Dynamic Representation of Eye Position in the Parieto-Occipital Sulcus

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Nakamura, K., H. H. Chung, M.S.A. Graziano, and C. G. Gross. Dynamic representation of eye position in the parieto-occipital sulcus. *J. Neurophysiol.* 81: 2374–2385, 1999. Area V6A, on the anterior bank of the parieto-occipital sulcus of the monkey brain, contains neurons sensitive both to visual stimulation and to the position and movement of the eyes. We examined the effects of eye position and eye movement on the activity of V6A neurons in monkeys trained to saccade to and fixate on target locations. Forty-eight percent of the neurons responded during these tasks. The responses were not caused by the visual stimulation of the fixation light because extinguishing the fixation light had no effect. Instead the neurons responded in relation to the position of the eye during fixation. Some neurons preferred a restricted range of eye positions, whereas others had more complex and distributed eye-position fields. None of these eye-related neurons responded before or during saccades. They all responded postsaccadically during fixation on the target location. However, the neurons did not simply encode the static position of the eyes. Instead most (88%) responded best after the eye saccaded into the eye-position field and responded significantly less well when the eye made a saccade that was entirely contained within the eye-position field. Furthermore, for many eye-position cells (45%), the response was greatest immediately after the eye reached the preferred position and was significantly reduced after 500 ms of fixation. Thus these neurons preferentially encoded the initial arrival of the eye into the eye-position field rather than the continued presence or the movement of the eye within the eye-position field. Area V6A therefore contains a representation of the position of the eye in the orbit, but this representation appears to be dynamic, emphasizing the arrival of the eye at a new position.

INTRODUCTION

The position of the eyes in the orbits affects the activity of neurons in a number of cortical areas in the primate brain. For example, in area 7a in the parietal lobe, eye position plays a modulatory role, increasing or decreasing the responses of the neurons to visual stimuli (Andersen and Mountcastle 1983; Andersen et al. 1985). A neuron in area 7a may be highly visually responsive when the eyes are in one position and relatively unresponsive when the eyes are in another position. For other neurons in the same area, the position of the eyes may influence the level of spontaneous activity. Similar effects of eye position were reported in area V3a, the lateral intraparietal area (LIP), the parieto-occipital area (PO), the ventral premotor cortex (PMv), area MT, and area MST (Andersen et al. 1990; Bremmer et al. 1997; Boussaoud et al. 1993; Galletti and Battaglini 1989; Galletti et al. 1993; Graziano et al. 1994b). In the dorsomedial frontal cortex (DMFC), the neurons are influenced by eye position but only when the monkey is performing a fixation task for a reward (Lee and Tehovnik 1995; Tehovnik et al. 1995). When the monkey makes spontaneous eye movements, the neurons no longer fire in association with eye position.

Areas V3a, LIP, 7a, PO, and DMFC are all monosynaptically interconnected, and PMv is connected to the other areas through multisynaptic routes (Cavada and Goldman-Rakic 1989a,b; Colby et al. 1988; Jones and Powell 1970; Kunzle 1978; Matelli et al. 1986; Mesulam et al. 1977). What is the purpose of this network of areas, and why do its neurons encode both visual stimuli and the position of the eyes? As Andersen and colleagues (1985) emphasized, the location of an object with respect to the head can be calculated by combining information about the position of the visual image on the retina with information about the position of the eye. Therefore one possible function of these areas may be to calculate the locations of objects in space. In support of this view, damage to these areas in the monkey brain and to comparable locations in the human brain produces a variety of deficits in processing the spatial locations of stimuli and in guiding movements toward spatial locations (for reviews see Andersen 1987; Gross and Graziano 1995).

Recently, eye position signals were reported in a region on the anterior bank of the parieto-occipital sulcus. This region was originally termed area PO (Covey et al. 1982), but subsequently PO was restricted to a more ventral part of the sulcal bank (Colby et al. 1988). The region just dorsal to the newly defined PO was termed V6A (Galletti et al. 1996). Galletti et al. (1993, 1995, 1996) found that ~65% of neurons in V6A were visually responsive. Of these, 61% were modulated by the position of the eyes, in that the visual responses were stronger when the eyes were in some positions than when the eyes were in other positions. In addition to this modulatory influence of eye position on the visual responses, for ~42% of the neurons the spontaneous activity depended on the position of the eyes.

We further examined the properties of eye-position–dependent neurons in area V6A in two ways. First, we tested whether the neurons were influenced by eye position during spontaneous eye movements in the dark. Second, we tested neurons in both a saccade task and a fixation task to distinguish activity related to eye position per se from activity related to the direction of the saccadic eye movement. In the course of these experiments, we also found that many neurons either in a subregion of V6A or in an area immediately adjacent to V6A were influenced by the movement and position of the arm. Galletti et al. (1997) also described neurons in the parieto-occipital sulcus related to the movement of the arm but did not report any spatial segregation between the eye- and the arm-related neurons.

A preliminary account of these experiments was published previously (Nakamura et al. 1996).

METHODS

Single neuron activity was recorded from four hemispheres of three male *Macaca fascicularis* (4–6 kg). All husbandry, surgical, and behavioral procedures were approved by the Princeton University Institutional Animal Care and Use Committee and were in accordance with the NIH Guidelines for Care and Use of Laboratory Animals (1985).

Initial surgery

For each monkey, an initial surgical operation was performed under ketamine 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 in diameter, was embedded in the acrylic over the parietal lobe for a vertical approach to the parieto-occipital sulcus. The approximate location of the sulcus for each monkey was determined from magnetic resonance images (MRI) (for details of MRI methods see Moore et al. 1995). A steel bolt for holding the head was also imbedded in the acrylic. Each animal recovered from the effects of the surgery within several days but was given 3 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 ~5 mm in diameter was drilled through the layer of acrylic and the bone, exposing the dura.

Recording procedures

During the daily recording sessions, the monkey sat in a primate chair with its head held in place by the head bolt and with a hydraulic microdrive (Narishige, type MO-95) mounted on 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 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 anterior bank of the parieto-occipital sulcus.

Once a cell was isolated, as indicated by the repeatability of its wave form on the oscilloscope, it was tested for any response related to the position or movement of the eyes. This was done first by turning off the room lamp and monitoring the neuron while the monkey made spontaneous eye movements in the dark. Eye position was measured with an infrared eye-tracking system (ISCAN Pupil Tracking System, model RK-416, resolution ~0.5°). The neuron was then tested while the monkey performed a fixation task and a saccade task (see *Fixation task* and *Saccade task*). Some of the cells were also tested for any response related to the position or movement of the arms (see *Reach task*). Finally, some cells were tested for visual and somatosensory responsiveness (see *Visual and somatosensory stimuli*).

Fixation task

The fixation task was performed in darkness. Figure 1*A* illustrates the events in the task. Each trial began with a warning tone (0.2 s), and then a fixation spot 0.5° in diameter was presented on a multiscan monitor (Liyama Electric, model MF-5221A) placed 28 cm in front of the monkey. For its reward, the monkey was required to fixate the spot within a 4 × 4° electronic window (ISCAN Pupil Tracking System) and maintain fixation until the end of the trial. Two of the three monkeys were trained on a fixation duration of 1.5 s. The third monkey was trained on a fixation duration of 1.2 s but partway through the experiment was promoted to a 1.5-s duration. At the end
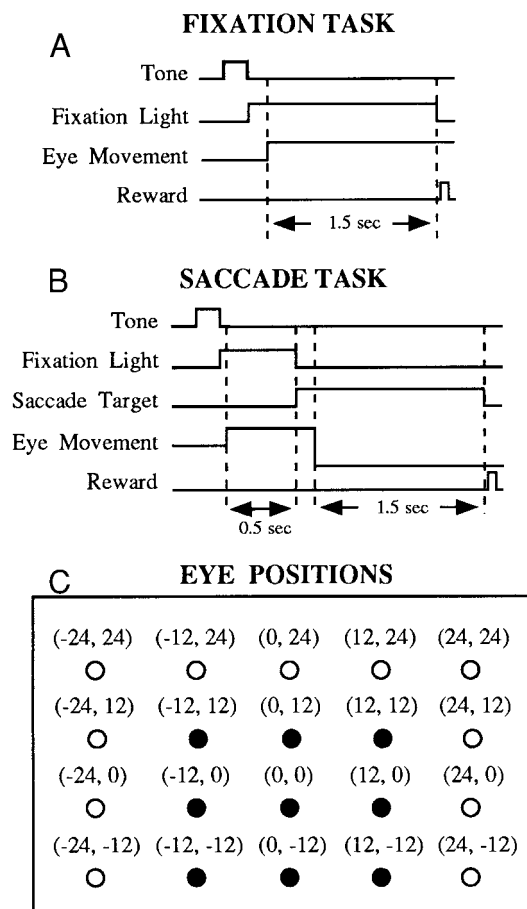

