

RESEARCH ARTICLE

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Visual responses with and without fixation: neurons in premotor cortex encode spatial locations independently of eye position

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Abstract The ventral premotor cortex (PMv) of the macaque monkey contains neurons that respond both to visual and to tactile stimuli. For almost all of these “bimodal” cells, the visual receptive field is anchored to the tactile receptive field on the head or the arms, and remains stationary when the eyes fixate different locations. This study compared the responses of bimodal PMv neurons to a visual stimulus when the monkey was required to fixate a spot of light and when no fixation was required. Even when the monkey was not fixating and the eyes were moving, the visual receptive fields remained in the same location, near the associated tactile receptive field. For many of the neurons, the response to the visual stimulus was significantly larger when the monkey was not performing the fixation task. In control tests, the presence or absence of the fixation spot itself had little or no effect on the response to the visual stimulus. These results show that even when the monkey’s eye position is continuously changing, the neurons in PMv have visual receptive fields that are stable and fixed to the relevant body part. The reduction in response during fixation may reflect a shift of attention from the visual stimulus to the demands of the fixation task.

Key words Attention · Fixation · Visual system · Motor system · Premotor cortex · Space coding

Introduction

Most neurons in the ventral premotor cortex (PMv) of the macaque monkey respond to tactile stimuli, and over one third also respond to visual stimuli (Rizzolatti et al. 1981; Gentilucci et al. 1988; Fogassi et al. 1996; Graziano et al. 1994, 1997). These bimodal, visual-tactile cells have tactile receptive fields on the face or the arms and corresponding visual receptive fields in the region of space

near the tactile receptive field. For 70% of the bimodal cells with a tactile response on the arm (arm + visual cells), the visual receptive field is anchored to the arm, moving when the arm is moved (Graziano et al. 1994, 1997). For 95% of the bimodal cells with a tactile response on the face (face + visual cells), the visual receptive field is anchored to the head, moving when the head is rotated (Graziano et al. 1997). In contrast, for almost all arm + visual and face + visual neurons (94%), when the eyes fixate different locations, the visual receptive field does not move (Gentilucci et al. 1983, Fogassi et al. 1992, 1996; Graziano et al. 1994). The bimodal neurons in PMv thus encode the locations of nearby visual stimuli with respect to the body, in body-part-centered coordinates, in a fashion that is independent of the position of the eyes.

Most experiments on the visual responses of PMv neurons, however, have been done either in anesthetized monkeys whose eyes are paralyzed, or in awake monkeys trained to fixate. That is, the visual responses have been tested under conditions when the eyes are stationary during stimulus presentation. How might the neurons in PMv respond under the more natural condition when the eyes are not stationary, but instead free to move? Would the neurons maintain clearly defined visual receptive fields anchored to the relevant body part? In this study, we compared the visual responses of bimodal neurons in PMv while the monkey was fixating for a reward and while the monkey was not performing any task and the eyes were free to move. We found that the neurons still maintained their visual receptive fields, and that the location of the visual receptive field near the body remained unchanged, when the eyes were free to move. We also found that, for many of the neurons, the visual response was significantly larger when the monkey was not performing the fixation task. One interpretation is that the fixation task captured the monkey’s attention, shifting it away from the visual stimulus, and that the reduction in the neuronal response reflects the reduction in attention to the stimulus.

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Materials and 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 NIH and USDA guidelines. Responses of single neurons in PMv were studied in two adult male *Macaca fascicularis* (6–7 kg).

Surgery

For each monkey, an initial surgical operation was performed under deep pentobarbital anesthesia and strict aseptic conditions, during which an acrylic skull cap was affixed to the skull with bone screws. A stainless steel recording chamber, 2.5 cm in diameter, was embedded in the acrylic over the frontal lobe for a vertical approach to the ventral premotor cortex. A steel bolt for holding the head was also imbedded in the acrylic. A scleral eye coil (Robinson 1963) was implanted in one eye. Each animal recovered from the effects of the surgery within a few days, but was given 3 additional weeks to allow the skull to grow tightly around the skull screws. (For details of surgical procedures see Graziano et al. 1997.)

In a subsequent procedure, also under deep anesthesia and aseptic conditions, the recording chamber was opened and a hole approximately 2 mm in diameter 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.

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-gauge syringe needle) was lowered through the hole in the skull and into the dura. Then a varnish-coated tungsten microelectrode (Frederick Haer; impedance 0.5–5 M Ω) was advanced from the guide cannula into the brain, in order to record from neurons in the cortex immediately below the dura.

