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Saccade-Related Activity in Monkey Superior Colliculus I. Characteristics of Burst and Buildup Cells

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SUMMARY AND CONCLUSIONS

1. In the monkey superior colliculus (SC), the activity of most saccade-related neurons studied so far consists of a burst of activity in a population of cells at one place on the SC movement map. In contrast, recent experiments in the cat have described saccade-related activity as a slow increase in discharge before saccades followed by a hill of activity moving across the SC map. In order to explore this striking difference in the distribution of activity across the SC, we recorded from all saccade-related neurons that we encountered in microelectrode penetrations through the monkey SC and placed them in categories according to their activity during the generation of saccades.

2. When we considered the activity preceding the onset of the saccade, we could divide the cells into two categories. Cells with burst activity had a high-frequency discharge just before saccade onset but little activity between the signal to make a saccade and saccade onset. About two thirds of the saccade-related cells had only a burst of activity. Cells with a buildup of activity began to discharge at a low frequency after the signal to make a saccade and the discharge continued until generation of the saccade. About one third of the saccade-related cells studied had a buildup of activity, and about three fourths of these cells also gave a burst of activity with the saccade in addition to the slow buildup of activity.

3. The buildup of activity seemed to be more closely related to preparation to make a saccade than to the generation of the saccade. The buildup developed even in cases when no saccade occurred.

4. The falling phase of the discharge of these saccade-related cells stopped with the end of the saccade (a clipped discharge), shortly after the end of the saccade (partially clipped), or long after the end of the saccade (unclipped).

5. Some cells had closed movement fields in which saccades that were substantially smaller or larger than the optimal amplitude were not associated with increased activity. Other cells tended to have open-ended movement fields without any peripheral border; they were active for all saccades of optimal direction whose amplitudes were equal to or greater than a given amplitude. We found both types of movement fields at all movement field eccentricities studied within the SC.

6. The activity of cells with open-ended movement fields did not result from the smear of the visual target as it swept across the retina during a saccade because the discharge of the cell was still present when saccades were made in the dark to remembered rather than visual targets. The activity of these cells was also not due to the occurrence of corrective saccades because the activity was visible whether or not there was one.

7. In penetrations through the intermediate layers of the SC, we usually found cells with a burst of activity and those with closed movement fields to lie more dorsally than those with a buildup of activity and open-ended movement fields.

8. We also compared the activity of the saccade-related cells with the activity of fixation cells located in the rostral pole of the SC. We found a transition between saccade-related cells with open-ended movement fields and fixation cells. Cells within this transition zone were tonically active during fixation but also discharged during small contraversive saccades. These fixation cells were encountered deeper in the intermediate layers, at the same level as the cells with open-ended movement fields and buildup of activity. We propose that fixation cells form a rostral extension of the layer of cells with a buildup of activity.

9. We conclude that these characteristics of the saccade-related cells overlap sufficiently to allow us to place the cells into two groups. Burst cells have a high-frequency burst occurring immediately before saccades and no buildup of activity; the majority have clipped activity at the end of the saccade and usually have closed movement fields. In contrast, buildup cells show activity beginning with the signal to make a saccade that continues until the generation of the saccade; the majority have partially clipped activity at the end of the saccade and have open-ended movement fields. Because we encountered the cells with burst activity and closed movement fields more dorsally than we did cells with buildup activity and open-ended movement fields, we hypothesize further that the burst and buildup cells can be regarded as separate functional sublayers with the burst layer on top and the buildup layer below. The buildup cells are similar to the saccade-related cells in the cat SC, but the burst cells may be an added feature of the primate SC.

INTRODUCTION

Neurons concentrated in the intermediate layers of the monkey superior colliculus (SC) discharge in relation to saccadic eye movements (for review, see Sparks and Hartwich-Young 1989). This discharge precedes saccades to an area of the visual field that defines the movement field of the cell. Within this movement field there is a gradient of cell discharge, with the peak discharge preceding saccades of a given amplitude and direction (Sparks and Mays 1980; Wurtz and Goldberg 1972). The amplitude and direction of this optimal discharge for different cells forms an orderly map spread across the SC, with the smallest saccades represented in the rostral SC and the largest in the caudal SC (Robinson 1972; Schiller and Stryker 1972). The most intensively studied cells have been those that show a vigorous burst of activity before the onset of saccades, and this burst is closely related in time to the initiation of saccades (Sparks 1978), although other saccade-related cells with a discharge less closely tied to the saccade have been described (Mohler and Wurtz 1976; Sparks 1978).

Where these burst cells fit into the brain circuit for the generation of saccades has been less certain. It is generally

believed that saccades are generated by a closed-loop control system (Jürgens et al. 1981; Robinson 1975). In the monkey, the characteristics of the falling phase of the high-frequency burst of SC cells led to the suggestion that the cells were inside the feedback loop controlling the amplitude of the saccade (Waitzman et al. 1988, 1991). The logic of this argument was that the clipped discharge of these cells (a discharge that ends as the saccade ends) resulted from feedback to the SC. In such a model of saccade generation, which included the SC in a feedback loop (Waitzman et al. 1988, 1991), the current change in eye position was compared with the initial desired change in eye position by the burst cell in the SC. The difference between these signals, dynamic motor error, fell as the saccade reached the target (T), as did the discharge of some SC burst cells (Waitzman et al. 1988, 1991).

In the cat, recent experiments have also led to the conclusion that the SC is within the feedback loop controlling the amplitude of saccades, but for reasons quite different from those described for the monkey. Munoz et al. (1991) described cells in the cat SC that discharged before the onset of saccades and more generally before shifts in gaze (combined eye and head movement) that had substantially different properties from the burst cells in the monkey SC. These cat SC cells had a slow buildup of activity preceding the shift of gaze rather than a discrete burst of activity. Most striking, however, was the observation that these cells seem to discharge as if the locus of activity were moving across the SC during the course of the saccade (the moving hill hypothesis). At the start of a large-amplitude gaze shift, neural activity was centered in the caudal SC, and during the gaze shift cells located progressively more rostral in the SC began to discharge. Munoz et al. (1991) argued that when this moving hill of activity reached the fixation cells located in the rostral SC, the saccade was terminated. This model of saccade generation also placed the SC in the feedback loop controlling the amplitude of the saccade. Thus, while the location of the SC in relation to a feedback control system for the amplitude of saccades had remained a puzzle for almost two decades, these two sets of experiments both reached the conclusion that the SC was in the feedback loop.

These results, however, leave striking differences between the cat and monkey because the activity of SC cells in the two species appears to be so different. The burst neurons studied in the monkey SC are rarely found in the cat (Munoz et al. 1991; Peck 1987), and the shifting of activity during a saccade seen in the cat SC has not been reported in the monkey.

We therefore revisited the issue of the relationship between the saccade-related activity in the monkey SC and the generation of saccadic eye movements. We recorded from all cells encountered in penetrations through the SC that changed their rate of discharge with saccades. We looked at the activity before the onset of the saccade, the activity at the end of the saccade, and the movement fields of saccade-related cells, and from these observations we hypothesize that the SC saccade-related cells can be regarded as falling into two largely separate groups of cells. The first group, the burst cells, had a burst of activity before the saccade, usually had clipped activity at the end of the saccade, and generally had closed movement fields. The second group, the buildup cells, had continuing activity between the signal for saccade initiation and saccade onset, usually had partially clipped activity at the end of the saccade, and tended to have open-ended movement fields. Because the burst cells tend to lie more dorsally than the buildup cells, we further hypothesize that these two cell types can be regarded as forming separate functional sublayers within the intermediate layers of the SC. We suggest that the buildup cells are sufficiently similar to the saccade-related cells in the cat that they could support a shift of activity during a saccade. The burst cells, on the other hand, may be an enhancement of the SC in the monkey and may contribute to the monkeys's higher velocity saccades.

In the companion paper (Munoz and Wurtz 1995), we examine the changes that occur across the population of burst and buildup cells during the generation of saccades. The separation of cell types allowed us to see a spread of activity in the buildup cells but not in the burst cells, and this distinction allows us to compare the SC activity in the monkey with that in the cat. The characteristics of these SC cell types and their population activity suggest an expanded concept of the role of the SC in the generation of saccades.

A brief report of the experiments described in this paper has appeared previously (Munoz and Wurtz 1992).

METHODS

Physiological and behavioral procedures

We recorded single-cell activity from saccade-related neurons in the SCs of four rhesus monkeys (*Macaca mulatta*) that weighed between 5 and 12 kg. The monkeys (3 males, 1 female: identification letters *c, p, g,* and *a*) were prepared for behavioral training and single-cell recording using the same procedures recently described (Munoz and Wurtz 1993). Eye movements were recorded using the magnetic search coil technique (Fuchs and Robinson 1966; Judge et al. 1980), which had a resolution of 0.1°. Horizontal and vertical eye position were digitized at 500 Hz. Single-cell recordings from the SC were made through an implanted recording cylinder angled 38° to the posterior of vertical; the center was directed at the midline 15 mm above and 1 mm posterior to the interaural line. All experimental protocols were approved by the Institute Animal Care and Use Committee and complied with Public Health Service Policy on the humane care and use of laboratory animals. The monkeys were under the care of the Institute veterinarian.

The animals were trained to perform several visuomotor tasks for liquid reward. During the experiments, monkeys were seated in a primate chair with the head restrained for the duration of the experiment (3–6 h). The monkey had an unobstructed view of 70 × 70° (±35° from center in any direction) of a tangent screen positioned 86 cm in front of it. Each behavioral trial lasted ~2–3 s and was preceded by an initial 2- to 3-s period in which the screen was diffusely illuminated (1.0 cd/m^2) and the monkey was not required to fixate. At the start of each behavioral trial the background light was extinguished, and the task was performed in total darkness except for the presence of the back-projected T spots produced by red light-emitting diodes (0.3 cd/m^2). This light-dark cycle prevented the monkey from becoming dark adapted. The first T spot, referred to as the fixation point (FP), came on 250 ms after the monkey was in the dark. The monkey had to look at the FP and maintain fixation (Fig. 1*A*) for 1.0–1.5 s before proceeding with one of the following saccade tasks. In the visually guided saccade paradigm (Fig. 1*B*), a new T appeared in the peripheral visual field at the same time that the FP was turned off and the

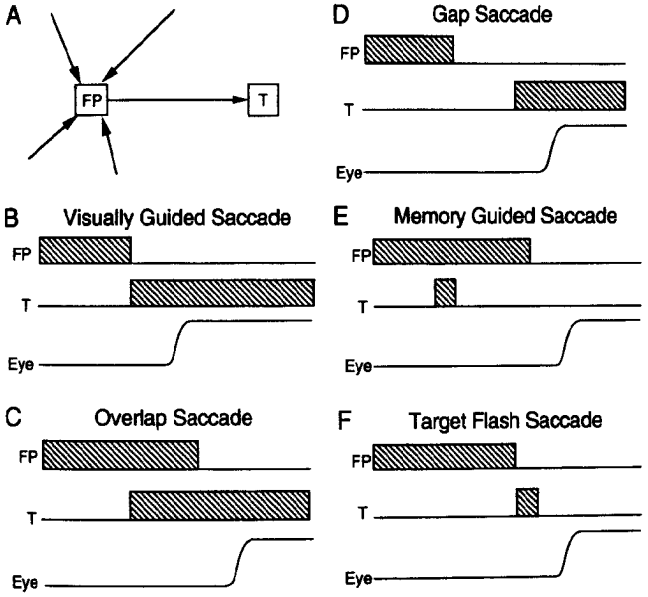

FIG. 1. Schematic representations of behavioral paradigms used in this study. *A*: all tasks began when the monkey looked at the fixation point (FP). A saccade was subsequently made to the target spot (T) in order to obtain the reward. *B–F*: paradigms varied in the temporal sequence of the FP and T illumination. See text of METHODS for details.

monkey had to look at the T. In the overlap saccade paradigm (Fig. 1*C*), the T came on while the FP remained illuminated. After a random period (500–1,000 ms) the FP was turned off and the monkey then had to look to the visible T. In the gap saccade paradigm (Fig. 1*D*) the FP was turned off but the T did not appear until after a period ranging from 200 to 400 ms. The monkey had to make the saccade to the T only after it came on. In the memory-guided saccade paradigm (Fig. 1*E*) the T was flashed for 50–80 ms while the FP remained illuminated. After a randomized period of time (400–800 ms) the FP was turned off and the monkey had to make a saccade to the remembered location of the T flash. In the T flash saccade paradigm (Fig. 1*F*) the FP was turned off as the T was flashed for 50–80 ms. The monkey had to immediately look to the location of the T flash. In both the memory-guided and the T flash saccade paradigms, the T was turned off before the saccade began.

In all tasks, the monkey was required to maintain fixation within a computer-controlled window of ±1 to ±5° during the periods of required fixation before and after the saccade in order to obtain the liquid reward. The smallest window (±1°) was used for small T offsets (<10°) and the largest window was used for the largest T offsets (>50°). If the monkey's eyes left this window, the trial was aborted and the monkey received no reward on that trial. The monkey was usually given up to 500 ms to initiate the saccade after receiving the final signal to go (FP offset in Fig. 1, *B, C, E,* and *F;* T onset in Fig. 1*D*) and an additional 500 ms to enter the computer controlled-window around the T. If both of these conditions were not met, then the trial was aborted and no reward was delivered. Each monkey typically performed between 1,500 and 3,000 trials in a 3- to 6-h experimental period as it worked to satiation. Records were kept of the weight and health status of the monkeys and supplemental fruit and water were provided as needed.

We studied every cell that we encountered within the SC that changed its discharge in relation to a saccade as determined by the use of an on-line raster display. For each cell, we first determined a T location that elicited the highest discharge rate with saccade initiation during the visually guided saccade task. The amplitude and direction of this T from the FP defined the cell's optimal saccade vector. We confined electrode penetrations to areas of the SC in which the optimal direction for saccades was the horizontal meridian. Therefore almost all cells (89%) had their preferred direction within ±30° of the horizontal meridian. We usually recorded each cell's activity when the monkey made saccades of the optimal amplitude and direction for that cell in four different saccade paradigms (visually guided, memory-guided, gap, and overlap) that were randomly interleaved in a single block of trials. The T was randomly placed at either the optimal location for the cell or 180° in the opposite direction. In other blocks of trials, the T was placed so as to generate saccades in the same direction as the optimal saccade, but larger or smaller; the Ts were presented in random order using only the visually guided, memory-guided, or T flash paradigms.

