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A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields

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Abstract. The macaque putamen contains neurons that respond to somatosensory stimuli such as light touch, joint movement, or deep muscle pressure. Their receptive fields are arranged to form a map of the body. In the face and arm region of this somatotopic map we found neurons that responded to visual stimuli. Some neurons were bimodal, responding to both visual and somatosensory stimuli, while others were purely visual, or purely somatosensory. The bimodal neurons usually responded to light cutaneous stimulation, rather than to joint movement or deep muscle pressure. They responded to visual stimuli near their tactile receptive field and were not selective for the shape or the color of the stimuli. For cells with tactile receptive fields on the face, the visual receptive field subtended a solid angle extending from the tactile receptive field to about 10 cm. For cells with tactile receptive fields on the arm, the visual receptive field often extended further from the animal. These bimodal properties provide a map of the visual space that immediately surrounds the monkey. The map is organized somatotopically, that is, by body part, rather than retinotopically as in most visual areas. It could function to guide movements in the animal's immediate vicinity. Cortical areas 6, 7b, and VIP contain bimodal cells with very similar properties to those in the putamen. We suggest that the bimodal cells in area 6, 7b, VIP, and the putamen form part of an interconnected system that represents extrapersonal space in a somatotopic fashion.

Key words: Space coding – Sensorimotor integration – Parietal cortex – Visually guided reaching – Monkey

Introduction

The macaque putamen is organized somatotopically (Crutcher and DeLong 1984a). 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 (DeLong 1973; Liles 1983; Crutcher and DeLong 1984b; Liles 1985; Liles and Updyke 1985; Alexander 1987; Schultz and Romo 1988). Furthermore, electrical stimulation of the putamen causes movement of the corresponding body part (Alexander and DeLong 1985a,b). The putamen receives a topographic projection from somatosensory and motor cortex, which is in register with the physiological map (Kemp and Powell 1970; Kunzle 1975, 1977, 1978; Jones et al. 1977; Liles and Updyke 1985). Because of these anatomical and functional properties, the putamen has been considered largely a somatomotor structure (e.g., Alexander et al. 1986). However, the putamen also receives direct projections from parietal area 7b (Weber and Yin 1984; Cavada and Goldman-Rakic 1991) and ventral premotor area 6 (Kunzle 1978; Parthasarathy et al. 1992). These cortical areas are somatotopically organized, but they also contain visually responsive neurons (Hyvarinen and Poranen 1974; Leinonen et al. 1979; Leinonen and Nyman 1979; Robinson and Burton 1980a,b; Hyvarinen 1981; Rizzolatti et al. 1981b; Gentilucci et al. 1988).

We recorded from the putamen in anesthetized macaque monkeys[1], and found a somatotopic organization similar to that previously reported for unanesthetized monkeys. In addition, we found visual responses in the face and arm region of the somatotopic map. Visual and tactile responses were often combined in a single neuron, and for these bimodal neurons, the visual receptive field (RF) usually matched the location of the tactile RF.

Brief accounts of some of this material have been published elsewhere (Gross and Graziano 1990; Graziano and Gross 1992a,b).

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[1] Originally we had intended to study visual properties in the claustrum, but the intriguing visual properties of cells in the adjacent putamen soon led us to the project described here

Materials and methods

Animal preparation

All husbandry, surgical, and behavioral procedures were approved by the Princeton University Institutional Animal Care and Use Committee and the consultant veterinarian and were in accordance with NIMH and DA guidlines.

Single unit responses in the putamen were studied in three male *Macaca fascicularis* (3–7 kg) and one female *Macaca mulatta* (5.5 kg). Stainless steel recording chambers 2.5 cm in diameter were positioned bilaterally, one over each hemisphere, to allow for a vertical approach to any location in the putamen. The recording chambers and a stereotaxically positioned head bolt were fixed to the skull with screws and dental acrylic under pentobarbital anesthesia (30 mg/kg) and sterile surgical conditions. Recording began 1 week after surgery.

At the beginning of each recording session, the animal was given atropine sulfate (0.15 mg/kg), to reduce mucosal secretions, and a restraining dose of ketamine hydrochloride (10 mg/kg) with acepromazine (0.4 mg/kg). The animal was then intubated with a pediatric tracheal tube coated with 2% xylocaine jelly and given a 2:1 mixture of nitrous oxide and oxygen to which 2.5% halothane was added. The head was then fixed into a stereotaxic frame by means of the head bolt. This technique eliminated the need for ear bars and eye bars, and therefore there were no pressure points in the ear canals or orbits. The animal rested comfortably on heating pads wrapped in absorbent towels, and its body temperature was maintained at 37–38° C. EKG was continuously monitored through skin electrodes. The animal was immobilized with an intravenous infusion (0.03 mg/kg per hour) of pancuronium bromide (Pavulon) through a pediatric i.v. cannula and artificially respirated. Respiratory rate and volume were adjusted to give an end-tidal carbon dioxide level of 3.5–4.5%. The pupils were dilated with cyclopentolate (Cyclogyl, 1%), and the corneas were covered with contact lenses selected to focus the eyes on a rear projection tangent screen. The cap of the recording chamber was removed and a small hole was drilled through the skull, exposing the dura in the location planned for the electrode penetration. Halothane was then discontinued, and the animal was maintained under 2:1 nitrous oxide and oxygen in order to minimize discomfort. No surgery was performed after the halothane was discontinued. A stainless steel guide cannula was lowered through the dura, and a varnish-coated tungsten microelectrode was advanced through the cannula and into the brain. There was no change in heart rate from the introduction of the guide cannula or the electrode, suggesting that the animal felt no pain. Stimuli applied to the animal during the experiment, such as touching the skin, manipulating or gently squeezing the limbs, and moving objects toward or away from the face, also caused no change in heart rate. In control tests, when the animal was respirated with 2:1 nitrous oxide and oxygen but not immobilized with Pavulon, there were no motor signs of distress as a result of these visual and somatosensory stimuli.

Recording sessions lasted 15-18 h and were separated by a minimum of 4 days. Each animal was used for about ten recording sessions. After each session, the animal was attended during full recovery and then placed back in its home cage. Animals began eating normally within 6 h of recovery. They remained in good health between sessions and showed no signs of distress.

Stimuli

Once a cell was isolated, it was studied by presenting a standard battery of stimuli while monitoring its activity on an oscilloscope and over a loudspeaker. Somatosensory responses were studied using manual palpation, manipulation of joints, gentle pressure, and stroking with cotton swabs. RFs were plotted by repeated presentation of the most effective of these stimuli. Responses on the face were tested while the eyes were covered with opaque goggles.

Visual responses were tested with moving bars of light back-projected onto a tangent screen. Color filters were used to produce colored bars of light. Expanding and contracting squares of light were also presented. Since cells often appeared to be selective for the depth of the visual stimulus, the screen was placed at various distances from the animal ranging from 30 cm to 1 m, 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 in depth 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 repeatedly approaching the animal from various angles. Cells were also tested with squares of cardboard mounted on a rod and presented manually. To ensure that the responses to stimuli close to the body were not caused by inadvertant tactile stimulation, such as by static electricity or air movement, a removable plexiglass plate was placed in front of the animal. As an additional control, visual stimuli were presented while the eyes were covered.

