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J Neurophysiol 95:505-526, 2006. First published 28 September 2005;

doi: 10.1152/jn.00639.2005

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Effects of Eye Position upon Activity of Neurons in Macaque Superior Colliculus

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Submitted 20 June 2005; accepted in final form 26 September 2005

Campos, Michael, Anil Cherian, and Mark A. Segraves. Effects of eye position upon activity of neurons in macaque superior colliculus. *J Neurophysiol* 95: 505–526, 2006. First published September 28, 2005; doi:10.1152/jn.00639.2005. We examined the activity of neurons in the deep layers of the superior colliculus of awake behaving rhesus monkeys during the performance of standard oculomotor tasks as well as during self-guided eye movements made while viewing natural images. The standard tasks were used to characterize the activity of neurons based on established criteria. The natural viewing paradigm enabled the sampling of neuronal activity during saccades and fixations distributed over a wide range of eye positions. Two distinct aspects of eye-movement behavior contributed to the modulation of firing activity in these neurons. The well-established influence of saccade amplitude and direction was strongest and most prevalent surrounding the time of the start of the saccade. However, the activity of these neurons was also affected by the orbital position of the eyes, and this effect was best observed during intervals of fixation. Many neurons were sensitive to both parameters, and the directions of their saccade vector and eye position response fields tended to be aligned. The sample of neurons included visual, build-up, and burst activities, alone or in combination. All of these activity types were included in the subpopulation of neurons with significant eye-position tuning, although position tuning was more common in neurons with build-up or burst activity and less common in neurons with visual activity. The presence of both eye-position as well as saccade-vector signals in the superior colliculus is likely important for its role in the planning and guidance of combined movements of the eyes and head.

INTRODUCTION

The superior colliculus is an important component of the gaze control system the deep layers of which contain neurons with well-established saccade-related activity and an orderly topographic representation of the amplitude and direction of saccadic eye movements (for reviews, see Guitton 1991; Sparks and Hartwich-Young 1989; Wurtz and Munoz 1995). In addition to the well-known oculocentric representation generated by collicular activity, the activity of collicular neurons is sensitive to auditory and somatosensory inputs and to the generation of head movements (Freedman et al. 1996; Jay and Sparks 1984; Peck et al. 1995; Wallace et al. 1996). There are also a number of lines of evidence, both anatomical and physiological, to suggest that collicular activity includes a sensitivity to position of the eyes in the orbits. There are several potential sources for an eye-position signal in the

colliculus, including, for example, from the cortico-tectal projection of the lateral intraparietal cortex (Andersen et al. 1990; Paré and Wurtz 1997), from the oculomotor brain stem (Hartwich-Young et al. 1990; Robinson et al. 1994; Scudder et al. 2002), or even from the extraocular muscles themselves (Abrahams and Anstee 1979; Abrahams and Rose 1975). There have been only a few reports of effects of eye position on the activity of superior colliculus neurons. The most comprehensive examination was made by Van Opstal and colleagues (1995), who reported the effects of eye position on the activity of collicular saccade-related burst neurons, finding that eye position modulates the level of peri-saccadic activity in these neurons. In a study devoted primarily to examining the link between collicular activity and smooth-pursuit eye movements, Krauzlis and colleagues (2000) also observed that neurons in the rostral monkey superior colliculus could have a tuning that was sensitive to eye position. Paré and Munoz (2001) found an eye-position-sensitive bias in collicular neurons during a time interval surrounding target appearance in a gap saccade task that facilitated saccades that brought the eyes back to the center of gaze.

An eye-position signal is an important component of a number of oculomotor processes in which the colliculus is likely to play a significant role. These include the formation of a corollary discharge signal, particularly for the generation of sequences of multiple saccades (Li and Andersen 2001; Mays and Sparks 1980b; Sparks and Mays 1983; Walker et al. 1995), the integration of sensory input from different modalities (Jay and Sparks 1987; Populin et al. 2004), and the need to compute the relative contributions of eye and head movements to generate gaze movements (Corneil and Elsley 2005; Cowie and Robinson 1994; Freedman et al. 1996). Although the majority of earlier work has focused on eye-position effects during the time that a saccade is being made, if one considers the potential sources of an eye-position signal in the colliculus, as well as the temporal dynamics of the functions that might be served by this input, it is unlikely that this influence is only present during the peri-saccadic interval. Whether an eye-position influence is derived directly from muscle proprioceptors or from a signal that is generated by another component of the oculomotor system, these signals are present continuously, leading to the possibility that eye position affects collicular activity during fixation as well as during saccades.

Our aim in this study was to obtain a continuous measure of saccade-vector- and eye-position-dependent activity of collicu-

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lus neurons during fixation as well as during saccades. Following the example of earlier work by Van Opstal and colleagues (1995), we employed a natural scanning paradigm that encouraged the monkeys to make multiple self-guided saccades, providing a large and diverse sample of stationary eye positions as well as saccade vectors. Using this approach, we found that the position of the eyes in the orbits had a significant influence on the activity of collicular neurons during periods of fixation. Moreover, the relative levels of the eye-position- and saccade-vector-related activities appeared to vary across time with the greatest influence of eye position on neural activity occurring during fixation, whereas the saccade-vector signal was more strongly expressed during saccades. In addition, we present preliminary evidence obtained using a more conventional oculomotor task designed to sample fixation period activity over a wide area of the oculomotor range, showing that eye-position activity is not unique to the self-guided saccades and fixations elicited with a natural scanning paradigm but is also found under more controlled behavioral conditions. In combination with the results of earlier reports, our findings strengthen the evidence for an eye-position influence on the activity of collicular neurons and demonstrate its availability at times where it could be used by a number of essential oculomotor processes.

Preliminary reports of these findings have appeared in abstract form (Campos et al. 2000, 2002; Cherian et al. 2001).

METHODS

Three female adult rhesus monkeys (*Macaca mulatta*) were used for these experiments. Northwestern University's Animal Care and Use Committee approved all procedures for training, surgery, and experiments performed. Each monkey received preoperative training followed by an aseptic surgery to implant a subconjunctival wire search coil, a stainless steel recording cylinder aimed at the superior colliculus, and a stainless steel receptacle to allow the head to be held stationary during behavioral and neuronal recordings. All of these methods have been described in detail elsewhere (Dias and Segraves 1999; Helminski and Segraves 2003). Surgical anesthesia was induced with the short-acting barbiturate Methohexital (11 mg/kg) injected through an intravenous line and maintained using halothane (1%) inhaled through an endotracheal tube.

Neuronal recordings and behavioral paradigms

The neuronal recordings focused on neurons in the deep layers of the superior colliculus. We define deep layers as the collicular layers located below the superficial layers (superficial gray and stratum opticum), including the intermediate and deep gray layers. At the beginning of each experimental session, the response fields of the encountered neurons were mapped with a task that allowed us to vary the position of a saccade target with a joystick. Next, the monkey was presented trials of gap and memory-guided saccade tasks with targets in the center of the movement field as well as in the opposite direction for the gap saccade task. The gap task began with a variable period of fixation; after the disappearance of the fixation light, a gap period of 400 ms was inserted before the appearance of the peripheral target light. When the peripheral target appeared, the monkey was required to make a saccade to it within 500 ms and was rewarded after the completion of the correct movement. The gap task was particularly useful for identifying build-up activity in collicular neurons. In the memory-guided saccade task, the central fixation light came on to start the trial, as before, and the monkey was required to fixate the central light until it was turned off. During the time that the central light was

on, a peripheral target was flashed for 500 ms. When the fixation light was turned off, the monkey was required to make a saccade to the position of the flashed peripheral target. The duration and time of occurrence of the flashed target was adjusted so that the target was extinguished while the monkey was still required to fixate the fixation light. The monkey maintained fixation for ≤ 950 ms after the disappearance of the flashed target light and then made a saccade to the remembered target location. This task was valuable for distinguishing between visually driven and saccade-related activity. Together, these tasks allowed us to classify the neuron's response profile as having visual, build-up, burst, or some combination of these activities (Munoz and Wurtz 1995). Next, a scanning paradigm was used during which eye-position and neuronal-activity data were collected for ≥ 30 min while the monkey viewed > 100 presentations of images (number of images: 118 ± 37 ; mean \pm SD) selected randomly from a large catalogue of images (Burman and Segraves 1994). These images included photographs of human and primate faces, landscapes, printed text, and animals in natural settings and were chosen with consideration to the placement of objects of visual salience such that the monkeys' scanpaths would include a sampling of central as well as eccentric fixations.

During the scanning paradigm, the presentation of each image was preceded by the display of a white fixation grid with a red fixation point illuminated at the center of the grid. After a randomly varied period of 0.5–2.5 s of fixation, the grid and fixation point disappeared, and an image was displayed for 10–20 s. During this time, the monkey was free to look wherever she wished. The monkeys were given a liquid reward before and after the presentation of each image. All images were generated by a CRT video projector (Sony VPH-D50, 75Hz vertical scan rate, $1,024 \times 768$ resolution) and rear projected onto a tangent screen in front of the monkey. The size of the projected image was $53 \times 40^\circ$.

The scanning paradigm was chosen for this study of eye-position and saccade-vector effects on collicular activity because of its capacity to efficiently generate a large sample of saccades initiated from a wide distribution of starting eye positions in a relatively short period of time. During the scanning paradigm, the monkeys made more than two to four saccades per second [mean: 2.36 ± 0.79 (SD) saccades/s], in agreement with known human scanning properties (Andrews and Coppola 1999). In a typical 30-min recording session for an isolated neuron, the monkey made an average of $> 3,000$ saccades ($3,369 \pm 1,390$). This frequency of saccades during a relatively short recording session allowed for multiple neuron recording sessions in a single day, providing a higher yield than would have been possible if the monkey were required to do a conventional task, where, in our experience, a maximum number of trials that can be achieved in a single day is 1,500–2,000 trials with a single saccade per trial.

Because the direction of gaze was not controlled during image presentation in the scanning paradigm, we examined all of the eye-position data recorded for the neurons included in this study to determine the percentage of time that the monkeys were looking at the images. We found that *monkey MAS03* had its eyes on the image 65% of the time and *monkey MAS07* 81%. The monkeys' eyes were within the boundaries of the white tangent screen 96 and 98% of the time. These percentages reflect the total amount of time spent looking at the image/screen over the course of all of the recordings. The times when the monkey was in the process of making a saccade as well as drifting fixations were excluded from this calculation.

The scanning paradigm was similar to that employed in an earlier report of eye-position effects on collicular activity where similar large samplings of eye movements were obtained by moving pieces of food and novel objects in front of the monkey to attract its attention (Van Opstal et al. 1995). For both paradigms, the goal was to obtain as large a sampling of eye-position data as possible over the limited period of time that isolation of each neuron as well as the behavioral motivation of the monkey could be maintained.

For one additional monkey (*MAS012*), we recorded collicular activity during performance of a multi-target task designed to sample a range of fixation positions. In this task, the video projector was used to project a red spot of light on a dark screen. At the start of a trial, the light spot was turned on at an initial fixation position. After the monkey fixated the spot, it remained on for an additional 700–1,000 ms. At the end of this period, the fixation point disappeared, and, after a gap of 50 ms, a target spot was turned on. Fixation point and target locations were chosen in random order from an array of locations that included the center of the screen ($0, 0^\circ$) and at eight positions spaced at intervals of 45° ($0, 45, 90, 135^\circ$, etc.) in each of three annuli located $7.5, 15.0$, and 22.5° away from the center (see sketch of fixation point and target locations at center of Fig. 16). Correct performance required the monkey to keep its eyes within criterion windows surrounding the fixation point and target locations. At the end of the trial, the target light was extinguished, the monkey was rewarded if performance was correct, and a fixation light appeared at a new location.

Data analysis

For this report, we restricted our observations to recording sites with neurons firing maximally for saccades with amplitudes of $<20^\circ$. This restriction was imposed to avoid the unequal distribution of preferred saccade starting and ending positions that would be obtained if recording sites representing larger eye movements were included in our study. Our results will demonstrate that the direction and amplitude of saccade-vector and eye-position tunings tended to overlap for a given cell. Thus neurons with preferred saccade vectors $>20^\circ$ could be expected to also prefer eye positions that were relatively eccentric near the limits of the oculomotor range. When this is the case, the range of saccades that can be initiated to reach that position is more limited. For example, one can only saccade to an eye position near the leftward limit of the oculomotor range with leftward saccades.

NEURON CLASSIFICATION. Mean discharge rates in intervals from the memory saccade trials were used to quantify visual (50-ms interval starting 50 ms after the onset of the target stimulus) and burst (interval beginning 8 ms before saccade start and continuing until 8 ms before saccade end) activity. Mean discharge rates during the final 100 ms preceding target onset in the gap saccade trials were used to quantify the presence of build-up activity (Munoz and Wurtz 1995). These were compared with the background mean discharge rates (final 200 ms before disappearance of the fixation point) with a Wilcoxon rank sum test.

SCANNING PARADIGM ANALYSIS. Off-line analysis of scanning data used velocity criteria to separate the scanning sequences into individual saccades surrounded by intervals of fixation of ≤ 400 ms before and after the saccade. For the example cell illustrated in this report (Figs. 1–6), the mean fixation duration was 284 ± 107 ms. For analysis of fixation period activity both before and after a selected saccade, only the firing activity that took place 100 ms after the end of the previous saccade and 100 ms before the start of the next saccade was included. This requirement was meant to eliminate contamination of activity from saccades other than the one to which the firing rate estimates were aligned. To analyze fixation period activity during the interval 200 ms before the start of the saccade, all fixations >300 ms in duration were used. For the example cell there were 1854 (of 5,085) such fixations in the data set.

REGRESSION ANALYSIS TO MODEL CONTRIBUTIONS OF EYE POSITION AND SACCADE VECTOR TO NEURONAL ACTIVITY. We used standard quantitative models implemented with MATLAB to evaluate the dependence of collicular firing rate on eye-position and saccade parameters (Draper and Smith 1981; Press et al. 2002; Van Opstal et al. 1995; Zar 1974). First, the natural scanning data were divided into individual saccades and surrounding fixations. Saccades were identified with velocity and amplitude criteria. For each entry in the spike

index, a sequence of three saccades were considered. The first and last saccades (S1 and S3) were used to define the duration of the fixation intervals surrounding the middle saccade (S2) to which we aligned the spike times. Neuronal spikes that occurred ≥ 100 ms after the end of the previous saccade (S1) and 100 ms before the start of the next saccade (S3) in the scanning sequence were assigned times referenced to the start of the current saccade (S2). Thus each entry in the index consisted of the spike times for the interval that began 100 ms after S1 to include the fixation interval before the current saccade (S2) and extended until 100 ms before S3 to include the fixation interval that followed S2. A separate index assigned times of the spikes relative to the end of the saccade.

The spikes trains were smoothed by convolving with a Gaussian ($\sigma = 20$ ms) to estimate the instantaneous firing rate for individual fixations and saccades. Thus all spikes within ~ 50 ms of the start of the saccade influenced the estimate of the firing rate at the start of the saccade although the spikes that were closer in time to the saccade start had a larger weight. This spike smoothing was used for all of the regression analysis.

