Cues to move increase information in superior colliculus tuning curves

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Li X, Basso MA. Cues to move increase information in superior colliculus tuning curves. J Neurophysiol 106: 690–703, 2011. First published May 18, 2011; doi:10.1152/jn.00154.2011.—Shifts in the location of spatial attention produce increases in the gain and sensitivity of neuronal responses to sensory stimuli. Cues to shift the line of sight have the same effect on sensory responses in a motor area involved in the control of eye movements, the superior colliculus. Evidence has shown that shifts of gaze and shifts of attention are linked, suggesting there may be similar underlying mechanisms. Here, we report on a novel way in which cues to move the eyes (top-down signals) can influence sensory responses of neurons by altering the variability of their discharge rate. We measured the spatial tuning of superior colliculus neuronal activity in trials with cues to either make or withhold saccadic eye movements. We found that tuning curve widths both increased and decreased, but that the information conveyed by the neuronal discharge about the stimulus increased with a cue to make a saccade. The increase in information resulted partly from decreases in the trial-to-trial variability of neuronal discharges for stimuli located at the flanks of the tuning curves rather than from increases in the discharge rate for stimuli located at the peak of the tuning curves. This result is consistent with theoretical work and provides a novel way for cognitive signals to influence sensory responses within motor regions of the brain.

saccades; movement preparation; attention; Fisher information; movement selection; action choice; signal detection; discrimination

The discharge rate of neurons is often well described by tuning curves, radially symmetric functions of particular stimulus parameters. In the visual system, neurons often discharge maximally for particular stimulus orientations and discharge with reduced vigor in response to orientations that differ from the optimal (Hubel and Wiesel 1959; Wurtz 1969). In the somatosensory system, the stimulus parameters include touch or pressure (Mountcastle 1957; Talbot et al. 1968). In the arm movement system, the parameters include movement force, velocity, or direction (Evarts 1981; Georgopoulos et al. 1986). Why neurons in so many brain regions have tuning curves remains an enigma (Salinas 2006). Nevertheless, a common theme in the literature is that when tuning curves are sharper, more information is available within the population. For example, as information is processed at increasingly higher levels within the auditory system, neurons show increasingly sharp tuning curves. The sharpening is associated with an increase in population coding accuracy (Fitzpatrick et al. 1997). A related idea found in the literature is that when an animal pays attention to or exerts effort toward a particular stimulus parameter, the neurons encoding that parameter develop shaper tuning curves (McAdams and Maunsell 1999a; Moran and Desimone 1985). Because this phenomenon is often correlated with better behavioral performance, it is considered that tuning curve sharpening enhances the ability of the population to encode the parameter (Spitzer et al. 1988). Thus, sharper tuning curves are considered to be better for a population code and ultimately for behavioral or perceptual accuracy.

Others have argued that it is difficult to know whether sharper is better because noise correlations among neurons (those trial-to-trial fluctuations in the spike counts from one neuron that predict trial-to-trial fluctuations in spike counts of a second neuron) are often unknown. As such, measuring only the width of tuning curves is an inadequate measure of the information contained within the population because it ignores the contribution of noise (Series et al. 2004). Therefore, a more thorough measure of information that includes a measure of noise or variability is required to determine whether changes in tuning curves convey better information for the population.

Here, we address the issue of tuning width and information content using the superior colliculus (SC) as a model system, since neurons in the SC are known to be involved in population coding (Sparks 1986; Sparks et al. 1976; Sparks et al. 1990) and SC neuronal activity is modulated by top-down signals (Basso and Wurtz 1998; Li and Basso 2005; Li and Basso 2008; Dorris and Munoz 1998). First, we asked whether providing a cue to make a saccadic eye movement influences the width of tuning curves of SC neurons. Second, we calculated the information content of tuning curves of visual responses in individual SC neurons using Fisher information and a threshold analysis based on signal detection theory. In so doing, we could determine the amount of information about the stimulus location for each SC neuron. Third, we asked whether providing a cue to make a saccadic eye movement influences the information conveyed by SC neurons. We then compared the change in information for individual neurons in saccade-cue and no-cue trials. We found that providing a cue to make a saccade resulted in sharper tuning curves for many SC neurons, but that many also had wider tuning curves. However, providing a cue to make a saccade increased the Fisher information conveyed by SC neurons regardless of the tuning curve width. A discrimination analysis confirmed that the thresholds of neurons in the “Go” condition were lower than those in the “NoGo” condition at the flanks. The increase in Fisher information resulted in part from decreases in the trial-to-trial variability of the discharge rates of neurons encoding stimuli at the flanks of the tuning curves. These results provide a novel way for cognitive signals to influence sensory responses within a motor region of the brain.
MATERIALS AND METHODS

Surgical procedures. For electrophysiological recording of single neurons and monitoring eye movements, cylinders and eye movement-measuring loops were implanted in three rhesus monkeys (Macaca mulatta) using procedures previously described (Li and Basso 2005, 2008). All experimental protocols were approved by the Institutional Animal Care and Use Committee of the University of Wisconsin (Madison, WI) and complied with or exceeded standards set by the Public Health Service policy on the humane care and use of laboratory animals.

Behavioral procedures. We used a real-time experimental data-acquisition and visual stimulus generation system (Tempo and Video-Sync, Reflective Computing) to create the behavioral paradigms and acquire eye position and single neuron data as previously described (Li and Basso 2005; Li et al. 2006). Visual stimuli appeared on a display with a native resolution of 1,024 × 768, operating at 60 Hz, and located at 51-cm distance from the monkeys. The visual stimuli were controlled by VideoSync software (Reflective Computing) running on a dedicated personal computer with a 1,024 × 768 VGA video controller (Computer Boards). Accurate timing was assured by a photocell placed on screen, which sent a TTL pulse to the personal computer within 1 ms.