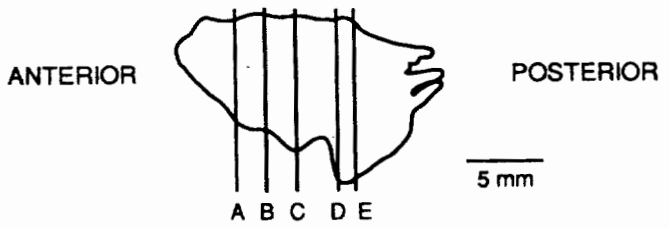
Single unit spike trains were recorded in order to generate peristimulus time histograms. An automatic track (throw of 70 cm, speed of 23.3 cm/s) under computer control was used to move the visual stimulus toward or away from the animal, while responses were stored on each trial. For testing somatosensory responses, the animal's eyes were covered and the track was used to bring a tactile probe in contact with the skin. In some cases, the computer initiated each trial by producing a signal click, which cued the experimenter to present the visual or tactile stimulus manually. Since only one of 354 putamen neurons responded to the click, this auditory signal did not interfere with the results.

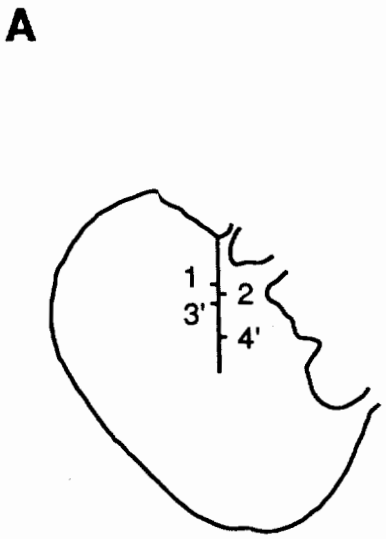
Histology

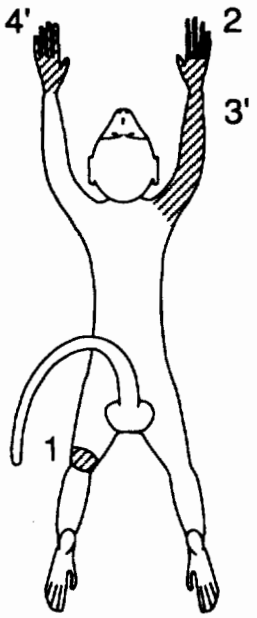
At the completion of the experiment, each animal was given an overdose of sodium pentobarbital (100 mg/kg) and perfused transcardially with saline and then formalin. The brain was blocked in a stereotaxic apparatus and sectioned in the coronal plane on a freezing microtome. Sections were cut at 50 μm and stained with cresylecht violet. Damage from the microelectrode was clearly visible as streaks of gliosis in the tissue, and therefore we were able to determine the location of every electrode penetration. The location of each neuron along an electrode penetration was reconstructed within about a millimeter accuracy in the following fashion. During the recording session, a depth measurement was made as the electrode first encountered cellular activity at the top of the brain; as the electrode reached a silent region indicating that it had been lowered through the top bank of cortex and entered the underlying white matter; as the electrode passed through regions of cellular activity corresponding to parts of the central sulcus or the lateral sulcus; and finally when the electrode had reached the neurons at the top of the putamen. This pattern of cellular activity and silence was then matched with the pattern of cortex and white matter that we observed in the histological sections. In each case, the various landmarks matched within a millimeter accuracy. In this fashion, we were able to reconstruct the approximate depth of each neuron that we studied. In some cases, these estimates of depth were verified with marking lesions.

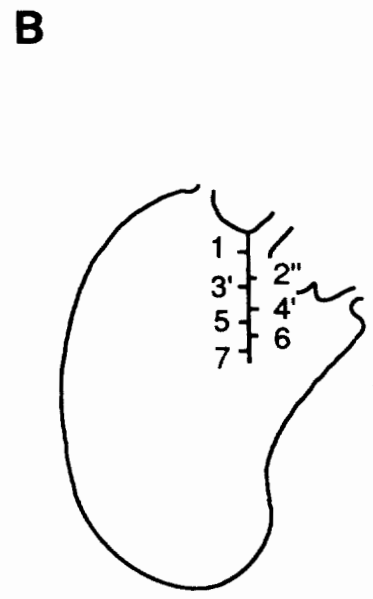
Results

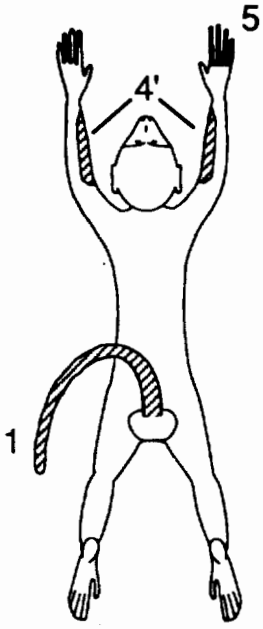
We recorded from 354 putamen neurons in six hemispheres of four anesthetized macaque monkeys. Locations of penetrations ranged from AP 10 to AP 22, and from ML 10 to ML 14. We found three main types of responsive cells: somatosensory cells (n = 143, 40%), vi-

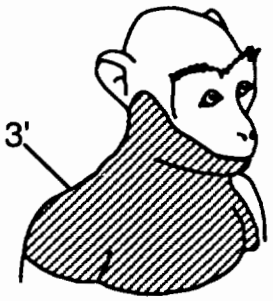












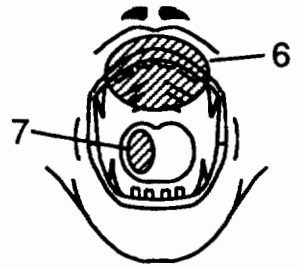


Fig. 1A–E. Somatotopic organization of the putamen. Five representative electrode penetrations (**A-E**) are shown. The locations of the penetrations are indicated on the lateral view of the putamen (*top*). Each of the sections to the *left* is a composite tracing of several adjacent brain sections, showing the electrode penetration and the approximate location of the responsive neurons. The corresponding receptive field locations are shown to the *right*. Cells numbered with single quotes (e.g., **3'**) responded to visual as well as tactile stimuli. Cells numbered with double quotes (e.g., **2"**) responded only to visual stimuli

