Selective activation of visual cortex neurons by fixational eye movements: Implications for neural coding

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Abstract

During normal vision, when subjects attempt to fix their gaze on a small stimulus feature, small fixational eye movements persist. We have recorded the impulse activity of single neurons in primary visual cortex (V1) of macaque monkeys while their fixational eye movements moved the receptive-field activating region (AR) over and around a stationary stimulus. Three types of eye movement activation were found. (1) Saccade cells discharged when a fixational saccade moved the AR onto the stimulus, off the stimulus, or across the stimulus. (2) Position/drift cells discharged during the intersaccadic (drift) intervals and were not activated by saccades that swept the AR across the stimulus without remaining on it. To activate these neurons, it was essential that the AR be placed on the stimulus and many of these cells were selective for the sign of contrast. They had smaller ARs than the other cell types. (3) Mixed cells fired bursts of activity immediately following saccades and continued to fire at a lower rate during intersaccadic intervals. The tendency of each neuron to fire transient bursts or sustained trains of impulses following saccades was strongly correlated with the transiency of its response to stationary flashed stimuli. For one monkey, an extraretinal influence accompanying fixational saccades was identified. During natural viewing, the different eye movement classes probably make different contributions to visual processing. Position/drift neurons are well suited for coding spatial details of the visual scene because of their small AR size and their selectivity for sign of contrast and retinal position. However, saccade neurons transmit information that is ambiguous with respect to the spatial details of the retinal image because they are activated whether the AR lands on a stimulus contour, or the AR leaves or crosses the contour and lands in another location. Saccade neurons may be involved in constructing a stable world in spite of incessant retinal image motion, as well as in suppressing potentially confusing input associated with saccades.

Keywords: Fixational eye movements, Neural coding, Macaca, V1, Receptive fields

Introduction

Ever since the initial experiments with stabilized retinal images in the 1950s, it has been generally accepted that retinal image motion is necessary to maintain visibility of visual stimuli (Ditchburn, 1973). When the head is immobilized, and the subject attempts to fixate steadily on an object, the motions that maintain visibility are provided by the fixational eye movements. These involuntary movements consist of slow drifts interspersed with small fixational saccades that impart higher velocities to the image. The slow drifts are thought to maintain visibility in the fovea, but fixational saccades do not appear to be necessary for foveal visibility (Steinman, 1975). In fact, when performing demanding visual tasks,

fixational saccades may be detrimental (Rattle & Foley-Fisher, 1968). Subjects typically reduce their frequency of fixational saccades while performing high-acuity visual tasks (Winterson & Collewijn, 1976; Bridgeman & Palca, 1980), perhaps to improve their performance. These data have led some authors to conclude that fixational saccades are mere "busy work" and contribute nothing to the visual process (Steinman et al., 1973; Kowler & Steinman, 1980).

Other results, however, suggest that fixational saccades may contribute to maintaining stimulus visibility, especially in the parafovea (Clarke & Belcher, 1962; Gerrits & Vendrik, 1974). There is also evidence that fixational saccades may be needed to maintain perception of hue differences, whereas drifts do not seem sufficient (Ditchburn, 1980). Thus, fixational saccades and drifts may make complementary contributions to visual functions.

In addition to their effects on visibility, fixational eye movements must be considered in another context—namely, how do we

perceive the world as stable, in spite of the incessant motions of the retinal image (Jung, 1972)? It is likely that the stabilization process utilizes computations by neurons that are responsive to the retinal image motions imparted by fixational eye movements (Murakami & Cavanagh, 1998).

Recent physiological investigations of the effects of fixational eye movements have focussed on their effects on the firing patterns of cortical neurons. We have shown that fixational eye movements contribute to the variability of cortical responses because they move receptive fields of cortical neurons over the visual scene in unpredictable ways (Gur et al., 1997; Gur & Snodderly, 1997). Fixational saccades, in particular, can suppress activity or elicit bursts of high-frequency firing (Livingstone et al., 1996; Bair & O'Keefe, 1998; Martinez-Conde et al., 2000) that alter the temporal statistics of the spike train and must be accommodated in neural coding schemes. Furthermore, Leopold and Logothetis (1998) recently reported that fixational saccades have different effects in different cortical areas. In V1, fixational saccades have mainly inhibitory effects, but in the extrastriate areas V2 and V4, they have strong excitatory effects. However, most of these physiological studies have not attempted to distinguish the influence of image motion from the influence of retinal position and how these two factors interact with the visual response properties of the cells.

In this paper, we show that responses of V1 neurons to fixational eye movements are more specific and more diverse than previously appreciated. Some cells are activated only by saccades, others discharge during the drift periods, and most show a mixture of these two influences. The patterns of activity reflect the interactions between the stimulus, the receptive-field activating region, the temporal response characteristics of the neuron, and the retinal positions and image motions imparted by the eye movements. An extraretinal influence accompanying fixational saccades can also modulate ongoing firing of V1 neurons. The diversity of the activity patterns suggests that during natural viewing of a stationary scene some cortical neurons are carrying information about saccade occurrences and directions while other neurons are better suited to coding the details of the retinal image.

Methods

Action potentials were recorded from neurons in area V1 of three adult female macaque monkeys that were trained to hold visual fixation. Most of the data were from one monkey (M45, *Macaca mulatta*); the main patterns of stimulus-related activation were confirmed with a second monkey (F42, *Macaca fascicularis*), and comparisons of extraretinal influences were made with a third monkey (M42, *Macaca mulatta*). Details of training (Snodderly & Kurtz, 1985; Gur & Snodderly, 1987) and recording (Snodderly & Gur, 1995) procedures have been published. To summarize briefly, monkeys were trained to fixate on a light-emitting diode for 5 s while test stimuli were presented in the visual field. Position of the dominant eye was monitored by a double Purkinje image eye tracker (2–3 minarc resolution; 100-Hz sampling rate) and recorded in a computer file. In the same file, spike shapes were recorded as analog samples collected at 10–20 kHz (Gur et al., 1999).

Visual stimuli were displayed on a Barco 7351 monitor (60 Hz noninterlaced frame rate) and were red, green, blue, gray or black bars of optimal orientation, velocity, color, and spatial configuration 0.9 log units brighter or darker than the background of 1 cd/m^2. The optimal values of the parameters were defined as those that evoked the most impulses when the stimulus bar was swept across the receptive field (Snodderly & Gur, 1995). Luminance

was measured with a Gamma Scientific telephotometer. Chromatic stimuli were generated by activation of individual guns of the color video monitor. Incremental (bright) stimuli were presented on a neutral gray background; decremental (dark) stimuli were presented on a background of a single color (Snodderly & Gur, 1995). Stimuli were usually viewed binocularly.

Electrophysiological recordings

Fiber electrodes made from quartz-insulated platinum-tungsten alloy (Eckhorn & Thomas, 1993) with bare tip lengths of 5 μm or less and impedance at 1 kHz of 2–3 MΩ were most frequently used to record single-unit activity. In some experiments, glass-insulated platinum-iridium electrodes (Snodderly, 1973) with a tip diameter of 1–1.5 μm, and bare tip length of 5–7 μm, were used. For the present experiments, recording sites have not been histologically localized, and tentative laminar assignments were based on a combination of electrode depth in the cortex and physiological criteria previously described (Snodderly & Gur, 1995). Based on this evidence, the recording sites included a broad sample of laminar locations.

Visual stimulation in relation to eye position and eye movements

Measurements using image stabilization

For mapping the size of the receptive-field activating region (AR), incremental and decremental bars of optimal orientation were swept at 1.5–4 deg/s forward and back across the receptive field in a direction orthogonal to the long axis of the AR. The eye position signal from the eye tracker was added to the stimulus position signal from the computer at the beginning of each video frame to compensate for changes in eye position during the trial ("image stabilization", Gur & Snodderly, 1987, 1997; Snodderly & Gur, 1995). Because the delay in the feedback loop compensating for eye position (eye tracker-computer-video generator) could be as long as 28 ms, data were selected as previously described (Snodderly & Gur, 1995) to exclude time periods containing saccadic eye movements that could cause position errors due to compensation delays. During the intersaccadic drift intervals, the compensation delay had little effect, and even with relatively rapid drifts the delay caused a position error less than 0.4 minarc (Gur & Snodderly, 1997). As a refinement to our earlier methods, the latencies of individual responses were adjusted to the mean value for the whole set of responses when the average response histogram was constructed. This procedure avoided inflating the AR size by residual errors in position compensation. The AR width was then measured as the region of the field in which 95% of the spikes were elicited by the stimulus sweep (Snodderly & Gur, 1995). In addition to the width of the AR, these data provided an estimate of the location and eccentricity of the receptive field.

To characterize cells that had two subfields, one subfield responding to incremental and the other subfield responding to decremental stimuli, we measured the degree of overlap between the subfields mapped with stabilized, sweeping bars. We calculated an overlap index (Schiller et al., 1976) using the ratio: [(Mean width of the two subfields) − (Center-to-center separation of the subfields)]/[(Mean width of the two subfields) + (Center-to-center separation of the subfields)]. This index ranges from 0 for no overlap to 1 for complete overlap, and it was used to identify simple cells in our sample (see Results). Total AR width was defined as the total width occupied by the increment and decrement subfields.

To assess direction selectivity we compared the cumulative response of the cell in the two directions of motion. The response in the nonpreferred direction was divided by the response in the preferred direction and this fraction was subtracted from 1 to create an index (*DI*) that ranged from 1 for a very selective cell to 0 when responses in the two directions were identical. We classified cells as direction selective when the number of spikes fired in the preferred direction was at least twice the response in the nonpreferred direction ($DI \geq 0.5$, Snodderly & Gur, 1995).

A subset of cells was also stimulated with a stabilized flashing bar placed at the center of the receptive field to measure the temporal characteristics of the response.

Measurements without image stabilization

For all other measurements, compensation for eye position (image stabilization) was turned off so that the eye movements of fixation moved the receptive field over and around a stationary stimulus (Gur & Snodderly, 1997). To determine the effects of fixational eye movements, a stationary bar of optimum width, orientation, color, and sign of contrast was placed at the estimated mean position of the receptive field. If necessary, the position was adjusted slightly after listening to the firing patterns of the cell. The bar was usually 2–3 times the estimated length of the AR to maximize the probability that it would stimulate the cell over a moderately wide range of movements.

Analyses

Constructing a map of the AR in eye position coordinates

For very precise analyses, we wanted to distinguish clearly when the stimulus was on the AR and when it was near, but outside the AR. Therefore, a measure of the AR location in eye position coordinates was obtained for a representative subset of the cells. A stationary, nonstabilized stimulus, either flashing or steadily illuminated, was placed at the mean location of the receptive field and the cell's activity was recorded while the fixational eye movements placed the stimulus at various locations within and around the AR (cf. Livingstone et al., 1996; Martinez-Conde et al., 2000). A map of the AR was constructed off-line in a manner analogous to the reverse correlation procedure that was developed to map receptive fields in anesthetized animals (Jones & Palmer, 1987).

The principle of the method is illustrated in Fig 1A, left, for a flashed stimulus. Each spike was correlated with an eye position using a fixed delay. A delay time of 40–60 ms was chosen based on the latency of the cell's response. Spikes that occurred in the 100-ms interval following the onset of a saccade were specifically excluded when constructing the map. Consequently, the exact delay for the correlation was not critical, because data were accepted only during the intersaccadic periods when the eye was stable or drifting slowly.

A filled pixel in the eye position plane (Fig. 1A, right) indicates that one or more spikes were generated when the eye was in that position in the appropriate time period before the spike. Darkness of the pixel is proportional to the number of spikes centered on that eye position, accumulated from multiple trials. An example of a trial recorded with a flashed stimulus is shown in Fig. 1B. In Fig. 1C (lower left), a spatial histogram compiled from this trial and four others like it is shown. The spike counts at their respective eye positions constitute a map of the AR in eye position coordinates. We assumed that the stationary bar was located at the center (judged by inspection) of the AR map. The AR map therefore

allowed the stationary bar to be put into eye position coordinates and it served as a position reference for AR width measurements made with a sweeping bar as described below.

The stimuli used to study the cell are shown at the correct spatial scale. The sweeping bar (stabilized) was used to generate the average response histogram from which the width of the receptive field was measured, whereas the stationary bar (nonstabilized) was flashed to generate the gray-scale map. For this cell, which had a tiny AR, the sweeping bar and the stationary bar gave very similar AR widths. However, in some cells with larger ARs, the stationary bar was not positioned over the whole AR by the distribution of eye positions, so the sweeping bar histogram provided a better measure of the AR size. For that reason, our procedure was to use the stationary bar as our position reference, and the histogram generated with the moving bar to obtain the width of the AR. In the Results, the AR of the cell is represented by an ellipse with the minor axis equal to the width of the AR measured with the moving bar (Fig. 1D). The major axis of the ellipse simply includes the loci where a response was obtained with the stationary bar. Because the mapping bar is longer than the AR, this major axis can be an overestimate of the true length of the AR, but it is not important because our analyses concentrated on eye movements that were perpendicular to the stimulus bar.

Note that the gray-scale map is intended to indicate the position of the receptive field when the eye is at the mean fixation position, which we take as the zero location. Errors in estimating the mean fixation locus or in measuring the eye position will result in the AR being displaced slightly from zero, for this cell by about 5 minarc. This small offset applies to both the stimulus and the receptive field so it does not affect their positions relative to each other.

Spike train analyses

For all analyses of neuronal impulse activity, a time resolution of 1 ms was used. Histograms of stimulus-related firing and saccade-triggered histograms for individual cells were plotted with a 10-ms bin width.

Saccade detection

From the eye position data, the occurrence of fixational saccades during the trial was detected using a vector velocity threshold of 10 deg/s (similar to Bair & O'Keefe, 1998). We also required a period of 50 ms stable fixation before the saccade; for the first 30 ms eye velocity could not exceed 7 deg/s, and for the 20 ms prior to saccade onset, velocity could not exceed the 10 deg/s threshold. These values were chosen empirically for convenience in eliminating false positives in the saccade detection. Because different fixation windows were used at various times, we restricted our analyses to saccades that were not larger than 100 minarc on either the horizontal or the vertical axis and that did not displace the eye more than 100 minarc from the mean fixation locus on either axis. If a saccade had a looping trajectory, the maximum displacement was taken as the measure of its amplitude rather than the final position. The resulting saccade population had a mean vector amplitude of about 40 minarc (see Results), which is typical of monkeys fixating within a window of ± 1.5 deg (Bair & O'Keefe, 1998).

Stimulus-related activation by saccades

For purposes of illustration, saccades were separated into those resulting in increased activity (more spikes in the 250-ms period after the saccade than in the 250 ms before it), decreased activity (fewer spikes after than before), and no effect (exactly equal numbers of spikes before and after the saccade) while a stationary,
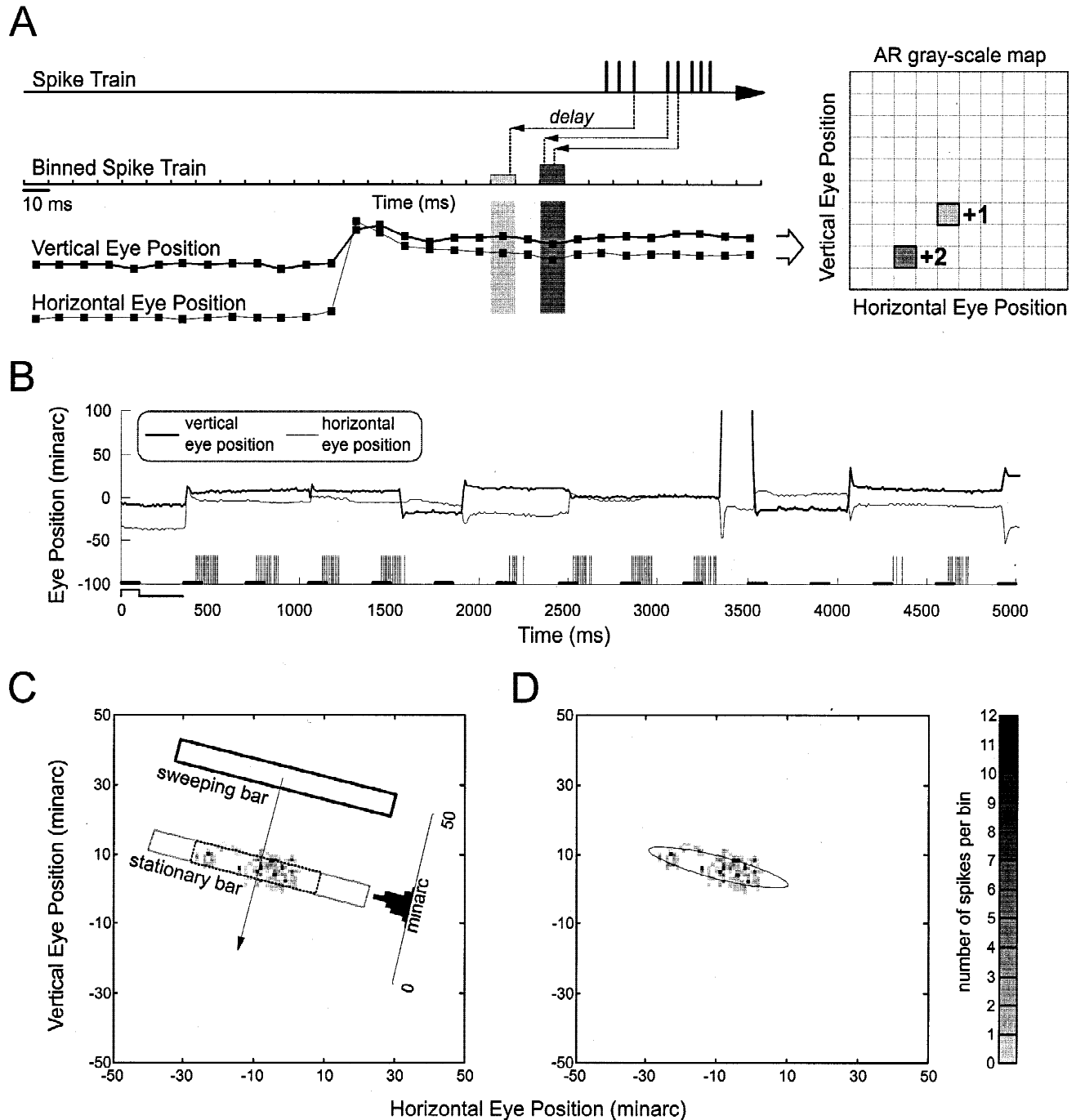
Fig. 1. Constructing a map of the receptive-field activating region (AR) in eye position coordinates. (A) Method of constructing a gray-scale map of the AR. An optimally oriented, stationary bar was flashed repeatedly in the receptive field of the cell. Schematic spike train is shown at the top. Spikes were shifted back in time by a delay corresponding to the visual latency and a spike histogram with bins of ±5 ms centered on eye position sampling times was constructed. A spatial histogram was prepared (right) where the darkness of each spatial bin (1 × 1 minarc) corresponded to the number of spikes fired with the appropriate delay when the eye was in this particular position. A spatial map was accumulated from several trials like the one shown in panel B. (B) Actual behavioral trial of about 5-s duration (file 2568f010). Eye position (thick line, vertical, thin line horizontal) is plotted along with the spike train (short vertical lines underneath the eye position traces). The stimulus was flashed (short, thick horizontal lines under spike train), on for 100 ms and off for 250 ms repeatedly during the trial. Response of the cell depended strongly on vertical eye position because its optimal orientation was near horizontal. (C) A sweeping bar was used to generate a response histogram (on right side of panel) from which AR width was measured (thick dashed rectangle). A stationary bar was flashed as shown in panel B to generate responses from which the gray-scale map of the AR was constructed in eye position coordinates. (D) An elliptical outline of the AR is used for the subsequent analyses. Minor axis of the ellipse equals width of AR as measured with the sweeping bar (see panel C).

steadily illuminated stimulus was presented. Increased or decreased activity corresponded to movement of the AR onto, off of, within, or across the AR. Equal numbers of spikes before and after saccades occurred primarily when the saccade trajectory did not bring the AR into contact with the stimulus. Firing patterns of the saccades causing increased activity were compared with excitatory responses to a stationary, flashed stimulus.