Stimuli

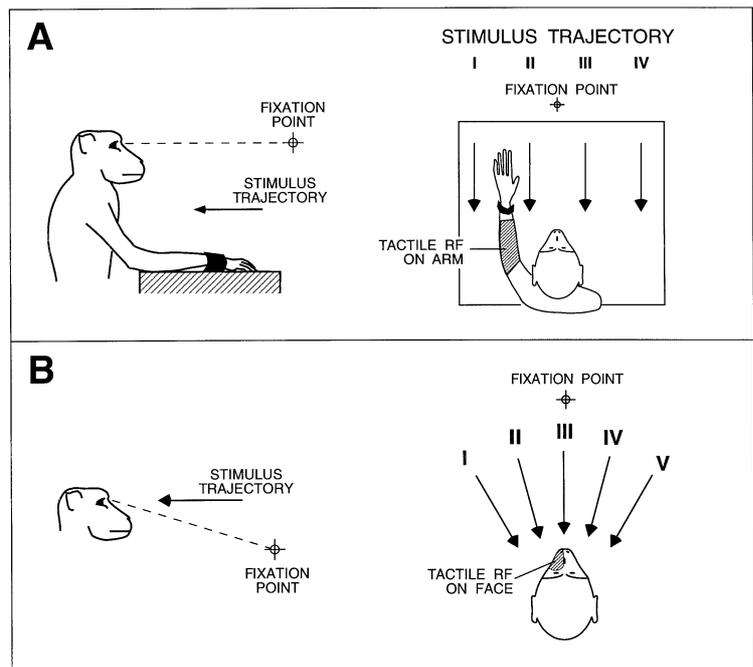
Once a cell was isolated, as indicated by the repeatability of its wave form on the oscilloscope, it was studied by presenting a standard battery of stimuli. Somatosensory responsiveness was studied using manual palpation, manipulation of joints, gentle pressure, and stroking with cotton swabs. Somatosensory 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.

Most bimodal PMv neurons do not respond to stimuli projected onto a tangent screen, even when the screen is placed close to the face, within 20 cm (Graziano et al. 1997). Instead they respond best to objects near the animal. Therefore we used real objects, such as a ping-pong ball mounted on the end of a rod, in order to plot visual receptive fields. To insure that the responses to stimuli close to the body were not caused by inadvertent tactile stimulation, for example 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 by releasing the monkey's arm from the arm holder and enticing him to reach toward pieces of fruit, by inducing him to make threat faces at the experimenters, by holding up objects (such as a bulb syringe sometimes used to blow air on the face) that 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 his 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 0.025 mm). A black drape hung between the robot and the monkey, and a 1 cm diameter rod, on which the stimulus was mounted, protruded through a slit in the drape. Various stimuli were used, such as a white ball 5 cm in diameter, a ping-pong ball, a cotton swab, and a 4 × 4 cm square of white cardboard. In order to present the visual stimulus within the strongest part of the visual receptive field, two different sets of stimulus trajectories were used: one for bimodal neurons with a tactile response on the arm (arm + visual cells), and another for bimodal neurons with a tactile response on the face (face + visual cells). For arm + visual neurons, the stimulus was moved toward the monkey for 10 cm at 14.5 cm/s along one of four trajectories (Fig. 1A). These trajectories were arranged 10 cm below the level

Fig. 1A, B Stimulus positions for testing visual responses of bimodal, visual-tactile neurons. **A** Four stimulus trajectories used for bimodal neurons with a tactile response on the arm. Each trajectory was 10 cm. The stimulus was moved 14.5 cm/s by means of a computer-controlled robot. The fixation point was 28.5 cm in front of the monkey. **B** Five stimulus trajectories used for bimodal neurons with a tactile response on the face. Each trajectory was 10 cm and the fixation point was 28.5 cm in front of the monkey. *RF* Receptive field



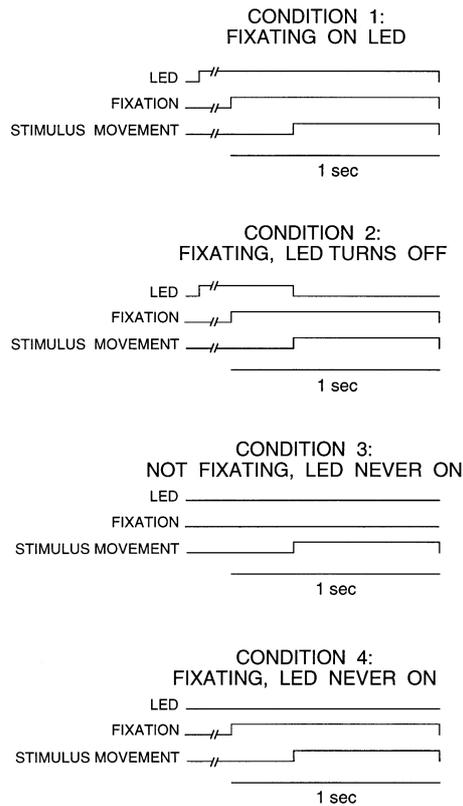


Fig. 2 Four fixation conditions used to test the visual responses of bimodal, visual-tactile cells in ventral premotor cortex (PMv). The conditions were presented in non-interleaved blocks. *Condition 1*: The fixation light-emitting diode (LED) turned on at the start of the trial and the monkey was required to fixate on the LED. Then, 0.3 s after the onset of fixation, the stimulus began to move in the cell's visual receptive field. The monkey was rewarded for fixating throughout the 1-s trial. *Condition 2*: As for condition 1 but the fixation LED was turned off during stimulus movement. The monkey was required to fixate on the unilluminated LED. *Condition 3*: The LED was never illuminated, the monkey never received a reward, and the stimulus was presented regardless of the position of the monkey's eyes. *Condition 4*: As for condition 1, except that the fixation LED was never illuminated. The monkey was trained to fixate on it for 1 s every 10 s