Go/NoGo task. Monkeys were trained to make saccades or hold gaze based on a central cue at the fixation point (Fig. 1A). After the onset of a centrally located, white fixation spot for a random time of 1,000–1,500 ms, either a triangle or a square stimulus appeared in the response field (RF) of a SC neuron for a random delay of 800–1,000 ms. The fixation point then changed to a triangle or square cue. After another 800- to 1,000-ms delay, the cue changed back to the white fixation spot. Monkeys were trained to make saccades to the visual stimulus located in the periphery if the central cue appeared as a triangle (Go condition) or to remain holding gaze if the cue appeared as a square (NoGo condition). The triangle and square were iso-pixel and iso-luminant (2.17 cd/m²) and elicited statistically indistinguishable responses from SC neurons (Li and Basso 2005). Conditions were presented in interleaved blocks, ruling out the possibility that measured changes in neuronal activity resulted from fatigue or other motivational factors.

Data acquisition. Using the magnetic induction technique (Fuchs and Robinson 1966) (Riverbend Instruments), voltage signals proportional to horizontal and vertical components of eye position were filtered (8-pole Bessel, −3 dB, 180 Hz), digitized at 16-bit resolution, and sampled at 1 kHz (CIO-DAS1602/16, Measurement Computing). The data were saved for offline analysis using an interactive computer program designed to display and measure eye position and calculate eye velocity. An automated procedure defined saccadic eye movements by applying velocity and acceleration criteria of 20°/s and 8,000°/s², respectively. The experimenter verified the adequacy of the algorithm on a trial-by-trial basis and made adjustments as necessary. Single neurons were recorded with tungsten microelectrodes (Frederick Haer) with impedances between 0.3 and 1.0MΩ measured at 1 kHz. Electrodes were aimed at the SC through stainless steel guide tubes held in place by a plastic grid secured to the cylinder (Crist et al. 1988). A window discriminator (Bak Electronics) returned a TTL pulse for each waveform that met amplitude and voltage criteria. TTL pulses were sent to a digital counter (PC-TIO-10, National Instruments) and were stored with a resolution of 1 ms.

RF assessment and neuronal classification. We mapped the RF of SC neurons and assessed the center of the RF by listening for the neuronal discharge as a spot of light from a 9 × 9 location array array appeared on the screen. During the appearance of the spot, monkeys
maintained fixation centrally. In this array, the stimulus positions were separated by 1–2° depending on the size of the RF. Therefore, the error of the estimated center location was within 1 or 2°. To ensure accurate assessment of the border of a RF, the separation of the stimulus positions was increased until the array covered the RF. The edge of the RF was determined by the lack of neuronal responses to the stimulus. In the same way, we also assessed the center of the movement fields of neurons by having monkeys make saccades to the different stimulus positions. In general, the centers of the receptive and movement fields were aligned. Once the border and center of the RF were determined, the stimulus appeared along a vertical axis through the RF. The diameter of the RFs of all SC neurons recorded was >5°; 14 of 46 neurons had RF centers >5° vertically, and 32 of 46 neurons had RF centers between 0 and 5° vertically. For all the neurons, at least one to two stimulus locations appeared outside of the borders of the RF.

We classified neurons as buildup or visual tonic using the following statistical criteria (Li and Basso 2005, 2008). We computed a baseline interval (average discharge rate 200–0 ms before the onset of the stimulus), a visual interval (50–250 ms beginning at the stimulus onset), a delay interval (300–800 ms after the stimulus onset), and a saccade interval (−50 to 0 ms before the saccade onset). Using only correct Go trials, we defined buildup neurons as those neurons with a significantly greater activity in the delay interval compared with the baseline (t-test, P < 0.05) and a significantly greater activity in the saccade interval compared with the delay interval (t-test, P < 0.05). If a neuron had a visual response and a significantly greater level of activity in the delay interval than in the baseline interval (t-test, P < 0.05), but had no significant difference in activity between the saccade and delay intervals, we classified the neuron as visual tonic. Only data from buildup and visual tonic neurons contributed to this report. Based on the neuronal response properties and the depth of the recordings (between 1 and 3 mm from the SC surface), we are confident that these neurons were all within the intermediate and deep layers of the SC.

Data analysis. We used the data from the 50- to 250-ms visual epoch for quantification and normalization unless otherwise stated. This epoch was the first 200-ms visual response since the visual latency of SC neurons is ~50 ms. Statistical analyses and curve fits were performed using MATLAB 2007b. Standard parametric descriptive and inferential statistics were used [ANOVA and t-tests with modified Bonferroni corrections (Keppel 1991)]. If the data failed to pass normality tests, nonparametric statistics such as Wilcoxon signed-rank tests or Mann-Whitney U-tests were used.

We used a nonlinear least-square optimization procedure (MATLAB 2007b) to fit Gaussian functions \( f(x) \) to the neuronal discharge measured during the 50- to 250-ms epoch after the onset of the stimulus, as follows:

\[
f(x) = ae^{-\frac{(x - b)^2}{2\sigma^2}} + c
\]

where \( a \) is the amplitude of the Gaussian, \( \sigma \) is the SD, \( b \) is the mean, and \( c \) is the lower asymptote of the Gaussian. We used the SD as an estimate of the width of the tuning curve. We used the mean of the Gaussian function as the center location of the tuning curve and refer to this as the “actual center” of the RF. The empirical center of the tuning curve was the location identified by the RF mapping procedure described in the preceding text. The goodness of the fit was estimated by the percentage of variance explained (Carpandini et al. 1997; Heuer and Britten 2002). Only neurons with goodness of fits explaining >60% of the variance of the tuning curves in both conditions were included in the data analysis set. The majority of the neurons in our sample exceeded goodness of fits of 80%.