The presaccadic eye position, (x_{pre}, y_{pre}) , was the position of the eyes at the start of the saccade. The postsaccadic eye position, (x_{post}, y_{post}) , was the position of the eyes at the end of the saccade. The horizontal/vertical component of a saccade vector (x_{vec}, y_{vec}) was defined as the difference between the horizontal/vertical eye position at the end of the saccade and the start of the saccade

$$x_{vec} = x_{post} - x_{pre} \quad (1)$$

$$y_{vec} = y_{post} - y_{pre} \quad (2)$$

Inter-saccadic drift, d , was calculated for each saccade, s , as the difference in eye position for the presaccadic interval of the current saccade and the eye position for the postsaccadic interval of the previous saccade

$$d_x(s, s-1) = x_{post}(s-1) - x_{pre}(s) \quad (3)$$

$$d_y(s, s-1) = y_{post}(s-1) - y_{pre}(s) \quad (4)$$

$$d(s, s-1) = \sqrt{d_x^2 + d_y^2} \quad (5)$$

To avoid contamination by drifting fixations or failures of the saccade detection algorithm, when the inter-saccadic drift exceeded 2° of visual angle, that fixation period and the two saccades occurring before and after it were removed from the saccade index as well as the fixation intervals before and after those saccades. In total, each time intersaccadic drift exceeded 2° , three fixation periods and two saccades were removed from the data set.

To establish the center of each neuron's saccade vector response field, firing rates at the start of the saccade were regressed on the components of the saccade vectors using the following function

$$F_{vec(t=0)} = b_0 + b_1 \cdot \exp\left(-\frac{(x_{vec} - b_3)^2 + (y_{vec} - b_4)^2}{b_2^2}\right) \quad (6)$$

An initial estimate of the center of the response field (b_3, b_4) was calculated as the vector average of all of the saccades with associated firing rates that were $>50\%$ of the maximum firing rate. Initial estimates of the remaining parameters were chosen arbitrarily, $b_0 = 100, b_1 = 4, b_2 = 3$. The values obtained from the nonlinear fit for b_3 and b_4 were then used in the remainder of the analysis as the defined center of the neuron's saccade vector response field (x_{ctr}, y_{ctr}). Establishing the center of the response field diminished the chance of spurious regressions, and restricted the model to three parameters, instead of five

$$x_{ctr} = b_3 \quad (7)$$

$$y_{ctr} = b_4 \quad (8)$$

The next step was to perform a bootstrapped regression analysis at many points in time, t , relative to the start of the saccade, $t = 0$. First

consider the regression at the time 200 ms before the start of the saccade. All saccades for which the preceding fixation interval was <300 ms (200 ms + 100 ms buffer) in duration were eliminated from the sample as were all saccades for which there was excessive drift in the preceding or following fixation intervals. The spike data for the remaining saccades and associated fixation intervals were then used as the population on which three functions were regressed: the saccade vector function, F_{vec} , and two firing rate models based on presaccadic, F_{eyepr} , and postsaccadic, F_{eyepost} , eye position

$$F_{\text{vec}(t)} = b_0 + b_1 \cdot \exp\left(-\frac{(x_{\text{vec}} - x_{\text{ctr}})^2 + (y_{\text{vec}} - y_{\text{ctr}})^2}{b_2^2}\right) \quad (9)$$

$$F_{\text{eyepr}(t)} = b_0 + b_1 x_{\text{pre}} + b_2 y_{\text{pre}} \quad (10)$$

$$F_{\text{eyepost}(t)} = b_0 + b_1 x_{\text{post}} + b_2 y_{\text{post}} \quad (11)$$

These functions returned values for the regression coefficients (b_0 , b_1 , b_2), r^2 values, and P values. Each regression was bootstrapped to establish confidence intervals (Efron and Tibshirani 1993). To do this, 200 fixations and associated firing rates were chosen at random with replacement from the sample. The regression was computed, and the values for the parameters were stored along with the r^2 values describing the goodness-of-fit for the regressions. This procedure was repeated 100 times. The means \pm SE were then estimated from the 100 bootstrapped samples of the regression parameters, r^2 values, and P values.

ANALYSIS OF TUNING STRENGTH. In addition to the regression analysis, we performed a second analysis that evaluated the strength of eye-position- and saccade-related tuning across time by generating a tuning metric. The metric was related to the population vector found in the Raleigh test of nonuniformity of circular data (Batschelet 1981). In two separate analyses that organized firing rate data with respect to saccade vectors (x_{vec} , y_{vec}) and eye position (x_{pre} , y_{pre}) or (x_{post} , y_{post}), data were divided into eight angular bins and two 15°-wide amplitude bins. Averaged firing rates associated with angular bins were used in place of firing rates of individual saccades or eye positions to remove from the analysis the effects of unequal distributions resulting from a monkey's potential saccade-vector or eye-position preferences during scanning. The function for the tuning metric was as follows

$$\tau = \frac{\sqrt{\left(\sum_{\theta} \rho(\theta) \cos(\theta)\right)^2 + \left(\sum_{\theta} \rho(\theta) \sin(\theta)\right)^2}}{\sum_{\theta} \rho(\theta)} \quad (12)$$

$$\alpha = \arctan\left(\frac{\sum_{\theta} \rho(\theta) \cdot \sin(\theta)}{\sum_{\theta} \rho(\theta) \cdot \cos(\theta)}\right) \quad (13)$$

Averaged firing rates (ρ) were used in the calculation of the tuning (τ) by calculating a population vector composed of individual vectors pointing to the center of each of eight angular bins with length equal to the firing associated with the saccade vectors or eye positions in its direction (θ) in central (<15°) and eccentric (15–30°) annuli. The magnitude of this vector was normalized by the sum of the firing rates for all directions so that the strength of tuning could be compared across cells with different firing rates. The angle, α , is the angle of the weighted population vector for which τ is the amplitude.

To compare the relative strength of saccade-vector and eye-position signals across time, the strength of tuning of a cell's firing was quantified separately in the saccade-vector and eye-position reference frames. The two reference frames would be in register when the monkey makes a saccade from the straight ahead position, which happens when she fixates a point at the center of the tangent screen as is normally the case in conventional oculomotor experiments. During

scanning eye movements, however, the origins of the two reference frames frequently do not coincide.

Although the distributions of sampled eye position and saccade vectors obtained from the very large sample of fixation positions and saccade vectors generated during the course of viewing a variety of images were not homogeneous, they were devoid of obvious discontinuities, irregularities, or holes, and included high frequencies of data points throughout the distribution. The method of using large angular and eccentricity bins to divide the data and the averaging of firing activity within these bins compensated for differences in distribution that might have existed between these bins and removed a bias that might have been introduced by variability in the number of saccades for different directions.

RESULTS

For this report, we completed a full analysis of the activity of 73 neurons in the deep layers of the superior colliculus for two rhesus monkeys (*MAS03*: 32; *MAS07*: 41). We characterized the activity of each of these neurons using memory-guided and gap saccade tasks (Fig. 1). This sample included neurons classified as having visual and burst activity alone (Fig. 1, *A* and *B*), or in combination with build-up activity (Fig. 1, *C–E*). Table 1 summarizes the visual, build-up, and burst activities seen in this cell population.

After characterizing the activity of these neurons during the performance of conventional oculomotor tasks, activity was recorded while the monkey performed a scanning paradigm (METHODS). This paradigm allowed the monkey to make series of unrehearsed, self-guided eye movements from a wide range of starting eye positions and gave us the opportunity to examine the activity of these neurons in relationship to both a large population of saccade vectors of all amplitudes and directions as well as a large distribution of orbital positions of the eyes during the intervals between saccades. As expected, we found that increases in activity for many neurons could be associated with a small range of saccade vectors, defining the movement fields for these neurons. In addition, we made the unexpected observation that the activities of many collicular neurons were tuned to a restricted range of positions of the eyes in their orbits during the intervals between saccades.

To first provide a qualitative illustration of saccade-vector and eye-position influences on a single collicular neuron, we plotted eye-position traces for saccade and fixation intervals that were associated with the highest level of firing for a cell (Fig. 2). Epochs of spike traces aligned to saccade start times were sorted to identify the epochs with the largest number of spikes within the saccadic (Fig. 2*A*) or fixation (*B*) time intervals. In this figure, data are shown for only the top 10 selected saccadic and fixation periods from a sample that included 5,085 saccades recorded during the scanning paradigm for this neuron. The 10 epochs of data used for this figure represent 0.2% of the entire data sample.

Figure 2*A*, detailing eye movements and neuron activity chosen for highest activity during the saccade interval, shows the neuron's tuning for saccade vector. Activity during saccades is highest for saccades made to the left (yellow eye-position traces). Note that the starting and ending eye positions for these saccades as well as the vectors of preceding saccades (black dots) varied over a wide range. When these saccades associated with high activity are referenced to a common starting point (Fig. 2*A*, *bottom right inset*), it is possible to

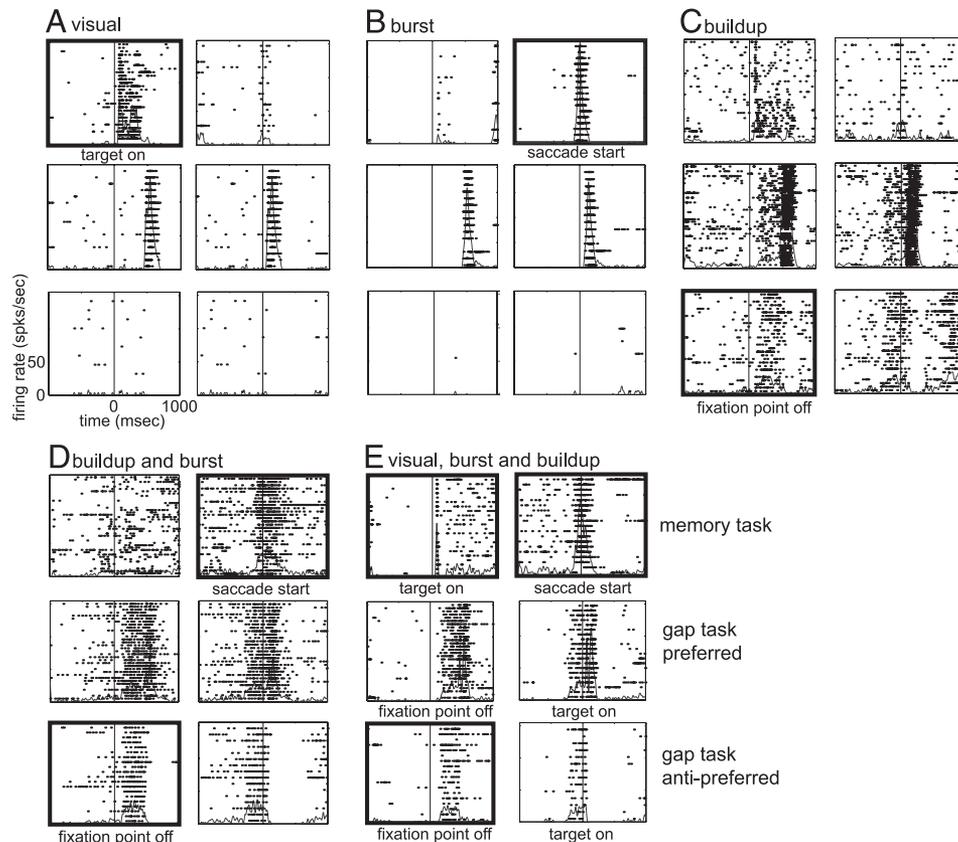


FIG. 1. Neuron classification. Examples of neurons classified as having visual or burst activity alone (*A* and *B*) or in combination with build-up activity (*C*–*E*). Activity shown was recorded during performance of both memory-guided saccade and gap saccade tasks. Each panel shows rasters of spiking activity (black dots) and smoothed estimates of the average firing rates (solid lines), aligned to multiple events in the 2 tasks to illustrate different types of neural activity. *E* includes labels to indicate the time point of the raster alignments for all panels. Target on, time when the target light was turned on; saccade start, start of the saccade to the target location; fixation point off, time when the fixation point light was turned off. For the memory-guided saccade task, the target appeared for 500 ms after which the fixation point remained on for an additional 350–950 ms before it was extinguished allowing the monkey to make a saccade to the remembered location of the target flash. For the gap task, a gap of 400 ms between disappearance of fixation point and onset of target was used. Visual and burst activity were dissociable in the memory-guided saccade task because the peripheral target was briefly flashed and the monkey was required to delay making an eye movement until the disappearance of the fixation point. When the eye movement was cued, there was no longer a visual stimulus present to drive the activity of the neuron. To quantify visual activity, the 50-ms interval starting 50 ms after the onset of the target was compared with baseline firing. To quantify burst activity, the peri-saccadic interval beginning 8 ms before the start of the saccade and lasting until 8 ms before the end of the saccade was compared with baseline (see METHODS). Visual and burst activities could not be dissociated in the gap saccade task because the monkey was instructed to acquire the target as soon as it appeared. Build-up activity occurred during the gap task in the interval between the disappearance of the fixation point and the appearance of the peripheral target light. To quantify build-up activity, we compared the neural activity in the 200-ms interval before target appearance with a baseline interval (see METHODS). *A*: neuron with predominant visual activity (07213, $p_{\text{visual}} < 10^{-9}$, $p_{\text{burst}} = 0.58$, $p_{\text{build-up}} = 0.85$). *B*: neuron with predominant burst activity and weak but significant visual activity (03445, $p_{\text{visual}} = 0.009$, $p_{\text{burst}} < 10^{-6}$, $p_{\text{build-up}} = 1.0$). *C*: neuron with significant build-up activity in addition to visual and burst activities (03440, $p_{\text{visual}} < 10^{-9}$, $p_{\text{burst}} < 10^{-4}$, $p_{\text{build-up}} = 10^{-4}$). *D*: neuron with a combination of statistically significant build-up and burst activity (03423, $p_{\text{visual}} = 0.06$, $p_{\text{burst}} < 10^{-4}$, $p_{\text{build-up}} < 10^{-4}$). *E*: neuron showing a combination of significant levels of visual, build-up, and burst activity (03418, $p_{\text{visual}} < 10^{-6}$, $p_{\text{burst}} < 10^{-5}$, $p_{\text{build-up}} < 10^{-3}$). Thickened outlines surround rasters that best demonstrate the characteristics of a particular activity type, and the alignment event for these rasters is indicated. For example, in *A*, the top left raster is outlined to highlight the visual activity after the appearance of the target light, and in *C*, the bottom left raster is outlined to highlight activity after the disappearance of the fixation light in trials when the target would appear in the anti-preferred direction.

observe that these movements share similar amplitudes and directions, whereas their preceding saccades do not share these similarities. In Fig. 2*B*, eye positions associated with the highest fixation interval activity for this neuron are plotted (red eye-position dots). These fixation positions tend to be located within the bottom left quadrant of the image, suggesting a tuning for eye positions that held the eyes within the bottom-

left portion of the orbits. Note that both the preceding (black) and following (yellow) saccade vectors were variable in amplitude and direction (Fig. 2*B*, bottom right inset), suggesting that the elevated activity during fixation could not be attributed to activity tuned to the previous or upcoming saccades. In several instances, however, the fixation period was either preceded or followed by a saccade that matched the preferred vector for this neuron. In these cases, there was the possibility that elevated activity at the beginning or end of the fixation period could be attributed to the adjacent saccade. For this report, the analysis of fixation activity is restricted to an interval of fixation period activity that is separated by ≥ 100 ms from saccades that occur before and after the fixation period.

