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# Activity of Rostral Superior Colliculus Neurons During Passive and Active Viewing of Motion

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**Krauzlis, Richard J.** Activity of rostral superior colliculus neurons during passive and active viewing of motion. *J Neurophysiol* 92: 949–958, 2004. First published March 17, 2004; 10.1152/jn.00830.2003. The superior colliculus (SC) has long been known to be important for the control of saccades, and recent findings indicate that the rostral SC (rSC) plays some role in pursuit as well. The recent finding that the prelude activity of some SC neurons exhibits directional selectivity suggests that the rSC might process visual motion signals relevant for the control of pursuit. We have now tested the activity of buildup neurons in the rSC during the passive viewing of motion stimuli placed within their response field and also during the previewing of visual motion stimuli that were subsequently tracked with pursuit eye movements. We found that rSC buildup neurons typically responded well to motion stimuli, but that they exhibited essentially no selectivity for the direction or speed of visual motion, and that they also responded well to stationary flickering dots. However, during the previewing of visual motion prior to the onset of pursuit, many neurons did exhibit a buildup of activity similar to that exhibited before saccades. These results are inconsistent with the notion that the rSC mediates visual motion signals used to drive pursuit, but instead support the idea that visual motion signals can be used by rSC neurons as part of a mechanism for selecting targets for pursuit and saccades.

## INTRODUCTION

The intermediate and deep layers of the monkey superior colliculus (SC) are known to be important for the control of saccadic eye movements (Moschovakis and Highstein 1994; Sparks and Hartwich-Young 1989; Sparks and Mays 1990; Wurtz and Albano 1980). The rostral SC, which represents the central portion of the retinotopic map (Robinson 1972), also appears to participate in the generation of pursuit eye movements. Activation and inactivation of the rostral SC alters the metrics of pursuit and saccades (Basso et al. 2000; Munoz and Wurtz 1993b), providing evidence for a causal role in both types of eye movements. Neurons in the rostral SC with "buildup" activity (Munoz and Wurtz 1995) change their firing rate before and during pursuit eye movements, as well as during fixation and small saccades (Krauzlis and Dill 2002; Krauzlis et al. 1997, 2000). One explanation for these observations is that the activity of rostral SC neurons helps define the goal for eye movements involving parafoveal locations, regardless of whether this goal is achieved by saccades, pursuit, or maintained fixation (Krauzlis et al. 1997). In support of this interpretation, we have recently shown that rostral SC neurons exhibit higher activity for target than for distractor stimuli and that this preference can account for the target choices made by the pursuit and saccadic systems (Krauzlis and Dill 2002).

Alternatively, rostral SC neurons might provide a signal that directly modifies the metrics of pursuit and saccades. In particular, the SC receives visual motion information that could be used to guide pursuit. The middle temporal area (MT) and the medial superior temporal area (MST) process visual motion signals crucial for the control of pursuit (Dürsteler and Wurtz 1988; Newsome et al. 1985), and both areas project to the SC (Boussaoud et al. 1992; Fries 1984; Ungerleider et al. 1984). Recent physiological studies support the idea of directionally selective inputs to saccade-related neurons in the SC (Horwitz and Newsome 1999, 2001a,b). In these studies, monkeys indicated their judgment about a random-dot motion display by making a saccade to the target that was spatially aligned with the perceived direction of motion. The prelude activity of some SC neurons exhibited directionally selective visual responses that predicted the choices made during the task and that pointed toward the spatial location of the neuron's response field. Thus the pursuit-related activity of rostral SC neurons might be due to similar directionally selective visual inputs, rather than to information about target location. In this study, we tested this possibility by recording the activity of rostral SC neurons during passive viewing of visual motion stimuli and also during the previewing of motion stimuli that were subsequently tracked. We report that rostral SC neurons showed essentially no selectivity for the direction or speed of motion, although many exhibited a marked buildup of activity during previewing of visual motion prior to the onset of smooth tracking.

## METHODS

### *General procedures*

Data were collected from two adult male rhesus monkeys (*Macaca mulatta*) weighing 9–15 kg. All experimental protocols for the monkeys 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 prepared and studied using standard surgical and recording techniques that have been described in detail previously (Krauzlis 2003). In brief, spikes form single neurons were recorded in the intermediate and deep layers of the SC (1.0–3.5 mm below the collicular surface) with tungsten microelectrodes with impedances of 0.7–1.5 MΩ measured at 1 kHz (Frederick Haer) and converted to timing pulses using a multi-channel spike sorting system (Plexon). Spike events were converted to a continuous record of firing rate by replacing each spike with a replica

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of a postsynaptic potential (1-ms rising time constant, 20-ms decaying time constant) (Hanes et al. 1998). The experiments were controlled by a computer using the Tempo software package (Reflective Computing), and a second computer using VisionWorks software (Swift et al. 1997) acted as a server device for presenting the visual stimuli. Stimuli were presented with a video monitor (Eizo FX-E7, 120 Hz, ~20 pixels/°) at a viewing distance of 41 cm. Eye movements were recorded using scleral search coils (Judge et al. 1980) and the electromagnetic induction technique (Fuchs and Robinson 1966) using standard phase detector circuits (Riverbend Instruments). All neuronal spike data, eye movement data, and events related to the onset of stimuli were stored on disk during the experiment (1-kHz sampling rate, A/D converter, ComputerBoards) and transferred to a FreeBSD Linux-based system for off-line analysis.

### *Neuron classification*

Response fields were mapped based on the visual responses to spot stimuli (0.2° diam) as the monkey performed a block of visually guided saccades. The locations of the visual stimuli were set by hand, and it typically required about 40 visually guided saccades to identify the center and edges of each neuron's response field. After this mapping of the response fields, neurons ($n = 57$; 38 and 19 for monkeys W and A, respectively) were tested using the fixation blink paradigm (Munoz and Wurtz 1993a) and memory-guided saccades (Hikosaka and Wurtz 1983) in separate blocks of trials. This study focused on neurons ($n = 51$) that had the same functional properties as those described previously for "rostral buildup neurons" (Krauzlis 2003; Krauzlis et al. 2000), but also included a few "buildup" neurons (Munoz and Wurtz 1995) from more caudal locations. The remaining neurons were active only during the motor execution of saccades ($n = 1$) or during the presentation of visual stimuli ($n = 5$). Many of the neurons selected for study ($n = 30/51$) met the criteria defined for "fixation" cells (Munoz and Wurtz 1993a)—they maintained a firing rate of ≥10 spikes/s during blinks imposed during fixation. This maintained activity was documented by comparing the firing rate in a 100-ms blink interval (starting 100 ms after the onset of the blink) to the firing rate in a 100-ms visible interval (starting 100 ms before the onset of the blink), as shown in Fig. 1*A* and described previously (Krauzlis 2001, 2003). A majority of neurons ($n = 32/51$) also showed an increase in activity before and during small memory-guided saccades (Fig. 1*B*). These neurons were tested during saccades to remembered stimuli placed in the center of the response field of the neuron, which was typically within the central 5° of the contralateral hemifield. As found for buildup neurons in the caudal SC (Munoz and Wurtz 1995), the "burst" activity for these neurons (defined as the average firing rate in an interval from 8 ms prior to saccade onset until 8 ms prior to saccade end) was generally preceded by lesser "buildup" activity (defined as the average firing rate in a 75-ms interval starting 100 ms before saccade onset). These memory-guided saccades did not always produce large increases in activity, because the endpoints were chosen to be large enough to elicit reliable memory-guided saccades and thus did not always fall in the center of the neuron's response field. However, to be classified as a buildup neuron, the "buildup" activity had to be significantly greater (Wilcoxon rank-sum test, $P < 0.05$) than the "baseline" activity during fixation (defined as the average firing rate in a 100-ms interval starting 100 ms before fixation point offset). Of the 30 neurons with tonic activity during fixation, 11 also exhibited increased activity during memory-guided saccades.