To determine the statistical significance of the parameters of fitted curves, we used a bootstrapping procedure adopted from McAdams and Maunsell (1999a). We created one data set by randomly choosing three trials from each of the stimulus locations. We then fitted a Gaussian function to the data to get one set of parameters [we chose three trials instead of one trial as done by McAdams and Maunsell (1999a) to ensure better fits]. By repeating this procedure 1,000 times, we obtained 1,000 sets of parameters for each condition. A Wilcoxon signed-rank test was applied to determine the significance of the differences between the parameters in the Go and NoGo conditions.

To compute the Fisher information contained in the tuning curve of the neurons in the Go and NoGo conditions, we adapted formulae used by others (Nover et al. 2005; Pouget et al. 1999). For one neuron and a specific stimulus location \( i \), the Fisher information \( (F_i) \) is as follows (see Fig. 3):

\[
F_i = \frac{R_i^2}{\sigma_i^2}
\]

where \( R_i \) is the derivative (slope) of the tuning function for location \( i \) and \( \sigma_i \) is the trial-to-trial variance of neuronal responses at location \( i \). For each location of each condition, we used the data from at least 10 correct trials, most commonly 15–20 trials. The number of stimulus locations could depend on the size and location of the RF for each neuron. However, this did not influence the results or conclusions since we compared relative rather than absolute changes in Fisher information between the Go and NoGo conditions.

We also calculated a measure of discrimination to determine whether neurons could discriminate the stimulus better in the Go condition compared with the NoGo condition. To do this, we adopted a method used by Snowden and colleagues (1992). We first fitted neuronal responses and neuronal response variances of individual neurons with the following power function:

\[
\text{variance} = x^{\text{response}^k}
\]

Only neurons showing significant correlations between log(response) and log(variance) \( (P < 0.05, \text{Matlab function Corrcoef}) \) in both conditions were included in the data set. We then simulated neuronal responses of an individual neuron at each stimulus location 1,000 times. These simulated responses were randomly picked from a Gaussian distribution with its mean at a neuronal response value from the neuron’s fitted Gaussian tuning curve \( (Eq. 1) \) and its SD as the square root of a corresponding variance, which was calculated by \( Eq. 3 \). We chose different locations along the tuning curve every 0.01° for the simulations and chose 40 criteria evenly distributed from 0 spikes/s to the neuron’s maximum response. For a certain criterion, we calculated the probability that the simulated responses were higher than the criterion to generate a neurometric function. Thus, for each neuron, a total of 40 neuromeric functions were created.

Every neurometric function yields a discrimination threshold. To do this, each function was fitted as follows:

\[
p = \gamma - (\gamma - \delta) \times \exp\left[\frac{-1 \times (d/\alpha)\theta}{\tau}\right]
\]

where \( p \) is the probability that 1,000 simulated responses were greater than the criterion, \( d \) is the distance of the stimulus to the center of a tuning curve, \( \alpha \) is the location at which \( p \) decreases 63.2% from the maximum to the minimum, \( \delta \) is the lower asymptote, and \( \gamma \) is the upper asymptote. The discrimination threshold was defined as the location in which the probability changed from 0.5 to 0.25 (Snowden et al. 1991). This yielded a group of discrimination thresholds for different stimulus locations.

RESULTS

We recorded 46 neurons from 3 monkeys while they performed a delayed, visually guided, Go-NoGo task (Fig. 1A; see MATERIALS AND METHODS). We classified 35 neurons as buildup neurons and 11 neurons as visual tonic neurons. Since visual tonic and buildup neurons showed similar tuning modulation in the task, we combined the data in this report.

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Because SC RFs are asymmetric along the horizontal plane (Cynader and Berman 1972; Ottes et al. 1986), it is difficult to accurately measure the width of the tuning curves along this axis. Additionally, some buildup neurons have “open” movement fields along the horizontal axis precluding an accurate measure of the RF border (Munoz and Wurtz 1995). For these reasons, we elected to measure tuning along a vertical slice through the RF (Fig. 1A). Neuronal responses were measured 50–250 ms after the onset of the visual stimulus for each stimulus position (Fig. 1B). Gaussian functions were fitted to the neuronal discharge data, and 97.8% of the median variance was explained by the Gaussian fits across the sample of 46 neurons. Such good fits indicate that vertical tuning curves of SC neurons can be considered approximately symmetric. Furthermore, 97.4% of the variance was explained for the fits of the Go data, whereas 98.1% of the variance was explained for the fits of the NoGo data. These result indicate that the fits were equally good for the data measured in both conditions of the experiment. We used the parameters of the Gaussian fits to quantify the properties of SC neuronal RFs.

Width changes of SC tuning curves. We first asked whether a cue to make a saccade altered the width of the tuning curves of SC neurons. Figure 1B shows raster plots and tuning curves from one example buildup neuron (see MATERIALS AND METHODS, RF assessment and neuronal classification). We chose three points in the Go condition and three points in the NoGo condition for illustration. The points marked as points 1, 2, and 3 in Fig. 1B show the mean of the neuronal discharge for the stimuli located close to the center of the RF (peak of the tuning curve) and on one of the edges of the RF (flanks of the tuning curve). The points marked as points 4, 5, and 6 in Fig. 1B show the neuronal discharge for the same stimulus positions in the NoGo trials. At $x = -1°$ (where $0°$ is the empirical center of the RF), the mean neuronal discharge rate measured in the visual interval of the Go trials was 120.0 spikes/s (Fig. 1B, point 1). This rate was higher than the neuronal discharge rate measured during the same interval on the NoGo trials (91.0 spikes/s; Fig. 1B, point 4). At $x = 2°$, the mean neuronal discharge rate measured in the visual interval of the Go trials was 81.0 spikes/s (Fig. 1B, point 2). This discharge rate was closer to the rate measured in NoGo trials for the same stimulus location (point 5) in Fig. 1B (90.0 spikes/s). When the stimulus was positioned further on the flank of the tuning curve ($x = 6°$; Fig. 1B, points 3 and 6), the neuronal discharge on Go trials was smaller than the discharge measured on NoGo trials (46.0 vs. 62.0 spikes/s). This observation is consistent with the idea that when a cue to make a saccade appears, the visual response of SC neurons shows an enhanced peak of the tuning curve and a reduction of activity at the flanks of the tuning curve (Fig. 1B, inset).