TABLE 1. Cell counts for visual, build-up, and burst activity

Monkey	Visual Activity	Build-up Activity	Burst Activity
MAS03	19	3	20
MAS07	33	11	20

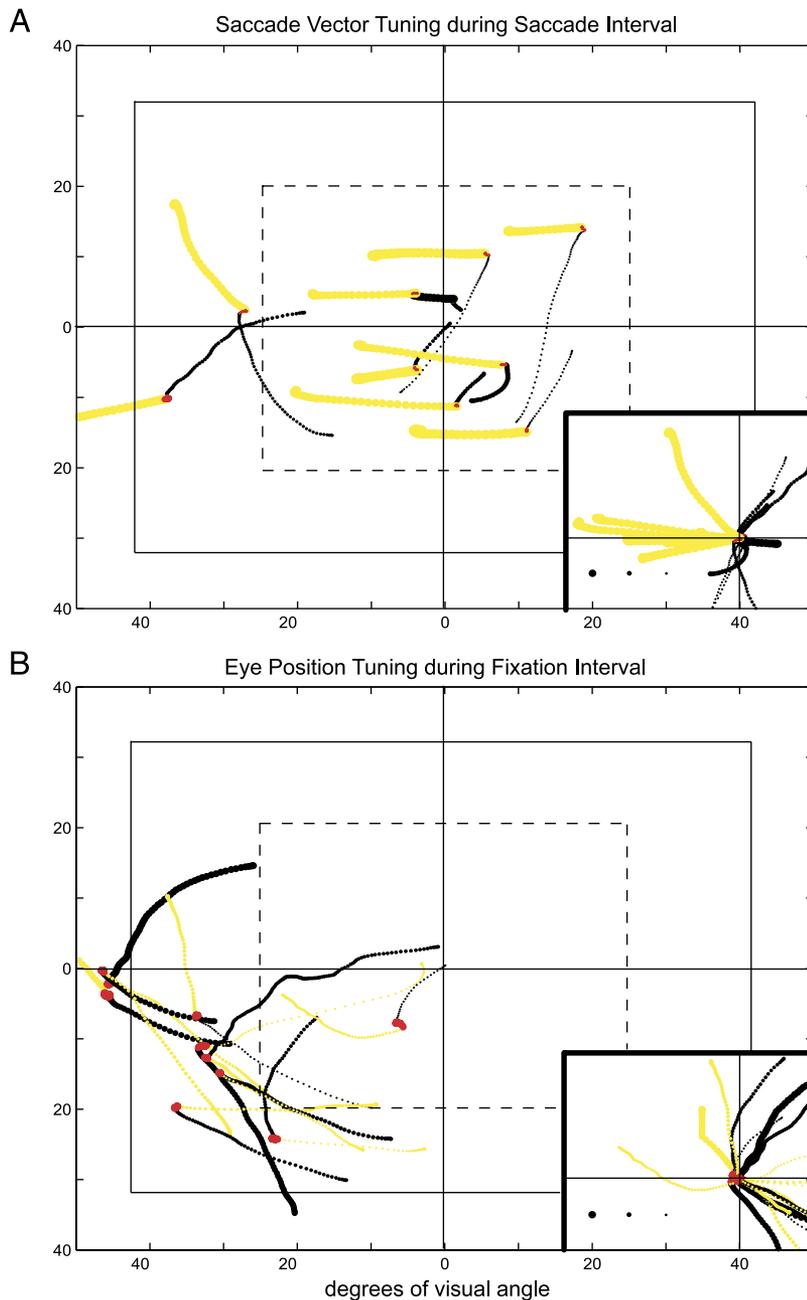


FIG. 2. Eye-movement epochs with high levels of associated neuronal activity. The 10 eye-movement epochs that were accompanied by the highest levels of spike activity from a single superior colliculus neuron during saccade (A) or fixation (B) time intervals are shown. Same neuron as for Fig. 1C. In A, eye position (sampled at 1 kHz) during saccades associated with high activity is colored yellow. Eye position during fixation is colored red, and eye position during saccades that preceded the fixation is colored black. In B, fixation periods with intervals of highest activity are plotted in red with eye position during preceding and following saccades in black and yellow. Dot size used to plot eye position is proportional to the amount of activity found in each of the saccade or fixation intervals. Sample dot sizes plotted in the bottom right corner correspond to firing frequencies of 30, 50, and 100 Hz. Data plotted were saccades and fixations with the highest level of activity from a sample of 5,085 saccades recorded from this neuron during a single scanning session. During this time, the monkey viewed 202 separate image presentations with each presentation randomly selected from a catalogue of 110 different images. Saccade interval was defined as the time from 25 ms before the start of the saccade until 25 ms after saccade end. Fixation interval was defined as the time extending from 225 ms until 175 ms before the start of the saccade. Insets: eye-position component of the fixation period removed thereby referencing the preceding saccades to a common endpoint and the following saccades to a common starting point. Some eye traces extend beyond the boundaries of the insets and main panels. Dashed and shaded line rectangles mark the outer limits of the projected image and the white tangent screen.

For this neuron, activity during the fixation interval tended to be present when the animal fixated within a restricted range of eye positions as demonstrated by a series of histograms that plot the activity for eight different directions of eye position (Fig. 3A). ANOVA of the average firing rates plotted in Fig. 3B grouped according to direction (8-way), show a highly significant dependence of firing rate on eye position during the fixation interval ($P < 10^{-20}$).

Polar plots of the level of activity associated with eye position and saccade vector during fixation and saccade intervals for the entire recording period of the cell illustrated in Figs. 1C, 2, and 3 demonstrate the separate tunings for both eye position and saccade vector in this neuron (Figure 4). For this cell, there was a sharper tuning for the position of the eyes in the orbits during the fixation interval (Fig. 4, left, top and bottom rows) versus a well-defined tuning for the amplitude

and direction of the saccade during the saccade interval (Fig. 4, right, middle row). The plots of these data in Fig. 4 illustrate several characteristics of the eye-position and saccade-vector tuning of these neurons that will be confirmed quantitatively later in this report. First, they demonstrate that the directions of the saccade-vector and eye-position response fields were aligned with one another. The response fields in both vector and eye-position reference frames were in roughly the same direction (saccade vector field = 175° ; eye-position field = 180°), and this trend tended to be true for the whole population of neurons (see Figs. 11 and 15). Because the directions of the response fields were similar, the saccade vectors preceding the fixations where activity was elevated tended to be similar to the preferred saccade vector of the cell. For this reason, many of the fixation intervals with higher activity in the post saccade period followed leftward saccade vectors (right, bottom row).

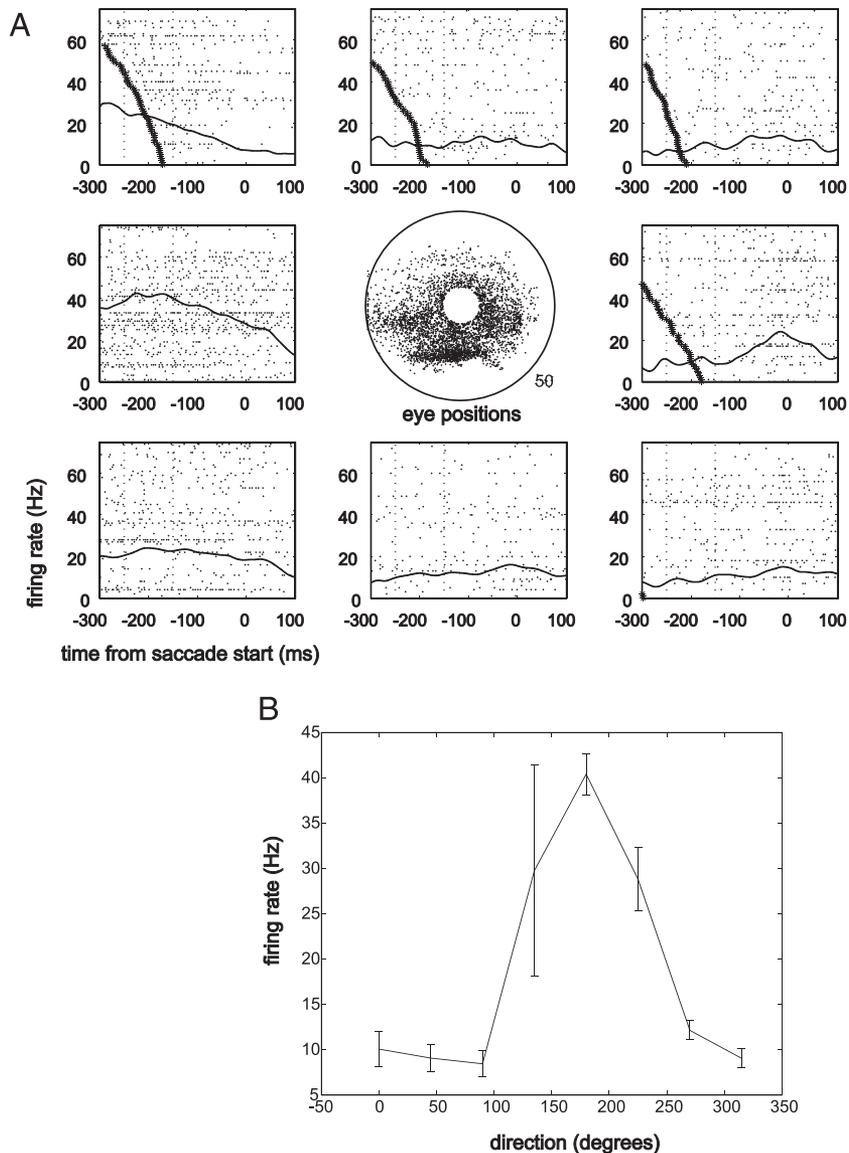


FIG. 3. Eye-position tuning during fixation. *A*: rasters and smoothed spike density histograms arranged for 8 directions of eye position from central gaze. Data are presented from all eye positions $>10^\circ$ from straight ahead position (*center*). The 8 raster/histograms of neuron activity are aligned to the beginning of saccades from the corresponding regions of eye position space. The 0° direction is to the right. *Middle right*: data from all eye positions located between angles of -22.5° and $+22.5^\circ$. *Top right*: data from all eye positions located between angles of $+22.5^\circ$ and $+67.5^\circ$ (i.e., centered at 45°), etc. Vertical dotted lines mark the portion of the fixation interval used for the analysis, centered at 200 ms before the start of the saccade. From top to bottom of each histogram, raster lines are ordered by larger to smaller period of time since the end of the previous saccade. For trials with relatively shorter intersaccadic intervals, heavy black dots indicate the point in time 100 ms after the end of the previous saccade. Only neural activity after this point is considered in the tuning analysis. *B*: tuning curve consisting of the average firing rates during the fixation intervals for the 8 directions shown in *A*. Error bars show SE. This cell (same cell as for Figs. 1C and 2) was located in the right superior colliculus and exhibited a combination of visual, build-up, and burst activities in the gap and memory-guided saccade tasks.

However, when we separately considered preferred and neutral saccade vectors (Fig. 5), we saw that for the preferred vector saccades, only those that ended in the preferred eye-position field were accompanied by increased activity 200 ms after the end of the saccade (Fig. 5A). Neutral saccades, for which the cell was not active during the saccade interval, tended to be followed by increased activity 200 ms after saccades only when those saccades ended in the preferred eye-position field (Fig. 5B, bottom left quadrant). It should be noted that because saccades tagged as neutral in this example were directed down and to the right, there were relatively few neutral saccades that landed within the preferred eye-position field of the cell that was near the limits of the oculomotor range in the bottom left quadrant.

The second characteristic of eye-position and saccade vector tuning demonstrated by the plots in Fig. 4 was that the direction of the eye-position tuning for this neuron was the same for both the pre- and postsaccadic fixation intervals. This finding addresses the possibility that an eye-position sensitivity could be attributed to correlations between eye positions and saccade vectors and that activity during the fixation period

might be a spill-over of saccade-related activity. In examining our data, we found a correlation between eye position and saccade vector that could be described as a re-centering bias. The pattern we observed was that fixations at eccentric eye positions tended to be followed by saccades that would bring the eyes back near the center of the orbits. Because the neurons are known to be tuned for a restricted range of saccade vectors, if an eccentric eye position tends to be followed by saccades that bring the eyes back to primary position, one might mistakenly identify an eye-position sensitivity that is instead attributable to the re-centering bias that we observed. However, if the re-centering bias was the basis for the observed eye-position tuning, the presaccadic eye-position sensitivity would be in the direction opposite to the preferred saccade vector, and the postsaccadic eye-position sensitivity would be in the same direction as the preferred vector. Instead, we found that eye-position sensitivity tended to be in the same direction as the preferred saccade vector and was always at the same orbital position before and after the saccade, indicating that the eye-position sensitivity was independent of correlations between eye position and preferred saccade vector. In addition, our

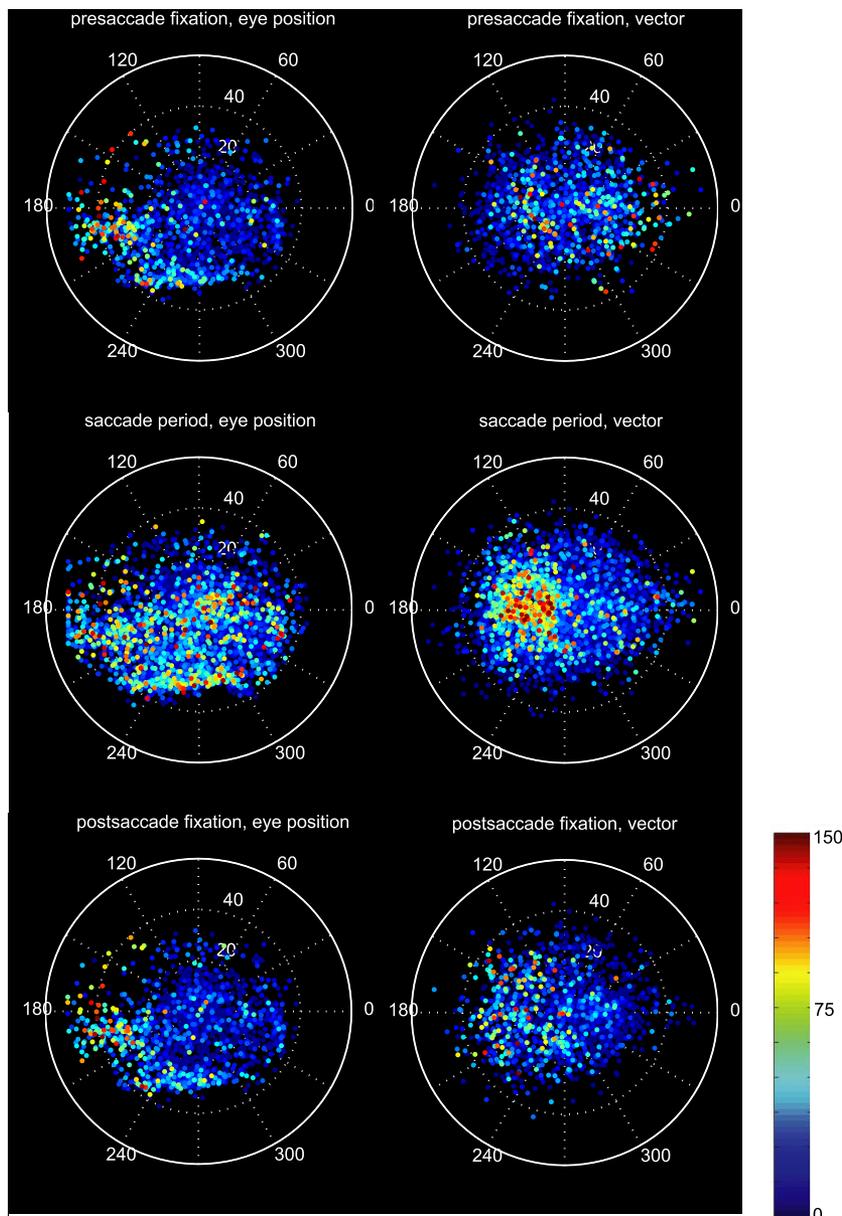


FIG. 4. Eye-movement and saccade-vector activity fields. A demonstration of the full saccade-vector movement field and eye-position response field for the same neuron as used in Figs. 1C, 2, and 3. *Left*: eye positions referenced to central fixation (orbital position of the eyes), using presaccadic eye position for the *top* and *middle* rows and postsaccadic eye position for the *bottom* row. *Right*: the endpoints of saccade vectors referenced to the start of each saccade. Color-level of dots indicates the firing rate associated with each eye position (*left*) or saccade vector endpoint (*right*). *Top*: instantaneous firing rates observed 200 ms before the start of a saccade. *Middle*: firing rates observed at the time of saccade start. *Bottom*: firing rates observed 200 ms after the end of the saccade. Color-bar indicates firing rate in spikes/s.

study avoids the potential effects of spill-over by imposing a 100-ms buffer between the saccade and the fixation interval that was used in our analysis.