To describe the range of discharge patterns evoked by saccades, we created an index that was intended to rank the cells in the simplest manner possible according to the difference between mean firing rates immediately after saccades (*FRpost*) and mean firing rates later in the drift periods (*FRdrift*). All saccades meeting the amplitude criteria during presentation of a stationary, steadily illuminated stimulus were included in the ranking index regardless of whether they caused increases or decreases in firing. The firing rate in a fixed period 250 ms after each saccade (*FRpost*) was computed. If the next saccade (saccade #2) occurred within this 250-ms period, no *FRdrift* value was computed for saccade #1, but the *FRpost* value was retained. If saccade #2 occurred more than 250 ms after saccade #1, the firing rate from 250 ms after saccade #1 until the time of occurrence of saccade #2 was calculated as *FRdrift*. The drift period was therefore of variable duration and there were unequal numbers of *FRpost* and *FRdrift* values contributing to the overall averages.

For more detailed analyses of the transiency and time courses of neuronal discharge patterns, other perisaccadic intervals were used as described in the Results. For all analyses except the ranking index described above, trial segments were also excluded if they had saccades that were too close together. We required that each saccade not be preceded by another saccade by less than 350 ms and not be followed by another saccade by less than 250 ms when measuring stimulus-related activity. This was done to avoid contamination of saccade-triggered averages by the overlapping influences of adjacent saccades.

Extraretinal activation associated with saccades

For assessing extraretinal influences in the absence of deliberate stimulation, the monkey viewed either a blank gray video screen or the room was completely dark except for the fixation target. Before the dark condition, the monkey was light adapted to the 1 cd/m^2 background, so the measurements were made during transient dark adaptation, when sensitivity to any dim stray light would be minimized. In the dark, the video monitor was not visible to human observers who were in the room with the monkey. To ensure that there was no unintended stimulation of the AR by the fixation target, we checked the visual field locations of the cells studied. For ten cells with the strongest extraretinal modulation, five most strongly modulated in the light, and five most strongly modulated in the dark, all had ARs located at least 4.4 deg from the center of fixation. Because the saccades we analyzed under these conditions had maximum amplitudes no greater than 2.3 deg, none of the ARs would be stimulated by the fixation point. In fact, for all cells the mean amplitude of saccades selected for analysis of extraretinal effects in the light was only 37 minarc, and 86% of the saccades were <1 deg in amplitude, so the AR was usually well separated from the fixation point. In addition, the AR was always farther from the edge of the monitor screen than the largest saccades analyzed. Thus, we are confident that the presumed extraretinal effects are not due to stimulation by either the fixation point in the dark or the border of the video monitor in the light.

To avoid temporally overlapping influences, we required that each saccade evaluated for extraretinal influences not be preceded by another saccade by less than 500 ms and not be followed by

another saccade by less than 400 ms. These long time periods were required because the extraretinal effects had a slower time course than stimulus-related modulations.

In summary, our saccade selection procedure detected all saccades, but accumulated for further analysis only those perisaccadic trial segments that fulfilled the additional criteria for small saccade amplitude, limited displacement from the mean fixation locus, and an appropriate temporal spacing relative to adjacent saccades.

All analyses were done with custom software written in Matlab 5.2 (MathWorks). For stimulus-related activation, we analyzed data from a total of 4438 perisaccadic intervals, and for extraretinal activation we analyzed data from 865 perisaccadic intervals.

Results

Types of neuronal activity related to fixational eye movements

When a stationary, optimally oriented stimulus was placed in the receptive field and the eye movements of fixation moved the image of the stimulus about the retina, V1 neurons discharged in characteristic patterns. Three examples that represent the range of firing patterns evoked by a steadily illuminated bar are shown in Fig. 2. The upper panel illustrates a fixation trial recorded while monitoring a neuron that discharged vigorously during the intersaccadic drift periods. This cell was activated by the presence of the stimulus on the AR. Because some of the activation may be due to the slow drifts that occur in these periods, we refer to this type of cell as "position/drift-activated". The middle panel illustrates the activity of a cell that fired bursts of impulses restricted primarily to short periods immediately following saccades. We refer to this type of cell as "saccade-activated". Position/drift- and saccade-activated cells represent the extremes of a range encompassing many cells that respond like the "mixed" cell whose activity is illustrated in the bottom panel. (For brevity, we will shorten the names of the three groups to "position/drift", "mixed", and "saccade"). Mixed cells are activated during the intersaccadic drift periods and they also fire bursts of spikes with shorter interspike intervals when saccades occur. To aid in analyzing the effects of fixational saccades on neuronal activity, the times of occurrence of fixational saccades were determined by a velocity criterion as described in the Methods. These time points (indicated in Fig. 2 by inverted triangles) were used to establish perisaccadic windows for constructing spike histograms. The amplitudes of the saccades had a mean of 41 minarc (SD 23), which is similar to the value previously reported with similar inclusion criteria and it corresponds to a mean speed of about 30 deg/s during the saccade (Bair & O'Keefe, 1998).

Initially, the three types of activation—position/drift, saccade, and mixed—were identified by inspection of experimental records like those of Fig. 2. For an unbiased confirmation of the assignment of cortical neurons to these three groups, firing rates in different time periods relative to the eye movements were analyzed quantitatively as described later in the Results. First, we illustrate how the motions and positions of the retinal image imparted by fixational eye movements interact with the response properties and the receptive fields of the neurons to produce the characteristic firing patterns.

Position/drift cells

In addition to the temporal relationships between neuronal activity and fixational eye movements, it is essential to consider the spatial relationships between the receptive field and the stim-
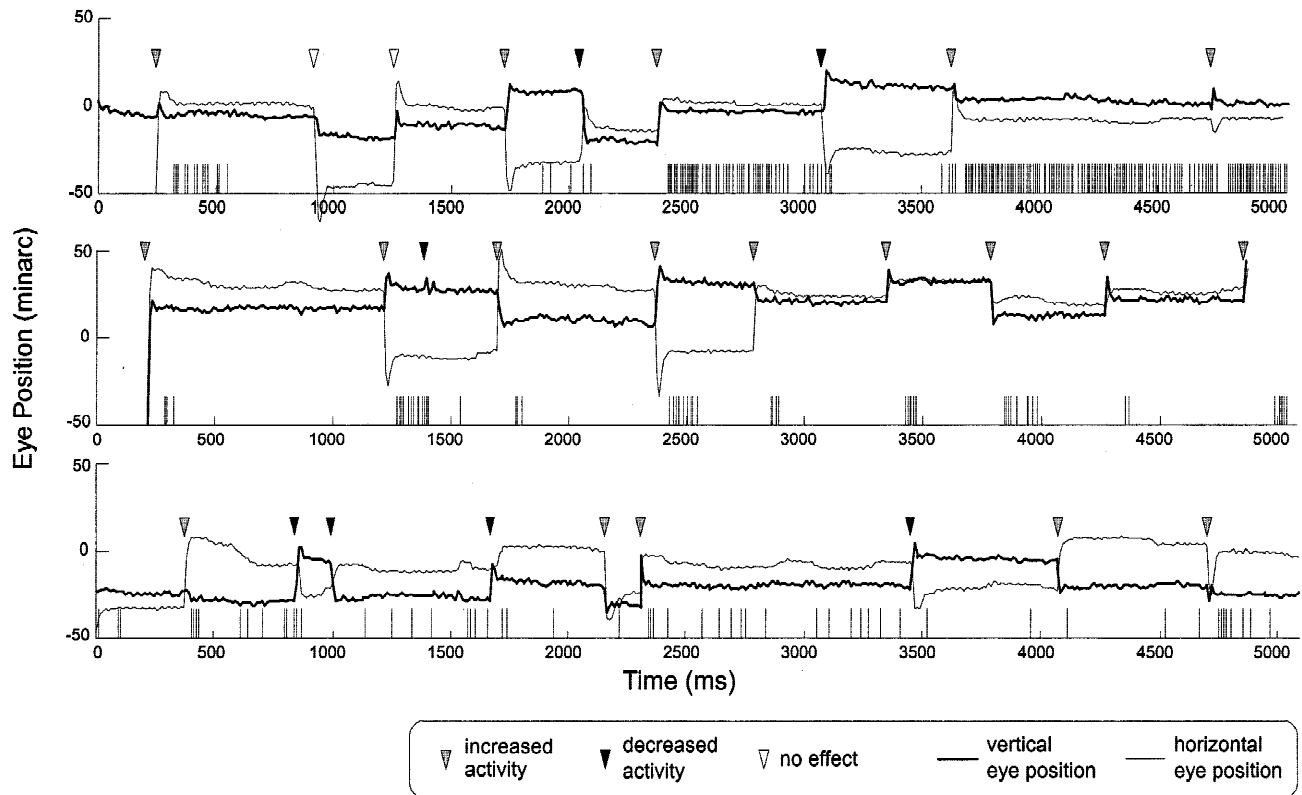
Fig. 2. Eye position and spike trains from cells with three different types of eye-movement-related activity. During behavioral trials of about 5-s duration, the receptive field was moved over and around a stationary, steadily illuminated bar of optimal size, color, and orientation by the fixational eye movements. *Top panel*. Position/drift cell 25683 (file 11). This cell had a tiny AR about 6 minarc wide and no spontaneous activity. *Middle panel*. Saccade cell 26682 (file 8). This cell had an AR about 20 minarc wide and no spontaneous activity. *Bottom panel*. Mixed cell 30682 that was activated during drifts and also fired bursts after saccades (file 15). This cell had an AR about 30 minarc wide, 0.5 spikes/s spontaneous activity, and it was direction selective. Inverted triangles above the eye position traces denote saccade occurrences. Saccades were classified according to the influence they exerted on the neuron's activity as described in Methods: Black triangles—saccades followed by decreased activity. Gray triangles—saccades followed by increased activity. White triangles—saccades that had no effect (equal numbers of spikes in the 250 ms before and the 250 ms after the saccade).

ulus that are established by the eye movements. In Fig. 3, these spatial relationships are illustrated for the same position/drift cell used for Fig. 1 and the top panel of Fig. 2.

For Fig. 3, short segments of fixation trials were selected that represent the different ways that the fixational eye movements moved the stimulus in and around the AR of the cell. Recall that this cell had no ongoing activity. In panel A, the temporal relationships are shown (I–IV). The firing of the cell could increase after a saccade (I a–b, III e–f), decrease after a saccade (II c–d, III f–g), or be unaffected by saccades (IV, h–i–j). The alterations in firing were due to the placement of the AR with respect to the stimulus as described below.

The time courses of the firing patterns are illustrated in panel B, where saccade-triggered spike histograms accumulated from several behavioral trials are plotted. Separate histograms were calculated for saccades followed by increased activity and saccades followed by decreased activity. Saccades causing no effect were not included. Our justification for grouping the neuronal responses into separate categories of activity increases and decreases is based on the observation that they represented different spatial relationships. The activity increases resulted from movement of the AR onto the stimulus (or better centering over the stimulus) whereas decreases resulted from movements of the AR off the stimulus (or poorer centering over the stimulus).

Note that when saccades followed by increases or by decreases of activity are combined in the same histogram ("*both*"), the result is a flat temporal profile, which obscures the dramatic effects of the eye movements. The flat temporal profile of the combined activity is due to two things: (1) The increased activity when the AR lands on a stimulus balances the decreased activity when the AR leaves the stimulus. (2) This type of cell has a very sustained response to stimulation, as demonstrated by the histogram for a flashed stimulus ("*flashes*").

The spatial relationships between the AR and the stimulus during the trial segments are illustrated in the next two panels of Fig. 3. The AR mapped with a stationary bar is shown in panel C with the ellipse whose minor axis represents the AR width. The small fringe of scattered pixels outside the elliptical profile is due to the difference between the estimates of the AR width derived from the sweeping bar and the stationary bar; these small differences do not influence the overall interpretation. The bar that was used to generate the AR map is drawn to the same spatial scale. In panel D, two-dimensional plots show how the eye movements in the trial segments of panel A move the AR in space while a stationary stimulus is present.

The situations that are illustrated represent the following conditions resulting from fixational saccades (left to right). *On*: The AR is moved onto the stimulus (I, a–b). *Off*: The AR is moved off
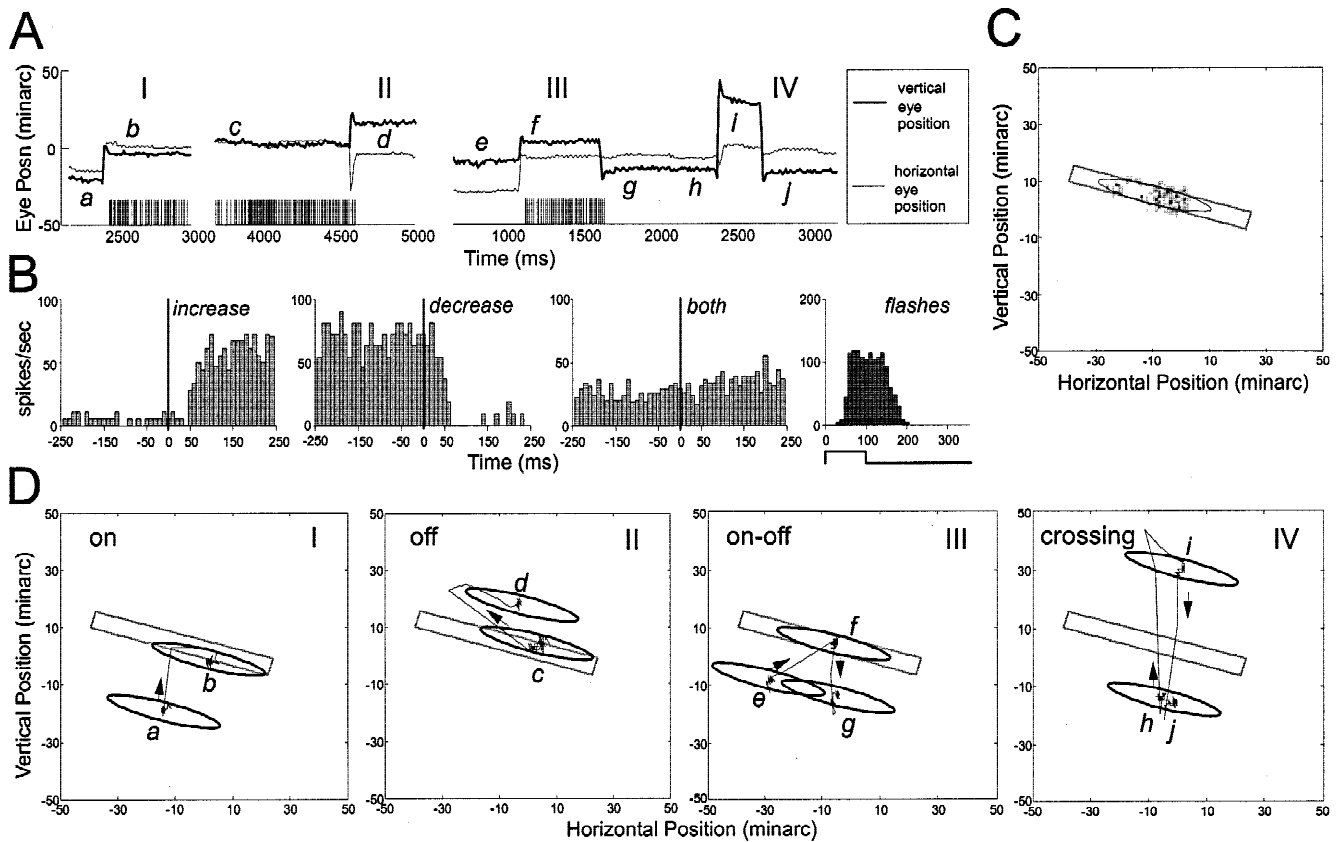
Fig. 3. Characteristics of a position/drift cell (25683). (A) Activation of the cell by a green incremental stationary bar 6 min wide of optimal orientation, placed at the mean receptive field position (file 11). Four separate time segments (I–IV) from different trials are shown. (B) Saccade-triggered histograms of average spike frequency. Separate histograms are presented for saccades followed by increased activity (*increase*, n = 18), saccades followed by decreased activity (*decrease*, n = 12), and all saccades combined (*both*, n = 30). Saccades occurred at *t* = 0. Also shown is the average response histogram of the cell to flashing the bar (file 10; n = 25, stimulus on 100 ms, off 250 ms for each repetition; temporal profile indicated under time axis). (C) Gray-scale map of AR in eye position coordinates, along with elliptical outline used in subsequent panels. Stimulus bar used to generate the map is drawn to the same spatial scale. Minor axis of ellipse is width of cell's AR measured with a stabilized bar sweeping across its receptive field as described in Fig. 1. (D) Spatial interactions between stimulus and AR during the trial segments in panel A. The eye position data shown as a function of time in panel A are plotted here in space, along with the stimulus bar that evoked the activity. I—Saccade brings the AR onto the stimulus. II—Saccade takes AR off the stimulus. III—AR moves onto the stimulus (first saccade), stays on the stimulus briefly, and then moves off it (second saccade). IV—Pair of saccades sweeping AR rapidly (50 deg/s) across the stimulus and back.

the stimulus (II, c–d). *On–off*: Successive saccades move the AR on and then off the stimulus (III, e–f–g). Note that there is no activation when the stimulus leaves the field. *Crossing*: Saccades move the AR across the stimulus, but the AR is not on the stimulus during the intersaccadic drift periods (IV, h–i–j). This last condition is particularly informative, because it shows that the retinal image motions imparted by the saccades are not sufficient by themselves to activate this neuron. For this type of cell, the activation associated with saccades is caused by moving the AR onto the stimulus.

