusts in order to remain attached to the tactile receptive field.

Summary of Bimodal Properties As described above, neurons in the putamen, area 7b, and inferior area 6 have many properties in common. All three areas are somatotopically organized, although the map in area 7b is relatively crude. In addition to the somatosensory neurons, all three areas contain bimodal, visual-tactile neurons. In the putamen, 24% of the cells were bimodal; in area 7b, 34% were bimodal; and 27% of the cells in area 6 were bimodal (see figure 67.1). For these bimodal cells, the visual and tactile receptive fields corresponded, and visual stimuli near the animal drove the cells best. For bimodal cells that had tactile receptive fields on the arm, we tested whether the visual receptive field moved as the arm moved. In the putamen, the visual receptive field was modulated by the position of the arm for 20% of the cells tested. Sixty-seven percent of the cells in inferior area 6 were modulated by arm position. However, in area 7b, none of the 30 cells tested showed any modulation of the visual response by the position of the arm.

There appears to be a fourth brain area with bimodal, visual-tactile responses nearly identical to those in the putamen, area 7b, and area 6. Neurons in the ventral intraparietal area (VIP) respond to tactile stimuli, primarily on the face, and to visual stimuli presented within a few centimeters of the tactile receptive field (Colby and Duhamel, 1991; Colby, Duhamel, and Goldberg, in press; Duhamel, Colby, and Goldberg, 1991). For at least some of these neurons, the visual receptive field appears to be fixed with respect to the face, even when the eyes move to a new location (Colby, Duhamel, and Goldberg, in press). For example, one neuron preferred a stimulus moving toward the chin, but not the forehead; this was so whether the animal's gaze was directed downward or upward. Since VIP has few if any tactile receptive fields on the arm, it may not be possible to test the dependence of the visual receptive field on arm position, as we did for the other three areas.

Could the sensory responses have been motor?

In the awake monkey, cells in the putamen, area 7b, and inferior area 6 respond during voluntary movement (e.g., Hyvarinen, 1981; Crutcher and DeLong, 1984b; Gentilucci et al., 1988; Rizzolatti et al., 1988). Could the responses to visual and tactile stimuli that we observed in these three areas have actually been motor rather than sensory responses, representing the animal's attempt to avoid or to reach for the stimulus? Because the animal was immobilized with Pavulon, such attempts to move could not have been noticed. However, in control tests when the animal was respirated with nitrous oxide and oxygen but not immobilized with Pavulon, there was no obvious motor response to these stimuli. Furthermore, the characteristics of the responses we observed suggest that they are sensory and not motor. As described above, both the tactile and visual responses had discrete receptive fields that varied from one cell to the next. Many cells were directionally selective in the tactile modality, the visual modality, or both. It is difficult to imagine how such stimulus selectivity could have been caused by the animal attempting to move.

Although a motor explanation of the responses we observed is thus inherently implausible, we directly tested the possibility. We recorded in the putamen of an awake monkey whose head was fixed by a head bolt and whose arms were loosely constrained in padded arm rests. Eye position was measured with a scleral search coil, and electrical activity was measured through surface electrodes pasted over various muscles of the upper and lower arm, using electromyography (EMG). First, the animal was trained to fixate an LED during presentation of visual and tactile stimuli. These stimuli included cotton swabs that were brought near the face, shoulders, arms, or hands at various speeds and then touched the skin. After several weeks the animal became so habituated to the situation that it sat quietly and continued to fixate the LED even during presentation of these stimuli.

We then recorded from single neurons in the putamen while simultaneously taking EMG recordings from the arm. As in the anesthetized animals, we found neurons that responded to visual and tactile stimuli, and the location of the visual and tactile receptive fields corresponded. For example, the neuron shown in figure 67.12 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 67.12A show the response as the visual stimulus was moved toward the tactile receptive field. An EMG record during one trial is also shown. There is clearly no change in EMG activity during the presentation of the stimulus. By contrast, figure 67.12B shows the EMG activity when the animal was fondling a grape that was