Data analysis

To evaluate the relation between cell discharge and specific events (such as T onset or eye movement), we produced rasters and a continuously varying spike density function (MacPherson and Aldridge 1979) aligned on these events. To generate the spike density function for each trial (Richmond et al. 1987), a Gaussian pulse of fixed width was substituted for each spike and then all of the Gaussians were summed together to produce a continuous function in time. Large values of the spike density function represented a greater probability of the occurrence of a spike, and the peak of the function represented the peak discharge of the cell. A mean spike density function was derived, averaging the spike densities over a series of trials. The effect of changing the standard deviation of the Gaussian pulse (σ) can be seen in Fig. 2 for pulses with a σ 1, 4, and 10 ms in width. We used a Gaussian pulse of 4 ms for all figures and analyses except those used to determine the peak discharge of a cell during a saccade (Figs. 11 and 12). To determine this peak, we used a spike density profile with a σ of 10 ms because this σ provided considerable smoothing of the averaged spike density and made it easier to determine a single peak.

Saccades were identified and marked during off-line analysis, using a previously described computer program that identified the onset and termination of each saccade using velocity and acceleration threshold criteria (Waitzman et al. 1991). The saccade recognition was reviewed by the experimenter.

We computed cell discharge for different amplitude saccades by counting the number of action potentials recorded in the interval beginning 8 ms before saccade onset and ending 8 ms before its termination. We shifted the sampling period backward in time by 8 ms because we inferred that this was the minimum period in which collicular activity contributes to a saccade, because stimulation of the deeper layers of the extrafoveal SC in the monkey altered the trajectory of an ongoing saccade within 8–10 ms (Munoz and Wurtz, unpublished observations). For most quantitative measures of saccade-related activity we used spike frequency (spikes/s), except when plotting movement fields, when we used spike count to show the activity for saccades of all amplitudes. Some cells were active for a very wide range of saccadic amplitudes, and a frequency measure would make similar spike counts diminish as saccade duration increased. We therefore plotted spike count against saccade amplitude to obtain a measure of activity across the movement field and used a smoothing cubic spline function to fit a curve through the data (de Boor 1978).

RESULTS

We recorded from 203 cells that changed their discharge rates in association with saccadic eye movements. Of these 203 cells within the SCs of four monkeys, 139 increased their discharge rate with saccades, and we will refer to these cells as saccade-related cells. The remaining 64 cells de-

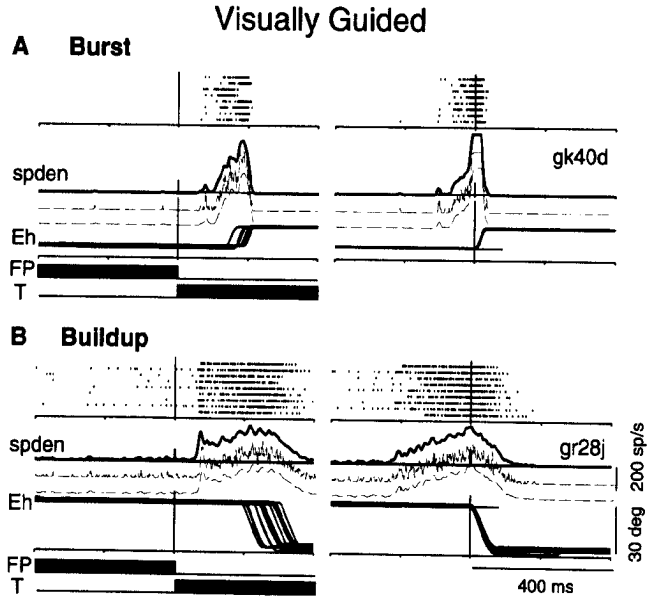

FIG. 2. Difference between burst activity (*A*) and a buildup of activity (*B*) during visually guided saccades. Each panel shows the individual rasters, the spike density profile, and the horizontal eye position traces (Eh) for 8 or 9 trials. Three Gaussian widths are shown for the spike density (——— at *top*, σ = 4 ms; — — — in *middle*, σ = 1 ms; — — — at *bottom*, σ = 10 ms). In this and subsequent figures, the amplitude of the trigger line on the spike density trace indicates 100 spikes/s/trial; flat-topped spike density traces result from truncation to allow maximum display of the rate of change at the beginning and end of the saccade-related discharge. The traces are aligned on T onset in the *left column*, and the same data are aligned on saccade onset in the *right column*. *A*: presaccadic activity consisted only of the burst before the saccade. The cell was in the left superior colliculus (SC) and the 10° rightward saccades shown were the optimal direction and amplitude for the cell. *B*: buildup of activity followed onset of the visual stimulus and ended after the saccade. The cell was in the right SC and had an optimal saccadic amplitude and direction of 25° to the left; the saccades shown were 30° to the left. Cell identification numbers are indicated at *right*.

creased their discharge rate during saccades but were tonically active during visual fixation, and we classified these as fixation cells using the criteria described previously (Munoz and Wurtz 1993).

Burst and buildup activity

For each saccade-related cell studied, we first identified the direction and amplitude of the saccade that generated the most intense saccade-related discharge, which we refer to as the optimal vector of the cell. We then examined the discharge that preceded this optimal vector saccade, and we were able to distinguish two types of saccade-related discharge. One type was a high-frequency burst of action potentials immediately before saccade onset. The other type was a long-lead buildup of activity before saccade initiation. We used the set of saccade tasks shown in Fig. 1 to separate and characterize these two types of saccade-related activity.

We determined the activity of cells in the visually guided saccade task in which the FP went out at the same time that a peripheral visual T appeared and the monkey then was required to make a saccade to the T. Figure 2 shows the discharge of a cell with a burst of activity (Fig. 2*A*) and a cell with a buildup of activity (Fig. 2*B*). The *left column* shows the cell discharge aligned on the onset of the visual T and the *right column* shows the same traces aligned on the saccade onset. Both cells began to discharge ~60–70 ms after T onset, a presumed visual response (Fig. 2, *left*), and then generated a more robust discharge in association with saccade onset (Fig. 2, *right*). Notice that the cell with burst activity (Fig. 2*A*) had a brief pause between its weak visual response and robust movement-related activity, whereas the cell with only a buildup of activity (Fig. 2*B*) lacked any clear pause.

To separate the visual response to T onset from the subsequent saccade-related activity, we used the overlap saccade paradigm (Fig. 3, *A* and *B*), in which we turned on the T long before the saccade to it was required. The cell with a

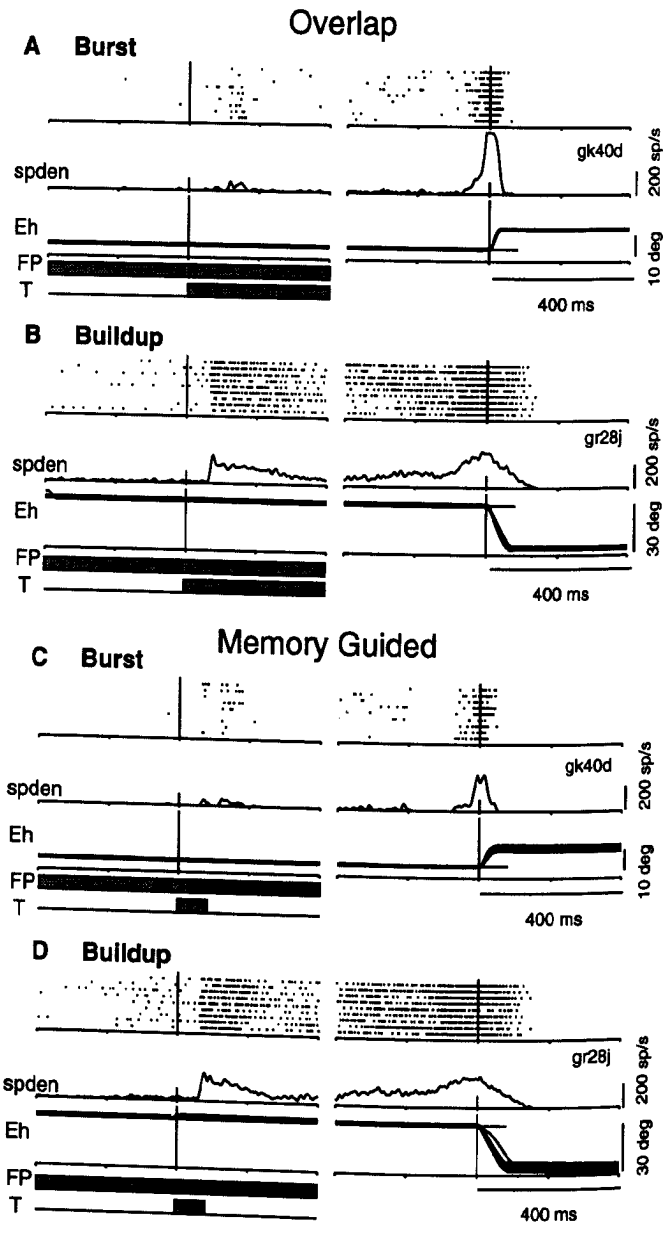

FIG. 3. Difference between a burst and a buildup of activity in 2 delayed saccade tasks that allowed separation of activity related to T onset from that related to saccade onset. Same organization and cells as in Fig. 2; for the spike density (spden) calculation, σ = 4 ms. Cell discharge in both the overlap saccade paradigm (*A* and *B*) and the memory-guided saccade paradigm (*C* and *D*) continued during the interval between T presentation and saccade onset for the cell with a buildup of activity (*B* and *D*) but not for the cell with a burst of activity (*A* and *C*).

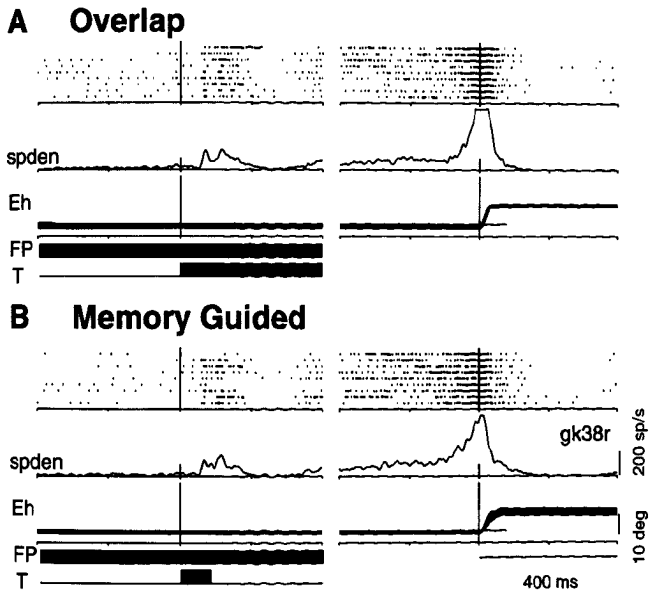

FIG. 4. Example of a cell showing a buildup of activity and an added burst of activity before the saccade. Same organization as in Fig. 2; for the spike density calculation, $\sigma \approx 4$ ms. The cell was located in the left SC and preferred 10° rightward saccades.

burst of activity (Fig. 3*A*, *left:* same cell shown in Fig. 2*A*) had a weak visual response shortly after T onset, remained only sporadically active until after the offset of the FP, and then gave a burst of activity synchronized with saccade initiation (Fig. 3*A*, *right*). In contrast, the cell with a buildup of activity began to discharge ~60–70 ms after T onset (Fig. 3*B*, *left:* same cell as in Fig. 2*B*), continued to discharge tonically until after the FP went off, and then increased its discharge rate at the time of saccade initiation (Fig. 3*B*, *right*). The major difference between the two cells was the increased rate of discharge during the delay period for the cell with a buildup of activity (Fig. 3*B*) and the lack of that increase in the cell with a burst of activity (Fig. 3*A*).

To determine the extent to which the buildup of activity was related to the continued presence of a visual stimulus, we used the memory-guided saccade paradigm in which the T was flashed briefly and the monkey later had to make a saccade to the spatial location of the T. In this task, the cell with a burst of activity (Fig. 3*C*, *left*) gave only a weak response to the T flash and then a burst with the saccade to the remembered location of the T flash (Fig. 3*C*, *right*). The cell with a buildup of activity discharged in a sustained manner from the time of the flash (Fig. 3*D*, *left*) until the saccade was made, even though the T was no longer visible (Fig. 3*D*, *right*).

Many cells showing a buildup of activity also had a burst of activity at the time of the saccade. For example, the cell shown in Fig. 4 had a buildup of activity that long preceded the saccade but also had a burst of activity with the saccade. This buildup and then burst was clear in both the overlap (Fig. 4*A*) and memory-guided saccade tasks (Fig. 4*B*).

The extent to which the buildup of activity was in anticipation of a given saccade was revealed by using the gap saccade paradigm in which the T position was randomly presented at two locations in opposite hemifields. During the 250-ms gap the monkey presumably knew that a T would appear and what saccade amplitude would be required to reach it, but did not know the direction of the required saccade. Figure 5 shows the activity of two cells during the gap saccade paradigm, one having only burst activity and one having both a burst and a buildup of activity. Ts always appeared in one of two locations; trials in which the T appeared in the ipsilateral visual field (left field) are shown in the *left column* (Fig. 5, *A* and *C*), and those in which it appeared in the contralateral field (right field) are shown in the *right column* (Fig. 5, *B* and *D*). The cells were both isolated in the left SC, so it is not surprising that the cell showing only a burst of activity before saccades did so to a T in the contralateral (right) visual field (Fig. 5*B*), but not before those that appeared in the ipsilateral field (Fig. 5*A*). The cell with a buildup of activity showed increased activity during the gap period (Fig. 5, *C* and *D*) regardless of the side on which the T would eventually appear. It then showed an additional increase of activity only with a saccade to the contralateral field (Fig. 5*D*). The intensity of this buildup of activity during the gap was similar to that seen for this cell in the overlap and memory-guided tasks when the T had appeared but the saccade was delayed (Fig. 4).

