Visuospatial Properties of Ventral Premotor Cortex

MICHAEL S. A. GRAZIANO, XIN TIAN HU, AND CHARLES G. GROSS
Department of Psychology, Princeton University, Princeton, New Jersey 08544

Graziano, Michael S. A., Xin Tian Hu, and Charles G. Gross. Visuospatial properties of ventral premotor cortex. *J. Neurophysiol.* 77: 2268–2292, 1997. In macaque ventral premotor cortex, we recorded the activity of neurons that responded to both visual and tactile stimuli. For these bimodal cells, the visual receptive field extended from the tactile receptive field into the adjacent space. Their tactile receptive fields were organized topographically, with the arms represented medially, the face represented in the middle, and the inside of the mouth represented laterally. For many neurons, both the visual and tactile responses were directionally selective, although many neurons also responded to stationary stimuli. In the awake monkeys, for 70% of bimodal neurons with a tactile response on the arm, the visual receptive field moved when the arm was moved. In contrast, for 0% the visual receptive field moved when the eye or head moved. Thus the visual receptive fields of most ''arm + visual'' cells were anchored to the arm, not to the eye or head. In the anesthetized monkey, the effect of arm position was similar. For 95% of bimodal neurons with a tactile response on the face, the visual receptive field moved as the head was rotated. In contrast, for 15% the visual receptive field moved with the eye and for 0% it moved with the arm. Thus the visual receptive fields of most ''face + visual'' cells were anchored to the head, not to the eye or arm. To construct a visual receptive field anchored to the arm, it is necessary to integrate the position of the arm, head, and eye. For arm + visual cells, the spontaneous activity, the magnitude of the visual response, and sometimes both were modulated by the position of the arm (37%), the head (75%), and the eye (58%). In contrast, to construct a visual receptive field that is anchored to the head, it is necessary to use the position of the eye, but not of the head or the arm. For face + visual cells, the spontaneous activity and/or response magnitude was modulated by the position of the eyes (88%), but not of the head or the arm (0%). Visual receptive fields anchored to the arm can encode stimulus location in ''arm-centered'' coordinates, and would be useful for guiding arm movements. Visual receptive fields anchored to the head can likewise encode stimuli in ''head-centered'' coordinates, useful for guiding head movements. Sixty-three percent of face + visual neurons responded during voluntary movements of the head. We suggest that ''body-part-centered'' coordinates provide a general solution to a problem of sensory-motor integration: sensory stimuli are located in a coordinate system anchored to a particular body part.

INTRODUCTION

Premotor cortex, also called area 6, is thought to be involved in the planning and execution of movements (e.g., Kalaska and Crammond 1992; Wise 1985). It projects in a topographic fashion to primary motor cortex (M1) and also directly to the spinal cord (Barbas and Pandya 1987; Dum and Strick 1991; Godschalk et al. 1984; He et al. 1993; Leichnetz 1986; Matelli et al. 1986; Matsumura and Kubota 1979; Muakkassa and Strick 1979). Premotor neurons are active during specific voluntary movements, and electrical stimulation of different parts of the somatotopic map will evoke muscle movement in the corresponding part of the body (Caminiti et al. 1990; Gentilucci et al. 1988; Hepp-Raymond et al. 1994; Weinrich et al. 1984).

In addition to these motor properties, premotor cortex receives somatosensory and visual input. The secondary somatosensory areas SII and 5 project to portions of premotor cortex (Matelli et al. 1986). The visual areas 7a, lateral intraparietal area (LIP), ventral intraparietal area (VIP), and medial superior temporal area (MST) all project to area 7b, which in turn projects to premotor cortex, mainly to the ventral half (Cavada and Goldman-Rakic 1989a,b; Jones and Powell 1970; Kunzle 1978; Matelli et al. 1986; Mesulam et al. 1977). This ventral region (see Fig. 1) has several names, including ventral premotor cortex (PMv), 6Va, and PMa (see He et al. 1993). Here we refer to it as PMv.

PMv contains a somatotopic representation of the arms, hands, face, and mouth (Gentilucci et al. 1988; Matelli et al. 1986; Muakkassa and Strick 1979). Many of these tactile neurons also respond when a visual stimulus is placed in the region of space near the tactile receptive field (Fogassi et al. 1996; Gentilucci et al. 1988; Rizzolatti et al. 1981). Such bimodal neurons are especially numerous in the posterior part of PMv, which Gentilucci et al. (1988) have termed area F4.

In most visual brain areas, the receptive fields are anchored to the retina and move as the eye moves. Such receptive fields encode the position of a visual stimulus on the retina in ''retinocentric'' coordinates. Rizzolatti and colleagues (Fogassi et al. 1992; Gentilucci et al. 1983) found that the bimodal, visual-tactile neurons in PMv behaved in a different fashion. For most PMv neurons, when the eye moved, the visual receptive field did not move. Instead, it remained in the same region of space, near the tactile receptive field. Fogassi et al. (1992) suggested that these visual receptive fields may be anchored to the head, or possibly to the body, rather than to the retina. According to this hypothesis, visual space is encoded in PMv in ''head-centered'' or ''body-centered'' coordinates. The hypothesis, however, was not directly tested. Although the visual receptive fields did not move with the eye, and therefore were not anchored to the retina, they might have been anchored to the head, the chest, the arm, the leg, or even to an external landmark such as the frame of the primate chair.

To determine the spatial coordinate system used by neurons in PMv, in the present study we varied the position of the monkey's eye, arm, and head. We found that most bimodal neurons with a tactile response on the arm (termed ''arm + visual'' cells) had a visual receptive field that was anchored to the arm, moving as the arm was moved. Most bimodal cells with a tactile response on the face (termed

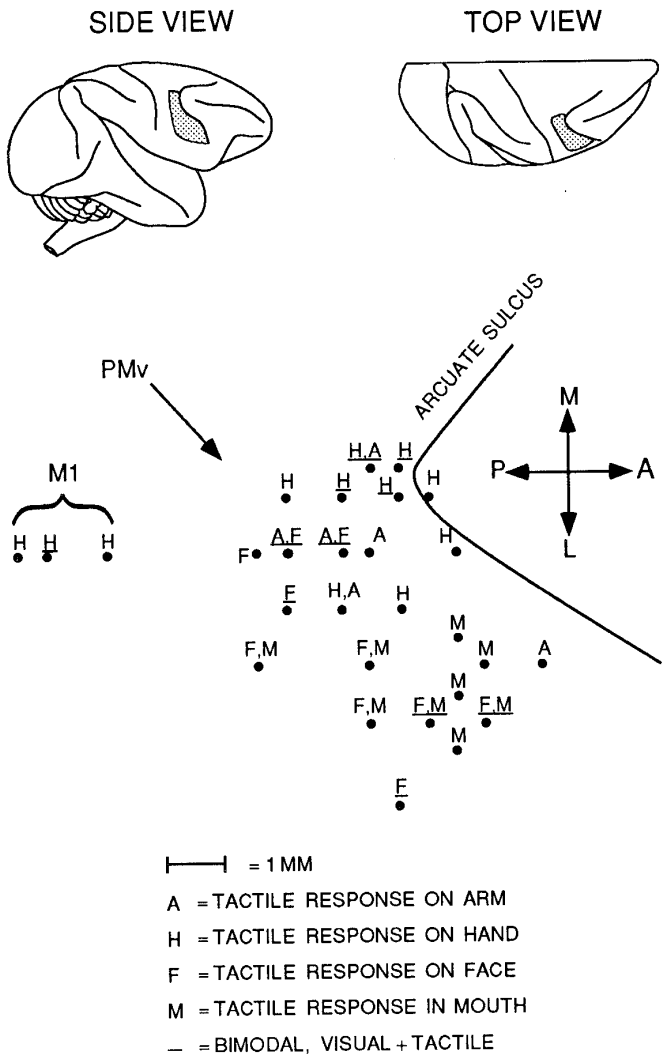

FIG. 1. *Top*: location of ventral premotor cortex (PMv; shaded area) on side view and top view of macaque monkey brain. *Bottom*: top view of arcuate sulcus and PMv in an anesthetized monkey, showing somatotopic organization. Black dots: locations of electrode penetrations for which the tactile receptive fields were located on the arm (A), hand (H), face (F), or inside of the mouth (M). Underlines: penetrations on which bimodal, visual-tactile cells were located. One penetration first entered cortex anterior to the arcuate sulcus, but then continued into PMv in the posterior bank of the sulcus. Three posterior penetrations were presumably in motor cortex (M1). Because the electrode penetrations were not perpendicular to the cortical surface, deeper recordings were sometimes at a different somatotopic location than superficial recordings. Therefore only responses within 1 mm of the surface are included here. Seven penetrations, for which no responses were found in the 1st mm, are not shown.

''face + visual'' cells) had a visual receptive field that was anchored to the head, moving as the head was rotated. The bimodal neurons in premotor cortex, therefore, appear to encode visual space in ''body-part-centered'' coordinates.

Body-part-centered information about the locations of nearby visual stimuli could help to guide movements. To test this possibility, we also studied the responses of face + visual neurons while the monkey turned its head. Some neurons showed motor-related activity, responding selectively to one direction of head movement. We suggest that these neurons may play a role in the visual guidance of head movements, such as for flinching, biting, or, in the case of humans, kissing.

In this paper we also describe some of the basic visual properties of the neurons, including latency, selectivity for direction of motion, and selectivity for the distance to the stimulus.

Preliminary accounts of some of these results were published previously (Graziano and Gross 1992; Graziano et al. 1994).

METHODS

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 National Institutes of Health and U.S. Department of Agriculture guidelines.

Responses of single neurons in PMv were studied in three adult male *Macaca fascicularis* (6–7 kg). As briefly described below, *monkey 1* was studied while under anesthesia and *monkeys 2* and *3* were studied while awake and fixating.

Initial surgery

For each monkey, an initial surgical operation was performed under deep pentobarbital sodium anesthesia and strict aseptic conditions, during which the top of the skull was cleared of skin and muscle, titanium screws were screwed into the bone, and the exposed bone was covered with a layer of dental acrylic ~1 cm thick. A stainless steel recording chamber, 2.5 cm diam, was embedded in the acrylic over the frontal lobe for a vertical approach to PMv. A steel bolt for holding the head was also embedded in the acrylic. For *monkeys 2* and *3* the conjunctiva of one eye was cut open, a scleral eye coil was inserted, and the incision was sutured closed again. The leads to the eye coil were passed under the skin to an electrical connector embedded in the acrylic implant. Each animal recovered from the effects of the surgery within several days, but was given three additional weeks to allow the skull to grow tightly around the skull screws.

In a subsequent procedure, also under deep anesthesia and aseptic conditions, the recording chamber was opened and a hole ~2 mm diam was drilled through the layer of acrylic and the bone, exposing the dura. As the experiment progressed, new holes were added to allow access to different portions of premotor cortex.

Anesthetized recording procedures

At the beginning of each recording session, the animal was given an intramuscular injection of atropine sulfate (0.15 mg/kg) to reduce mucosal secretions, and then given 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 on heating pads wrapped in towels, and its body temperature was maintained at 37–38°C. Electrocardiogram was continuously monitored through skin electrodes. The animal was immobilized with an intravenous infusion ($0.03\ mg \cdot kg^{-1} \cdot h^{-1}$) of pancuronium bromide (Pavulon) through a pediatric intravenous cannula and was artificially respired. 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, exposing the dura. Halothane was

then discontinued, and the animal was maintained under 2:1 nitrous oxide and oxygen. No surgery or potentially painful procedures were performed after the halothane was discontinued.

A micromanipulator was fixed to one rail of the stereotaxic frame and was used to lower a stainless steel guide cannula (an 18-gauge syringe needle) vertically through the dura at the location planned for the electrode penetration. Then a varnish-coated tungsten microelectrode (Frederick Haer, impedance 0.5–5 MΩ) 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 under these conditions. 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 respired 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.

The animal was used for nine weekly recording sessions, 15–18 h each. After each session, the animal was attended during full recovery and then placed back in its home cage. The animal began eating normally within 6 h of return to its home cage. It remained in good health between sessions and showed no signs of distress.

(For a more detailed description of the anesthetized recording procedures, see Desimone and Gross 1979.)

Awake recording procedures

During the daily recording sessions, the monkey's head was held in place by the head bolt and a hydraulic microdrive was mounted to the top of the recording chamber. A steel guide cannula (an 18-ga. syringe needle) was lowered through the hole in the skull and into the dura. Then the varnish-coated tungsten microelectrode (Frederick Haer, impedance 0.5–5 MΩ) was advanced from the guide cannula into the brain, to record from neurons in the cortex immediately below the dura. We believe that the stability of the electrode and the guide tube was markedly enhanced by the use of a narrow hole through the acrylic and skull. This procedure not only reduced the heartbeat pulsation of the brain, but also allowed a column of tough connective tissue to fill the entire 1-cm-deep, 2-mm-wide hole, thus forming a matrix to stabilize the guard tube. This stability was particularly important in experiments in which the head bolt was loosened and the animal was allowed to turn its head freely from side to side. Even sudden head movements did not displace the electrode enough to interfere with single-neuron recording. (For a more detailed description of some of the awake recording procedures, see Rodman 1991).

Stimuli

Once a cell was isolated, as indicated by the repeatability of its wave form on the oscilloscope, it was tested with a standard battery of stimuli. Somatosensory responsiveness was studied with the use of manual palpation, manipulation of joints, gentle pressure, and stroking with cotton swabs. Somatosensory receptive fields were plotted by repeated presentation of the most effective of these stimuli. Responses on the face were tested while the eyes were covered.

Visual responsiveness was tested with bars, spots, expanding and contracting squares, and random dot patterns back-projected onto a tangent screen. None of these stimuli were effective in eliciting neuronal responses, even when the tangent screen was moved to within 10 cm of the animal's eyes. Instead, visual cells responded best to real objects near the animal, and therefore these stimuli were used to plot visual receptive fields. To ensure that the responses to stimuli close to the body were not caused by inadvertent tactile stimulation, such as by static electricity or air movement, the visual stimuli were also presented while the eyes were covered, while the animal was shielded with a piece of clear Plexiglas, or under both conditions.

Motor-related activity was assessed in the awake preparation by releasing the monkey's arm from the arm holder and enticing the monkey to reach toward pieces of fruit, by inducing the monkey to make threat faces at the experimenters, by holding up objects (such as a bulb syringe sometimes used to blow air on the face) which elicited a cringing response, and by observing the monkey's frequent spontaneous movements. In some cases the head bolt was loosened and the monkey was allowed to turn its head.

After the initial testing for tactile, visual, and motor-related activity, the cell was then tested quantitatively with stimuli presented on the end of a computer-controlled robot arm (Sands Technology R15 cartesian format robot, repeatability to 0.001 in.). A black drape hung between the robot and the monkey, and a 1-cm-diam rod, on which the stimulus was mounted, protruded through a slit in the drape. Unless indicated otherwise, the stimuli were presented while the monkey fixated a light-emitting diode (LED). During different phases of the experiment, different stimuli were used, such as a white ball 5 cm diam, a ping-pong ball, a cotton swab, and a 4×4 cm square of white cardboard. In addition, the stimuli were presented at different speeds and along different trajectories. These stimulus details, and also the details of the training procedure, are given below.

Behavioral training: monkeys 2 and 3

Each animal was trained by means of fruit rewards to climb out of the home cage and to sit in a primate chair. The animal was restrained in the chair by a rigid Plexiglas collar bolted to the sides of the chair. The monkey was then trained to extend one arm, allowing the arm to be strapped down with Velcro strips to a metal arm holder. The head was held in place by the head bolt. During 4-h daily sessions over several weeks, the animal was trained to sit quietly while restrained in this manner and while being touched with cotton swabs on the face, around the eyes, or on other parts of the body. Visual stimuli (described below) were mounted on the end of the robot arm and moved toward and away from the face until the monkey became fully accustomed to them and ignored them. This lack of any visible motor response to the visual stimuli was crucial for the experiment, because many neurons in PMv respond during voluntary movement.

The animal's ad libitum daily water intake was measured, and on the basis of this measurement the animal was placed on a water schedule in which liquids were received under three conditions only: as a reward (apple juice) during the experimental session; as a supplement immediately after each session; and free water for two consecutive days each week.

The monkey was trained on a fixation task. To monitor the position of the eye, we used a standard eye coil technique, in which a current was induced in the eye coil by means of an oscillating magnetic field and measured at a sampling rate of 100 Hz (C-N-C Engineering, Dual Power Oscillators, 3-ft-diam magnetic coils). As described below, the monkey was required to fixate on a spot of light within a 5°-diam electronic window. However, the monkey's spatial accuracy was much better than the size of the window. During fixation, the SD of eye position was 0.6° in the *X* dimension and 0.2° in the *Y* dimension, both at the limits of the resolution of this eye coil system.

Behavioral paradigm for arm + visual cells in the awake monkey

The monkey sat with the head fixed by the head bolt and the arm contralateral to the recording electrode strapped to an arm holder with Velcro strips (see Fig. 5, *top*). The arm holder could

be adjusted to different positions. Three LEDs were spaced 20° apart along the horizontal meridian at eye level and positioned 28.5 cm in front of the monkey. Each trial began with one of the LEDs turning on and blinking at a frequency of 4 Hz. As soon as the animal fixated the LED within a 5°-diam window, the blinking stopped and the LED remained on. If the animal maintained fixation for the remainder of the trial (randomly varied between 1.2 and 1.5 s), the LED would turn off, a valve would release ~0.2 ml of juice into the animal's mouth, and the 10-s intertrial interval would commence. If the animal broke fixation at any time during the trial, the LED was extinguished, no reward was given, and the intertrial interval would commence. As described above, the monkey fixated within 1° of the fixation spot, much better than the required 5°.

A 10-cm-diam white sphere was used as the visual stimulus. It was mounted on the end of the computer-controlled robot arm described above. The stimulus began to move at a variable time (0.3–0.6 s) after the onset of fixation and continued toward the monkey for 10 cm at 14.5 cm/s along one of four trajectories (see Fig. 5, *top*). These trajectories were arranged 10 cm below the level of the fixation lights and 10 cm above the level of the arms. During the first 2 s of the 10-s intertrial interval, the stimulus was moved to its next starting position.

The three eye positions and four stimulus positions yielded 12 conditions, which were presented in an interleaved fashion, usually 10 trials per condition. The effect of arm position was studied by running a block of trials while the arm was in one position, and then adjusting the arm holder to a new position and running a second block. For some neurons, these blocks were repeated to control for any possible order effect. We always found the same pattern of results on repeated blocks.

Behavioral paradigm for face + visual cells in the awake monkey

The task used for testing face + visual cells was the same as the one described above for testing arm + visual cells, except as follows. The monkey fixated one of three lights, FIX A, FIX B, or FIX C, spaced 15° apart horizontally and positioned ~20° below eye level. During fixation, the visual stimulus (usually a ping-pong ball, sometimes a cotton swab) was advanced toward the monkey for 1 s at 10 cm/s along one of five trajectories (see Fig. 13, *top*). These trajectories were arranged at eye level. The three eye positions and five stimulus positions yielded 15 conditions, which were presented in an interleaved fashion, usually 10 trials per condition. In separate blocks of trials, the monkey's head was fixed straight (shown), or rotated 15° to the right or the left. The arm contralateral to the recording electrode was fixed straight ahead or bent across the chest.