FIG. 1. Paradigms used to test eye-related neurons. *A*: fixation task. Each trial began with a warning tone (0.2 s) followed by the onset of the fixation light. After the monkey achieved fixation (indicated by the Eye Movement line), the trial continued for 1.5 s, and then the fixation light was extinguished and a reward was given. The trial was aborted if fixation was broken. *B*: saccade task. Similar to the fixation task, except that the monkey was required to fixate on the fixation light for only 0.5 s, at which time the fixation light was extinguished and the saccade target appeared. The monkey was then required to fixate the saccade target within 1 s and to remain fixated for 1.5 s to receive a reward. *C*: 20 possible positions for the fixation light and the saccade target. Positions are indicated in *x* and *y*° from the straight ahead. ●: central fixation position and 8 saccade targets tested in the saccade task. For some cells the saccade task was also run at other screen locations.

of the trial, the fixation spot was turned off, a valve released ~0.2 ml of juice into the animal's mouth, and the intertrial interval (ITI) began. The ITI was 1.5–2.5 s. If the animal broke fixation at any time during the trial, the fixation spot was turned off, no reward was given, and the ITI began. Two of the monkeys were trained to press a lever after the warning tone, at the start of the trial, with the contralateral hand, and to maintain pressing until the end of the trial. If the monkey released the lever during the trial, the trial was aborted without a reward, and the ITI began. The purpose of the lever press was to keep the contralateral hand stationary because we found that some neurons were sensitive to the monkey's arm position and arm movement. In this way we could isolate the effects of eye position and eye movement on neuronal activity.

The fixation spot was presented at 1 of 20 possible positions. These positions were arranged in a 4 × 5 grid and were 12° apart from each other (see Fig. 1*C*). However, not all 20 positions were tested for every neuron. Usually 18 fixation positions were tested, but some neurons were tested with 9 or 12 fixation positions.

Statistical analysis for fixation task

For each neuron, we analyzed the firing rate (spikes/s) from the period beginning when the monkey's eye first entered the fixation window and ending 1,500 ms later, at the end of the required fixation period. To determine if this firing rate was significantly different for different fixation positions, a one-way Kruskal-Wallis test was performed. For example, the neuron illustrated in Fig. 3 was tested at 18 eye positions, with 10 trials at each eye position. A Kruskal-Wallis test on the 18 groups showed that the firing rate varied significantly with eye position ($n = 180$, df $= 17$, $H = 6,181$, $P < 0.0001$).

All neurons that showed a significant dependence on eye position with the Kruskal-Wallis test were then tested as follows. The fixation position at which the neuron gave the highest mean spikes/s was selected. The 1.5-s fixation period was then divided into two analysis periods, the first 0.5 s and the subsequent 1.0 s. The data from these two periods were compared with the Wilcoxson nonparametric test for correlated subjects. If the firing rate in the first period was significantly greater than the firing rate in the second period, the cell was considered to have a response that was strongest immediately after the onset of fixation and then decayed over the period of fixation. If the firing rate in the first period was not significantly different from the firing rate in the second period, the neuron was considered to have a response that was sustained throughout the fixation period. None of the neurons responded significantly more in the second period.

Saccade task

In the fixation task described in the previous section, the monkey's eye position and saccadic eye movements before the onset of fixation varied from trial to trial. The saccade task was designed to control these variables. Figure 1*B* illustrates the events in the saccade task, which was performed in darkness. Each trial began with a warning tone (0.2 s). Then a fixation spot 0.5° in diameter was presented on the monitor. The monkey was required to fixate the spot within a $5 \times 5°$ electronic window and maintain fixation for 0.5 s. Then the fixation spot disappeared, and simultaneously another spot, the saccade target, appeared. The monkey was required to saccade to the target within 1,000 ms and then to maintain fixation on the target for another 1.5 s. At the end of the trial the target spot disappeared, a valve released ~0.2 ml of juice into the animal's mouth, and the 1.5- to 2.5-s ITI began. If the monkey broke fixation during the trial or failed to saccade to the target within the required time, the trial was aborted without a reward, and the ITI began. Two of the monkeys were trained to press a lever after the warning tone, at the start of the trial, with the contralateral hand, and to maintain pressing until the end of the trial. If the monkey released the lever during the trial, the trial was aborted without a reward, and the ITI began.

The saccade target could be presented at one of nine possible positions (Fig. 1*C*, ●). These positions were arranged in a 3×3 grid with 12° separation between each position. The central position for the saccade target was the same as the position of the fixation point. Therefore, on trials when the target appeared at the center, the monkey was not actually required to saccade anywhere but instead to maintain fixation at the same position for the entire trial. Most cells were tested with all nine saccade target positions, but some cells were tested with fewer positions. For each neuron, each position was tested with ≥10 trials.

In separate blocks of trials, the starting fixation position and the entire set of saccade target positions were shifted to a different location, and the neuron was tested again. In this fashion we could study the effect of eye position on the saccadic activity of the neurons.

Statistical analysis for saccade task

All analyses were performed on the firing rate in the period after the saccade, beginning when the monkey's eye first entered the saccade target window and ending 1.5 s later, at the end of the required fixation period. The reason for using this time period is that for all responsive neurons the response began postsaccadically, after the onset of fixation (see RESULTS). For each neuron, the following statistical tests were performed.

1) Was the activity of the neuron during fixation dependent on the direction of the saccade that preceded fixation? Each fixation position could be approached by many different directions of saccade. We selected the fixation position that gave the largest mean response for that neuron (but some exceptions are described subsequently) and sorted the data into different groups corresponding to the different directions of saccade that were used to approach that fixation position. We then performed a one-way Kruskal-Wallis test to determine if there was any significant difference between these groups. A significant difference would indicate that the firing rate of the neuron during fixation at that position depended significantly on the direction of the saccade that preceded the fixation.

In many cases the neuron preferred a fixation position at the edge of the test grid, which could only be approached by a limited range of saccade directions. In these cases, we selected a fixation position closer to the center of the test grid to test for saccadic dependence. Some neurons did not respond at all near the center of the test grid, and these neurons could not be tested for saccadic dependence.

2) Was the activity of the neuron during fixation dependent on the position of the fixation point? For this test we selected the saccade direction that gave the maximal overall response. We then sorted the data into groups corresponding to the different fixation positions reached by that direction of saccade. We performed a one-way Kruskal-Wallis test on these groups to determine if there was any significant difference between them. For example, Fig. 9 shows the responses of a neuron that preferred downward saccades. Six different fixations positions were approached by a downward saccade (Fig. 9, *A–F, bottom positions*). We performed a one-way Kruskal-Wallis test on these six conditions and found that the response was significantly different in the different conditions ($H = 15.71$, $P = 0.0004$), that is, the response depended significantly on the position of the fixation point.

Some neurons responded equally well to all directions of saccade, and in these cases the data for all saccade directions were combined for this test.