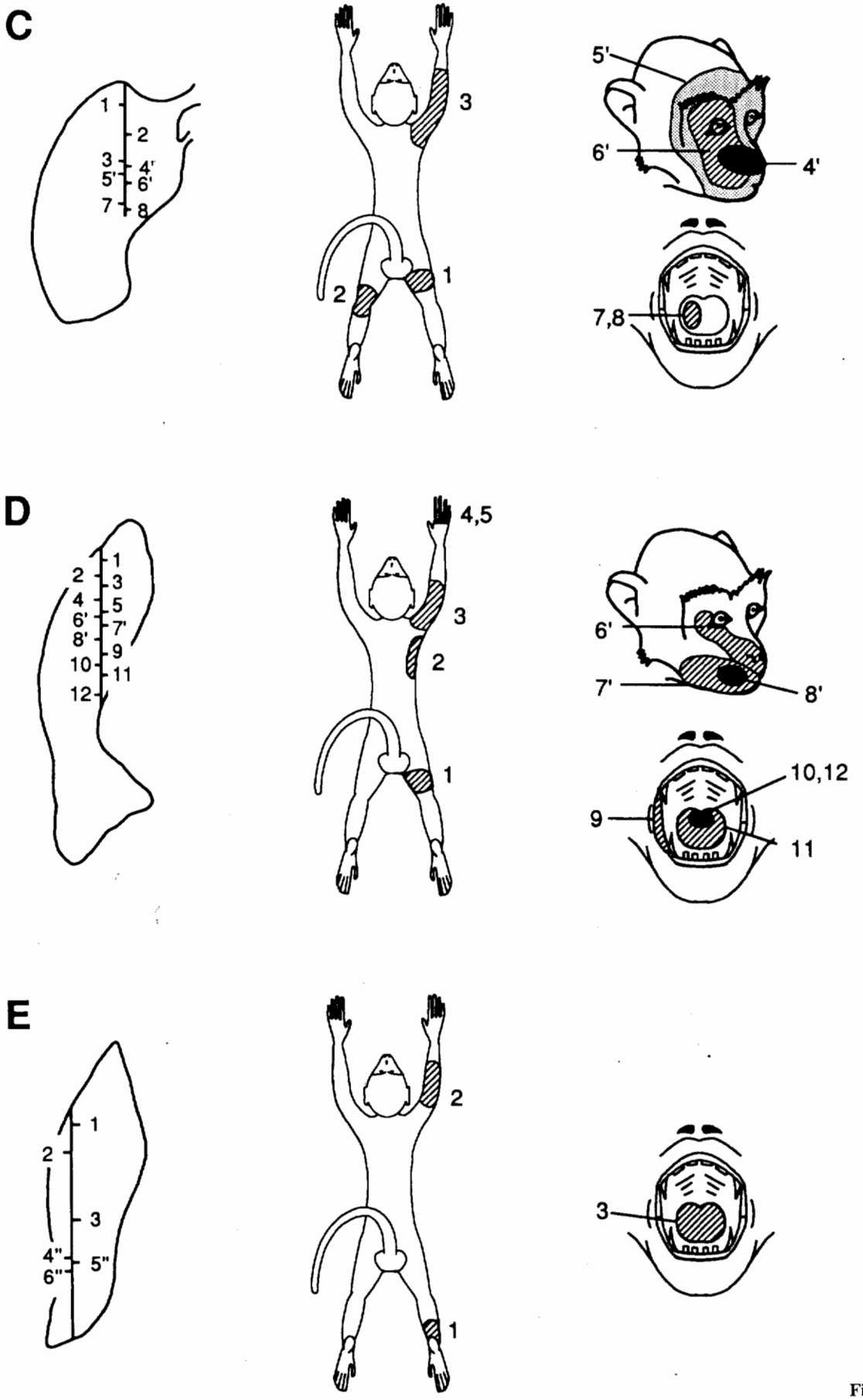

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Fig. 1C–E

sual cells (n = 42, 12%), and bimodal, visual-somatosensory cells (n = 86, 24%). In addition, one cell responded both to visual and auditory stimuli. The remaining 82 cells (23%) did not respond to any of the stimuli tested.

Somatosensory cells

Cells in the putamen were somatotopically organized in a manner similar to that described by Crutcher and Delong (1984a). On vertical electrode penetrations, the first cells encountered had RFs on the tail or lower legs. As the electrode moved ventrally, cells had RFs on the trunk, then the shoulders and upper limbs, then the face, and finally inside the mouth. Figure 1 shows five representative penetrations, projected onto a "standardized" drawing of the putamen. The same somatotopic progression was found at all AP levels in the putamen, from AP 10 to AP 22.

We studied 143 purely somatosensory cells, and categorized these by the type of response: light touch, deep pressure, or joint movement. Of these 143 cells,124 could be unambiguously assigned to one categories: 45 cells (36%) responded to light touch, 37 (30%) responded to deep pressure, and 42 (34%) responded to joint manipulation. The sizes of the RFs shown in Fig. 1 are typical. It was sometimes difficult to tell the laterality of a response, especially for RFs located inside the mouth; but of 126 cells with clear laterality, 86 (68%) were contralateral, 34 (27%) were bilateral, and 6 (5%) were ipsilateral. One cell was suppressed by somatosensory stimulation, and the remaining 142 gave excitatory responses.

Bimodal cells

In addition to somatosensory responses, we found visual responses in the face and arm region of the somatotopic map. Eighty-six neurons were bimodal, that is, they responded both to visual and to somatosensory stimuli. These bimodal neurons usually responded to light touch (86%) rather than to joint rotation (8%) or to deep muscle pressure (6%). As shown in Fig. 2, of the 81 cells with somatosensory RFs on the face, 57 (70%), termed face + visual cells, were bimodal; of the 77 cells with RFs on the arm, 25 (32%), termed arm + visual cells, were bimodal; 8 cells had RFs that encompassed the entire body, and 4 (50%) of these also responded to visual stimuli. All 4 body + visual cells were located in the arm and face region of the somatotopic map. Bimodal cells were not found either in the dorsal part of the penetration, before entering the arm region, or in the ventral part, after the RFs had progressed from the front of the face into the mouth. The large proportion of face and arm cells reflects our concentration on that region of the map.

Face + visual cells. We first describe the properties of several individual face + visual cells, and then characterize this entire category. A typical example of a face + visual cell is shown in Fig. 3. The tactile RF was plotted while the animal's eyes were covered. The cell was activated by lightly touching the facial hairs, and the responsive region covered most of the contralateral cheek and the area around the mouth (Fig. 3A, 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 RF, and the cell began responding when the stimulus was within about 10 cm of the face (Fig. 3C). This response was not caused by inadvertent tactile stimulation, such as by air movement, since it was eliminated by covering the eyes (Fig. 3D). In addition, the spontaneous activity of the cell was higher when the eyes were open (Fig. 3C) than when the eyes were closed (Fig. 3B, D). This increase of spontaneous

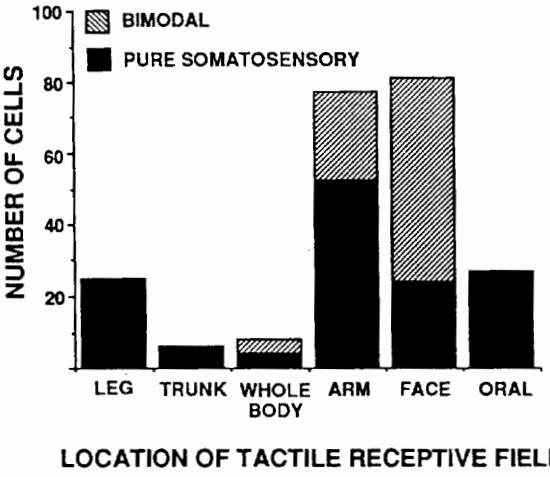

Fig. 2. Categorization of cells by the location of their somatosensory RFs. Bimodal cells always had tactile RFs that included the face or arms. The large proportion of face and arm cells reflects our concentration on that region of the putamen