of the fixation lights and 10 cm above the level of the arms. The four trajectories were presented on interleaved trials, usually ten trials per trajectory. During the first 2 s of the 10-s inter-trial interval, the stimulus was moved to its next starting position. For face + visual neurons, the stimulus was moved toward the monkey for 10 cm along one of five trajectories, arranged at eye level (Fig. 1B). For some neurons only one of the above stimulus trajectories was presented, chosen to match the region of strongest visual response.

Behavioral training

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. It 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 mounted on the end of the robot arm were 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, since many neurons in PMv respond during voluntary movement.

The animal's ad libitum daily water intake was measured, and based on this measurement the animal was placed on a water schedule in which he received liquids 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. In order to monitor the position of the eye, a standard eye-coil technique was used, 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; 1 m diameter magnetic coils). The monkey was required to fixate on a light-emitting diode (LED) within a 5° diameter electronic window. However, the monkey's spatial accuracy was much better than the size of the window. During fixation, the standard deviation 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.

We tested bimodal neurons under the four behavioral conditions described below. The experiment proceeded in three stages. We first tested 44 neurons with conditions 1 and 2, in order to determine whether the presence or absence of a lighted fixation point affected the visual responses. These conditions were presented in two non-interleaved blocks and the order of blocks was varied between neurons. We then tested 46 neurons with conditions 2 and 3, in order to determine whether the presence or absence of the requirement to fixate affected the visual responses. Again, the conditions were presented in non-interleaved blocks and the order of blocks was varied between neurons. Finally, we tested 15 neurons with conditions 3 and 4, as a second method of determining whether fixation affected the visual responses. Again, the conditions were presented in non-interleaved blocks and the order was varied between neurons.

Condition 1: fixating on LED

The monkey sat with its head immobilized by the head bolt. In the case of neurons with a tactile receptive field on the arm, the arm was strapped to a holder to prevent it from moving. Eye position was monitored through a scleral search coil as described above. An LED was positioned 28.5 cm in front of the monkey. Each trial began with the LED turning on (Fig. 2, condition 1). The animal was required to fixate the LED within a 5° spatial window. As described above, the actual performance was within 1° – much better than the required 5°. There was no time constraint for the onset of fixation: the LED remained on until the animal fixated. The animal was then required to maintain fixation for 1 s in order to be rewarded. At the end of the trial, the LED was turned off, a valve released approximately 0.2 cm³ of juice into the animal's mouth, and the 10-s inter-trial interval (ITI) began. If the animal broke fixation during the trial, the LED was turned off, no reward was given, and the ITI began.

The visual stimulus mounted on the end of the robot arm (described above) began to move 0.3 s after the onset of fixation and continued toward the monkey for 10 cm.

Condition 2: fixating, LED turns off

This task was the same as condition 1 (Fixating on LED), except that the LED was extinguished 0.3 s after the onset of fixation, at the beginning of the movement of the stimulus, and remained unlit for the remainder of the trial (Fig. 2, condition 2). The animal was required to maintain fixation on the same location until the end of the trial. Because the LED itself was visible, though unlit, the animal was able to perform the task easily.

Condition 3: not fixating, LED never on

The LED, though constantly visibly, was never illuminated, a reward was never given, and the stimulus was presented every 10 s regardless of the position of the animal's eyes (Fig. 2, condition 3). In some cases the juice tube was pulled away from the mouth, in order to inform the monkey that the block of trials involved no reward and required no fixation. In other cases, the monkey determined within the first few trials that the reward had been turned off, and therefore stopped fixating. The results were the same in both cases. During this condition, eye movement records showed that the monkey made apparently random fixations, unassociated with the timing of events in the trial and with no tendency to cluster in any one location. The monkey appeared to ignore both the LED and the robotic stimulus, in that he did not fixate on them any more than on any other point.

Condition 4: fixating, LED never on

The LED, though constantly visible, was never illuminated. The animal was trained to fixate for 1 s every 10 s on this target. The reward followed a standard fixed interval schedule, with an interval of 10 s. That is, there was a 10-s ITI during which fixation on the target had no effect. After the ITI a "ready" period commenced. During the ready period the animal's eye position was monitored, and as soon as the eye entered a window of 5° around the LED, the ready period was terminated and the trial commenced. During the trial, the animal was required to maintain fixation for 1 s to receive a reward. The stimulus began to move during the trial 0.3 s after the onset of fixation and continued toward the monkey for 10 cm. However, if the monkey broke fixation at any time during the trial, the trial was aborted and the ITI commenced (Fig. 2, condition 4).