3) Many neurons showed a significant effect of both saccade direction and eye position, as determined by test 1 and 2. Therefore an index was calculated to quantify whether the neuron was more "saccade related" or "eye-position related." We first selected a fixation position near the center of the test grid that gave the largest mean response for that neuron and sorted the data into different groups corresponding to the different directions of saccade that were used to approach that fixation position. We then calculated the variance between these groups, *VS*. A neuron that responds differently to different saccade directions should have a large value of *VS*, and a neuron that is unselective for saccadic direction should have a small value of *VS*. In a similar fashion, we selected the saccade direction that gave the maximal response and sorted the data into groups corresponding to the different fixation positions reached by that direction of saccade. We then calculated the variance between these groups, *VP*. A neuron that responds differently to different fixation positions should have a large value of *VP*, and a neuron that is unselective for fixation position should have a small value of *VP*. Finally, we calculated the index, $I = (VP - VS)/(VP + VS)$. For an eye-position cell, that is, a cell that responds in relation to the fixation position and has no dependence on the direction of the saccade, *VS* will be small compared with *VP*, and $I \sim 1$. For a saccade-related cell with no dependence on eye position, *VP* will be small compared with *VS*, and $I \sim -1$. For a cell that is equally influenced by eye position and saccadic direction, $VP \sim VS$ and $I \sim 0$.

4) Many neurons showed a clear border between preferred eye positions and nonpreferred eye positions. A nonpreferred eye position

was defined as a position at which the neuron gave less than one-half of its response at the most preferred eye position. We tested whether the neuronal response was greater when the eye saccaded from a nonpreferred to a preferred eye position than when the eye saccaded between two positions that were already both within the preferred range. All the data recorded when the eye saccaded from a nonpreferred to a preferred position were grouped and compared with all the data recorded when the eye saccaded from a preferred position to another preferred position. A Mann-Whitney U test was then performed on these two groups to determine if they were significantly different.

Reach task

Many of the neurons in the PO sulcus seemed to respond during movements of the arm. Therefore each monkey was trained as follows. The experimenter held a jeweler's screwdriver in front of the monkey, and the monkey was required to reach out and touch the screwdriver. The experimenter then rewarded the monkey by pressing a button that opened the juice valve and released juice into the monkey's mouth. By using this simple method, any direction or magnitude of reach could be studied. Most of the reach-related neurons were studies in this fashion.

In addition, one monkey was trained to touch illuminated circles on a touch-sensitive screen placed 28 cm away. For this task, the monkey first pressed a lever that was centered and at waist level just in front of its body while also fixating a central fixation spot on the screen within a $4 \times 4°$ fixation window. After 500 ms, the fixation spot disappeared, and a target circle (8 deg in diameter) was presented on the screen. The monkey was required to saccade to the target circle and maintain fixation. Then after a delay of 500 ms the monkey was required to release the lever, reach out with the same hand, and touch the target circle. The task was performed in darkness so that movement of the arm was not visible. This paradigm was used to study only four reaching-related neurons but is described here because it allowed us to collect quantitative data confirming the existence of the reach-related response and showing that it was independent of the sight of the arm, the position or movement of the eyes, and the onset of the target stimulus (see Fig. 13).

Visual and somatosensory stimuli

Visual receptive fields were tested with bars, spots, squares, and complex colored images such as a picture of a monkey's face, back-projected onto a $160 \times 160°$ tangent screen 28 cm in front of the monkey. During stimulus presentation, the monkey performed the same fixation task described previously (fixation task) except that the fixation spot in this case was a light-emitting diode (LED) 1 cm in diameter, taped to the projection screen.

Somatosensory responsiveness was studied with manual palpation, manipulation of joints, gentle pressure, and stroking with cotton swabs.

Behavioral training

Training on all tasks was done with a liquid reward. First the animal's ad lib 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 (cranberry juice) during the experimental session, as a supplement immediately after each session, and free water for 2 consecutive days each week. Two of three animals were first trained to press a lever with the contralateral hand and hold it for 1.5 s. For the third animal, this step was omitted. All three animals were trained to fixate a central fixation spot for 0.5 s. Next they were trained to fixate any of the 20 positions shown in Fig. 1C. They were then trained to saccade to a target

presented just after the offset of the fixation spot. Finally, the fixation time was increased to the full 1.5 s.

Histology

In the last week of recording from each monkey, marking lesions and iron deposits were made by passing a 20-μA current through a stainless steel electrode at two different depths at four to six locations. At the conclusion of recording, the monkey was given an overdose of pentobarbital and perfused transcardially with saline followed by 10% formalin. Ferrocynaide (2%) was mixed with the formalin to color the iron deposits. The brains were serially sectioned at 100 μm in the coronal place and then stained with cresyl violet. Electrode tracks were identified with the lesions as reference points. As shown in Fig. 2A for each monkey, the recording sites were located mainly in the top one-half of the anterior bank of the parieto-occipital sulcus but also extended onto the dorsal and medial surface of the superior parietal lobe. This area corresponds roughly to V6A of Galetti et al. (1996). It may overlap the dorsal border of area PO of Colby et al. (1988). The recording site in monkey AL extended more laterally and anteriorly than in the other two monkeys and did not include the medial surface of the hemisphere. Figure 2B shows representative coronal sections through the right parietal lobe of two of three monkeys. Each section shows a representative track along which electrodes penetrated the cortex and the region along the track in which neurons were recorded (thickened portion of track).
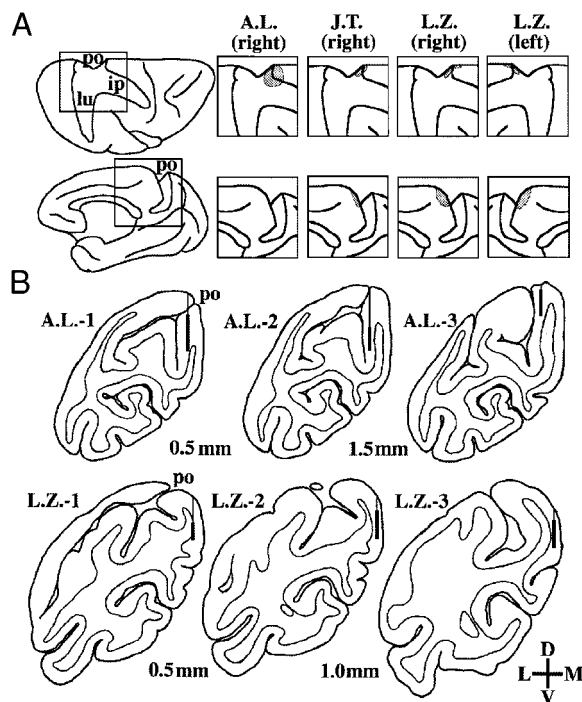

FIG. 2. Recording sites for all 3 monkeys. A: parieto-occipital sulcus (po), intraparietal sulcus (ip), and lunate sulcus (lu) are opened up to show the buried cortex. Both dorsal view (*top row*) and medial view (*bottom row*) are shown. The recording site (shaded) in monkey A. L. was larger and extended more laterally and anteriorly than the recording sites in monkeys J. T. and L.Z.B. Representative coronal sections through the right parieto-occipital sulcus (po) in monkeys A. L. and L. Z. For each monkey, the section shown on the left is the most posterior, and the section shown on the right is the most anterior. The numbers indicate the spacing in millimeters between the sections. Vertical lines: location of representative electrode penetrations. The thickened part of each line indicates the region in which responsive neurons were studied.