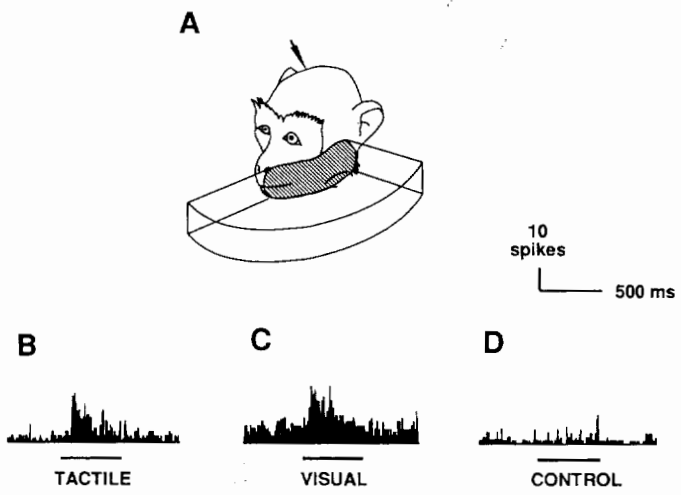

Fig. 3A–D. Post-stimulus time histograms, summed over 10 trials, for a typical *face + visual* cell. **A** The tactile RF (*stippled*) and the visual RF (*boxed*) are in register. The *arrow* indicates the hemisphere recorded from. **B** Response to a cotton swab touching the face while the eyes are 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

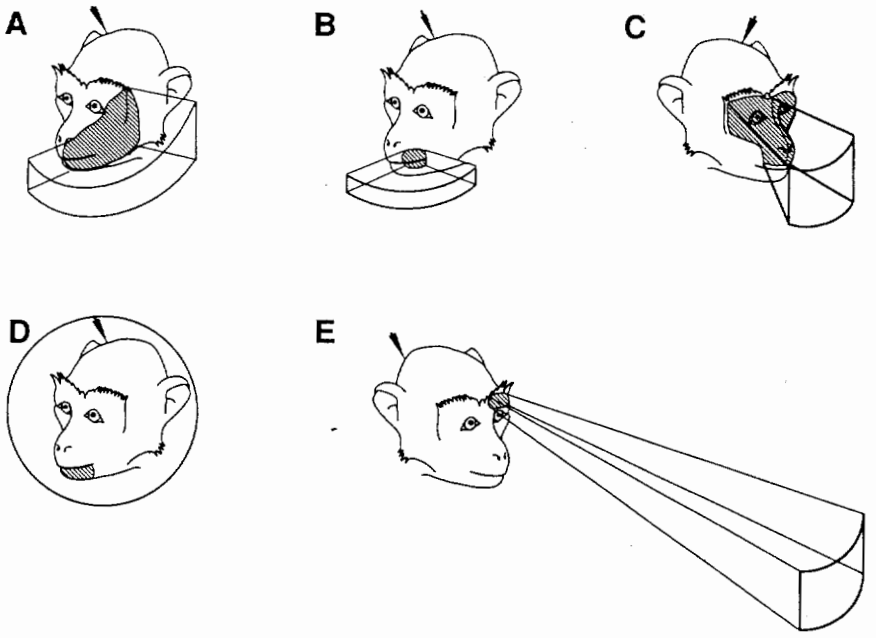

Fig. 4A, B. A, B, Typical *face + visual* cells in that the visual and tactile RFs correspond and the visual RF extends about 10 cm from the face. **C** and **E** Atypical face + visual cells because in **C** the tactile RF is bilateral and the visual RF is contralateral, and in **D** the tactile RF is confined to the lower jaw but the visual RF extends from the face in all directions. In both, the visual RF extends about 10 cm from the face. In **E**, the visual RF is atypical in that it extends about 100 cm from the tactile RF

activity in the light was typical of the bimodal cells that we studied.

By approaching the tactile RF 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 Fig. 3A, the visual RF as thus defined was a solid angle centered at the tactile RF and extending out approximately 10 cm. The response was weak and erratic toward the edges of the visual RF. The response was better to a stimulus moving toward the face than to a stimulus moving away. The cell gave no response to conventional visual stimuli, such as bars of light projected onto a tangent screen, colored bars of light, or expanding or contracting squares of light. The shape or color of the object approaching the face did not affect the response.

Fig. 4A, B shows two more examples of typical face + visual cells. As in the previous example, these cells had cutaneous RFs on the face and responded to a light touch on the hairs. They also responded to visual stimuli moving toward the tactile RF, within a distance of about 10 cm. Again, these responses were not caused by inadvertent tactile stimulation, since they were eliminated by covering the animal's eyes but not by placing a plexiglass shield in front of the face. Both cells preferred stimuli moving toward the face, and did not respond to light stimuli projected onto the tangent screen. They were not sensitive to the form or color of the visual stimulus.

Figure 4 also shows several cells that differed slightly from this basic pattern. Figure 4C shows a cell with a bilateral tactile RF, but a contralateral visual RF. Stimuli moving toward the ipsilateral side of the face did not activate the cell, even though touching the ipsilateral side of the face did. Figure 4D shows a cell with a small bilateral tactile RF covering the chin, and a visual RF covering the entire visual field but extending outward only about 10 cm from the face. An object approaching any part of the face, even the upper face, caused a visual response. Figure 4E shows a cell with a tactile RF on the contralateral brow, and a visual RF in the contralateral half of space. The visual RF extended out about one meter from the monkey, and stimuli at that distance would drive the cell as they moved toward the face.

All 57 face + visual cells responded to light cutaneous stimulation, usually to bending of the facial hairs. By definition, they also responded to visual stimuli, and we were able to characterize the receptive fields in 38 cases. Of these, 31 (82%) responded best or only to objects within 20 cm of the face, while 7 (18%) responded well to objects at greater distances. We found no selectivity for the form or color of the stimulus.

All 57 cells were tested for their directional preference, and 22 (39%) were directionally selective. All 22 preferred motion in depth, toward the tactile RF. This directionality might have resulted from the habituation displayed by most cells: as the stimulus first entered the RF and moved toward the face, the cell responded; when the stimulus was drawn back away from the face, the cell had already habituated and no longer responded. Alternatively, the gradual increase in stimulus size, or other cues for motion in depth, might have activated the cells. Fourteen directional cells were further tested by presenting expanding and contracting squares of light on the tangent screen. Only eight cells responded; all eight responded to the expanding stimulus and not to the contracting stimulus.