To determine whether the tuning curve of this neuron changed between the Go and NoGo conditions, the neuronal discharge data were fitted with Gaussian functions, and the parameters of the fits were measured. For the example neuron shown in Fig. 1B, the amplitude of the tuning curve ($a$ of the Gaussian function) increased 27.6%, from 68.7 spikes/s in the NoGo condition to 87.6 spikes/s in the Go condition. Similarly, the width of the tuning curve ($\sigma$ of the Gaussian function) decreased 4.24° in the NoGo condition to 2.43° in the Go condition. From this example neuron, we conclude that saccade cues can alter the tuning properties of SC neurons.

Note also that this example neuron showed a slight change in its preferred stimulus location. This observation was not consistent across our sample of neurons ($P = 0.47$, Wilcoxon signed-rank test; data not shown).

We fit all 46 of our SC neurons with Gaussian functions and measured the SD ($\sigma$) of each. Figure 2A shows the best-fit Gaussian function for each of the 46 neurons in the Go trials normalized to the NoGo trials, with lower asymptotes removed for display. Figure 2B shows the same for the NoGo condition. Across the sample of neurons in the Go condition, the tuning curves appeared sharper, although there was considerable vari-

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**Fig. 2. SC tuning curves differ in Go and NoGo trials.**

**A:** normalized discharge rate plotted against the vertical eccentricity of the stimulus location. The neuronal discharge measured in the visual interval in the Go condition was normalized to the activity measured in the visual interval of the NoGo condition. The curves show the fitted Gaussians.

**B:** same as in **A** for the discharge rate measured in the NoGo condition. The neuronal discharge on Go trials was smaller than the discharge measured on NoGo trials (46.0 vs. 62.0 spikes/s). This observation is consistent with the idea that when a cue to make a saccade appears, the visual response of SC neurons shows an enhanced peak of the tuning curve and a reduction of activity at the flanks of the tuning curve (Fig. 1B, inset).

**C:** frequency histograms of the width ratios between the Go and NoGo conditions. Only the width ratio for the neurons in which a Gaussian function provided good fits (the percentage of variance explained $>60%$; most are $>80%$) are shown ($n = 46$). The solid bars show the width ratio for neurons with statistically significant width changes between the Go and NoGo conditions (bootstrapping, $P < 0.05$). The open bars indicate neurons with no significant change in width. $n$, Number of neurons.
ability (cf. Fig. 2, A and B). To determine whether individual neurons had sharper or wider tuning curves in the Go condition compared with the NoGo condition, we plotted the ratio of the SD of the Gaussian in the Go condition to the SD of the Gaussian in the NoGo condition for each neuron (Fig. 2C). Width ratios of >1.0 indicate a widening of the tuning curve, whereas width ratios of <1.0 indicate a sharpening of the tuning curve. The solid bars in Fig. 2C show the SC neurons with statistically significant changes in SDs between the Go and NoGo conditions. The open bars in Fig. 2C show neurons without significant changes. Across the sample, 23 of 46 (50%) neurons had significantly smaller SDs in the Go condition compared with the NoGo condition (bootstrapping test, \( P < 0.05 \)), and 20 of 46 (43.5%) of SC neurons had significantly larger SDs in the Go condition compared with the NoGo condition (bootstrapping test, \( P < 0.05 \)); 3 of 46 neurons showed no change. Thus, the tuning curves of SC neurons are as likely to show sharpening as widening with cues to make saccades. Across the sample, neither the width change nor the amplitude change of the tuning curves between the Go and NoGo conditions were statistically significant (width: \( P = 0.823 \) and amplitude: \( P = 0.087 \), Wilcoxon rank-sum test).

**Fisher information and SC neurons.** In attention tasks, neurons in extrastriate cortex show increases, decreases, or little change in tuning curve width (Haenny et al. 1988; McAdams and Maunsell 1999a; Spitzer et al. 1988). Like these previous results, neurons in the SC also show increases, decreases, or little change in tuning curve width with a cue to make a saccade. Although decreases in tuning curve width are commonly considered to increase the accuracy of a population code, changes in tuning properties do not a priori indicate changes in information (Pouget et al. 1999). This is because changes in variability among neuronal discharge rates that might affect tuning would also result in changes in information content. However, information measures are not made routinely. Therefore, it remains unknown whether the changes in tuning properties observed previously or here in the SC correspond to changes in information conveyed by the neurons to the population.

To determine whether cues to make saccades change the amount of information conveyed by SC neurons, we calculated Fisher information for each stimulus position for each SC neuron in the Go and NoGo conditions. We hypothesized that Fisher information would increase in the Go condition compared with the NoGo condition regardless of whether the width of the tuning curve sharpened or broadened. We reasoned this because increases in information can occur independently of width changes if, for example, there are changes in the variance of the neuronal discharge rate. This is because tuning curve widths reflect the amount of overlapping inputs among neurons, which, in turn, is related to the correlated noise among neurons within a population. Therefore, we speculated further that the increases in Fisher information resulted from changes in the trial to trial variability of neuronal discharge rates. Below, we describe each of these results in turn.