The qualitative demonstrations of separate eye-position and saccade-vector tunings in these neurons, added to the background of earlier reports demonstrating eye-position influences on superior colliculus neuron activity, motivated us to pursue two separate quantitative analyses of the effects of eye position and saccade vector on collicular activity. In the first analysis, we used standard regression methods to model the eye-position and saccade-vector effects on cell activity. In the second analysis, we used circular statistics to quantify the magnitude and tuning of the position and vector contributions.

Analysis of the contributions of eye position and saccade vector to collicular neuron activity

We applied the models represented by Eqs. 9–11 to the activity of the same neuron as shown in Figs. 1C and 2–5 (Fig.

6) and produced idealized response profiles based on the optimal regression coefficients for eye position (Fig. 6A) and saccade vector (B) effects on activity. These demonstrate a best neuronal response for eye positions that are near horizontal and to the left of primary position. Best response for saccade vector is for leftward, horizontal saccades of $\sim 14^\circ$ amplitude. These response profiles agree with a qualitative assessment of the plots included in Fig. 4 (Fig. 4, *left column, top row* for Fig. 6A; Fig. 4, *right column, middle row* for Fig. 6B). Plotting changes in the regression coefficients for x_{pre} and y_{pre} (b_1 and b_2) across time referenced to the start of the next saccade (Fig. 6C) demonstrated that most of the effect of eye position on firing activity could be attributed to the horizontal component. This contribution to the cell's activity was initially elevated during the fixation period but dropped quickly to near-zero levels beginning 150–100 ms before the start of the saccade. Finally, r^2 values, a measure of the “goodness-of-fit” of these models, plotted over time (Fig. 6D), demonstrated the rela-

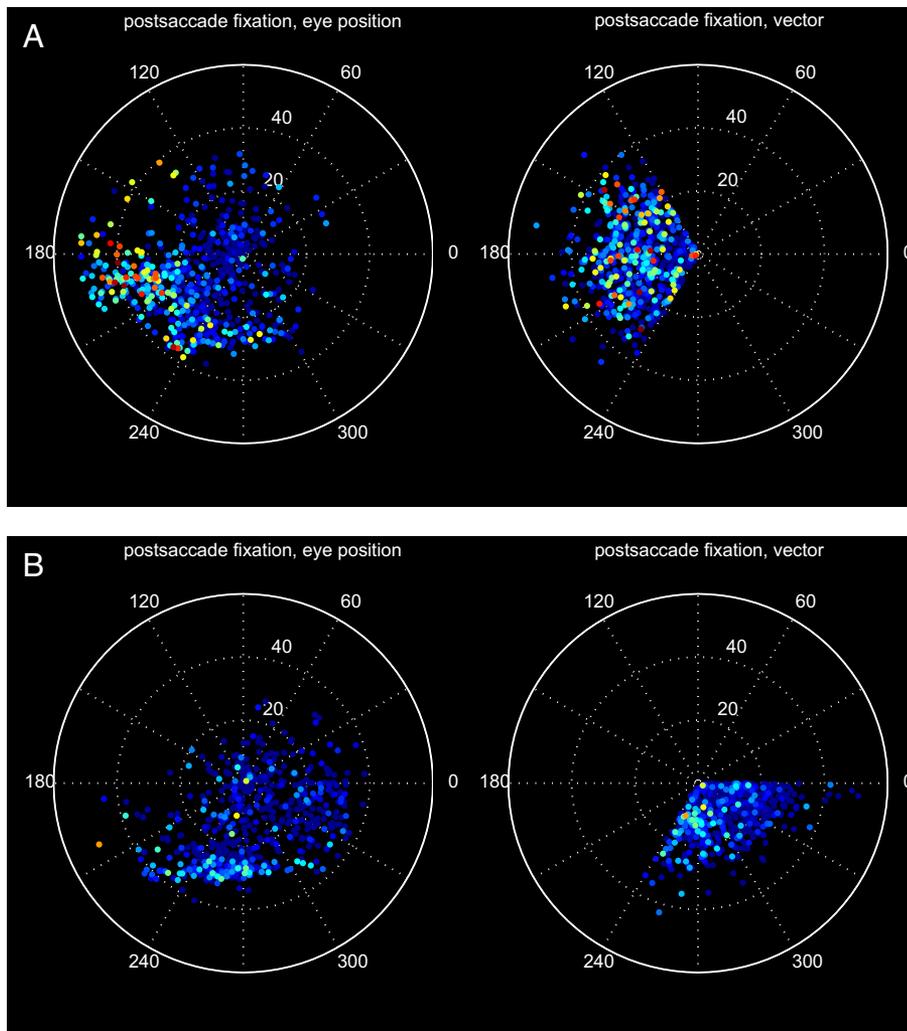


FIG. 5. Fixation interval activity after preferred and neutral saccades. Subsets of the data points from the bottom row of Fig. 4 are shown. *A*: plots activity for the postsaccadic fixation interval referenced to eye position (*left*) and saccade vector (*right*) for saccades that were in the preferred direction for this neuron (120–240°) *B*: same format as *A*, for saccades made in a neutral direction for this neuron (240–360°). Color code for firing rate is identical to that used in Fig. 4.

tively higher dependence of activity on eye position during the initial period of fixation, a drop in eye-position dependence beginning ~150 ms before the start of a saccade, and a simultaneous rise in dependence on saccade vector which peaked at the start of the saccade and then diminished during the course of the next 300 ms. The r^2 value for postsaccadic eye position (Fig 6D, red trace) was low during fixation prior to the saccade (time ≤ 0) indicating a lesser component of the activity tuned to future eye position. This value reaches a higher level after the saccade (time ≥ 100) as it then represents the new current eye position.

Examination of the dynamics of eye position and saccade vector r^2 values for each of the remaining cell types included in Fig. 1 revealed that the eye-position sensitivity was not restricted to a single cell type (Fig. 7). For these neurons, all except a cell with purely visual activity (Fig. 7A, same neuron as plotted in Fig. 1A) had some sensitivity to eye position during the presaccadic fixation period. Although it showed little sensitivity to eye position before or after the saccade, the activity of the visual cell was strongly dependent on saccade vector, suggesting a role in saccade target selection during scanning. This lack of eye-position sensitivity in a neuron classified as purely visual attenuated a concern that the activity we have characterized during fixation periods of the scanning paradigm was visually driven activity that was mistakenly

characterized as nonvisual eye-position dependent activity. Conversely, cells with weak or no visual activity in standard tasks showed significant eye-position sensitivity during the scanning paradigm (Figs. 1B/7B; 1C/6D; 1D/7C). The relative level of dependence on saccade vector versus eye position was considerably higher for two of these cells (Fig. 7, B and D), whereas for the remaining cell, saccade vector and eye position appeared to have made roughly equal contributions to the cell's activity although at separate times in the cycle of saccade and fixation (Fig. 7C).

For the example cells shown in Fig. 7, as well as for our examination of the entire population of cells in this study, it was apparent that the eye-position sensitivity we observed was not a property that could be attributed to neurons with a specific subtype of activity as characterized by the standard tasks used to classify collicular neurons (Fig. 8). From a total of 73 neurons for which we were able to fully characterize their activity in the memory-guided and gap saccade tasks (Fig. 8A), 16 (22%) met our criteria ($r^2 > 0.1$ and $P < 0.01$) for significant eye-position tuning during the fixation period (Fig 8B). For the total population of cells, 41% (30/73) were characterized as having a combination of more than one activity type. Regardless of whether or not they exhibited one or more activities, cells with build-up (4/14, 29%) or burst activity (13/39, 33%) were more likely to have a significant eye-

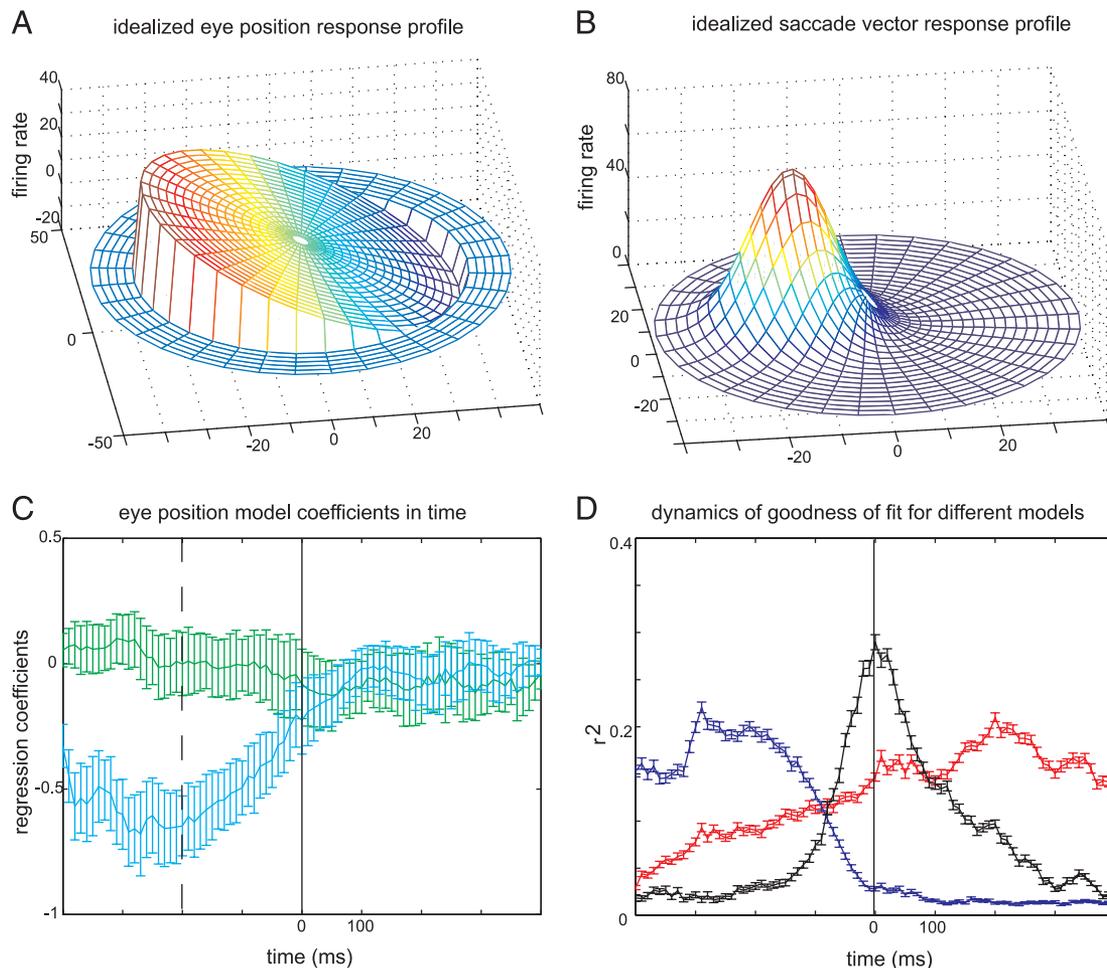


FIG. 6. Regression analysis for separate firing rate models based on eye-position and saccade-vector metrics. Idealized responses according to optimal regression coefficients for models based on eye positions (*A*) and saccade vectors (*B*). *C*: regression coefficients for the eye-position model plotted at 10-ms intervals relative to saccade start, for the horizontal (cyan) and vertical (green) components. Error bars are SD of 100 bootstrapped calculations. The vertical dashed line marks the time point 200 ms prior to the saccade where fixation period activity was sampled for many of the comparisons described in the text (e.g., Fig. 9–12). *D*: regression fits (r^2 values) at 10-ms intervals relative to saccade start are plotted for presaccadic eye-position (blue), postsaccadic eye-position (red), and saccade-vector (black) models. Error bars are SE of 100 bootstrapped calculations. Same neuron as for Figs. 1C and 2–5.

position tuning than were cells with visual activity (10/50, 20%).

For the entire population of cells in our sample, a comparison of r^2 values and P values for saccade vector and eye-position models demonstrated that the activity of these neurons at the time of saccade start was best fit by the saccade vector model, whereas fixation period activity 200 ms before the start of the saccade was best fit by the eye-position model (Fig. 9).

A comparison of r^2 values for eye position during the fixation interval versus at the start of the saccade demonstrates that these values decrease at the start of the saccade (Fig. 10A). The vast majority of dots plotted below the diagonal line indicate that the eye-position tuning (as modeled with Eq. 10) was almost always weaker at saccade start compared with the fixation interval. This was true even for cells whose saccade vector signal was weak. Further examination of the saccade-related activity showed that, although it was high during the saccade, this activity had dropped substantially by 100 ms after the end of the saccade (Fig. 10B).

To compare the topography of saccade-vector and eye-position activities for individual neurons, we compared the direction for optimal saccade vector tuning to the direction of

the gradient of the fitted eye-position tuning plane (Fig. 11; see Fig. 6A for example eye-position tuning plane). Here, a symbol for each of the 73 cells in our sample was plotted with radius equal to the fixation interval r^2 value (200 ms before the saccade start) obtained with the eye-position model and angle equal to the difference between the angles for the centers of saccade-vector and eye-position tuning fields. The distribution of preferred direction differences for the sample of collicular neurons with significant eye-position tuning ($n = 16$) was significantly nonuniform (Rayleigh test for nonuniformity, $P < 10^{-4}$) and centered near 0° (mean angle: -14.6° , circular SD: 42.7°). For 13 of these 16 neurons, the preferred eye-position and saccade vector directions were within 30° of one another.