We used the characteristics of the saccade-related discharge during these series of paradigms to classify the cells as having a burst of activity or a buildup of activity. We identified a cell as having a buildup of activity if it was active between the onset of a visual stimulus and the onset of the saccade to that stimulus. This activity was seen most clearly in the delay period in the overlap, memory-guided, and gap tasks (e.g., see Figs. 3, *B* and *D*, 4, and 5). Although some cells with this long-lead buildup had activity wane momentarily after a visual response (e.g., Fig. 4), all cells with buildup activity discharged >30 spikes/s ≥100 ms before a saccade of the optimal amplitude and direction in the delayed saccade paradigms (overlap and memory-guided paradigms). We identified a cell as having only burst activity if it discharged <30 spikes/s ≥100 ms before a saccade of the optimal amplitude and direction in the delayed saccade paradigms. We could sometimes distinguish a stopping of activity from continued activity in the visually guided task (as in Fig. 2*A*), but if there was not a clear pause between the visual and saccade-related responses we could not classify the activity with certainty. Of the 94 saccade-related cells that we could classify, 68% (64 of 94) were classified as having only burst activity, whereas 32% (30 of 94) had a sustained response, and we classified them as having a buildup of activity. Twenty-four of these cells with a buildup of activity also had a high-frequency burst synchronized with saccade onset (as in Figs. 4 and 5), whereas the remaining six cells lacked the high-frequency burst component (as in Figs. 2 and 3). These groupings are summarized in Table 1. For the remaining 45 of the 139 saccade-related cells in our sample, we could not determine whether they had a buildup of activity because we only recorded activity in the visually guided saccade paradigm and these cells did not have a clear pause between the visual and saccade-related responses.

We quantified the differences in the cells with a burst or a buildup of activity along with the visual response of 29 cells that we had studied in both the overlap and gap tasks (Fig. 6). We first divided the cells using the criteria described in the preceding paragraph. We used the discharge rate of cells after the T came on in the overlap task as a

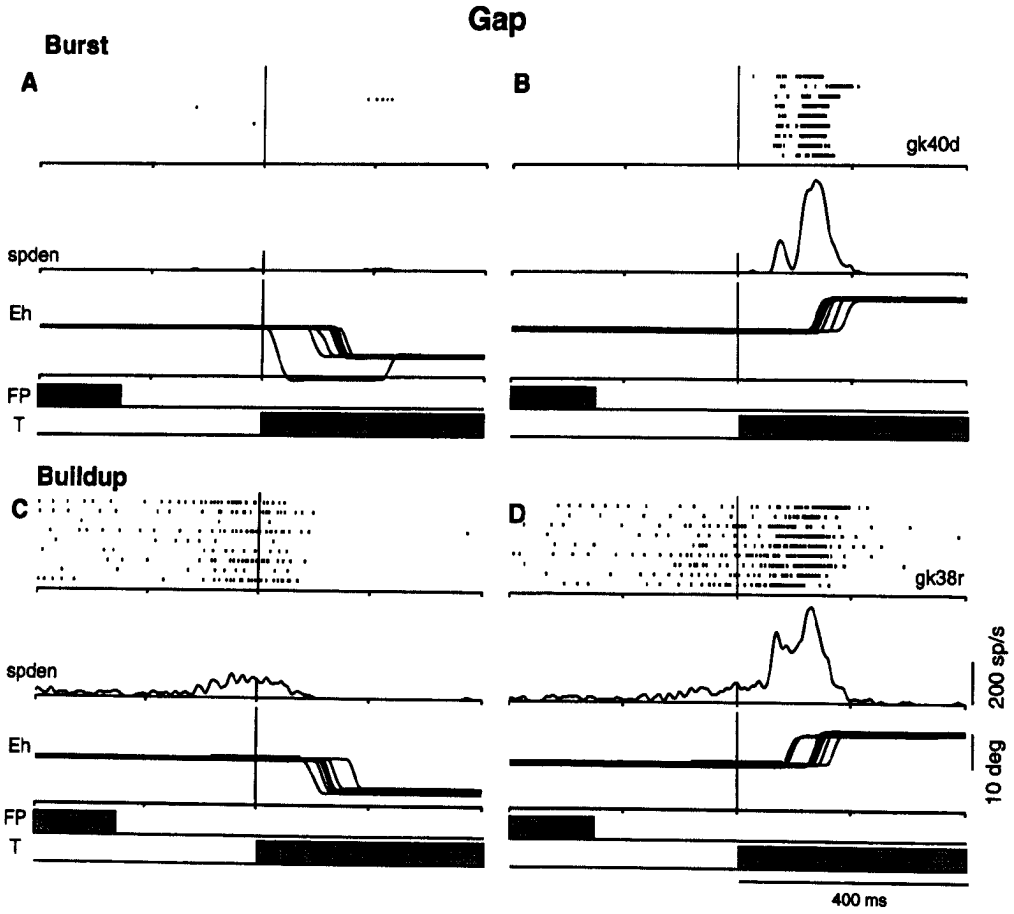

FIG. 5. Buildup of activity during the period of saccade preparation in the gap saccade task. All traces are aligned on T onset after the gap period. *Left columns*: trials when the T appeared in the ipsilateral visual field. *Right column*: trials for contralateral Ts. *A* and *B*: in the gap period between the time the FP went off and the T came on, the cell was silent and a burst of activity only occurred when the monkey made a saccade to the T in the contralateral (right) visual field. *C* and *D*: buildup of activity increased during the gap preceding both ipsilateral and contralateral saccades, but a burst of activity came only before the contralateral (rightward) saccade. Within a block of trials, the T location was randomly presented on the right or left and visually guided, memory-guided, overlap, and gap paradigms were randomly interleaved. Same organization as in Fig. 2; for the spike density calculation, σ = 4 ms.

measure of visual activity, the discharge rate during the gap for the buildup of activity, and the discharge rate during the saccade for burst activity (see Fig. 6 legend for calculation). Both the cells with burst activity (Fig. 6, *top graphs*) and a buildup of activity (Fig. 6, *bottom graphs*) had visual responses with about equal intensities (Fig. 6*A*). For the saccade-related measures, the buildup measure (Fig. 6*B*) separated the cells but the measure of burst activity (Fig. 6*C*) did not. Thus, in our sample of cells, it is the presence or absence of the buildup of activity that clearly separates the classes of saccade-related discharge.

Clipping of saccade-related activity

In a previous study, saccade-related cells were classified by comparing the timing of the end of the discharge to the end of the saccade (Waitzman et al. 1991). The saccade-related discharge was classified as clipped if activity was ≥90% over by the end of the saccade, partially clipped if activity decreased during the saccade but <90% of the activity had occurred by the end of the saccade, and unclipped if the activity slowly decreased after the saccade. Table 1 shows the results of this classification applied to the 139 saccade-related cells in our sample: 45% (63 of 139) were clipped, 48% (66 of 139) were partially clipped, and 7% (10 of 139) were unclipped.

We also determined the relationship between the clipping of responses and the burst and buildup types of activity (Table 2). Of the 64 cells with a burst of activity, 62% (40 of 64) were clipped and 38% (24 of 64) were partially clipped. The distribution was different for the 30 cells with buildup of activity: 27% (8 of 30) were classified as clipped, 60% (18 of 30) as partially clipped, and 13% (4 of 30) as unclipped. Thus the majority of cells with a burst of activity was clipped, whereas the majority of cells with a buildup of activity was partially clipped.

Movement fields of saccade-related cells

CLOSED AND OPEN-ENDED MOVEMENT FIELDS. The saccade-related cells in the SC have movement fields—that part of the visual field where a saccade is accompanied by an increase in cell discharge (Wurtz and Goldberg 1972). We found that we could also classify saccade-related cells on the basis of their movement fields. For a given cell, we first qualitatively determined the movement field and the optimal

TABLE 1. *Distribution of cell types*

	n	Percent
Burst and buildup activity*		
Buildup only	6	6%
Buildup and burst	24	26%
Burst only	64	68%
Total cells classified	94	
Cells not classified	45	
Total	139	
Clipped responses		
Clipped	63	45%
Partially clipped	66	48%
Unclipped	10	7%
Total	139	
Movement fields†		
Closed	63	56%
Open	38	34%
Other	11	10%
Total cells tested	112	
Cells not tested	27	
Total	139	

n is number of cells. * Cells with a buildup of activity were active between the onset of a visual stimulus and the onset of the saccade to that stimulus. Although some cells with this long-lead buildup had activity wane momentarily after a visual response, all cells with buildup activity discharged >30 spikes/s ≥100 ms before a saccade of the optimal amplitude and direction in the delayed saccade paradigms (overlap and memory-guided saccade paradigms). We identified a cell as having only burst activity if it discharged <30 spikes/s ≥100 ms before a saccade of the optimal amplitude and direction. † Cells whose movement fields were well enough studied to determine whether they had closed movement fields (those with a peripheral border) or open-ended fields (those with no peripheral border). The movement fields labeled "other" had discharge rates that declined with larger saccades, as do closed movement fields, but had much larger and more skewed movement fields than closed movement fields. Only cells with optimal amplitudes <32° are plotted because we were unable to determine for certain whether cells preferring greater amplitudes had open or closed fields; our monkeys only made saccades out to 60–70°, which was still within the movement field of all cells preferring >32°.

direction and amplitude of saccades within this field (the optimal vector). We then studied the movement fields of these cells by measuring the activity with saccades of increasing amplitudes aligned with the optimal vector.

In Fig. 7 we compare the activity of two cells with different movement fields and show activity associated with six different saccadic amplitudes along the optimal direction for each cell. Saccades of ~8° in amplitude produced the highest activity for both cells. The cell shown in Fig. 7*A* discharged maximally for saccades that were close to this amplitude, and its activity diminished when saccade amplitude was substantially more or less than this optimum. Most importantly, note that this cell was silent for saccades that were considerably greater than the optimal amplitude. The discharge of the cell shown in Fig. 7*B* also diminished if the amplitude of the saccade was smaller than the optimum, but the cell continued to discharge for saccades whose amplitudes were greater than the optimum.

The saccade-related activity of both cells in Fig. 7 also diminished when saccade direction deviated from the cell's optimal direction (not shown), but we did not systematically study the discharge of the cells in directions other than the optimal. On the same penetration through the SC, the cells with open and closed movement fields tended to have similar optimal amplitudes and directions.

The differences in movement fields are seen more easily in Fig. 8, which shows cell discharge for the duration of the saccade plotted against saccadic amplitude along the optimal direction. Figure 8, *C* and *D*, shows the activity along a line through the optimal vector of the movement fields and the solid line spline curves fitted to the data for the same two saccade-related cells shown in Fig. 7. The plot of the cell in Fig. 8*C* shows a movement field that was closed, that is, one that had both a central and peripheral border because the cell did not discharge for very small or very large saccades. The cell shown in Fig. 8*D* had an open-ended movement field; it did not discharge with small saccades but did for all saccades that were equal to or greater than a minimum amplitude. The same basic shapes of movement fields were observed for cells that preferred smaller saccadic amplitudes (2°, Fig. 8, *A* and *B*) and larger saccadic amplitudes (20°, Fig. 8, *E* and *F*). The closed movement fields all had clearly defined central and peripheral borders (Fig. 8, *A*, *C*, and *E*). Cells classified as open-ended did not have a peripheral border to their movement fields (Fig. 8, *B*, *D*, and *F*). The same distinction between open-ended and closed movement fields could be made regardless of whether the smoothing splines were based on number of spikes during the saccade (solid lines) or on average firing frequency (dashed lines). Note that the width of the closed fields increased with eccentricity and was presumably related to the nonhomogeneous mapping of saccadic amplitude across the SC (Munoz and Wurtz 1995; Ottes et al. 1986; Sparks et al. 1976).

Our sample of cells had optimal amplitudes ranging from from 0.3 to 50°. In Fig. 9*A* we plot the activity of each cell at its optimal amplitude for the cells with optimal amplitudes out to 32°—those for which we could determine with certainty whether the fields were open-ended or closed. Both closed and open-ended fields are represented at all eccentricities, although a higher proportion of cells with smaller optimal saccadic amplitudes has closed fields. We found no relation between the number of spikes at the optimal amplitude and the eccentricity of the optimal amplitude for the sample of cells with closed and open-ended fields, as indicated by the similarity of the regression lines. In contrast, Fig. 9*B* shows a striking difference between cells with closed and open-ended movement fields when the discharge of each cell at the optimal saccadic amplitude is compared with the activity of the cell at 3 times that amplitude. As saccadic amplitude increased beyond the optimum, the mean values of the cells with open-ended movement fields were scattered around 1, whereas the average values of the cells with closed fields fell to 0.