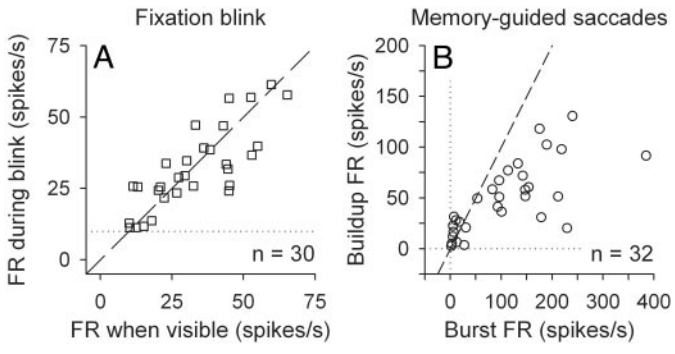


FIG. 1. Classification of neurons reported in this study. *A*: activity during the fixation blink paradigm of rostral superior colliculus (SC) neurons that met the criteria for "fixation cells." Firing rate during fixation with target blinked off (a 100-ms interval starting 100 ms after onset of blink) is plotted against firing rate during fixation with target visible (a 100-ms interval starting 100 ms before onset of blink). Dashed line indicates unity slope; dotted horizontal line indicates 10 spike/s, the criterion minimum firing rate for fixation cells (Munoz and Wurtz 1993a). *B*: activity during memory-guided saccades of rostral SC neurons identified as buildup neurons. Buildup firing rate (average activity during a 75-ms interval starting 100 ms before saccade onset) is plotted against burst firing rate (average activity during an interval spanning 8 ms prior to saccade onset until 8 ms prior to saccade end). Overall, 30 neurons exhibited fixation-related activity, and 32 neurons exhibited buildup activity. A subset of these neurons ($n = 11$) exhibited both fixation and buildup activity, for a total of 51 neurons.

### *Behavioral paradigms*

Neurons identified as rostral or caudal buildup neurons were studied with random-dot motion stimuli under two behavioral conditions presented in separate blocks. For the "passive viewing" condition, monkeys maintained fixation of a central stimulus while we presented random dot motion stimuli in the response field of the neuron. The monkey initiated these trials by fixating a small red spot (0.2° diam) that appeared at the center of the display. After maintaining fixation for 750 ms, a random dot motion stimulus was presented in the response field of the neuron for 1 s, after which the random dot stimulus was removed and the monkey was required to maintain fixation for an additional 750 ms. The flanking periods of fixation were included to ensure that the monkey was actively maintaining fixation during the presentation of the motion stimulus and not planning saccades in anticipation of the end of the trial. Throughout the entire trial, the monkey was required to remain with 2.0° of the central fixation spot; otherwise, the fixation spot was extinguished, and the paradigm reverted to the initial fixation period after a 1-s timeout. The monkey was given a liquid reward at the end of each correctly performed trial. The location and dimensions of the random dot motion stimuli were based on the mapping of the response fields using visually guided saccades. For cases in which the random dot motion stimulus spatially overlapped the center of the screen, the red fixation spot occluded the moving white dots of the motion stimulus, so that the monkey's view of the fixation spot was uninterrupted. On each trial, we presented dots that moved at one of six possible speeds (0, 4, 8, 16, 32, 64°/s) and that moved in one of eight possible directions of motion (left, right, up, down, left-up, left-down, right-up, and right-down), resulting in 41 unique trial conditions. On a given trial, every dot in the random dot motion stimulus (density: 3 dots/$^{\circ 2}$) moved at the same constant speed and in the same direction. The lifetime of each dot was limited to 50 ms. Our stimuli therefore included a substantial flicker component, which is known to affect motion processing in the middle temporal and medial superior temporal areas (Britten et al. 1993; Churan and Ilg 2002; Lagae et al. 1994; Qian and Andersen 1994). Although we did not systematically examine the interaction between flicker and motion processing, we did document the responses to stationary flicker (i.e., the 0°/s condition).

For the "previewing" condition, monkeys viewed the random dot motion stimulus during a period of maintained fixation before actively tracking the motion with a smooth pursuit eye movement. As before, the monkey initiated these trials by fixating a small red spot (0.2° diam) that appeared at the center of the display. After maintaining fixation for 250 ms, we presented a strip of stationary random dots, 5° high by 44° wide that straddled the horizontal meridian. After 1 s, the

stationary dots in the strip were replaced by dots moving either leftward or rightward, but the monkey was required to maintain fixation of the central red spot (the "preview" interval). After an additional 1 s, the central red spot adopted the motion of the random dots, effectively merging with the random dot motion stimulus. The motion stimulus was presented for an additional second, and the task of the monkey was to smoothly track the combined spot and random dot motion (the "track" interval). Once the red spot began to move, the monkey was allowed 500 ms to get his eye position within 3° of the position of the moving red spot and he was required to keep within 3° of the spot for the remainder of the trial. Coincident with the onset of the red spot's motion, its location was offset in the direction opposite to its motion, and this offset was adjusted so that the elicited pursuit contained few or no accompanying saccades (Rashbass 1961). On each trial, we presented dots that moved at one of three possible speeds (10, 15, 20°/s) and either leftward or rightward. The dimensions of the strip of stationary and moving dots were always fixed at 5° high by 44° wide.