Statistical procedures

The experiments on arm + visual neurons used a $4 \times 3 \times 2 \times 2$ factorial design (4 stimulus trajectories × 3 eye positions × 2 arm positions × 2 data collection periods, the prestimulus period and the stimulus period). The experiments on face + visual neurons used a $5 \times 3 \times 2 \times 2$ design (5 stimulus trajectories × 3 eye positions × 2 head positions × 2 data collection periods). Many neurons were only tested on some conditions, and in these cases an overall analysis of variance (ANOVA) was impossible. In any case, our specific hypotheses would not have been addressed by examining the main effects or interaction terms in an overall ANOVA, but could only be addressed by specific comparisons. Therefore for each neuron we performed four types of specific comparisons (described below). The level of α was adjusted to compensate for the number of comparisons, with the use of the following approximation: we assumed that the ''experimentwise error rate'' $= 1 - (1 - \alpha)^N$, where N = the number of comparisons performed on that neuron. We then adjusted α until the experimentwise error rate was 0.05. This method provides a relatively conservative test for significance (Linton et al. 1975). Because of the nature of the specific comparisons (e.g., ANOVAs on subsets of the data), it was not possible to use the other methods of controlling the α level that are generally used on simple pairwise comparisons.

For each experimental condition, the prestimulus activity was defined as the mean spikes/s in the period from 0.3 to 0.0 s before stimulus onset. The response was defined as the mean spikes/s in the period from 0.2 s after stimulus onset until the end of the stimulus movement.

For each neuron, we asked four types of questions. *1*) Did the neuron respond significantly to any of the stimulus trajectories? *2*) Did the visual receptive field move with the eye, arm, or head? *3*) Was the magnitude of the visual response modulated by the position of the eye, arm, or head? *4*) Was the level of spontaneous activity modulated by the position of the eye, arm, or head? *Neuron S86* (Fig. 5, *bottom*) can be used to illustrate all of the statistical procedures.

t-TEST FOR VISUAL RESPONSE. *Neuron S86* responded to stimulus trajectory IV (see Fig. 5, *bottom, row A1*). To test the significance of this response, we compared the mean spikes per second in the prestimulus period to the mean spikes per second in the stimulus period with the use of a paired *t*-test. The result was significant ($t = 10.18$, $P < 0.05$). Neurons that did not respond significantly to at least one trajectory were not analyzed further.

CONTRAST ANALYSIS FOR MOVEMENT OF VISUAL RESPONSE. In Fig. 5, *row A1*, the visual response was best at trajectory IV. In contrast, in *row A2*, the visual response was best at trajectory III. That is, when the arm moved, the visual receptive field also moved. To test whether this movement was significant, a standard contrast analysis was used (Rosenthal and Rosnow 1985). The four means in *row A2* were compared with a pattern of weights derived from the means in *row A1*. This specific comparison showed a significant match ($F_{\text{match}} = 31.89$, $P < 0.01$), but also a significant residual, or nonmatching, variance ($F_{\text{residual}} = 50.79$, $P < 0.01$). That is, the pattern of response in *row A1* significantly overlapped the pattern in *row A2* (reflected in the significance of F_{match}), but the two patterns also had significant differences (reflected in the significance of F_{residual}). To show that the visual receptive field shifted significantly, it is sufficient to show the significance of F_{residual}. Therefore, in this case, the visual receptive field moved significantly with the arm.

In Fig. 5, *rows A1, B1, and C1*, the visual response was best at trajectory IV. That is, when the eye moved, the visual receptive field did not appear to move. To test the significance of this result, we compared *rows B1* and *C1* with a pattern of weights derived from *row A1*. These comparisons showed that both *rows B1* and *C1* significantly matched *row A1*, and had no significant residual variance. That is, the visual response did not move when the eyes moved. In general, to show that the visual receptive field remained in the same location, it is necessary to show both that F_{match} is significant and that F_{residual} is not significant. (For *row B1*, $F_{\text{match}} = 52.69$, $P < 0.01$, and $F_{\text{residual}} = 1.03$, $P > 0.05$; for *row C1*, $F_{\text{match}} = 177.98$, $P < 0.01$, and $F_{\text{residual}} = 2.87$, $P > 0.05$.)

ANOVA FOR MODULATION OF RESPONSE MAGNITUDE. The visual response to trajectory IV is larger in Fig. 5, *row A1* than in *rows B1* or *C1*. That is, the position of the eye may have modulated the magnitude of the visual response. Note that we consider only the stimulus trajectory that gave the best response. This selection is necessary to avoid analyzing the spontaneous activity represented by the nonresponding positions. (As described below, a separate method was used to test for modulation of spontaneous activity.) To characterize the amount of modulation, we calculated

the percent change in response between *row A1*, trajectory IV (eye position with highest response), and *row B1*, trajectory IV (eye position with lowest response). We used the following formula: % change = 100 × (response at best eye position − response at worst eye position)/response at worst eye position. In this case, the change was 18%. To test the statistical significance of the modulation, we analyzed the response to trajectory IV with the use of a one-factor ANOVA with 3 levels (Fig. 5, *rows A1, B1,* and *C1*). The result, however, was not significant ($F = 0.59$, $P > 0.05$). Thus, for this neuron, the position of the eye did not modulate the magnitude of the visual response.

On the basis of the data from this neuron, it is not possible to determine whether the position of the arm modulated the magnitude of the visual response. The reason is that the visual receptive field moved with the arm. If the magnitude of the response were to increase when the arm moved, it might be caused by the visual receptive field moving into alignment with one of the stimulus trajectories.

ANOVA FOR MODULATION OF SPONTANEOUS ACTIVITY. We also tested whether the spontaneous activity of the neuron (the activity in the prestimulus period) was modulated by the position of the eyes. We first calculated the percent change in spontaneous activity by the use of the formula: % change = 100 × (mean spontaneous activity at best eye position − mean spontaneous activity at worst eye position)/mean spontaneous activity at worst eye position. In this case, the change was 27%. To test the statistical significance of the change, we analyzed the prestimulus period with the use of a 4 × 3 ANOVA (4 stimulus positions × 3 eye positions, *conditions A1, B1,* and *C1*). The main effect of eye position for *cell S86* was not significant ($F = 0.17$, $P > 0.05$), indicating that eye position did not affect the magnitude of the spontaneous activity.

To test whether arm position modulated the spontaneous activity, we first calculated the percent change with the use of the formula: % change = 100 × (mean spontaneous activity at best arm position − mean spontaneous activity at worst arm position)/mean spontaneous activity at worst arm position. In this case the change was 25%. We then analyzed the prestimulus activity with the use of a 4 × 2 ANOVA (4 stimulus positions × 2 arm positions, *conditions A1* and *A2*). There was no significant main effect of arm position ($F = 3.43$, $P > 0.05$); thus the spontaneous activity of this cell was not significantly modulated by arm position.

All the statistical procedures described above were also used for face + visual cells, except that five stimulus trajectories were used instead of four.

Active and passive movement of the head

To study the effect of head movement, we loosened the clamp on the head bolt, allowing the head to turn freely side to side but not in any other direction. In the active movement condition, the monkey made frequent spontaneous head movements while we recorded single neuron activity. In the passive movement condition, the experimenter stood behind the monkey, grasped the head bolt with a pair of pliers, and turned it. To measure the head position, we used a 15-mm-diam coil of insulated wire (Cooner Wire, 15 strand, No. AS632), similar to the eye coil, but attached directly to the acrylic implant. An oscillating magnetic field was used to induce a current in the wire coil, which was measured at a sampling rate of 50 Hz (C-N-C Engineering, Dual Power Oscillators, 3-ft-diam magnetic coils).

Histology

At the completion of the experiment, *monkeys 1* and *2* were given an overdose of pentobarbital sodium (100 mg/kg) and perfused transcardially with saline and then 10% Formalin. The head was put in a stereotaxic apparatus, the skull was opened, and the brain was exposed. The positions of the arcuate and central sulci were measured stereotaxically. Figure 1 shows the entry locations of the electrode penetrations in relation to the sulci for *monkey 1.* Most recording sites were within the posterior portion of PMv, on the cortical surface, in an area that Rizzolatti and colleagues have termed F4 (Gentilucci et al. 1988; Rizzolatti et al. 1988). Some sites entered the cortex anterior to the arcuate sulcus and then passed into the posterior bank, into a region of PMv that Rizzolatti et al. have termed F5. Several penetrations were also made just anterior to the central sulcus, within 1 mm of the sulcus, presumably in M1.

The brains were fixed in 10% Formalin and sectioned in the coronal plane on a freezing microtome. Sections were cut at 50 mm and stained with cresyl violet. Damage from the microelectrode was clearly visible as streaks of gliosis in the tissue, confirming the locations of recording sites.

As of this time, we are still collecting data from *monkey 3* and therefore we do not have histology for that case. Instead, magnetic resonance images (MRIs) of the frontal lobe were obtained both in coronal and in sagittal sections. The scans were performed in a GE Signa 1.5-T magnet with the use of an inversion recovery sequence with an echo time of 12 ms, a repetition rate of 2,000 ms, an inversion time of 708 ms, and a data matrix of 192 × 256. Field of view was 16 × 16 cm with two excitations. Slice thickness was 3 mm and three separate acquisitions were interleaved to produce a resolution of 1 mm. (For details of the MRI methods, see Moore et al. 1995). Vitamin E pills were glued to the monkey's scalp at several stereotaxic reference points. Because vitamin E is visible in the MRI scan, we were able to use these reference points to estimate the stereotaxic location of the arcuate sulcus. Some of the skull holes were also visible in the MRI, thus confirming that they were positioned directly over PMv, that is, just posterior to the lower limb of the arcuate sulcus.

RESULTS

Response categories

We studied 604 neurons in PMv in four hemispheres of three monkeys. *Monkey 1* was studied under anesthesia and *monkeys 2* and *3* were studied while awake and fixating. Neuronal responses were classified as somatosensory, visual, bimodal (somatosensory + visual), or auditory. In the awake preparation, we were also able to test activity related to the monkey's spontaneous movements. Table 1 shows the proportions of these different response types. Thirty-one percent of the neurons were classified as bimodal, and are the main focus of this paper.

Somatotopic organization

Most of the neurons that we studied in PMv (409 of 604, 68%) responded to somatosensory stimuli. These neurons were somatotopically organized. As shown in Fig. 1 for *monkey 1,* studied under anesthesia, when electrode penetrations were made in the medial part of PMv, near the genu of the arcuate sulcus, the somatosensory receptive fields were usually located on the arm (labeled A) or hand (labeled H). When penetrations were made a few millimeters laterally, the tactile receptive fields were usually located on the face (labeled F) or inside the mouth (labeled M). A similar somatotopic organization was found in *monkey 3,* tested while the monkey was awake. In *monkey 2,* however, we

TABLE 1. *Categories of neurons in the anesthetized and awake preparations*

	Cells From Anesthetized Monkey	Cells From Awake Monkeys
Somatosensory only	58 (41.0)	65 (14.0)
Motor only		46 (10.0)
Somatosensory + motor		49 (10.5)
Visual only	2 (1.5)	18 (4.0)
Somatosensory + visual	39 (27.5)	146 (31.5)
Motor + visual		4 (1.0)
Somatosensory + motor + visual		50 (10.5)
Trimodal (somatosensory + visual + auditory)	0 (0.0)	2 (0.5)
Unresponsive	42 (30.0)	83 (18.0)
Total	141 (100.0)	463 (100.0)

Values are number of cells, with percentages in parentheses. Percents are rounded to the nearest 0.5.

did not record from enough locations in PMv to test the somatotopic organization.

Twenty-eight percent of the neurons that we studied in PMv of this monkey were bimodal, responding both to visual and to somatosensory stimuli. Bimodal cells were found on penetrations scattered throughout the face and arm parts of the somatotopic map. These penetrations are labeled with an underline.

We also recorded from 28 neurons just anterior (within 1 mm) of the central sulcus. These neurons were therefore probably in M1, and were located in the hand representation. Because these recordings were made in an anesthetized monkey, we could not test whether the neurons responded during voluntary movement. Sixteen of the cells, however, responded to tactile stimuli. Of the 16, 1 was bimodal, also responding to visual stimuli. This proportion of bimodal cells in M1 was significantly smaller than in PMv ($\chi^2 = 6.91$, $P < 0.01$).

Bimodal responses

A typical example of a bimodal, somatosensory + visual cell, studied in the anesthetized preparation, is illustrated in Fig. 2*A*. The tactile receptive field was plotted while the animal's eyes were covered. The cell was activated by lightly touching the facial hair, and the responsive region covered most of the contralateral cheek and the area around the mouth. When the animal's eyes were uncovered, the response began as the stimulus (a cotton swab) approached the face, but before it had touched. By approaching the face from various angles, we determined the three-dimensional structure of the visual receptive field. The boxed region in Fig. 2*A* shows the region of greatest response, a solid angle centered at the tactile receptive field and extending out ~10 cm. Outside of this region, the response was weak and erratic, grading into spontaneous activity at a distance of ~20 cm from the face. The visual response was not caused by inadvertent tactile stimulation, such as by air movement or static electricity, because it was eliminated by covering the eyes. 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, color, motion, or texture of the object placed near the face did not affect the response. If a stimulus was held stationary near the face, the cell responded in a sustained fashion for ≥15 s, although we did not test longer than that. Presumably the response would have habituated eventually, because parts of the stereotaxic apparatus near the face did not elicit a response, judging by the cell's near-zero spontaneous activity.

Figure 2, *B–F*, shows several more examples of bimodal responses. As described in the figure legend, some of these neurons were studied in the anesthetized preparation and some were studied in the awake preparation. We could see no difference in the bimodal response properties between these two experimental conditions.

The latency of the visual response was studied for 15 bimodal neurons in the awake preparation. The stimulus was a 10-cm-diam sphere approaching the monkey at 14.5 cm/s. Each neuron was tested with 10 trials and the data were collapsed into 20-ms time bins. The latency was defined as the first time bin, after the onset of stimulus motion, for which the mean number of spikes per second was >2 SD above the baseline. The mean latency for the 15 neurons was 197 ± 54 (SD) ms. The shortest latency was 100 ms and the longest latency was 280 ms.

Other types of visually responsive neurons, such as the purely visual neurons, had visual response properties indistinguishable from those described above for somatosensory + visual neurons.

Selectivity for the direction of stimulus motion

We used the following paradigm to test the directional selectivity of bimodal neurons in the awake preparation. While the animal fixated, a ping-pong ball mounted on the end of the robot arm was moved for 0.5 s at 10 cm/s along one of six possible trajectories, arranged such that their midpoints intersected ~20 cm in front of the monkey. The directions of motion were as follows: toward, away, left, right, up, and down. These stimulus trajectories were presented in an interleaved fashion, usually 10 trials per condition.

We tested 27 bimodal neurons, and of these, 24 responded significantly above baseline to at least one of the stimulus trajectories (paired *t*-test between prestimulus and stimulus period, $P < 0.05$). Figure 3 shows the results for three typical neurons. The six columns correspond to the six directions of motion, and the three rows show the responses of the three neurons. The cell shown in *row A* responded best to inward motion. This cell was highly selective, responding significantly above baseline to only one of the six stimulus directions. The cell in *row B* responded to a greater range of stimuli, including upward, rightward, leftward, and outward motion. It did not respond at all to inward motion. The cell in *row C* responded significantly to all six stimuli. It had a weak directional preference, responding significantly better to rightward motion than to leftward motion.

Of the 24 neurons tested, 4 preferred motion toward the monkey, 1 preferred motion away, and 19 preferred motion in the frontoparallel plane, either left, right, up, or down. However, most (17) were broadly tuned, responding significantly to more than one direction of motion. Only seven

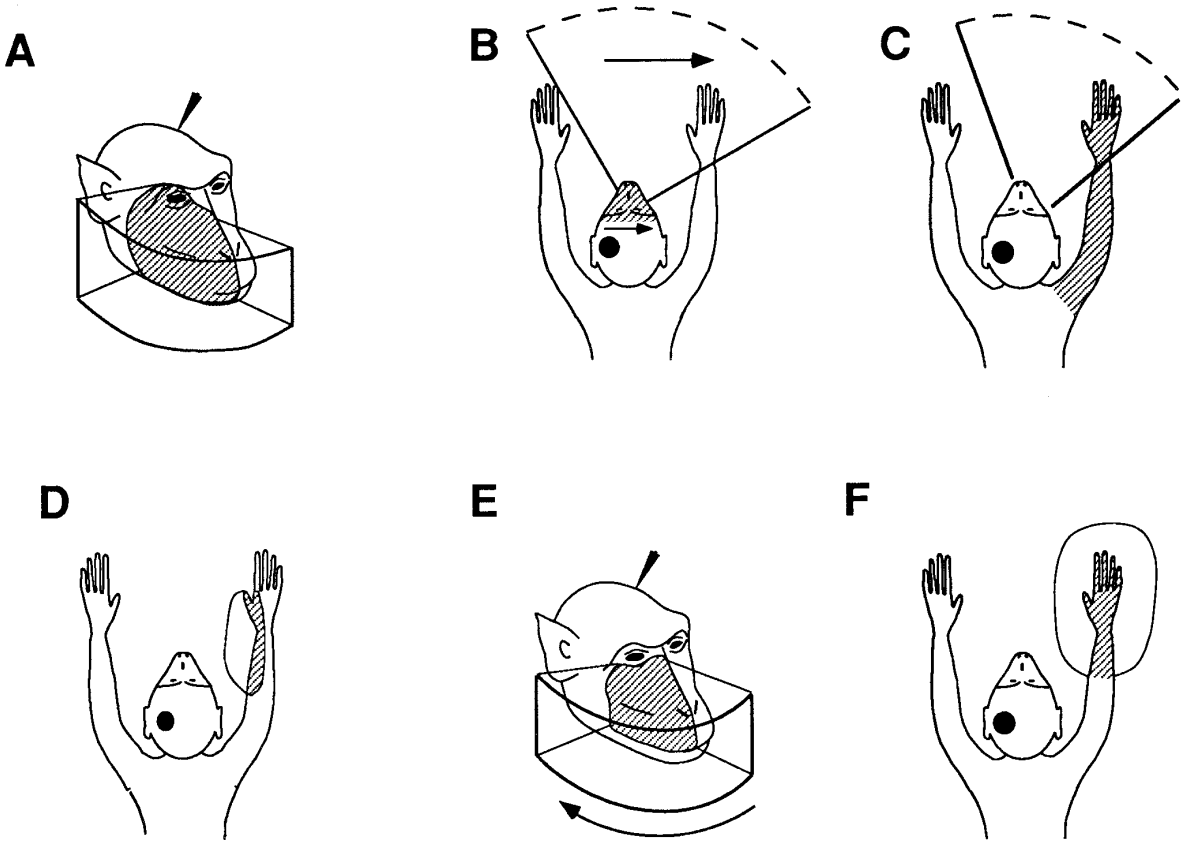

FIG. 2. Six examples of bimodal, visual-tactile neurons from PMv. *A–D* were studied in the anesthetized preparation. *E* and *F* were studied in the awake preparation. The tactile receptive fields (cross-hatched) and the visual receptive fields (boxed) matched in location. Dotted line: visual receptive field extended beyond 1 m from the monkey. Black wedges (e.g., in *A*) and dots (e.g., in *B*): hemisphere recorded from. Arrows in *B*: preferred direction for tactile and visual stimuli. Curved arrow in *E*: preferred direction for both tactile and visual stimuli.

cells were highly selective, responding significantly to just one direction of motion.