Although most of the focus of this presentation has been on eye-position tuning during the current fixation period, we also examined tuning for future eye position after the upcoming saccade. Comparing r^2 values for the link between firing frequency and eye position during the current fixation (Eq. 10) versus the position where the eye would land at the end of the upcoming saccade (Eq. 11), indicated that the location of the eyes during the current fixation period was the better predictor of cell activity (Fig. 12A, ★). Likewise, when looking at r^2

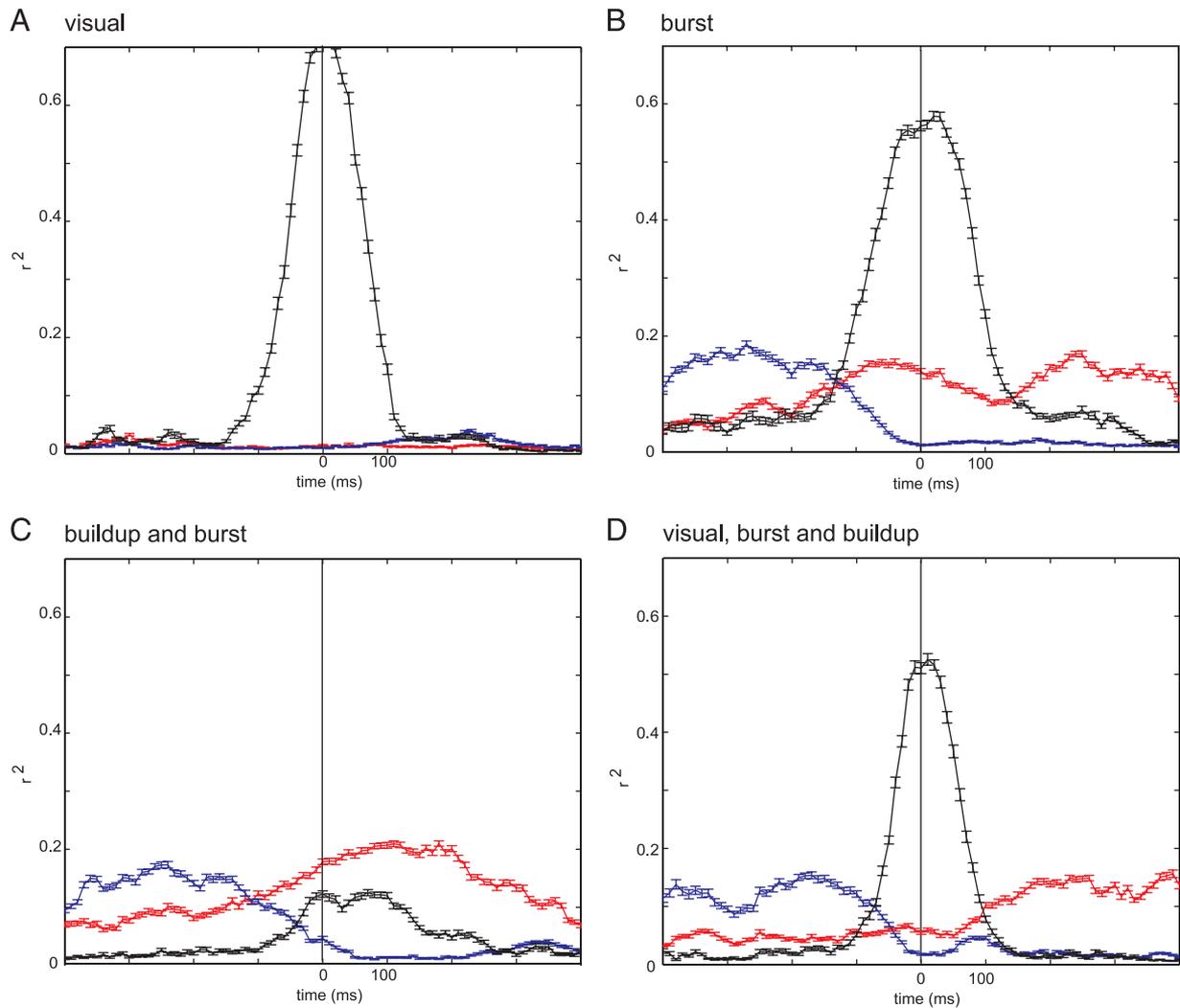


FIG. 7. Regression analysis examples for other types of neuronal activities. Example neurons with visual activity (A), saccade-related burst activity (B), combined build-up and burst activity (C), and combined visual, build-up and burst activities (D). As for Fig. 6, regression fits (r^2 values) at 10-ms intervals relative to saccade start are plotted for presaccadic eye-position (blue), postsaccadic eye-position (red), and saccade-vector (black) models. Error bars are SE of 100 bootstrapped calculations. Activity for these neurons in conventional tasks is plotted in Fig. 1.

values for eye position 200 ms after the end of the saccade (Fig. 12A, □) we noted that activity was better predicted by eye position after the saccade (Eq. 11) than it was by eye position

before the saccade (Eq. 10). Both comparisons reveal that eye-position-related activity during fixation is best predicted by the current position of the eyes not prior or future eye position.

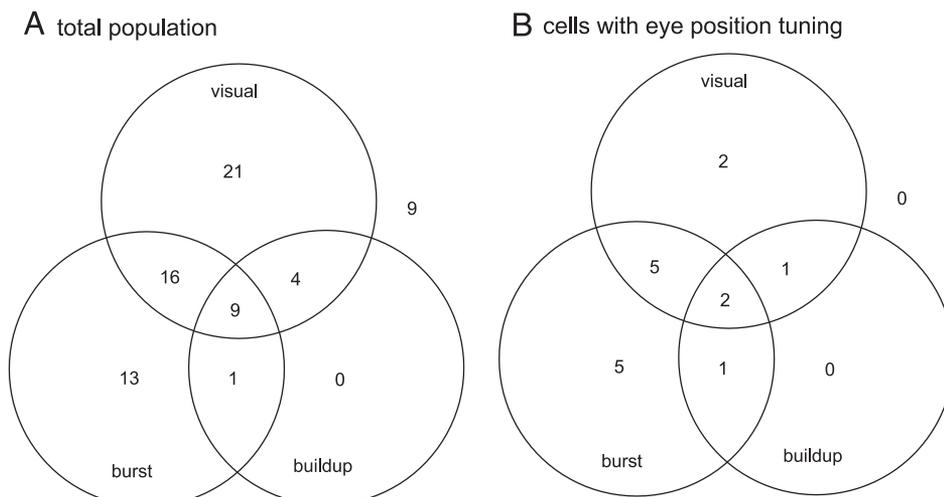


FIG. 8. Distribution of activity types. Venn diagrams of the distributions of visual, build-up, and burst activity types in the entire sample population used for this study (A) as well as for the subpopulation of cells with significant eye-position tuning (B).

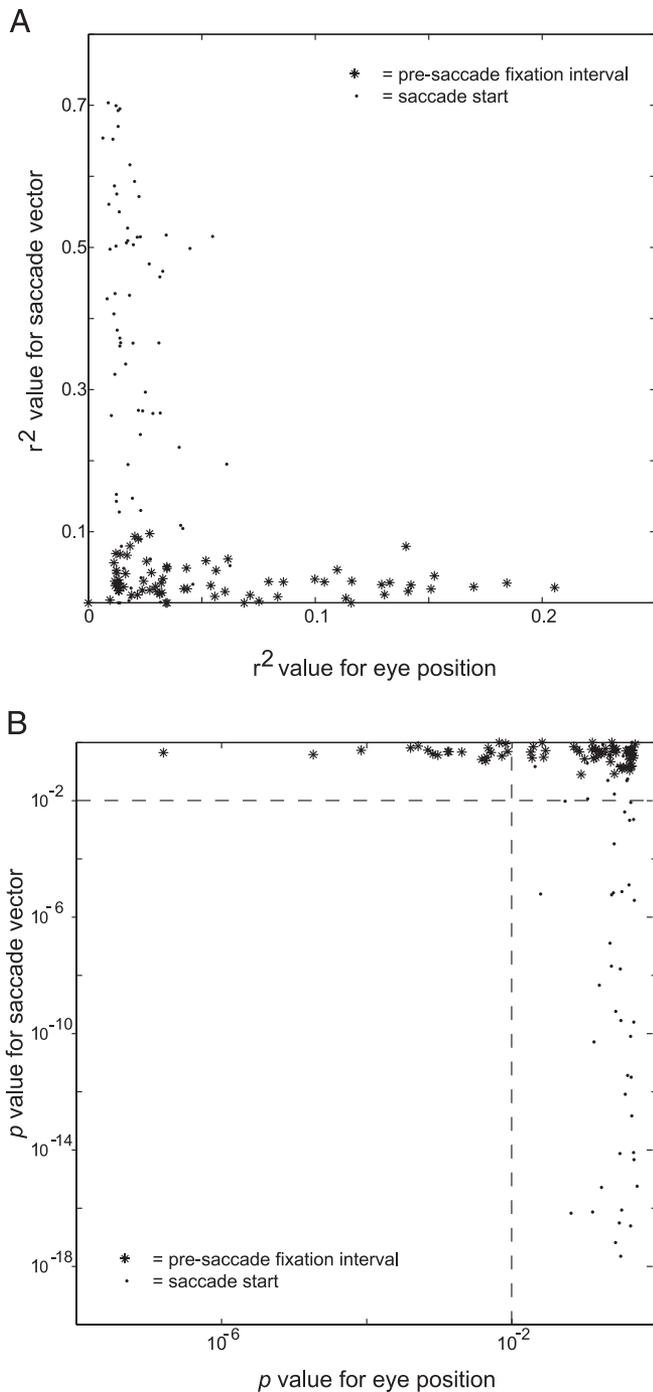


FIG. 9. Population results. Comparison of firing rate models based on eye positions or saccade vectors. *A*: distribution of r^2 (goodness-of-fit) values for firing rate models based on presaccade eye position (horizontal axis; equivalent to blue line in Figs. 6*D* and 7) and saccade vector (vertical axis; black line in Figs. 6*D* and 7). Values are plotted for regressions on firing rates at saccade start (●) and 200 ms before the start of the saccade (*) for individual neurons. Note that r^2 values are higher for the saccade vector model than the eye-position model at the start of the saccade and that this relationship is reversed for the fixation interval centered 200 ms before saccade start. *B*: distribution of p (significance of regression) values for firing rate models based on presaccade eye position (horizontal axis) and saccade vector (vertical axis).

In other words, the eye-position sensitivity is not a record of previous eye positions or an indication of where the eyes will be in the future. Rather, the eye-position sensitivity represents the current location of the eyes in their orbits.

We compared the preferred direction of the eyes from primary position for eye-position tuning in pre- and postsaccadic fixation intervals (Fig. 12*B*). The difference between these two directions clustered near 0°, indicating that the tunings for eye position before and after the saccade were the same. The distance from the center of this plot equals the r^2 value for the eye-position model in the presaccadic interval.

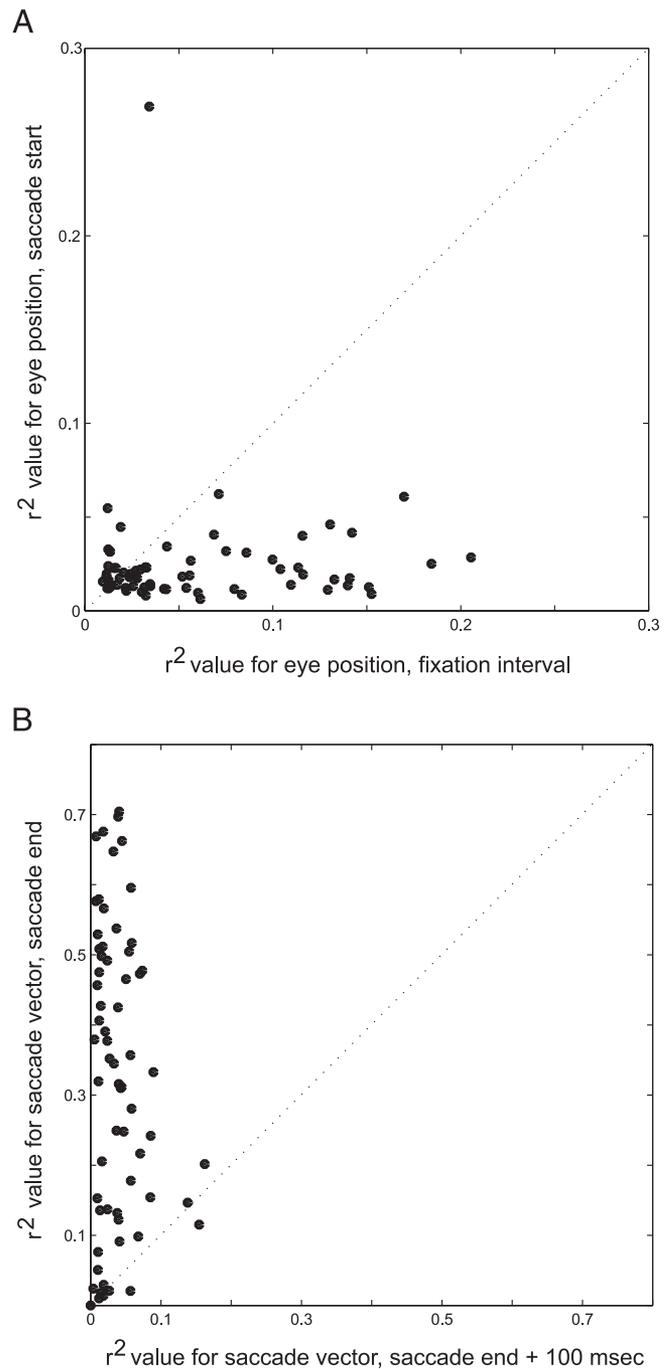


FIG. 10. Decrease in eye-position tuning at the start of the saccade and decrease in saccade vector tuning 100 ms after the saccade. *A*: ●, the r^2 values for the eye-position model during the presaccadic fixation interval (horizontal axis; blue lines in Figs. 6*D* and 7, value at $t = -200$) and at the time of saccade start (vertical axis; blue lines in Figs. 6*D* and 7, value at $t = 0$). *B*: ●, the r^2 values for the saccade vector model (black lines in Figs. 6*D* and 7) for firing rates at the end of the saccade (vertical axis) and at the time 100 ms after the end of the saccade (horizontal axis).

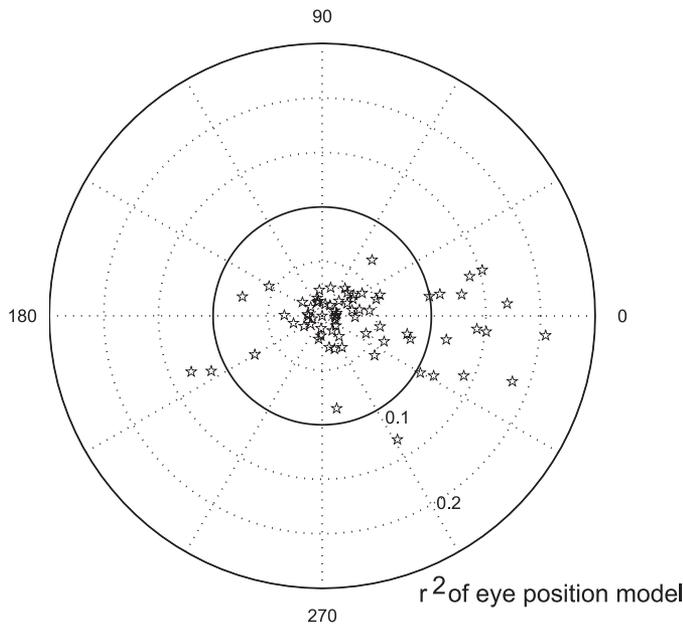


FIG. 11. Angular difference of preferred saccade vector and preferred eye position directions. Angle of the eye position tuning field is defined as the arctangent of the regression coefficients (Eq. 10) of the vertical divided by horizontal components, or $\theta = \arctan(b_2/b_1)$. Angle of the saccade vector tuning field is defined as the arctangent of the regression coefficients (Eq. 9) of the vertical center divided by horizontal center, or $\theta = \arctan(y_{ctr}/x_{ctr})$. The distance from the center of this plot equals the r^2 value for the eye-position model in the presaccadic fixation interval. The solid-line circle at $r^2 = 0.1$ marks our criteria for neurons with significant eye-position tuning during the presaccadic fixation interval.