We obtained sufficient data from 81% (112 of 139) of the saccade-related cells to quantitatively evaluate their movement fields and to classify them as having closed or open-ended movement fields. Table 1 illustrates the relative distribution of cells: 56% (63 of 112) had closed movement fields, 34% (38 of 112) had open-ended movements fields, and the remaining 10% (11 of 112) had characteristics of both types of fields and were classified as "other" (cells that had movement fields with discharge rates that declined with larger saccades, as do closed movement fields, but with movement fields much larger and more skewed than the closed fields). Table 2 shows the relationship between movement fields and the burst or buildup of activity for the 78 saccade-related cells

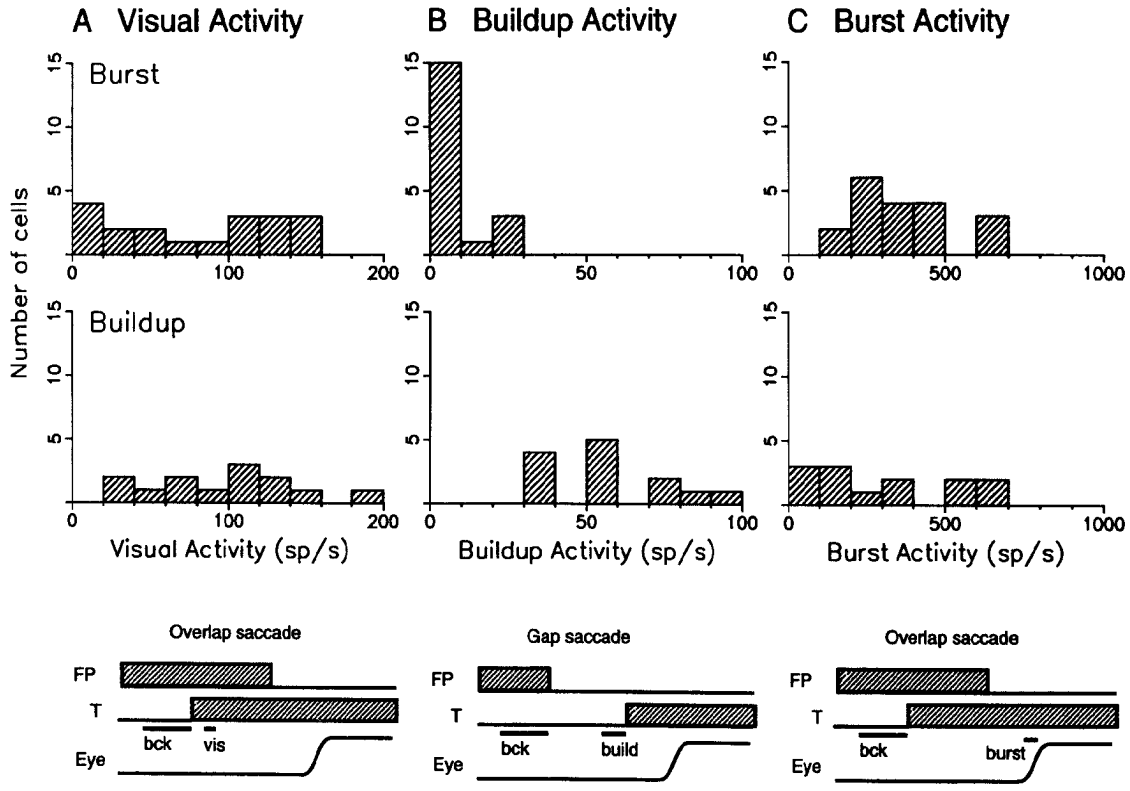

FIG. 6. Quantitative measures of visual (*A*), buildup (*B*), and burst (*C*) activity. The 16 cells with burst activity (*top graphs*) and the 13 cells with a buildup of activity (*bottom graphs*) had all been tested on both the gap and overlap tasks. The schematic drawings below each graph indicate when we measured the discharge rate. The visual activity is the mean discharge rate between 50 and 100 ms after T onset minus the background rate in the 200 ms preceding T onset for a T in the center of the visual receptive field. We used the overlap saccade paradigm because the onset of the visual stimulus preceded the visually guided saccade by several hundred milliseconds. The buildup of activity is the mean discharge rate in the final 100-ms period of the gap in the gap saccade paradigm minus the background discharge rate in the final 200 ms before offset of the FP. We used the gap paradigm for this activity because the T appeared at either of 2 locations and the monkey could not anticipate the location of the T before any stimulus appeared at that site; the activity was therefore most closely related to the buildup of activity rather than any visual or burst activity. The burst activity is the mean discharge rate between 8 ms before saccade onset and 8 ms before saccade end minus the background rate in the 200 ms before T onset in the overlap saccade paradigm. This mean rate for the duration of the saccade was shifted backward in time by 8 ms because we infer that this is the minimum period in which collicular activity contributes to a saccade (see METHODS). For the buildup activity measure, the mean was 7 spikes/s (range 0–27 spikes/s) for the cells with a burst activity and 58 spikes/s (range 30–94 spikes/s) for the cells with a buildup of activity, and these were significantly different (*t*-test, $P < 0.0005$). The mean visual activity measures of the cells with a burst and a buildup of activity were 80 and 100 spikes/s, respectively, whereas the mean burst activity measure was 375 and 305 spikes/s, respectively (neither difference was significant: *t*-test, $P > 0.05$).

in which we could both evaluate the movement fields and classify cells by their burst or buildup of activity. For 53 cells with only burst activity, 85% (45 of 53) had closed movement fields, and for 25 cells with a buildup of activity, 88% (22 of 25) had open-ended movement fields. Figure 10 shows the overlap between the cells for which we found burst activity, a clipped response, and closed movement fields (Fig. 10*A*) and buildup, partially clipped, and open-ended movement fields (Fig. 10*B*). Thus, although we have kept the analysis of these three characteristics separate, we think there is a clustering of characteristics: the cells with only burst activity nearly always had closed movement fields and most had clipped responses; the cells with a buildup of activity nearly always had open-ended movement fields and about half had partially clipped responses.

TABLE 2. *Relation of burst and buildup activity to clipping and movement fields*

	Burst	Buildup
Clipping of activity		
Clipped	40 (62)	8 (27)
Partially clipped	24 (38)	18 (60)
Unclipped	0 (0)	4 (13)
Total	64	30
Movement fields		
Closed	45 (85)	0 (0)
Open	4 (7.5)	22 (88)
Other	4 (7.5)	3 (12)
Total	53	25

Values are number of cells, with percentages in parentheses.

TIMING OF PEAK SACCADIC DISCHARGE. After we divided cells into those with closed and open-ended movement fields, we found that these cell types had differences in the time between saccade onset and their peak discharge when larger saccades were executed. For example, the cell with the closed movement field in Fig. 11*A* had a peak discharge that

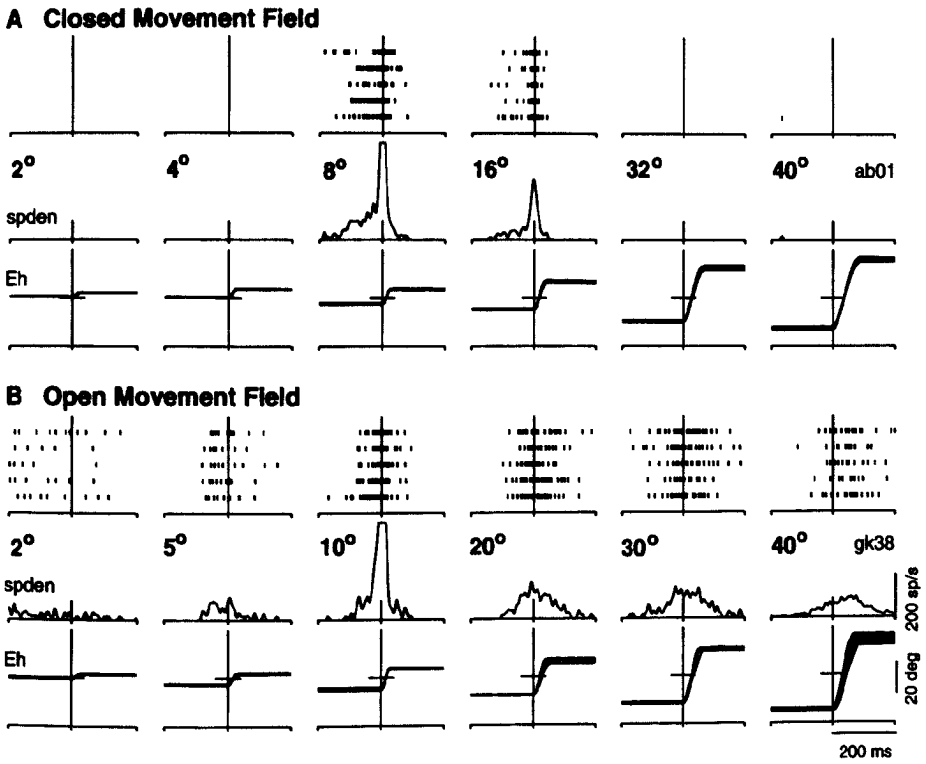

FIG. 7. Saccade-related activity of a cell with a closed movement field (*A*) and an open-ended movement field (*B*) as saccade amplitude increased along the optimal direction across the movement field. Each panel shows the response of the cell to 6 saccades of identical amplitude; the optimal amplitude for both cells was ~8°. The spike density profile was computed with σ = 4 ms. Records of >6 saccades are shown to indicate the consistency of the saccades; only saccades that were single and accurate were selected for this and subsequent figures. The cell with a closed movement field increased discharge to saccades of intermediate amplitudes, whereas the cell with the open-ended movement field discharged with saccades equal to or greater than the optimal amplitude.

occurred close to saccade onset for the optimal amplitude (5°) and for all other amplitudes for which it was active. In contrast, for the cell with the open-ended movement field (Fig. 11*B*) and an optimal amplitude of 8°, the time from saccade onset to peak discharge tended to increase as saccadic amplitude increased.

Figure 12 shows this change in timing quantitatively for cells with closed (Fig. 12, *left column*) and open-ended (Fig. 12, *right column*) movement fields. For the two cells shown in Fig. 11, the curves in Fig. 12, *A* and *B*, quantify the time from saccade onset to peak discharge for saccades of increasing amplitudes. The curves in Fig. 12, *C* and *D*, are for all cells in which we were able to test a wide enough range of amplitudes. The cells are divided into two groups: those having optimal amplitudes between 2 and 10° (solid lines) and those with optimal amplitudes between 10 and 20° (dashed lines). Figure 12, *E* and *F*, shows the spline fits through the data points for the curves in Fig. 12, *C* and *D*. For all cells with open-ended movement fields (Fig. 12, *B*, *D*, and *F*), the time between saccade onset and peak discharge increased as saccade amplitude increased. The peak discharge occurred only when saccadic amplitude was greater than the optimal amplitude of the group of cells (2–10° and 10–20°). For example, the cell in Fig. 11*B* shows a clear increase in the time to peak discharge for 40 and 50° saccades; this is much less so for 24° saccades. Some of the curves for cells with optimal amplitudes in the 10–20° range in Fig. 12*D* do not bend up because these cells have optimal amplitudes near 20° and we would not expect these curves to turn up until saccades were even larger than the 50° shown on the graph. Most importantly, note that for a given amplitude saccade, those cells having optimal amplitudes <10° (solid lines) achieved peak discharge later than the cells whose optimal amplitudes were <20° (dashed lines). That is, the solid lines curved upward before the dashed lines. For the cells with closed movement fields, the timing of the peak discharge relative to saccade onset occurred around the time of saccade onset (Fig. 12, *A*, *C*, and *E*), irrespective of saccade amplitude.

CONTROLS. Two factors in our experiments might have produced open-ended movement fields as a result of artifacts: visual stimulation during the saccade or corrective saccades. We ran control tests to investigate each of these points.

The activity of a cell during a saccade might be generated not in relation to saccade initiation but in response to the smear of the visual T as it was swept across the retina during a saccade. To determine whether this factor was significant, we compared the movement fields of cells with saccades to visual Ts, when such a visual smear could be present, to the discharge with saccades to a remembered or flashed T, when visual smear was not present. Figure 13 illustrates the discharges of two cells, one with a closed movement field (Fig. 13*A*) and one with an open-ended movement field (Fig. 13*B*), when saccades were made to visible Ts (visually guided saccades) and in darkness (T flash saccades). The presence or absence of the T made no difference for the saccade-related portion of the discharge of either cell.

For 28 saccade-related cells, we were able to compare the saccade-related activity from visually guided and memory-guided or T flashed saccades. All cells had a similar discharge for saccades to visible and remembered Ts. The only difference in the two conditions was that the frequency of discharge for some cells was lower when the saccade was made to a remembered T. This was noted previously and was attributed to the lower saccadic velocity of these movements

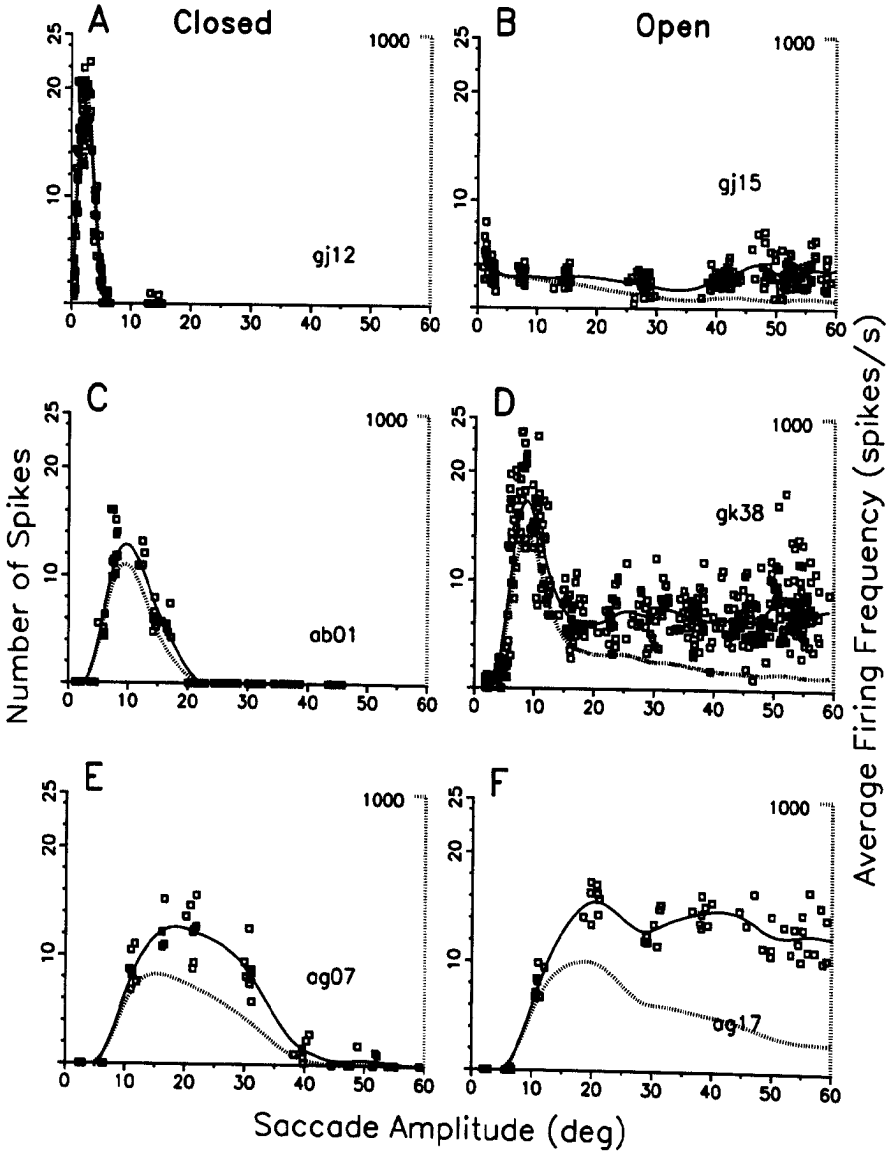

FIG. 8. Quantitative response of cells with closed movement fields (*A*, *C*, and *E*) and open-ended movement fields (*B*, *D*, and *F*) with increasing amplitude of saccades. The number of spikes obtained in the interval spanning 8 ms before saccade onset to 8 ms before saccade termination is plotted against the amplitude of saccades in the optimal direction. Solid lines: cubic splines fitted to the number of spikes in this saccade duration. Dashed lines: cubic spline fits to the same data but using spike frequency (spikes/s) rather than spikes per saccade duration. The optimal saccadic amplitude for the cells in *A* and *B* was 2°, in *C* and *D* it was 8°, and in *E* and *F* it was 20°. The peak of activity with small saccades in *B* is barely visible but can be seen in Fig. 16*A*, which more clearly shows the activity with a 2° saccade for the same cell. The cells with the open-ended movement fields discharged for all saccades greater than the optimum saccadic amplitude, whereas the cells with closed movement fields did not.