Arm + visual cells. A typical arm + visual cell is shown in Fig. 5A. The somatosensory RF, plotted while the eyes were covered, was located on the contralateral arm. The cell responded to light touch, and when the eyes were uncovered it responded to visual stimuli moving in the

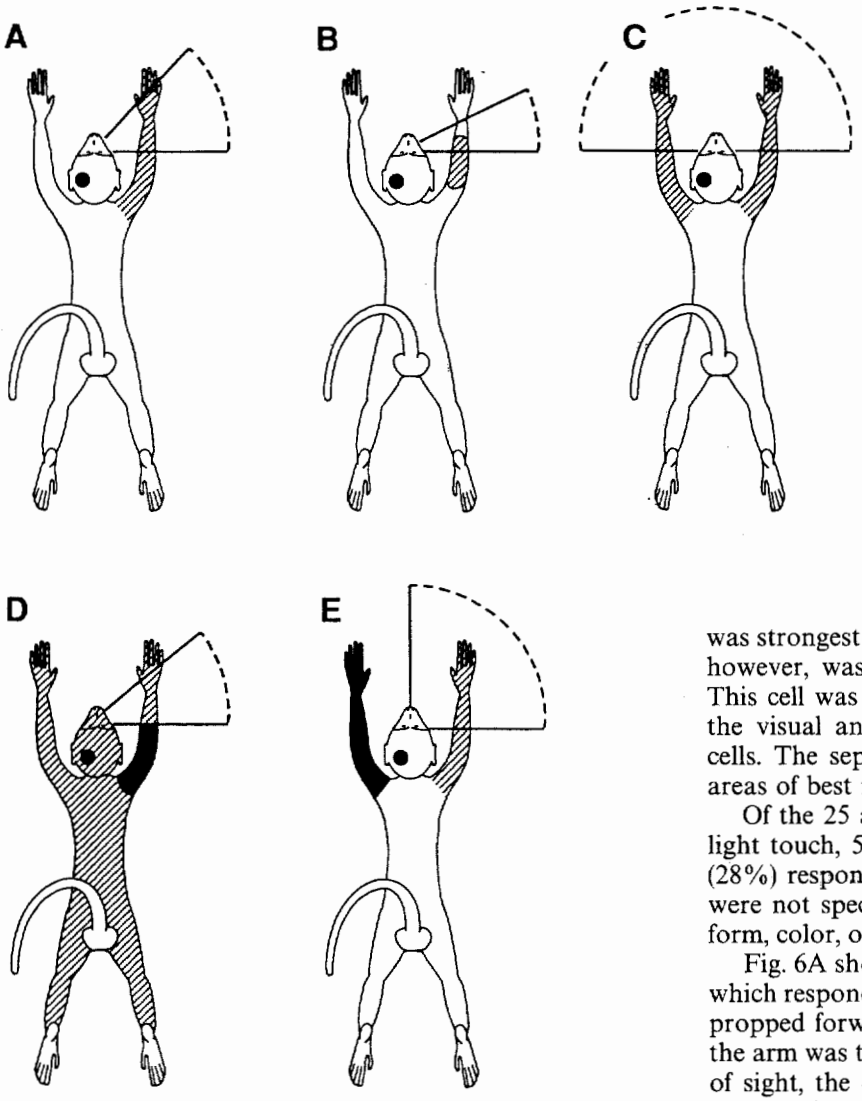

Fig. 5A–E. *Arm + visual* cells. The *lines* indicate the angles subtended by the visual RFs in the horizontal plane. The *dashed lines* indicate that the RFs extend for several meters or more. The *stippling* indicates the tactile RFs, the *blackening* shows the region of maximal response. The *black circles* on the head indicate the hemisphere recorded from. **A-C** Typical arm + visual cells for which the visual and tactile RFs correspond. **D-E** Atypical cells for which the tactile RFs are bilateral but the visual RFs are unilateral

contralateral periphery. This cell could be activated by objects at all distances tested, out to the wall of the room 1.5 m away. The response did not depend on the direction of motion, the shape, or the color of the visual stimulus. Figure 5B shows a second typical example. The tactile RF covered part of the contralateral arm, and the visual RF lay in the contralateral periphery. Again, the cell responded to objects at any distance out to the wall of the room, 1.5 m from the animal, and the response did not depend on the direction of motion, or the shape or color of the visual stimulus.

Figures 5C, D, and E show the responses of several cells that differed slightly from this basic pattern. The cell shown in Fig. 5C responded to a touch on either arm; the visual RF was bilateral, and included both peripheries. The cell shown in Fig. 5D responded to touch almost everywhere on the body, but the response was strongest on the contralateral shoulder and upper arm, and the visual response was confined to the contralateral periphery. The cell shown in Fig. 5E responded to touch on either arm and on a part of the chest, but the response was strongest on the ipsilateral arm. The visual response, however, was restricted to the contralateral half field. This cell was the only instance of a mis-match between the visual and somatosensory RFs, for arm + visual cells. The separation was not complete, since only the areas of best response were mis-matched.

Of the 25 arm + visual cells, 13 (52%) responded to light touch, 5 (20%) responded to deep pressure, and 7 (28%) responded to joint motion. The visual responses were not specific: none of the cells was sensitive to the form, color, or direction of motion of the visual stimulus.

Fig. 6A shows an interesting type of arm + visual cell which 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 RF 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. Of the 25 arm + visual cells that were tested by placing the arm in different positions, five (20%) had visual responses that were gated by the position of the arm. All five preferred stimuli near the animal, within 20 cm, while all other arm + visual cells responded to more distant stimuli.

The cell shown in Fig. 6B had a particularly close match between the tactile and visual RF; the visual RF extended 5 cm from the hand. When the arm was moved to different locations within the animal's sight, the visual RF 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.

Correspondence of tactile and visual RFs. As noted above, the location of the tactile RF usually approximately matched the location of the visual RF, for both arm + visual and face + visual cells. Table 1 summarizes this relationship for the 70 bimodal neurons that had sufficiently complete plots of tactile and visual RFs. The cells are categorized by their region of best response; contralateral, bilateral, or ipsilateral. Most cells ($n = 59$,

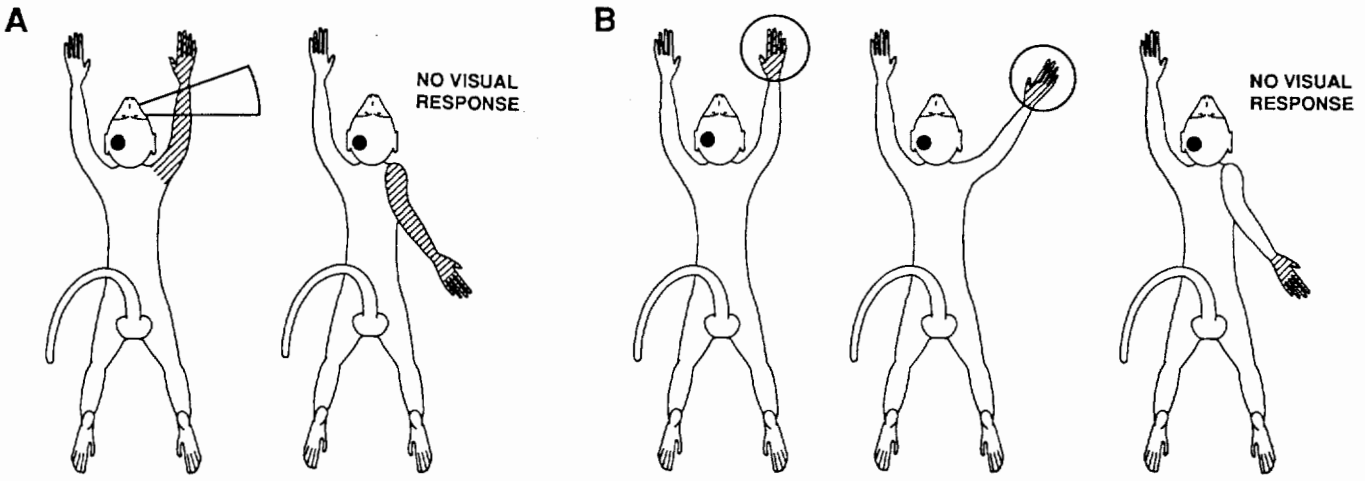

Fig. 6A, B. Two examples of a special type of arm + visual cell. These cells responded visually when the arm was within the monkey's field of view (*left*), but did not respond when the arm was moved out of view (*right*). For the cell shown in **B**, the visual RF moved as the hand moved

Table 1. Number of bimodal neurons with corresponding and non-corresponding tactile and visual RFs. Laterality of tactile response versus laterality of visual response

Area of best or only visual response	Area of best or only tactile response		
	Contra	Bi	Ipsi
Contra	37	5	1
Bi	2	16	3
Ipsi	0	0	6

Table 2. Face or arm tactile response versus central or peripheral visual response

Area of best or only visual response	Area of best or only tactile response	
	Face	Arm
Central (<45°)	36	2
Peripheral (>45°)	4	19

84%) fell along the diagonal positions in the chart, showing that the tactile response usually had the same laterality as the visual response. This match in laterality was not simply because most responses were contralateral, since even ipsilateral responses tended to match.