We calculated Fisher information as described in MATERIALS AND METHODS and shown schematically in Fig. 3A. Fisher information is a way to calculate how well an ideal observer can estimate a stimulus given the neuronal discharge. Importantly, Fisher information takes into account the slope of a tuning curve and the variability in the neuronal discharges underlying the tuning curve. Therefore, the inverse of Fisher information is related to the amount of variability or the discriminability; higher information means less noise and higher discriminability. Figure 3B shows the Fisher information calculated for the different stimulus locations for one example buildup neuron. The neuron shown in Fig. 3B is the same neuron as shown in Fig. 1B. For this neuron, the Go tuning curve was sharper than the NoGo tuning curve (Fig. 1B, cf. black and blue curves). The biggest change of Fisher information between the Go and NoGo conditions occurred for stimulus positions -4 and 2°, on the flanks of the tuning curve. At the peak of the tuning curve, 0°, Fisher information changed

![Figure 3](http://jn.physiology.org/)

**Fig. 3.** Calculating Fisher information. A: example tuning curve showing how we calculated Fisher information. Each group of rasters is the set of trials measured for that stimulus location. In the rasters, each tick is an action potential and each row of ticks is a trial. The data points and fitted Gaussian function (see MATERIALS AND METHODS) are shown by the open circles and dashed gray line, respectively. The vertical line through the circles is 1 SE. The variance of the discharge rate measured across the trials provided an estimate of the variance \( \sigma^2 \) for each stimulus location (i). The thick black line indicates the derivative of the tuning curve schematically \( \sigma_i \). B: Fisher information of an example neuron plotted for each stimulus location for the Go (black line) and NoGo (gray line) trials. Fisher information was calculated for the 50- to 250-ms time interval after the stimulus onset. ML403 is a file identifier.
Fisher information differed little between the Go and NoGo conditions. The interesting finding was that for the stimulus position \(-4^\circ\), the mean discharge rate of the neuron in the Go condition was only slightly greater than the mean discharge rate in the NoGo condition (57.0 spikes/s in the NoGo condition and 54.0 spikes/s in the Go condition; Fig. 1B). Similarly, at the \(+2^\circ\) stimulus position, the mean discharge rate of the neuron in the Go condition was lower than the mean discharge rate in the NoGo condition (position marked 6, 90.0 spikes/s in the NoGo condition and 81.0 spikes/s in the Go condition; Fig. 1B). However, at both of these stimulus positions, the Fisher information was considerably larger in the Go condition compared with the NoGo condition (Fig. 3B). This result suggests that the change in the discharge rate alone cannot account for the changes in Fisher information. We explore this more fully below.

To determine whether changes in Fisher information were consistent across our sample of SC neurons, we aligned all tuning curves with their centers and normalized the stimulus eccentricities based on the SDs of tuning curves. A normalized stimulus eccentricity therefore equals its distance to the center of its RF divided by the SD of the RF. We then plotted the Fisher information for all neurons in our sample (Fig. 4). Figure 4A shows the calculated Fisher information (calculated from the 50- to 250-ms interval) in the Go condition for all neurons. Figure 4B shows the same for all neurons in the NoGo condition.

To compare these values directly across all neurons, we binned the data across eccentricity every 1 SD from \(-4.5\) to 4.5 SD, as shown in Fig. 4A (1–9 bins). We then normalized the Fisher information value to the maximum Fisher value computed in the NoGo condition for each neuron individually and plotted the median Fisher information values of each bin (Fig. 4C). Across the sample, the values of Fisher information for bins 3, 4, 6, and 7 (\(-2.5\) to 1.5 SD, \(-1.5\) to \(-0.5\) SD, 0.5 to 1.5 SD, and 1.5 to 2.5 SD) were greater in the Go condition than in the NoGo condition. In the other bins, in particular the center bin, which included the peak of the RF, the values of Fisher information differed little between the Go and NoGo conditions. To confirm this observation statistically, we plotted the Go Fisher information from bins 3, 4, 6, and 7 against the NoGo Fisher information for the same bins (Fig. 4D). Across the sample, the Fisher information was greater in the Go condition (median = 0.64) than in the NoGo condition (median = 0.52). This difference was statistically significant (Wilcoxon signed-rank test, \(P = 0.001\)). We also assessed the Fisher information change in an early visual epoch (50–100 ms) and a later visual epoch (100–250 ms). In both epochs, the differences in Fisher information between the Go and NoGo conditions were statistically significant (\(P = 0.026\) and 0.008, respectively). Thus, we conclude that a cue to make a saccade increases the information contained in SC tuning curves along the flanks and does not affect the information contained at the peak of the tuning curve or at locations beyond the tuning curve (outside of the RF). Importantly, the changes in information were independent of the direction of the change in the tuning curve, sharpening or widening. Figure 4E shows the ratio of the Fisher information in the Go condition to the NoGo condition plotted against the ratio of the width change in the Go condition to the NoGo condition for the flanking bins. The data points were distributed fairly evenly around a value of 1 along the horizontal axis. This indicates that the width changes in the two cueing conditions are equally likely to be sharpening as widening (\(P = 0.940\)). In contrast, more points lay above a value of 1 along the vertical axis than below, consistent with an increase in Fisher information (\(P = 0.001\)). This result directly shows that Fisher information increases largely for the flanking positions with a cue to make a saccade. This change occurred regardless of how the tuning curve changed, consistent with the idea that “sharper is not necessarily better” (Series et al. 2004).

Because the changes in Fisher information in the Go condition were small, we performed a second analysis to assess whether the changes in information were meaningful across the population. Using a method based in signal detection theory, we assessed how well the responses of SC neurons could discriminate whether the task was Go or NoGo. This ability is dependent on the rate with which a neuron discharges and the reliability of the discharge for each stimulus position in the different task conditions. We implemented a procedure to determine neurometric functions and calculated the thresholds of discrimination (see MATERIALS AND METHODS). Briefly, the relationship between the mean discharge and the variability of discharge was determined to be linear for 31 of 46 of the neurons in our sample, and discrimination thresholds were measured for these 31 neurons. An example is shown in Fig. 5 for a single neuron. Figure 5A shows the Go condition, and Fig. 5B shows the NoGo condition (only 10 neurometric functions are shown for clarity). For each of these neurometric functions, a threshold can be determined. The threshold as a function of stimulus position can then be plotted (Fig. 5C). This revealed two things. First, the lowest threshold occurred for stimulus positions slightly off the center of the tuning curve, in other words, on the flank of the curve. This is similar to what was found in middle temporal (Snowden et al. 1992). Second, a lower minimum threshold was found for the Go condition compared with the NoGo condition (cf. open circles and solid line).