Do cells generally respond better to inward motion than to outward motion? Eighteen cells gave a significant response to inward and/or outward motion. Of these, nine responded significantly better to inward motion, four responded significantly better to outward motion, and for five cells the response to inward motion was not significantly different from the response to outward motion.

Bimodal neurons in PMv were also often directionally selective in the tactile modality. Ninety-five neurons with a tactile receptive field on the face were tested with a cotton swab moved across the skin in various directions. During these tests, the monkey's eyes were covered. Fifty-four cells (57%) responded in a directionally selective fashion. Of these, 27 were also tested for directional preference with hand-held visual stimuli. That is, the eyes were uncovered and the cotton swab was moved in the space within a few centimeters of the tactile receptive field. For 23 cells, the tactile directional preference matched the visual directional preference. For four cells, there was no observable directional preference in the visual modality, even though the cell was clearly directional in the tactile modality.

These results suggest that most bimodal cells in PMv are sensitive to the direction of motion of the stimulus, and that a wide range of directional preferences is represented. However, although most neurons responded best to moving stimuli, many neurons also responded to a stationary object placed within the space near the tactile receptive field, as described below.

Selectivity for the distance to the stimulus

Figure 4 shows the responses of a typical bimodal neuron studied in the awake preparation. The cell had a bilateral tactile receptive field on the eyebrows and a bilateral visual receptive field. Figure 4*A, top histogram,* shows the result when a 2×2 cm white cardboard square, mounted on the robot arm, was advanced toward the face from a distance of 37.5 cm to a distance of 2 cm, over 4.3 s. The monkey did not fixate during this period because the stimulus would have blocked the fixation LED from view. (As described below, the magnitude and specificity of the visual response is as good or better when the animal is not fixating.) At the onset of stimulus motion, the cell gave a transient response and then returned to its baseline activity. When the stimulus had approached within ~25 cm of the face, the cell began to respond again. This response increased as the stimulus neared the face. When the stimulus stopped moving, the firing rate dropped but still remained well above baseline.

Figure 4*A, bottom histogram,* shows the result for interleaved trials when the stimulus was retracted at the same

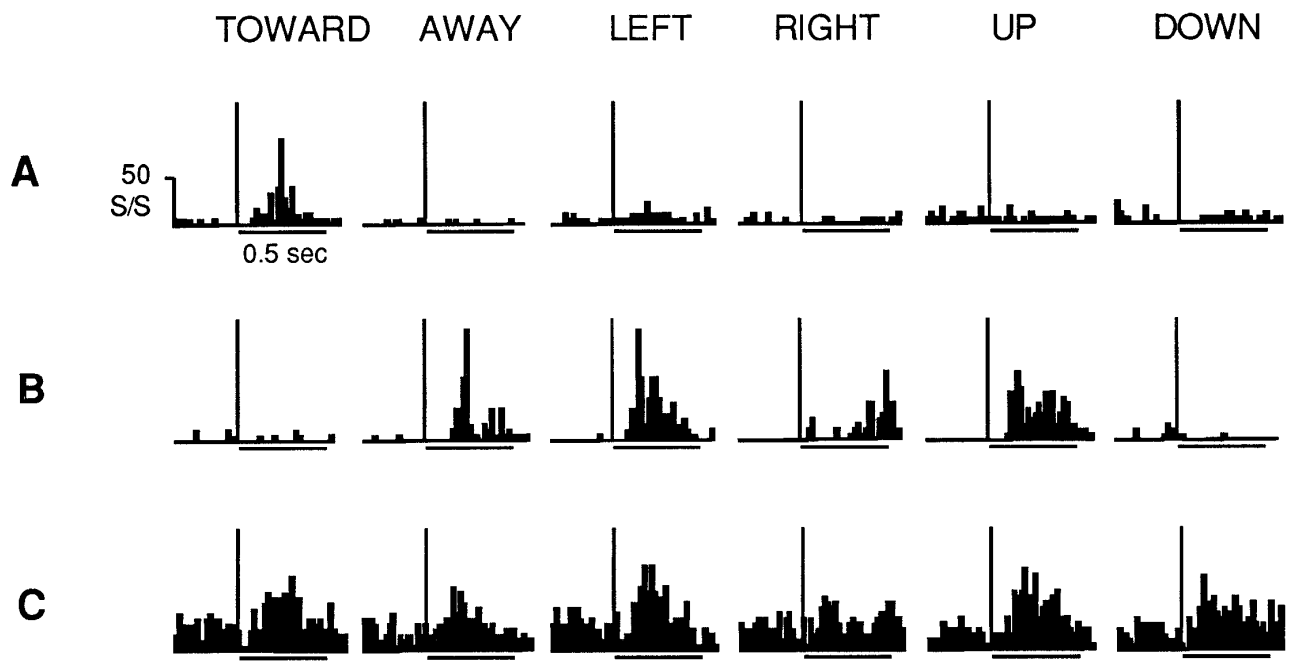

FIG. 3. Responses of 3 bimodal PMv neurons (*rows A–C*) to 6 different directions of stimulus movement. Each histogram is based on 10 trials. Vertical lines: time of stimulus onset. The stimulus moved at 10 cm/s for 0.5 s (indicated by the horizontal lines).

speed. The elevated activity before the start of the stimulus motion indicates that the cell was still responding to the stationary stimulus near the face, even by the end of the 10-s intertrial interval. At the onset of stimulus motion, the cell gave a transient response, and then the activity quickly dropped to baseline as the stimulus receded.

Figure 4*B* shows the result when the ipsilateral eye was covered with an eye patch. The baseline activity increased, because the patch was stimulating the tactile receptive field. The pattern of the response, however, was the same; the cell responded better as the stimulus neared the face. Stereopsis, therefore, is not necessary for the cell's sensitivity to distance. Figure 4*C* shows the result when both eyes were open and the stimulus was changed to a 4 × 4 cm white square, twice as large as in Fig. 4*A*. The response, however, is not twice as large, nor does it extend twice as far from the monkey; instead, the pattern of response is the same. Therefore the retinal size of the stimulus is not a necessary cue for distance. Finally, Fig. 4*D* shows the response to a stationary stimulus (2 × 2 cm square) placed at eight different distances. The stimulus was first moved into position, and then, 5 s later, data collection was begun and continued for another 3 s. Thus the activity that was measured corresponds to the sustained response to the stimulus 5 s after it had stopped moving. The cell responded better to closer stimuli. That is, motion cues, such as the rate of expansion of the stimulus, are not necessary for the cell's distance sensitivity. The response may have depended on other monocular cues for depth, such as occlusion, texture, or accommodation; or it may have depended on a combination of cues, such that eliminating any one would have had little or no effect. Clearly none of the main cues for depth is sufficient, by itself, to account for the properties of the cell.

Eighteen bimodal neurons were tested with approaching and receding stimuli. None showed a sharp outer border to the visual receptive field; instead, as the stimulus approached, the response began to increase gradually, reaching a maximum when the stimulus reached its closest approach. Twelve cells continued to respond even when the stimulus was stationary, near the face. However, in all cases this sustained response to a stationary stimulus was significantly smaller than the response to a moving stimulus.

Ten cells gave a response at the onset of stimulus motion when the stimulus was at its maximum distance and beginning to approach the monkey. In these cases the response to stimulus onset was transient; the firing rate returned to baseline and then began to increase again when the stimulus had approached closer to the face.

For an additional 73 neurons, the furthest distance at which we could elicit a sustained visual response was plotted with hand-held stimuli. (Some of these cells also gave a transient response at stimulus onset to more distant stimuli.) Thirty-four neurons gave a sustained response only within 5 cm of the animal, 29 responded within 20 cm, 5 responded within 1 m, and 5 responded at all distances tested, out to the wall of the room 2 m away. We did not find any neurons that responded exclusively to distant stimuli and not to nearby stimuli.

Visual receptive fields that move with the arm but not the eye or head

In this section we present the results for arm + visual neurons studied in the awake preparation. As described in METHODS, the monkey fixated one of three lights, FIX A, FIX B, or FIX C, while the visual stimulus was advanced along one of four trajectories, I–IV (Fig. 5, *top*). The arm contralateral to the recording electrode was strapped to an

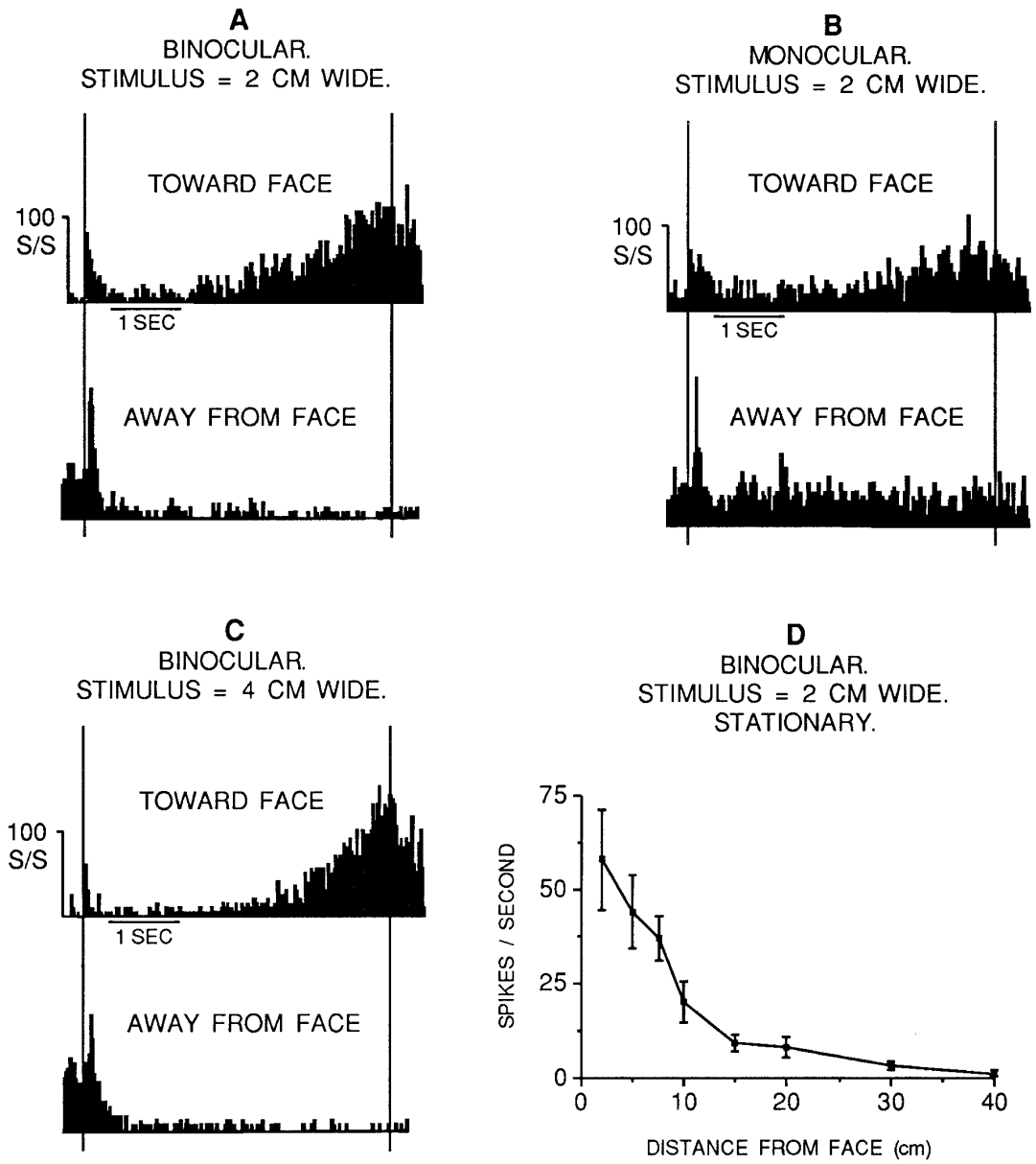

FIG. 4. Responses of a bimodal neuron from PMv with a tactile receptive field on the eyebrows. Each histogram is based on 10 trials. Stimuli were presented while the monkey was not performing the fixation task. In *A–C* the visual stimulus was advanced toward the face from in front at 8.25 cm/s and retracted on alternate trials. Stimulus farpoint = 37.5 cm, nearpoint = 2 cm, intertrial interval = 10 s. Vertical lines: onset and offset of stimulus movement. In *A,* the stimulus was a 2 × 2 cm square of cardboard viewed binocularly. The cell responded better as the stimulus approached. In *B,* 1 eye was covered, but the cell was still sensitive to depth. The baseline activity increased because the eye cover touched the tactile receptive field. In *C,* the stimulus was a 4 × 4 cm square of cardboard viewed binocularly. The increase in stimulus size did not cause a corresponding increase in response. In *D,* stationary stimuli were tested at 8 different distances. The cell still preferred nearby stimuli, even though all motion cues for depth had been eliminated. Error bars: means ± SE. Each point is based on 10 trials.

arm holder and positioned on the right (contralateral) or bent toward the left (ipsilateral). The cross-hatching on the arm shows the location of the tactile receptive field for one arm + visual neuron. The responses of this neuron to the visual stimulus are shown in Fig. 5, *bottom.*

Figure 5, *bottom, rows A1, B1,* and *C1,* shows the visual response when the arm was fixed to the right. The cell gave a strong, sustained response only when the stimulus was presented on the far right, along trajectory IV. That is, the visual response matched the location of the tactile response on the lateral surface of the upper arm. The visual response remained at trajectory IV, whether the eyes looked to the left (*row A1*), to the center (*row B1*), or to the right (*row C1*). (This spatial constancy of the visual receptive field was significant. See METHODS for details of this and subsequent statistical procedures. A contrast analysis on *rows B1* and *C1* with the use of a pattern of weights derived from *row A1* showed a significant match and no significant residual variance. For *row B1*, $F_{match} = 52.69$, $P < 0.01$, and $F_{residual} = 1.03$, $P > 0.05$; for *row C1*, $F_{match} = 177.98$, $P < 0.01$, and $F_{residual} = 2.87$, $P > 0.05$.)

The arm was then bent toward the left and the cell was

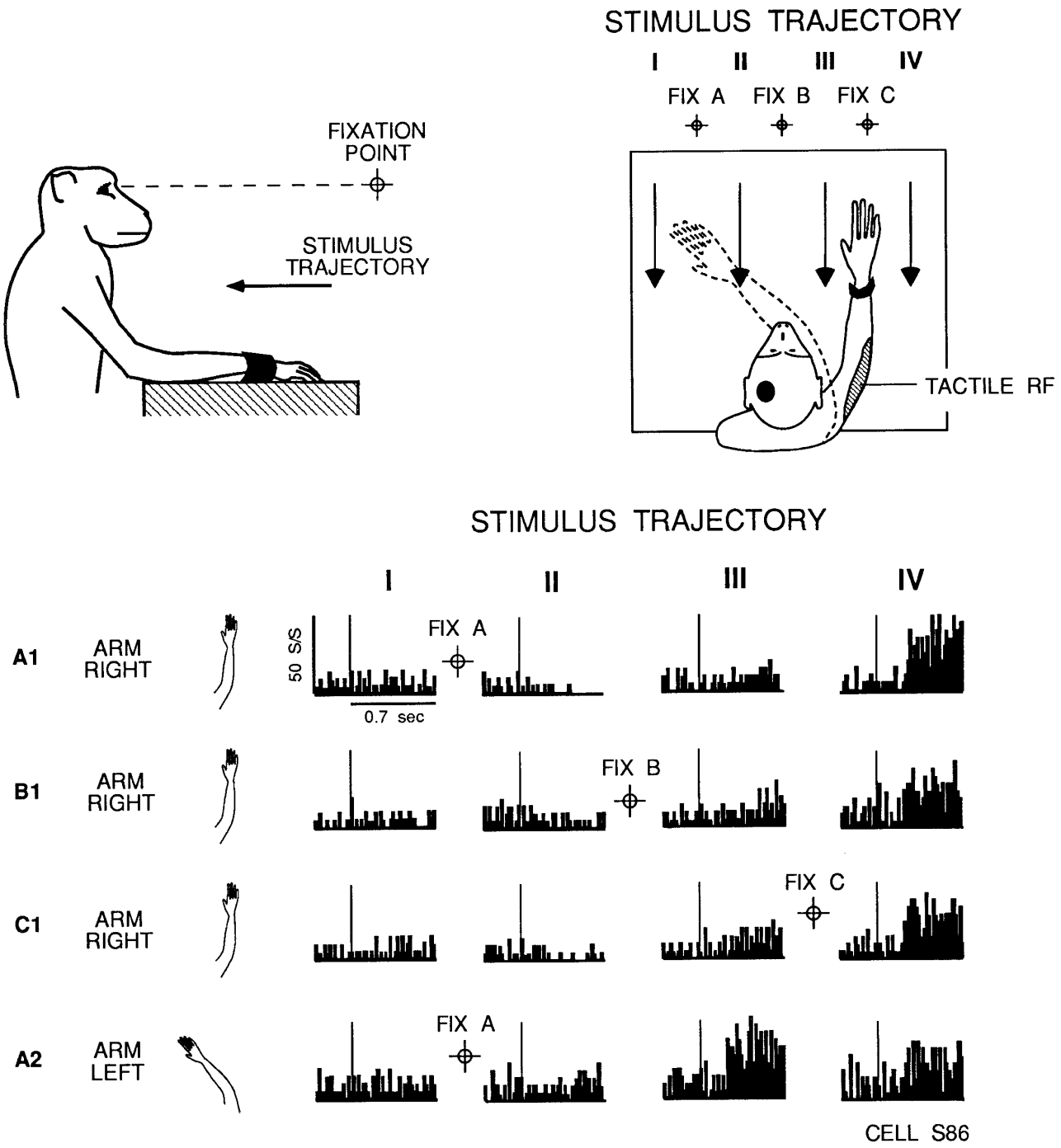

FIG. 5. *Top*: experimental paradigm for testing the effect of arm position. On each trial the animal fixated 1 of 3 lights spaced 20° apart (FIX A, FIX B, or FIX C) and the stimulus was advanced along 1 of 4 trajectories (I–IV). The arm was fixed in 1 of 2 positions. Trajectories and monkey are drawn to the same scale. Stippling: tactile receptive field (RF) of the cell whose responses are illustrated at *bottom. Bottom*: histograms of neuronal activity, summed over 10 trials, as a function of eye position (A–C), stimulus position (I–IV), and arm position (to the right in *rows A1, B1,* and *C1,* and to the left in *row A2*). Vertical lines: stimulus onset. When the arm was fixed to the right, the neuron responded best to the rightmost stimulus trajectory (IV), whether the eye looked to the left (as in *row A1*), to the center (as in *row B1*), or to the right (as in *row C1*). However, when the arm was fixed to the left (*row A2*), the neuron responded best to stimulus trajectory III. That is, the visual receptive field moved toward the left with the tactile receptive field. Results for *conditions B2* and *C2,* not shown, were similar.