TABLE 1. *Categories of neurons*

	Monkey A. L.	Monkey L. Z.	Monkey J. T.	Total
Eye	33 (34.5)	33 (40.5)	4 (40.0)	70 (37.5)
Visual	6 (6.0)	12 (15.0)	0 (0.0)	18 (9.5)
Arm	17 (17.5)	1 (1.0)	0 (0.0)	18 (9.5)
Eye + visual	3 (3.0)	3 (3.5)	0 (0.0)	6 (3.0)
Eye + arm	6 (6.0)	1 (1.0)	0 (0.0)	7 (3.5)
Visual + arm	3 (3.0)	0 (0.0)	0 (0.0)	3 (1.5)
Arm + tactile	1 (1.0)	0 (0.0)	0 (0.0)	1 (0.5)
Undefined	4 (4.0)	6 (7.5)	1 (10.0)	11 (6.0)
Unresponsive	23 (24.0)	25 (31.0)	5 (50.0)	53 (28.5)
Total	96 (100)	81 (100)	10 (100)	187 (100)

Only the 187 neurons tested for all categories are represented here. Eye, neurons that responded in relation to position or movement of the eyes; Visual, visually responsive neurons; Arm, neurons that responded in relation to position or movement of the arm; Tactile, tactually responsive neurons; Undefined, neurons with a response that could not be specified; Unresponsive, neurons that had no detectable response. Values are number of cells, with percentages in parentheses. Percents are rounded to the nearest 0.5.

RESULTS

Response categories

We studied 354 neurons in 4 hemispheres of 3 monkeys. Table 1 shows the proportions of neurons in each response category. Although 354 neurons were tested, not all neurons were tested for every response property. Table 1 shows the results only for the 187 neurons that were tested for all of the properties listed. "Eye" neurons responded only in relation to the position or movement of the eyes; "visual" neurons responded only to visual stimuli; "arm" neurons responded only to the position or movement of the arm. Other neurons responded under more than one of these conditions (e.g., eye + visual, eye + arm). One neuron had a tactile response over most of the body, strongest on the contralateral hand; this neuron also responded in relation to arm movement. For 11 neurons, we failed to determine the effective stimulus. Most of these "undefined" neurons fired as the monkey moved in the chair.

Eye-related neurons

Three hundred ten neurons were tested for the effect of eye position and movement, and 149 (48%) responded. Some of

these neurons, such as the eye + visual neurons, also had other response properties. Figure 3 shows the responses of a typical eye-related neuron, tested during the fixation task. This cell was most active while the monkey was fixating the top right position (position 12, 24). The elevated firing started after the onset of fixation (indicated by the horizontal line) and was sustained throughout the 1.5-s fixation period. In contrast, the neuron showed little or no firing when the monkey was fixating the other 17 positions. This difference in firing rate between the different positions was statistically significant (Kruskal-Wallis test, $H = 6181$, $P < 0.0001$; see METHODS for details).

Figure 4 shows the response profiles for another 20 typical neurons. Some (Fig. 4, *A–D*) fired most when the eyes were within a small range of preferred positions and responded less well or not at all to the surrounding positions. Some (Fig. 4, *E–H*) showed response profiles that increased monotonically from one edge of the test grid to the other. These four examples had discharge rates that increased smoothly as the eyes fixated more toward the top-left (Fig. 4, *E*), right (*F*), bottom (*G*), and top (*H*). The remaining 12 examples showed a variety of complex response profiles. Almost all of them (Fig. 4, *I–R*) fired most when the eyes were at the edge of the range that we tested. In these cases, we could not determine if the cell had a peak in the response profile or if the response continued to increase as the eye position became more eccentric.

Of the 149 eye-related neurons, 83 were tested with at least the central 9 fixation positions. For each neuron we determined which of these nine positions gave the greatest response. Figure 5 shows a frequency histogram of the results. None of the 83 neurons preferred the central eye position. Instead all responded better to eye positions that were deviated from the center of gaze. This tendency was highly statistically significant (χ^2 test, $P < 0.001$).

The results presented so far suggest that the eye-related neurons in V6A encode the position of the eye during steady fixation. However, at least two alternative hypotheses remain to be tested. First, the activity of these neurons might be caused by the visual stimulation of the fixation spot. Second, the activity might represent the timing or direction of the saccadic eye movement that brought the eye to the fixation position. In the following sections we examine these two alternative hypotheses.
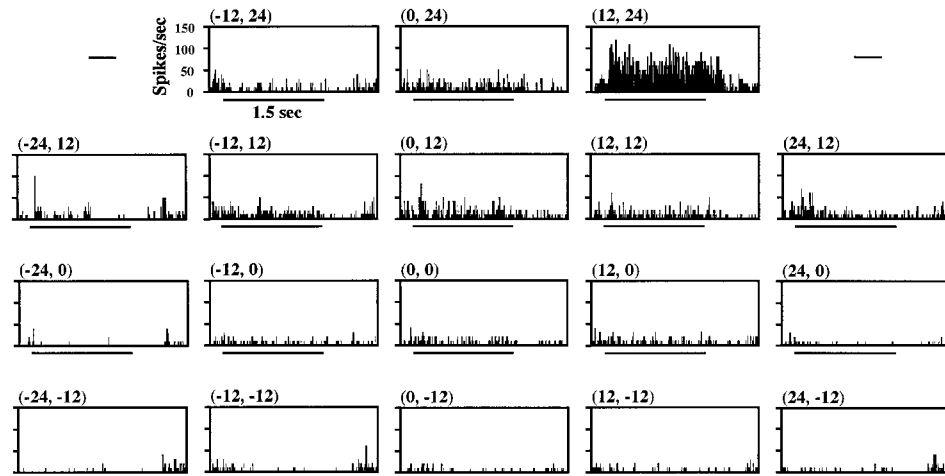

FIG. 3. Responses of an example eye-related neuron while the monkey fixated 18 different locations. The horizontal bar beneath each histogram indicates the period beginning when the eye first entered the fixation window and ending 1.5 s later when the monkey was rewarded.
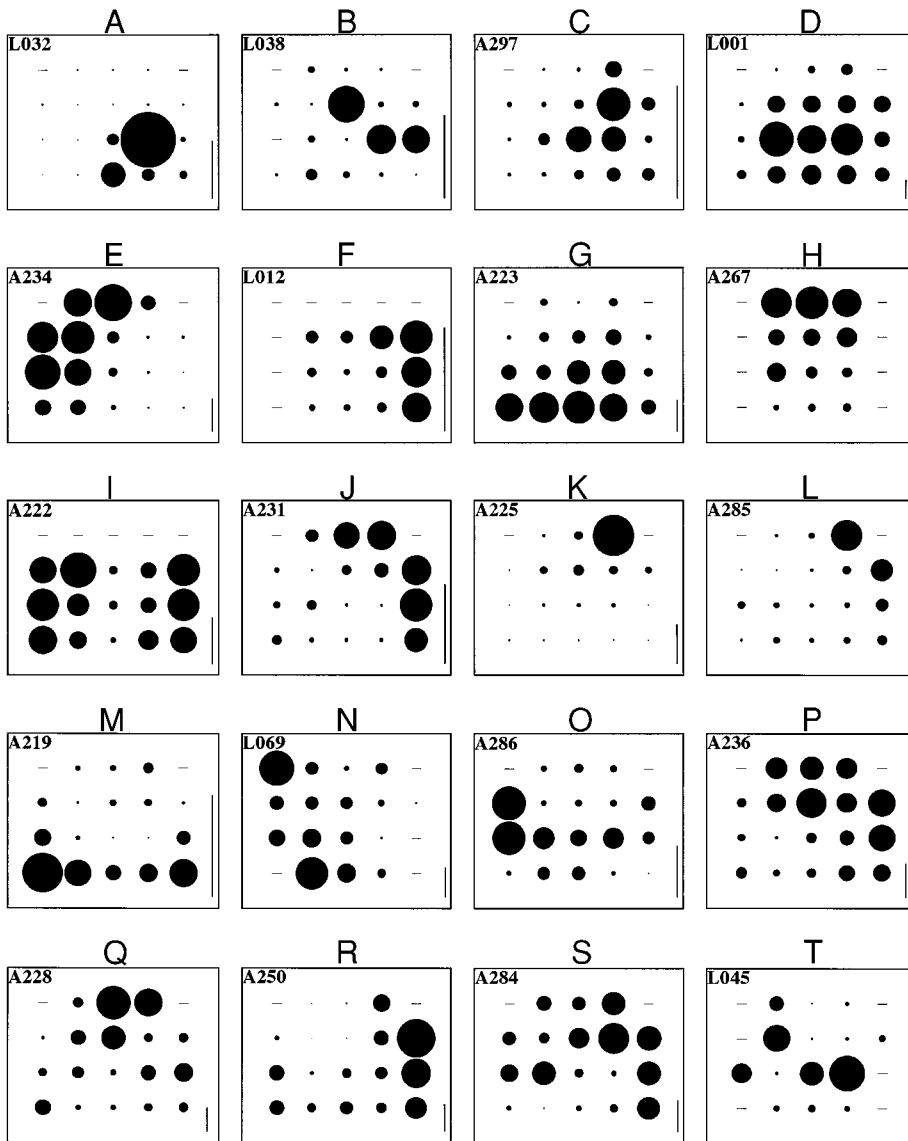
FIG. 4. Responses of 20 eye-related neurons during fixation at different positions. Radius of each solid circle is proportional to the firing rate at that fixation position. Scale bar on bottom right of each box shows 50 spikes/s. Short horizontal lines indicate positions that were not tested. Neurons *A–D* preferred a small range of eye positions and responded less to surrounding positions. Neurons *E–H* had response profiles that increased monotonically from 1 edge of the test grid to the other. Neurons *I–T* responded in a variety of complex patterns, and all but *S* and *T* responded better at the edge of the test grid.