(Rohrer et al. 1987; Waitzman et al. 1991). We did not test these cells for small shifts in the vertical position of movement fields that have been reported recently (Stanford and Sparks 1994). We conclude that the sensitivity to the visual T does not produce closed and open-ended movement fields.

The activity recorded from cells with open-ended movement fields during saccades that were larger than the optimal amplitude was not due to subsequent corrective saccades. Figure 14 compares the discharge of a cell with a closed movement field (*left column*) with that of a cell with an open-ended movement field (*right column*). On single trials, both cells discharged a high-frequency burst in association with small movements that were close to the optimal saccadic amplitude (~6°; Fig. 14, *A* and *B*). When the monkey made a very large saccade (~60°; Fig. 14, *C–F*), the cell with the open-ended movement field was active during the movement, regardless of whether there was a subsequent corrective saccade (Fig. 14*F*) or not (Fig. 14*D*), although the corrective saccade was also associated with subsequent activity. We found that all cells with open-ended movement fields were active for very large saccades regardless of whether subsequent corrective saccades were made or not. The cell with the closed movement field only discharged if there was a small corrective saccade of the appropriate amplitude (Fig. 14*E*), but not when there was none (Fig. 14*C*). We conclude that the activity of cells with open-ended movement fields was not dependent on the generation of corrective saccades.

Location of cells

We determined the relative location of saccade-related cells by measuring the depth at which we recorded cells below the dorsal surface of the SC. Figure 15*A* shows the distribution of cells with only a burst of activity and cells with a buildup of activity, as well as the fixation cells we have described previously (Munoz and Wurtz 1993). The depth of each cell is plotted relative to the depth of the first multiunit visual responses that we encountered on that penetration as the electrode entered the SC. Its location on the abscissa corresponds to its optimal amplitude converted to millimeters from the foveal representation. Cells with a

burst of activity were found immediately beneath the cells with only a visual response, ~1.0–2.0 mm below the dorsal surface. The cells with a buildup of activity were located ventral to, and somewhat intermingled with, the cells with burst activity, mainly 1.5–2.5 mm below the dorsal surface of the SC. Fixation cells were confined to the rostral pole of the SC ~1.5–2.7 mm below the dorsal surface, immediately ventral to cells that burst for very small contraversive saccades. Thus the depth of the fixation cells is similar to that of the cells with a buildup of activity.

Figure 15*B* shows the distribution of the same cells classified by whether they had closed or open movement fields. Once again each data point represents the depth of each cell below the first multiunit response encountered plotted against the cell's optimal amplitude. Notice that the cells with open-ended and closed movement fields tended to be found at separate depths within the SC. Cells with closed movement fields were found ~1.0–2.0 mm below the surface, whereas cells with open-ended movement fields occupied a region spanning ~1.5–2.7 mm below the surface.

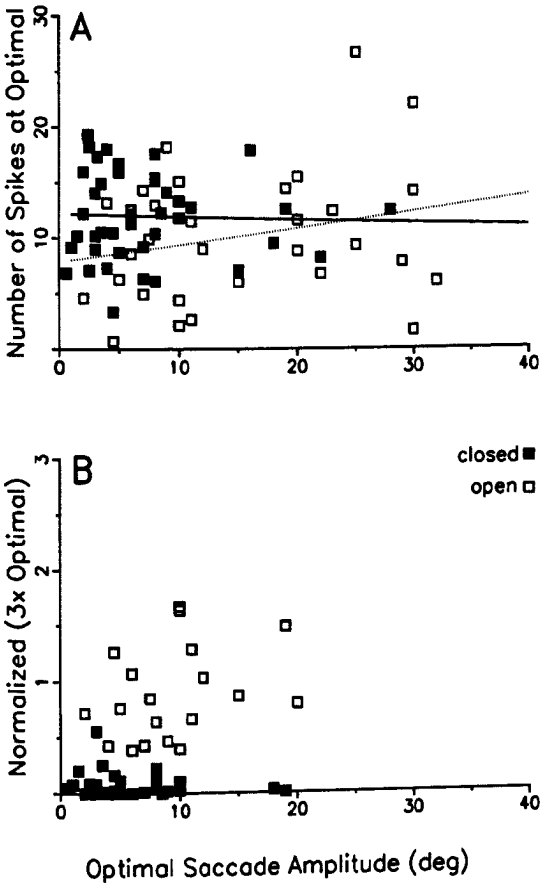

FIG. 9. Quantitative comparison of movement fields for the sample of cells with open-ended (□) and closed (■) movement fields. We divided cells into closed and open-ended classes by looking at the shapes of their movement fields as in Fig. 8. Only cells with optimal amplitudes <32° are plotted because we were unable to determine for certain whether cells preferring greater amplitudes had open or closed fields; our monkeys only made saccades out to 60–70°, which was still within the movement field of all cells preferring >32°. We determined the number of spikes at the optimal saccadic amplitude from the spline curves, like those shown in Fig. 8. *A*: for each cell, the number of spikes at the optimal saccadic amplitude (ordinate) is plotted against that optimal saccadic amplitude (abscissa). Solid line: regression line through the data points for the closed movement fields (■). Dotted line: regression line through the data points for the for the open-ended movement fields (□). The slope, *Y*-intercept, and correlation values were −0.03, 12.18, and −0.04 for the solid line and 0.15, 7.88, and 0.23 for the dotted line. *B*: ordinate is the normalized value (spike count at 3 times the optimal saccade amplitude divided by the spike count at the optimal amplitude) plotted against the cell's optimal amplitude (abscissa). We normalized the spline curve through the movement field to the value of the spike count at the optimal amplitude. The values for cells with closed fields fall at ~0, indicating that these cells no longer responded with large saccades, whereas the values for the open-ended cells remain scattered at ~1, indicating their continuing activity with large saccades.

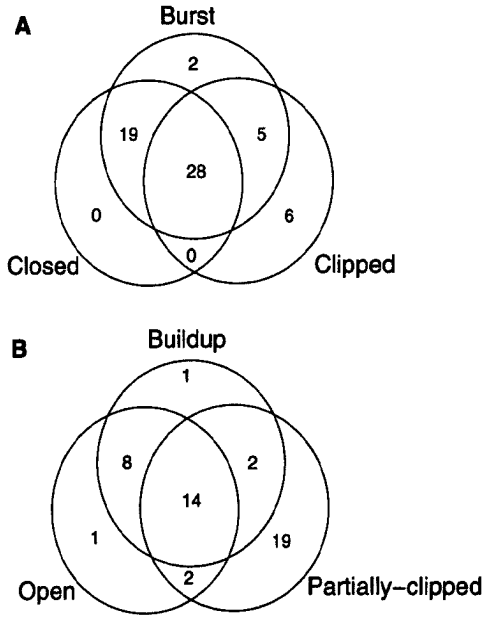

FIG. 10. Relation of cell characteristics for the sample of cells with burst (*A*) and buildup (*B*) activity. *A*: relation of sample of cells with burst activity to those with clipped activity and closed movement fields. *B*: relation of cells with buildup activity to those with partially clipped activity and open movement fields. We have only included cells in which the response type (burst or buildup), amount of clipping (clipped, partially clipped, or unclipped), and type of movement field (closed, open, or hybrid) were fully characterized so that the total numbers in each group are frequently smaller than the total sample listed in Tables 1 and 2. Areas of sectors within circles are not proportional to the number of cells indicated. Note that nearly all of the cells with burst activity have closed movement fields and most have clipped activity, whereas the cells with a buildup of activity nearly always have open-ended movement fields and about half have partially clipped activity.

Comparison with fixation cells

We recently described the discharge characteristics of a subpopulation of neurons in the rostral pole of the monkey SC that we called fixation cells. The defining characteristic of these cells was that they discharged tonically when the monkey actively fixated a T of interest and that they paused for most saccades (Munoz and Wurtz 1993). In the present experiments we have found that some of the cells we categorized as fixation cells shared a salient characteristic with some of the saccade-related cells: open-ended movement fields. This similarity can be best described by comparing the activity of a saccade-related cell with an open-ended movement field (Fig. 16*A*), a fixation cell that paused for all saccades (Fig. 16*C*), and a fixation cell that also had an increase in activity for small contraversive saccades (Fig. 16*B*).

For saccades to the contralateral visual field, the saccade-

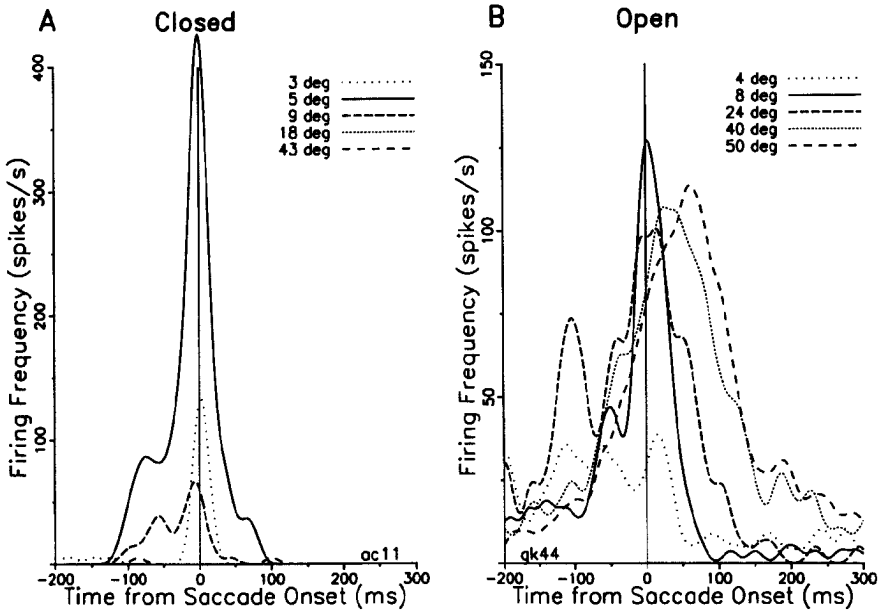

FIG. 11. Time between saccade onset and peak discharge for saccades of different amplitudes for a cell with a closed (*A*) and an open-ended (*B*) movement field. Solid line: amplitude closest to the optimal amplitude for each cell (5° in *A*, 8° in *B*). The spike density traces are averages over 8–10 single saccades of identical amplitude and direction using σ = 10 ms to smooth the curves in order to more easily identify a single peak in the neuronal discharge train. We computed 2 spike density profiles, 1 aligned on saccade onset and the other aligned on saccade termination, and then measured the latency from saccade onset and termination to the peak. The cell with the open-ended movement field showed peak activity that came later and during the saccades of larger amplitude.

related cell shown in Fig. 16*A* showed maximal activity with saccades of 2° amplitude, but it also discharged with all saccades that were larger in amplitude. The activity of this cell also occurred later and later for larger saccades. The fixation cell shown in Fig. 16*C* paused for all contraversive saccades as it did for all ipsiversive saccades (not shown). For the fixation cell shown in Fig. 16*B*, the change of activity shows aspects of the cells in both Fig. 16, *A* and *C*. This cell paused with all ipsilateral saccades and all large contralateral saccades, like the fixation cell in Fig. 16*C*. This fixation cell, like many of those described previously (Munoz and Wurtz 1993), also increased its activity for small contraversive saccades (the 2° saccade in Fig. 16*B*), and this activity is not very different from the activity before a 2° saccade for the cell with the open-ended movement field (Fig. 16*A*). For the fixation cell in Fig. 16*B*, the pause with saccades became clearer for larger saccades (like the fixation cell in Fig. 16*C*), but there was also a late increase of activity with large saccades that was similar to the activity of the saccade-related cell in Fig. 16*A*. Thus the fixation cell in Fig. 16*B* has some characteristics of both the fixation cell (Fig. 16*C*) and the saccade-related cell with the open-ended movement field (Fig. 16*A*).

We therefore regard some of the fixation cells (such as that in Fig. 16*B*) as a transition between the fixation cells that actively discharge during fixation and pause with all saccades and the saccade-related cells with open-ended movement fields that have no tonic activity during fixation but discharge with saccades in a given direction. Rostral to these transition cells are the "pure" fixation cells, and caudal to these cells are the pure saccade-related cells with open-ended movement fields. This transition between these cell types is consistent with the fixation and the open-ended movement field cells lying at about the same depth within the SC (Fig. 15). We find that such transition activity occurs with cells that respond best to saccades of ~0.5–2°.

The time of the initial change in activity of fixation cells before saccade onset also allows comparison between the saccade-related cells. Figure 17 shows examples of the discharge of a cell with burst activity (same cell as in Fig. 4, *A* and *B*), one with a buildup of activity (same cell as in Fig. 4, *C* and *D*), and a fixation cell. The fixation cell had a long-lead decrease in activity during the gap before T appearance at the same time that the buildup of activity began its long-lead increase in activity. Subsequently, there was also a close temporal correlation between the cessation of fixation cell activity and the high-frequency activity of the burst cell (seen also in the cell with a buildup of activity).

The burst of activity in the burst cells and the cessation of activity in the fixation cells were closely related. Figure 18 compares the burst onset and end with fixation cell pauses. We show the time from saccade onset to burst onset (Fig. 18*A*) and the time from saccade end to burst end (Fig. 18*B*) for each of 34 burst cells. The mean time from saccade onset to burst onset for each of 34 burst cells was −23 ± 6 (SD) ms, whereas the mean time from saccade end to burst end was −7 ± 8 (SD) ms. The mean times of the burst cells (Fig. 18, *A* and *B*) can be compared with the mean times of pause onset and pause end for 31 fixation cells (Fig. 18, *C* and *D*). Note the similarities between pause onset and burst onset, and between burst end and pause end.