retested. As shown in Fig. 5, *row A2* for one eye position, the visual response moved with the arm. Because of the large size of the visual receptive field, the cell responded both to trajectory III and to trajectory IV. The peak response, however, moved to trajectory III, shifting to the left by approximately the same amount that the tactile receptive field shifted. (This shift in the visual response with the arm was significant. Contrast analysis on *row A2* with the use of

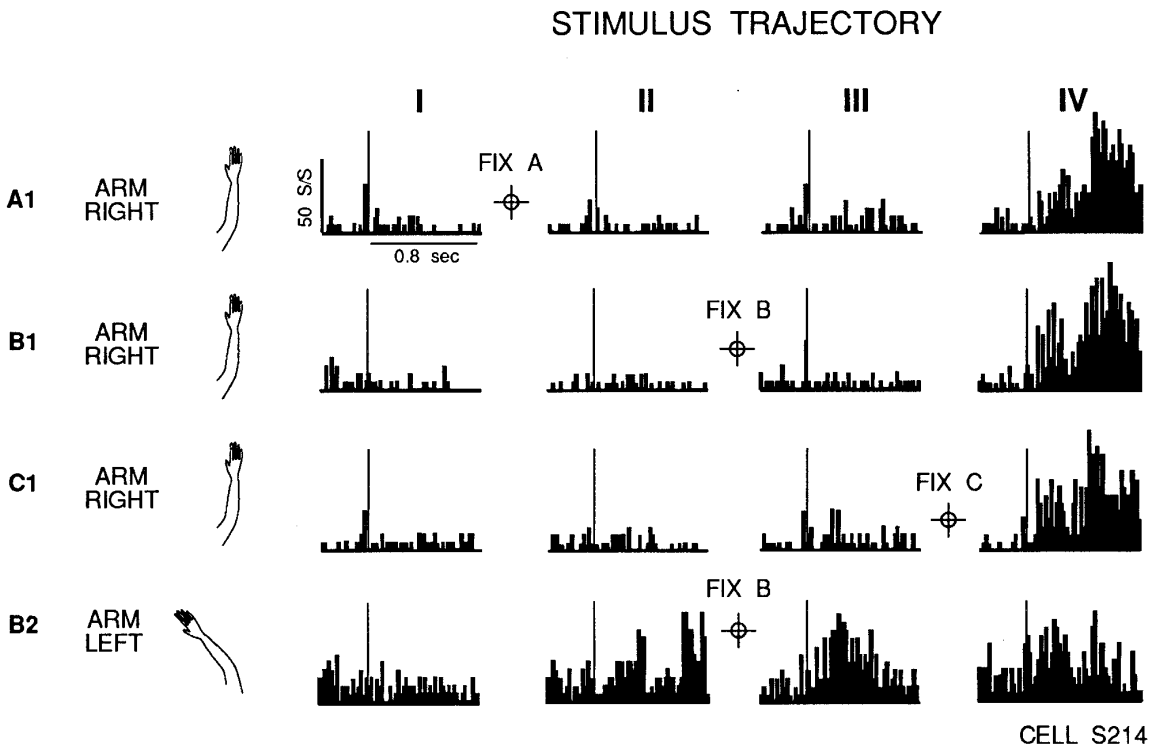

FIG. 6. Responses of a bimodal PMv neuron with a tactile receptive field that covered the entire contralateral arm. When the arm was fixed to the right (*rows A1, B1,* and *C1*), the visual response was strongest at trajectory IV, near the arm. The response remained at position IV despite the change in eye position (FIX A, FIX B, and FIX C). When the arm was extended leftward, the visual receptive field also extended leftward, to trajectories II and III. See also legend to Fig. 5.

weights derived from *row A1* had a significant residual. $F_{match} = 31.89$, $P < 0.01$, and $F_{residual} = 50.79$, $P < 0.01$.)

Responses from a second arm + visual neuron are shown in Fig. 6. Just as for the previous example, the visual receptive field did not move with the eyes. The cell responded best to trajectory IV whether the eyes fixated to the left (*row A1*), to the center (*row B1*), or to the right (*row C1*). (This spatial constancy of the visual response was significant, because *rows B1* and *C1* significantly matched a pattern of weights derived from *row A1* with no significant residual variance. For *row B1*, $F_{match} = 348.92$, $P < 0.01$, and $F_{residual} = 1.27$, $P > 0.05$; for *row C1*, $F_{match} = 255.29$, $P < 0.01$, and $F_{residual} = 0.12$, $P > 0.05$.) The tactile receptive field for this cell covered the entire arm. Therefore, when the arm was bent toward the left, the tactile field extended from the monkey's shoulder on the far right, across the midline, and partly into the ipsilateral half of space. The visual responses matched this pattern exactly. When the arm was bent to the left (Fig. 6, *row B2*), the visual receptive field encompassed trajectories II–IV. (This movement of the visual receptive field was significant, because a contrast analysis on Fig. 6, *row B2* with the use of weights derived from *row A1* had a significant residual. $F_{match} = 4.38$, $P > 0.05$, and $F_{residual} = 11.68$, $P < 0.01$.)

In addition, this cell was tested while the monkey's view of its arm was occluded with a piece of cardboard. Under this condition, the visual receptive field still moved significantly with the arm, suggesting that the effect of arm position is mediated at least partly by proprioception ($F_{match} = 53.73$, $P < 0.01$; $F_{residual} = 9.29$, $P < 0.01$).

The same cell (Fig. 6) illustrates yet another property of many arm + visual cells, namely the modulation of neuronal activity by joint angle. For this cell, the spontaneous activity increased by 202% when the arm was bent to the left. This modulation by arm position was significant ($F = 23.11$, $P < 0.01$).

Responses from a third arm + visual neuron are shown in Fig. 7. Again, the visual receptive field for this neuron did not move with the eyes. (*Rows A* and *B* significantly matched a pattern of weights derived from *row C*, with no significant residual. For *row A*, $F_{match} = 11.52$, $P < 0.01$, and $F_{residual} = 1.77$, $P > 0.05$; for *row B*, $F_{match} = 31.55$, $P < 0.01$, and $F_{residual} = 1.13$, $P > 0.05$.) However, unlike in the previous cells, the magnitude of the response was modulated by eye position, increasing by 86% when the eyes fixated toward the right ($F = 6.88$, $P < 0.01$).

Figure 8 shows an example of an arm + visual cell that was tested by turning the head. The cell responded best to trajectory IV whether the eyes fixated to the left (*row A1*), center (*row B1*), or right (*row C1*). When the head was rotated 20° to the left (*row A2*), the cell still responded best to trajectory IV. That is, the visual receptive field for this cell did not move with the head. (*Rows B1, C1,* and *A2* significantly matched a pattern of weights derived from *row A1*, with no significant residual. For *row B1*, $F_{match} = 57.59$, $P < 0.01$, and $F_{residual} = 1.63$, $P > 0.05$; for *row C1*, $F_{match} = 77.91$, $P < 0.01$, and $F_{residual} = 1.39$, $P > 0.05$; for *row A2*, $F_{match} = 55.05$, $P < 0.01$, and $F_{residual} = 1.27$, $P > 0.05$.) For this neuron, both the spontaneous activity and the magnitude of the response were modulated by the position of the

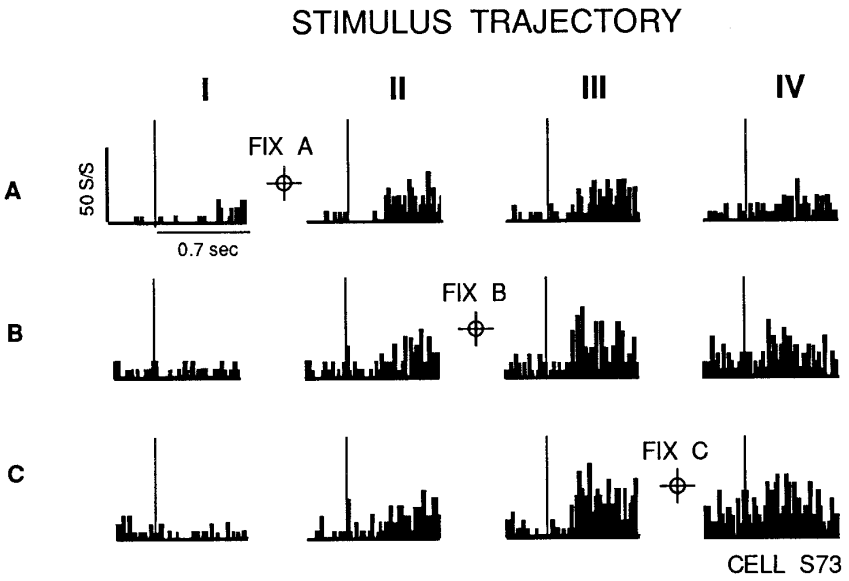

FIG. 7. Responses of a bimodal PMv neuron with a tactile receptive field on the contralateral elbow. The visual receptive field remained in the same location whether the eyes fixated light A, B, or C. However, the magnitude of the visual response was modulated by eye position. The response was significantly greater when the eyes fixated light C. The contralateral arm was fixed to the right during these tests. See also legend to Fig. 5.

head. The spontaneous activity was 194% larger when the head was straight than when the head was rotated to the left ($F = 35.44$, $P < 0.01$; analysis on *conditions B1* and *A2*). The visual response at trajectory IV was 130% larger when the head was straight than when the head was rotated to the left ($F = 22.01$, $P < 0.01$; analysis on trajectory IV, *conditions B1* and *A2*).

For all of the examples described above, the visual receptive field did not move with the eyes. Therefore fixation should not have been necessary to position a stimulus within the receptive field. Figure 9 shows the responses of a neuron tested with and without fixation. The cell had a tactile receptive field on the contralateral forearm and a matching visual receptive field in the space within ~20 cm of the forearm. This visual response did not move when the eye moved. *Conditions C1* and *C2* show the result when the monkey fixated point C, on the right. When the arm was strapped on the right (*row C1*), the visual response was strongest at stimulus position III. When the arm was strapped on the left (*row C2*), the visual response was strongest at stimulus position II. Thus the visual receptive field was anchored to the forearm, and moved as the forearm moved. *Conditions NF1* and *NF2* show the result when the fixation light did not come on at the start of the trial, the monkey was not required to fixate, and no reward was given at the end of the trial. When tested in this fashion, the response was larger, and in particular, the movement of the visual receptive field with the arm was more pronounced. Similar

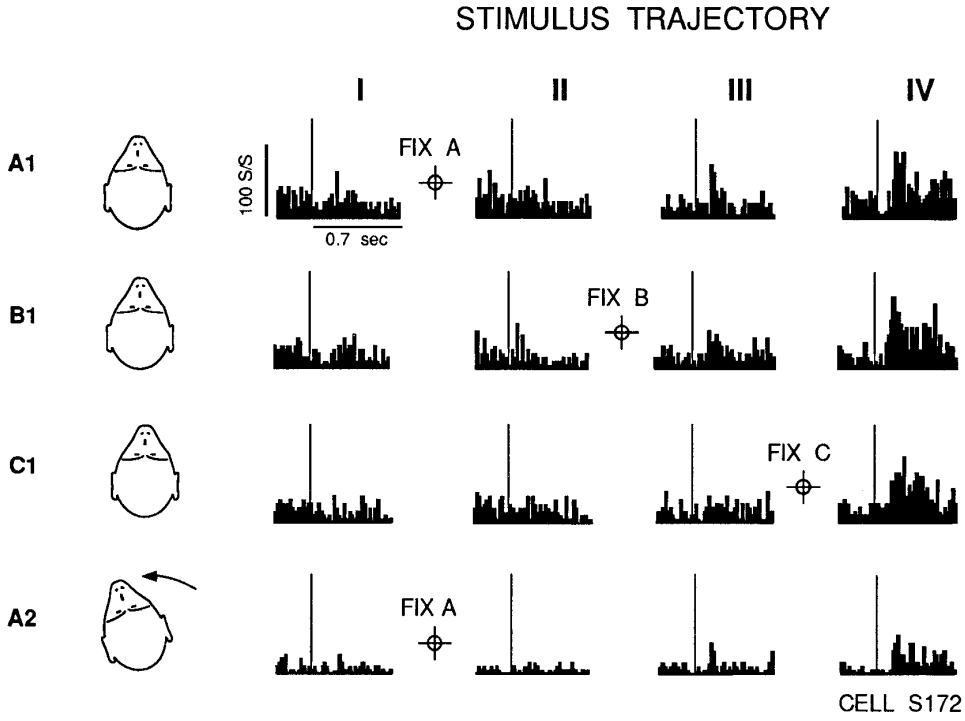

FIG. 8. Responses of a bimodal PMv neuron with a tactile receptive field on the contralateral arm. The visual response was strongest to trajectory IV, independent of the position of the eyes (*rows A1, B1,* or *C1*) or of the head (*row A2*). However, the activity of the neuron was modulated by the position of the head. Both the response and the spontaneous activity were reduced when the head was turned to the left. See also legend to Fig. 5.

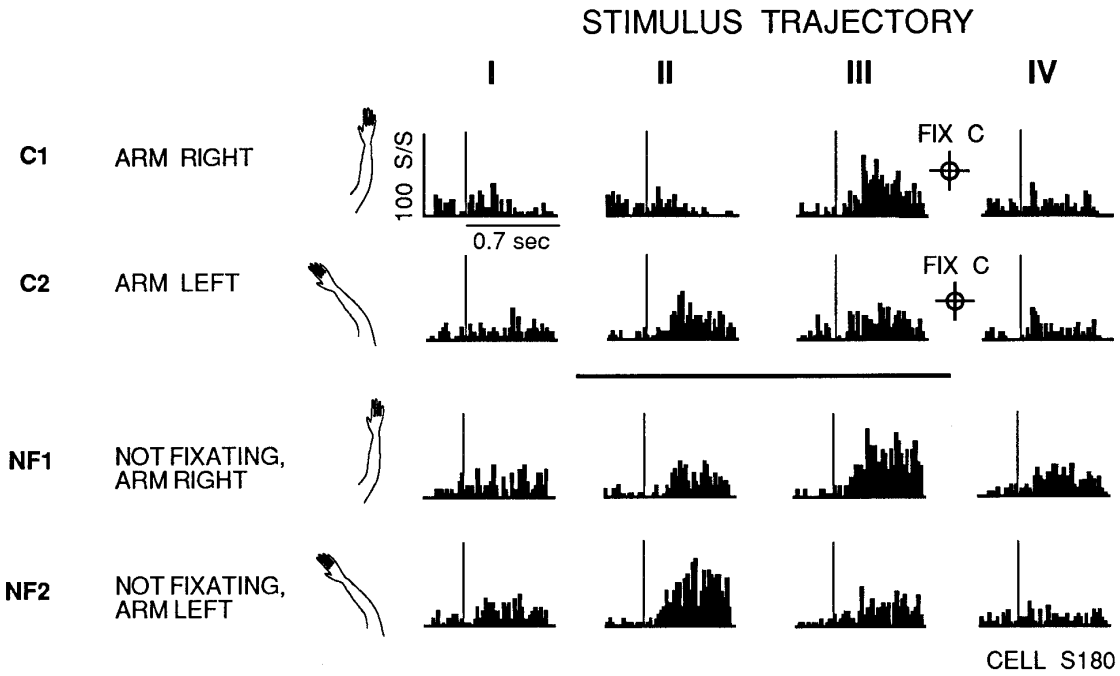

FIG. 9. Responses of a bimodal neuron with a tactile receptive field on the right forearm. In *rows C1* and *C2*, the fixation light-emitting diode (LED) was illuminated at the beginning of the trial and then extinguished during the presentation of the stimulus. The monkey was required to maintain fixation on the unilluminated LED until the end of the trial. When the arm was bent toward the left (*row C2*), the visual response moved with the arm toward the left. In *rows NF1* and *NF2*, the fixation light was never illuminated and the monkey was not required to fixate. The response increased, and the movement of the visual receptive field with the arm was more pronounced.

tests were performed in 46 bimodal neurons. Of the 46 neurons, 30% responded significantly better to the visual stimulus when the monkey was not performing the fixation task; 7% responded better when the monkey was performing the fixation task; and 63% showed no significant difference. Thus fixation control may not be necessary to study most bimodal PMv neurons, and indeed often reduces the magnitude of the visual response. Instead, the position of the relevant body part is far more important to control.

For some cells, when the visual receptive field moved with the arm, it moved out of range of the robotic stimuli. Figure 10 shows one example. The tactile receptive field was located on the inner surface of the upper arm. When we tested this neuron with hand-held visual stimuli, we obtained a vigorous response, especially when the stimulus was within 10 cm of the tactile receptive field. When we fixed the arm in different positions, the visual receptive field moved with the arm. In particular, when the arm was bent to the left, the visual response was strongest in the region of space between the arm and the chest. However, when we tested the cell with our standard set of robotic stimuli, the result was quite different. When the arm was fixed to the right (*row C1*), the cell responded best to stimulus position III. When the arm was fixed to the left (*row C2*), most of the visual receptive field was hidden behind the arm, and the cell did not respond well to any of the stimulus positions. It fired only a few spikes to position III. On the basis of these histograms, the visual receptive field does not appear to have shifted with the arm; instead, the response magnitude appears to have been modulated by arm position. The reason, however, is that the robotic stimuli did not enter the strongest part of the visual receptive field. As described below, this was the case for at least five neurons. Clearly, to test the receptive field properties of these neurons, the stimulus must be carefully chosen to enter the correct part of near, personal space.

Table 2 summarizes the results of moving the eye, head, and arm in the awake monkey preparation. In total, 27 arm + visual neurons were tested by placing the arm in two positions and presenting stimuli along four trajectories. For 19 (70%) of these neurons, the visual response moved significantly with the arm, and for 8 (30%) the visual response did not move with the arm. Of these eight neurons, five were further tested with hand-held stimuli. In all five cases, we were able to demonstrate that the visual receptive field was indeed arm-centered, moving as the arm was moved, but that the robotic stimuli had not entered the optimal part of the visual receptive field. Therefore we suggest that the actual proportion of visual receptive fields that move with the arm, for arm + visual cells, may be much higher than 70%. In support of this suggestion, we tested 26 neurons (including the 5 just described) with hand-held stimuli, and for 24 of these (92%) the visual receptive field moved with the arm.