Eye position or visual response?

The eye-related neurons in V6A responded when the monkey fixated on a spot of light. Was this response caused by the visual stimulation of the fixation spot? For example, the cells might have a visual response that is stronger for some eye positions and weaker for others. Such modulation of the visual response by eye position is common in this brain area (Galletti et al. 1993, 1995, 1996). However, two control tests demonstrated that the responses of the eye-related neurons were not dependent on the fixation light. First, the neurons responded in darkness during spontaneous eye movements. For example, consider the neuron that is shown in Fig. 3. This neuron was most active while the monkey fixated the top right position (position 12, 24). Figure 6 shows the result for the same neuron when the monkey sat in the dark and did not perform any task. No fixation light was presented. Each tic mark represents an action potential, and the horizontal lines indicate the time during which the monkey was looking within 5° of the preferred eye position for the cell. The neuron fired at a high rate when the eyes were within this preferred position. Thus neither

the presence of a fixation light nor the performance of a fixation task was necessary to make the cell respond. All of the eye-related neurons responded during spontaneous eye movements in the dark, in a fashion that matched the responses during the parametric tests.

Second, we tested the effect of blinking off the fixation light while the monkey was fixating. Figure 7 shows the result for a cell tested at its preferred eye position. In Figure 7*A*, the fixation light turned on and remained on while the monkey fixated for 1.5 s. The neuron's firing rate increased after the onset of fixation and was sustained throughout the entire fixation period. In Fig. 7*B*, the fixation light turned on, the monkey fixated for 1.5 s, but the light was extinguished for 0.4 s during the period of fixation. The neuron did not show any decrease in firing when the light was extinguished. We compared the data during the 0.4 s that the light was extinguished with the data during the subsequent 0.5 s with the Wilcoxson test for correlated data and found that there was no significant difference in the neuronal activity between these two time periods ($T = 21$, $P = 0.51$).
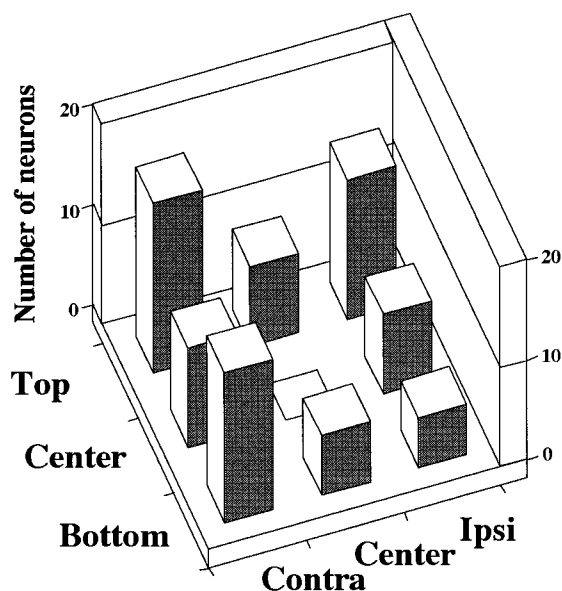
FIG. 5. Frequency histogram for 83 neurons showing the fixation position at which each neuron responded most. Only the central 9 fixation positions are plotted (see Fig. 1, ●). Ipsi, Center, Contra, Top and Bottom indicate fixation positions relative to the monkey's straight ahead. No neurons preferred the central position.

Fifteen eye-related neurons were tested in this fashion, and the firing of all 15 neurons remained constant even while the fixation spot was turned off, as long as the eye was still fixating the preferred position. These results show that the activity of the eye-related neurons was not due to the visual stimulation of the target spot.

Eye position or saccadic vector?

Does the activity of eye-related neurons reflect the position of the eye during fixation, or does it reflect the vector of the saccade that brought the eye to that position?

Figure 8 shows the results for a neuron tested in the saccade task. In Fig. 8A, the monkey fixated the central position (0,0) and then saccaded to one of four surrounding positions, 12° up, down, right, or left. The central histogram (0,0) shows the result when the monkey did not make a saccade but maintained fixation at the initial location. The neuron did not respond under this condition. Instead, the neuron responded best when the monkey saccaded to the top position (0,12) and the right-
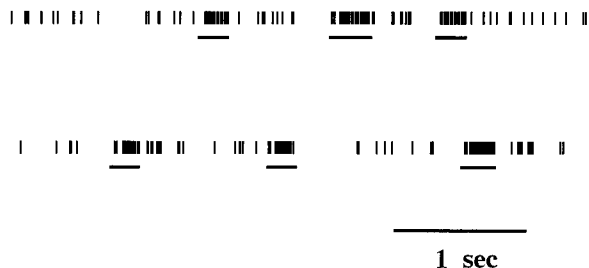

FIG. 6. Responses of an eye-related neuron during spontaneous eye movements in the dark. Each tic mark indicates an action potential. Short horizontal bars indicate when the eye was within 5° of position 12, 24, the preferred eye position for this neuron (see Fig. 3 for responses of this neuron during the fixation task).
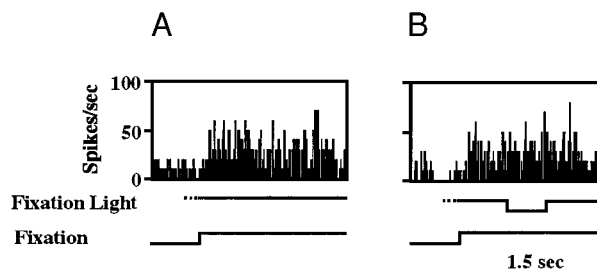

FIG. 7. Responses of an eye-related neuron during fixation at its preferred eye position. Top horizontal bar (Fixation Light) indicates when the fixation light was illuminated. Bottom horizontal bar (Fixation) indicates the time during which the eye was within the fixation window. Fixation light was at position 0, 12. *A*: fixation light was illuminated during the entire period of fixation. *B*: fixation light was extinguished for 0.4 s during fixation. This neuron responded during fixation even while the fixation light was extinguished.

ward position (12,0). The response began after the eye reached the target position. Did this activity reflect the saccadic vector that preceded fixation, that is, was it caused by an upward and a rightward saccade, or was it an eye-position response, caused by the final position of the eye after the saccade was completed? To answer this question we changed the initial fixation position and then retested the cell. In this second test (Fig. 8*B*), the monkey fixated a new starting position (12,12) and then saccaded to one of four surrounding target positions. Under these conditions, the cell responded best when the eye saccaded to the leftward position (0,12) and the downward position (12,0). These are the same two positions that elicited a response previously, that is, the firing of the cell depended on the final position of the eyes, not on the direction of saccade that preceded the fixation. Indeed, each direction of saccade—up, down, right, or left—elicited a response when it terminated at a preferred position; likewise, no direction of saccade gave a response when it terminated at a nonpreferred position. (The dependence on eye position was significant: test 1, $H = 22.64$, $P < 0.0001$. The dependence on saccade direction was not significant: test 2, $H = 1.029$, $P = 0.794$. See METHODS for details. See also next section for more data on and further analysis of this neuron.)