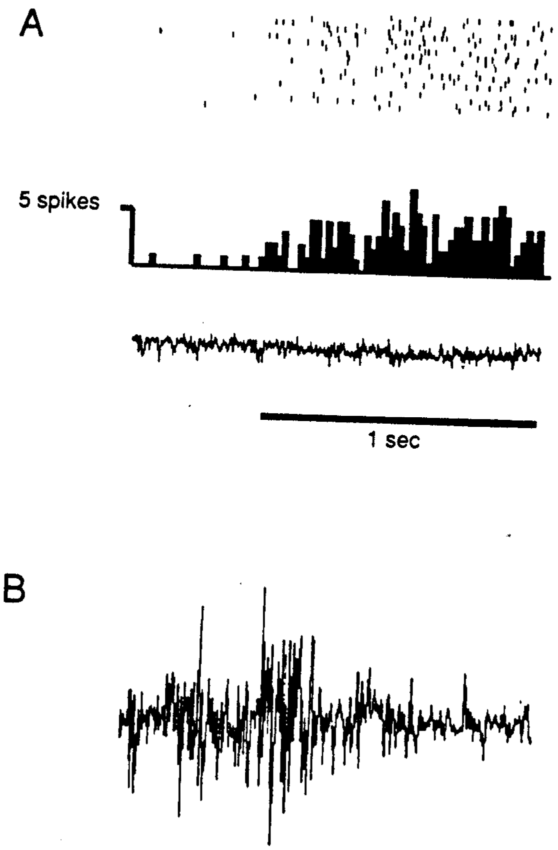

FIGURE 67.12 A bimodal neuron recorded from the putamen of an awake, fixating monkey. (A) The neuronal response, based on 20 trials, as the visual stimulus approached the tactile receptive field on the arm. The EMG trace (palmaris longus muscle), taken from one of the 20 trials, shows that the arm was stationary during stimulus presentation. (B) EMG trace while the animal touched a grape presented near its fingers.

placed near its fingers. The number of cells we have sampled so far is insufficient to assess any possible quantitative differences between bimodal putamen cells in the anesthetized and unanesthetized monkeys. However, these results demonstrate that bimodal responses with corresponding visual and tactile receptive fields occur in awake monkeys, unassociated with arm movements.

An interconnected system of bimodal areas

At the cortical level, the initial convergence of vision and somesthesis appears to occur in the parietal lobe. Somatosensory areas project to the medial bank of the intraparietal sulcus (area MIP) (Jones and Powell, 1970; Vogt and Pandya, 1978), visual areas project to the lateral bank (area LIP) (Selzer and Pandya, 1980; Maunsell and Van Essen, 1983; Ungerleider and Desimone, 1986; Neal, Pearson, and Powell, 1988; Cavada and Goldman-Rakic, 1989a; Boussaoud, Ungerleider, and Desimone, 1990; Baizer, Ungerleider, and Desimone, 1991), and both projections overlap in the fundus (area VIP) (Maunsell and Van Essen, 1983; Ungerleider and Desimone, 1986; Colby and Duhamel, 1991; Duhamel, Colby, and Goldberg, 1991). All three intraparietal areas innervate 7b (Jones and Powell, 1970; Mesulam et al., 1977; Cavada and Goldman-Rakic, 1989a), which also receives other somatosensory input, primarily from the second somatosensory area (SII) (Stanton et al., 1977; Cavada and Goldman-Rakic, 1989a). Inferior area 6 and area 7b are heavily interconnected (Mesulam et al., 1977; Kunzle, 1978; Matelli et al., 1986; Cavada and Goldman-Rakic, 1989b), and both project to the putamen (Kunzle, 1978; Weber and Yin, 1984; Cavada and Goldman-Rakic, 1991; Parthasarathy, Schall, and Graybiel, 1992).

These connections suggest that bimodal responses may be generated in area VIP and area 7b from convergent visual and somesthetic input. Area 7b may then transmit its bimodal properties to inferior area 6 and the putamen, where further processing is done. In the next section we propose that these areas form a system for representing extrapersonal space.

Bimodal cells may code extrapersonal visual space

The putamen, inferior area 6, area 7b, and area VIP form a distributed system of bimodal cells. Each of these areas is somatotopically organized, except perhaps for VIP, where the organization is not known. In each map, neurons in the arm portion have visual receptive fields around the arm, while neurons in the face portion have visual receptive fields around the head. That is, each area contains a somatotopically organized map of the visual space near the animal. We suggest, therefore, that these areas encode near extrapersonal visual space. This view is supported by the results of lesion experiments. Lesions to inferior area 6 impair the ability to localize nearby visual stimuli, but leave intact the ability to localize stimuli that are beyond reaching distance (Rizzolatti, Matelli, and Pavesi, 1983; Rizzolatti and Berti, 1990). Lesions to the parietal lobe cause a whole constellation of spatial deficits, including deficits in processing extrapersonal space. For example, parietal lesions in humans often produce optic ataxia, an inability to judge the locations of stimuli for the purpose of reaching toward them (Newcombe and Ratcliff, 1989).

What spatial coordinate system do these bimodal areas use to encode the location of visual stimuli? Several different visual coordinate systems have been described for other regions of the brain. In the primary visual cortex, visual space is mapped retinocentrically; that is, neurons in V1 have visual receptive fields that are fixed with respect to the retina. In parietal area 7a, the receptive fields are also retinocentric, but the response magnitude is modulated by eye position (Andersen, Essick, and Siegel, 1985). A population of such neurons could encode the location of stimuli with respect to the head, that is, in craniocentric space (Zipser and Andersen, 1988). Finally, visual receptive fields in inferior area 6 remain in the same location even when the eyes move (Fogassi et al., 1992; Gentilucci et al., 1983). That is, they appear to encode space in a way that is explicit at the level of single neurons.