Figure 11*A* shows the mean result for the 19 neurons whose visual responses moved significantly with the arm. For each neuron, the data were first expressed as a percentage of the maximum response for that neuron. Two curves were then obtained: one curve for the ARM RIGHT condition and one curve for the ARM LEFT condition. These data were shifted to the left or to the right, until the peak response in the ARM RIGHT condition was aligned on the location marked by the arrow. For 10 neurons the data were shifted

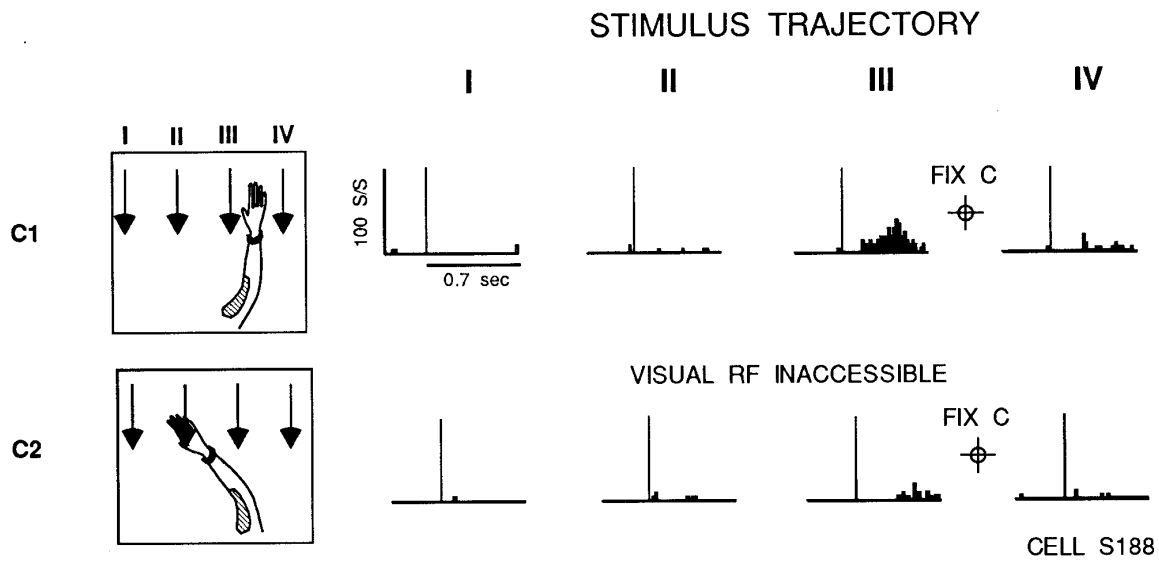

FIG. 10. Responses of a bimodal PMv neuron with a tactile receptive field on the upper medial surface of the arm. When tested with hand-held stimuli, the cell responded best to visual stimuli within ~10 cm of the tactile receptive field. This visual receptive field moved when the arm was moved, remaining attached to the upper arm. However, the 4 robotic stimulus trajectories were not adequate to test this visual receptive field. When the arm was fixed on the right (*row C1*), the neuron responded to trajectory III. When the arm was fixed on the left (*row C2*), the visual receptive field was blocked by the arm, and the neuron no longer responded strongly to the stimuli presented by the robot.

to the left, and for 17 neurons the data were shifted to the right. Because of the partial overlap of these two data sets, Fig. 11 shows five stimulus positions, even though each neuron was tested with only four stimulus positions. The results for all 19 neurons were then averaged together. The population of visual receptive fields clearly moved to the left with the arm. Six of these neurons were also tested when the monkey's view of the arm was occluded, and for five the visual receptive field still moved significantly with the arm.

Figure 11*B* shows the result for the eight neurons whose visual responses did not move significantly with the arm. We suggest that the graph in Fig. 11*A* is more representative of the arm + visual neurons in PMv, because the graph in Fig. 11*B* contains at least five neurons for which the robot could not adequately reach the visual receptive field. In these cases, the visual responses obtained with the robot did not appear to move with the arm, even though the visual receptive field, tested with hand-held stimuli, clearly moved as the arm moved.

TABLE 2. *Bimodal neurons*

	Arm + Visual Cells	Face + Visual Cells
Moved with eye	0/31 (0)	3/20 (15)
Modulated by eye position	18/31 (58)	15/17 (88)
Moved with head	0/4 (0)	19/20 (95)
Modulated by head position	3/4 (75)	0/20 (0)
Moved with arm	19/27 (70)	0/7 (0)
Modulated by arm position	10/27 (37)	0/7 (0)

Values are number of neurons, with percentages in parentheses, for bimodal neurons with visual receptive fields that moved significantly with the eye, head, or arm, and cells whose level of activity (spontaneous and/or visual response) was modulated by eye, head, or arm position. Data from awake monkey preparation only.

As shown in Table 2, for 10 of 27 arm + visual neurons (37%), the spontaneous activity changed significantly when the arm was moved. For one neuron, the spontaneous activity was greatest when the arm was fixed to the right (contralateral). For nine neurons, the spontaneous activity was greatest when the arm was fixed to the left (ipsilateral). We could not test whether the magnitude of the visual response was also modulated by arm position. This was because the visual receptive field usually moved with the arm. For example, in Fig. 10, the response magnitude appeared to change when the arm moved, but only because the visual receptive field moved out of range of the stimulus trajectories.

Four arm + visual cells were tested by rotating the head. In all four cases the visual receptive field remained in the same location in space. That is, it did not move with the head. For three of the cells, both the spontaneous activity and the visual response were significantly modulated by head position.

Thirty-one arm + visual cells were tested for the effect of eye position. (This sample includes 26 of the 27 neurons that were tested for the effect of arm position.) In all 31 cases, the visual receptive field remained at the same location in space, despite the 40° shift in eye position. Figure 12 shows the mean result for all 31 neurons. The data corresponding to the central fixation (□) have been aligned on the position marked by the arrow. If the visual receptive fields were retinocentric, as they are in most visual areas, then the data for the left-hand fixation (×) should be shifted toward the left of the arrow, and the data for the right-hand fixation (■) should be shifted toward the right of the arrow. Instead, all three curves fall at the same location. The entire population of receptive fields, therefore, remained stationary in space when the eyes moved.

Although none of the visual receptive fields moved with the eye, 18 neurons (58%) were modulated by eye position,

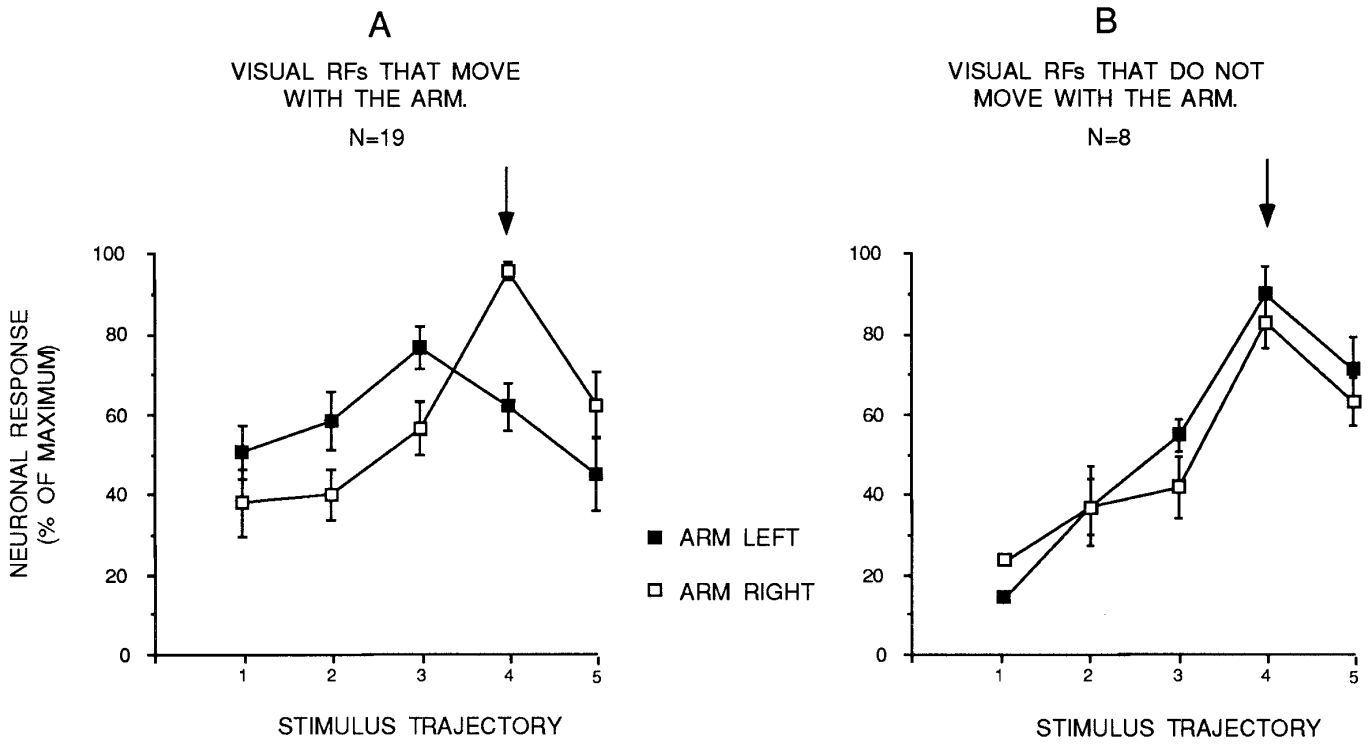

FIG. 11. *A*: mean responses of the 19 arm + visual neurons for which the visual receptive field moved significantly with the arm. Responses are expressed as % of the maximum response for each neuron. Error bars: means ± SE. Visual receptive fields plotted while the arm was fixed on the right (□) have had their peaks aligned on the arrow, at position 4. When the arm was fixed to the left, the visual receptive fields moved to the left (■). *B*: mean responses of the 8 arm + visual neurons for which the visual response to the robot did not move significantly with the arm. For 5 of these 8 neurons, when the arm moved, the visual receptive field shifted out of the range of the robotic stimuli. When the cells were tested with hand-held stimuli, the visual receptive fields did move with the arm.

in that either the spontaneous activity (6 cells), the response magnitude (8 cells), or both (4 cells) was significantly greater for some eye positions than for others. In most cases, the spontaneous activity was greatest when the monkey fixated one of the extreme positions, either to the contralateral side (5 cells) or to the ipsilateral side (4 cells). In only one cell, the spontaneous activity was significantly greater when the monkey fixated the central position. Similarly, in most cases the magnitude of the visual response was greatest when the monkey fixated the contralateral side (8 cells) or the ipsilateral side (3 cells), and in only one case the activity was significantly greater when the monkey fixated the central position.

In summary, almost all of the neurons in premotor cortex with tactile responses on the arm have arm-centered visual receptive fields, which move as the arm is moved but not as the eye or the head is moved (see Table 2). When the tactile receptive field is on the upper arm, the visual receptive field moves with the upper arm (Figs. 5 and 10). When the tactile response is on forearm, the visual receptive field moves with the forearm (Fig. 9). When the tactile receptive field includes the whole arm, the visual receptive field moves with the whole arm (Fig. 6). The level of activity of many of the neurons is modulated by the angle of the eyes, the head, and the arm, perhaps reflecting a proprioceptive input from these joints. We have found similar results for arm + visual cells studied in the anesthetized monkey (Graziano and Gross 1995; Graziano et al. 1994).

Visual receptive fields that move with the head, not with the eye or the arm

To test whether cells with tactile responses on the face had head-centered visual receptive fields, we varied the position of the head, the arm, and the eyes. The monkey fixated one of three lights, FIX A, FIX B, or FIX C, spaced 15° apart horizontally (Fig. 13, *top*). During fixation, the visual stimulus was advanced toward the monkey along one of the five trajectories shown (I–V).

Figure 13, *bottom*, shows the result for a cell that had a tactile receptive field on the contralateral side of the snout. When the head was straight (*rows A1, B1, C1,* and *B2*), the neuron responded best to stimulus trajectory II, regardless of eye or arm position. When the head was rotated 15° to the right (*row B3*), the neuron responded best to trajectory III. Thus the visual receptive field moved toward the right with the head. (Specific comparisons with contrast analyses showed that *rows A1, B1,* and *B2* significantly matched a pattern of weights derived from *row C1,* with no significant residual; that is, the visual response did not move with the eyes or the arm. However, *row B3* did not significantly match *row C1,* but instead had a significant residual, indicating that the visual response moved with the head. For *row A1,* $F_{match} = 152.50$, $P < 0.01$, and $F_{residual} = 2.41$, $P > 0.05$; For *row B1,* $F_{match} = 267.15$, $P < 0.01$, and $F_{residual} = 2.78$, $P > 0.05$; For *row B2,* $F_{match} = 518.49$, $P < 0.01$, and $F_{residual} = 5.39$, $P > 0.05$; For *row B3,* $F_{match} = 5.55$, $P > 0.05$, and, $F_{residual} = 165.6$, $P < 0.01$.)

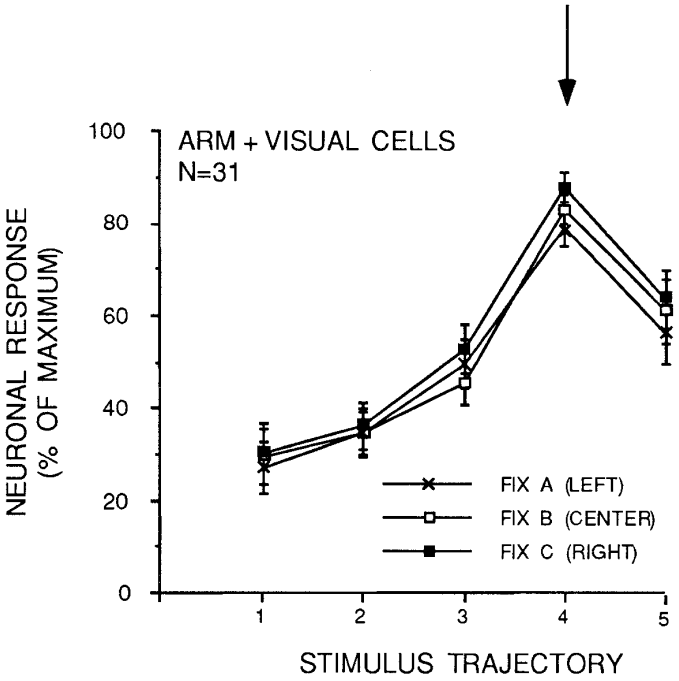

FIG. 12. Mean responses of all 31 arm + visual neurons tested with 3 eye positions. Visual receptive fields plotted while the eye fixated the central position (FIX B, □) have had their peaks aligned on the arrow, at position 4. When the eye fixated 15° to the left (FIX A) or 15° to the right (FIX C), the visual receptive fields remained in the same location. That is, the visual receptive fields did not move as the eye moved. Responses are expressed as percents of the maximum response for each neuron. Error bars: means ± SE.

Although the visual receptive field of this neuron did not move with the eyes, the spontaneous activity depended on eye position, increasing by 1744% when the eyes fixated toward the left ($F = 175.2$, $P < 0.01$). The magnitude of the visual response, however, was not significantly modulated by eye position (27% change, $F = 4.89$, $P > 0.05$).

It has been suggested (Fogassi et al. 1992, 1996) that such modulation of activity in PMv neurons is not caused by the position of the eye per se, but rather caused by the tension in the neck muscles, which is known to vary depending on the angle of gaze. According to this hypothesis, the purpose of the modulation is to encode the position of the head on the trunk. However, this hypothesis cannot be true for the example in Fig. 13. The activity of the neuron is clearly modulated by the position of the eye in the orbit, not by the position of the head on the trunk. In *row A1,* the head is straight and the eyes are 15° to the left. In *row B3,* the head has been rotated to the right, but the eyes are still at the same orbital position, that is, 15° to the left with respect to the head. Despite this change in head position, there is no significant change in spontaneous activity (8% change, $F = 0.78$, $P > 0.05$).

Figure 14 shows the result for another cell. When the head was rotated 15° to the left (*row B1*), the neuron responded best to trajectory I. When the head was straight (*row B2*), the response was best to trajectory II. When the head was rotated 15° to the right (*row B3*), the response was best to trajectory III. Thus the visual receptive field was anchored to the head and moved as the head moved. (*Rows B1* and *B3* significantly matched a pattern of weights derived from *row B2,* but there was also a significant residual variance, that is, a significant movement of the visual receptive field. For *row B1,* $F_{match} = 10.84$, $P < 0.01$, and $F_{residual} = 22.03$, $P < 0.01$; For *row B3,* $F_{match} = 13.19$, $P < 0.01$, and $F_{residual} = 7.87$, $P < 0.01$.) As was the case for all other face + visual cells (see Table 1), the spontaneous activity of this cell was not modulated by head position (16% change, $F = 2.11$, $P > 0.05$).

Figure 15 shows an example of a visual receptive field that moved partially with the eyes and partially with the head. In *row A1,* when the eyes fixated to the left, the cell responded best to stimulus trajectory II. In *row B1,* when the eyes fixated to the center, the cell responded best to trajectory III. However, in *row C1,* when the eyes fixated to the right, the visual response was still best at trajectory III. That is, the visual response moved toward the right as the eye moved, but not by the full amount that the eye did. (*Rows B1* and *C1* had a significant residual when compared with a pattern of weights derived from *row A1.* That is, the visual receptive field moved significantly with the eye. For *row B1,* $F_{match} = 11.14$, $P < 0.01$, and $F_{residual} = 4.07$, $P < 0.05$; for *row C1,* $F_{match} = 16.66$, $P < 0.01$, and $F_{residual} = 12.72$, $P < 0.01$).

Figure 15, *row B2,* shows the result of rotating the head toward the right. Compared with *row B1,* the response to trajectory I decreased and the response to trajectory III increased, although the peak response stayed at trajectory III. That is, the visual receptive field did not move by the full amount that the head moved. (*Row B2* had a significant residual when compared with a pattern of weights derived from *row B1;* thus the visual receptive field moved significantly with the head. $F_{match} = 150.03$, $P < 0.01$, and $F_{residual} = 30.68$, $P < 0.01$.)

As shown in Table 2, 20 neurons were tested by rotating the head toward the right, and for 19 of these (95%) the visual receptive field moved significantly with the head. Figure 16 shows the mean result for all 20 neurons. The population of visual receptive fields moved 15°, maintaining precise register with the head. Four neurons were also tested by rotating the head 15° to the left, and in these cases the visual receptive field moved to the left with the head in a similar fashion.

The position of the head did not modulate the spontaneous activity in any of the 20 neurons. We could not usually determine whether the position of the head modulated the magnitude of the visual response, because the visual receptive field generally moved with the head. For example, in Fig. 15, the neuron responded more when the head was turned to the right (*row B2*); but this increase in response may be due to the visual receptive field moving into range of stimulus trajectory III.