Figure 9 shows the results for a second neuron. In Fig. 9*A*, the monkey fixated an initial position $(-12,12)$ and then saccaded to one of four surrounding positions. This cell responded best after the monkey saccaded downward and leftward. Figure 9, *B–F*, shows the result when the initial fixation position was changed. In every case, the neuron preferred the same direction of saccade, that is, downward and leftward. This neuron therefore responded in relation to saccadic vector. In addition, the magnitude of the response was modulated by the position of the eyes. The response was larger in Fig. 9, *A* and *D*, when the eyes were deviated toward the left side of the screen, and smaller in *C* and *F*, when the eyes were deviated toward the right side of the screen. These data show that both eye position and the direction of saccadic eye movement influenced the activity of this neuron. (Dependence on eye position was significant: test 1, $H = 43.69$, $P < 0.0001$. Dependence on saccade direction was significant: test 2, $H = 15.71$, $P = 0.0004$.)

Forty-six eye-related neurons were tested with multiple starting positions in the saccade task. Of these, 19 responded
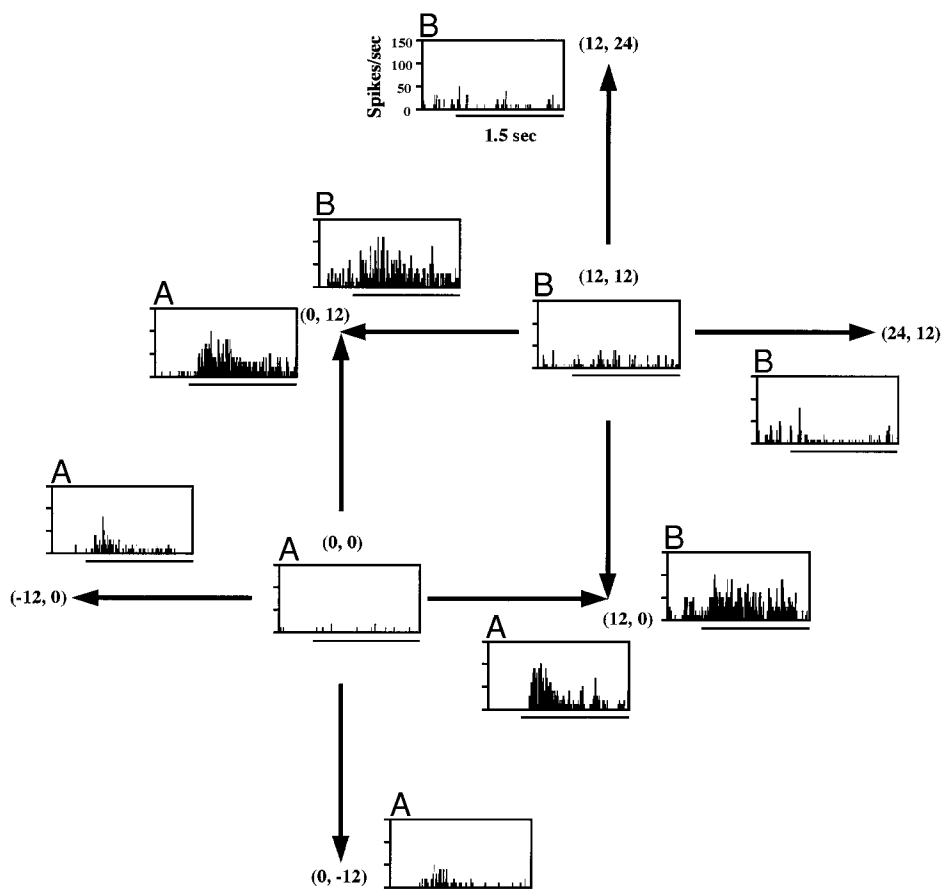
FIG. 8. Responses of an eye-position neuron tested with the saccade task. *A*: 5 histograms showing the results when the monkey began fixation at position 0,0 and then saccaded 12° up, down, right, or left or remained fixated on the central point. The horizontal bar beneath each histogram indicates the time during which the eye was within the fixation window around the final target position. *B*: results when the central fixation point in the saccade task was shifted to position 12,12. This neuron responded when the monkey saccaded to and fixated positions 0,12 and 12,0. It did not respond in relation to the direction of saccade. Each direction of saccade—up, down, right, or left—could either elicit a response or not, depending on the position to which eye saccaded.

only at the extreme edge of the test grid and therefore could not be analyzed for saccadic and eye-position dependence (see METHODS). Of the remaining 27 neurons, all were significantly affected by the position of the eye during fixation. These cells responded significantly better at some fixation positions than at others. Eighteen of these cells (66%) also responded in relation to the direction of saccade that preceded fixation.

For all 46 neurons tested, the response began after the eye entered the final fixation window. None of the cells, not even the 18 cells that were dependent on saccadic vector, responded before or during the saccadic eye movement.

For each neuron we calculated an index to quantify whether the neuron was more dependent on saccade direction or on eye position. An index of +1 indicates that the response of the neuron is dependent solely on fixation position; an index of −1 indicates that the response is dependent solely on saccade direction; and an index of 0 indicates that the response is equally dependent on both (see METHODS). For example, the neuron in Fig. 8 had an index of 0.89, indicating that it was highly dependent on eye position and not on saccade direction. The neuron in Fig. 9 had an index of 0.18, indicating that it was approximately equally dependent on eye position and saccade direction. Figure 10 shows the results for all 27 neurons tested. The distribution is skewed toward 1. The index ranges from −0.33 to +0.96, and only five neurons (19%) had negative indices. The population of neurons is therefore more influenced by eye position than by saccade direction.

Steady-state eye position, or saccades to a preferred eye position?

Figure 11 shows data from the same neuron illustrated in Fig. 8. As described previously, this neuron had an eye position field that encompassed positions 0,12 and 12,0. When the eye saccaded into this region, the neuron responded. The histograms in Fig. 11, however, show that, if the eye was already in the eye position field and then saccaded to a second location also within the eye position field, the neuron responded less well. That is, the neuron was most sensitive to the movement of the eyes into the borders of the eye position field and relatively insensitive to the movement of the eyes within the borders.