Tuning analysis with circular statistics

In addition to the analysis with regression models, we evaluated the eye-position and saccade-vector tunings and their strengths across time using a tuning metric related to the population vector used in the Rayleigh test of nonuniformity of circular data (see METHODS, Eq. 12). The results from the regression analysis described up to this point were confined by the model's prediction that the eye-position sensitivity conforms to a linear profile (Eqs. 10 and 11). In fact, this is a first approximation of the position tuning, and the task remains for future work to provide a better model to define the representation of eye-position tuning across the superior colliculus. Both the regression analysis and the tuning metric analysis have their unique advantages. While the regression analysis has the advantage that it generates r^2 values that gauge the contribution of eye position to the total activity of a neuron, the main advantage of the tuning metric analysis was that it did not require that the eye-position response fields conform to a shape that was predetermined by a quantitative model.

To assess the strength of tuning, the average activity was computed for all of the saccades in each of eight angular bins, and two amplitude bins ($<15^\circ$ and $15\text{--}30^\circ$), then focus was placed on the amplitude bin that had the strongest tuning across the population of recorded neurons. Division into amplitude bins increased the "signal-to-noise" ratio to a level higher than would be obtained if an average of activity associated with all saccades for a given range of directions were considered. Most (53 of 73, χ^2 test, $P < 0.01$) of the preferred eye positions were

in eccentric locations, and so the eccentric annulus was used for the population analysis of eye-position sensitivity. Likewise, the majority (46 of 73, χ^2 test, $P < 0.05$) of the neurons showed a preferred saccade vector directed to locations in the central annulus, and so the central annulus was used for the population analysis of saccade vectors. During the neuronal recordings for these experiments, we purposely selected collicular neurons with best vectors the amplitudes of which were $<20^\circ$ to avoid the unequal distribution of preferred saccade starting and ending positions that would be obtained if recording sites representing larger eye movements were used. This selection criterion was largely responsible for the majority of preferred saccade vectors having amplitudes within the central annulus ($<15^\circ$).

TEMPORAL DYNAMICS OF TUNING IN DIFFERENT REFERENCE FRAMES.

In a manner similar to the presentation of our regression analysis results, we'll first present results from the circular statistics analysis for a single neuron, followed by presentation of the results for the subpopulation of cells with significant eye-position sensitivity. In agreement with numerous descriptions of saccade-related activity in the superior colliculus, a plot of a sample neuron's activity taken from the time period surrounding the start of the saccade varied continuously with the angle of the saccade vector, reaching a maximum for a preferred direction of 245° (Fig. 13A, top row). Firing rates of collicular neurons were also sensitive to the amplitude of the saccade, and so the firing rates are shown as they varied with direction for both small ($<15^\circ$)- and large ($15\text{--}30^\circ$)-amplitude ranges. As can be seen in the top two rows of Fig. 13A, the neural activity was more strongly tuned for short-amplitude saccades (inner ring) compared with large-amplitude saccades (outer ring). Taken together, the familiar saccade vector tuning is demonstrated in the top row of Fig. 13A. In contrast, the tuning for activity at saccade start associated with the eye-position coordinates was weak and poorly localized (Fig. 13A, bottom 2 rows). The strength of saccade vector and eye-position tuning (Eq. 12, τ) is indicated by the magnitude of the tuning vectors shown as the values of the curves at $t = 0$ in Fig. 13C. For the time period surrounding the start of the saccade, the length of the tuning vector was large when the firing activity was referenced to saccade vector coordinates (Fig. 13C, $\cdot\cdot\cdot\cdot$ at $t = 0$). In contrast, when the same activity was referenced to eye-position coordinates at the start of the saccade, the tuning vector was relatively small (Fig. 13C, — at $t = 0$). Superimposed on these values in Fig. 13C are arrows showing the relative magnitude (τ , Eq. 12) and the direction (α , Eq. 13) of the weighted resultant vector. The comparatively stronger tuning for saccade vector information during the epoch surrounding the start of the saccade confirms that this neuron generated the expected saccade-vector signal during this time period.

Conversely, when the activity during fixation was examined, we found the opposite result. Plots of the activity of the same neuron, but from a time window centered 200 ms before the start of the saccade, demonstrates this finding (Fig. 13B). The relative magnitude of the tuning vectors for firing activity referenced to saccade vector versus eye-position coordinates is reversed in comparison to what was seen for the saccade period, indicating that an eye-position signal dominated this neuron's activity during fixation (200 ms before saccade start).

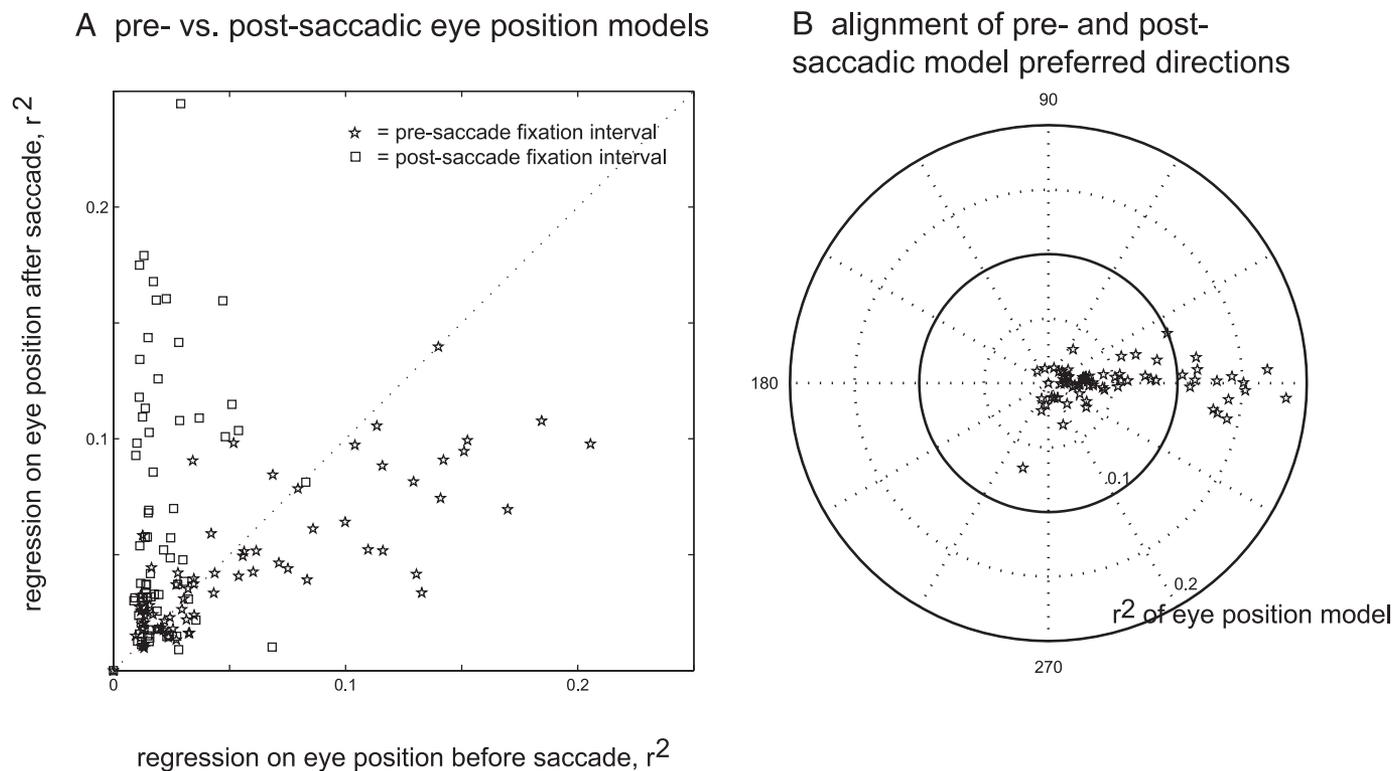


FIG. 12. Comparison of firing rate models based on current and future eye positions. *A*: distribution of r^2 (goodness-of-fit) values for firing rate models based on presaccade eye position (Eq. 10, horizontal axis) and postsaccade eye position (Eq. 11, vertical axis). Values are plotted for regressions in the presaccade fixation interval 200 ms before saccade start (\star) and the postsaccade fixation interval 200 ms after the saccade end (\square) for individual neurons. *B*: angular difference of eye-position response fields before and after the saccade. The distance from the center equals the r^2 value for the eye-position model during the presaccadic interval.

Activity during this interval of fixation tended to be present when the animal fixated within a restricted range of eye-position directions, as demonstrated in the bottom rows of Fig. 13*B*. The eye-position tuning was also dependent on amplitude, showing greater tuning for eye position in the outer versus inner rings.

To obtain the firing rates used in the circular statistics analysis, spike trains were first smoothed with a Gaussian as was done in the regression analysis (see METHODS). Because the data sample contains fixation intervals with variable durations, the average firing rates were calculated every millisecond using only the fixation intervals for which there were ≥ 100 ms of fixation following the previous saccade. The smoothed values for firing rates were then fed into the tuning metric equation (Eq. 12) to produce a value for the tuning index at every millisecond. Figure 13*C* plots the progression of tuning indices for saccade vector ($- \cdot - \cdot -$) and eye position ($-$) over a time period extending from 300 ms before until 100 ms after the start of the saccade. In a manner similar to the regression analysis (see Figs. 6*D* and 7, *B-D*), this plot of eye position and saccade vector tuning across time demonstrates a high level of eye-position tuning during fixation that decreased rapidly as the start of the saccade approached. This decrease in position tuning was matched by a rapid rise in saccade vector tuning that reached a maximum at the start of the saccade.

POPULATION RESULTS. When data for the sample of collicular neurons with significant eye-position tuning ($r^2 > 0.1$ and $P < 0.01$ for fit to eye-position model in fixation interval) are combined (Fig. 14*A*, $n = 16$), the pattern of tuning demon-

strated for the single neuron the data of which are illustrated in Fig. 13 is reflected in the tuning for this larger sample of neurons. An elevated eye-position tuning during fixation diminishes and is rapidly replaced by strong saccade vector tuning surrounding the time of the saccade.

The distribution of tuning indices for the population of neurons with significant eye-position tuning demonstrates the preference of the majority of cells for eye-position tuning during the fixation interval (Fig. 14*B*, \star , Wilcoxon rank sum test, $P < 10^{-2}$), and vector tuning during the time surrounding saccades (Fig. 14*B*, \bullet , Wilcoxon rank sum test, $P < 10^{-4}$).

In Fig. 15, the relationship between the response field directions for both coordinate frames is shown. In a manner similar to that generated with the regression models (see Fig. 11), the direction of the eye-position and saccade-vector response fields tended to be aligned with each other for individual cells. The distribution of preferred direction differences for the sample of collicular neurons with significant eye-position tuning ($n = 16$) is significantly nonuniform (Rayleigh test for nonuniformity, $P < 10^{-6}$) and centered on 0° (mean angle: $-2.85 \pm 29^\circ$) (Batschelet 1981).

Eye-position tuning during a fixation task

In one additional monkey (*MAS012*), we tested the effects of eye position on collicular activity using a task that did not involve scanning of images but required the monkey to fixate a spot of light positioned at locations chosen at random from an array of 25 positions extending in amplitude from 0 to 22.5°

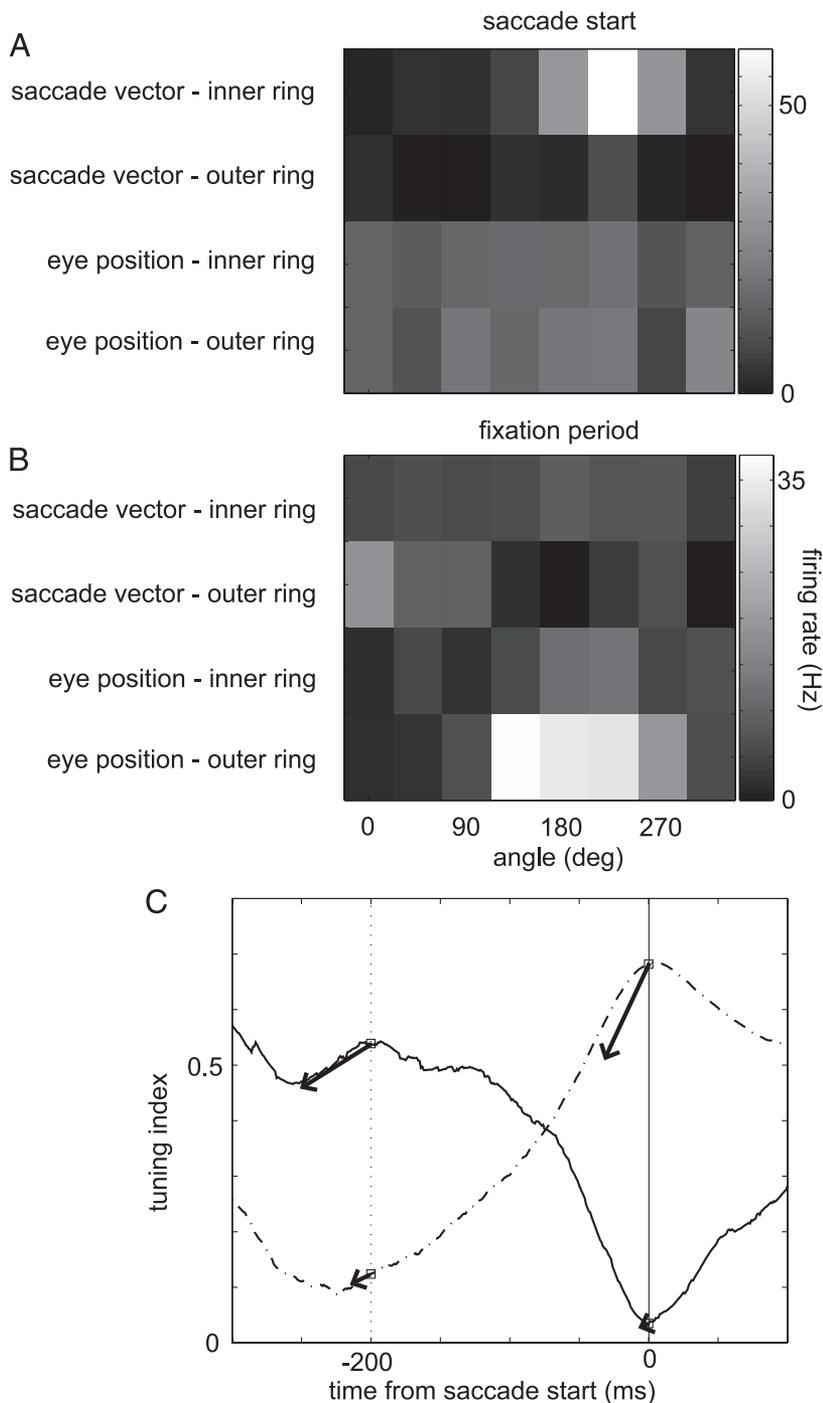


FIG. 13. Saccade-vector and eye-position tuning of a single collicular neuron. Firing rates associated with saccade vectors (A and B, top 2 rows) and eye position (A and B, bottom 2 rows) at saccade start (A) and a point during fixation 200 ms prior to the start of the saccade (B). C: dynamics of eye position (—) and vector (- · - ·) tuning aligned with respect to saccade start at time = 0. Eye-position tuning is calculated from the range of saccades that began 15–30° from the center of the tangent screen (A and B, bottom row, outer ring), and vector tuning from vectors of amplitude 0–15° (A and B, top row, inner ring). The tuning vectors superimposed on the — and - · - · indicate the direction and relative magnitude of the population vector where magnitude is equal to the value of the tuning index at –200 and 0 ms (height of curves in C). See text for additional details.

and at angular increments of 45° (Fig. 16; see METHODS for task description).