Seven neurons were tested by moving the arm, and in all cases, the visual receptive field did not move with the arm. Arm position also did not modulate the magnitude of the response or of the spontaneous activity. There was no significant effect at all of moving the arm.

Twenty cells were tested for the effect of eye position. (This 20 includes 17 of the cells that were tested for the effect of head position.) For 17 cells (85%), the visual receptive field did not move with the eye. For the remaining

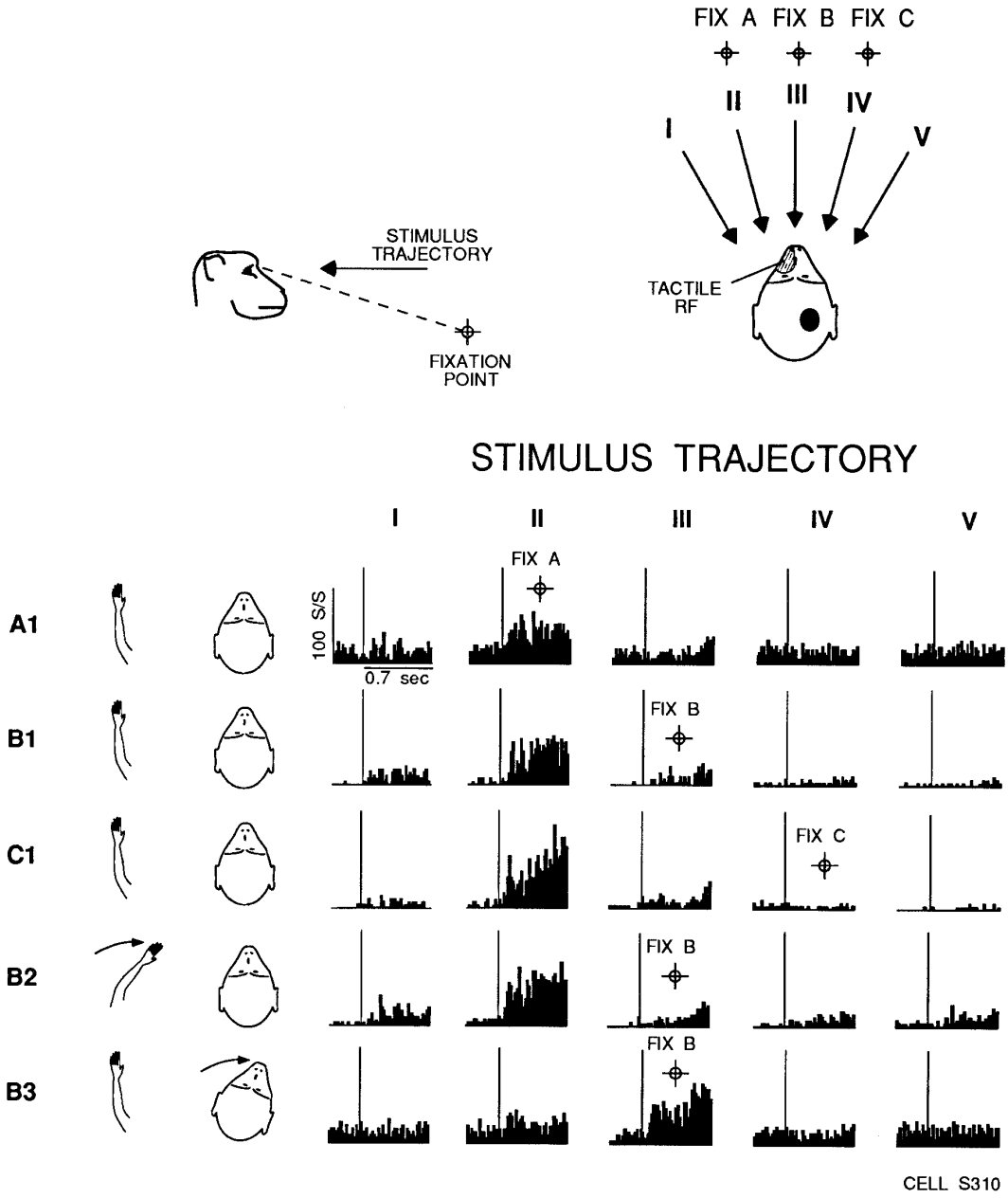

FIG. 13. *Top*: experimental paradigm for testing the effect of head, arm, and eye position. The monkey fixated 1 of 3 lights (FIX A, FIX B, or FIX C) spaced 15° apart. The stimulus was presented along 1 of 5 trajectories (I–V). The trajectories and the monkey are drawn to the same scale. The monkey's head was held straight (shown), or rotated 15° to the right or the left. The arm was strapped to a movable holder and held straight ahead or bent rightward across the chest. Black dot: hemisphere recorded from. Stippling: tactile receptive field of the cell whose responses are illustrated beneath. *Bottom*: histograms of neuronal activity, summed over 10 trials, as a function of eye position (FIX A, FIX B, FIX C), stimulus position (I–IV), arm position (to the right in *row B2*, to the left in all other conditions), and head position (to the right in *row B3*, straight in all other conditions). Vertical lines: stimulus onset. When the head was straight (*rows A1, B1, C1,* and *B2*), the neuron responded best to stimulus trajectory II, regardless of eye or arm position. When the head was rotated 15° to the right (*row B3*), the neuron responded best to trajectory III. Thus the visual receptive field moved toward the right with the head. The spontaneous activity was greatest when the eyes were angled 15° to the left of the head (*rows A1* and *B3*).

three cells, the visual receptive field showed a partial movement with the eye. Figure 17 shows the mean for all 20 neurons. Whether the eyes fixated the central position (□), the right-hand position (×), or the left-hand position (■), the population of visual receptive fields remained in the same location. That is, the population of cells coded visual space with respect to the head, not with respect to the eye.

Although for most neurons the visual receptive field did not move with the eyes, the position of the eyes did have a significant effect on the overall level of activity. It was not possible to test this effect in the three neurons whose visual receptive fields moved partially with the eye. But of the remaining 17 neurons, 15 (88%) were modulated by eye position; that is, either the spontaneous activity (5 cells),

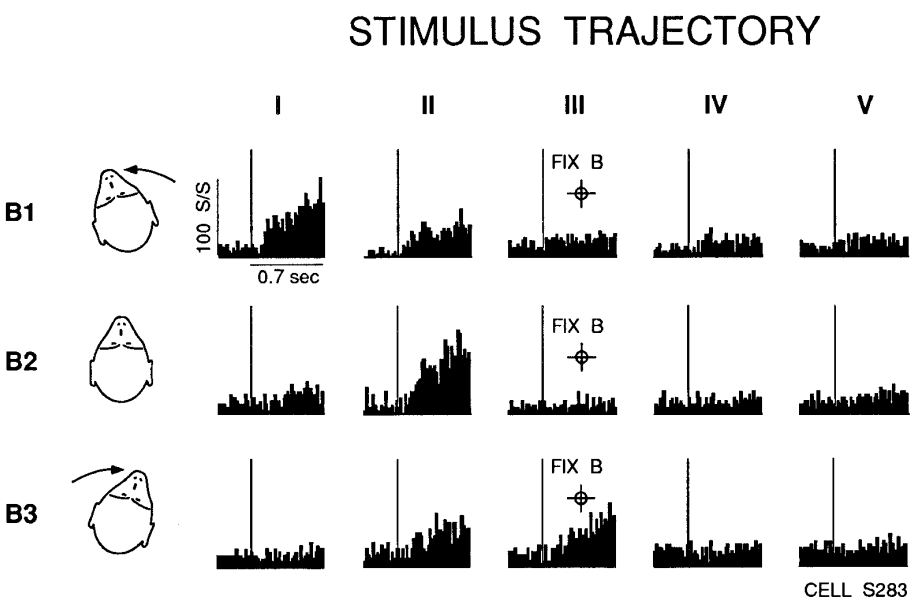

FIG. 14. Responses of a bimodal PMv neuron with a tactile receptive field on the contralateral snout. When the head was rotated 15° to the left (*row B1*), the neuron responded best to trajectory I. When the head was straight (*row B2*), the response was best to trajectory II. When the head was rotated 15° to the right (*row B3*), the response moved to trajectory III. Thus the visual receptive field was anchored to the head and moved as the head moved.

the response magnitude (1 cell), or both (9 cells) were significantly greater for some eye positions than for others. The spontaneous activity was usually greatest when the monkey fixated the contralateral side (8 cells) or the ipsilateral side (5 cells), rather than the central position (1 cell). The magnitude of the visual response was also usually greatest when the monkey fixated the contralateral side (5 cells) or the ipsilateral side (3 cells), rather than the center (2 cells).

In summary, most neurons in PMv with a tactile response on the face have a visual receptive field that is head centered (see Table 2). These visual receptive fields are anchored to the head and move as the head is rotated, but not as the arm moves or as the eye moves. Although the visual receptive fields do not move with the eyes, for many neurons the level of activity is modulated by the position of the eyes. Unlike the case for arm + visual cells, however, we did not find any evidence that face + visual cells were modulated by the position of the head or of the arm.

Responses during voluntary movement of the head

We recorded from face + visual neurons while the monkey turned its head to the right or the left, or reached with the contralateral arm toward pieces of fruit. Of the 27 face + visual neurons tested in this fashion, none responded in association with movements of the arm. In contrast, 17 (63%) responded significantly above baseline as the monkey turned its head (*t*-test, $P < 0.05$).

Figure 18 shows the result for one neuron tested for movement-related activity. The visual and tactile responses were

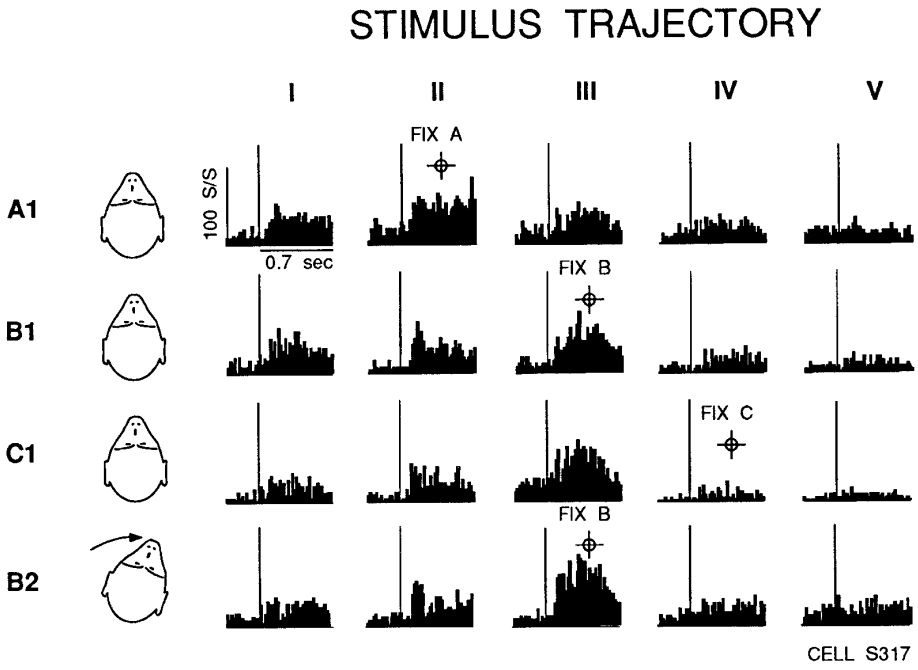

FIG. 15. Responses of a bimodal PMv neuron with a tactile receptive field on the contralateral snout and a visual receptive field that moved partly with the eyes and partly with the head. When the eyes fixated location A, the neuron responded best to trajectory II. When the eyes fixated location B, the neuron responded best to trajectory III. However, when the eyes fixated location C, the cell still responded best to trajectory III. When the head was rotated 15° to the right (compare *rows B1* and *B2*), the visual receptive field did not move by the full amount that the head moved.

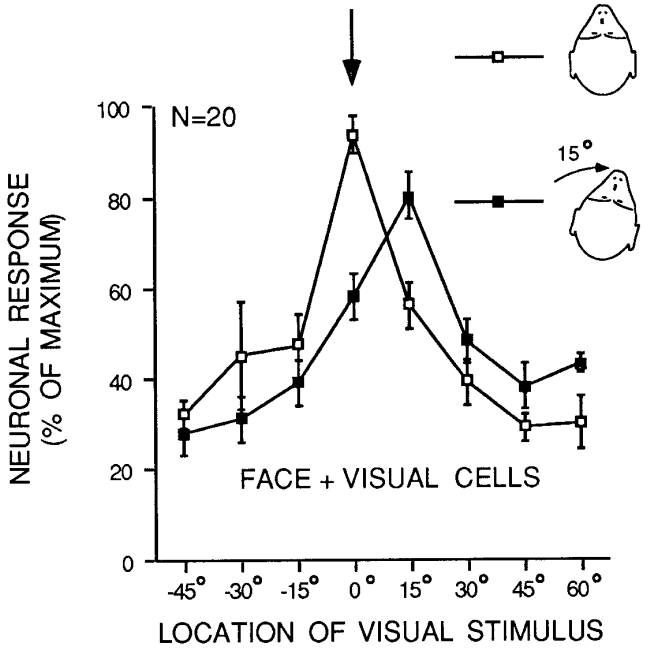

FIG. 16. Mean responses of all 20 face + visual neurons tested with multiple head positions. Visual receptive fields plotted while the head was straight (□) have had their peaks aligned on the arrow, at 0°. When the head was rotated 15° to the right, the visual receptive fields also shifted an average of 15° to the right (■). Responses are expressed as % of the maximum response for each neuron. Error bars: SE. Of these 20 neurons, 4 were also tested by rotating the head toward the left, and in these cases the visual receptive fields moved to the left with the head in a similar fashion.

strongest on the left (contralateral) side of the face (*A*). When the head bolt was loosened, the animal turned its head freely from side to side. The cell responded as the head rotated to the right but not as it rotated to the left (*B*). To determine whether this movement-related response was caused by sensory stimulation, such as proprioceptive stimulation of the neck or tactile stimulation caused by the hair rubbing against the chair, we turned the head passively, producing similar sensory conditions (*C*). The neuron no longer responded. Thus the neuronal activity was associated with active movement of the head.

Of the 17 neurons that responded significantly above baseline during active head rotation, 16 were directionally specific, responding in association with only one direction of head rotation. Eight preferred movement away from the tactile and visual receptive field; six preferred movement toward the tactile and visual receptive field; two responded equally well to tactile and visual stimuli on both sides of the head but preferred head movement in only one direction; and one responded to visual and tactile stimuli on both sides of the head and also responded to both directions of head movement. This range of cells could serve a range of visuomotor functions, such as reaching toward or flinching away from nearby stimuli.

Fourteen of the cells that responded during active head movement were also tested with passive head movement. Of these, 13 responded significantly more during active movement (*t*-test, $P < 0.05$). Indeed, nine of these cells responded only during active movement. One cell responded equally well under both active and passive conditions.

DISCUSSION

Visual and tactile responses in premotor cortex

We studied the sensory properties of neurons in PMv, both in the anesthetized and in the awake macaque. The recording sites were located on the cortical convexity posterior to the arcuate sulcus, corresponding mainly to area F4 as defined by Rizzolatti and colleagues (Gentilucci et al. 1988; Rizzolatti et al. 1988). We found that the cells responded to somatosensory stimuli, visual stimuli, or both, i.e., were bimodal. In addition, many neurons in the awake monkey (32%) responded during voluntary movement.

The bimodal, visual-somatosensory cells usually responded to visual stimuli positioned close to the tactile receptive field. Some cells responded only if the stimulus was within a few centimeters of the tactile receptive field, whereas others responded to stimuli as far away as 1 m; but all cells responded better to closer stimuli. None of the cells responded to stimuli projected onto a screen, such as spots, slits, expanding squares, and expanding random dot patterns. Only objects, either moving or stationary, could drive the neurons. These results are very similar to those of Rizzolatti and colleagues (Fogassi et al. 1996; Gentilucci et al. 1988; Rizzolatti et al. 1981).

We also studied a small sample of neurons ($n = 28$) in the hand representation of M1 in an anesthetized monkey, and found one bimodal visual-tactile neuron. Wannier et al. (1989) also found bimodal neurons in the hand representa-

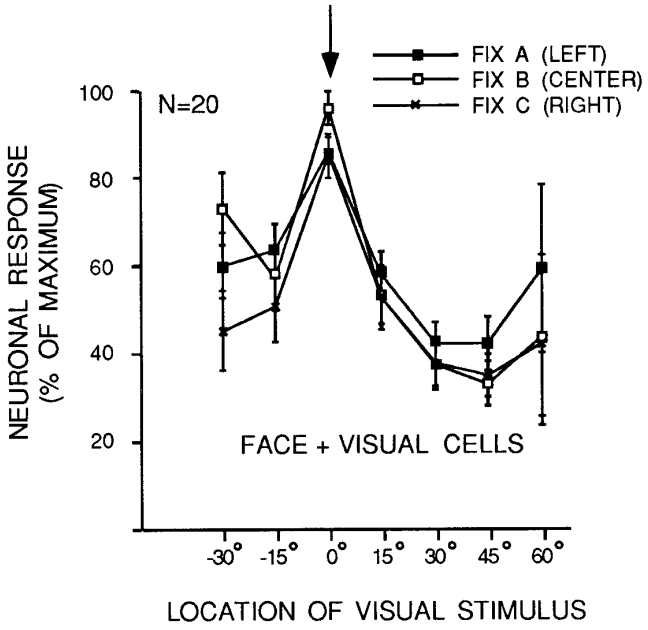

FIG. 17. Mean responses of all 20 face + visual neurons tested with 3 eye positions. Visual receptive fields plotted while the eye fixated the central spot (FIX B, □) have had their peaks aligned on 0°. When the eye fixated location A, 15° to the left, or location C, 15° to the right, the visual responses remained in the same location. That is, the visual receptive fields did not move with the eyes. Responses are expressed as % of the maximum response for each neuron. Error bars: SE.