In Fig. 11*A*, the monkey fixated three different starting positions and then saccaded to position 12,0, inside the cell's eye position field. The cell responded best when the starting positions were 0,0 or 12,12, outside the eye position field. The response just after the arrival of the eyes almost disappeared when the starting position was already inside the eye position field, at 0,12. In Fig. 11*B*, the monkey fixated five different starting positions and then saccaded to position 0,12, inside the eye position field. Again, the only condition that elicited little or no response was when the starting position for the eye was already inside the eye position field, at 12,0. A Mann-Whitney *U* test showed that the responses when the eye began outside and then entered the eye position field were significantly greater than the responses when the eye began and ended in the
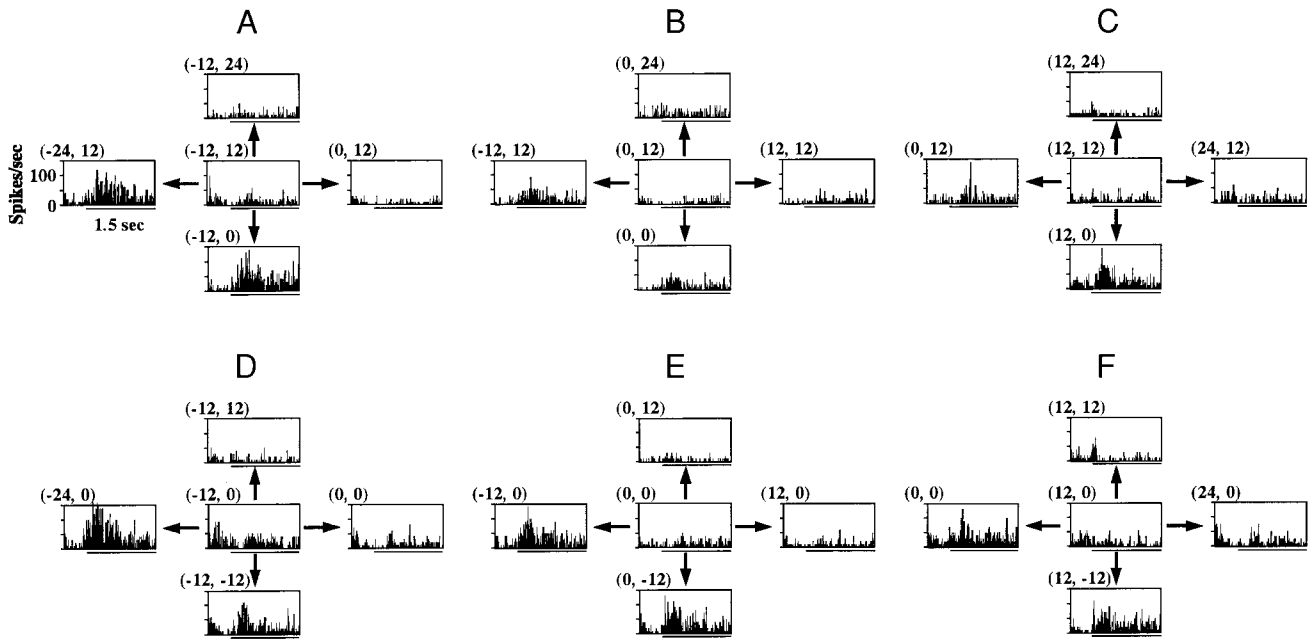
FIG. 9. Responses of a saccade-related neuron tested in the saccade task at 6 different positions. *A*: 5 histograms showing the results when the monkey began fixation at position −12,12, and then saccaded 12° up, down, right, or left or remained fixated on the central point. The horizontal bar beneath each histogram indicates the time during which the eye was within the fixation window around the final target position. *B–F*: results when the saccade task was presented at 5 other positions. This neuron responded best during fixation after downward and leftward saccades. It also responded best when the eyes were in the bottom left part of the test grid.

eye position field ($Z = 6.64$; $P < 1 \times 10^{-7}$; the Z value was used instead of the U value because of the large sample size; $n1 = 20$, $n2 = 60$).

We performed similar tests on 22 neurons with eye position fields. For 18 neurons (82%), the response was significantly larger when the eyes started outside the eye position field and then saccaded to a point inside the eye position field. These results indicate that the eye-related neurons in area V6A preferentially code the arrival of the eyes into the eye-position fields.

A related property is that many of the neurons tested in the fixation task or the saccade task (53/118 cells, 45%) responded best or only within the first 500 ms of fixation. For these cells

the firing rate dropped significantly in the subsequent 1,000 ms of fixation (see METHODS for statistical details). These cells therefore appear to emphasize the initial arrival of the eyes at the preferred position, that is, they preferentially code a change in status rather than a steady state.
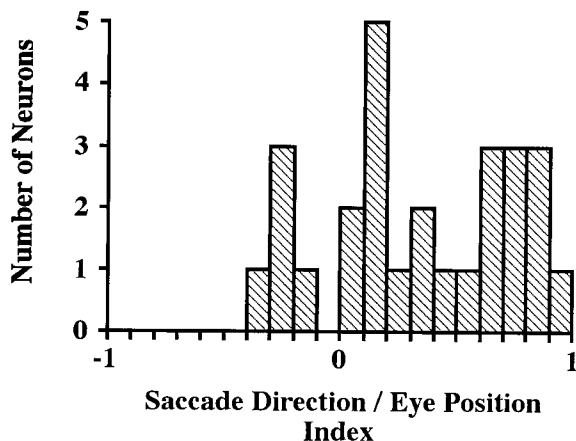

FIG. 11. Responses of an eye-position neuron that responded best at positions 0,12 and 12,0. See Fig. 8 for more data on the same neuron. *A*: responses when the eye saccaded to position 12,0 from 3 different initial positions. The horizontal bar beneath each histogram indicates the period during which the eye was fixating on the final position. *B*: responses when the eye saccaded to position 0,12 from 5 different positions. This neuron responded best after saccades from a nonpreferred position to a preferred position. After saccades that both began and ended on a preferred position (from 0,12 to 12,0 or vice versa) the neuron gave little or no response.

FIG. 10. Frequency histogram showing Saccade Direction vs. Eye Position Index for 27 neurons. An index of +1 indicates a neuron influenced by eye position but not saccade direction. An index of −1 indicates a neuron influenced by saccade direction but not eye position. An index of 0 indicates a neuron equally influenced by both. See METHODS for details of index.
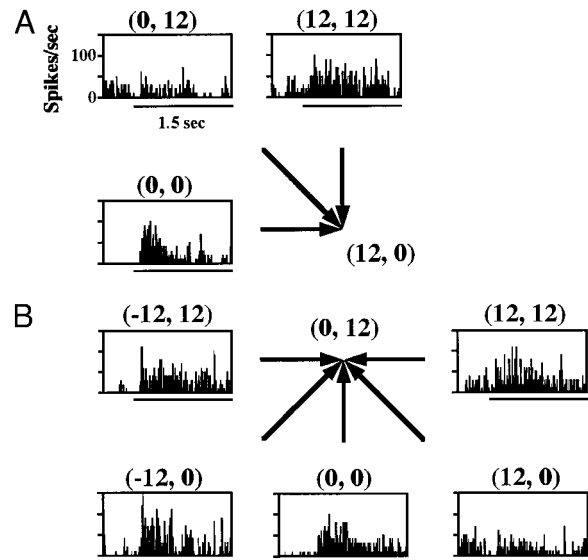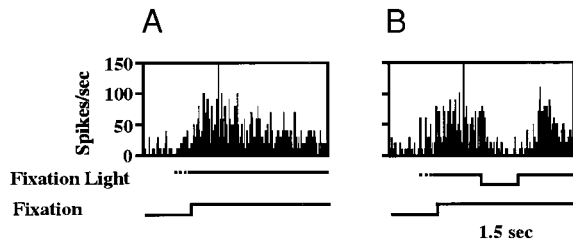
FIG. 12. Responses of a visual neuron during fixation on a fixation light. Top horizontal bar (Fixation Light) indicates when the fixation light was illuminated. Bottom horizontal bar (Fixation) indicates time during which the eye was within the fixation window. *A*: fixation light was illuminated during the entire period of fixation. *B*: fixation light was extinguished for 0.4 s during fixation. This neuron responded during fixation, but only when the fixation light was illuminated.

Visually responsive neurons

Three hundred thirty-four neurons in V6A were tested for visual responsiveness, and 73 (23%) responded. Of these, 56 were exclusively visual, and 17 also had other response properties, such as eye-position or reaching-related responses. One type of visual neuron that we found responded to the fixation spot during the fixation task. Figure 12 shows the responses of one of these cells. This neuron did not respond during spontaneous eye movements in the dark and therefore was not classified as an eye-related neuron. In Fig. 12*A*, the fixation light turned on and remained on while the monkey fixated on it for 1.5 s. The neuron responded during this period of fixation. In Fig. 12*B*, the light was extinguished for 0.4 s during fixation. The neuron stopped responding when the light was turned off. Therefore the cell responded to the visual stimulation caused by the fixation light. This pattern of response is quite different from the pattern for eye-related neurons (see Fig. 7).

Many of the visual neurons also responded to the onset of a room lamp or to moving or stationary bars projected onto a tangent screen. We did not systematically plot visual receptive fields or systematically test if the visual responses were modulated by eye position.