We recorded from a total of 19 neurons during the performance of this task, 8 in the right colliculus and 11 in the left. From this total, 14 neurons had sufficient data recorded to allow us to perform a regression analysis of the effects of fixation position on cell activity. We analyzed average spike activity in a 100-ms window centered at 500 ms after the monkey's eyes moved to the fixation point. This was a time period when fixation was well established and roughly midway between the saccade that brought the eyes to the fixation point and the saccade that would move the eyes to the upcoming

target. Four of these neurons (29%) had a significant eye-position regression ($P < 0.01$) when the analysis was performed on the entire data set. Higher levels of significance were obtained when the analysis was restricted to the ring of fixation locations that best matched the amplitude of the optimal saccade vector for the site (outer ring of dots at 22.5° in sketch at center of Fig. 16 for 3 of the units, and middle ring of dots at 15° for 1 unit). For the data illustrated in Fig. 16, recorded from a cell in the right colliculus, we obtained an r^2 value of 0.27 with $P = 1.8 \times 10^{-7}$. The rate of change of cell activity as eye position moved from right to left along the horizontal meridian was 0.43 spikes/s/deg (Eq. 10, $b_1 =$

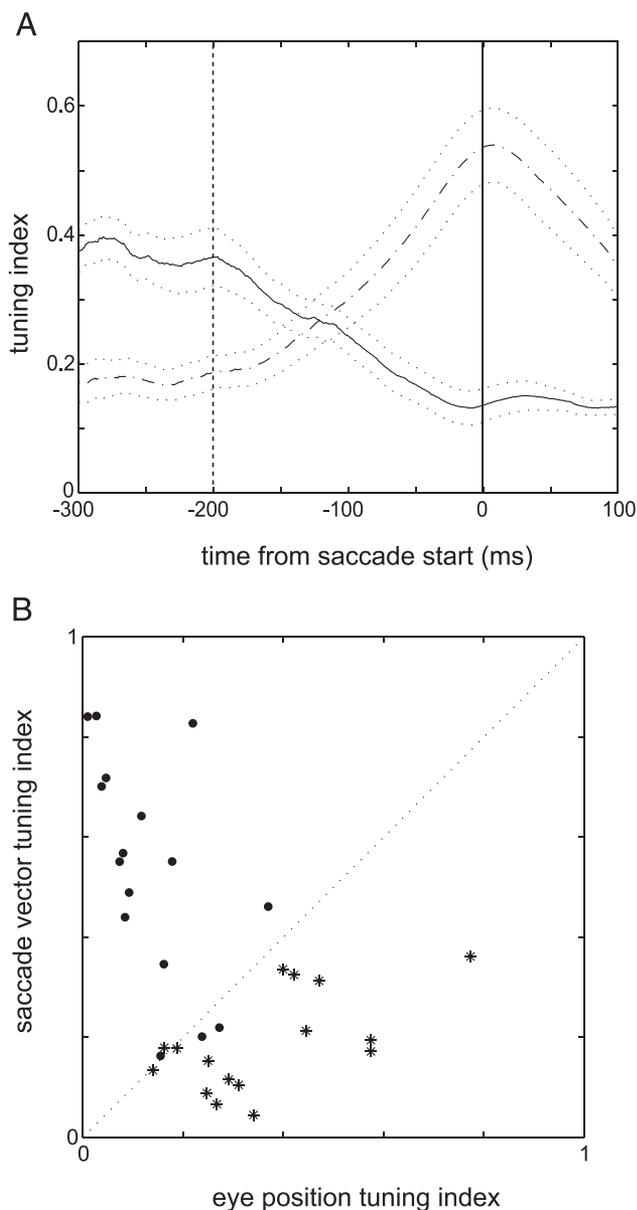


FIG. 14. Population results for circular statistics analysis. *A*: tuning dynamics for the sub-sample of collicular neurons with significant eye position tuning. Eye position (—) and vector (---) tuning dynamics \pm SE (\cdots), aligned with respect to saccade start at time = 0. *B*: distribution of saccade-vector and eye-position tuning indices for the same population of cells as used for *A*. For each individual neuron, the plot includes tuning indices for eye position (x axis) vs. saccade vector (y axis) reference frames, at saccade start (\bullet) and 200 ms preceding the start of the saccade (\star).

-0.43 , $b_2 = 0.00$). For another cell recorded in the left colliculus, $r^2 = 0.35$ and $P = 5.7 \times 10^{-4}$. Rate of change of cell activity as eye position moved up and slightly to the right was 0.52 spikes/s/deg ($b_1 = 0.12$, $b_2 = 0.51$). Both indicate that when the eyes were eccentric, a large component of the activity during fixation could be attributed to the position of the eyes in their orbits.

A comparison of saccade vector direction to the direction of the gradient of the fitted eye-position tuning plane for the four neurons with significant eye-position tuning is provided in Table 2. For each of these neurons, there was a close overlap ($<30^\circ$) between the directions of saccade-vector and eye-

position tuning. This overlap was very similar to what was seen for the scanning paradigm neurons using both the regression and circular statistics analyses.

DISCUSSION

This study examined the effects of saccade vector and eye position on the activity of neurons in the deep layers of the monkey superior colliculus. The saccade vector activity of superior colliculus neurons has been long established (Robinson 1972; Schiller and Stryker 1972; Sparks et al. 1976; Wurtz and Goldberg 1972). In contrast, there have been fewer reports of a sensitivity of collicular activity to eye position, and they have appeared more recently. A sensitivity to eye position has been reported for both cat (Peck 1986; Peck et al. 1995) and monkey superior colliculus where Van Opstal and colleagues (1995) demonstrated an eye-position modulation of saccadic activity reminiscent of the gain fields described for the inferior parietal lobule (Andersen et al. 1985). Krauzlis and colleagues (2000) also reported a sensitivity to eye position for cells in the rostral colliculus in monkeys. The best orbital positions for these cells were located just a few degrees from primary position matching the rostral colliculus' retinotopic representation of points nearby and including the fovea. This topographical correspondence is in agreement with the finding of this report that the directions of the eye-position and saccade vector fields for the cells we studied tended to be aligned, a property referred to as colinearity. In addition, the number of cells where an eye-position effect could be demonstrated in rostral colliculus (26%) was similar to the number found in this report (22% using scanning paradigm, 29% using multi-target task). Van Opstal and colleagues (1995) found that 53% (30/57) of their sample of collicular neurons was influenced by eye position, and reported that slightly more than half (17/30) had saccade vector and eye-position tunings that were in alignment. Finally, Paré and Munoz (2001) reported an eye-position effect on neuronal excitability that was associated with saccades that would bring the eyes back to primary position. For example, eye positions to the left of primary position

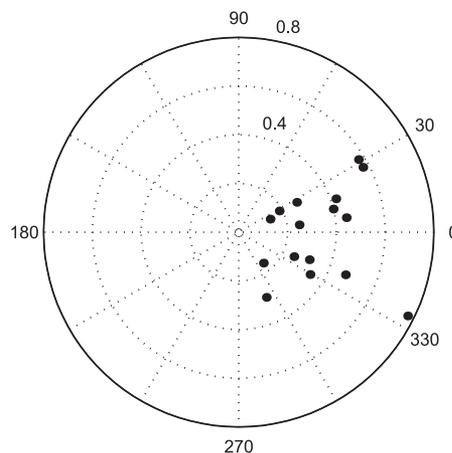


FIG. 15. Alignment of the preferred directions. \bullet , the direction of the preferred saccade vector minus the direction of the preferred eye position. Direction is given by the angle of the weighted population vector (Eq. 13). The distance from the center equals the mean value of the tuning metric during the fixation interval (200 ms before saccade start). Grouping of the data points near 0° indicates that vector and position directions tend to be aligned.

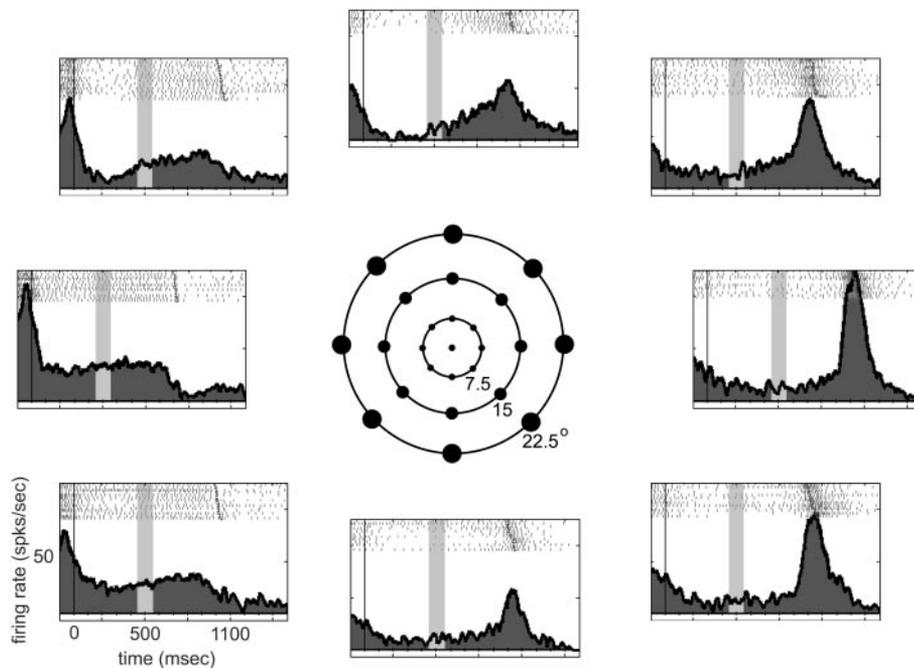


FIG. 16. Eye-position tuning demonstrated with a fixation task. Activity from a neuron in the right superior colliculus recorded while a monkey fixated locations 22.5° away from the center of the screen and spaced at angular increments of 45° . Rasters and spike density histograms are aligned to the time when the monkey's eye entered the criterion window surrounding the fixation point at time = 0 ms. Heavy black marks in the raster plots indicate the start of the saccade to a target that could be located at any of the locations in the array except for the current fixation location. Shaded bar indicates the 100-ms time interval used for the regression analysis described in RESULTS. The response field for the combined visual and saccade-related burst activity of this neuron was centered at $15\text{--}20^\circ$ amplitude to the left and horizontal. The bursts of activity associated with the target-directed saccades in the data illustrated here were due to saccades being made to targets that were within the cell's response field. This was most often the case when the eyes were fixated at the most rightward fixation point location ($22.5, 0^\circ$). The sketch in the center of the figure shows the entire array of potential fixation point and target locations for this task. The 3 circles of fixation point/target locations have radii of 7.5, 15, and 22.5° from the center of the screen.

would facilitate rightward saccades that would bring the eyes back to center of the orbits. At first glance, this finding appears to contradict the findings of this report as well as those of Van Opstal and Krauzlis and colleagues, however, the task used by Paré and Munoz was designed to encourage short-latency saccades and the position bias they observed was likely to have been associated with the upcoming re-centering saccade.

The current results add to earlier observations by demonstrating a relatively stronger eye-position signal during fixation at intervals where the cell's activity does not appear to be affected by either preceding or following saccades. Moreover, we examined the dynamics of these tunings, finding that eye-position sensitivity comprises a relatively larger component of cell activity during the inter-saccadic interval and that the population of collicular neurons, as well as individual neurons, becomes dominated by saccade vector driven activity as the time of saccade initiation approaches.

Evaluation of METHODS and RESULTS

The scanning paradigm used for these experiments allowed for a sampling of a large range of self-guided eye movements used to demonstrate the effect of eye position on collicular cell activity. This method is similar in many respects to that of Van Opstal and colleagues (1995) who used "food and novel gadgets" to elicit eye movements over a wide range. In their experiments as well as in our own, a major advantage of the behavioral approach was that, in a short period of time, it

TABLE 2. Preferred directions of cells in multi-target task

Neuron	Saccade-Vector Direction	Eye-Position Direction	r^2	P
52605lu2	180°	179°	0.27	<0.001
53105lu2	70°	100°	0.17	<0.001
60105lu4	70°	76°	0.35	0.002
81705lu7	135°	162°	0.31	0.003

yielded a very large number of saccades and fixations distributed throughout the oculomotor range. In our experiments, >3,000 saccades were recorded in the recording session for each individual neuron at a rate of >2 saccades/s. An equivalent sample would be difficult to attain using conventional oculomotor tasks. This large and widely distributed sample of saccades and eye positions with associated neural activity was essential to the analyses performed in these studies.

Although we feel the evidence for eye-position sensitivity presented in this study is strong and is corroborated by a number of earlier reports, we would like to address several alternative explanations for the modulation of collicular neuron activity that we have attributed to the influence of eye position.

The first alternative explanation is that the increases in activity observed during fixation were a remnant of activity associated with the preceding saccade. Waitzman and colleagues (1991) reported that 56% of collicular neurons with saccade-related activity continued to fire for 30–100 ms after the end of the saccade. Figure 10B demonstrates that by 100 ms after the end of the saccade, the activity is not tuned to the previous saccade vector, and so to avoid the effect of activity related to the prior saccade, the fixation interval used in our analysis was set to exclude all spikes that occurred within 100 ms of the end of the previous saccade. Furthermore, as shown in the insets of Fig. 2, A and B, as well as in Fig. 4 (top right), the population of saccades preceding the intersaccadic intervals with elevated activity during the fixation period was topographically heterogeneous, including a majority of saccades, both ipsiversive and contraversive, that did not match the cell's saccade vector tuning. This diverse distribution of the preceding saccades provides additional assurance that increases in a cell's activity during fixation was not a remnant of preceding saccade vector activity.

A second alternative explanation, mentioned in RESULTS, is that the position of the eyes during fixation and the saccade vectors that precede and follow those fixations are not independent. One could argue that an apparent eye-position tuning

was attributable to a group of eye positions being correlated with a neuron's preferred saccade vector. We have looked at the correlations between eye position and saccade vector and find that they are dominated by a tendency for saccades originating from eccentric eye positions to bring the eyes back to the center of the orbits. If this correlation was to have a dominant effect on the tunings of these neurons, one would expect to see a preponderance of eye-position tuning fields the centers of which were in a direction opposite to that of the saccade vector tuning. In fact, this is rarely the case, and it is most common to see colinear saccade-vector and eye-position response fields for a given neuron (see Figs. 11 and 15). The resistance of the sampled neurons' position and vector tunings to this correlation in eye movement behavior underlines the separate and independent nature of these tunings.