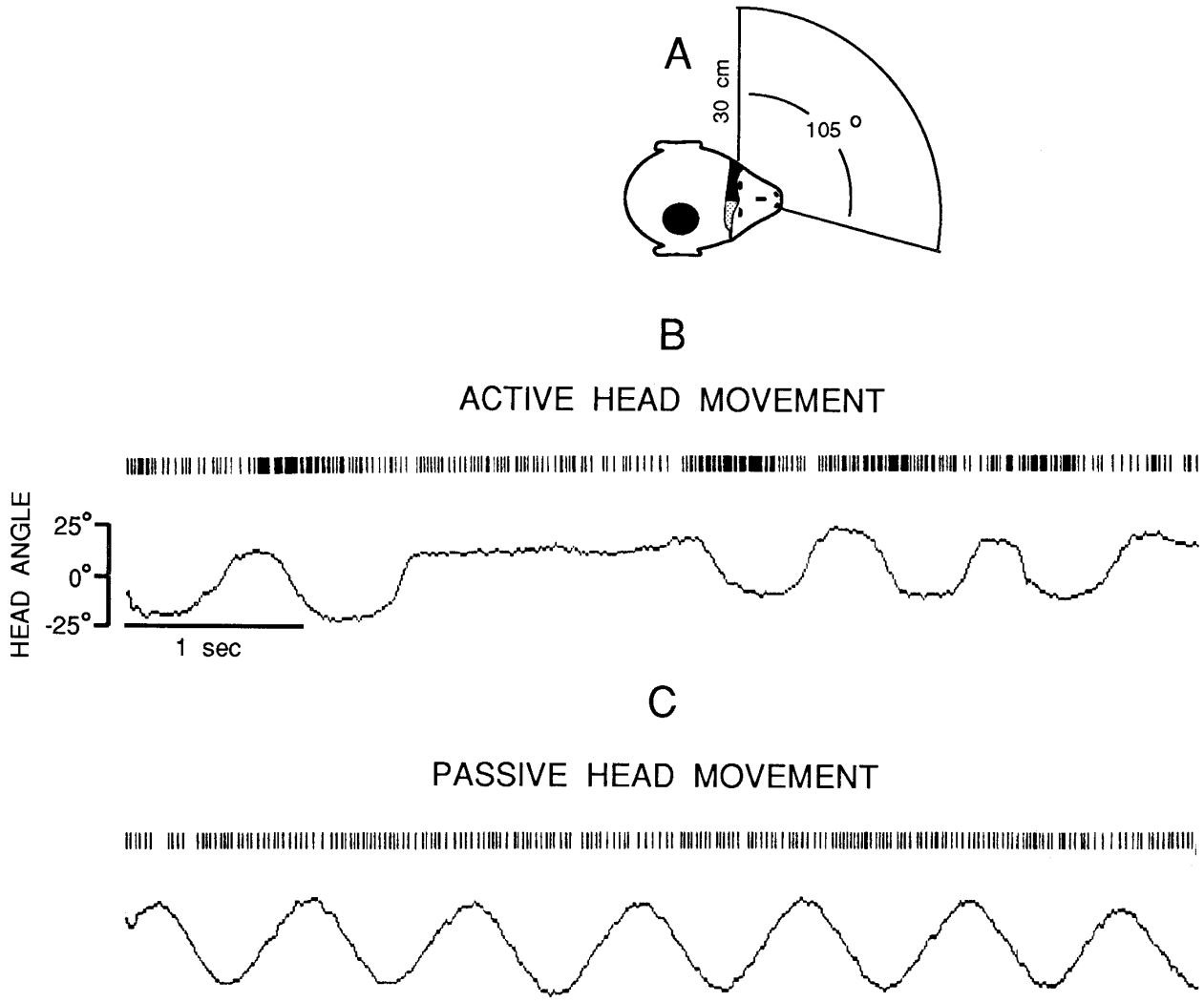

FIG. 18. Responses of a bimodal PMv neuron to active and passive rotation of the head. *A*: tactile receptive field (black shading: region of strongest response; gray shading: region of weaker response) and the visual receptive field (outlined) are strongest on the left side of the face. *B*: head bolt was loosened and the animal turned its head freely side to side. Downward direction of the trace: rightward head movement. Upward direction of the trace: leftward head movement. Vertical lines above trace: neuronal discharges. The neuron responded as the head turned toward the right, away from the visual receptive field. *C*: head was turned passively and the neuron no longer responded during the movement.

tion of M1. Because PMv projects directly to M1, it is not surprising to find at least some bimodal neurons in M1.

Motor versus sensory response

The neuronal activity during stimulus presentation might not be sensory at all, but instead might represent the monkey's attempt to flinch. Indeed, a large proportion (32%) of the neurons in the awake preparation responded during voluntary movements of the arm, mouth, or head.

However, the characteristics of the responses we observed suggest that they are sensory and not motor (see also Fogassi et al. 1996). Both the tactile and visual responses had delimitable receptive fields that varied from one cell to the next. In the case of the visual responses, the receptive fields were not only confined in their angular spread, but also in their distance from the monkey. Some neurons responded only to stimuli within centimeters of the body, whereas others responded to stimuli >1 m away. It is unlikely that the monkey would flinch only to near stimuli, and then when the electrode had advanced to the next cell, suddenly change strategy and flinch to more distant stimuli as well. Similarly, if responses were ''motor'' rather than sensory, why should adjacent cells have varied in whether they responded only to visual stimuli, only to tactile stimuli, or to both?

Furthermore, 41 neurons studied in the awake preparation had clear motor-related activity but no responses to tactile or visual stimuli. If the ''flinch'' hypothesis were correct, then these neurons should have responded to visual and tactile stimuli. For example, one neuron responded in association with voluntary movement of the eyebrow. However, the cell gave no response to our standard tactile stimulus, a gentle stroking with a cotton swab, applied to the eyebrow. The cell also gave no response to visual stimuli, including a robotically presented stimulus that approached the face. The reason is that the monkey had habituated to these standard stimuli and therefore the eyebrow did not move in response to them.

Indeed, if the flinch hypothesis were correct, then motor neurons in M1 should have been equally responsive to visual stimuli. However, we found that only 1 of 28 neurons in our sample from M1 responded to visual stimuli. Similarly, we have now recorded from a sample of 33 neurons in dorsal premotor cortex in an awake monkey (unpublished observations). None were bimodal, whereas 30 responded in association with voluntary movements of the arm. Thus motor properties, by themselves, cannot account for the responses to visual and tactile stimuli that we observed in PMv.

A major prediction of the flinch hypothesis is that PMv neurons should respond best to stimuli that approach the animal. However, we found that PMv neurons were selective for a wide range of stimulus directions, including motion away from the monkey's body. We also found that many neurons (57%) were selective for the direction of the tactile stimulus. It is difficult to explain how a flinch might result in different neurons having different selectivity for the direction of visual and tactile stimuli.

Another prediction of the flinch hypothesis is that PMv neurons should respond to any cue that predicts a touch, and not exclusively to a visual cue. We tested 21 bimodal neurons with a robotically presented stimulus that approached and touched the tactile receptive field in the dark. The sound of the robot motors indicted that the stimulus had begun to move. However, for 20 neurons, there was no response to the sound of the robot. Only one neuron responded significantly to the sound. Further testing showed that this response was not caused by anticipation of touch; instead the neuron responded to any auditory stimulus, and was one of the two auditory neurons that we found in PMv.

A final prediction of the flinch hypothesis is that the neurons should not respond when the animal is anesthetized. However, at least under nitrous anesthesia, we found a high proportion of somatosensory and bimodal neurons in PMv. In control tests, when the animal was anesthetized with nitrous oxide but not paralyzed with pavulon, the presentation of the visual stimuli did not elicit any noticeable motor response from the monkey. That is, the anesthesia was sufficient to prevent any obvious attempts to flinch from or grab the stimulus.

This evidence suggests that neurons in PMv respond to tactile and visual stimuli, independent of any motor-related activity that they may also have. As described below, we suggest that these sensory responses serve the function of guiding movements.

Coding of space in body-part-centered coordinates

In most visual areas of the brain, the cells encode the locations of visual images on the retina, that is, in retinocentric coordinates. When the eye moves, the visual receptive fields also move. For most of the bimodal, visual-tactile neurons in PMv, however, the visual receptive fields were not anchored to the retina. Instead, we found that most bimodal cells with a tactile response on the arm had a visual receptive field that was anchored to the arm; and most bimodal cells with a tactile response on the face had a visual receptive field that was anchored to the head. These cells can therefore encode the locations of visual stimuli with respect to the arm, that is, in ''arm-centered'' coordinates, or with respect to the head in head-centered coordinates. We expect that neurons in a more dorsal part of premotor cortex, in a possible leg representation (Kurata 1989; Kurata et al. 1985; Muakkassa and Strick 1979), might have visual receptive fields that are anchored to the leg or foot, locating stimuli in ''foot-centered'' coordinates.

More recently, Fogassi et al. (1996) have shown that when the monkey's chair is turned, the visual receptive fields of PMv neurons move with the chair. This study demonstrates that the visual receptive fields are not anchored to any external feature of the room, but rather to some part of the monkey's body or of the chair. The result is therefore consistent with our current and previous data showing that most visual receptive fields in PMv are body part centered (see Graziano and Gross 1992; Graziano et al. 1994).

In agreement with our results, Boussaoud et al. (1993) found that the activity of most PMv neurons was modulated by the position of the eyes. However, those authors also suggested that the visual receptive fields in PMv are anchored to the retina and move as the eye moves. Our findings contradict this suggestion. Boussaoud et al. gave three examples of receptive fields that moved with the eye and one example of a receptive field that did not move with the eye. Given the small number of cells those researchers described, it is difficult to compare these proportions with our own results. In any case, as Boussaoud et al. discuss, they do not appear to have tested the visual responses of bimodal, visual-somatosensory neurons. Rather, they tested responses of a subset of neurons associated with the monkey's performance of a lever-press task. Therefore the type of neuron and the type of response studied by Boussaoud et al. are unlikely to be the same as the ones that we studied.

Visual receptive fields that are not anchored to the retina have been reported in several different brain areas and species. Galletti et al. (1993) reported them in area PO of the monkey parietal cortex, Pigarev and Rodionova (1986) reported them in the parietal cortex of the cat, and Schlag et al. (1980) reported them in the thalamus of the cat. However, although these visual receptive fields did not move when the eyes moved and therefore were not anchored to the retina, it is not clear what part of the body or world they might have been anchored to. In the crayfish, Weirsma (1966) reported visual receptive fields that were fixed with respect to the gravitational vertical. Visual receptive fields influenced by the direction of gravity have also been reported in striate cortex of the cat (Horn and Hill 1969).

Possible functions of the tactile receptive fields: locating stimuli in space

If bimodal neurons in PMv encode the visual space near the body, then what is the function of their tactile responses? The tactile and visual receptive fields of a bimodal neuron are continuous, detecting the presence of a stimulus anywhere within the critical region of space. A strictly tactile neuron has a spatial receptive field that extends only a short distance from the skin, $\sim$1 cm, the length of the hair. A bimodal neuron has a spatial receptive field that may extend farther from the body, in some cases beyond a meter. This range of receptive fields would be useful for encoding the distance from the body part to the stimulus.

As described below, the tactile responses could also serve a developmental function.

Possible functions of the tactile receptive fields: ontogeny of spatial perception

One of the central puzzles in cognitive development is how an infant learns to interpret patterns of light on the retina as a three-dimensional space and how it learns to use that information to guide movement (e.g., Epstein and Rogers 1995; Millar 1994). Although some of this spatial and visuomotor ability is thought to be present at birth, much of it develops through experience.

The somatotopic organization in PMv could act as a hard-wired, stable framework on which to build the visual receptive fields used for encoding space near the body. On this view, the tactile receptive fields would provide a training signal for calibrating the visual receptive fields. Salinas and Abbot (1995) have described a multilayer network that uses Hebbian-type synapses to develop body-part-centered visual receptive fields. The network learns partly through its experience with combined visual and tactile stimuli.

If such a mechanism exists in PMv, the adaptation must be slow and require many trials of training, or, perhaps, be limited to a critical period early in development. When a visual stimulus repeatedly approached and touched the tactile receptive field of a bimodal neuron, the neuron did not become more responsive to that visual stimulus (Graziano and Gross, unpublished observations of 27 neurons). Even when tested with 100 trials of paired visual and tactile stimulation, the neurons still did not change their visual responsiveness. This resistance to change suggests that the system is designed to be relatively stable at least in the adult animal. It will be interesting, however, to test whether bimodal neurons can change their response properties with more extended training, as well as to see whether they are more plastic in infant monkeys.

Visual guidance of movement

We suggest that body-part-centered receptive fields provide a general solution to a central problem of sensory-motor integration (Graziano and Gross 1994; Gross and Graziano 1995). As described above, the body-part-centered visual receptive fields in PMv can encode the distance and direction from a body part to a nearby visual stimulus. Such information is sometimes called ''motor error'' because it specifies the distance and direction the body part must move to reach or avoid the stimulus (e.g., Bruce 1990). Arm + visual neurons would therefore be useful for guiding the arm toward or away from nearby stimuli. Face + visual neurons would be useful for guiding the head.

We found that 63% of the face + visual cells responded during voluntary movements of the head. These motor responses were usually specific to one direction of head movement, supporting the hypothesis that face + visual neurons contribute to the visual guidance of head movements. Further support comes from a study by Rizzolatti et al. (1983) in which lesions of PMv disrupted the monkey's ability to avoid or to bite nearby visual stimuli.

Other evidence supports the hypothesis that reaching with the arm may be controlled in an arm-centered coordinate system. Caminiti et al. (1990) recorded from an area on the border of PMv and dorsal premotor cortex and found that each neuron responded best as the monkey reached in a particular direction. That is, the neuron had a motor field. When the arm was moved to a different position, the motor field also moved, rotating roughly with the arm. Therefore the motor fields were arm centered, just as the visual receptive fields in our experiments were arm centered.

Psychophysical studies in humans also suggest that visually guided reaching may be organized in arm-centered coordinates. Soechting and Flanders (1989) analyzed the pattern of errors when human subjects reached toward visual and remembered targets, and concluded that reaching must be controlled in a coordinate system centered roughly on the shoulder. Tipper et al. (1992) found that the attended region of space during a reaching task is anchored to the hand. Paillard (1991) tested human subjects who were wearing displacing prisms. As expected, by repeatedly pointing toward visual targets the subjects were able to adapt to the prisms. Paillard then showed that the movements of each body part, such as the hand, the forearm, the upper arm, and the head, could be separately adapted. All of these experiments suggest that arm movements may be organized in a body-part-centered coordinate frame.

Other body parts may also be guided by body-part-centered coordinates. For example, in the frontal eye field, area LIP, and the superior colliculus, movements of the eye appear to be guided by visual, auditory, and tactile receptive fields that are anchored to the eyeball (Bruce 1990; Duhamel et al. 1992; Groh and Sparks 1996; Mazzoni et al. 1996; Sparks 1991). Thus a general principle of sensory-motor control appears to be that the sensory stimulus is located in a coordinate frame centered on the relevant body part.

An interesting test of the generality of body-part-centered coordinates would involve species of animals that have unique motor hardware. For example, an elephant might use a proboscocentric coordinate system, a capuchin monkey might use a caudocentric coordinate system, and an aardvark might use a glossocentric coordinate system.

Modulation of the response magnitude by the position of the eye, arm, and head: a possible mechanism for computing body-part-centered coordinates

Andersen and colleagues (Andersen and Mountcastle 1983; Andersen at al. 1985, 1990) studied the visual responses of neurons in posterior parietal areas 7a and LIP, and found that the visual receptive fields were retinocentric, moving as the eye moved. Those researchers also found that for some cells the magnitude of the visual response was modulated by the position of the eye. [A similar modulation by eye position has since been reported for a number of other visual areas, including PO, area V3a, primary visual cortex, and the lateral geniculate nucleus (Galletti and Battaglini 1989; Galletti et al. 1993; Lal and Friedlander 1989; Trotter et al. 1992)]. Modulation of neuronal activity by the position of the head has now been reported in area 7a and LIP (Andersen et al. 1993; Brotchie et al. 1995). There is even some evidence that neurons in area 7a may be modulated by the position of the arm (MacKay 1992).

It has been suggested that the proprioceptive and visual information carried by these parietal neurons could be used to construct head-centered, trunk-centered, and arm-centered visual receptive fields similar to the ones we found in PMv (Andersen et al. 1993; Brotchie et al. 1995; Gross and Graziano 1995; Pouget et al. 1993; Salinas and Abbot 1995). Area 7a and LIP do not project directly to PMv, but they do project to parietal area 7b, which then projects to PMv (Cavada and Goldman-Rakic 1989a,b; Kunzle 1978; Matelli et al. 1986; Mesulam et al. 1977). Proprioceptive input to PMv about head and arm position could also come via projections from other sources, such as the supplementary motor cortex and M1 (e.g., Matelli et al. 1986; Muakkassa and Strick 1979; for review, see Kalaska and Crammond 1992).

To construct a visual receptive field that is anchored to the arm, it is necessary to take into account the position of the arm relative to the eye; that is, the angle of the eye in the orbit, the angle of the head on the trunk, and the angle of the arm with respect to the trunk. We found that the activity of arm + visual neurons was often modulated by exactly these signals: eye position, head position, and arm position (see Table 1). In contrast, to construct a visual receptive field that is anchored to the head, it is necessary to take into account only the position of the eye relative to the head. It is not necessary to take into account the position of the head on the trunk or the position of the arm with respect to the trunk. We found that most face + visual neurons were modulated by the position of the eyes, but that none was modulated by the position of the head or of the arm. These results strongly support the idea that the modulation of neuronal activity by eye position, head position, and arm position is part of the mechanism through which body-part-centered receptive fields are constructed.

Interconnected system of bimodal areas

Several other areas of the macaque brain contain bimodal, visual-tactile neurons that are strikingly similar to the bimodal neurons in PMv. These areas include area 7b in the posterior parietal lobe, VIP, which lies on the floor of the intraparietal sulcus, and the putamen. Area 7b, VIP, and PMv are monosynaptically interconnected, and all three project to the putamen (Cavada and Goldman-Rakic 1989a,b, 1991; Kunzle 1978; Matelli et al. 1986; Mesulam et al. 1977; Parthasarathy et al. 1992; Weber and Yin 1984). We suggest that these four areas form a bimodal, visual-somesthetic system that processes the space on and near the body, for the purpose of guiding movement.

PUTAMEN. Most neurons in the monkey putamen respond to a touch on the skin, rotation of the joints, or deep muscle pressure, and many will respond only when the animal makes a voluntary movement (e.g., Alexander 1987; Crutcher and Delong 1984a,b; Liles 1985). These somatosensory and motor fields are organized somatotopically. We recorded from the putamen both in anesthetized and awake macaque monkeys (Graziano and Gross 1993, 1995) and found that ~30% of the cells with a somatosensory response on the face or arms also responded to visual stimuli. For these bimodal, visual-tactile neurons, the location of the visual receptive field closely matched the location of the tactile receptive field, extending outward from the skin into the space surrounding the body. In some cases, when the tactile response was on the arm, the visual receptive field was anchored to the arm, moving through space when the arm was moved. Responses in the putamen were somewhat different from the responses that we observed in PMv, in that the tactile and visual receptive fields were usually smaller in the putamen, and therefore the somatotopic map was more clear and had less overlap between the representations of different body parts.

VIP. Colby et al. (1993) studied neurons in area VIP and found that ~70% were bimodal, responding to tactile stimuli on the face and to visual stimuli near the face. Some cells responded to visual stimuli only within a few centimeters of the tactile receptive field, whereas others responded to more distant stimuli. Most cells were directionally selective in both modalities, and the preferred direction in the tactile modality usually matched the preferred direction in the visual modality. For at least one neuron, the visual response did not change when the eyes moved. This neuron preferred a visual stimulus approaching the chin but not the forehead, regardless of whether the animal's gaze was directed upward or downward.