Arm-related neurons

Of 263 neurons tested, 56 (21% of total) responded in association with the movement or position of the contralateral arm. We found these neurons unexpectedly during the first months of the experiment and studied them qualitatively, training the monkey to reach toward a target that was held in the experimenter's hand; therefore we do not know the precise parameters of their responses. However, the relatively high incidence of reaching-related responses suggests that these neurons form an important part of the makeup of this portion of the parietal lobe. The following observations may help to clarify the nature of their responses. Of the 56 reaching-related neurons, 41 were exclusively related to the arm, whereas 15 also had other properties, such as eye-position–related responses. Some reaching-related neurons (20, 36%) responded only during the arm movement itself and stopped responding after the arm reached its final position, whereas other neurons (36, 64%) continued to respond for as long as the monkey maintained its arm in an outstreched position. The preferred direction of arm movement (toward the contralateral or ipsilateral side) was determined for 42 of the arm-related neurons. Most (27, 57%) responded best when the monkey reached toward the contralateral side, but some responded best to ipsilateral reaching (10, 21%), and some responded equally well to either direction of reaching (5, 11%). The reaching-related neurons were also tested when the monkey's eyes were covered or when view of the arm was blocked through some other means such as with a sheet of cardboard. Under these conditions the neurons still responded during the arm movement, indicating that the neurons were not responding to the visual stimulus of the arm in motion.

Figure 13 shows the responses of a typical reaching-related neuron. In this case, the monkey was trained to reach out with the contralateral hand and touch an illuminated circle on a touch-sensitive screen (see METHODS for details). Eye position was controlled, and the reach was performed in darkness. The monkey reached 20° to the left (Fig. 13*A*), toward the midline (*B*), or 20° to the right (*C*). As shown in the figure, this neuron was most active before the leftward (contralateral) reach and least active before the rightward (ipsilateral) reach.

Almost all of the arm neurons (46/50, 92%) were found in monkey A. L. As shown in Fig. 2, the recording site in A. L. extended more laterally and also more anteriorly onto the cortical surface of the superior parietal lobe. Most of the arm neurons were found in this lateral, anterior region. In Fig. 2*B* three representative coronal sections from monkey A. L. are shown. In the most posterior section, 36 neurons were studied, of which only 2 (6%) responded in relation to the arm. In the next example section shown, 0.5 mm more anterior, 21 neurons were studied, of which 13 (62%) responded in relation to the arm. Finally, in the most anterior section, another 1.5 mm anterior, 24 neurons were studied of which 21 (88%) were related to the arm. These results suggest that there may be a separate arm area located anterior to the eye-related neurons in area V6A. However, more extensive mapping studies will be necessary to confirm the existence of an arm area.

DISCUSSION

We found two principal types of neuronal responses in area V6A; 48% of the neurons responded in relation to the movement or position of the eyes, and 23% responded to visual
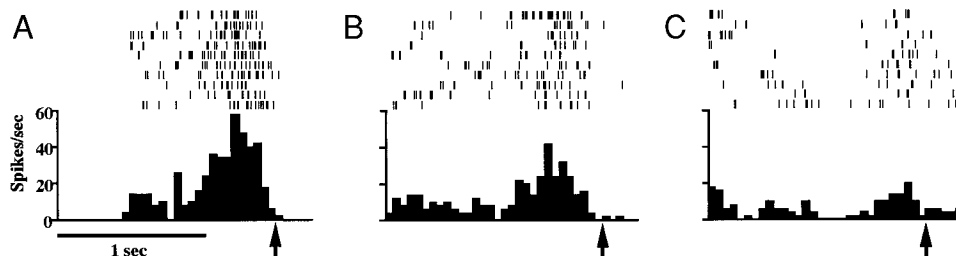

FIG. 13. Responses of an arm-related neuron during reaching 20° to the left (*A*), to the center (*B*), and 20° to the right (*C*). Arrow indicates the time at which the monkey's hand made contact with the target on the touch-sensitive screen. See METHODS for details of the reaching task.

stimuli. Previous studies by Galletti et al. (1993, 1995, 1996) found that 42% of the neurons responded in relation to the position of the eyes, and 65% were visually responsive. In addition, they reported that 61% of the visual neurons were modulated by eye position, in that the visual responses were stronger for some eye positions than for others. Although we encountered the same phenomenon, we did not systematically study it.

We also found neurons that responded in relation to the movement or position of the arm. These arm-related neurons were located mainly in what was either a subregion of V6A or an area adjacent to V6A, more anterior and lateral than the location of most of the eye-related neurons. Galletti et al. (1997) also reported arm-related activity in V6A but did not report any spatial segregation between eye neurons and arm neurons.

A representation of eye position

As described previously, 48% of the V6A neurons in this study were classified as eye related. When tested in a fixation and a saccade task, these cells responded according to the position of the eyes, that is, each cell had a preferred range of eye positions or an eye position field. The responses were not caused by the visual stimulation of the fixation light because when the fixation light was turned off the cells continued to respond. Even when the monkey made spontaneous eye movements in the dark, the firing of these neurons continued to provide an accurate account of the changing position of the eyes. The population of cells in V6A therefore appears to form a representation for eye position.

However, we found that 66% of the eye-position neurons were also influenced significantly by the direction of the saccade that preceded fixation. This sensitivity to the direction of the saccade was surprising because all of the responses were postsaccadic. None of the cells responded before or during saccades.

We suggest that the saccade direction information may contribute to the representation of eye position, that is, it may be used by V6A neurons to help calculate the position to which the eyes just arrived. The next section discusses one way in which saccade information might influence the representation of eye position.

A stronger signal when the eye moves than when the eye is stationary

Many of the eye position neurons (45%) responded best within the first 500 ms after the eye made a saccade to a preferred position. The response then dropped off while the eye remained at that position. These neurons therefore preferentially encoded the arrival of the eye in the eye position field rather than the continued presence of the eye in the eye position field. Furthermore, when the starting and ending point of the saccade were both inside the eye position field, most neurons (82%) responded less well; however, when the saccade began outside and then entered the eye position field, the neurons responded vigorously. Therefore these neurons did not encode the static position of the eyes so much as the dynamic arrival of the eyes at the preferred site. This emphasis on a change in status, rather than on the steady state, may be a fundamental property of sensory processing. For example, in the visual system, neurons are most sensitive to the borders between two luminances or colors rather than to a region of uniform luminance or color (Hubel 1988). In view of the current data, the same emphasis on encoding a change in status appears to apply to the representation of eye position. One possible function of the eye position information in V6A is discussed in the final section.

Where is the "where" pathway?

In 1982, Ungerleider and Mishkin proposed that extrastriate visual cortex is organized in two processing streams, a ventral stream that processes the identity of objects and a dorsal stream that processes the spatial locations of objects. Subsequent work has shown that, in the ventral stream, neuronal responses to shape, color, and texture increase in complexity along a sequence of interconnected areas including V1, V2, V4, and IT (for review see Desimone et al. 1985; Gross et al. 1993). The dorsal stream, however, was more difficult to specify. Neuronal responses to visual motion increase in complexity along a sequence of areas including V1, V2, MT, MST, and STP (for review see Graziano et al. 1994a). However, there is little evidence that these areas are involved in processing spatial location per se. Indeed lesions to MT seem to affect the processing of motion rather than spatial location (Newsome and Pare 1988). Where is the where system, that is, what are the areas that process spatial location, and are they organized in a hierarchical fashion?

Areas that process space must carry more than just visual information. They must also carry information about the position of the eyes and other body parts to reconstruct the location of visual stimuli with respect to the body. Because of its combination of visual and proprioceptive information, parietal area 7a is considered an important processing station for space (Andersen 1987). Recently several other areas, including V3a, PO, and V6A, were found to carry similar spatial information (Galletti et al. 1993, 1995, 1996). Therefore we suggest that these areas may be part of the missing spatial processing stream and that area V6A, with its high proportion of eye-position sensitive neurons, may serve as one source of the eye-position information that is critical for spatial processing in other parietal areas.

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