Because the fixation target was never illuminated in this task, there was no visual signal to tell the monkey when to begin fixating. Eye position traces indicated that the animals did not fixate on the target during the beginning of the ITI; toward the end of the ITI, within the last few seconds, the animals would begin to fixate intermittently; finally the ITI would end, the ready period would begin, and at the next fixation attempt the trial would commence. Once the robot began to move, 0.3 s after the onset of fixation, the animal seemed to realize that the fixation had "taken effect" and thus would maintain fixation until the reward 1 s later. That is, the animal's behavior followed the "scalloped" profile typical of fixed interval reward schedules (Ferster and Skinner 1957). The monkeys learned this task readily and performed with near 100% accuracy, that is, with less than 1% of the trials aborted due to a break in fixation.

Histology

At the completion of the experiment, monkey 1 was given an overdose of sodium pentobarbital (100 mg/kg) and perfused transcardially with saline and then 10% formalin. The head was put in a stereotaxic apparatus, the skull opened and the brain exposed. The positions of the arcuate and central sulci were measured stereotaxically. The 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).

The brain was fixed in 10% formalin and sectioned in the coronal plane on a freezing microtome. Sections were cut at 50 µm 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.

At the time of writing, monkey 2 is still in experimental use and therefore we do not have histological details for that case. Instead, the implant and all associated metal parts were drilled off the head and magnetic resonance imaging (MRI) of the frontal lobe was performed in both coronal and sagittal planes. (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. Since vitamin E is visible on the MRI scan, we were able to use these reference points to estimate the stereotaxic location of the arcuate sul-

cus. Some of the skull holes through which we had recorded were also visible on the MRI scan, thus confirming that our recording site was in PMv, just posterior to the lower limb of the arcuate sulcus.

Results*Effect of the presence or absence of the fixation light*

Our main objective was to compare the visual responses of bimodal, visual-tactile neurons when the monkey was required to fixate throughout the trial and when the monkey was not required to fixate. Therefore, as a control, we first tested whether the fixation light itself might affect the responses. Forty-four bimodal neurons were tested with condition 1 (Fixating on LED) and condition 2 (Fixating, LED Turns Off). As described in Materials and methods, in both conditions the LED was turned on at the start of the trial and the animal was required to fixate on it throughout the trial. However, in condition 1 the LED remained on throughout the trial, while in condition 2 the LED was turned off during the presentation of the stimulus.

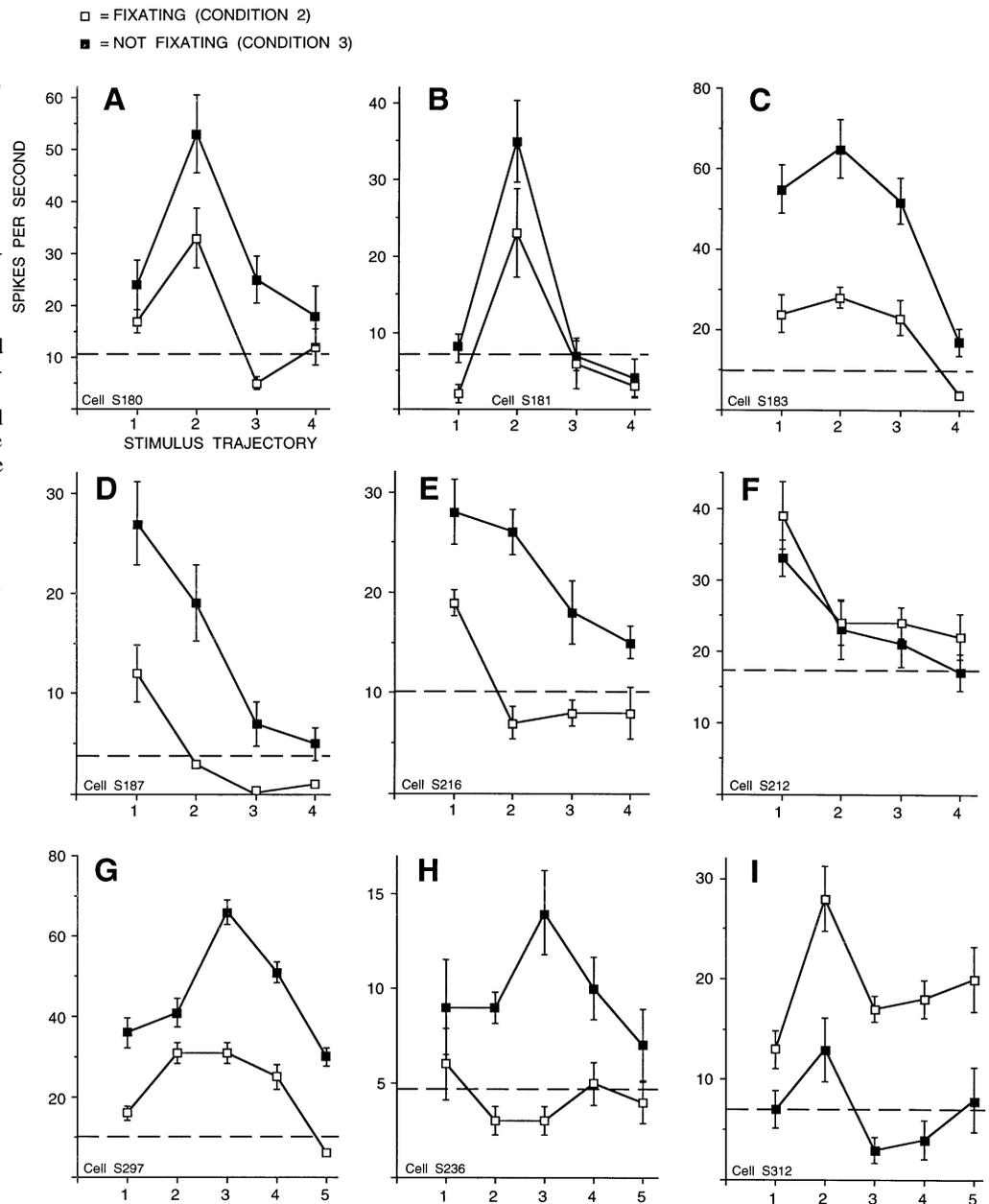
For most neurons, only one stimulus trajectory was tested. This trajectory was chosen to pass through the center of the visual receptive field. For neurons tested with multiple stimulus trajectories, we analyzed the results for the trajectory that gave the strongest visual response. Using these data, we found that for almost all cells (42/44), there was no significant difference in the visual response between condition 1 and condition 2 (*t*-test on mean spikes per second in stimulus period, $P > 0.05$, α adjusted for 44 independent tests; see Linton et al. 1975). Of the remaining two cells, one responded significantly better in condition 1, and the other responded significantly better in condition 2. Thus the presence or absence of the fixation light had no consistent effect on the magnitude of the visual response.