One explanation for these visual receptive fields that remain stationary when the eyes move is that they represent space in craniocentric coordinates (Fogassi et al., 1992). Our own work, however, suggests that the mapping of extrapersonal visual space in area 6 (and in the putamen) is not exclusively craniocentric. In both areas, we found bimodal neurons with visual receptive fields that move with the arm. These cells could encode the location of visual stimuli in arm-centered coordinates. More generally, we suggest that these bimodal areas may encode stimuli in a body part–centered fashion. According to this view, bimodal cells with tactile receptive fields on the face encode the location of stimuli with respect to the head; bimodal cells with tactile receptive fields on the arm encode the location of stimuli with respect to the arm; and bimodal cells with tactile receptive fields on the chest encode the location of stimuli with respect to the trunk. That is, the visual space near the animal is represented as if it were a gelatinous medium surrounding the body that deforms whenever the head rotates or the limbs move. Such a map would give the location of the visual stimulus with respect to the body surface, in somatotopic coordinates.

This hypothesis of body part–centered coordinates for the mapping of near extrapersonal visual space yields the following predictions. If a bimodal cell has a tactile receptive field on the face, then the visual receptive field would move as the head is rotated, but it would not move with the eye or the arm. If a bimodal cell has a tactile receptive field on the chest, then the visual receptive field would move as the trunk is rotated, but not with the head, the eyes, or the arm. We would expect to find neurons with these visual properties in some or all of the bimodal areas described above.

Relationship between sensory and motor properties

Cells in the putamen, area 7b, and inferior area 6 have motor functions as well as sensory functions (e.g., Hyvarinen, 1981; Crutcher and DeLong, 1984b; Gentilucci et al., 1988; Rizzolatti et al., 1988). Indeed, the same neurons often have both sensory and motor activity. These areas are probably best described as sensory-motor interfaces, which help to encode the location of sensory stimuli and to generate the motor responses to those stimuli. Are the sensory and motor responses expressed in a common coordinate system? There is some evidence that this is the case for area 6. Many neurons in inferior area 6 respond when the monkey reaches toward a target (Caminiti, Johnson, and Urbano, 1990). These neurons are broadly tuned to a preferred direction of reach, and this motor field moves as the arm moves, rotating at roughly the same angle that the shoulder has rotated. That is, just as for the visual receptive fields, the motor response fields for arm movements appear to be arm centered. The relevant experiment has not been done for neurons in area 7b or the putamen. However, there is psychophysical evidence from humans that, whatever portion of the brain may control reaching movements, it is done in an arm- or shoulder-centered coordinate system (Soechting and Flanders, 1989a, 1989b).

Another area with both sensory and motor responses in the same neurons is the superior colliculus (for review, see Sparks, 1991; Stein and Meredith, 1993). Neurons in the deep layers of the superior colliculus respond to visual, auditory, and tactile stimuli, and they also respond during saccadic eye movements. Many neurons are multimodal, and in these cases the response fields for the saccadic eye movements and the receptive fields for the different sensory modalities correspond spatially. Exactly how the location of a stimulus is encoded in the colliculus has been an issue of great interest. It appears that saccade targets are encoded by sensory receptive fields that are fixed with respect to the retina. This retinocentric organization was particularly clear in experiments by Jay and Sparks (1987), who recorded from neurons that had auditory receptive fields. When the monkey moved its eyes to different locations, these auditory receptive fields also moved, and thus remained at the same retinal coordinates.

Retinocentric coordinates are particularly appropriate for encoding the location of saccadic targets, because these coordinates give the distance and direction between the fovea and the desired target location. That is, they encode the saccadic "motor error" (Sparks, 1991). Similarly, arm-centered responses are appropriate for reaching toward an object, because they give the motor error between the current arm position and the desired arm position. However, retinocentric and arm-centered coordinate systems are not the only useful choices. When a monkey reaches toward another monkey with its teeth, it must encode the spatial relationship between its mouth and the target. When a soccer player butts a ball with his head, he must encode the changing relationship between the ball and his forehead. When he elbows a fellow player, he must encode the distance and direction between his elbow and the other player's stomach. Indeed, it would be useful to have a visual coordinate frame fixed to every part of the body surface, for the purpose of hitting, grasping, or avoiding visual stimuli in extrapersonal space. We hypothesize that the bimodal portions of the brain provide exactly such a somatotopically organized map of space. The arm and face portion of this map is clearly exaggerated. Indeed, in the putamen, we did not find any visual responses in the leg or trunk portions of the somatotopic map. However, they may exist in much lower proportions. In area 7b and area 6, the leg and trunk representations have not been adequately explored.

Two types of spatial maps have generally been distinguished (e.g., Hein and Jeannerod, 1983; Stiles-Davis, Kritchevsky, and Bellugi, 1988; Paillard, 1991). The first is an egocentric map, in which objects are located with respect to the body—usually with respect to a point in the middle of the forehead. The other is an allocentric map, in which objects are located in a fixed, external frame. The bimodal system proposed in this chapter contains a type of egocentric representation, a body part–centered one rather than a head-centered one.

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