Fig. 4. Fisher information across the sample. A: Fisher information plotted for each stimulus location for all the neurons in the Go condition. The stimulus positions were normalized to the widths (SD) of the best-fit Gaussian function to the neuronal tuning curves. Zero is the center/peak of the tuning curves. B: same as A for the NoGo condition data. The dashed lines show tuning for C. C: average Fisher information after being normalized to the maximum Fisher value in the NoGo condition for each neuron and each stimulus position. Data were binned over locations every 1 SD from \(-4.5\) to 4.5 SD, as indicated by the dashed lines (1–9) in A and B. Each circle is the median Fisher information across the sample in a 1 SD bin. \(n = 46\), but numbers of neurons in each bin may vary. D: Fisher information values (not normalized) for flanking bins 3, 4, 6, and 7 (\(-2.5\) to \(-1.5\) SD, \(-1.5\) to \(-0.5\) SD, 0.5 to 1.5 SD, and 1.5 to 2.5 SD) were greater in the Go condition than in the NoGo condition. The black line is the unity line. Fisher information values were significantly different between the Go and NoGo conditions (Wilcoxon signed-rank test, \(P = 0.001\)). E: ratios of Fisher information between the Go and NoGo conditions plotted against the ratios of the widths of neuronal tuning curves between the Go and NoGo conditions. The data points are taken from flanking bins 3, 4, 6, and 7 (\(-2.5\) to \(-1.5\) SD, \(-1.5\) to \(-0.5\) SD, 0.5 to 1.5 SD, and 1.5 to 2.5 SD, as shown in C). The two dashed lines represent no change (ratio of 1). Fisher information values in the Go condition were significantly larger than those in the NoGo condition (Wilcoxon signed-rank test, \(P = 0.001\)). Widths in the two conditions were not significantly different (Wilcoxon signed-rank test, \(P = 0.940\)).
triangles in Fig. 5C). In total, 19 of the 31 SC neurons showed lower minimum thresholds for the Go condition compared with the NoGo condition. We took the thresholds falling in flanking bins 3, 4, 6, and 7 and plotted histograms of the thresholds in the Go and NoGo conditions in Fig. 5D. The Go condition had significantly lower thresholds than the NoGo condition (P < 0.001, Wilcoxon rank-sum test). This result is consistent with the idea that SC population activity better discriminates the position of the stimulus in the Go trials compared with the NoGo trials, particularly for the flanking stimulus positions.

Fisher information and discharge variability. Fisher information depends on the slope of a tuning curve and the trial-
to-trial variability of the discharge rate across stimulus locations (see Eq. 2 in MATERIALS AND METHODS). We wanted to determine whether changes in variance of the discharge rate could contribute to the change of Fisher information. We were also interested in exploring changes in neuronal discharge rate variability because recent reports have suggested that shifting attention either has little or some influence on the discharge variance of extrastriate cortical neurons (McAdams and Maunsell 1999b; Mitchell et al. 2007).

Taking the data from the stimulus locations falling in bins 3, 4, 6, and 7 and using the epoch 50–250 ms after the onset of the visual stimulus, we calculated the median slope2 in the Go and NoGo conditions. Figure 6A shows the distribution of differences in slope2 between the Go and NoGo conditions for each stimulus location for all the neurons [(NoGo − Go)/(NoGo + Go)]. An index smaller than 0 indicates a higher slope2 in the Go condition and a sharpening of the tuning curve. A Wilcoxon signed-rank test of these data showed that the difference of the indexes between the conditions was significant (Wilcoxon rank-sum test, P < 0.001).

second analysis shows that the difference in Fisher information we observed was due, in part, to changes in the slope of the tuning curve between the Go and NoGo conditions. Next, we assessed the influence of changes in the variability of the neuronal discharge rate to the Fisher information. Using the same flanking bin data as used for the slope analysis, we found that the distribution of differences in the discharge variance had a slight rightward shift (cf. dashed and solid vertical lines in Fig. 6B). This indicates that the variances of the discharge rates were lower in the Go condition compared with the NoGo condition (P = 0.003, Wilcoxon signed-rank test).

It is well known that the variance of the discharge rate is correlated positively with the amplitude of the discharge rate (see also Fig. 8A). Therefore, it is possible that the decrease in the variances in the Go condition compared with the NoGo condition results from the overall lower discharge rate for stimuli appearing at the flanks of the tuning curves. To assess this, we plotted the discharge rates for the responses measured in bins 3, 4, 6, and 7. The median discharge rate was 25.0 spikes/s in the Go condition. In the NoGo condition, the median discharge rate was 27.9 spikes/s. These differences in
discharge rate between the Go and NoGo conditions were not statistically significant (Wilcoxon signed-rank test, \( P = 0.142 \)). The difference index we calculated also showed no significant difference between the Go and NoGo conditions (Wilcoxon signed-rank test, \( P = 0.077 \); Fig. 6C). Therefore, we conclude that the changes in Fisher information at the flanks of the SC tuning curves result mainly from changes in neuronal discharge rate variability and that changes in discharge rate contribute little, if at all, to the increase in information of the SC tuning curves in the Go condition compared with the NoGo condition.