In order to characterize the entire sample of neurons we used the following procedure. For each neuron we first calculated the average spikes per second during the stimulus period for condition 1 and condition 2. We then calculated the percentage change between condition 1 and condition 2 using the formula: $100 \times (\text{Response in condition 2} - \text{Response in condition 1}) / (\text{Response in condition 1})$. The mean percentage change for all 44 neurons was 9, and was not significantly different from zero as determined by *t*-test (SEM = 8, $t = 1.09$, $P = 0.28$). That is, the presence or absence of the fixation light did not affect the population response.

Effect of the requirement to fixate

We tested the visual responses of 46 bimodal neurons while the monkey was performing a fixation task (condition 2) and while the monkey was not performing any task (condition 3). The results for nine example neurons are shown in Fig. 3. Some of these example neurons had

Fig. 3A–I Responses of nine cells tested during condition 2 (Fixating, LED Turns Off) and condition 3 (Not Fixating, LED Never On). Each *point* is based on ten trials. *Error bars* show the standard error of the mean. *Dotted horizontal line* shows mean baseline firing rate. **A–F** Data from arm + visual cells, tested with four stimulus trajectories. **G–I** Data from face + visual cells, tested with five stimulus trajectories. The location of the visual receptive field was the same whether the monkey performed the fixation task or not. In most cases, the visual response was stronger when the monkey was not performing the fixation task. In **H**, the neuron did not respond significantly above baseline during fixation but exhibited a visual receptive field when the monkey was not fixating. In **I** the neuron responded significantly better when the monkey was fixating



a tactile receptive field on the arm and were tested with four stimulus trajectories near the arm (Fig. 3A–F), while others had a tactile receptive field on the face and were tested with five stimulus trajectories near the face (Fig. 3G–I). For the neuron whose responses are shown in Fig. 3A, the visual response was best at trajectory 2. The location of this peak in the visual receptive field was the same whether the monkey performed the fixation task (open squares) or was free to move his eyes throughout the trial (filled squares). The only systematic difference between the two conditions is that the visual response was stronger when the monkey was not performing the task. Thus the spatial tuning of this neuron was not affected by the position or movement of the animal's eyes. The neuron encoded the same region of

space near the body in both conditions. In particular, the visual receptive field did not become less well defined or less consistent in any way as a result of removing the requirement to fixate; indeed, quite the opposite, the strength of the visual signal increased when the monkey was not required to fixate.

The examples shown in Fig. 3B–E are similar. In all cases, the visual receptive field remained at the same location, but the magnitude of the visual response increased significantly, when the monkey was not required to fixate. The neuron whose responses are shown in Fig. 3F, however, responded equally well whether the animal was performing the fixation task or not.