The relationship between the three cell types (burst, buildup, and fixation) can be summarized by using the same visual, buildup, and burst activity measures we used previously to compare the cells with burst and buildup activity. Figure 19 shows these measures plotted against each other for cells with burst activity (■), cells with buildup activity (□), and fixation cells (×). On the graphs, values of the activity >0 indicate increased activity; values <0 indicate decreased activity. For each comparison there is some separation among the groups of cells. On the visual versus burst activity graph (Fig. 19*A*), cells with burst activity and cells with buildup activity were indistinguishable (as shown in Fig. 6). The fixation cells have negative values on the burst measure (Fig. 19*A*) because they decrease their activity during the saccade, but had values of ~0 on the visual measure because they show little change in activity after the appear-

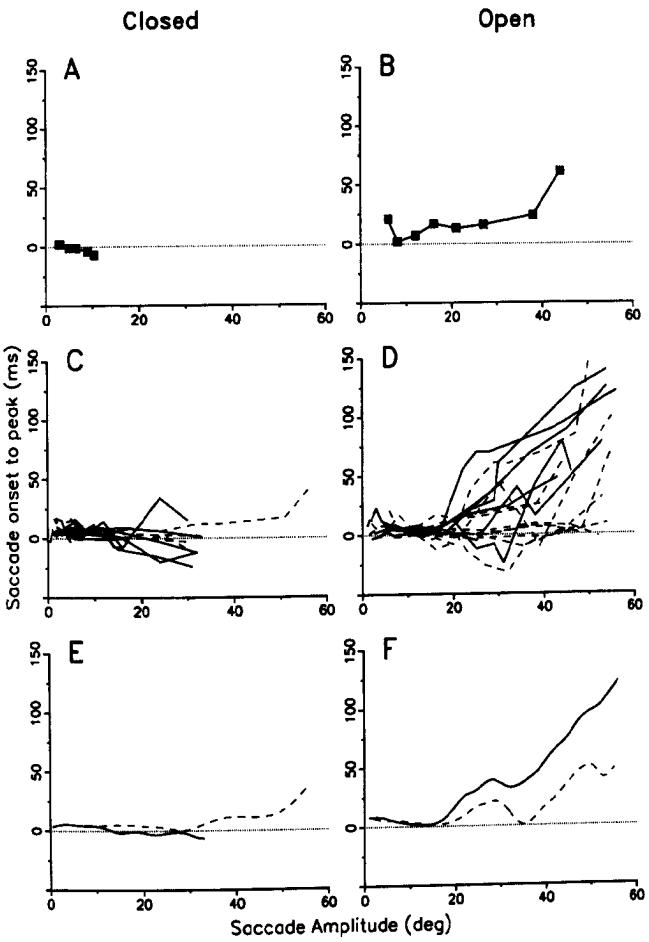

FIG. 12. Plots of time of saccade onset to time of peak discharge for cells with closed movement fields (*left column*) and for those with open-ended movement fields (*right column*). *A* and *B*: time from saccade onset to the peak discharge for the cells illustrated in Fig. 11. We used the spike density profile (σ = 10 ms) accompanying 8–10 saccades of identical amplitude to determine each point. This method allowed for considerable smoothing of the spike density profile and thus it was easier to determine the true peak of activity. The peak discharge was determined by a computer program that scanned along the instantaneous spike density profile from 100 ms before saccade onset to 100 ms after saccade end on each trial. If 2 peaks were detected, that with the highest value was designated as the peak, and if the 2 peaks were of identical height, the first encountered was designated as the peak. *C* and *D*: curves for each cell were derived as in *A* and *B*. All cells for which a wide enough range of amplitudes were tested are included. Solid lines: cells with optimal saccade amplitudes between 2 and 10°. Dashed lines: cells with optimal saccade amplitudes of 10–20°. *E* and *F*: spline fit through the data points for the curves shown in *C* and *D*. Same key as in *C* and *D*. The time to peak discharge was delayed as saccade amplitude increased for cells with open-ended movement fields.

ance of a peripheral visual stimulus. On the buildup versus visual activity graph (Fig. 19*B*) and on the burst versus buildup activity graph (Fig. 19*C*), the cells were more separated into three groups. Only the buildup activity measure adequately separated cells with burst from those with buildup activity (as in Fig. 6*B*), and on this measure the fixation cells most closely resembled those with a buildup of activity in that they too had changed values, the values were just negative.

DISCUSSION

Burst cells, buildup cells, and SC organization

We studied all of the saccade-related cells we encountered in penetrations through the SC and determined their activity during saccade generation, their movement fields, and their relative depth within the SC. We were able to distinguish two broad categories of activity that preceded the saccade. One was a burst of activity just before saccade onset with little or no activity between the time the signal was given to make the saccade and the saccade onset. The other was a buildup of activity that was present continuously between the time that the signal to make a saccade was given and saccade initiation. About three fourths of the cells that showed a buildup of activity also showed a burst just before the saccade. When we looked at the relation of the activity of the cells to the end of the saccade, we saw cells that had activity clipped off at the end of the saccade as well as those with partially clipped or unclipped activity. Some cells had closed movement fields in which saccades that were substantially shorter or longer than the optimum were not associated with increased activity, whereas other cells had open-ended movement fields in which saccades larger than the optimal amplitude continued to be associated with increased activity.

Although we deliberately evaluated each of these saccade-related characteristics separately for each cell, we also observed a clustering of these characteristics. We therefore hypothesize that the saccade-related cells in the monkey SC can be regarded as falling into two groups, which we name after their discharge characteristics before saccades. The first are the burst cells, which had a high-frequency burst occurring immediately before saccades. Of these burst cells 85% had closed movement fields, and a majority also had clipped activity (Table 2). The second are the buildup cells, which had continuous activity between the signal to make a saccade and its onset. Of these buildup cells 88% had open-ended movement fields, and a majority had partially clipped activity (Table 2). Because we usually encountered the cells with burst activity and closed movement fields more dorsally than cells with buildup activity and open-ended movement fields (Fig. 15), we hypothesize further that the burst and buildup cells lie in separate functional sublayers within the SC.

This hypothesis about the organization of the SC is summarized by the multilayered SC shown schematically in Fig. 20. The most dorsal layer contains visually responsive cells, which we have not studied in the present experiments and which correspond anatomically to the superficial gray and dorsal part of the optic layer of the SC (Ma et al. 1991). The deeper-lying saccade-related cells, which probably lie within the ventral optic layer and the intermediate gray and white layers (Ma et al. 1991), we show divided into a burst cell layer and a buildup cell layer.

In Fig. 20 we placed the fixation cells at the rostral pole of the buildup layer, because from our present and previous (Munoz and Wurtz 1993) experiments we think the fixation cells are most similar to buildup cells and can be regarded as a rostral extension of the buildup cells. Both fixation and buildup cells *1*) have open-ended movement fields (Fig. 16), *2*) change their activity long before the onset of the saccade (Fig. 17), and *3*) are encountered at about the same depth within the SC (Fig. 15*A*).

Comparison of burst and buildup cells to cells in previous studies

The burst cells are presumably the same neurons that have been most frequently studied and illustrated in the initial

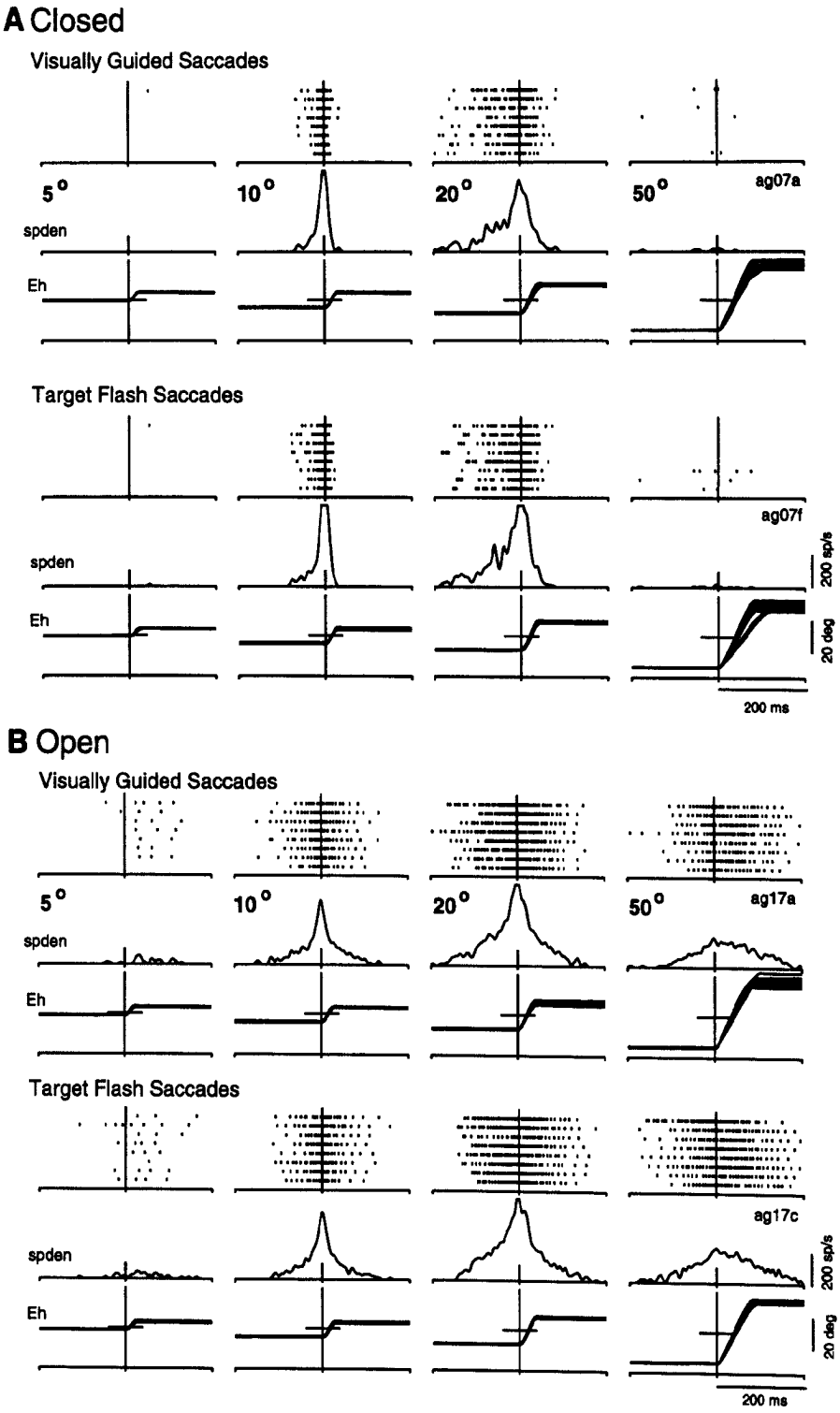

FIG. 13. Similar activity for saccades made to a continually present visual T (visually guided saccades) and to a T removed before the saccade began (T flash saccades). *A*: cell with a closed movement field. *B*: cell with an open-ended movement field. The optimal amplitude of both cells was 20°. Because the T had been turned off before the saccade began in the T flash paradigm, the response of the cell could not have resulted from the sweep of the T across the receptive field of the cell. Rasters, spike density (σ = 4 ms), and horizontal eye position traces are for saccades in the optimal direction for each cell.

investigations of the monkey SC; they are largely silent during fixation and discharge a high-frequency burst of spikes immediately before onset of saccades having the appropriate amplitude and direction (Schiller and Koerner 1971; Sparks 1975; Sparks et al. 1976; Wurtz and Goldberg 1971, 1972). This class of cells almost certainly includes the saccade-related burst neurons described by Sparks (1978), because they have "low levels of spontaneous activity and a discrete burst of activity tightly coupled to saccade onset" as do the type I saccade-related cells of Sparks et al. (1976). The burst cell grouping probably also includes the cells Sparks (1978) identified as having visual receptive fields and movement fields, because they appear to have had a pause between visual and saccade-related activity. The burst neurons also would include the visually triggered movement cells (Mohler and Wurtz 1976) that only discharged before saccades made to visual Ts and not before spontaneous saccades, because these neurons clearly had a pause in their

activity between the visual and saccade-related activity. We did not, however, record the activity of burst cells with spontaneous saccades in this study, so we could not tell which were visually triggered movement cells.

More recently it was suggested that the termination of the burst in some SC cells was an active process because it was clipped off at the end of the saccade in many cells (Waitzman et al. 1988, 1991). The majority of the burst cells had clipped activity and all had either clipped or partially clipped activity, which strongly suggests that cells with such clipped activity can be regarded as burst cells. Finally, the burst neurons we studied nearly always had closed movement fields, as did a number of cells studied by Wurtz and Goldberg (1972), Schiller and Koerner (1971), and Sparks and colleagues (Sparks 1975; Sparks and Mays 1980; Sparks et al. 1976).

In summary, we think that a type of colliculus cell can be identified in our experiments, as well as in previous ones, that has a burst of activity before saccades of the appropriate amplitude and direction, clipped responses, and closed movement fields.