Saccade cells

Saccade neurons have firing patterns that are complementary to those of the position/drift cells. In this section, we describe the properties of two saccade cells with different response properties recorded on the same penetration in different laminar locations. One of the cells was direction selective and judged to be in layer 4B. It had a maintained discharge rate of 1 spike/s with a blank field of our standard luminance. Its eye movement-related prop-

erties are illustrated in Fig. 4. The trial segments were chosen to include particularly informative spatial interactions between the AR and the stimulus produced by the fixational eye movements. With a stationary stimulus in the field, this cell fired very transient bursts after most saccades (Fig. 4A, I–IV). It also discharged very transient bursts at ON and OFF of a flashed stimulus (Fig. 4B). Because there was no ongoing activity and no activation during the drift periods, all saccades that influenced the firing of the cell were followed by increased activity, so there is no separate histogram for decreased activity. The position and width of the AR were determined as previously described, using a narrow bar (Fig. 4C).

This direction-selective cell was activated when the AR moved off the stimulus or onto the stimulus, provided the direction of eye motion conferred retinal image motion in the preferred direction (I, II, c–d, III). However, saccades that produced retinal image motion in the null direction elicited no activity (II, d–e). Direction selectivity for activation by fixational saccades has been reported previously for MT cells (Bair & O'Keefe, 1998), and our results show that the selectivity is already present in V1.
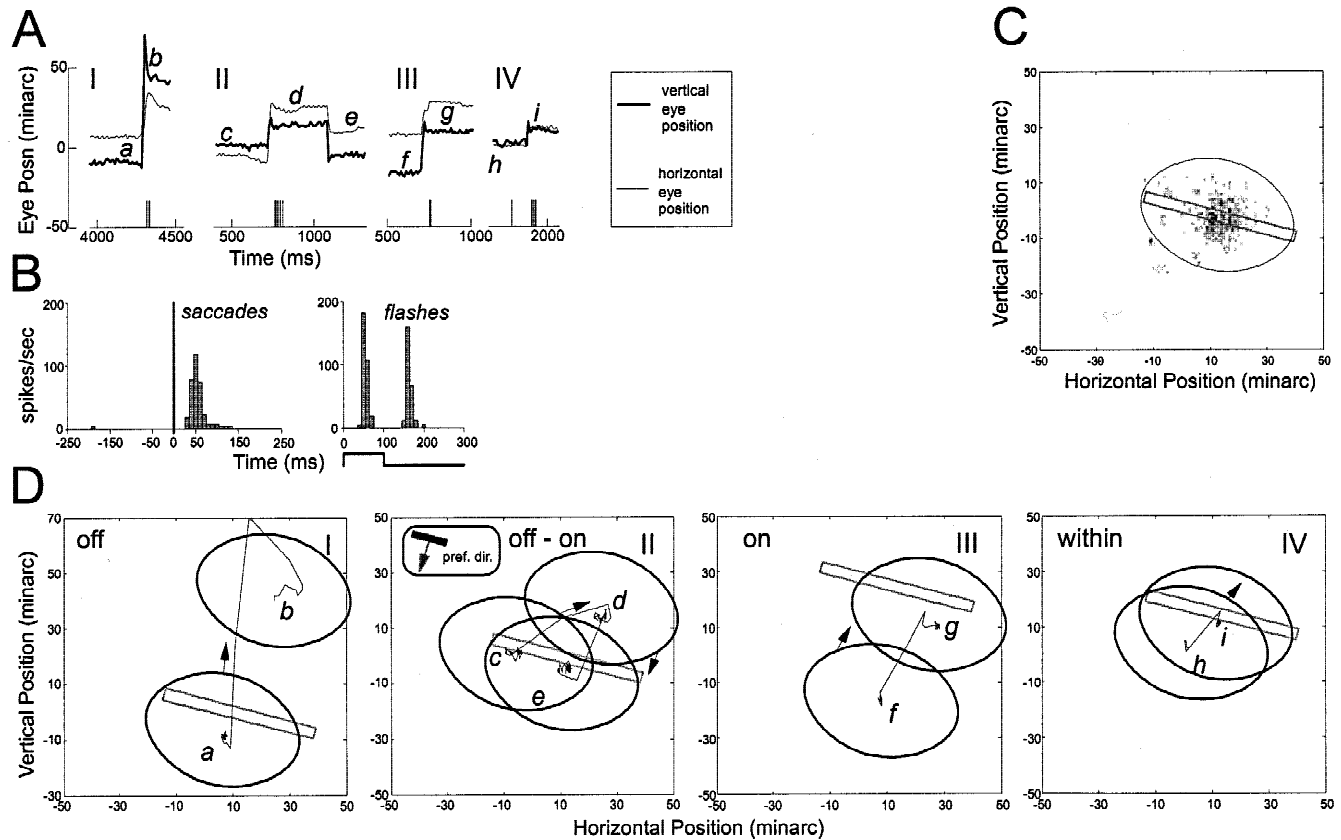
Fig. 4. Characteristics of a saccade cell with a transient discharge (26683). Conventions are the same as in Fig. 3. (A) Activation of the cell by an optimally oriented, red incremental stationary bar 4 min wide, placed at the mean receptive-field position (file 13). Four separate time segments (I–IV) from different trials are shown. (B) Saccade-triggered averaged spike histograms for all saccades followed by increased activity ($n = 110$) compared with responses of the cell to a stationary flashing bar (file 11; $n = 75$; stimulus on 100 ms, off 200 ms for each repetition). (C) Gray-scale map of AR in eye position coordinates, along with elliptical outline used in subsequent panels. Stimulus bar used to generate the map is drawn to the same spatial scale. Minor axis of ellipse is width of cell's AR measured with a stabilized bar sweeping across its receptive field. (D) Spatial interactions between stimulus and AR during the trial segments in panel A. The eye position data shown as a function of time in panel A are plotted here in space, along with the stimulus bar that evoked the activity. I—Saccade takes AR off the stimulus. II—Effect of directional selectivity for saccade-induced motion: Saccade c–d takes AR off the stimulus and saccade d–e puts AR back onto the stimulus. Preferred direction for external stimulus motion is shown. Saccade d–e generates image motion in the null direction and elicits no activity. III—Saccade putting AR onto stimulus with preferred direction of image motion (opposite to eye motion) produces sharp burst of spikes. IV—Small amplitude (about 10 minarc) saccade moves stimulus within AR to generate discharges. Positions of stationary bar in segments I and II differ from that of panels III and IV.

The sensitivity of this saccade cell for small motions was exquisite. Sharp bursts of spikes were elicited by saccades that moved the AR by only a small fraction of its width, so that the stimulus remained within the AR for the entire movement (IV).

For the second example (Fig. 5), we illustrate the characteristics of the saccade neuron used for the second panel of Fig. 2. Recall that the cell had no spontaneous activity and it was not direction selective. Its AR was about half as wide as the previous saccade cell (Fig. 5C). From its cortical depth, it was judged to be in layer 2 or 3. Bursts of activity occurred in association with most saccades (Fig. 5A, I–III), but the cell was not activated during the intersaccadic drift periods (IV). Its saccadic activation was fairly prolonged, as was its flash response (Fig. 5B).

Spatial interactions are illustrated in Fig. 5D. A saccade that moved the AR off the stimulus generated a discharge (I, *off*). Motion that did not bring the AR into contact with the stimulus elicited no spikes (IIa, *missing*), but even a brief jerk of the AR on and off the stimulus produced a couple of spikes (IIb, *on–off*). In general, it was only necessary for the AR to remain on the stimulus for a brief moment to activate the cell, as indicated by a burst of activity following a saccade that rapidly displaced the AR across the stimulus from one side to the other (III). For this cell, it was clearly the fast motions of the eye that were important, and maintaining the AR on the stimulus was ineffectual. When a saccade moved the AR abruptly onto the stimulus, followed by slow drift for more than 2 s (IV), and then a saccade that abruptly moved the AR off the stimulus, the only discharges were associated with the rapid saccadic movements.

Note that both saccade cells fired when a saccade moved the AR either on or off the stimulus. This was a common property of all cells that discharged in association with saccades, including the mixed cells as shown below. Such behavior may complicate the interpretation of neuronal activity when the subject is viewing a natural scene, because both the image feature leaving the AR and the feature entering the AR may influence the cell in similar ways when the eye moves.
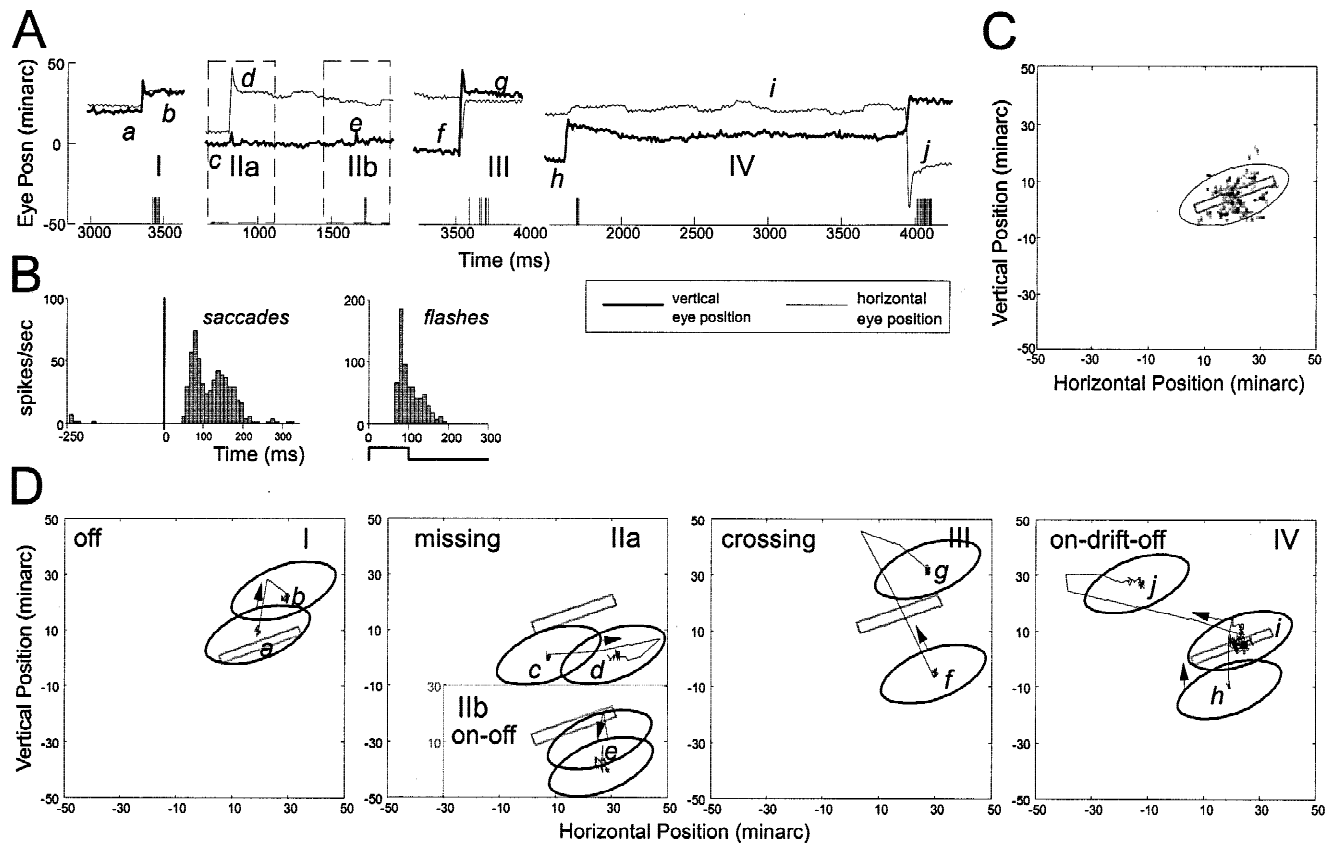
Fig. 5. Characteristics of a saccade cell with a relatively prolonged discharge (26682). Conventions are the same as in Figs. 3 and 4. (A) Activation of the cell by an optimally oriented, green stationary bar 3 min wide, placed at the mean receptive-field position (file 8). Four separate time segments (I–IV) from different trials are shown. (B) Saccade-triggered averaged responses for all saccades followed by increased activity ($n = 136$) compared with response of the cell to stationary flashing bar (file 7; $n = 75$; on 100 ms, off 200 ms for each repetition). (C) Gray-scale map of AR in eye position coordinates, along with elliptical outline used in subsequent panels. Stimulus bar used to generate the map is drawn to the same spatial scale. Minor axis of ellipse is width of cell's AR measured with a stabilized bar sweeping across its receptive field. (D) Spatial interactions between stimulus and AR during the trial segments in panel A. Eye position data shown as a function of time in panel A are plotted here in space, along with the stimulus bar that evoked the activity. I—Saccade a–b takes AR off the stimulus. II—Time periods IIa and IIb indicated by the dashed boxes in panel A are plotted separately. IIa—AR misses stimulus during saccade c–d. IIb—Small saccade pair e takes AR briefly onto stimulus and then off again. III—AR crosses stimulus. IV—AR lands on stimulus, remains there for a long drift period, and then is moved off the stimulus by next saccade. Note that stationary bar's position in panels II and III differs slightly from that of panels I and IV.

Mixed cells—activated by both position/drift and saccades

The largest group of cells in our sample had mixed properties. They fired bursts of spikes after saccades, but were also activated during the intersaccadic drift periods. Characteristics of a cell with mixed properties are illustrated in Fig. 6. This cell was not direction selective and it had a maintained discharge rate of 2.6 spikes/s with a blank field of our standard luminance. It was tentatively assigned to layer 5.

For the mixed cells, the bursts that follow individual saccades (Fig. 6A) were sometimes difficult to distinguish from the irregular, but more sustained activity during the drift periods. However, saccade-triggered histograms (Fig. 6B) for the cases where activity either increases or decreases after the saccades show clear bursts in addition to changes in the maintained firing rate. When data from both types of saccades are combined (*both*), the burst of activity evoked by the saccades is still evident in the histogram, but the changes in the more sustained components of the activity are not evident because the increases and decreases balance each other. For demonstrating the position/drift activation of mixed cells by

fixational eye movements, it was useful to separate increased and decreased activity just as it was for cells that were activated *only* during the drift periods (e.g. Fig 3B). Note that the flash response of the mixed cell is intermediate in form between the position/drift cell and the saccade cells, displaying a transient at ON with a sustained component as well. There may also be an OFF transient, but the flash duration was too short to be sure.

When the eye movements placed the AR of the mixed cell on the stimulus (Fig. 6D, left panel), there was a moderate level of sustained activity. The saccade-related bursts were evoked by motions that moved the AR onto the stimulus (I) or off the stimulus (II). As previously illustrated in Fig. 5, small motions of the stimulus bar within the AR were effective (III, IV).