The dimensions of the stimulus were not tailored to the response field of the neuron under study, because this would have resulted in stimuli that were inappropriate to elicit pursuit. In particular, for neurons with response fields near the fovea, tailored stimuli would have been too small to support pursuit for more than a few hundred milliseconds, whereas for neurons with response fields away from the fovea, tailored stimuli would have required parafoveal pursuit. Instead, we used a fixed elongated stimulus and focused this experiment on neurons whose response fields fell within a portion the stimulus ($n = 19$), and for comparison, included a few neurons whose response fields fell outside of the stimulus ($n = 6$). In addition, by keeping the stimulus constant, it was easier for monkeys to learn to maintain fixation during the "preview" interval, despite the large size of the motion stimulus, and to generate essentially saccade-free pursuit during the "track" interval. In all other respects, the dot motion stimulus was the same as in the "passive viewing" condition.

### *Data analysis*

To document the changes in neuronal activity during the "passive viewing" condition, we measured the average firing rate in four epochs. *1*) We defined the "baseline" activity as the average firing rate in a 200-ms interval starting 200 ms before the appearance of the random dot motion stimulus. *2*) We defined the "response" activity as the average firing rate in a 1,000-ms interval starting 70 ms after the appearance of the random dot motion stimulus. The purpose of the 70-ms delay is to compensate for the delay in the visual response to the motion stimulus. For the "preview" condition, we measured the firing rate in two epochs during the preview interval. *1*) We defined the "early preview" activity as the average firing rate in a 200-ms interval starting 300 ms after the stationary dots were replaced by moving ones. This interval was therefore placed 500–700 ms before the fixation spot merged with the moving random dots. *2*) We defined the "late preview" activity as the average firing rate in a 200-ms interval starting 800 ms after the moving dots appeared. This interval was therefore placed 0–200 ms before the fixation spot merged with the moving random dots. The statistical significance of differences between measurements made from individual trials and across conditions was assessed using commercially available software (Matlab and SigmaStat). To eliminate any saccade-related modulation from these measurements, we excluded all spikes that occurred from 100 ms before to 25 ms after the occurrence of saccades. We detected saccades by applying a set of amplitude criteria to the eye velocity and eye acceleration signals, as described previously (Krauzlis and Miles 1996). Signals encoding horizontal eye velocity and acceleration were obtained by applying a finite impulse response (FIR) filter (−3 dB at 54 Hz for monkeys) to the calibrated horizontal eye position signals. This algorithm permitted us to detect saccades with amplitudes as small as ~0.15°.

## RESULTS

Of the neurons we studied ($n = 51$), the majority (30) had response fields centered within the central 5° of the visual field, as shown by the scatterplot in Fig. 2. On average, the neurons in the central 5° had smaller response fields (average size: 3.5 ± 1.3° horizontal by 3.5 ± 1.4° vertical) compared with neurons with centers lying outside of the central 5° (average size: 8.8 ± 2.9° horizontal by 8.9 ± 3.6° vertical).

### *Changes in neuronal activity during passive viewing*

Most buildup neurons showed a marked increase in activity shortly after the onset of the random dot motion stimulus, although the responses were not very selective for the direction of motion. A sample rostral buildup neuron is shown in Fig. 3. This unit was recorded in the left superior colliculus and had a response field located in the right visual field at an eccentricity of 1° along the horizontal meridian; the size of the response field was 3° by 3°. The individual graphs of spike density show an increase in activity after the appearance of the random dot motion stimulus, which contained dots moving at 8°/s and was presented for the temporal interval indicated by the black bar at the bottom of the plots. The neuron responded vigorously during presentation of the motion stimulus and exhibited a slight preference for the left-downward direction, but overall was not particularly selective for the direction of motion.

We quantified these responses by measuring the average firing rate during a "baseline" interval (a 200-ms interval starting 200 ms before the appearance of the motion stimulus) and a "response" interval (a 1,000-ms interval starting 70 ms after the appearance of the motion stimulus). As shown by the polar plot in Fig. 3, the firing rate of the neuron increased from a baseline level of ~20 spikes/s (dotted line) to a level of 30–50 spikes/s (solid line) in the presence of the motion

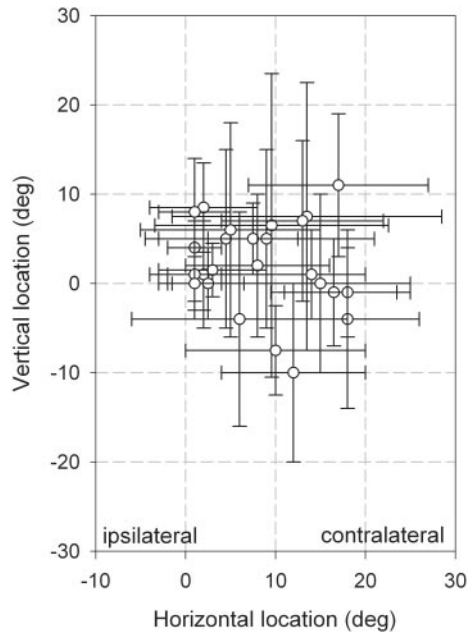


FIG. 2. Response fields of the neurons. Each circle indicates location of response field center with respect to recording site (all contralateral), and error bars indicate horizontal and vertical edges of response field. Number of circles plotted is smaller than number of neurons because the same response field was sometimes found for multiple neurons.

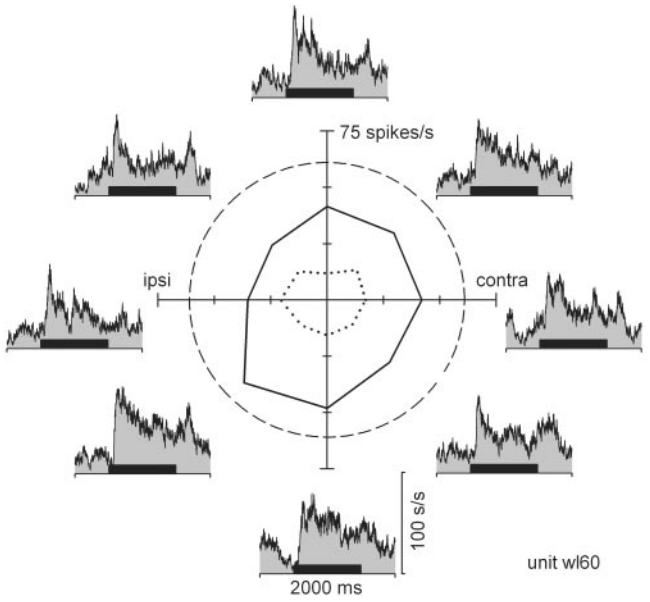


FIG. 3. Activity of a sample rostral SC buildup neuron during passive viewing of motion stimuli. Individual spike density plots show average firing rate plotted as a function of time during presentation of 8 directions of motion of the random dot stimulus at a speed of 8°/s. Black bar along abscissa of each plot indicates the 1-s interval during which motion stimulus was presented. Central polar plot summarizes activity of neuron. Dotted line indicates baseline activity measured in a 200-ms interval before appearance of motion stimuli. Solid line indicates average activity in a 1,000-ms interval starting 70 ms after appearance of motion stimuli. Dashed line indicates average activity in a 1,000-ms interval starting 70 ms after appearance of stationary dots, with the same dot lifetime as in motion stimuli. Data are from unit wl60, recorded in the left SC.

stimulus. Also shown is the firing rate during the response interval during presentation of stationary dots (dashed line, 61 spikes/s). Although stationary, the dots in this stimulus flickered because, as in the motion stimulus, each dot had a 50-ms dot lifetime. Thus in addition to exhibiting only weak directional selectivity, the neuron actually responded more vigorously to stationary flickering dots than to moving flickering dots.