The data shown in Fig. 3G–I are from face + visual neurons, tested with five stimulus trajectories. The exam-

ple shown in Fig. 3G is similar to the example shown in Fig. 3A, in that the visual receptive field remained in approximately the same location but the magnitude of the visual response increased when the monkey was not required to fixate. The example shown in Fig. 3H was unusual in that the neuron did not respond significantly above baseline (dotted line) when the monkey was performing the fixation task, but exhibited a significant visual response and a clear visual receptive field when the monkey was not required to fixate. We found two neurons that behaved in this fashion. For these neurons, the performance of the fixation task appears to have completely inhibited the visual response. Finally, the example shown in Fig. 3I is unusual in that the visual response was significantly stronger when the monkey was required to fixate.

For each of the 46 neurons, we analyzed the results for the stimulus trajectory that gave the strongest visual response. Fourteen cells responded significantly better to the visual stimulus when the monkey was not fixating; three cells responded better when the monkey was fixating; and 29 cells showed no significant difference (significance determined by *t*-test on mean spikes per second in stimulus period, $P < 0.05$, α adjusted for 46 independent tests). Thus the fixation task reduced the responses of 30% of the neurons and enhanced the responses of 7%.

To characterize the entire sample of neurons we used the following procedure. For each neuron, we calculated the average spikes per second during the stimulus period for condition 2 and condition 3. We then calculated the percentage change between the two conditions using the formula: $100 \times (\text{Response in condition 3} - \text{Response in condition 2}) / (\text{Response in condition 2})$. The mean percentage change for all 46 neurons was 100, and was highly significantly above zero as determined by *t*-test (SEM = 28, $t = 3.54$, $P = 0.0009$). Thus the population response of the neurons was greater when the monkey was not fixating.

Effect of the requirement to fixate: a second test

We also performed an independent experiment on a smaller sample of neurons ($n = 15$) using a variant of the experimental procedures described above. In this experiment, two conditions were used: condition 3 (Not Fixating, LED Never On) and condition 4 (Fixating, LED Never On) (Fig. 2). These two conditions were identical except in their reward contingencies. In one case, the animal was rewarded for fixating on the target for 1 s every 10 s; in the other case, no reward was given. Unlike in the experiments described above, the fixation target was never illuminated and thus there was no signal to distinguish the two conditions. Eye position traces showed that in condition 4, the animal fixated within 1° of the target during the trial. In condition 3, the animal fixated on the target only for the first one or two trials of the block. After receiving no reward, the animal

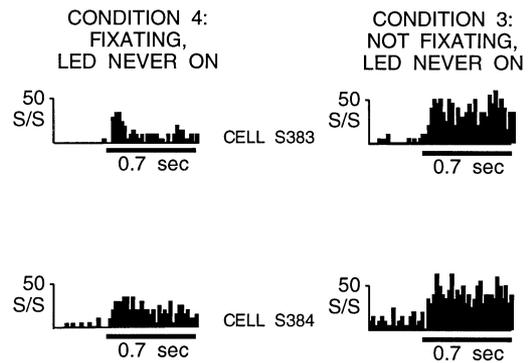


Fig. 4 Responses of two cells tested during condition 4 (Fixating, LED Never On) and condition 3 (Not Fixating, LED Never On). Both cells responded significantly better when the monkey was not fixating (*t*-test, $P < 0.05$). The horizontal bar indicates the 0.7-s period of stimulus movement. All histograms are based on ten trials

stopped performing the task for the remainder of the block (see Materials and methods for details).

Of the 15 neurons tested, seven responded significantly better to the visual stimulus during condition 3, when the monkey was not performing the fixation task. One neuron responded significantly better during condition 4, when the monkey was performing the task. The remaining seven cells showed no significant difference (significance determined by *t*-test on mean spikes per second in stimulus period, $P < 0.05$, α adjusted for 15 independent tests). Thus the requirement to fixate reduced the responses of 47% of the neurons and enhanced the responses of 7%.

Figure 4 shows histograms of neuronal activity for two example cells tested with and without fixation. In both cases, the response was significantly greater when the animal was not required to fixate.

For each neuron, we calculated the percentage change in response between conditions 3 and 4 using the formula: $100 \times (\text{Response in condition 3} - \text{Response in condition 4}) / (\text{Response in condition 4})$. The mean percentage change for all 15 neurons was 47, and was significantly above zero as determined by *t*-test (SEM = 17, $t = 2.78$, $P = 0.015$). Thus, again, the population response of the neurons was greater when the monkey was not fixating.

Discussion

In the present study, we tested bimodal, visual-tactile neurons in PMv under several different fixation conditions. Under some conditions, the monkey was required to fixate during the presentation of the visual stimulus. Under other conditions, the monkey was not required to fixate, and the stimulus was presented while the monkey was not performing any task. We found that the visual receptive fields remained in the same location, near the associated tactile receptive field, whether the monkey was required to fixate or not. In particular, the visual receptive fields did not become any less well defined or any less reliable while the monkey's eyes were free to move. In-

stead, the population of bimodal neurons became more responsive to the visual stimulus. For one experiment, 30% of the neurons became significantly more responsive, and for a second experiment, 47% of the neurons became significantly more responsive. Control tests showed that the presence or absence of an illuminated fixation light in front of the monkey had little or no effect on the neurons. These results show that the neurons in PMv can encode the spatial locations of visual stimuli near the body even when the visual input from the retina is constantly changing as a result of movements of the eye.