Quantitative analyses of activation by fixational eye movements

For 50 cells, we recorded neuronal activity while fixational eye movements moved the AR over and around a stationary visual stimulus with no image stabilization. For a subset of 28 cells, the
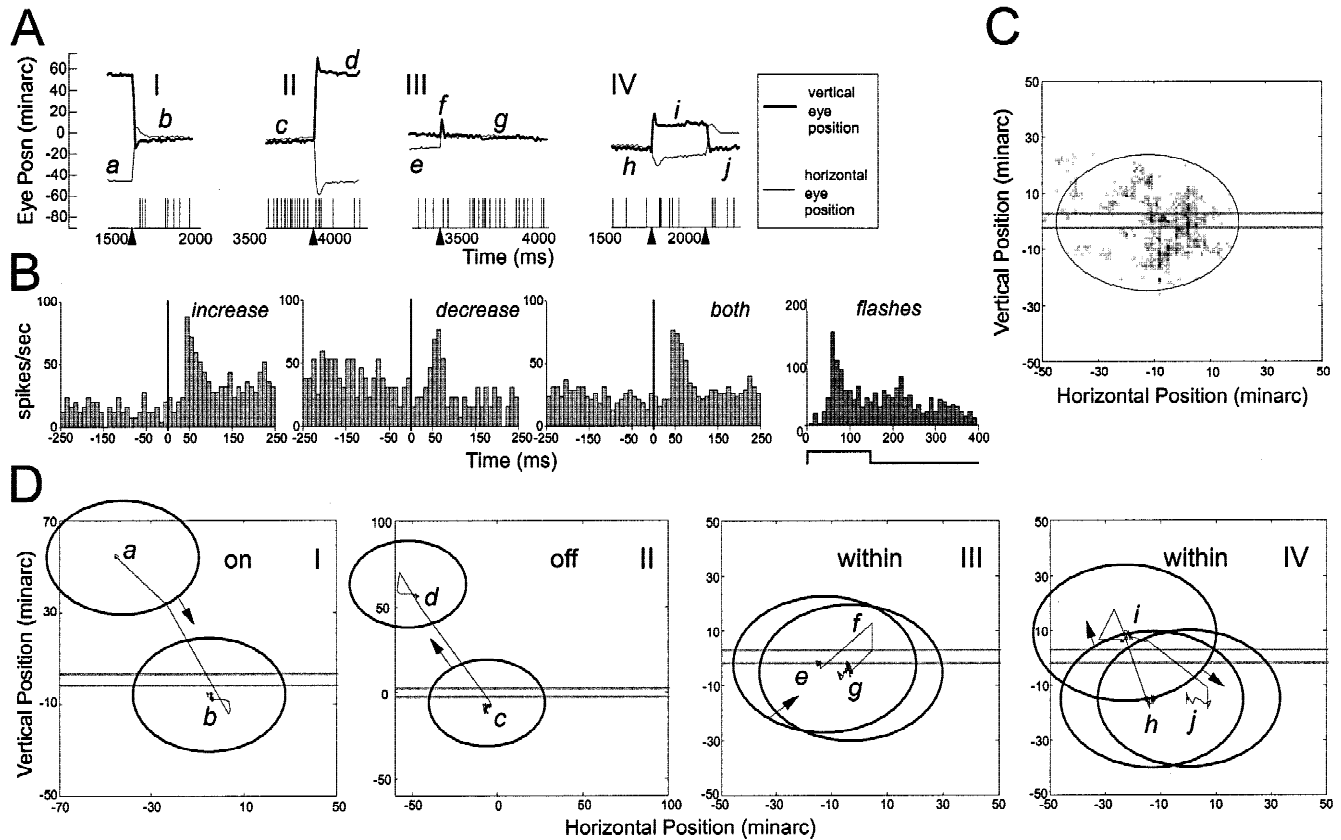
Fig. 6. Characteristics of a mixed cell (25684). Conventions are the same as in Figs. 3–5. (A) Activation of the cell by an optimally oriented green incremental stationary bar 5 min wide, placed at the mean receptive-field position (file 20). Four separate time segments (I–IV) from different trials are shown. Arrowheads under the time axis indicate the times of saccade occurrences. (B) Saccade-triggered histograms of average spike frequency for saccades that were followed by increased activity ($n = 23$), saccades followed by decreased activity ($n = 11$), and all saccades combined (*both*, $n = 34$). Saccades occurred at $t = 0$. Also shown is the average response histogram of the cell to flashing the stimulus bar (file 18; on 150 ms, off 250 ms for each repetition). (C) Gray-scale map of AR in eye position coordinates, along with elliptical outline used in subsequent panels. Stimulus bar used to generate the map is drawn to the same spatial scale. (D) Spatial interactions between stimulus and AR during the trial segments in panel A. AR moves onto stimulus. II—AR moves off the stimulus. Eye position axis has a different scale in this panel to accommodate large saccade. III—Small looping saccade pair moves AR so that stimulus remains within the AR. IV—Successive small saccades move AR, keeping stimulus within the AR.

AR location in eye position coordinates was determined by reverse correlation so that saccades could be separated into those that caused the AR to land on the stimulus, leave the stimulus, or cross the stimulus as illustrated in Figs. 3–6. We begin with analyses of this well-characterized subset, and then show how to include data from the other 22 cells for which less precise position information was available.

Analysis of specific, known saccadic displacements

From inspection of saccade-triggered histograms of neuronal firing, we selected time periods for quantitative analyses designed to test the validity of our qualitative assignment of V1 neurons to the three eye movement categories. We quantified the transient activation (peak) as the mean firing rate in the period 40–250 ms after the saccade, and the sustained activation (tail) as the firing rate in the period 250–500 ms after the saccade. The mean firing rate in the 250-ms period just before the saccade was taken as the baseline (base), and it was subtracted from the other two measures. We found that the population of 28 cells could be segregated into three classes by comparing the peak activation for crossing sac-

cades with the tail of the sustained activation for landing saccades. When we plotted these measures in a two-dimensional space (Fig. 7), the cells segregated into three nonoverlapping clusters with only one outlier. The outlier (25682) was a position/drift cell in the upper right quadrant that had a high maintained discharge rate of 28 spikes/s and a relatively strong extraretinal input evidenced by inhibition 250–300 ms after a saccade (see later).

For landing saccades, we expected sustained activation for position/drift and mixed cells but not for saccade cells. Accordingly, the firing rate in the tail minus the baseline firing rate for landing saccades was less than 0.8 spikes/s for all saccade cells, greater than six for all the mixed cells, and greater than 12 for all the position/drift cells. Thus, the lack of sustained activation of the saccade cells after a landing saccade segregated them completely from the other two cell types. The means of tail minus base for landing saccades for the three groups were statistically different (*t*-test, $P < 0.01$).

At the other extreme, for crossing saccades we expected a transient activation of mixed and of saccade cells but not of position/drift cells. Accordingly, the peak firing rate minus the
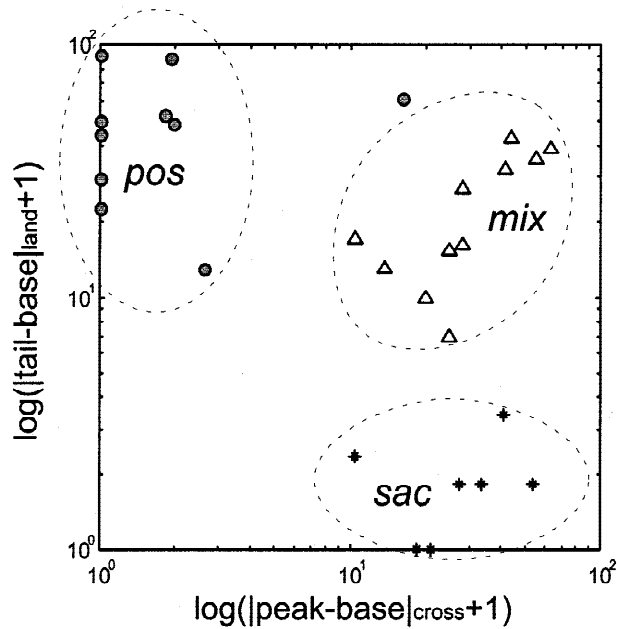
Fig. 7. Separation of cortical neurons into eye movement classes based on activation by fixational saccades that caused the AR to land on the stimulus (vertical axis) compared with activation by saccades that caused the AR to cross the stimulus without remaining on it (horizontal axis). Each point represents data from a single cell. *Peak* is the mean firing rate 40–250 ms after the saccade, and *tail* is the mean firing rate in the period 250–500 ms after the saccade. The baseline firing rate in the period 250 ms before the saccade (base) was subtracted from both peak and tail, and the absolute values of these differences were used to avoid negative numbers so that a log scale could be used to display the results. One was added to this absolute difference to avoid an inadmissible log of zero.

baseline firing rate for crossing saccades was less than 1 spike/s for all position cells, whereas for all mixed and for all saccade cells it was greater than 9. Consequently, the lack of a transient response to a crossing saccade segregated the position/drift cells completely from the other two cell types, and the means of peak minus base for position/drift cells for crossing saccades were statistically different from saccades and mixed cells (*t*-test, $P < 0.001$). The result of these quantitative comparisons confirmed our qualitative separation of V1 neurons into three classes based on their patterns of activity during fixational eye movements.

For each cell, we computed saccade-triggered histograms of neuronal firing in the perisaccadic period for the three types of saccadic displacements. We then averaged the histograms across cells in each of the eye movement categories to create the summary shown in Fig. 8. The different patterns of activation illustrated in Fig. 8 are summarized in Table 1.

Analyses based on all fixational saccades

For the other 22 neurons in our sample of 50 V1 neurons, the exact relationship between the saccadic displacements and the AR location was not known with sufficient precision to distinguish landing, leaving, and crossing saccades. Nevertheless, it was clear that the cells spanned a range from those activated only immediately after saccades, to those exclusively activated during drift periods, with mixed cells in between. To describe this distribution of neuronal activation patterns, we created an index to rank the cells according to the difference between the mean firing rates in the postsaccade period (250 ms) and the drift period (250 ms to next saccade; see Methods). To minimize the effect of spontaneous activity, the maintained discharge rate (*MDR*) during 5–30 s of viewing our standard uniform background with no stimulus bar was subtracted from both the postsaccadic firing rate, *FRpost*, and the drift firing rate, *FRdrift*. In addition, to minimize confounding by differences in mean firing rates from cell to cell, the index was normalized by dividing by the sum of *FRpost* and *FRdrift*, with *MDR* subtracted from each.

The rank of each cell was thus calculated according to the following formula:

$$Rank = \frac{(FRpost - MDR) - (FRdrift - MDR)}{(FRpost - MDR) + (FRdrift - MDR)}$$
$$= \frac{(FRpost - FRdrift)}{(FRpost + FRdrift - 2MDR)}.$$

The distribution of these ranks based on all saccades for our entire sample of 50 V1 neurons is shown in Fig. 9 (top row). The different symbols indicate our prior qualitative classification into three groups. For comparison, the bottom row of Fig. 9 shows the distribution of ranks for the subset of 28 cells where analyses of specific saccadic displacements provided evidence for three eye movement groups. The boundaries indicated by the vertical dashed lines are based on results from these 28 cells derived from saccades that caused the AR to land on the stimulus or to cross the stimulus. Thus the results of the analyses of known saccadic displacements, the tentative qualitative assignments to eye movement categories, and the ranking index are consistent with each other.

Given the modest number of cells in our sample, the pattern that we have found is probably artificially neat, and a larger sample may show more overlap at the boundaries between the classes. However, the important question is not whether our criteria will always completely separate the classes, but what functional roles the different types of cells may play. In the next sections, we describe several functional properties of our sample of 50 V1 neurons, using the eye movement classifications based on the ranking index as indicated in the top row of Fig. 9.

Table 1. *Effects of saccades causing specific displacements of the AR with respect to the stimulus*

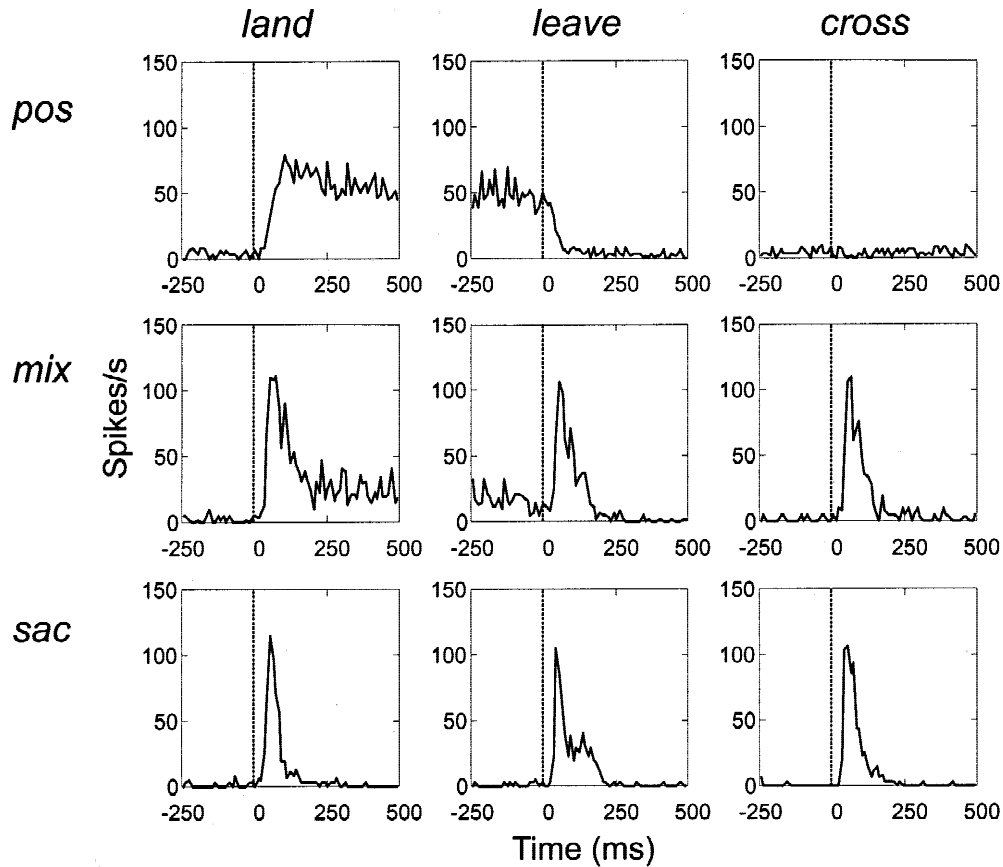|	AR land on stimulus	AR leave stimulus	AR move across stimulus
Position/Drift Cells	Sustained activation	Reduced activity	No activation
Mixed Cells	Transient and sustained activation	Transient activation, then reduced activity	Transient activation
Saccade Cells	Transient activation	Transient activation	Transient activation

Fig. 8. Saccade-triggered average spike histograms for position/drift activated cells (pos, $n = 10$), mixed cells (mix, $n = 11$), and saccade cells (sac, $n = 7$) when saccades caused the AR to land on the stimulus (first column), leave the stimulus (second column), or cross the stimulus without remaining on it (third column). Saccades occurred at $t = 0$. For each cell, data were based on five saccades causing the AR to land on the stimulus and five saccades causing the AR to leave the stimulus. Because the monkeys maintained gaze within a compact region, saccades sweeping the AR across the stimulus without remaining on it were less frequent. Four or five crossing saccades were analyzed for 15 cells, three saccades for four cells, and two saccades for nine cells.

Comparison of saccadic activation with responses to flashed stimuli

A saccade that abruptly moves the AR onto the stimulus elicits a discharge that is very similar to an abruptly flashed stimulus centered on the AR. To compare these two situations, we computed a transiency index for each cell based on the spike histograms for the subset of saccades that led to increased firing. This group included landing saccades for the position/drift neurons, and a
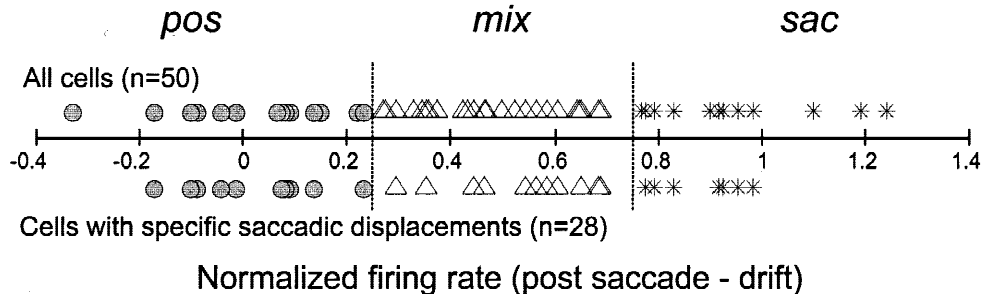

Fig. 9. Ranking of V1 neurons according to the difference between the normalized firing rates in the postsaccade period (250 ms) and the drift period (250 ms to next saccade). *Top row*. All cells ($n = 50$) divided into one of the three categories—position/drift (pos, filled circles), mixed (mix, triangles), or saccade (sac, asterisks). *Bottom row*. Subset of cells previously classified based on activation by landing saccades and by crossing saccades ($n = 28$, same cells used for Figs. 7 and 8). Vertical dashed lines are dividing lines between mixed cells and the other two eye movement classes.

mixture of saccade types for the saccade and mixed neurons. Because the saccades were selected to be small, few of them cleanly crossed the AR. The transiency index (*TI*) was computed from three measures: *MDR*—the maintained discharge rate with a blank, lighted field, *peak*—average firing rate in the three highest 10-ms bins that occurred within 120 ms after the saccade, and *tail*—mean firing rate during the period from 120–250 ms after the saccade. Note that the exact time period used for estimating the peak firing rate was individually chosen for each cell to insure that the maximum rate was correctly estimated. This refinement was introduced to allow for latency variations that were in part linked to the unpredictable nature of the saccade patterns. The index was calculated according to the formula:

$$TI = \frac{(peak - MDR) - (tail - MDR)}{(peak - MDR) + (tail - MDR)}$$
$$= \frac{(peak - tail)}{(peak + tail - 2 \cdot MDR)}.$$

Thus the transiency index is the difference between peak and tail scaled by the postsaccadic firing rate, with both peak and tail being corrected for the maintained discharge rate. Values close to one are indicative of a transient excitatory response, values approaching zero are indicative of uniform firing after the saccade, and intermediate cases are scattered between these two extremes. (Among the 50 cells, there were two exceptional cases, one mixed, and one position/drift cell, whose index values were negative because the maximal firing rates occurred later than 120 ms after the saccade.)

For comparison with saccadic activation, a corresponding transiency index was computed for the flash responses of cells for which flash data were available ($n = 29$). The stimulus was the same color and sign of contrast, although sometimes of slightly different size. The same formula was used to compute the flash transiency index, but values for the peak were derived from the period 0–100 ms after flash onset and values for the tail were calculated for the period 100–150 ms after flash onset. We used shorter time periods for these analyses because the latency of the peak was less variable after flashes and because many of the flashes were of shorter duration than the time periods that were analyzed after saccades.