Many neurons in our sample exhibited significant changes in firing rate after the appearance of the motion stimulus, but they also showed significant changes with stationary flickering dots. The results we obtained with a dot speed of 8°/s are summarized by the graphs in Fig. 4, which plot the average firing rate during the response interval as a function of the average firing rate during the baseline interval for each neuron. Across the eight directions of motion (each shown by 1 of the 8 outer graphs), an average of 36% of the neurons showed a significant change in activity between the two intervals (filled circles, Wilcoxon rank-sum test, $P < 0.05$). The gray filled circle indicates the measurements from the sample unit shown in Fig. 3. In comparison, the appearance of the stationary flickering dots caused a significant change in activity in 45% of the neurons. In fact, across neurons, the response to stationary flicker was linearly related to the response to motion in the preferred direction (linear regression, $r = 0.89$, $P < 0.001$); the slope of this regression was just slightly greater than unity (1.09), indicating a tendency for neurons to emit somewhat larger responses for stationary flicker than for the motion stimulus. We found similar results with every combination of speed and direction tested.

To document the quality of direction tuning across our sample, we computed average tuning curves (Fig. 5). We generated these average curves by rotating each individual tuning curve so that the best direction (the direction associated with the highest activity during the response interval) was defined as 0°. Across our sample of neurons, the average responses to the motion stimuli (open circles) were elevated modestly with respect to the baseline activity (dotted lines), but tended to be lower than the responses to the stationary flickering dots (dashed lines). The direction of motion did not have a significant effect on firing rate for any of the five speeds tested (ANOVA $F_{(7,400)} < 0.64$, $P > 0.72$ for each of the 5 speeds).

The relatively modest degree of directional selectivity could be due to the presence of neurons in our sample that did not respond significantly to the motion stimulus. To test this possibility, we identified a subset of our neurons that were "motion sensitive," which we defined as those neurons that showed a significant increase in activity over baseline for at least one combination of direction and speed and which also showed a significantly larger response for moving dots than for the stationary flickering dots. Only a small minority of the neurons in our sample—14% (7/51)—met this criterion for "motion sensitive." To assess the directional selectivity of this subset, we generated an additional set of average tuning curves based on these seven "motion sensitive" neurons, and found average tuning curves (shaded circles in Fig. 5) that differed slightly in overall firing rate, but otherwise showed essentially the same weak tuning for direction as that obtained using our complete sample. Thus even the minority of neurons identified

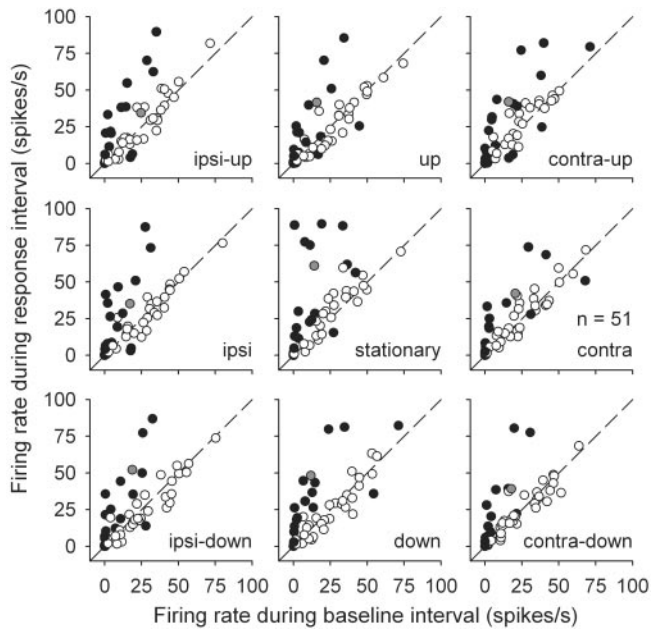


FIG. 4. Changes in activity during passive viewing of the 8°/s motion stimulus. Average firing rate during response interval (1,000-ms interval starting 70 ms after the appearance of motion stimuli) is plotted against average firing rate during baseline interval (200-ms interval before appearance of motion stimuli) for each neuron ($n = 51$). Outer plots are arranged according to the corresponding 8 directions of motion, and the central plot shows data obtained with stationary flickering dots. Filled circles indicate significant differences (Wilcoxon rank-sum test, $P < 0.05$). Gray filled circle indicates unit wl60, the sample neuron shown in Fig. 3.

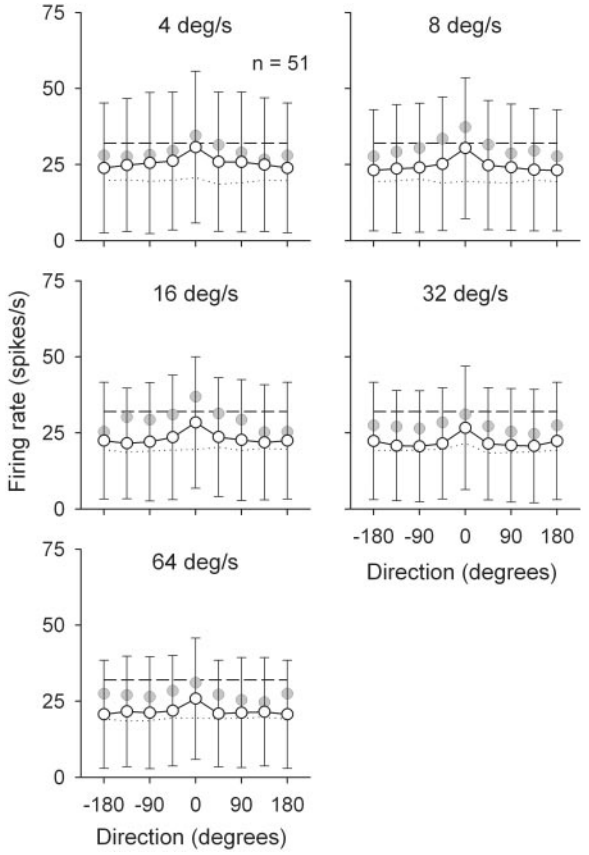


FIG. 5. Average direction-tuning curves of rostral SC buildup neurons. Each plot shows average tuning exhibited for 1 speed of motion. Average activity during response interval (1,000-ms interval starting 70 ms after appearance of motion stimuli) is plotted as a function of direction, relative to the best direction for each neuron, which is defined as 0°. Open circles show activity for entire population of neurons ($n = 51$). Dotted line shows activity during baseline interval (200-ms interval before appearance of motion stimuli). Dashed line shows average activity during response interval when stationary flickering dots were presented. Shaded circles show activity for the 7 neurons that were classified as "motion sensitive."

as "motion sensitive" did not exhibit a strong preference for the direction of motion.