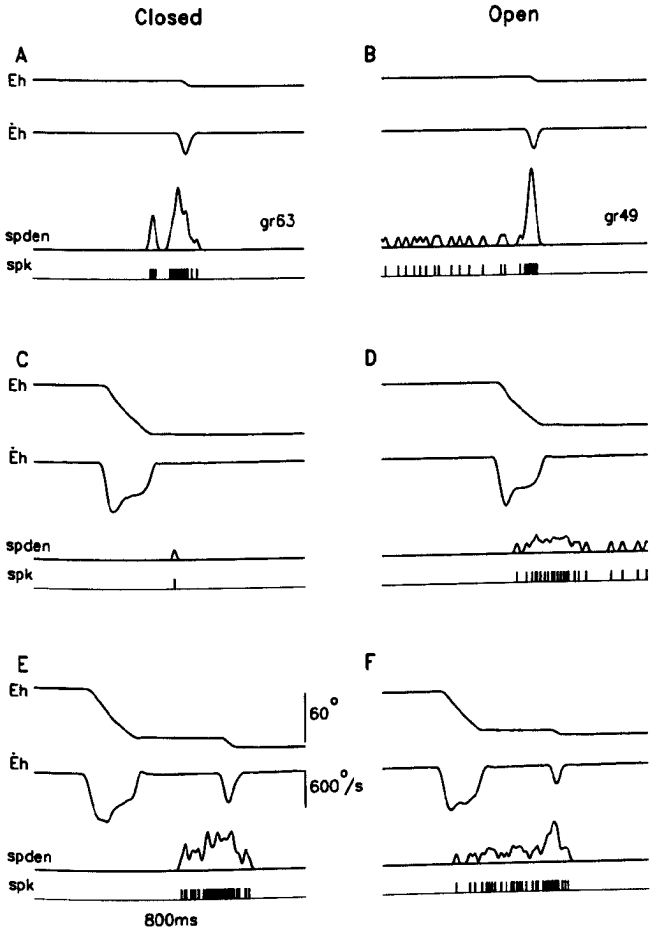

FIG. 14. Open-ended movement fields are not dependent on the generation of corrective saccades. *Left column*: activity of a cell with a closed movement field. *Right column*: activity for a cell with an open-ended movement field. *A* and *B*: saccades of ~6° were the optimal for both cells. *C* and *D*: only the cell with the open-ended movement field responded during a large (~60°) saccade. *E* and *F*: when a small corrective saccade was elicited, both cells increased their discharge rate; however, the cell with the open-ended movement field still began to discharge during the large saccade. For the spike density calculation, σ = 4 ms.

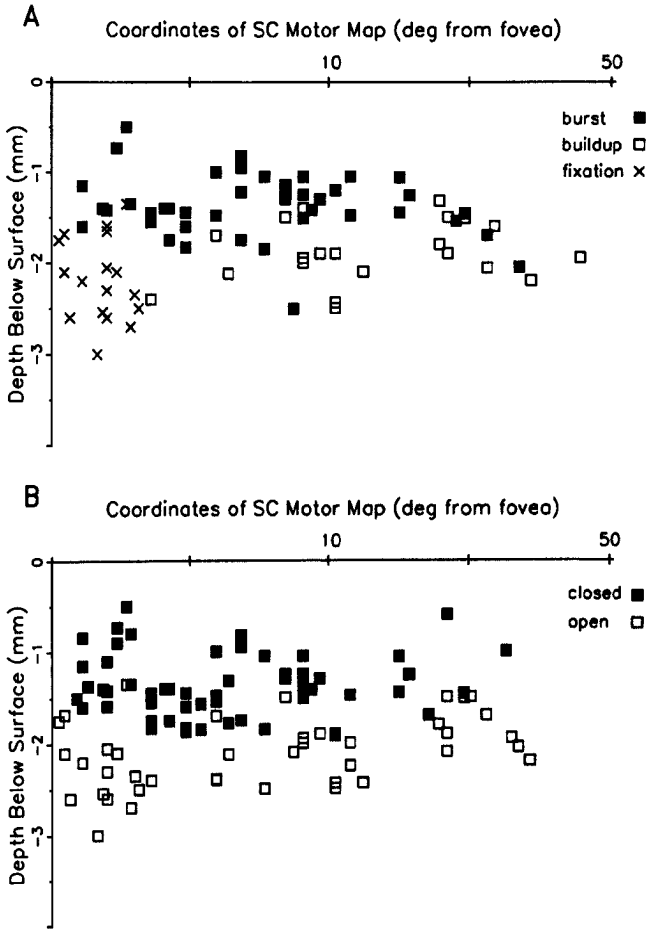

FIG. 15. Location of cells within the SC. The depth of each cell is plotted relative to the depth at which multiunit visual activity was encountered as the recording electrode first entered the SC. The anteroposterior coordinate corresponds to the cell's optimal amplitude from the foveal representation on the motor map. Visual cells, lacking saccade-related activity, were located in the 1st 1.2 mm of electrode travel through the SC (not shown). *A*: location of 81 cells with only burst activity (■), a buildup of activity (□), or fixation activity (×) across the anteroposterior extent of the SC. *B*: location of 99 cells with closed movement fields (■) or open-ended movement fields (□). Open-ended sample includes fixation cells. Points were derived from a total of 68 penetrations in 29 guide tubes in 3 monkeys.

Cells having a buildup of activity before the saccade and open-ended movement fields have also been described, but not identified as a separate category of saccade-related cell. Mohler and Wurtz (1976) showed a series of cells at increasing depths in the SC, and the two deepest cells they illustrated (see Fig. 5 in Mohler and Wurtz 1976) had both a buildup of activity before saccades and open-ended movement fields. These cells would certainly coincide with what we have called buildup cells. Sparks et al. (1976) also identified a class of movement-related neurons (class II) that were "characterized by a gradual increase in spike frequency beginning approximately 80–100 ms before saccade onset . . .". They emphasized that these cells never had a discrete burst of spikes, so that they are most comparable with the one fourth of the buildup cells in our sample without such a burst. More recently, cells having long-lead activity have been described in the monkey, where they have been named prelude bursters (Glimcher and Sparks 1992). The prelude activity could be present for several seconds before

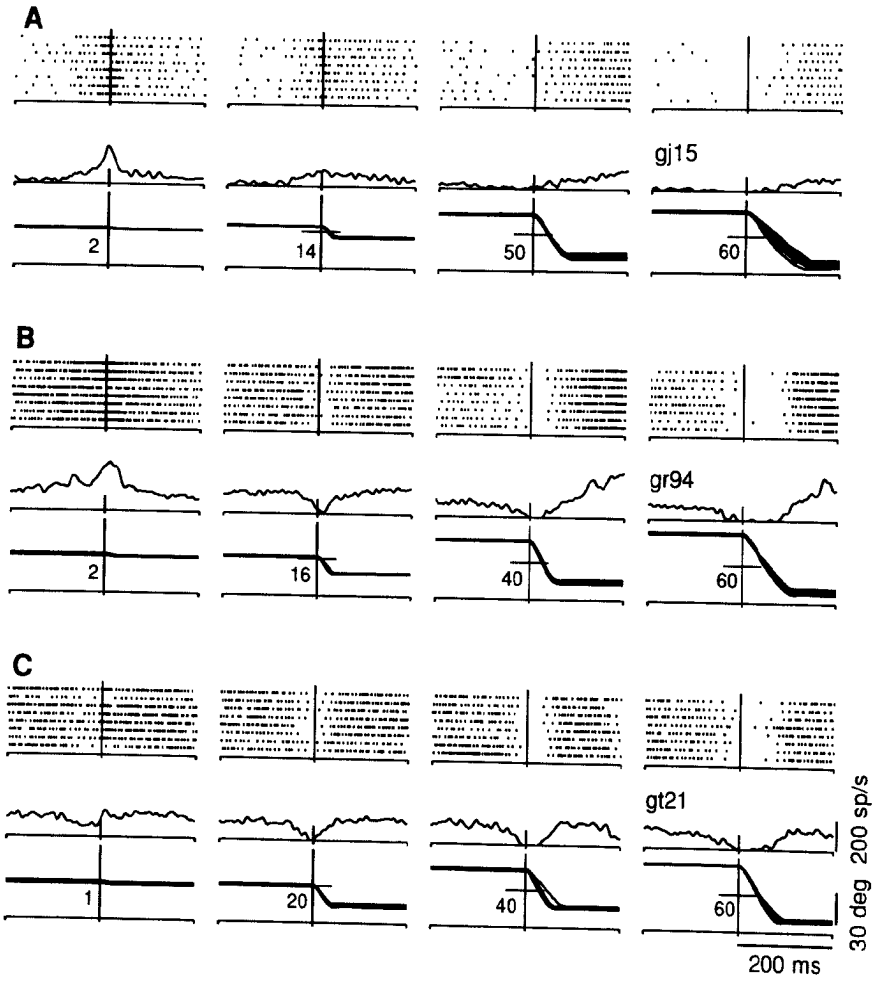

FIG. 16. Comparison of the open-ended movement field of a saccade-related cell (*A*) with the movement fields of 2 fixation cells (*B* and *C*) to reveal the transition between the saccade-related cells and fixation cells. *A*: optimal saccade direction was oblique, 45° down and to the left. Only the horizontal eye position traces are shown. The optimal amplitude for the cell is 2°, and its movement field is plotted in Fig. 8*B*. *B*: this fixation cell discharged a burst for small contraversive saccades and paused for all large contraversive saccades. The optimal amplitude for this fixation cell was 1°. *C*: this fixation cell paused for all saccades including the contraversive ones shown. Note that the cell in *B* represents a transition between the cells in *A* and *C*. All cells were in the right SC. For the spike density calculations, σ = 4 ms.

saccade initiation, and the cells also had high-frequency bursts in association with saccade execution. Because of their long-lead activity, we would be inclined to categorize these prelude bursters as buildup cells, but some caution is required because the movement fields of prelude bursters are closed rather than open as we would expect for buildup

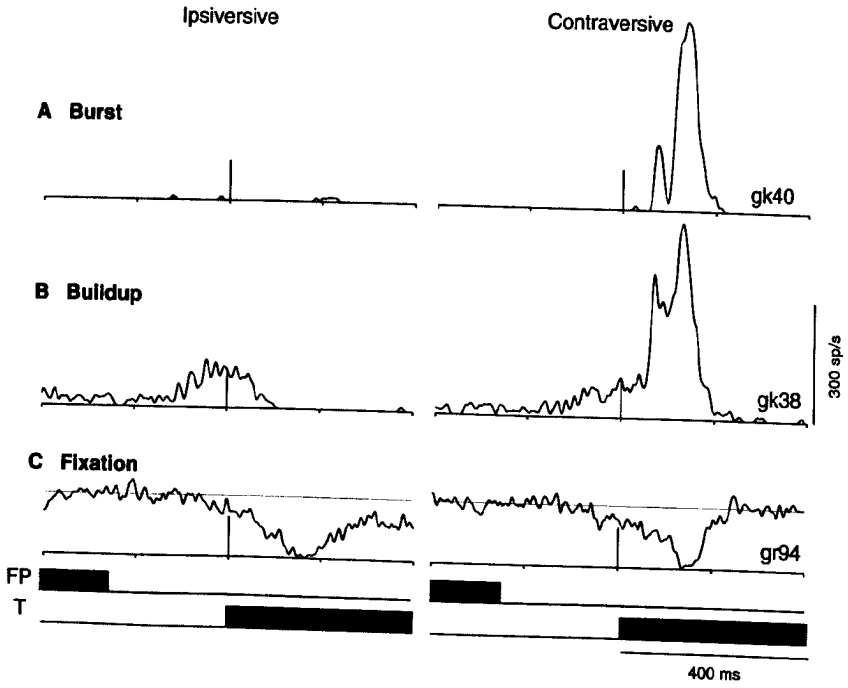

FIG. 17. Comparison of 3 cells with burst (*A*), buildup (*B*), and fixation (*C*) activity. Saccades were made during the gap saccade task to Ts in the ipsilateral (*left column*) and contralateral (*right column*) visual fields. The change in both the buildup of activity (*B*) and the decrease of fixation activity (*C*) began long before the saccade. The thin horizontal lines on the fixation cell traces are added for reference. The cessation of fixation activity also coincides with the peak of the burst activity. The spike density traces had σ = 4 ms.

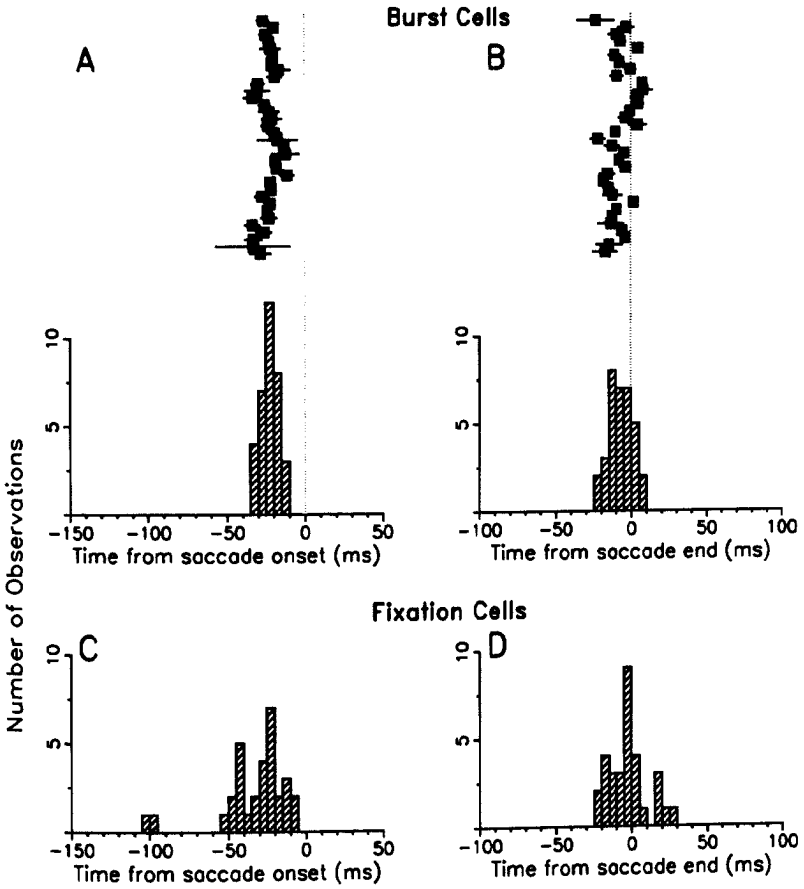

FIG. 18. Comparison of timing of the saccade-related burst for cells with only burst activity (*A* and *B*) and timing of the saccade-related pause for cells with fixation activity (*C* and *D*). *A*: time from saccade onset to burst onset for 34 cells with burst activity. We first computed the spike density (σ = 4 ms) for each trial and then measured the time from burst onset (50% of peak of spike density) to saccade onset. The means ± SD are shown for each cell at the *top*, and the histogram at the *bottom* represents the means of all 34 cells analyzed. The mean time from saccade onset to burst onset for the 34 cells was −23 ± 6 (SD) ms. *B*: time from saccade end to burst end for the same burst cells. Burst end was defined as when the spike density traces fell to 50% of the peak. The mean time from saccade end to burst end was −7 ± 8 (SD) ms. *C* and *D*: for reference, we have included the histogram of mean times from saccade onset to pause onset and saccade end to pause end obtained from 31 fixation cells for contraversive saccades (Munoz and Wurtz 1993).

cells (P. W. Glimcher and D. L. Sparks, personal communication). Thus cells with the characteristics we have used to categorize buildup cells have been observed in a number of previous studies of the SC.