Because we found changes in Fisher information as well as changes in tuning curves of SC neurons, and because we found no consistent change in response amplitude of SC neuronal activity (data not shown), we reasoned that the changes in the tuning curves of SC neurons and thus information must result mainly from changes in trial-to-trial variability. To explore the relationship between the discharge rate and discharge variance further, we plotted the trial-to-trial variance of the discharge rate measured in the 50- to 250-ms visual interval in the Go condition normalized to the same measurement in the NoGo condition against the stimulus position (Fig. 7A). Zero is the center of the RF for each neuron. Figure 7B shows the same for the variances measured in the NoGo condition. For most neurons, variances were greater in the center of the RFs and smaller at the peripheral locations, forming bell-shaped distributions. To assess the pattern of this result across the sample of neurons, we normalized the stimulus locations and binned the variances as we did in Fig. 4C. The mean and SE of the variance for each bin are shown in Fig. 7C. The black lines show the results for the Go condition, and the gray lines show the results for the NoGo condition. The trial-to-trial variance of the discharge rate in the Go condition was greater for the stimulus position located at the center of the RF than in the NoGo condition. In the other bins except the two tails (bins 1 and 9), the means of the trial-to-trial variance were smaller in the Go condition than in the NoGo condition (cf. black and gray lines; Fig. 7C). Discharge rates across stimulus positions followed a similar trend (Fig. 7D).

A comparison of the results shown in Fig. 7, C and D, showed that, although the overall pattern appeared similar, there was a small but important difference between the distributions in the Go and NoGo conditions. From the center to the periphery of the RF (peak to flank of the tuning curve), the decrease in variance was more robust than the decrease in the discharge rate in the Go condition. To make this point clear, we calculated the ratios of the mean and variances of the discharge rates between the Go and NoGo conditions using the same binning procedure as before (Fig. 7E). In bin 5, the center of the RF, a cue to make a saccade increased the variance of the discharge rate more than it increased the magnitude of the discharge (cf. gray and black circles at 0 in Fig. 7E). In the flanking bins (bins 2–4 and 6–8), a cue to make a saccade decreased the variance of the discharge rate.

Fig. 6. Changes of Fisher information result from changes in discharge variance and tuning curve slope. A: histogram of slope2 indexes \((\text{NoGo} - \text{Go})/(\text{NoGo} + \text{Go})\). Data were measured in the 50- to 250-ms time interval after the stimulus onset and were taken from the stimulus locations falling on the flanks of the tuning curves (bins 3, 4, 6, and 7). The black vertical line is 0, and the dashed vertical line indicates the median index value. An index smaller than 0 means a greater slope2 in the Go condition and thus a sharper tuning curve. This median value was statistically smaller than 0 (Wilcoxon signed-rank test, \( P = 0.009 \)). B: histogram of variance indexes. The format is the same as in A. The median index was significantly greater than 0 (Wilcoxon signed-rank test, \( P = 0.003 \)), meaning lower variances in the Go condition. C: same as in A for indexes of neuronal discharge rates. The differences were statistically indistinguishable (Wilcoxon signed-rank test, \( P = 0.077 \)).
more than it decreased the magnitude of the discharge (cf. gray and black circles in Fig. 7E).

To confirm this observation statistically, we plotted the ratio of the variance in the Go and NoGo conditions against the ratio of the discharge rate in the Go and NoGo conditions for the flanking bins for all neurons (Fig. 7F). In Fig. 7F, the points below the line (quadrants I–III) are those in which the variance ratio of the discharge rate was lower than the magnitude ratio of the discharge rate, indicating that the variance decreased more than the magnitude of the discharge rate in the Go condition.
condition compared with the NoGo condition. In quadrant II of Fig. 7F, the ratios of the discharge rate lie above the unity line and the ratios of variance lie below the unity line. These are the cases in which the discharge rate increased in the Go condition but the variance of the discharge rate decreased. For the cases lying in quadrant III, both the discharge rates and variances increased in the Go condition, but the variances increased slightly less than the discharge rates. Note, however, that only a few cases fell into this quadrant. A Mann-Whitney U-test across the sample confirmed that the ratio of the variances was significantly lower than the ratio of the discharge rates between the Go and NoGo conditions ($P = 0.038$). Thus, a saccade cue resulted in a decrease in the trial-to-trial variability of SC neuronal responses to visual stimuli. The decrease in variability was not linked to changes in neuronal discharge rates.

Since the effect shown in Fig. 7F was small, we also analyzed the relationship of the variance and discharge rate (Fig. 8). As shown in Fig. 8A, the spike variance was plotted against the spike count in a log plot. The data from the Go condition are marked in red, and the data from the NoGo condition are marked in black (Fig. 8A). Two power functions ($Eq. 3$) were fitted to the data. Although the powers of these two functions were not significantly different, the slope in the Go condition was slightly smaller than that in the NoGo condition, indicating a tendency for the variance to increase more slowly than the discharge rate in the Go condition compared with the NoGo condition. When we plotted the Fano factors in the NoGo condition against the Go condition (Fig. 8B), we found that the Fano factors in the NoGo condition were significantly higher than those in the Go condition (Wilcoxon sign-rank test, $P = 0.006$). The Fano factor was defined as the spike variance in a time period divided by the spike count in the same time period (in our case, the 50- to 250-ms epoch). This result confirmed that, across the sample, neurons in the Go condition had a systematically lower spike variance than neurons in the NoGo condition.

Epoch length and fisher information. Increasing the length of the epoch over which Fisher information is calculated has the effect of reducing the variability. Because longer epochs would also include more of the tonic activity of SC neurons, it also has the effect of reducing the mean discharge rate. We reasoned that comparing changes in Fisher information with increasing epochs might provide further insights into whether changes in variability underlie the changes in Fisher information. We calculated Fisher information at time epochs from 50–150 to 50–750 ms in 100-ms increments. In Fig. 9, we show only four time intervals in the Go condition. The normalization was based on the maximum value from the 50- to 150-ms epoch, and binning procedures were performed as previously described (see Fig. 4C).