We summarized the selectivity for the direction of motion using a directionality index, which was defined by the equation

$$\textit{Directionality Index} = 1 - \{(\text{Response to non-preferred direction}) \div (\text{Response to best direction})\}$$

As shown by the histograms in the *left column* of Fig. 6, the majority of neurons had directionality indexes $<0.5$ regardless of the speed of the motion stimulus. The numbers in each graph indicate the median value for each speed; across all speeds, the median directionality index was 0.25, indicating that the response to motion in the preferred direction was typically about one-third larger than the response to motion in the nonpreferred, or opposite, direction. The distributions of index values at each speed were not significantly different from one another (Kruskal-Wallis, $P = 0.186$), indicating that the strength of tuning did not vary with the speed of motion. There was also no tendency for neurons to favor one direction of motion over others. As shown by the histograms in the *right column* of Fig. 6, the best directions of our neurons were mostly uniformly distributed across the eight directions of motion tested. The distributions of best directions did not indicate a significant preference for any particular direction, and there was no apparent relationship between the best direction and motion speed ($\chi^2$ test, $P = 0.293$). Overall, we conclude that buildup neurons in the rostral SC are responsive to motion stimuli, but are not particularly selective for the direction or speed of motion.

### *Changes in neuronal activity during previewing of motion*

In addition to their modest responses during passive viewing of motion stimuli, we found that buildup neurons in the rSC exhibited strong modulation of their activity during the previewing of motion stimuli that were subsequently tracked with a smooth-pursuit eye movement. Sample data from one unit are shown in Fig. 7. This neuron was recorded in the right rSC and had a small centrally located receptive field (3° by 3°) that fell inside the strip of motion, as indicated by the black square in Fig. 7*A*. The receptive field of the neuron was too close to the fixation spot to probe directly with memory-guided saccades, but we did test the neuron with larger rightward (i.e., ipsiver-

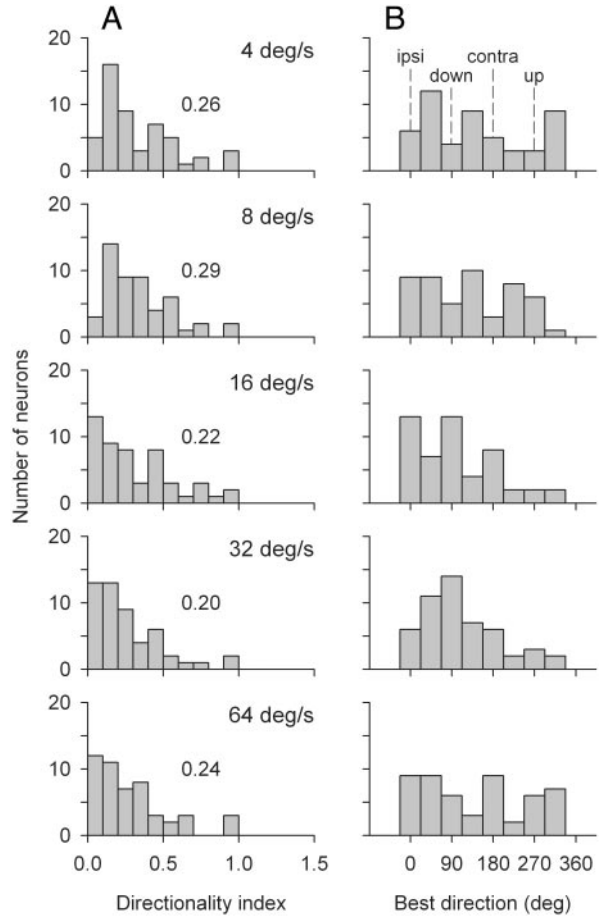


FIG. 6. Summary of directional selectivity of rostral SC buildup neurons. *A*: distribution of directionality indexes (DI). Each plot shows range of DIs found for a particular speed of motion, indicated by *top* label. Median DI for each distribution is indicated by the number in the center of each plot. *B*: distribution of best directions, sorted according to speed of motion, as in *A*. Directions of motion were defined with respect to the side of recording, such that 0° corresponds to ipsilaterally direction motion, 180° corresponds to contralaterally direction motion, 90° corresponds to downward motion, and 270° corresponds to upward motion.