Using the transiency index, *TI*, for saccadic activation, the cells were sequentially ordered and the spike histograms from a systematically selected group of neurons are presented in Fig. 10. The 14 pairs of histograms in Fig. 10 were derived from the four neurons with the highest values of *TI*, the four neurons with the lowest values of *TI*, and approximately every third neuron in between. The reader may recognize that ordering according to the *TI* does not completely separate the different classes. This incomplete separation happens because the *TI* does not incorporate as long a time epoch during the drift period as the ranking index used for classification purposes.

The obvious correlation between the transiency of the saccadic activation and the flash activation is further illustrated in Fig. 11 (Pearson $r = 0.81$; $P < 0.0001$). The correspondence between the saccade-evoked and the flash-evoked activity of the cells indicates that the abrupt retinal image motions imparted by the fixational saccades affect the time course of neuronal activity in a manner similar to the abrupt temporal transient of a flashed stimulus. It also suggests that extraretinal influences (see later) are not major determinants of the time course of saccade-evoked activity when a strong stimulus is present.

Relationship of eye movement activation to stimulus selectivity and AR dimensions

We did not make detailed measurements of orientation tuning for all cells, but most were clearly orientation selective (at least twice as many spikes fired at the optimal orientation as at the orthogonal orientation). Some other characteristics of the cells that were related to eye movement activation are summarized in Table 2 and discussed below.

Saccade neurons

For the saccade cells, the saccadic transiency index was strongly correlated with the direction index ($r = 0.89$, $P < 0.001$). Nearly half (5/12) of the saccade cells had a $DI \geq 0.5$, which is the traditional criterion for designating a cell as direction selective (Snodderly & Gur, 1995). Eight saccade cells were localized to the two silent, output supragranular layers 2/3 and 4B, and had maintained discharge rates of 0 to 2.6 spikes/s. Three other cells were localized to layer 4Cα and had maintained discharge rates of 12–23 spikes/s.

Mixed cells—activated by both saccades and position/drift

The mixed cells were a heterogeneous group including a small percentage of direction-selective cells that were assigned to layers 4B and 6. Maintained discharge of mixed cells in the light had a

Table 2. *Characteristics of V1 cells showing different types of eye movement activation*[a]

Eye movement activation	Number of cells	Percent direction selective	AR subfield width (minarc)	AR total width (minarc)
Saccade	12	41%	45 ± 34 ($n = 12$)	54 ± 34 ($n = 10$)
Mixed	24	12%	33 ± 21 ($n = 22$)	37 ± 22 ($n = 20$)
Position/drift	14	14%	13 ± 11 ($n = 14$)	14 ± 10 ($n = 11$)

[a]The term "AR subfield" refers to single regions responsive to increments or decrements. AR width values are means ± standard deviations. Data for direction selectivity were collected for all cells listed. In some cases AR widths were not measured, and the reduced number of neurons used to compute the statistics are indicated.
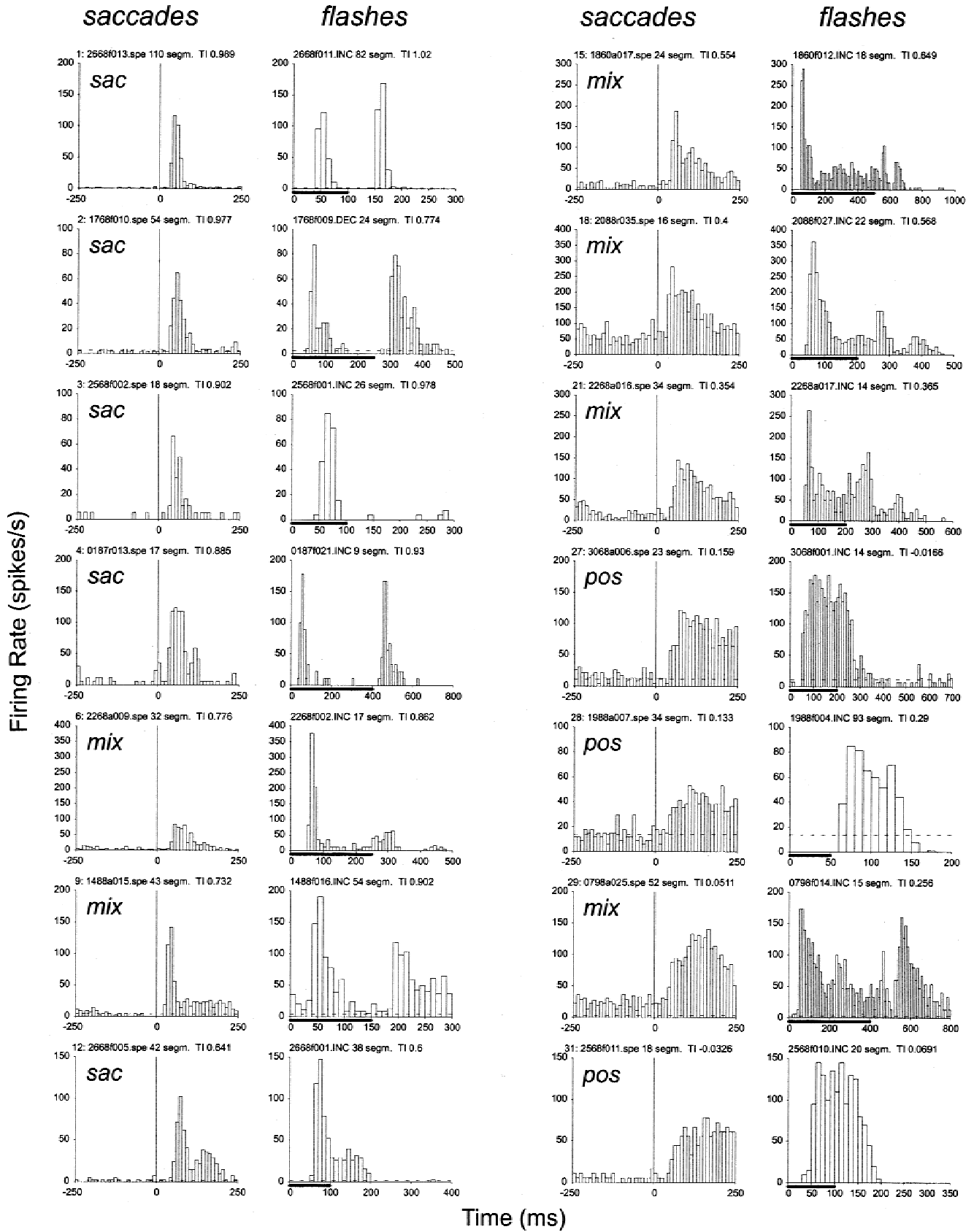
saccades   flashes   saccades   flashes

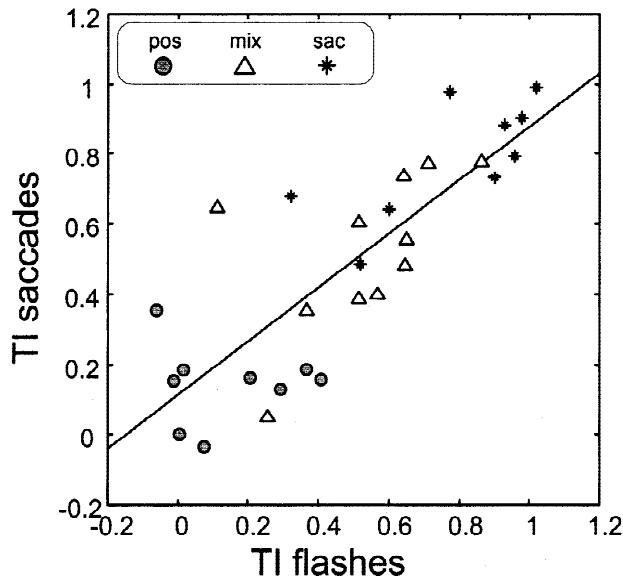**Firing Rate (spikes/s)**

Time (ms)

FIGURE 10

Fig. 11. Transiency index, TI, for saccadic activation with a stationary, steadily illuminated stimulus compared with activation by a briefly flashed stimulus. Each data point is derived from one neuron and a least-squares regression line has been fit to the data. Flash durations ranged from 50–450 ms. Numbers of neurons in each category are nine saccade-activated, nine position/drift-activated, and 11 mixed.

wide range (0–14 spike/s) and the neurons were broadly distributed over the cortical layers.

Position/drift neurons: Comparisons with other eye movement classes

Like the mixed cells, the position/drift neurons included a few direction-selective cells, which surprised us, because it implies that there are functionally distinct subpopulations among the direction-selective neurons in V1. Position/drift cells had a wide range of maintained discharge rates with a lighted blank field (0–28 spikes/s), and they were broadly distributed across the cortical layers.

The position/drift cells had mean AR widths less than half those of the saccade and mixed cells (Table 2, $P < 0.001$, Mann–Whitney U Test). However, the failure of crossing saccades to activate position/drift cells does not seem to be due to inadequate stimulation related to the small AR widths. Position/drift neurons with AR widths 15–16 minarc were not activated by

crossing saccades, whereas saccade and mixed cells with AR widths only 2–4 minarc wider were clearly activated.

Because the position/drift neurons were so different from the other two classes, we combined data from the saccade cells and the mixed cells for purposes of comparison. Contributing to the smaller AR widths of the position/drift neurons is the fact that nearly half of them (6/14) had ARs with only one subfield, either increment- or decrement-responsive, but not both. This configuration was significantly rarer in the other two eye movement groups, where only 2/30 cells tested had receptive fields with one subfield ($P < 0.02$, chi-square test).

To characterize more precisely cells that had two subfields, we measured the degree of overlap between the subfields for 32 cells using sweeping bars (see Methods). Six neurons with an overlap index <0.3 were considered simple cells; the remaining 26 cells had an overlap index >0.6. Of the cells with two subfields, three of five position/drift cells, and three of 27 cells in the other groups were simple cells. The probability of this distribution of receptive-field types arising by chance is only $P = 0.03$ (Fisher's exact test). Thus, the position/drift group is more likely to respond to only one sign of contrast at each point of the AR, because position drift neurons are more likely to be simple cells or to have only one subfield. Conversely, most cells among the saccade and mixed classes had strongly overlapping increment and decrement sub-fields, and responded to both signs of contrast at most points within the AR.

Extraretinal influences of fixational saccades

Although much of the activity associated with fixational eye movements clearly resulted from interactions between the stimulus and the AR of the neuron, we also tested for extraretinal influences. We analyzed spike activity recorded during fixation trials with only a tiny red (3 minarc) fixation target and a lighted blank gray monitor screen or a completely dark field. Saccade-triggered histograms of neuronal discharges were constructed for cells that had an ongoing discharge of at least 9 spikes/s and at least five saccades whose modulatory effects did not overlap temporally with the effects of adjacent saccades (see Methods.) These analyses were carried out for data from M45, the monkey from which most of the data showing stimulus-related eye movement activation was recorded (Fig. 12, left column), and for an additional sample of 34 cells recorded from M42, another rhesus monkey (Fig. 12, right column).

For M45, the average across all cells (third row) showed a clear modulation of neuronal firing by fixational saccades, both in the light and in the dark. The ongoing activity was reduced 60–70 ms after saccade onset followed by an increase in firing for 200–

Fig. 10. Saccade-triggered activity during presentation of a stationary, steadily illuminated stimulus compared with activity evoked by flashing a stimulus of the same color and sign of contrast. Each pair of histograms is derived from one neuron. The left member of the pair is the saccade-triggered spike histogram. The eye movement classification is indicated in the upper left corner of the histogram (saccade = *sac*, mixed = *mix*, position/drift activated = *pos*). The right member of each pair is the spike histogram of flash-evoked activity. The thick horizontal line under the time axis indicates flash duration. In most cases the stimulus was stabilized during the flash presentation. All spike histograms have 10-ms bins, but some bins of the flash-evoked responses appear wider than others because flash durations and time scales differ from cell to cell. The histogram pairs are ranked according to the transiency index, TI, for the saccade-related activity (see text). High TI values begin at the top of the left column, and low TI values are at the bottom of the right column. The text above each histogram gives the TI rank for saccade activation, the file number, the number of trial segments used, and the TI value. The mean maintained discharge rate with a blank field is indicated by a horizontal dashed line for those cells with nonzero ongoing rates.
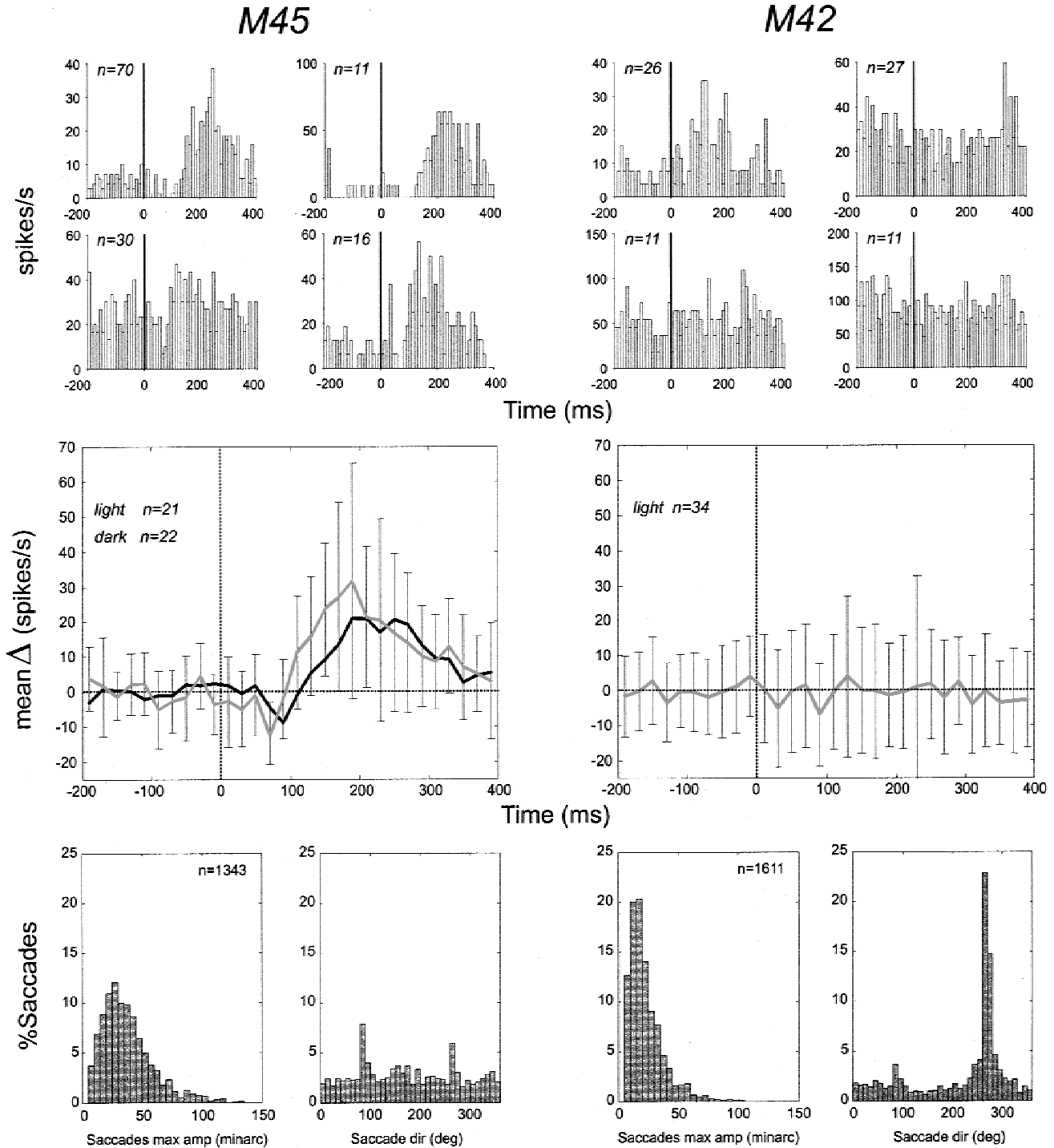
Fig. 12. Modulation of maintained discharge by fixational saccades. *Left column*. Data from M45. *Top row*. Saccade-triggered spike histograms for two individual cells recorded in the dark. For this and all other histograms from individual cells in this figure, data from the cells with the maximal number of trial segments (*n*) meeting our criteria are presented (see text). *Second row*. Saccade-triggered spike histograms for two individual cells recorded with a blank gray field. *Third row*. Average across all cells with at least five acceptable trial segments. Unlike other spike histograms in this paper, a 20-ms bin width is used here to smooth the waveform. Data recorded in the light (*n* = 18, light line) are plotted together with data recorded in the dark (19 cells, black line). For each cell, the mean spike rate in the period 200 ms before the saccades was subtracted before averaging across cells. Error bars are standard deviations of the means across cells recorded in the light. Standard deviations in the dark were similar in size. *Bottom row*. Histograms from trials recorded in the light for saccade amplitudes (left) and directions (right) expressed as percentages. If a saccade had a looping trajectory, the maximum vectorial displacement was taken rather than the final position. *Right column*. Data from M42. Same conventions as left column; all data from M42 were collected in the light.

300 ms. The mean peak-to-trough difference in both illumination conditions was significantly different from 0 ($P < 0.0001$, two-tailed t-test).

The degree of extraretinal influence was also examined on a cell-by-cell basis by subtracting the mean firing rates of each cell in the period from 50 to 100 ms after each saccade (trough) from the mean firing rate in the period 100 to 300 ms after the saccade (peak). For M45, the mean peak-to-trough difference was greater than 0 for all 21 cells in the light and 21 of 22 cells in the dark. The probability of such an outcome occurring by chance is less than 0.001 (sign test, two-tailed) for both illumination conditions. These results show that an extraretinal influence was consistently present in the data from this monkey, both in the light and in the dark.