AREA 7B. Neurons in area 7b respond to somatosensory stimuli such as touch, deep pressure, joint rotation, and pain (Dong et al. 1994; Robinson and Burton 1980a,b). About 30% of the neurons in area 7b also respond to visual stimuli; that is, they are bimodal (Hyvarinen 1981; Hyvarinen and Poranen 1974; Leinonen and Nyman 1979; Leinonen et al. 1979). These bimodal neurons have tactile receptive fields on the arm, the face, or both, and visual receptive fields that roughly match the locations of the tactile receptive fields. We recorded from area 7b in anesthetized monkeys (Graziano and Gross 1995; Graziano et al. 1996) and found that for most bimodal cells the tactile and visual receptive fields were bilateral and so large that it was difficult to assess whether the two matched. The visual receptive fields, however, often had a smaller region of best response. When the arm was moved, the region of best visual response did not move with it. Instead, the visual receptive field remained in the same place, unassociated with the arm.

In summary, there are at least four interconnected areas of the macaque brain—area 7b, VIP, PMv, and the putamen—that contain similar bimodal, visual-somesthetic responses. What, if any, are the differences between these areas? It is difficult to compare VIP with the other areas because it was studied under different conditions. The bimodal properties in the putamen, PMv, and area 7b, however, are not identical. In PMv and the putamen, many of the arm cells had visual receptive fields that were anchored to the arm, moving as the arm was moved; in area 7b, this was never the case. The tactile and visual receptive fields were smallest in the putamen, intermediate in PMv, and largest in area 7b. The somatotopic map was most clear in the putamen, with very little overlap between the representations of different body parts, and was almost undetectible in area 7b. These differences suggest that each bimodal area serves a different function. One speculation is that area 7b forms an early stage in the processing of space near the body, where the information is not as fully processed, perhaps coarse-coded in the form of large receptive fields that are not anchored to specific body parts. The output from area

7b might then be used to help construct the body-part-centered visual receptive fields found in the putamen and PMv.

We thank G. Yap, H. Biola, D. Evert, N. Rebmann, H. Rodman, D. Prentice, and G. Rizzolatti for help in different phases of the study.

This work was supported by National Eye Institute Grant EY-11347 and McDonnell Pew 90-16.

Address for reprint requests: M. Graziano, Dept. of Psychology, Green Hall, Princeton University, Princeton, NJ 08544.

Received 11 June 1996; accepted in final form 14 January 1997.

REFERENCES

ALEXANDER, G. E. Selective neuronal discharge in monkey putamen reflects intended direction of planned limb movements. *Exp. Brain Res.* 67: 623–634, 1987.

ANDERSEN, R. A., BRACEWELL, R. M., BARASH, S., GNADT, J. W., AND FOGASSI, L. Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. *J. Neurosci.* 10: 1176–1196, 1990.

ANDERSEN, R. A., ESSICK, G. K., AND SEIGEL, R. M. The encoding of spatial location by posterior parietal neurons. *Science Wash. DC* 230: 456–458, 1995.

ANDERSEN, R. A. AND MOUNTCASTLE, V. B. The influence of the angle of gaze upon the excitability of the light-sensitive neurons of the posterior parietal cortex. *J. Neurosci.* 3: 532–548, 1983.

ANDERSEN, R. A., SNYDER, L. H., LI, C.-S., AND STRICANNE, B. Coordinate transformations in the representation of spatial information. *Curr. Opin. Neurobiol.* 3: 171–176, 1993.

BARBAS, H. AND PANDYA, D. N. Architecture and frontal cortical connections of the premotor cortex (area 6) in the rhesus monkey. *J. Comp. Neurol.* 256: 211–228, 1987.

BOUSSAOUD, D., BARTH, T. M., AND WISE, S. P. Effects of gaze on apparent visual responses of frontal cortex neurons. *Exp. Brain Res.* 93: 423–434, 1993.

BROTCHIE, P. R., ANDERSEN, R. A., SNYDER, L. H., AND GOODMAN, S. J. Head position signals used by parietal neurons to encode locations of visual stimuli. *Nature Lond.* 375: 232–235, 1995.

BRUCE, C. J. Integration of sensory and motor signals in primate frontal eye fields. In: *From Signal to Sense: Local and Global Order in Perceptual Maps*, edited by G. M. Edelman, W. E. Gall, and W. M. Cowan. New York: Wiley-Liss, 1990, p. 261–314.

CAMINITI, R., JOHNSON, P. B., AND URBANO, A. Making arm movements within different parts of space: dynamic aspects in the primate motor cortex. *J. Neurosci.* 10: 2039–2058, 1990.

CAVADA, C. AND GOLDMAN-RAKIC, P. S. Posterior parietal cortex in rhesus monkey. I. Parcellation of areas based on distinctive limbic and sensory corticocortical connections. *J. Comp. Neurol.* 287: 393–421, 1989a.

CAVADA, C. AND GOLDMAN-RAKIC, P. S. Posterior parietal cortex in rhesus monkey. II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. *J. Comp. Neurol.* 287: 422–445, 1989b.

CAVADA, C. AND GOLDMAN-RAKIC, P. S. Topographic segregation of corticostriatal projections from posterior parietal subdivisions in the macaque monkey. *Neuroscience* 42: 683–696, 1991.

COLBY, C. L., DUHAMEL, J.-R., AND GOLDBERG, M. E. Ventral intraparietal area of the macaque: anatomic location and visual response properties. *J. Neurophysiol.* 69: 902–914, 1993.

CRUTCHER, M. D. AND DELONG, M. R. Single cell studies of the primate putamen. I. Functional organization. *Exp. Brain Res.* 53: 233–243, 1984a.

CRUTCHER, M. D. AND DELONG, M. R. Single cell studies of the primate putamen. II. Relations to direction of movement and pattern of muscular activity. *Exp. Brain Res.* 53: 244–258, 1984b.

DESIMONE, R. AND GROSS, C. G. Visual areas in the temporal cortex of the macaque. *Brain Res.* 178: 363–380, 1979.

DONG, W. K., CHUDLER, E. H., SUGIYAMA, K., ROBERTS, V. J., AND HAYASHI, T. Somatosensory, multisensory, and task-related neurons in cortical area 7b (PF) of unanesthetized monkeys. *J. Neurophysiol.* 72: 542–564, 1994.

DUHAMEL, J. R., COLBY, C. L., AND GOLDBERG, M. E. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science Wash. DC* 255: 90–92, 1992.

DUM, R. P. AND STRICK, P. L. The origin of corticospinal projections from the premotor areas in the frontal lobe. *J. Neurosci.* 11: 667–689, 1991.

EPSTEIN, W. AND ROGERS, S. *Perception of Space and Motion.* San Diego, CA: Academic, 1995.

FOGASSI, L., GALLESE, V., DI PELLEGRINO, G., FADIGA, L., GENTILUCCI, M., LUPPINO, M., PEDOTTI, A., AND RIZZOLATTI, G. Space coding by premotor cortex. *Exp. Brain Res.* 89: 686–690, 1992.

FOGASSI, L., GALLESE, V., FADIGA, L., LUPPINO, G., MATELLI, M., AND RIZZOLATTI, G. Coding of peripersonal space in inferior premotor cortex (area F4). *J. Neurophysiol.* 76: 141–157, 1996.

GALLETTI, C. AND BATTAGLINI, P. P. Gaze-dependent visual neurons in area V3A of monkey prestriate cortex. *J. Neurosci.* 9: 1112–1115, 1989.

GALLETTI, C., BATTAGLINI, P. P., AND FATTORI, P. Parietal neurons encoding spatial locations in craniotopic coordinates. *Exp. Brain Res.* 96: 221–229, 1993.

GENTILUCCI, M., FOGASSI, L., LUPPINO, G., MATELLI, M., CAMARDA, R., AND RIZZOLATTI, G. Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements. *Exp. Brain Res.* 71: 475–490, 1988.

GENTILUCCI, M., SCANDOLARA, C., PIGAREV, I. N., AND RIZZOLATTI, G. Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position. *Exp. Brain Res.* 50: 464–468, 1983.

GODSCHALK, M., LEMON, R. N., KUYPERS, H.G.J.M., AND RONDAY, H. K. Cortical afferents and efferents of monkey postarcuate area: an anatomical and electrophysiological study. *Exp. Brain Res.* 56: 410–424, 1984.

GRAZIANO, M.S.A., GROSS, C. G., AND FERNANDEZ, T. A comparison of bimodal, visual-tactile neurons in parietal area 7b and ventral premotor cortex of the monkey brain. *Neurosci. Abs.* 22: 398, 1996.

GRAZIANO, M.S.A. AND GROSS, C. G. Coding of extrapersonal visual space in body-part centered coordinates. *Soc. Neurosci. Abstr.* 18: 593, 1992.

GRAZIANO, M.S.A. AND GROSS, C. G. A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Exp. Brain Res.* 97: 96–109, 1993.

GRAZIANO, M.S.A. AND GROSS, C. G. Mapping space with neurons. *Curr. Dir. Psychol. Sci.* 3: 164–167, 1994.

GRAZIANO, M.S.A. AND GROSS, C. G. The representation of extrapersonal space: a possible role for bimodal, visual-tactile neurons. In: *The Cognitive Neurosciences*, edited by M. S. Gazzaniga. Cambridge, MA: MIT Press, 1995, p. 1021–1034.

GRAZIANO, M.S.A., YAP, G. S., AND GROSS, C. G. Coding of visual space by premotor neurons. *Science Wash. DC* 266: 1054–1057, 1994.

GROH, J. M. AND SPARKS, D. L. Saccades to somatosensory targets. III. Eye-position-dependent somatosensory activity in primate superior colliculus. *J. Neurophysiol.* 75: 439–453, 1996.

GROSS, C. G. AND GRAZIANO, M.S.A. Multiple representations of space in the brain. *Neuroscientist* 1: 43–50, 1995.

HE, S., DUM, R. P., AND STRICK, P. L. Topographic organization of corticospinal projections from the frontal lobe: motor areas on the lateral surface of the hemisphere. *J. Neurosci.* 13: 952–980, 1993.

HEPP-REYMOND, M.-C., HUSLER, E. J., MAIER, M. A., AND QI, H.-X. Force related neuronal activity in two regions of the primate ventral premotor cortex. *Can. J. Physiol. Pharmacol.* 72: 571–579, 1994.

HORN, G. AND HILL, R. M. Modifications of receptive fields of cells in the visual cortex occurring spontaneously and associated with body tilt. *Nature Lond.* 221: 186–188, 1969.

HYVARINEN, J. Regional distribution of functions in parietal association area 7 of the monkey. *Brain Res.* 206: 287–303, 1981.

HYVARINEN, J. AND PORANEN, A. Function of the parietal associative area 7 as revealed from cellular discharges in alert monkeys. *Brain* 97: 673–692, 1974.

JONES, E. G. AND POWELL, T.P.S. An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. *Brain* 93: 739–820, 1970.

KALASKA, J. F. AND CRAMMOND, D. J. Cerebral cortical mechanisms of reaching movements. *Science Wash. DC* 255: 1517–1523, 1992.

KUNZLE, H. An autoradiographic analysis of the efferent connections from premotor and adjacent prefrontal regions (areas 6 and 8) in *Macaca fascicularis. Brain Behav. Evol.* 15: 185–236, 1978.

KURATA, K. Distribution of neurons with set- and movement-related activity before hand and foot movements in the premotor cortex of rhesus monkeys. *Exp. Brain Res.* 77: 245–256, 1989.

KURATA, K., OKANO, K., AND TANJI, J. Distribution of neurons related to a hindlimb as opposed to a forelimb movement in the monkey premotor cortex. *Exp. Brain Res.* 60: 188–191, 1985.

LAL, R. AND FRIEDLANDER, M. J. Gating of the retinal transmission by afferent eye position and movement signals. *Science Wash. DC* 243: 93–96, 1989.

LEICHNETZ, G. R. Afferent and efferent connections of the dorsolateral precentral gyrus (area 4, hand/arm region) in the macaque monkey, with comparison to area 8. *J. Comp. Neurol.* 254: 460–492, 1986.

LEINONEN, L., HYVARINEN, J., NYMAN, G., AND LINNANKOSKI, I. I. Functional properties of neurons in the lateral part of associative area 7 in awake monkeys. *Exp. Brain Res.* 34: 299–320, 1979.

LEINONEN, L. AND NYMAN, G., II. Functional properties of cells in anterolateral part of area 7 associative face area of awake monkeys. *Exp. Brain Res.* 34: 321–333, 1979.

LILES, S. L. Activity of neurons in putamen during active and passive movement of wrist. *J. Neurophysiol.* 53: 217–236, 1985.

LINTON, M., GALLO, P. S., AND LOGAN, C. A. *The Practical Statistician.* Monterey, CA: Brooks/Cole, 1975.

MACKAY, W. A. Properties of reach-related neuronal activity in cortical area 7a. *J. Neurophysiol.* 67: 1335–1345, 1992.

MATELLI, M., CAMARDA, R., GLICKSTEIN, M., AND RIZZOLATTI, G. Afferent and efferent projections of the inferior area 6 in the macaque monkey. *J. Comp. Neurol.* 255: 281–298, 1986.

MATSUMURA, M. AND KUBOTA, K. Cortical projection to hand-arm motor area from post-arcuate area in macaque monkeys: a histological study of retrograde transport of horseradish peroxidase. *Neurosci. Lett.* 11: 241–246, 1979.

MAZZONI, P., BRACEWELL, R. M., BARASH, S., AND ANDERSEN, R. A. Spatially tuned auditory responses in area LIP of macaques performing delayed memory saccades to acoustic targets. *J. Neurophysiol.* 75: 1233–1241, 1996.

MESULAM, M.-M., VAN HOESEN, G. W., PANDYA, D. N., AND GESCHWIND, N. Limbic and sensory connection of the inferior parietal lobule (area PG) in the rhesus monkey: a study with a new method for horseradish peroxidase histochemistry. *Brain Res.* 136: 393–414, 1977.

MILLAR, S. *Understanding and Representing Space: Theory and Evidence from Studies with Blind and Sighted Children.* Oxford, UK: Clarendon, 1994.

MOORE, T., RODMAN, H. R., REPP, A. B., AND GROSS, C. G. Localization of visual stimuli after striate cortex damage in monkeys: parallels with human blindsight. *Proc. Natl. Acad. Sci. USA* 92: 8215–8218, 1995.

MUAKKASSA, K. F. AND STRICK, P. L. Frontal lobe inputs to primate motor cortex: evidence for four somatotopically organized ''premotor'' areas. *Brain Res.* 177: 176–182, 1979.

PAILLARD, J. Motor and representational framing of space. In: *Brain and Space*, edited by J. Paillard. New York: Oxford Univ. Press, 1991, p. 163–184.

PARTHASARATHY, H. B., SCHALL, J. D., AND GRAYBIEL, A. M. Distributed but convergent ordering of corticostriatal projections: analysis of the frontal eye field and the supplementary eye field in the macaque monkey. *J. Neurosci.* 12: 4468–4488, 1992.

PIGAREV, I. N. AND RODIONOVA, E. I. Neurons with visual receptive fields independent of eye position in the caudal part of the ventral bank of cat cruciate sulcus. *Neurophysiology Kiev* 18: 800–804, 1986.

POUGET, A., FISHER, S. A., AND SEJNOWSKI, T. J. Egocentric spatial representation in early vision. *J. Cognit. Neurosci.* 5: 150–161, 1993.

RIZZOLATTI, G., CAMARDA, R., FOGASSI, L., GENTILUCCI, M., LUPPINO, G., AND MATELLI, M. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp. Brain Res.* 71: 491–507, 1988.

RIZZOLATTI, G., MATELLI, M., AND PAVESI, G. Deficits in attention and movement following the removal of postarcuate (area 6) and prearcuate (area 8) cortex in macaque monkeys. *Brain* 106: 655–673, 1983.

RIZZOLATTI, G., SCANDOLARA, C., MATELLI, M., AND GENTILUCCI, M. Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. *Behav. Brain Res.* 2: 147–163, 1981.

ROBINSON, C. J. AND BURTON, H. Organization of somatosensory receptive fields in cortical areas 7b, retroinsula, postauditory and granular insula of *M. fascicularis. J. Comp. Neurol.* 192: 69–92, 1980a.

ROBINSON, C. J. AND BURTON, H. Somatic submodality distribution within the second somatosensory (SII), 7b, retroinsular, postauditory, and granular insular cortical areas of *M. fascicularis. J. Comp. Neurol.* 192: 93–108, 1980b.

RODMAN, H. R. Methods for repeated recording in visual cortex of anesthetized and awake behaving infant monkeys. *J. Neurosci. Methods* 38: 209–222, 1991.

ROSENTHAL, R. AND ROSNOW, R. *Contrast Analysis: Focussed Comparisons in the Analysis of Variance.* New York: Cambridge Univ. Press, 1985.

SALINAS, E. AND ABBOTT, L. F. Transfer of coded information from sensory to motor networks. *J. Neurosci.* 15: 6461–6474, 1995.

SCHLAG, J., SCHLAG-REY, M., PECK, C. K., AND JOSEPH, J. P. Visual responses of thalamic neurons depending on the direction of gaze and the position of targets in space. *Exp. Brain Res.* 40: 170–184, 1980.

SOECHTING, J. F. AND FLANDERS, M. Sensorimotor representations for pointing to targets in three-dimensional space. *J. Neurophysiol.* 62: 582–594, 1989.

SPARKS, D. L. The neural encoding of the location of targets for saccadic eye movements. In: *Brain and Space*, edited by J. Paillard. New York: Oxford Univ. Press, 1991, p. 3–19.

TIPPER, S. P., LORTIE, C., AND BAYLIS, G. C. Selective reaching: evidence for action-centered attention. *J. Exp. Psychol. Hum. Percept. Perform.* 18: 891–905, 1992.

TROTTER, Y., CELEBRINI, S., STRICANNE, B., THORPE, S., AND IMBERT, M. Modulation of neural stereoscopic processing in primate area V1 by the viewing distance. *Science Wash. DC* 1257: 1279–1281, 1992.

WANNIER, M. J., MAIER, M. A., AND HEPP-REYMOND, M.-C. Responses of motor cortex neurons to visual stimulation in the alert monkey. *Neurosci. Lett.* 98: 63–68, 1989.

WEBER, J. T. AND YIN, T.C.T. Subcortical projections of the inferior parietal cortex (area 7) in the stump-tailed monkey. *J. Comp. Neurol.* 224: 206–230, 1984.

WEINRICH, M., WISE, S. P., AND MAURITZ, K. H. A neurophysiological study of the premotor cortex in the rhesus monkey. *Brain* 107: 385–414, 1984.

WEIRSMA, C.A.G. Integration in the visual pathway of crustecea. *Symp. Soc. Exp. Biol.* 20: 151–177, 1966.

WISE, S. P. The primate premotor cortex: past, present, and preparatory. *Annu. Rev. Neurosci.* 8: 1–19, 1985.