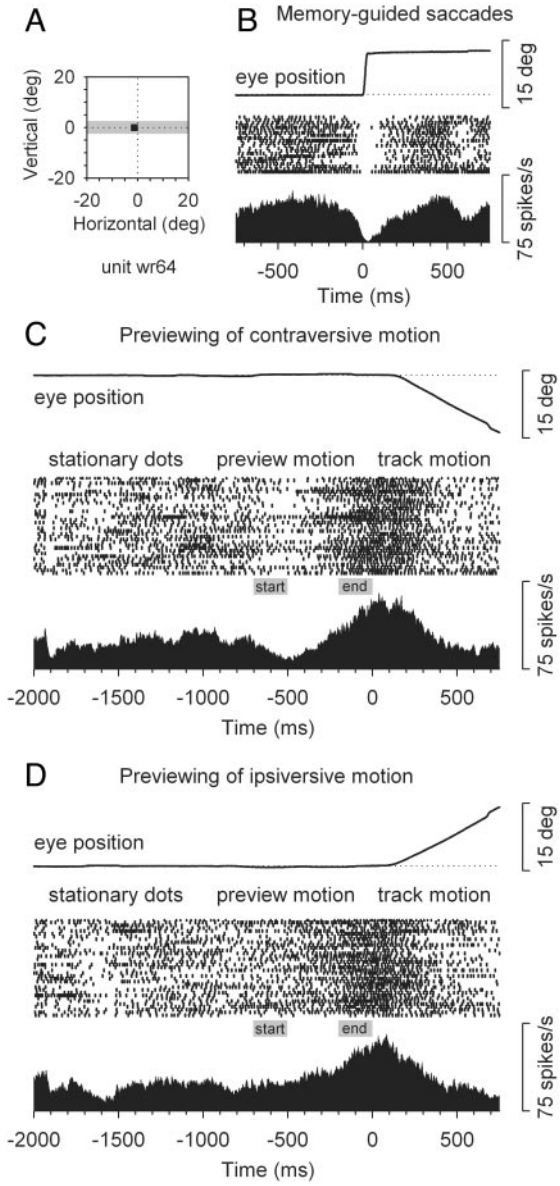


FIG. 7. Activity of a sample rostral SC neuron that exhibited "build up" of activity prior to smoothly tracking the motion stimulus. *A*: schematic diagram comparing location of the neuron's response field (filled square) and area occupied by the motion stimulus (gray rectangle). In this case, stimulus consisted of leftward motion at 20°/s. *B*: activity during memory-guided saccades. The neuron decreased its activity when the monkey made a saccade to a remembered stimulus placed 10° to the ipsilateral (right) side. Trace shows eye position from a single trial (dotted lines indicates 0°). Spike data below are aligned with respect to saccade onset (defined as 0 ms). *C*: activity during previewing of contraversive motion stimulus. As shown by the raster and spike density plot at *bottom*, the neuron increased its firing rate toward the end of the "preview motion" interval, hundreds of milliseconds before the onset of pursuit. Traces at top show eye velocity and eye position from a single trial. Boxes labeled "stationary dots," "preview motion," and "track motion" indicate temporal intervals during which the monkey viewed stationary dots during fixation, moving dots during fixation, and moving dots during pursuit, respectively. Gray boxes labeled "start" and "end" indicate temporal intervals used to quantify change in activity during preview motion interval. *D*: activity during previewing of ipsiversive motion stimulus. Despite reversal in the direction of motion, the neuron again increased its firing rate toward the end of the "preview motion" interval. Conventions are the same as in *C*.

sive) saccades. As shown in Fig. 7*B*, the neuron maintained tonic activity during fixation but exhibited a marked pause in activity around the time of the 10° memory-guided saccade away from its response field. This neuron also maintained its firing rate during fixation in the absence of a visual stimulus (data not shown) and therefore qualified as a "fixation cell" (see METHODS).

During the "previewing" condition, the monkey viewed a horizontally elongated strip of random dot motion (dimensions indicated by the shaded region in Fig. 7*A*) during a period of maintained fixation before actively tracking the motion stimulus with a smooth-pursuit eye movement. In the example shown in Fig. 7*C*, after a 1-s interval with "stationary dots," we presented 20°/s contraversive (i.e., leftward) motion during a 1-s "preview motion" interval and a 700-ms "track motion" interval (Fig. 7*C*). Conversely, in the example shown in Fig. 7*D*, we presented 20°/s ipsiversive (i.e., rightward) motion. As shown by the sample traces of eye position, the monkey maintained steady fixation during the "stationary dots" and "preview motion" intervals and generated a pursuit eye movement to follow the stimulus during the "track motion" interval. During this sequence of behavioral intervals, the neuron exhibited changes in firing rate that were characteristic of most of the neurons we studied with this paradigm. The neuron maintained a tonic level of activity of ~25 spikes/s during presentation of the "stationary dots," which persisted during the early portion of the "preview motion" interval. However, midway through the "preview motion" interval, the activity of the neuron began to steadily increase, reaching a peak firing rate of about 60 spike/s several hundred milliseconds later, at about the same time that the "track motion" interval began. This increase in activity was observed for both contraversive (Fig. 7*C*) and ipsiversive (Fig. 7*D*) motion. Thus the neuron exhibited a buildup of activity as the monkey maintained fixation and previewed the motion stimulus that was about to become the target of a pursuit eye movement, and this increase in activity was not selective for the direction of motion.

For a smaller number of neurons, we found the complementary pattern of activity. The neuron shown in Fig. 8 had a larger receptive field located outside of the motion stimulus, as indicated by the black square in Fig. 8*A*. The neuron increased its activity well before memory-guided saccades directed toward the center of its receptive field, as well as a burst of activity during the saccade itself. We identified this unit as a buildup neuron because of this elevated activity prior to memory-guided saccades. During the "previewing" condition (Fig. 8, *C* and *D*), this neuron showed the opposite pattern of activity as the unit shown in Fig. 7. The neuron had tonic activity of about 30 spikes/s during the "stationary dots" interval and the first half of the "preview motion" interval, but decreased its activity steadily so that it had almost completed ceased firing at the beginning of the "track motion" interval, for both contraversive and ipsiversive motion. This neuron therefore exhibited a "build-down" of activity as the monkey previewed the motion stimulus without making any saccades, and this decrease in activity was not selective for the direction of motion.

We found similar results across the sample of 25 neurons we tested with this stimulus. Following the distinctions between the sample units in Figs. 7 and 8, we divided the neurons into two classes based on the locations of the receptive fields: "inside" units with small centrally located receptive fields that