The temporal pattern of the extraretinal modulation is quite similar to the firing pattern reported by Leopold and Logothetis (1998). However, our data were collected with no visual stimulation, and therefore indicate that our saccade-related modulation is extraretinal in origin. Furthermore, the extraretinal influence has a very different form and time course from stimulus-activated firing patterns (Figs. 8 and 10; cf. Martinez-Conde et al., 2000) which is strong evidence that the modulation of the ongoing activity is not due to unintended visual stimulation (such as objects in the peripheral field).

Data from the other monkey, M42, were available only for fixation in the light. They did not show the same clear saccade modulation. Results from cell to cell were inconsistent (Fig. 12, right column, first and second rows), and the overall average had no clear pattern (third row).

The apparent lack of an extraretinal effect for M42 may be related to the spatiotemporal patterns of its fixational eye movements. M42 made ~38% of its saccades within 10 deg of the downward direction (260–280 deg) whereas only ~9% of M45's fixational saccades were within 10 deg of the downward direction (Fig. 12, bottom row). The downward saccades of M42 were part of a pattern of upward drifts corrected by downward saccades, a common pattern among monkeys (Skavenski et al., 1975; Gur & Snodderly, 1997). For M42, the drift rate was sufficiently high that a relatively high saccade frequency was necessary to compensate for it (Table 3). Interestingly, calculation of the standard deviation of eye position during the trial did not identify this instability because the monkey managed to maintain position near the mean fixation locus in spite of the rapid motions. However, we suggest that the higher drift rate and higher saccade frequency may spread the extraretinal influences more uniformly throughout the trial and hence make it more difficult to identify them. We hope this hypothesis will be tested by other investigators, who can compare the eye movement statistics of their monkeys to help clarify individual differences in the physiological results.

Discussion

Selectivity of eye movement activation: Implications for neural coding

The two components of fixational eye movements, saccades and drifts, activate different subpopulations of V1 neurons in distinctive ways. Saccade and mixed cells fire bursts of spikes when a fixational saccade moves the AR onto the stimulus, off the stimulus, or across the stimulus. The sign of contrast (light or dark) is unimportant. These characteristics imply that the burst responses are conveying rather crude information about the details of the stimulus. For example, if an appropriately oriented stimulus contour activated the neuron following a saccade, it would be difficult to determine whether the contour remained in the AR (saccade moved AR onto contour) or was outside it (saccade moved AR across the contour). This ambiguity would have particular relevance when viewing complex natural images (Gallant et al., 1998), because the neuronal discharge could be evoked either by a stimulus feature crossed by the AR during the saccade, or by a completely different feature on which the AR landed at the end of the saccade.

It has often been suggested that bursts of spikes convey more information about a stimulus than other measures of neuronal activity (Reich et al., 2000). This proposal could be interpreted to imply that the bursts (Martinez-Conde et al., 2000) fired by saccade and mixed cells following fixational saccades are the important sources of information about the visual scene. Although the bursts are important, understanding their role will require accommodating the ambiguities described above, as well as assessing the utility of the sustained activity of mixed and position/drift neurons. We have not yet presented complex or nonoptimal stimuli to the different eye movement classes, but the close correspondence between responses to flashed stimuli and to saccadic transients (Figs. 10 and 11) suggests that the neuronal responses will behave in a predictable manner.

An alternative role for the saccade neurons might be to participate in the suppression of visual input associated with saccades (Matin, 1974), which selectively affects the magnocellular pathway (Burr et al., 1994; Bridgeman & Macknik, 1995). Several of the saccade cells were assigned to layer 4B, which is part of the magnocellular pathway (Lund, 1988). Theoretically, they could participate in saccadic suppression by inhibiting other neurons that

Table 3. *Eye movement statistics for two rhesus monkeys, M42 and M45*[a]

Monkey	Number of trials	Sac. Freq. (sac/s)	Vertical SD (minarc)	Horizontal SD (minarc)	Vert Drift mean speed. (deg/s)
M42	133	2.34	8.48	8.32	2.14
M45	159	1.65	11.24	11.48	1.63

[a]The monkeys viewed a blank gray screen of luminance 1 cd/m^2. Only trials where eye position on both axes remained within ± 100 minarc of the mean fixation locus were included. SD = standard deviation of all eye position samples computed for each trial and averaged across all trials. Drift speed was computed from successive eye position samples by taking the mean of all speeds that did not exceed the criterion for saccadic movements (see Methods). This simple procedure results in higher estimates of drift speeds than would be produced by more stringent selection of trial segments and optimal noise reduction of the eyetracker signals, but it is adequate for comparisons between animals.

carry stimulus information, or by adding noise to the signal, thereby raising thresholds and making stimulus events undetectable at the times of saccades. This role would make the saccade neurons the source rather than the target of saccadic suppression, an idea previously suggested by Bair and O'Keefe (1998). To clarify this issue, our future experiments will test whether neurons that are activated by fixational saccades are suppressed or activated by the large saccades that have typically been used to study saccadic suppression.

An intriguing question is whether the saccade and mixed neurons could contribute to a perceptually stable visual world. Murakami and Cavanagh (1998) have proposed that the "motion signals" evoked by fixational eye movements are processed by the visual system to compute a local motion minimum, which is interpreted as a stationary region in the visual scene. For this computation, the details of the image are not important, and the selectivity for motion shown by the saccade cells and some mixed cells would be appropriate. Further investigation of this idea would be well justified.

The position/drift neurons must play a quite different set of roles that are complementary to those of the other eye movement classes. Because position/drift neurons do not respond to saccades, they may be spared the potentially detrimental effects of saccade-related activity. They signal accurately the position of stimulus features on the retina, and in many cases the sign of contrast. Thus, their activity could in principle be the basis for a reconstruction of the image (Stanley et al., 1999).

If position/drift neurons are coding details of the image, then their behavior constrains neural coding schemes that rely on very precise spike timing (Mainen & Sejnowski, 1995; Bair & Koch, 1999). Any timing scheme must accommodate the fact that the neuronal firing is strongly modulated by unpredictable eye drifts, as well as uncompensated head movements as discussed below.

Applicability of the results to natural viewing

Most studies of fixational eye movements immobilize the head of the subject to minimize the effects of head and body movements so that retinal image motions are primarily caused by eye movements. Under natural viewing conditions, however, head and body movements are unavoidable, and they are only partially corrected by the vestibulo-ocular reflex. As a result, for human subjects the retinal image speeds during maintained fixation in a natural viewing situation are about 2–4 times as high as they are with the head immobilized (Skavenski et al., 1979; Steinman et al., 1982). How would these higher speeds affect our characterization of eye movement activation?

In many respects, the patterns of activation by fixational eye movements can be predicted from the stimulus–response properties of the neurons. Saccade cells have transient responses and respond well to rapid retinal image motions. Position/drift cells have more sustained responses and are activated by slow retinal image speeds or by a stationary stimulus. Mixed cells are intermediate in their properties. Thus, it is likely that some cells would shift their firing pattern in a predictable manner when the head is free to move and retinal image speeds increase. For example, some saccade cells might fire during drift periods when the head is free and retinal image speeds are higher. However, we predict that the position/drift cells would continue to ignore the occurrence of saccades and only fire during the drift periods. In summary, we expect that with the head free, more cells would be activated during the drift periods, but the three types of eye movement activation we have described would still be distinguishable.

Retinal contributions

The sensitivity of cortical neurons to motions of the retinal image that are only a fraction of the receptive-field size is not surprising, because sensitivity to tiny image displacements is already present in the retina. Scobey (1981) has reported that all on-type retinal ganglion cells of anesthetized rhesus monkeys responded to image movements that were less than 1/10 the diameter of their receptive fields. Given this input from the retina, it is likely that most cortical cells should be activated by small stimulus motions, regardless of the sizes of their receptive fields. Furthermore, one should expect that the retinally based sensitivity to small motions could continue to be evidenced by cortical neurons in more central visual areas even though receptive fields are larger (Leopold & Logothetis, 1998).

Extraretinal influences

We are the first to demonstrate physiologically the presence of extraretinal influences associated with fixational saccades, but our results can be considered a logical extension of earlier studies based on large voluntary saccades. An extraretinal influence on cortical areas V1 and V2 was previously demonstrated by showing that spontaneous activity of neurons in these areas is modulated by saccades made in darkness (Duffy & Burchfiel, 1975; Kayama et al., 1979). In addition, a small percentage of V1 cells appear to give weaker responses during saccades than during fast stimulus motion (Fischer et al., 1981). In general, large saccades and high stimulus velocities have been found to activate poorly the supragranular cells in V1 that project to higher cortical areas (Judge et al., 1980).

Following up these studies with large saccades, Leopold and Logothetis (1998) examined the effects of small saccades on neurons in several cortical areas; they concluded that small saccades had a primarily inhibitory influence on about two-thirds of the V1 neurons that were influenced by small saccades. Their experimental conditions included presentation of a grating stimulus during a discrimination task in a binocular rivalry experiment and analysis of very small saccades (median 10 minarc). The time course of the spike train modulations that they observed is more comparable to our extraretinal effects (Fig. 12) than the saccadic activation that occurs when a near-optimal stimulus is present (Figs. 8 and 10). Thus, their results probably contain a mixture of stimulus-driven and extraretinal effects. The strong inhibitory effect that they observed may also be related to the high baseline firing rate indicated in their Fig. 2a.

In our experiments, activation by fixational saccades and flash responses are both brisk and of relatively short latency, usually on the order of 50 ms. The latencies of these stimulus-evoked discharges are sufficiently short that they clearly precede the main peak of extraretinal activation, which occurs near 200 ms. However the extraretinal influences could modulate the stimulus-driven activation and contribute to the later stages of firing for some cells. Given its longer latency, the extraretinal activation could conceivably be driven by descending inputs to V1 from extrastriate cortical areas (cf. Toyama et al., 1984).

Concluding remarks

Fixational eye movements have been primarily a methodological nuisance for most behavioral neuroscientists, because they are an uncontrolled factor that can contribute variability to the results (Gur et al., 1997). In this paper, we have shown that these same eye
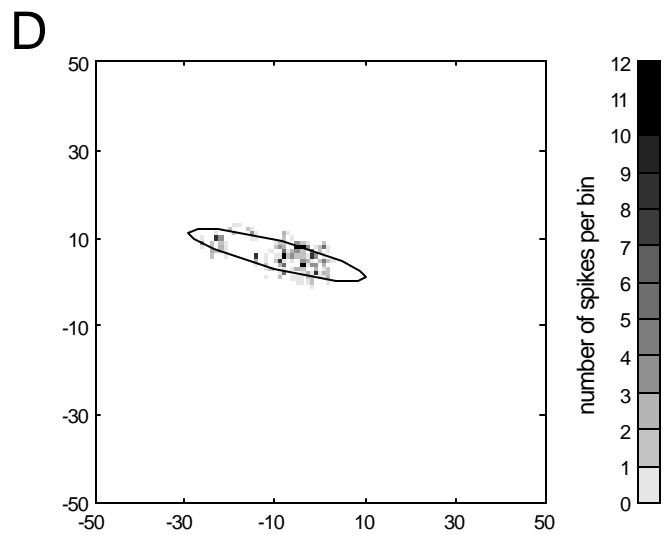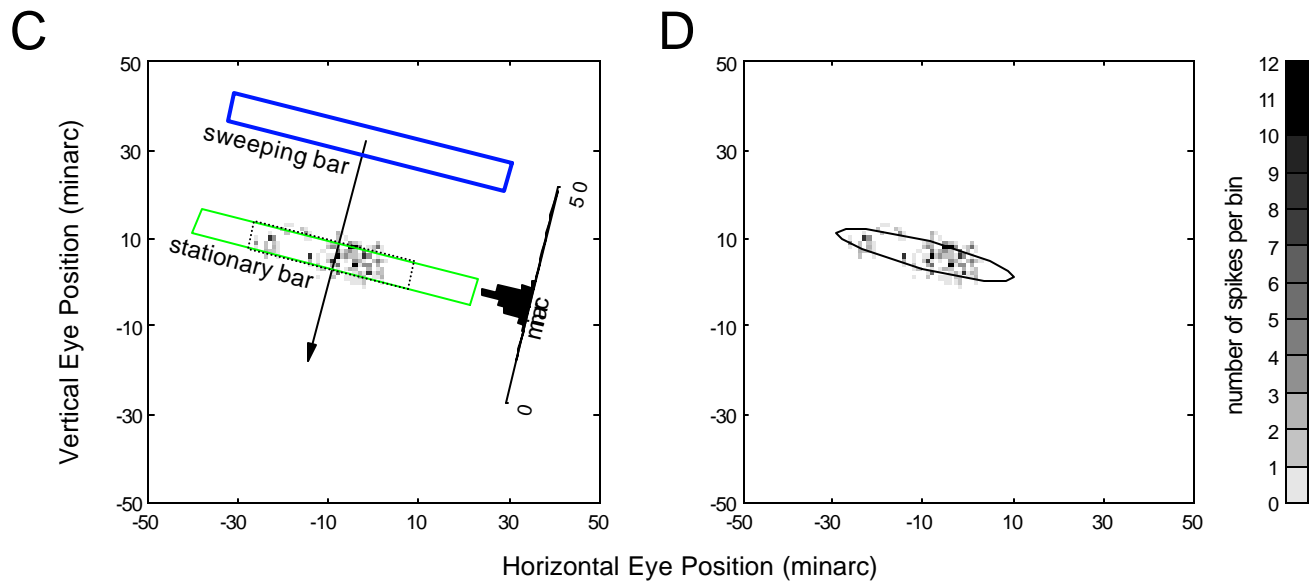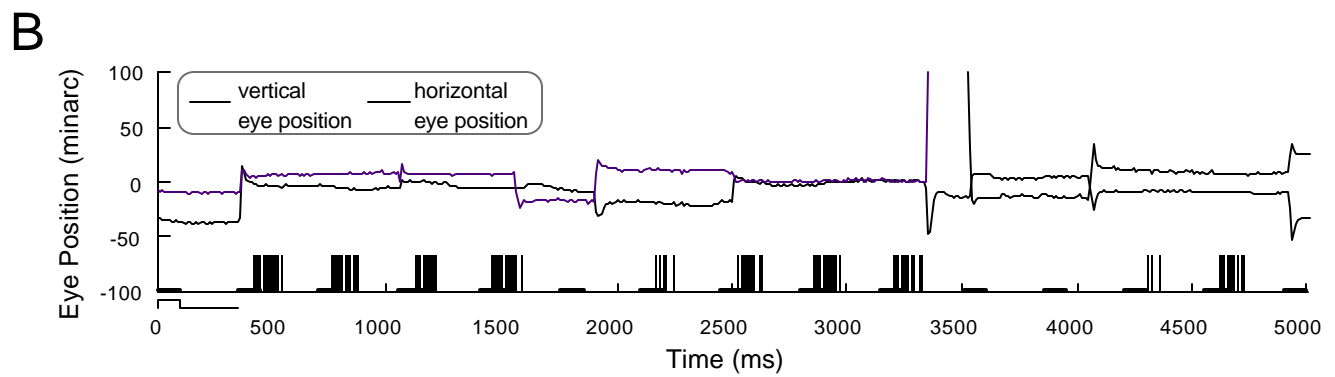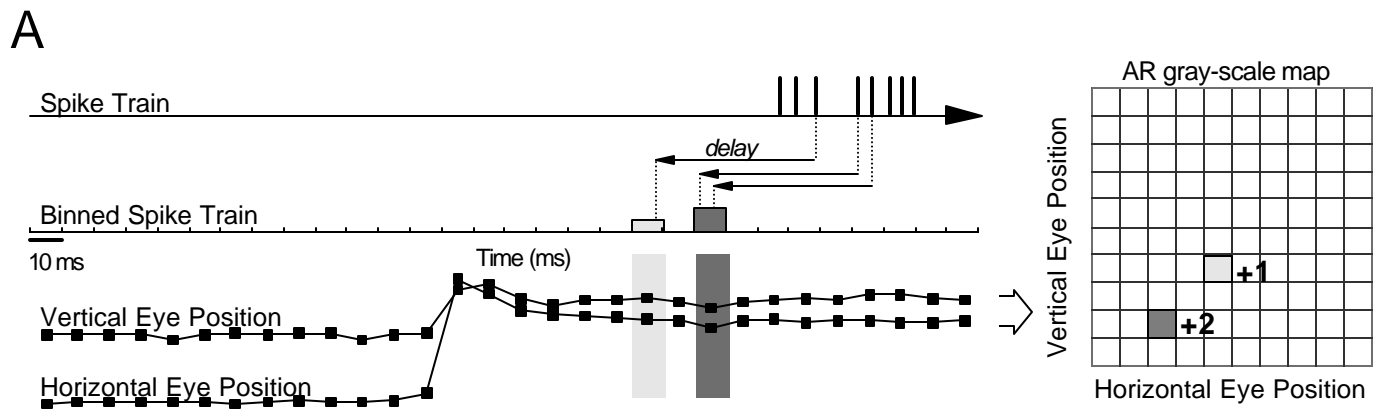
movements have strong and reliable effects that can be used to parse V1 neurons into classes with distinctive functional properties. Future research will need to determine the ways that the different eye movement classes participate in perceptual processes.
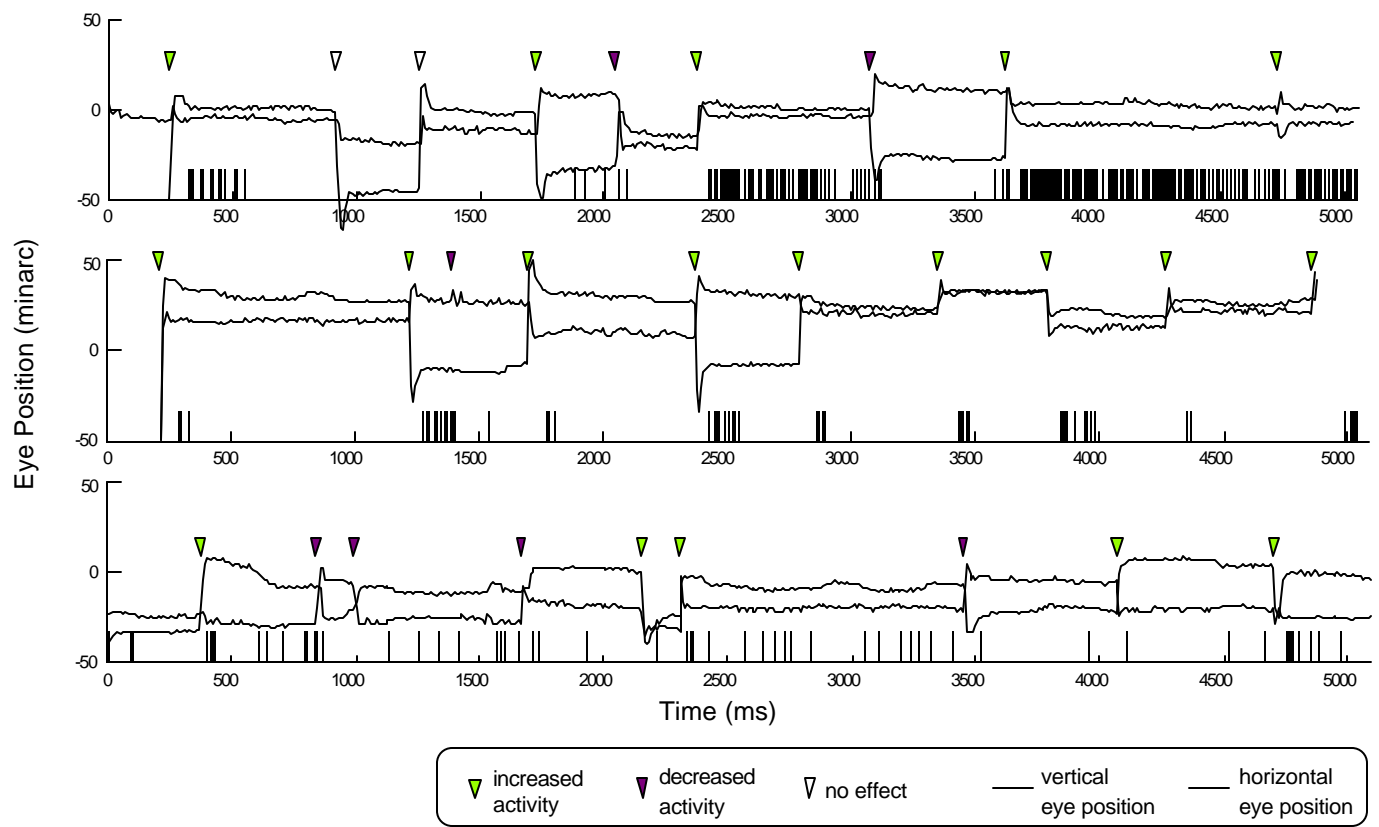
Acknowledgments