Motor attention

As described above, for many neurons the visual responses were reduced while the monkey was performing a fixation task. One interpretation is that the neurons were influenced by the monkey's attention. When the monkey performed the fixation task, his attention was presumably drawn to the LED and to the demands of the task. This capturing of the monkey's attention might have caused the neurons in PMv to respond less to the behaviorally irrelevant robotic stimulus.

Effects of attention have been reported in a number of brain areas, including V1, V2, V4, IT, MT, MST, LIP, the pulvinar, frontal eye fields, and the superior colliculus (Goldberg and Wurtz 1972; Lynch et al. 1977; Bushnell et al. 1981; Goldberg and Bushnell 1981; Richmond et al. 1983; Moran and Desimone 1985; Petersen et al. 1987; Goldberg et al. 1990; Andersen et al. 1990; Spitzer and Richmond 1991; Motter 1993; Schall and Hanes 1993; Steinmetz and Constantinidis 1995; Treue and Maunsell 1995; for review, see Desimone and Duncan 1995). In these brain areas, when the monkey's attention is explicitly drawn to a visual stimulus, such as when the animal is required to respond to that stimulus, the neuronal responses to the stimulus are often enhanced. When the monkey's attention is drawn away from the visual stimulus, to another location, the neuronal responses to the stimulus are often suppressed. Neurons in area 7a often respond better to unattended stimuli, and less well or not at all to stimuli that are positioned close to the locus of attention (Motter and Mountcastle 1981; Steinmetz and Constantinidis 1995; for a similar finding in area V4 see also Moran and Desimone 1985).

The phenomenon of attention can apply not only to sensory processing but also to motor coordination. It is notoriously difficult to perform two motor acts simultaneously, such as patting your head and rubbing your stomach, unless you practice each act until it becomes automatic and pre-attentive. That is, the motor system has a limited attentional capacity. Attention in the motor system has been studied in the superior colliculus and the frontal eye fields, both involved in the control of eye movements (Goldberg and Wurtz 1972; Wurtz and Mohler 1976a,b; Goldberg and Bushnell 1981; Schall and Hanes 1993). Neurons in these two oculomotor areas respond better to

a visual stimulus if the stimulus is to be the target of a saccadic eye movement. This enhancement is weak or absent if the monkey's attention is drawn to the stimulus in some other fashion, for example if the stimulus is to be the target for an arm movement or if the monkey must detect a dimming of the stimulus (Wurtz and Mohler 1976a,b; Goldberg and Bushnell 1981). That is, the neurons are not influenced merely by attention to a sensory stimulus, but by attention during a specific type of motor act. Motor-specific attention has been called "motor intention" (e.g., Boussaoud and Wise 1993). However, the word "intention" implies only that the monkey is planning to make a movement. The word "attention" better captures the concept that there is a limited processing resource, and that by selecting one movement, the monkey reduces its ability to plan another movement (Goldberg and Segraves 1987).

Our results suggest that the neurons in area PMv, thought to be involved in the control of head and arm movements, may also be influenced by the monkey's attention. The properties of these bimodal neurons can explain the results on humans subjects who are performing a reaching task. Tipper et al. (1992) asked subjects to reach toward a red light that was displayed at the same time as a yellow distracter light. Reaction times were longer when the distracter was placed in the region of space roughly between the hand and the target, and shorter when the distracter was placed in other regions of space. When the initial position of the arm was changed, the region of maximal distraction also changed, thereby remaining in the space between the hand and the target. That is, the spatial region to which the subject attended during the reaching task appeared to be anchored to the arm and extended outward from the arm to the target. This attended region is similar to the visual receptive fields of the arm + visual bimodal neurons in monkey PMv, suggesting that an enhancement of the visual responses in PMv may underlie the effect of attention during reaching.

We suggest that the visual responses of the bimodal neurons in PMv are modulated by motor-specific attention. Bimodal neurons with a tactile response on the arm are often active during reaching movements (Gentilucci et al. 1988; M.S.A. Graziano and X.T. Hu, unpublished observations); and bimodal neurons with a tactile response on the face are often active during rotations of the head (Graziano et al. 1997). For arm + visual neurons, we predict that the maximum visual response will be obtained when the visual stimulus is to be the target for an arm movement. For face + visual neurons, we predict that the maximum visual response will be obtained when the stimulus is to be the target for a head movement.