Table 2 shows that of the 61 bimodal neurons for which the peripheral edge of the visual RF was determined, most arm + visual cells (19/21, 90%) had peripheral visual RFs, while most face + visual cells (36/40, 90%) had central visual RFs. Again, this result demonstrates the correspondence between visual and somatosensory RFs, since in the resting position of the monkey on the recording platform, the hands were placed to either side of the head, in the visual peripheries.

Finally, the five arm cells that responded visually only when the arm was in sight demonstrate an even closer correspondence between the two modalities. The visual RF of one of these cells surrounded the tactile RF on the hand (Fig. 6B), and followed wherever the hand was placed in the visual field.

Visual cells

In addition to somatosensory cells and bimodal cells, we found 42 cells which responded only to visual stimuli. These visual cells were found in two locations in the putamen: in the face and arm region of the somatotopic map, where bimodal cells were located (e.g., Fig. 1B, cell 2); and ventral to the map, in a region without somatosensory responses (e.g., Fig. 1E, cells 4, 5, and 6). Twenty cells (48%) lay within the somatotopic map; and 17 cells (40%) lay beneath the most ventral tactile response found on their particular penetrations. Five cells (12%) lay along penetrations in which the body map was not clearly determined. We found no consistent difference between visual cells found within the somatotopic map and visual cells found ventrally.

An example of a visual cell located within the face part of the somatotopic map is shown in Fig. 7. On the same electrode penetration, bimodal face + visual cells were found both above and below it, within 0.5 mm, but this particular neuron had a visual response and no tactile response. The upper histogram in Fig. 7, based on nine trials, shows the response when a 5-cm sphere, mounted on a track, was moved toward the face at 23.3 cm/s from a distance of 78 cm to a distance of 8 cm. The response began when the stimulus was about 50 cm away and increased as the stimulus approached the face. Once the stimulus stopped moving, the response abruptly decreased, although the cell continued to fire above base-

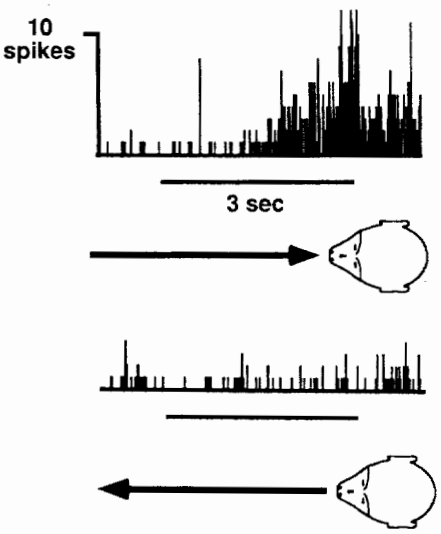

Fig. 7. Response of a visual cell to a 5 cm diameter brown sphere moving on a track at 23.3 cm/s toward or away from the face. Farpoint, 78 cm; nearpoint, 8 cm; duration, 3 s; based on nine trials with an intertrial interval of 15 s

line for several seconds. As shown in the lower histogram, there was no response on interleaved trials when the stimulus was moved away from the face.

We found only two visual cells that appeared to be selective for stimulus form and color. The cells were tested with numerous three-dimensional complex objects including life-sized models of human and monkey heads, a model of a hand, plastic flowers, a plastic snake, brightly colored brushes, and various junk items found around the lab. Both cells responded best to a large white rectangle (20° × 10°) presented at any orientation in the center of the visual field. The two cells lay along the same electrode penetration, within 0.3 mm of each other, and were located in the ventral putamen beneath the somatosensory map.

In general, visual cells responded to stimuli at any distance from the animal, including light stimuli projected onto the tangent screen. Fourteen cells (33%) were selective for the direction of motion: Five preferred motion in the frontoparallel plane, six preferred motion in depth toward the monkey, and three preferred motion in depth away from the monkey. These direction selective cells were not sensitive to the form or color of the moving stimulus. RF plots were obtained for 20 visual cells, and the mean RF width was 125°. Seventeen cells had RFs that crossed the midline, and ten covered the entire visual field.

Discussion

Somatosensory cells

We recorded from the putamen in anesthetized macaque monkeys, and found a somatotopic map similar to the one found in awake monkeys by Crutcher and Delong (1984a). On vertical electrode penetrations, the most dorsal cells had RFs located on the tail and lower limbs. As the electrode moved ventrally, it encountered cells with RFs on the trunk, then on the arms, then on the face, and finally in the mouth. This somatotopic progression was found at all AP levels in the putamen, from AP 10 to AP 22.

There were, however, several minor differences between the somatosensory properties that we found and those reported by Crutcher and Delong. First, these authors reported that most cells responded to joint movement or deep muscle pressure. They found only a small percentage of cells with cutaneous RFs (5% of arm cells, proportion unreported for other areas of the body map), and none that responded to touch on the hair of non glabrous skin. In our experiment, we found a higher percentage of cells with cutaneous RFs (28% of somatosensory and bimodal arm cells, 54% for all somatosensory and bimodal cells combined). In particular, most cells with RFs on the face (97%) responded when the facial hair was touched. Second, the few cutaneous RFs that Crutcher and DeLong found were relatively small, for example covering half of the palm. Most of the cutaneous RFs that we found were larger, often covering an entire arm, or half of the face, and several cells had RFs that encompassed the entire body. Finally, Crutcher and DeLong did not report any ipsilateral responses, while we found that 5% of the somatosensory responses were exclusively ipsilateral.

Since Crutcher and Delong used an awake preparation and we used an anesthetized preparation, the discrepancies might result from the anesthesia. Responses might become less specific and more sensitive under anesthesia, revealing an ipsilateral input and increasing the average receptive field size. Similar effects of anesthesia have been reported before; for example, Baker et al. (1971) reported that tactile RFs in the somatosensory and motor cortex of the cat enlarged under anesthesia. Another likely reason for the discrepancies is the difficulty of studying some types of somatosensory responses in an awake, active monkey. Facial responses would be particularly difficult to characterize, since the monkey might react to the stimulus, for example, by flinching.