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A

Spike Train

delay

Binned Spike Train

10 ms

Time (ms)

Vertical Eye Position

Horizontal Eye Position

AR gray-scale map

Vertical Eye Position

+1

+2

Horizontal Eye Position

B

Eye Position (minarc)

| vertical eye position | horizontal eye position |

100

50

0

-50

-100

0   500   1000   1500   2000   2500   3000   3500   4000   4500   5000

Time (ms)

C

Vertical Eye Position (minarc)

50

30

10

-10

-30

-50

sweeping bar

stationary bar

50

0

mac

-50   -30   -10   10   30   50

Horizontal Eye Position (minarc)

D

50

30

10

-10

-30

-50

-50   -30   -10   10   30   50

number of spikes per bin
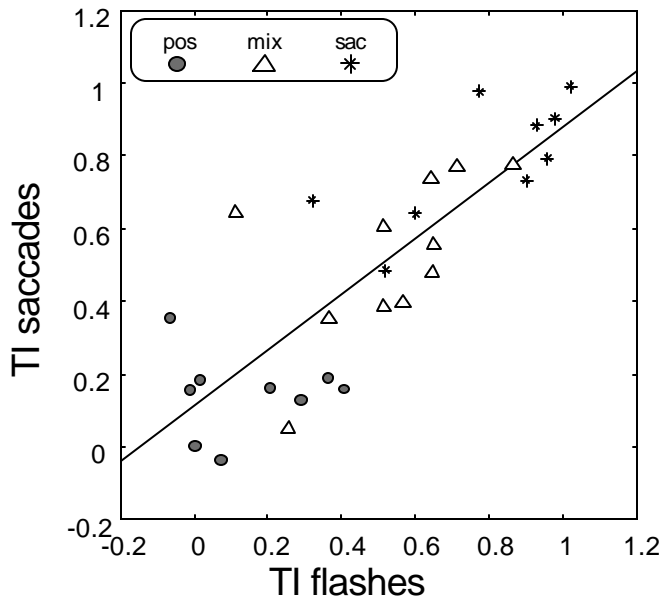
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Fixational eye movements and cortical activity, Figure 1, bottom, 2 columns

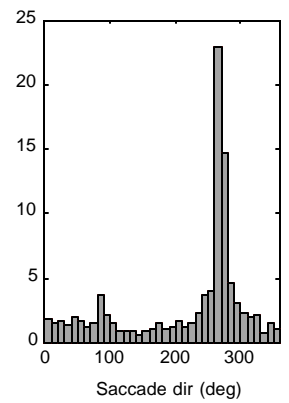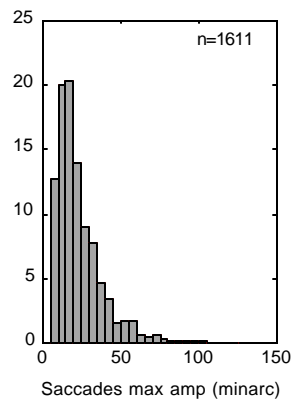Fixational eye movements and cortical activity, Figure 2, bottom, 2 columns
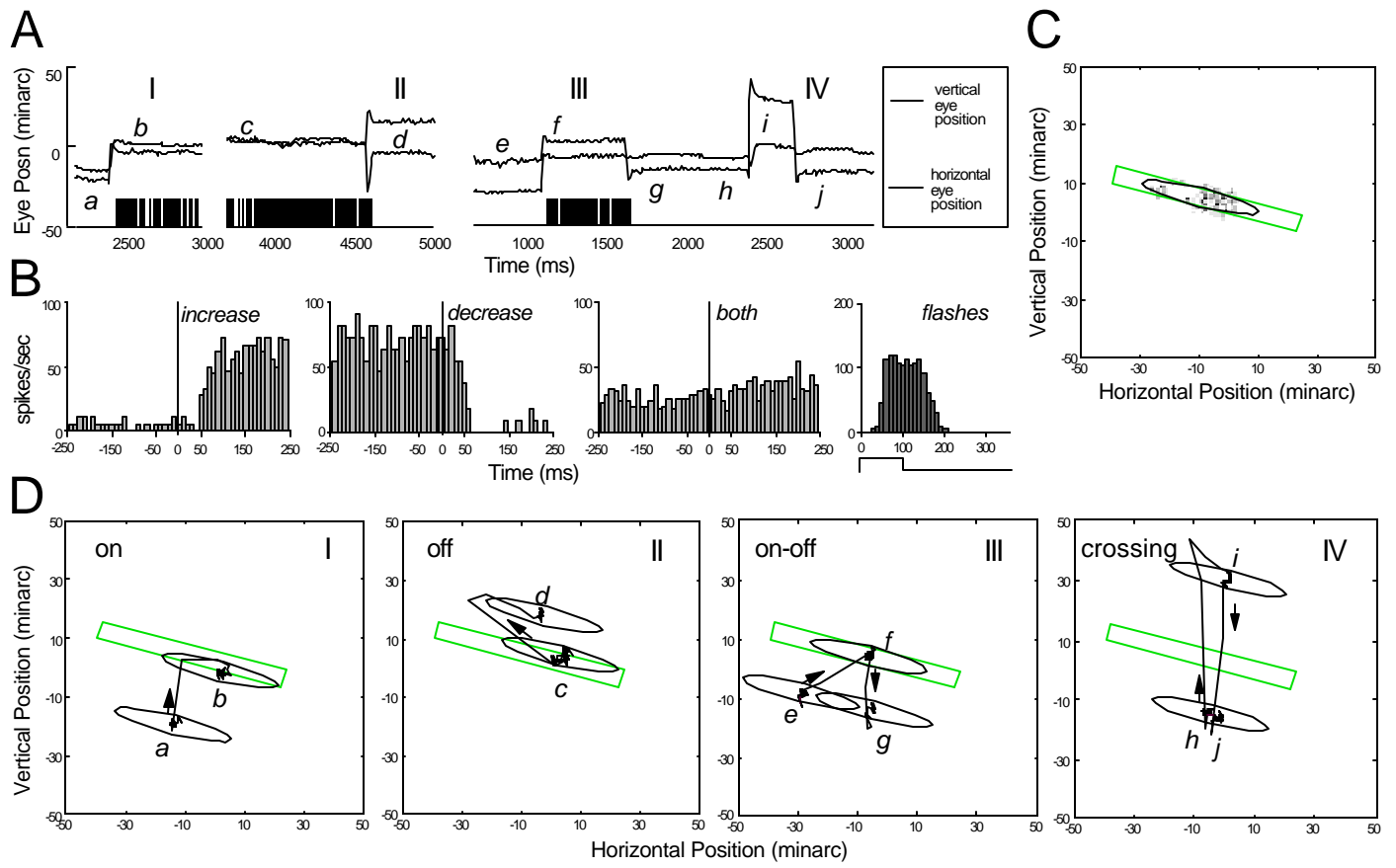
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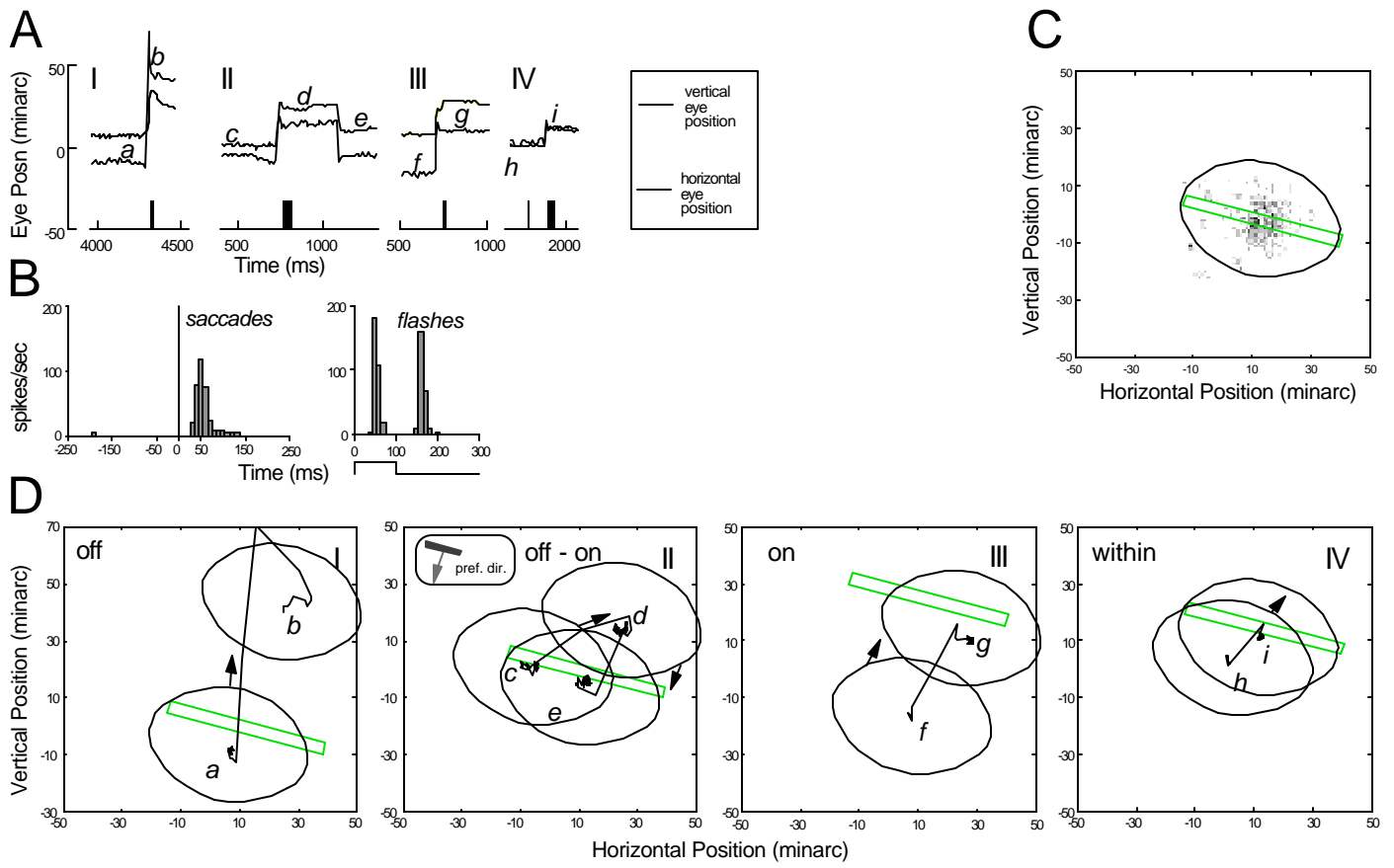
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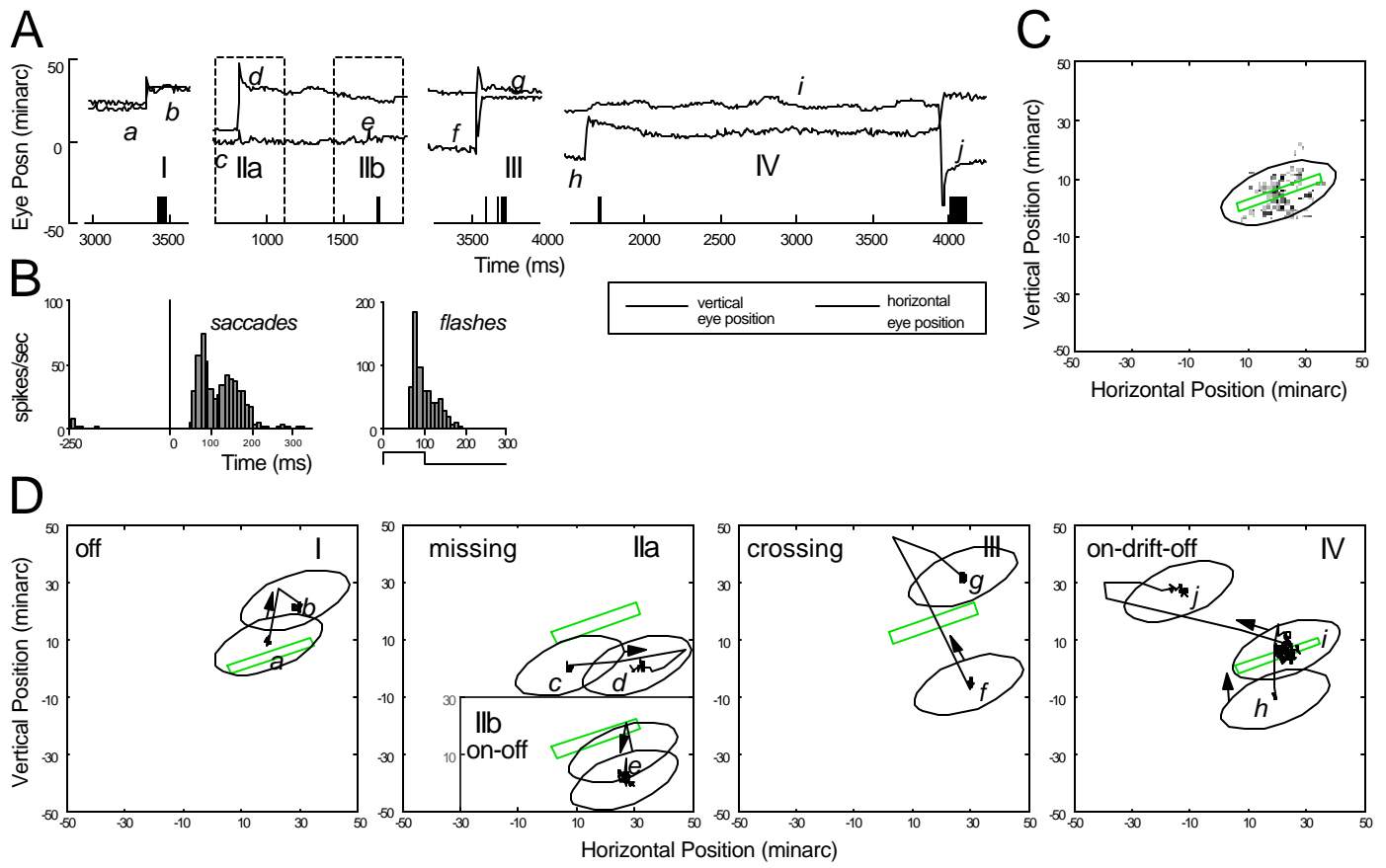
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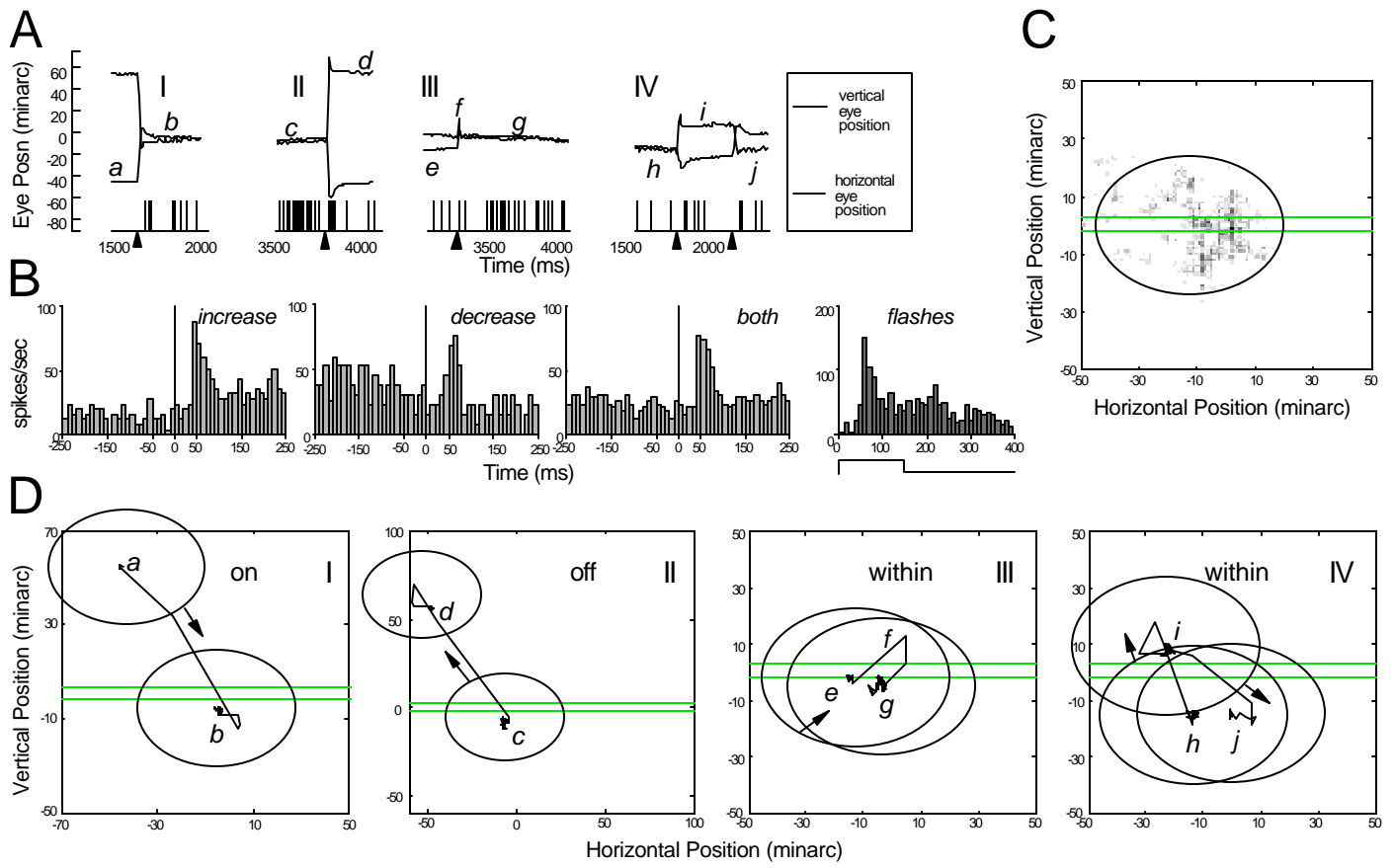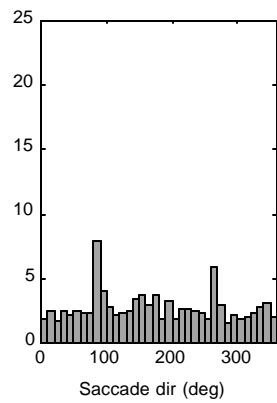
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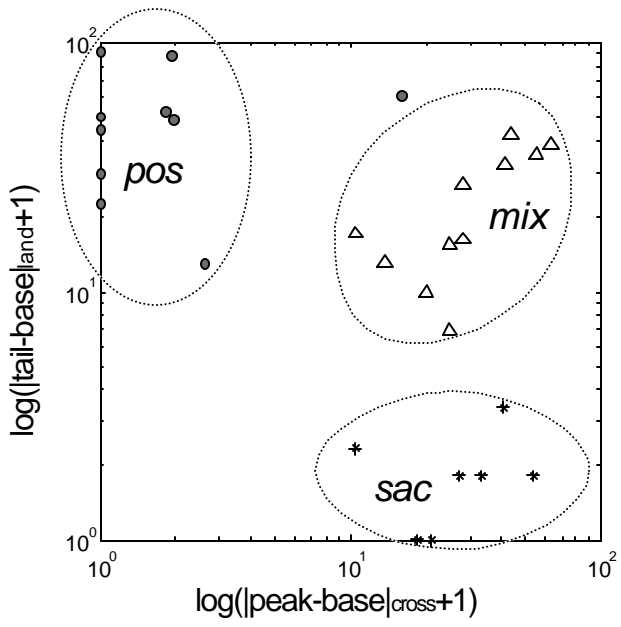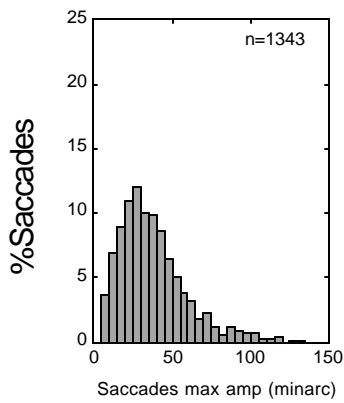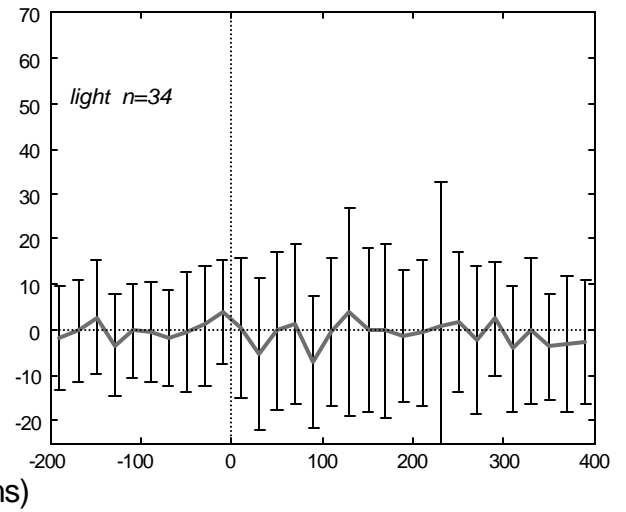
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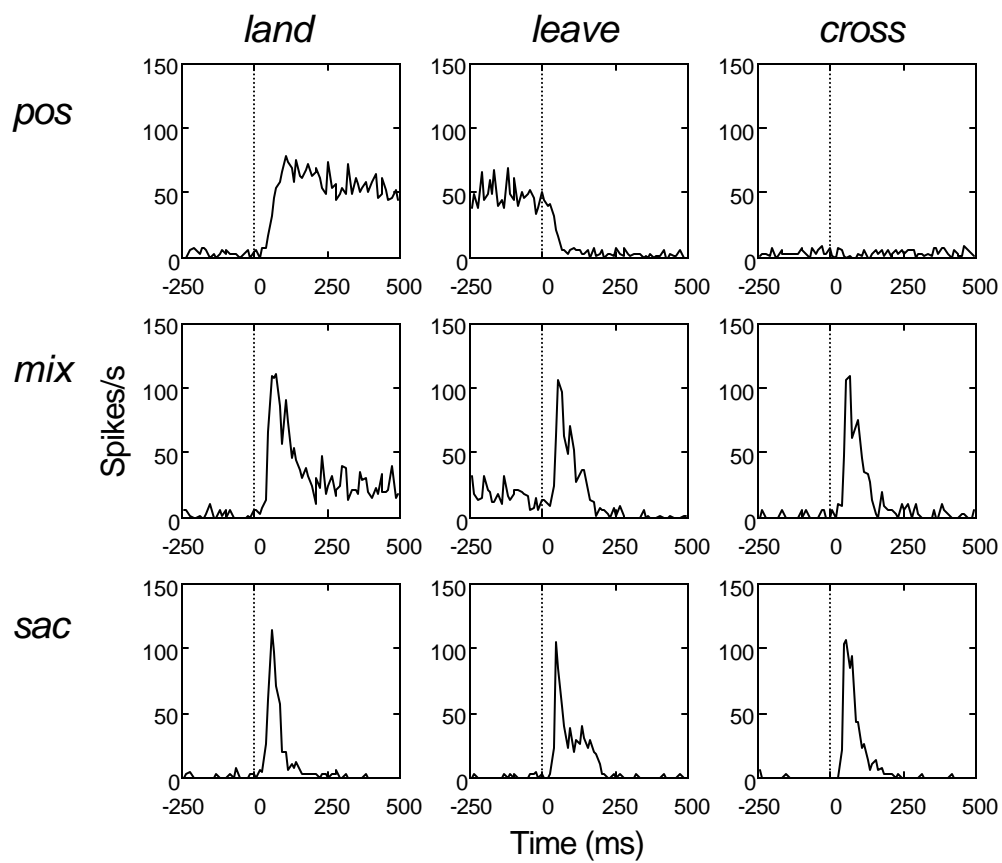
Fixational eye movements and cortical activity, Figure 8, bottom, 2 columns