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References

- Andersen RA, Graziano MSA, Snowden R (1990) Translational invariance and attentional modulation of MST cells. *Soc Neurosci Abstr* 16: 7
- Boussaoud D, Wise SP (1993) Primate frontal cortex: neuronal activity following attentional versus intentional cues. *Exp Brain Res* 95: 15–27
- Bushnell MC, Goldberg ME, Robinson DL (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. *J Neurophysiol* 46: 755–772
- Desimone R, Duncan J (1995) Neural Mechanisms of selective visual attention. *Annu Rev Neurosci* 18: 193–222
- Ferster CB, Skinner BF (1957) Schedules of reinforcement. Appleton-Century-Crofts, New York
- Fogassi L, Gallese V, di Pellegrino G, Fadiga L, Gentilucci M, Luppino M, Pedotti A, Rizzolatti G (1992) Space coding by premotor cortex. *Exp Brain Res* 89: 686–690
- Fogassi L, Gallese V, Fadiga L, Luppino G, Matelli M, Rizzolatti G (1996) Coding of peripersonal space in inferior premotor cortex (area F4). *J Neurophysiol* 76: 141–157
- Gentilucci M, Scandolara C, Pigarev IN, Rizzolatti G (1983) Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position. *Exp Brain Res* 50: 464–468
- Gentilucci M, Fogassi L, Luppino G, Matelli M, Camarda R, Rizzolatti G (1988) Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements. *Exp Brain Res* 71: 475–490
- Goldberg ME, Bushnell MC (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *J Neurophysiol* 46: 773–787
- Goldberg ME, Segraves MA (1987) Visuospatial and motor attention in the monkey. *Neuropsychologia* 25: 107–118
- Goldberg ME, Wurtz RH (1972) Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *J Neurophysiol* 35: 560–574
- Goldberg ME, Colby CL, Duhamel J-R (1990) The representation of visuomotor space in the parietal lobe of the monkey. *Cold Spring Harbor Symp Quant Biol* 55: 729–739
- Graziano MSA, Yap GS, Gross CG (1994) Coding of visual space by premotor neurons. *Science* 266: 1054–1057
- Graziano MSA, Hu XT, Gross CG (1997) Visuo-spatial properties of ventral premotor cortex. *J Neurophysiol* 77: 2268–2292
- Linton M, Gallo PS, Logan CA (1975) The practical statistician. Brooks/Cole, Monterey, Calif
- Lynch JC, Mountcastle VB, Talbot WH, Yin TCT (1977) Parietal lobe mechanisms for directed visual attention. *J Neurophysiol* 40: 362–389
- Moore T, Rodman HR, Repp AB, Gross CG (1995) Localization of visual stimuli after striate cortex damage in monkeys: parallels with human blindsight. *Proc Natl Acad Sci USA* 92: 8215–8218
- Moran J, Desimone R (1985) Selective attention gates visual processing in the extrastriate cortex. *Science* 229: 782–784
- Motter BC (1993) Focal attention produces spatially selective processing in the visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J Neurophysiol* 70: 909–919
- Motter BC, Mountcastle VB (1981) The functional properties of the light-sensitive neurons of the posterior parietal cortex studied in waking monkeys: foveal sparing and opponent vector organization. *J Neurosci* 1: 3–26
- Petersen SE, Robinson DL, Morris JD (1987) Contributions of the pulvinar to visual spatial attention. *Neuropsychologia* 25: 97–105
- Richmond BJ, Wurtz RH, Sato T (1983) Visual responses of inferior temporal neurons in awake rhesus monkey. *J Neurophysiol* 50: 1415–1432
- Rizzolatti G, Scandolara C, Matelli M, Gentilucci M (1981) Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses. *Behav Brain Res* 2: 147–163
- Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M (1988) 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
- Robinson (1963) A method of measuring eye movements using a scleral search coil in a magnetic field. *IEEE Trans Biomed Eng* 10: 137–145
- Schall JD, Hanes DP (1993) Neural basis of saccade target selection in frontal eye field during visual search. *Nature* 366: 467–469
- Spitzer H, Richmond BJ (1991) Task difficulty: ignoring, attending to, and discriminating a visual stimulus yield progressively more activity in inferior temporal neurons. *Exp Brain Res* 83: 340–348
- Steinmetz MA, Constantinidis C (1995) Neurophysiological evidence for a role of posterior parietal cortex in redirecting visual attention. *Cereb Cortex* 5: 448–456
- Tipper SP, Lortie C, Baylis GC (1992) Selective reaching: evidence for action-centered attention. *J Exp Psychol Hum Percept Perform* 18: 891–905
- Treue S, Maunsell JHR (1995) Attentional modulation of direction-selective responses in the superior temporal sulcus of the macaque monkey. *Soc Neurosci Abstr* 21: 1756
- Wurtz RH, Mohler CW (1976a) Organization of monkey superior colliculus: enhanced visual response of superficial layer cells. *J Neurophysiol* 39: 745–765
- Wurtz RH, Mohler CW (1976b) Enhancement of visual responses in monkey striate cortex and frontal eye fields. *J Neurophysiol* 39: 766–772