Previous reports of visual responses in the putamen

In addition to the somatosensory cells, we also found visual cells in the putamen, as had several previous investigators. Caan et al. (1984) recorded from single units in the ventral putamen, below the somatotopic map, and found responses selective for the shape, color and texture of complex three-dimensional visual stimuli. For example, several cells fired best to a human face. Seventeen of the visual cells that we studied lay in the ventral putamen, but only two were selective for the form or color of the stimulus. Both cells fired best to a large white rectangle presented centrally. The most likely explanation for the difference between our results and the results of Caan et al. is that, according to their figures, their recording site was far more ventral than ours.

Kimura and associates (Kimura et al. 1984; Kimura

1986) have reported that neurons in the putamen can respond to visual and auditory cues. For example, when the onset of a light cued the monkey to move his arm, cells in the arm region of the somatotopic map responded to the light. However, as soon as the stimulus lost its behavioral significance, the response disappeared or was greatly reduced. Since they did not report the visual properties of these cells, such as receptive fields or preferred directions of motion, it is not possible to compare their results to ours.

Finally, Crutcher and Delong (1984a) reported a few cells responsive to visual stimuli, but did not characterize them sufficiently to allow comparison to the cells in our study.

Bimodal cells

We found that a high proportion of cells in the face and arm region of the map were bimodal, that is, they responded to both visual and tactile stimuli. Bimodal cells were not reported by Crutcher and DeLong, or by other groups that have recorded from the putamen (DeLong 1973; Liles 1983, 1985; Liles and Updyke 1985; Alexander 1987; Schultz and Romo 1988). Perhaps the reason was their use of awake monkeys. In our experiment, the optimal visual stimulus was usually an object moving near the tactile RF. Because many cells in the putamen respond to voluntary movement, in an awake animal it might have been difficult to distinguish a visual response from a motor response if the stimulus was threatening, attractive, or otherwise likely to elicit a motor response from the animal.

Sensory versus motor responses

In the awake monkey, many cells in the putamen respond during voluntary movement (DeLong 1973; Liles 1983, 1985; Crutcher and DeLong 1984b; Liles and Updyke 1985; Alexander 1987; Schultz and Romo 1988). Could the responses to visual and tactile stimuli that we observed have actually been motor rather than sensory responses, representing the animal's attempt to avoid or to reach for the stimulus? Because of the immobilization due to the action of Pavulon, such attempts to move would not have been noticed. However, it is unlikely that the animal was trying to move while respirated with the high dose of nitrous oxide used here (66.7%). There was no change in heart rate during the presentation of stimuli, including objects slowly or rapidly approaching the face or arms, objects hovering within centimeters of the skin, cotton swabs touching or stroking the skin, and manipulation of the limbs. This lack of a cardiac response suggests that the animal was not attempting to grasp, approach, or avoid the stimuli. In control tests when the animal was respirated with nitrous oxide and oxygen but not paralyzed 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 delimitable RFs which varied from one cell to the next. It is unlikely that the monkey would attempt to move when touched in one region of skin on the arm but not when touched in another adjacent region. In the case of the visual responses, the RFs were not only confined in their angular spread, but also in their distance from the monkey. Some neurons only responded to stimuli within centimeters of the skin, while others responded to stimuli as distant as 1 m. It is unlikely that the animal would react only to near stimuli, and then when the electrode had advanced to the next cell, suddenly change his strategy and react to distant stimuli as well. Similarly, if the responses were "motor" rather than sensory, why should adjacent cells have varied in whether they responded only to visual stimuli, only to somatosensory stimuli, or to both visual and somatosensory stimuli? Finally, presentation of food items such as fruit or monkey biscuits, threatening items such as models of human heads or pictures of snarling monkeys, or neutral items such as balls of cotton or pieces of cardboard, did not differentially affect the responsiveness of the cells. If the monkeys had been attempting to react to the stimulus, and if the observed neuronal responses were actually motor in nature, then arousing stimuli should have caused a greater response than neutral stimuli.

Although a "motor" explanation of the responses we observed is thus inherently implausible, we have directly tested the possibility. In recent experiments carried out in our laboratory (Graziano and Gross, unpublished observations), we recorded in the putamen of an awake monkey. The animal's head was fixed by a head bolt and the arms were loosely constrained in padded arm rests. Eye position was measured with a scleral search coil, and electromyographic activity (EMG) was measured through surface electrodes pasted over various muscles of the upper and lower arm (biceps, triceps, brachioradialis, extensor carpi radialis, flexor carpi ulnaris, palmaris longus, and the digit extensors). First the animal was trained to fixate a small spot of light 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 light even during presentation of these stimuli.

We then recorded from single neurons in the putamen while simultaneously recording EMG from the arm. As in the anesthetized animals, we found neurons to respond to visual and tactile stimuli, and the location of the visual and tactile RFs corresponded. EMG activity was quiescent during stimulus presentation. By contrast, when a raisin was presented near the animal's fingers, a vigorous EMG invariably resulted. 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 RFs occur in awake monkeys, unassociated with arm movements.

Other bimodal areas

Several other regions of the monkey brain, including parietal area 7b, the ventral intraparietal area (VIP), and inferior premotor area 6, contain bimodal, visual-tactile responses that are almost identical to the responses that we have studied in the putamen. These areas are monosynaptically interconnected, and we suggest that they form a bimodal system. In this section, we briefly summarize the sensory responses of each of these areas, and compare them to the responses in the putamen. We then summarize the anatomical connections between them.

Area 7b. Most neurons in this area respond to somatosensory stimuli, and are organized somatotopically (Robinson and Burton 1980a). Visual cells and bimodal, visual-somesthetic cells have also been reported in 7b, primarily in the face and arm region of the map (Hyvarinen and Poranen 1974; Leinonen and Nyman 1979; Leinonen et al. 1979; Robinson and Burton 1980a,b; Hyvarinen 1981). Estimates of the proportion of bimodal cells range from 6% (Robinson and Burton 1980b), to 33% (Leinonen and Nyman 1979). Most of the bimodal cells responded to cutaneous stimulation, and to visual stimuli moving toward the animal within about 10 cm of the tactile RF. Leinonen et al. (1979) reported a particularly close correspondence between the two modalities when the tactile RF was on the arm. In these cases, when the arm was placed in different positions, the visual response appeared to change to stay in rough correspondence with the arm. However, these cases were not reported in detail. A small number of cells had matching directional selectivity in both the tactile and visual modalities. Finally, some bimodal cells responded to joint rotation.

The bimodal responses in area 7b are similar in several ways to the responses in the putamen. First, both areas are somatotopically organized. Second, the bimodal cells are concentrated in the face and arm region of the map. Third, the bimodal cells respond to visual stimuli near and approaching the tactile RF. Fourth, when the arm is moved, the visual RFs for some arm + visual cells appear to move to the new location. However, there was one response type found in 7b which we did not find in the putamen, namely, bimodal cells that were directionally selective in both modalities. We never found putamen cells that had directional tactile responses, and neither did Crutcher and Delong (1984a,b). Some of the recordings in area 7b appear to have encroached on the intraparietal sulcus (e.g., Leinonen et al. 1979), and one area now known to lie in the sulcus, VIP (discussed below), contains just such bimodal directional cells. On the available evidence, the directional cells reported by Hyvarinen et al. and Leinonen et al. could have been located in area VIP, and not within 7b as it is currently defined.