pos   *mix*   *sac*

All cells (n=50)

-0.4   -0.2   0   0.2   0.4   0.6   0.8   1   1.2   1.4

Cells with specific saccadic displacements (n=28)

Normalized firing rate (post saccade - drift)
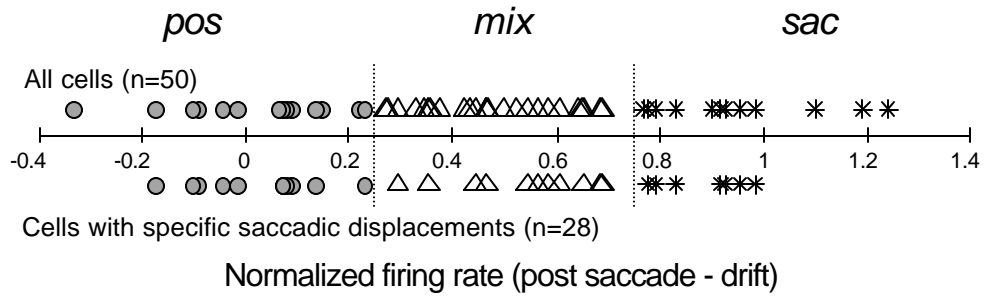
Fixational eye movements and cortical activity, Figure 9, bottom, 2 columns
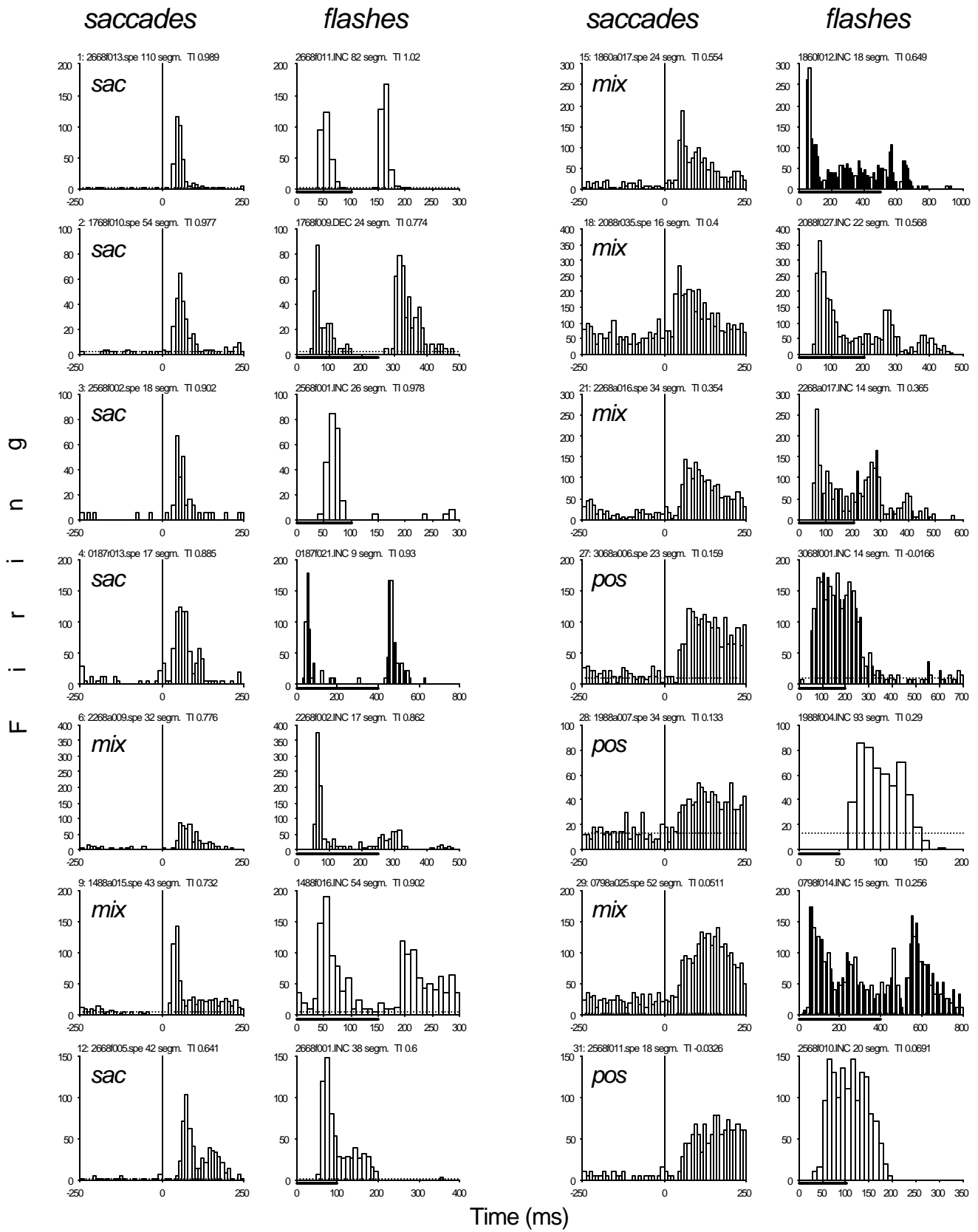
Fixational eye movements and cortical activity, Figure 10, bottom, 2 columns

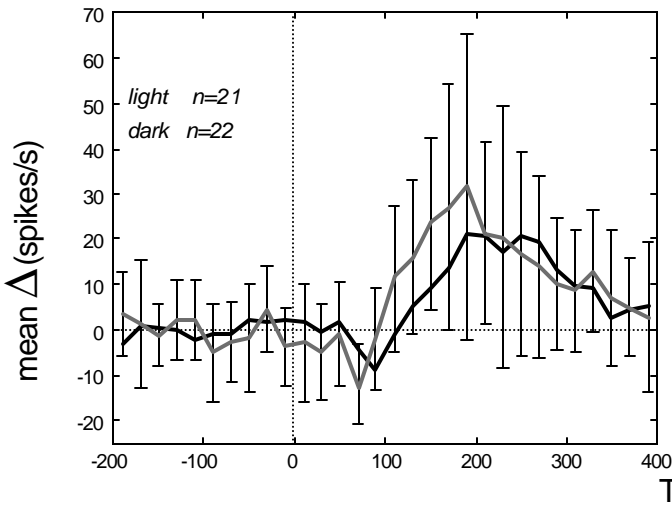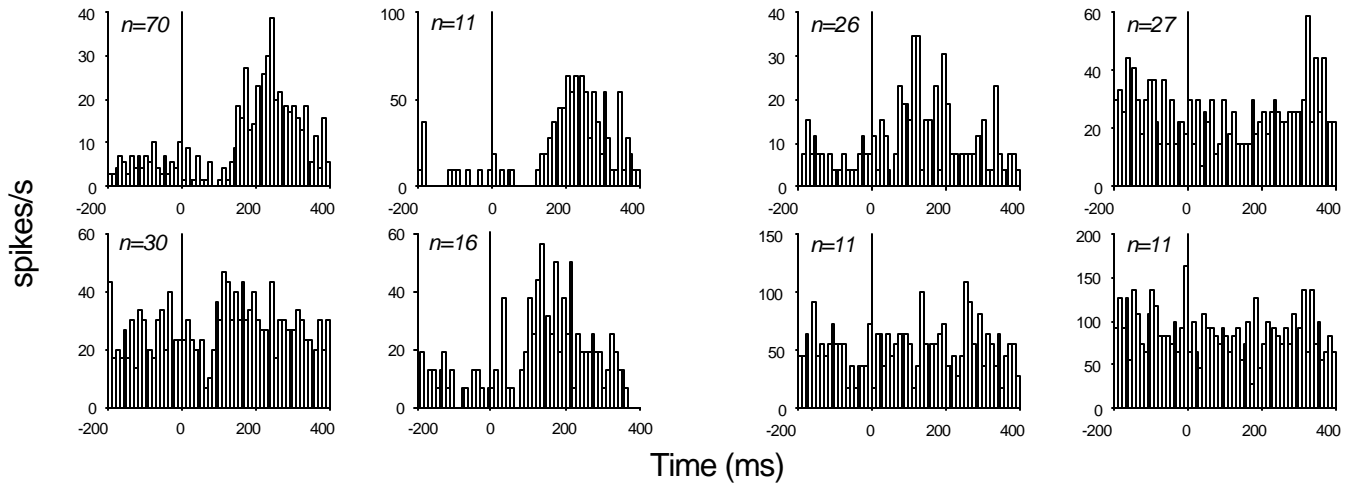Fixational eye movements and cortical activity, Figure 11, bottom, 1 column

Fixational eye movements and cortical activity, Figure 12, bottom, 2 columns