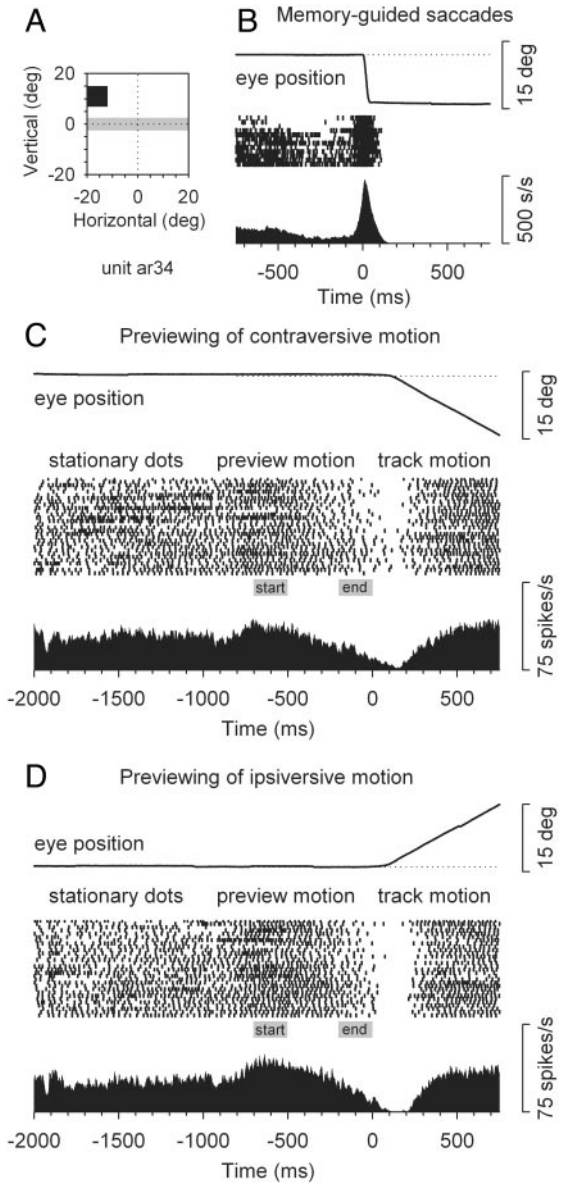


FIG. 8. Activity of a sample rostral SC neuron that exhibited "build down" of activity prior to smoothly tracking the motion stimulus. *A*: schematic diagram showing that location of the neuron's response field (filled square) lay outside of area occupied by motion stimulus (gray rectangle). *B*: activity during memory-guided saccades. The neuron increased its activity when the monkey made a saccade to a remembered stimulus placed 15° to the contralateral (left) side. *C*: activity during previewing of contraversive motion stimulus. The neuron decreased its firing rate toward the end of "preview motion" interval. *D*: activity during previewing of ipsiversive motion stimulus. The neuron again decreased its firing rate toward the end of "preview motion" interval. Other conventions are the same as in Fig. 7.

fell within a portion of the motion stimulus ($n = 19$), and "outside" units whose eccentric receptive fields fell outside of the stimulus ($n = 6$). We tested "inside" units during memory-guided saccades using targets located at 10° in the ipsilateral visual field, as with the sample neuron in Fig. 7, and found that the so-called "buildup" activity before the saccade was generally lower than the baseline activity (circles in Fig. 9*A*). We tested "outside" units with targets located at the centers of their receptive fields, as with the neuron in Fig. 8, and found that the buildup activity before the saccade was higher than the baseline activity (squares in Fig. 9*A*). We observed the complementary pattern for activity recorded while previewing the motion stimulus. "Inside" units had higher activity at the end of the preview interval than at its start (circles in Fig. 9, *B–E*, the measurement intervals are indicated by the gray bars in Fig. 7*C*), consistent with the buildup of activity shown for the sample neuron in Fig. 7. Conversely, "outside" units had lower activity at the end of the preview interval than at its start (squares in Fig. 9, *B–E*). This pattern of buildup and build-

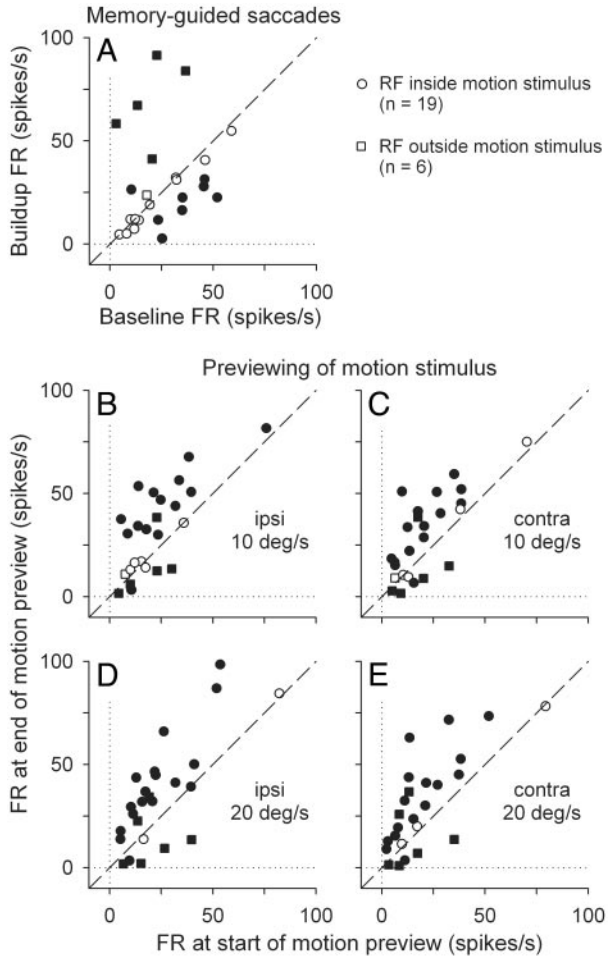


FIG. 9. Summary of the activity during previewing of motion stimuli. *A*: activity during memory-guided saccades. Buildup firing rate (average activity during a 75-ms interval starting 100 ms before saccade onset) is plotted against baseline firing rate (average activity in a 100-ms interval starting 100 ms before fixation point offset). "Inside" units (circles), defined as neurons with receptive fields that fell within the motion stimulus, were tested with saccades to remembered targets at 10° ipsilateral and generally exhibited buildup activity that was lower than baseline activity. "Outside" units (squares), defined as neurons with receptive field centers that fell outside of the motion stimulus, were tested with saccades to remembered targets at the centers of their response fields and generally exhibited buildup activity that was higher than baseline activity. *B–E*: activity during previewing of motion stimulus. Firing rate at the end of motion preview interval (average activity during the last 200 of preview interval, "end" in Figs. 7 and 8) is plotted against firing rate at the start of motion preview interval (average activity in a 200-ms interval starting 300 ms after motion onset, "start" in Figs. 7 and 8). Plots show data obtained for motion directed toward the ipsilateral (*B* and *D*) or contralateral (*C* and *E*) side and with speeds of either 10°/s (*B* and *C*) or 20°/s (*D* and *E*). "Inside" units (circles) tended to exhibit higher activity at the end of preview interval than at its start, whereas "outside" units (squares) tended to show the opposite effect. Filled circles indicate significant differences (Wilcoxon rank-sum test, $P < 0.05$).

down of activity was the same, regardless of whether the horizontal motion was directed toward the same side as the site of recording (Fig. 9, *B* and *D*) or away from the recording site (Fig. 9, *C* and *E*). We also observed essentially the same pattern for speeds of 10°/s (Fig. 9, *B* and *C*), 15°/s (data not shown), and 20°/s (Fig. 9, *D* and *E*). Across our sample of neurons, neither the direction nor the speed of motion had a significant effect on the firing rate recorded at the end of the preview interval (2-way ANOVA, $P = 0.39$ for direction of motion, $P = 0.73$ for speed). Thus as with the results obtained during passive viewing of motion, the buildup and build-down of activity during motion previewing did not depend on the direction or speed of the motion stimulus.

## DISCUSSION

We have shown that visual motion stimuli can elicit vigorous responses from buildup neurons in the rostral SC, but that this activity exhibits very little selectivity for the direction or speed of motion. For stimuli viewed passively during maintained fixation, only a small minority of neurons (14%) exhibited responses that could be considered "motion sensitive"—they showed a significant change in activity for at least one direction and speed of motion, and this response was larger than that evoked by stationary flickering dots. However, none of the neurons were particularly selective for the direction of motion. The median value of the directionality index was only 0.25; by comparison, neurons in the middle temporal area, an extrastriate region specialized for processing visual motion, exhibit directionality indices of ~1.0, reflecting a much stronger tendency for unidirectional excitation (Albright 1984; Maunsell and Van Essen 1983). There was no preference for particular speeds, and in fact, neurons responded about as well to stationary flickering dots as to moving flickering dots. Together, these results show that buildup neurons in the rostral SC respond to temporally modulated stimuli, but they are not selective for the speed or direction of motion.