VIP. Most cells in VIP respond to visual stimuli, and are directionally selective (Colby and Duhamel 1991; Duhamel et al. 1991; Colby et al. 1993). Furthermore, about 75% are bimodal, responding to tactile stimuli, primarily on the face, and to visual stimuli presented within a few centimeters of the tactile RF. The preferred direction in the tactile modality matches the preferred direction in the visual modality. For at least some neurons, the visual RF appears to be fixed with respect to the face, even when the eyes move to a new location (Colby et al. 1993). 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.

This area is similar to the putamen, in that it contains cells with tactile RFs on the face and matching visual RFs. It differs, however, in that most cells in VIP are directionally selective, in both the tactile and visual modalities. The only directional selectivity that we found among bimodal putamen cells was for visual stimuli moving in depth toward the face.

Inferior area 6. Most neurons in inferior area 6, in the premotor fields F4 and F5, respond to a touch on the face or manipulation of the arms (Rizzolatti et al. 1981a). About 60% also respond to visual stimuli (Rizzolatti et al. 1981b). For example, cells with tactile RFs on the face often respond to visual stimuli within about 20 cm and moving toward the tactile RF. Neurons with tactile RFs on the arm often respond to visual stimuli in the lower visual field, within reaching distance of the monkey (Rizzolatti et al. 1981b). For many neurons, the visual RF appears to remain fixed near the tactile RF, even when the monkey's eyes have rotated to a new location (Gentilucci et al. 1983; Fogassi et al. 1992).

The bimodal cells in area 6 are strikingly similar to neurons in the putamen. The emphasis on the face and arm representation, the correspondence between visual and tactile RFs, and the preference for visual stimuli near and approaching the monkey, are the same for both areas. In inferior area 6, cells with tactile RFs on the arm generally had lower field visual responses, whereas in the putamen, cells with tactile RFs on the arm generally had peripheral visual responses. However, in the studies by Rizzolatti et al., the monkeys were seated upright with their arms resting in the lower visual field, whereas in our experiment, the monkeys lay on a table with their arms resting in the visual peripheries. That is, in both experiments, the location of the visual RF matched the location of the tactile RF.

In summary, there are at least four areas with similar bimodal, visual-somesthetic responses: 7b, VIP, inferior area 6, and the putamen. In all four areas the visual responses lie primarly within a face or arm representation of the body. The visual and tactile RFs correspond, and visual stimuli near the animal drive the cells best. Area VIP appears to be slightly different from the other areas, in that its neurons are directionally selective in both the tactile and visual modalities.

Anatomical connections among 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 (MIP) (Jones and Powell 1970; Vogt and Pandya 1978), visual areas project to the lateral bank (LIP) (Selz-

er and Pandya 1980; Maunsell and Van Essen 1983; Ungerleider and Desimone 1986; Neal et al. 1988; Cavada and Goldman-Rakic 1989a; Boussaoud et al. 1990; Baizer et al. 1991), and both projections overlap in the fundus, where VIP is located (Maunsell and Van Essen 1983; Ungerleider and Desimone 1986; Colby and Duhamel 1991; Duhamel et al. 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 SII (Stanton et al. 1977; Cavada and Goldman-Rakic 1989a). Inferior area 6 and 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 et al. 1992).

These connections suggest the following flow of information: bimodal responses may be generated in VIP and 7b from convergent visual and somesthetic input. Area 7b may then transmit its bimodal properties to inferior area 6 and the putamen. In the next section we propose that these areas form a system for representing extrapersonal space. There are other multi-modal areas of the brain, such as the deeper layers of the superior colliculus (Meredith and Stein 1985; Sparks 1991) and the superior temporal polysensory area (Desimone and Gross 1979; Bruce et al. 1981). However, we do not yet have evidence that they are part of this system.

Coding of extrapersonal visual space

The brain contains a wide-spread and interconnected system of bimodal areas, including the putamen, inferior area 6, 7b, and VIP. The neurons in these areas respond best to visual stimuli near the animal, suggesting that they are involved in the representation of close personal space. What spatial coordinate system do these areas use? Is spatial location encoded with respect to the fovea, as Sparks and colleagues have shown in the superior colliculus for responses to visual, auditory, and remembered stimuli (Mays and Sparks 1980; Jay and Sparks 1987; Sparks 1991); is it encoded with respect to the head, as Rizzolatti and colleagues have suggested for visual responses in inferior area 6 (Gentilucci et al. 1983; Rizzolatti and Berti 1990; Fogassi et al. 1992 see also Schlag et al. 1980; Battaglini et al. 1990); or is there a complex population code, intermixing retinal position and eye position, such as Andersen and colleagues have suggested for parietal area 7a (Andersen et al. 1985)?

Each of the bimodal areas described above is somatotopically organized, except perhaps for VIP where the organization is not known. In each map, the arm region contains a representation of visual space around the arms, while the face region contains a representation of visual space around the head. That is, each area contains a *somatotopically* organized map of close, extrapersonal visual space.

These areas bring together eye position, limb position, vision and touch, and therefore the representation of extrapersonal space is probably not a simple head-centered one. Rather, we propose that it is a body-part-centered representation (Cf. Paillard 1991). In this view, bimodal cells with tactile RFs on the face encode the location of stimuli with respect to the head, while bimodal cells with tactile RFs on the arm encode the location of stimuli with respect to the arm. As the arm moves, visual RFs near the arm also move, to remain in register with the skin. That is, the visual space near the animal is represented as if it were a gelatinous medium surrounding the body, that deforms in a topology-preserving fashion whenever the head rotates or the limbs move. Such a map gives the location of the visual stimulus with respect to the body surface, in somatotopic coordinates.

Our view of the coding of extrapersonal space predicts the existence of bimodal areas that combine the following two unusual properties. First, the location of at least some of the visual RFs should be independent of eye position, and instead should be fixed in register with the tactile RFs. Second, for at least some arm + visual cells, the visual RFs should move as the arm moves, once again in order to remain in register with the tactile RFs. As described above, the first property has been reported in inferior area 6 (Gentillucci et al.1983; Fogassi et al. 1992), and in area VIP (Colby et al. 1993). The second property has been described for some cells in 7b (Leinonen et al. 1979), and, in the present study, in a small number of putamen cells. No area seems to have been tested systematically for both. We suggest that both properties may exist in some or all of the bimodal areas discussed above, namely inferior area 6, area 7b, VIP, and the putamen.

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 bimodal neurons in area 6 respond when the monkey reaches toward a target (Gentilucci et al. 1988; Rizzolatti et al. 1988). These neurons are broadly tuned to a preferred direction of reach, and this motor field appears to match the location of the visual RF. That is, the cell responds when the monkey reaches into the region of space that corresponds to the visual RF. Furthermore, Caminiti et al. (1990) have recorded from neurons in the dorsal region of area 6, and found that the motor field moves as the arm moves, rotating at roughly the same angle that the shoulder has rotated that is, the motor response fields for arm movements appear to be arm centered. Caminiti studied the dorsal part of area 6 while Rizzolatti studied ventral area 6, however the possibility remains that area 6, and perhaps other bimodal areas, encode both vision and movement in the same body part centered coordinates. That is, these areas may provide a common coordinate system for locating sensory targets and for guiding movements toward those targets. These questions, however, can only be answered by further research using the awake monkey preparation.

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