The buildup cells also have characteristics that overlap those of the quasivisual cells identified by Mays and Sparks (1980). These cells respond with a constant latency to onset of an appropriate visual stimulus, as do buildup cells. Quasivisual cells also begin discharging after a signal to make the saccade and continue to do so until the saccade occurs, just as do the buildup cells. For these reasons we are inclined to regard the quasivisual cells as one type of buildup cell. However, there are several points of uncertainty in this comparison. The first is that the quasivisual cells discharge during a double-step saccade paradigm when the initial presentation of the visual T is outside the visual receptive field of the cell. We did test three buildup cells in a double-step task and found that all three were active in this task, but the sample is too small to draw strong conclusions. Second, the quasivisual cells tended to be recorded at the top of the

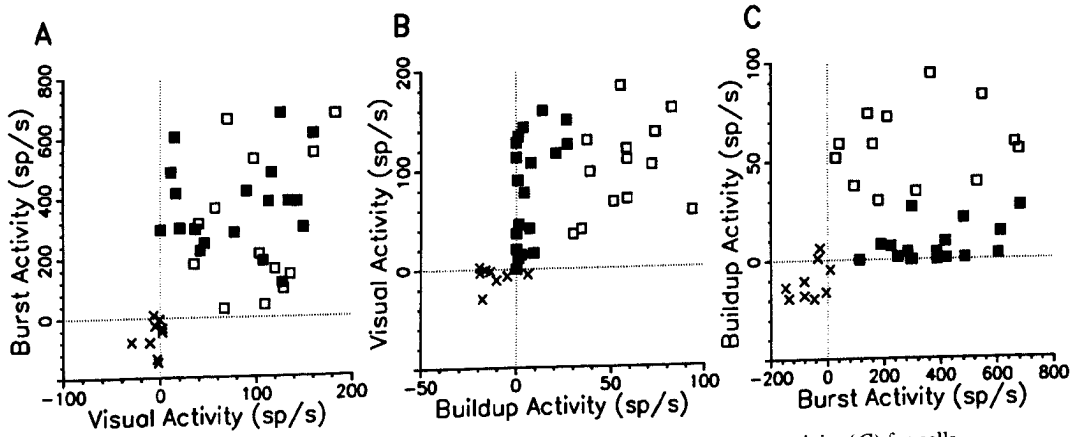

FIG. 19. Plots of burst vs. visual activity (*A*), visual vs. buildup activity (*B*), and buildup vs. burst activity (*C*) for cells with only burst activity (■), buildup activity (□), and fixation activity (×). The measures of activity were computed as in Fig 6. For cells with buildup activity and only burst activity, we used trials in which Ts were presented at the optimal amplitude and direction. For cells with fixation activity, we used trials in which the Ts were presented 10–20° in the periphery. Fixation cells had negative burst and buildup activities.

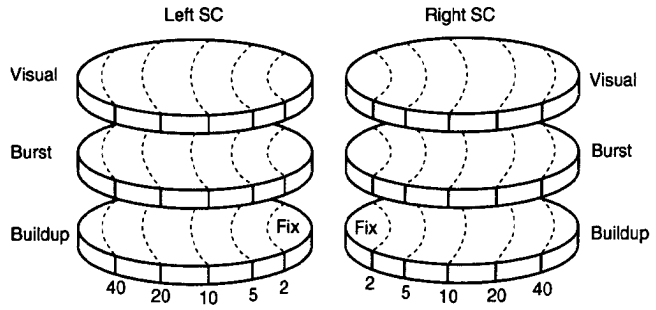

FIG. 20. Schematic drawing of visual, burst, and buildup cell layers of monkey SC. We hypothesize that there are 2 functional layers of saccade cells: a burst layer and a buildup layer. We suggest that the fixation cells are part of the buildup layer. See text of DISCUSSION for details.

intermediate layers (Mays and Sparks 1980), whereas we found buildup cells to be located deeper in the intermediate layers, beneath the burst cells.

The cells most similar to the buildup cells we describe in the monkey are the saccade-related cells recently described in the cat (Munoz and Guitton 1991; Munoz et al. 1991). The key features of these cells in the cat were *1*) the cells had long-lead preparatory activity, *2*) each cell appeared to achieve its peak discharge for a specific value of gaze motor error (the difference between current and desired gaze position), *3*) individual cells had open-ended movement fields, *4*) the peak in a cell's discharge occurred later in the movement for larger-amplitude movements, and *5*) there was a sequential activation of cells from the initially active caudal zone that moved rostrally toward the fixation cells. We saw many of these characteristics in the buildup cells: *1*) long-lead preparatory activity; *2*) peak discharge before saccades of a given amplitude; *3*) open-ended movement fields with discharge associated with saccades of optimal amplitude or larger; and *4*) peak discharge occurring later in the movement for larger than optimal saccades. The question of a sequential activation of cells cannot be determined from the observations described here on individual cells but can be assessed by looking at the population of cells as is done in the companion paper (Munoz and Wurtz 1995).

The buildup cells, and the fixation cells as the rostral extension of the buildup cells, appear comparable with the saccade-related cells and the fixation cells first described in the cat (Munoz and Guitton 1991; Munoz et al. 1991). The burst cells, however, appear to have little similarity to saccade-related cells in the cat.

In sum, the buildup cells have the key characteristics of a continuous buildup of activity after the signal to make a saccade and open-ended movement fields. It is also clear that the buildup cells form a more heterogeneous group than do the burst cells. Furthermore, it is not as easy to include previously studied neurons such as quasivisual cells and prelude bursters into the buildup category. These variants indicate that further (or different) divisions could be made in the population of buildup cells. We think, however, that by making this large division in the saccade-related cells, we can see differences in activity across the population of SC cells during the generation of saccadic eye movements, which we consider in the companion paper (Munoz and Wurtz 1995).

Anatomic correlates of burst and buildup cells

The burst and buildup cells may be related to the known anatomic cell types within the SC. Moschovakis and coworkers described two distinct classes of output cells that projected an axon from the SC to the predorsal bundle in both monkey (Moschovakis et al. 1988a) and cat (Moschovakis and Karabelas 1985). T cells were located in the ventral stratum opticum and dorsal stratum griseum intermedium. They had a projection into the collicular commissure, local collaterals within the SC, and an efferent projection from the SC into the predorsal bundle that branched into an ipsilateral ascending and contralateral descending component. X cells were located mainly in the stratum griseum intermedium. Their soma sizes and axon diameters were significantly larger than those of T cells. The axonal projections of X cells consisted of an axon in the predorsal bundle also having an ipsilateral ascending and contralateral descending component, an occasional recurrent collateral, and no commissural projection. Moschovakis and coworkers (1988b) found that in the alert squirrel monkey, T cells discharged high-frequency bursts associated with the generation of spontaneous saccades. T cells were presumably analogous to the previously studied saccade-related burst neurons and our burst cells. Indeed, Keller (1979) was able to antidromically activate collicular saccade-related burst neurons from the paramedian pontine reticular formation. Moschovakis and coworkers (1988b) could not determine a function for the X cells in the alert squirrel monkey making spontaneous saccadic eye movements. However, because in the cat almost all of the cells projecting an axon into the predorsal bundle are X cells rather than T cells (Moschovakis and Karabelas 1985) and because these collicular efferent cells in the cat have long-lead anticipatory discharges (Munoz et al. 1991), it seems reasonable to suggest that the X cells correspond to the long-lead cells in the cat. By analogy, the X cells may correspond to the buildup cells in the monkey, although this conclusion is less compelling than the correspondence between T cells and burst cells.

Additional evidence that the monkey SC gives rise to two descending projections to the contralateral brain stem has come from anatomic tracer studies (May and Porter 1992). One projection arises from dorsal intermediate SC and terminates in the medial reticular formation, whereas the other arises from the more ventral intermediate SC and terminates more laterally in the lateral reticular formation and spinal cord. The depths of these different projection neurons correspond to the depths of T and X cells described by Moschovakis and colleagues (1988a) and fit our anatomic description of burst and buildup cells. A similar laminar arrangement was also observed in the cat (Cowie and Holstege 1992).

Thus the anatomic evidence is consistent with the recognition of two major types of saccade-related cells within the SC of the monkey. Furthermore, the location of the cells with different projections at different depths in the SC is consistent with our hypothesis that saccade-related cells fall into two sublayers. As with the division of saccade-related cells into burst and buildup cells, this anatomically based division may also be subject to further subdivision.

Relation of buildup cells to head movement

Although initial stimulation studies of the monkey SC did not demonstrate a contribution of the SC to head movement (Robinson and Jarvis 1974; Stryker and Schiller 1975), more recent investigations have stimulated caudal regions of the SC and have produced both eye and head movements (Cowie and Robinson 1994; Freedman et al. 1993; Segraves and Goldberg 1992). Furthermore, there is some evidence that head movements are related to activity deeper in the SC because Cowie and Robinson (1994) have found that electrical stimulation elicited only saccades from the dorsal intermediate layers of the monkey SC but combined eye-head movements from more ventral intermediate layers. May and Porter (1992) speculated that it was the more ventral projection from the SC that was related to control of head movements, whereas the dorsal projection was more related to saccade generation. These observations not only indicate that the SC is related to the generation of head movement but that the relevant cells may lie deeper in the SC. Because the buildup cells lie deeper in the intermediate layers, this raises the possibility that these cells are also related to the generation of head movements.

We cannot contribute experimental observations on this point because in our experiments the monkey's head was always fixed. However, that the buildup cells probably are not related exclusively to the generation of head movements is clear from a consideration of the involvement of the head in the control of gaze shifts of differing sizes. Monkeys can look at Ts in the central visual field (±20°) with little if any movement of the head (Tomlinson and Bahra 1986) or attempted head movement (Richmond and Wurtz 1980). In this central range of ±20°, activity in the SC should be related to the generation of saccades rather than combined eye-head movements, yet within this range we observe many buildup cells (Figs. 9 and 15). The buildup cells cannot therefore be exclusively related to the generation of head movement.

The monkey has a full oculomotor range of ±50°, and for movements beyond this limit coordinated movements of the eyes and head are required. The buildup cells might contribute to the control of gaze (eyes and head) and be related to saccades only for small gaze shifts but to coordinated eye-head movement for the large gaze shifts. This relationship of the buildup cells to gaze would make the monkey similar to the cat. The saccade-related cells in the cat, which behave like the buildup cells in the monkey, are related to gaze, not just to eye movements (Munoz et al. 1991). But the cat has a limited oculomotor range (±25°) and relies on head movement to look at almost all visual Ts (Guitton et al. 1984, 1990), and stimulation of the cat SC always produces coordinated eye-head movement except when the stimulation is very close to the rostral pole (Roucoux et al. 1980). Therefore in the cat the saccade-related cells are always related to shifts in gaze, which nearly always involves head movement, whereas in the monkey the buildup cells might also be related to gaze shifts, which can be either eye alone or combined eye-head movements.

This leaves the burst cells apparently unneeded. One possible function of these cells is that they are related only to saccades, and it is their addition in the monkey that accounts for the higher-velocity saccades in the monkey (Fuchs 1967), compared with the cat (Evinger and Fuchs 1978).

Buildup cells and saccade preparation

The defining characteristic of the buildup cells is the development of activity over several hundred milliseconds before the onset of the saccade. The duration of the buildup varied somewhat from trial to trial under the same behavioral paradigm and varied markedly under different experimental paradigms.

We think that this buildup of activity is related to preparation to make a saccade. This preparation became evident when we used the gap paradigm with two potential Ts in which the monkey had the information after the FP went off that it was to make a saccade, but it did not know where the T was going to be or when the saccade was to be made until the onset of the T ended the gap period. During this gap between FP offset and T onset in our experiments (Figs. 5 and 17), the monkey presumably knew that the T would come on at a point in the ipsilateral or contralateral visual field during the several hundred milliseconds between the time the FP went off and the time the T appeared. During this gap period the activity of the buildup cells increased, but the monkey only knew that a saccade was required, not the direction and amplitude of the saccade. A burst of activity occurred only when the T came on in the contralateral visual field and a saccade was made to it. The buildup activity was therefore independent of the actual generation of the saccade; it was only related to the preparation to make a saccade.

When we looked at the activity of the fixation cells in the same gap paradigm, we saw a mirror image of the activity of the buildup cells (Fig. 17). The fixation cell activity decreased slightly as the buildup cell activity increased during the gap period, and then the fixation cell activity ceased during the burst just before the saccade. This initial change of activity in the fixation cells might also be regarded as preparation to make the saccade.

Thus in both the buildup and fixation cells we think that the long-lead increase or decrease of activity is related to early preparation to make a saccade. That activity would be present after planning for a saccade begins but before the goal and timing are specified. Our prediction would be that the higher the activity of the buildup cells (and the lower the activity of the fixation cells), the higher the probability of a saccade being made. The higher activity might also be predictive of when a saccade would be made. For example, we would predict that the short-latency express saccades would always be preceded by early and strong activity in the buildup cells.

The long-lead activity of the buildup cells might also be related to the selection of the next T for a saccade. This has been suggested for the monkey by Wurtz and Albano (1980) for long-lead SC cells, by Glimcher and Sparks (1992) for prelude bursters, and by Munoz and Guitton (1989, 1991) for tectoreticulospinal neurons in the cat. More recently Glimcher and Sparks (1992) concluded that the low-frequency activity of prelude bursters reflected a covert process of response selection that occurred early in the generation of a saccade. As we have indicated, our experiments using the gap paradigm led us to view the increased activity of

the buildup cells before the saccade as more closely related to a preparation to make a saccade rather than a selection of the T; the buildup of activity could not be related exclusively to response selection because that selection between the two alternative Ts had not yet been made when the buildup began. It may be, however, that because in our experiments the two Ts were always in the same two locations during a block of trials, the selection process was either minimized or had already taken place. All that was left was the preparation for any saccade, and so in our experiments this is what we observed. The activity of the buildup cells may in fact be related to both T selection and the subsequent preparation for movement. Both selection and preparation are related to the early activity preceding the saccade, and it is clear that the buildup cells are involved in this process. Furthermore, the relative contribution of these factors should be revealed by modifying the paradigms to separate the selection of Ts from the where and when of saccade generation.

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