Another potential shortcoming to the interpretation of our data are that activity during fixation might be visually driven by objects in the experimental setup. This possibility must be considered, since some of the cells within the deep layers of the superior colliculus include visually driven activity as a component of their responses. Almost 2/3 (10/16) of the neurons in our sample with significant eye-position related activity were visually responsive, with response fields of small to medium eccentricity. However, the sensitivity of a neuron to eye position did not depend on the degree to which it was visually responsive in conventional tasks (see DISCUSSION of Figs. 7 and 8 in RESULTS). In fact, cells with visual activity were less likely to have eye-position sensitivity than were cells with build-up or burst activity. Our full sample included a total of 50 neurons (68%, 50/73) the activity of which was sensitive to visual stimulation as tested in a memory-guided saccade task. Most of these neurons with visual activity (80%, 40/50) had no significant eye-position tuning. Finally, early studies of the activity of frontal eye field neuron visual activity during scanning did not reveal an effect of salient response field content on the activity of the neurons, instead, their activity seemed to be more specifically related to the choice of saccade targets (Burman and Segraves 1994). We expect this would also be the case for the superior colliculus the deep layers of which are, in our experience, less visually active than the frontal eye field.

It should be noted that for the present study, as well as the other study that has provided the most extensive evidence for eye-position tuning in the primate superior colliculus (Van Opstal et al. 1995), collicular neuronal data were collected during volitional, internally guided saccades made during the viewing of natural images or the presentation of novel objects in front of the monkey. In addition, we've presented preliminary evidence from a single monkey demonstrating that collicular eye-position tuning is present during a fixation task where the monkey fixates a spot of light presented on a dark background (Fig. 16). Furthermore, Krauzlis and colleagues (2000) have reported evidence for collicular eye-position tuning using conventional oculomotor tasks. It will be important for future experiments to expand the investigation of the degree to which an eye-position signal can be generated in the context of a conventional oculomotor task using spots of light as targets. These preliminary investigations suggest that the eye-position sensitivity we have demonstrated is a ubiquitous property of collicular activity that does not depend on whether the eyes are self-driven during the scanning of natural scenes or directed by a controlled oculomotor task.

Evaluation of saccade-vector and eye-position models

We chose a linear regression model for the eye-position sensitivity in these data as a first attempt to describe this characteristic of collicular activity. Although statistically significant, the r^2 values for the eye-position contribution to collicular neuron activity during fixation were low in comparison to those for saccade vector during the saccade period, suggesting that a linear model was less than optimal. In addition, it is likely that a regression model developed that is better able to approximate the actual shape of the eye-position response fields would yield a higher percentage of cells with significant eye-position tunings than is reported here. The saccade-vector sensitivity of superior colliculus neurons is well studied, and we know that a two-dimensional Gaussian is a good approximation of its response profile (Ottes et al. 1986). In contrast, the eye-position sensitivity has never been presented as an independent signal before, and so we purposely chose a simple linear model to provide a first approximation of the contribution of eye position to cell activity. Deriving the optimal profile for the eye-position response field will be an important goal for future studies.

Although the high r^2 values for saccade vector during the saccade suggest that this is the major factor affecting collicular activity at this time, the relatively low r^2 value for eye position during fixation suggests that other factors also contribute to activity during fixation. These are likely to include factors related to choice of saccade targets and preparation for a saccade (Carello and Krauzlis 2004; Hasegawa et al. 2004; Horwitz and Newsome 1999, 2001; Horwitz et al. 2004; Ratcliff et al. 2003) as well as activity driven by other modalities (Meredith and Stein 1986; Perrault et al. 2005; Stuphorn et al. 2000; Wallace et al. 1996).

Dynamics of collicular saccade-vector and eye-position tunings

This study provides evidence that the collicular representations of eye position and saccade vector are more evident during separate and distinct times during the continuous cycle of fixation and saccades. An eye-position signal prevails during fixation, and this is replaced by a saccade-vector signal during the time period surrounding the saccade. In addition to the well known saccade vector signal (Robinson 1972; Schiller and Stryker 1972; Sparks et al. 1976; Wurtz and Goldberg 1972) and the eye-position signal demonstrated here and in other reports (Krauzlis et al. 2000; Paré and Munoz 2001; Peck 1986; Van Opstal et al. 1995), cells within the deep layers of the superior colliculus are also known to have activity related to visual stimulation as well as anticipatory activity related to the probability that a saccade will be made to a target within the neuron's response field (Basso and Wurtz 1998; Mays and Sparks 1980a; Munoz and Wurtz 1995).

The ability of neurons to express different signals during different time periods is not unique to the collicular neurons we describe. Within the oculomotor system, for example, the burst-tonic activity of oculomotor neurons can be viewed as a signal that conveys both saccade-velocity and eye-position commands during separate time periods (Robinson 1970). For invertebrates, studies of the crab and lobster stomatogastric ganglion demonstrate that single neurons can switch their

functional roles and participate in different pattern-generating circuits during separate time periods (Hooper and Moulins 1989; Weimann and Marder 1994).

With more than one signal present in the activity of a single neuron, how is it possible for the downstream targets of these neurons to decipher collicular activity? Input from vector coded neurons in the superior colliculus is a substantial component of the input to preoculomotor neurons in the brain stem (Chimoto et al. 1996; Keller et al. 2000; Raybourn and Keller 1977). Although it has not been directly demonstrated that collicular cells with eye-position activity combined with saccade vector activity project to this region of the brain stem, our distribution of collicular cells with combined eye-position and saccade-vector signals include cells with build-up and burst activity in the deep layers of the saccade-related region of the colliculus, a region that is known to project to brain stem preoculomotor neurons. Gating neurons like the omnipause neurons might facilitate the separation of these signals for downstream elements by restricting the availability of a collicular neuron's signal to a limited time frame (Keller 1974). The tonic inhibition provided by omnipause neurons would prevent signals existing only during the fixation interval from directly affecting, for example, saccadic burst neurons. Mechanisms for the discrimination of the different signals may also involve low-pass filtering, achieved with long membrane time-constants integrated at the level of single neurons (Koch 1999). In the case of the superior colliculus, the saccade vector signal is a high-frequency burst. Neurons with long membrane time constants can ignore high-frequency bursting activity and still respond to the low-frequency eye-position signal.

We have reported that the influence of eye position on the firing activity is stronger during fixation and weaker near the time of the saccade. The eye-position signal may be diminished during the saccade period, or alternatively, the eye-position signal may be present continuously but obscured by the saccade vector signal during the saccade period. The firing rates associated with eye-position sensitivity are weaker than the firing rates associated with saccades and thus might still be present during the saccade interval although not detectable by the methods used in this study.

Origin and functional significance of eye-position tuning

In this section, we consider both the origin as well as the potential role for an eye-position signal in the collicular contribution to oculomotor behavior. An eye-position signal is required for processing taking place both within the superior colliculus as well as in structures receiving collicular projections (Freedman et al. 1996; Mays and Sparks 1980b; Sparks and Mays 1983). There are a number of potential sources for an eye-position signal in the colliculus. Early studies in cats demonstrated that the colliculus receives proprioceptive eye-position signals from extraocular muscles (Abrahams and Anstee 1979; Abrahams and Rose 1975). In primates, the *nucleus prepositus hypoglossi*, the site of the neural integrator for horizontal eye movements (Cannon and Robinson 1987), has been shown to have a strong projection to the superior colliculus (Hartwich-Young et al. 1990). In addition, the colliculus receives a number of other inputs from the oculomotor brain stem that could provide an eye-position signal (Robinson et al. 1994; Scudder et al. 2002). Eye-position input to the superior

colliculus may also be derived from cortex via direct projections from parietal cortex, frontal, and supplementary eye fields to superior colliculus as well as by indirect projections from parietal and supplementary eye field cortex to frontal eye field and then to colliculus (Andersen et al. 1985, 1990, 1997; Colby and Goldberg 1999; Moschovakis et al. 2004; Paré and Wurtz 1997; Shook et al. 1990). Eye-position signals are also part of the output of the colliculus as demonstrated by Grantyn and Berthoz (1985), who showed that the activity of tectoreticulospinal neurons is related to eye position as well as head movement and is relayed to the brain stem eye-movement centers and to the spinal cord.

An eye-position signal is essential to the formation of a corollary discharge signal that maintains a record of current eye position. Early studies by Sparks and colleagues (Mays and Sparks 1980b; Sparks and Mays 1983) demonstrated that the saccade initiation command in the colliculus can be updated by an eye-position signal and that the colliculus has access to a corollary discharge signal related to eye position even in the absence of direct proprioceptive input following afferent nerve section (Guthrie et al. 1983). Recent work by Sommer and Wurtz (2002, 2004a) demonstrates that the pathway from superior colliculus back to the frontal eye field via the thalamic medial dorsal nucleus carries a corollary discharge signal, although it is unknown whether this signal includes eye position. Sommer and Wurtz (2004b) propose that a corollary discharge signal may be present within several cortical areas involved in oculomotor processing, including posterior parietal cortex where an eye-position signal is known to exist. Eye-position activity has also been demonstrated to be essential for multimodal integration taking place within the colliculus where eye position modulates the response to auditory signals in both monkeys (Jay and Sparks 1987) and cats (Populin et al. 2004).

Information about current eye position may not be essential for single saccades initiated from primary position, particularly when the head is held stationary as it is in many experimental setups. Although Robinson's original model of the oculomotor plant featured a feedback signal representing eye position (Robinson 1975), some recent models of the saccadic system have eliminated eye position as an essential component (see for example Gancarz and Grossberg 1998). Nevertheless, once fixation is moved away from primary position, and particularly when gaze movements combining eye and head components are made, an eye-position signal becomes essential.

It is likely that eye-position signals are used to plan sequences of multiple saccades (Li and Andersen 2001; Walker et al. 1995). The use of corollary discharge signals in the performance of a double-step saccade task has been demonstrated by reversible inactivation studies (Li and Andersen 2001; Sommer and Wurtz 2004a,b). Sommer and Wurtz reported that delay period activity is filtered by the thalamic medial dorsal nucleus and that only visual and peri-saccadic activity is relayed to the frontal eye field. Thus an eye-position signal might be removed from the collicular feedback to the frontal eye field. In posterior parietal cortex, eye-position signals have been shown to combine with saccade vector signals to form gain fields (Andersen et al. 1985, 1987; Mullette-Gillman et al. 2005; Schlack et al. 2005). In addition, reversible inactivation of the lateral intraparietal area (LIP) leads to a more severe deterioration in performance of the double saccade task than is found from inactivation of the MD

input to the frontal eye field, and the magnitude of this deterioration following LIP inactivation is related to the eye position at the end of the first saccade and not the saccade vector (Li and Andersen 2001; Sommer and Wurtz 2004b).

As suggested by Van Opstal and colleagues (1995), a potential role for an eye-position signal in the colliculus might be to compensate for the variations in motor effort required to make a saccade as the eyes move away from primary position. For example, for the right colliculus, as eye position moves to the left, an increased motor signal is required to move the eyes a fixed displacement to the left, and as eye position moves rightward, less effort is required to generate the same movement. The colinear saccade vector and eye-position tunings that we report in this study are well-suited to this function. Although there is strong evidence to suggest that structures downstream of the colliculus are primarily responsible for this adaptation (Edelman and Goldberg 2002; Melis and Van Gisbergen 1996; Takeichi et al. 2005), it may be the case that the colliculus also plays a role in this process.

The eye-position sensitivity that we have described might also be accounted for by the "incomplete gaze hypothesis" put forth by Van Opstal and colleagues (1995). This hypothesis suggests that the eye-position sensitivity found in the superior colliculus reflects a head command that could not be executed while the monkey's head was restrained. In essence, the eye-position signal represents an error signal that would guide a head movement until the eyes are returned to the center of their orbits. If this was the case, a convenient way to organize separate representations for saccade vector and eye position in the colliculus would be for the two maps to be colinear. For example, the representation in rostral colliculus for the fovea and fixation would also correspond to a representation of primary position—the center of the oculomotor range, and a collicular site representing saccades directed up and to the right, would also represent eye positions that were up and to the right relative to primary position. Van Opstal and colleagues concluded that their data did not support this hypothesis because for almost 50% of the cells in their sample the saccade-vector and eye-position sensitivities were not colinear. In contrast, where we assessed eye-position tuning during intervals of fixation when the tuning strength was greater, we found that eye-position tuning and saccade-vector tuning were aligned for the vast majority of cells. Given this difference, our data give greater support to the incomplete gaze hypothesis than did the original findings of Van Opstal and colleagues. Further studies with head free or combined superior colliculus neuron and neck EMG recordings will be required to explore this possibility.

Eye-position signals may also be used to compute the relative contributions of eye and head movements to gaze shifts. Microstimulation at a single site in the superior colliculus can evoke gaze movements that consist of different relative contributions of eye and head movement with these contributions being dependent on the initial position of the eyes. This finding was first described in cats (Guitton et al. 1980; McIlwain 1986; Roucoux and Crommelinck 1976; Roucoux et al. 1980; Straschill and Rieger 1973) but was later shown to be true in monkeys as well (Cowie and Robinson 1994; Freedman et al. 1996; Segraves and Goldberg 1992). This suggests that a collicular eye-position signal may be used to adjust the relative contributions of eye and head to a particular gaze movement.

There are alternative hypotheses concerning how the colliculus might be involved in the control of movements of the eyes and head, and this bears on the degree to which a collicular eye-position signal might be involved in this process. In the gaze displacement hypothesis, a single gaze command is generated by the superior colliculus (Freedman and Sparks 1997). Although an eye-position signal may be used to separate a single gaze command into eye and head components, this input would be required downstream of the superior colliculus. A collicular eye-position signal might contribute only if it were contained in the output of the colliculus. In the separate channel hypothesis, separate eye and head commands are generated within the colliculus, requiring an eye-position input at the collicular level (Cowie and Robinson 1994). This proposed relationship to head movement planning is in agreement with a report by Corneil and colleagues (2002), demonstrating a link between fixation period activity of collicular neurons and the generation of head movements. Recently, Corneil and colleagues (2005) have proposed that eye and head commands are generated from a single source in the SC with the go signals of each effector triggered at different threshold levels. This model of head-movement initiation is in agreement with our findings in that it emphasizes the temporal dynamics of an eye-position signal. It also proposes that the initiation of a head-movement command can occur at times other than when the OPN inhibition is removed, corresponding to the time during fixation when our results suggest the eye-position signal is most evident in collicular activity. The issue of whether a single gaze command or separate eye- and head-movement commands are issued by the colliculus has not been resolved (Corneil and Elsley 2005; Freedman and Sparks 1997; Phillips et al. 1995; Scudder et al. 2002; Sparks et al. 2001); however, in either case, a collicular eye-position signal can contribute to this process either within the colliculus or in its efferent targets.

ACKNOWLEDGMENTS

We are grateful to R. Andersen, B. Breznen, B. Corneil, D. Ferster, and R. Ketner for helpful discussions concerning this work; J. Schall for suggesting the application of circular statistics to the data; A. Nitzke for participation in the preliminary fixation task experiments; the staff of Northwestern's Center for Comparative Medicine for animal care; Northwestern's Instrument Shop for machining; and the Dept. of Chemistry electronics shop for electronic hardware.

GRANTS

This work was supported by National Institutes of Health Grants EY-08212 and NRSA T32 GM-07737.

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