We also found that buildup neurons in the rostral SC exhibited a gradual change in activity during fixation as the monkey previewed motion stimuli that would soon become the target of a pursuit eye movement. Consistent with the results obtained during passive viewing of motion stimuli, these changes in activity also did not depend on the direction or speed of motion. However, the type of change in activity did depend on the location of the neuron's response field vis-à-vis the location of the motion stimulus, which was presented in a fixed window 5° high and 44° wide straddling the horizontal meridian. Neurons with response field centers located within the area delimited by the stimulus exhibited a "buildup" of activity, whereas neurons with response fields centers located outside this area exhibited a "build-down" of activity. These results show that, under the appropriate conditions, buildup neurons in the rostral SC can exhibit a buildup of activity prior to the onset of pursuit, similar to that observed prior to saccades (Munoz and Wurtz 1995).

### *Possible function of motion signals in the intermediate and deep layers of the SC*

The motion signals we observed could have reached the buildup neurons in the rostral SC by several possible paths. The middle temporal area (MT) is well known for its role in motion processing for pursuit and perception (Newsome and Pare 1988; Newsome et al. 1985) and projects to the superficial layers of the SC (Fries 1984; Ungerleider et al. 1984). The cell bodies of buildup neurons lie deeper than the termination sites from MT, but the dendrites of these neurons likely extend into the superficial layers (Moschovakis et al. 1988a,b). The medial superior temporal area is also a crucial area for motion processing (Celebrini and Newsome 1995; Dürsteler and Wurtz 1988) and projects directly to the intermediate and deep layers of the SC (Maioli et al. 1992). If the sensitivity to motion that we observed was due to these relatively direct projections, individual buildup neurons presumably receive approximately equal inputs from neurons with a variety of preferred directions, because they do not exhibit the strong directional preferences exhibited by neurons in MT and MST. In contrast, neurons in the nucleus of the optic tract (NOT), a nearby pretectal structure that receives similar cortical projections, exhibit strong selectivity for horizontal motion (Hoffman and Distler 1989; Ilg and Hoffmann 1993; Mustari and Fuchs 1990).

Alternatively, motion signals might have been combined in other cortical areas before reaching the rostral SC, namely, the lateral intraparietal area (LIP) and the frontal eye field (FEF), which receive inputs from areas MT and MST and also project to the intermediate and deep layers of the SC (Pare and Wurtz 2001; Tian and Lynch 1996; Wurtz et al. 2001; Yan et al. 2001). Some neurons in FEF and LIP respond well to motion stimuli and appear to play a role in applying motion information toward the planning of appropriate saccades (Kim and Shadlen 1999; Shadlen and Newsome 2001); it is possible that these or related areas play a similar role for the foveal and parafoveal portions of the visual field represented in the rostral SC. Our observation that stationary flicker was at least as effective as moving dots supports the idea that the motion sensitivity we observed could have been provided by areas that process motion signals according to their salience, rather than strictly according to their directional content.

In apparent contrast to our results, the prelude activity of some SC neurons exhibits selectivity for the direction of motion in monkeys trained to perform a direction-discrimination task (Horwitz and Newsome 1999, 2001a,b). In this two-alternative task, monkeys viewed a central motion stimulus and reported their choice by making a saccade to the visual target aligned with the direction of motion. About one-third of the SC neurons had prelude activity that predicted the upcoming saccade choice, and this activity was directionally selective, with preferred directions generally pointed toward the location of the neuron's response field (Horwitz and Newsome 2001a). One explanation for this activity is that it is simply due to the preparation of saccades, but Horwitz and Newsome (2001a) present several arguments that the direction-selective activity does not result from covert saccade planning, including the observation that this activity persists when the monkey prepares and executes a saccade away from the response field of the neuron under study. Instead, they conclude that these neurons play a role in saccade target selection and that the direction-selective responses are the result of changes in the wiring from cortical areas to the SC that occurred during the course of behavioral training. Consistent with this interpretation, our animals were not trained to plan saccades based on

discriminating the direction of motion, and we found that rSC neurons did not have a native selectivity for motion direction.

The distinction between covert saccade preparation and target selection is not entirely clear, especially since activity in the SC can represent multiple visual goals at the same time, at least under some conditions (McPeek and Keller 2002b). One possibility is that, for at least some SC neurons, the prelude or buildup activity is both covert and preparatory, but is not restricted to the control of saccades. For example, the activity of buildup neurons in the rostral SC is modulated by the early removal of a fixated stimulus that occurs in the "gap paradigm," and these changes are correlated with the changes in pursuit and saccade latencies observed with this paradigm (Krauzlis 2003). These results suggest that some of the same preparatory signals in the SC that can potentially trigger saccades may also gate the initiation of pursuit. In the "previewing of motion" condition of this study, by using an extended patch of motion that involves integration of motion signals across the visual field (Watamaniuk and Heinen 1999), the impending pursuit target was clearly identified, and the occurrence of saccades was largely eliminated. This condition produced dramatic changes in preparatory activity prior to the initiation of pursuit (Figs. 7 and 8), and as expected for a signal related to target selection, this activity increased for neurons whose response fields matched the upcoming moving target and decreased for neurons whose response fields did not.

Other recent results support the idea that the SC plays a role in target selection, distinct from its role in the direct control of saccades. Changing the probability that a visual stimulus will be selected as a visual target for a saccade alters the visual-evoked and the tonic activity of buildup neurons. This activity is predictive of the latency of the saccades, but is not related to saccade parameters such as amplitude or peak velocity (Basso and Wurtz 1997, 1998). During a visual search task using saccades, some SC neurons discriminate the target from the distractor with timing that does not depend on saccade latency, suggesting that they are involved in target selection in addition to saccade preparation (McPeek and Keller 2002a). During a two-alternative task using moving targets, some rostral SC neurons likewise exhibit selectivity for stimuli that will be the target of pursuit, and this selectivity can predict the timing of pursuit choices (Krauzlis and Dill 2002). Together, these results support the idea that one function of the SC is to specify the eye movement goal, regardless of the final motor strategy used to acquire that goal (Krauzlis and Carello 2003). From this viewpoint, the sensitivity to motion signals we observed is simply one example from a potentially endless list of sensory and other influences that could be used to specify or modify the representation of goals in the SC for orienting movements.

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