Fisher information increased at the flanks of the tuning curves and changed little at the peak of the tuning curve with increasing epoch length (cf. thin and thick solid lines in Fig. 9A). Not altogether surprisingly, both the discharge rate and variance of the discharge rate for these positions decreased with increasing epoch length (cf. thin and thick solid lines in Fig. 9, B and C). However, the relative changes between the discharge rate and variance differed. For example, the normalized discharge rate in bin 4 from the 50- to 150-ms epoch to the 50- to 250-ms epoch decreased from 0.70 to 0.59. This is a 16% decrease (Fig. 9B, bin 4). For the same bin, the normalized variance decreased from 0.61 to 0.28. This is a 54% decrease (Fig. 9C, bin 4). This shows that the changes in information content of SC neurons occur because of changes in the trial-to-trial variability in discharge rates primarily for stimulus positions located on the flanks of the tuning curves. This result is consistent with the idea that regardless of overall shape changes in tuning curves the variance of discharge rates arising from nearby neurons are important parameters to consider for the information content of neuronal responses. Future multiple neuron recording experiments will tackle this hypothesis directly.

**DISCUSSION**

We investigated how cues to make saccades alter tuning properties of SC neurons. We found that SC neurons are as likely to show sharper tuning curves as broader tuning curves with a cue to make a saccade. Despite this lack of consistency, the information content of SC neurons increased with saccade cues, a finding consistent with theoretical predictions. An
important and novel finding was that the increase in Fisher information with saccade cues occurred for the stimulus positions along the flanks of the tuning curves. This was associated with a decrease in discrimination threshold. The increase in information did not occur because of increases in discharge rate as might be expected from reports of extrastriate cortex neurons in attention tasks. Rather, the increased information occurred most likely because of reductions in the trial-to-trial variability of the discharge rate in response to stimuli located at positions along the flanks of the tuning curve. This finding points to a novel way for top-down signals to interact with local interconnections and regulate sensory responses in motor areas. In addition to the known influence of top-down signals on the amplitude of neuronal responses and therefore the ability of neurons to discriminate sensory inputs, our results suggest that top-down signals also enhance the discrimination ability of neurons by altering the variability of discharge rates of nearby neurons.

Neurons in the SC are arranged in a topographic map so that different regions of the SC encode saccadic eye movements of different amplitudes and directions (Robinson 1972). The tuning properties of SC neurons are well characterized by Gaussian functions, which can be quite broad: averaging 20° in diameter (Edelman and Keller 1996; Edelman and Keller 1998). However, saccades are very precise movements often rivaling perceptual accuracy (McGowan et al. 1998; Vishwanath and Kowler 2003). Therefore, it is likely that individual saccades are coded by the activity of large populations of active neurons with overlapping inputs (Sparks 1986; Sparks et al. 1976; Sparks et al. 1990). How the SC population activity determines precise saccades remains a matter of investigation (Edelman and Keller 1998; Glimcher and Sparks 1993; Groh 2001; Van Gisbergen et al. 1987; Van Opstal and Kappen 1993; Van Opstal et al. 1990).

Our sample of SC neurons showed robust discharges of action potentials immediately before and during saccades. These neurons likely participate in saccade generation (Munoz and Wurtz 1995; Schiller and Koerner 1971; Sparks 1975; Wurtz and Goldberg 1972). These neurons also had strong visual responses. We found that the tuning of the visual responses of these neurons was altered by a cue to make a saccade. The alterations of neuronal tuning curves indicate that SC tuning properties are dynamic. The classic view is that the shape and dimension of RF of SC neurons are determined by the dendritic geometry of superficial layer SC neurons and their retinal inputs (McIlwain 1975). Through convergent connections with the intermediate layers, the superficial layer neurons convey their RF geometry to the intermediate-layer neurons. However, increasing evidence has revealed that RFs are dynamic. For example, RFs of SC neurons shift their preferred location during performance of memory-guided saccades (Stanford and Sparks 1994) and smooth pursuit eye movements (Keller et al. 1996). Attention alters the RF of extrastriate cortex neurons (Ben-Hamed et al. 1997; Ben Hamed et al. 2002). Indeed, some of the original experiments in the monkey
SC showed that selecting a target for a saccade could stretch the RF of SC neurons (Goldberg and Wurtz 1972; Wurtz and Mohler 1976). Furthermore, results from our previous work showed that SC neuronal activity is influenced even by a stimulus presented in the opposite visual field (Basso and Wurtz 1998). Thus, a number of lines of evidence, including the results presented here, challenge the notion that the RFs of SC neurons are static. This has important implications for understanding the population code (Deneve et al. 2001; Pouget et al. 1999).

Based on results obtained over two decades ago, it was thought that RFs shrink around the location of an attended stimulus (Moran and Desimone 1985). Implicit in this idea is that a better representation of the stimulus and better behavioral performance result when a more tightly tuned population of neurons is activated. Although models based on biased competition (Reynolds and Chelazzi 2004; Reynolds et al. 1999) and remapping (Connor et al. 1996; Connor et al. 1997; Olshausen et al. 1993) replaced the idea of shrinking RFs, the idea that sharper is better generally remains.

Studies looking at tuning properties in attention tasks have found mixed results. In V1, V2, and V4, most neurons show an enhancement of responses to optimal stimuli consistent with a sharpening of tuning width from an increased discharge at the peak of the curve. For example, 35.0% of V1 neurons, 39.0% of V2 neurons, and 45.0% of V4 neurons showed increases in discharge rates for a stimulus with the preferred orientation in an experiment comparing attended and unattended conditions (Motter 1993), consistent with a sharpening. Similarly, 31.5% of V1 neurons and 71.0% of V4 neurons showed increases in discharge rates for preferred orientation stimuli and sharper tuning curves with attention (Haenny et al. 1988). Subsequent studies using measures that take into account differences in baseline discharge of neurons found that only a small fraction of V4 neurons (9.0%) change tuning and as many sharpen as widen. The differences between the results are thought to result from differences in measurements of width. Using the same measure of width as used by McAdams and Maunsell (1999a), we obtained similar results in the SC as they did in V4: although most SC neurons showed changes, as many neurons showed sharpening as widening with a cue to make a saccade. Despite the inconsistency in width changes, V4 neurons are still able to better discriminate stimulus orientation on attended trials compared with unattended trials (McAdams and Maunsell 1999a). Our findings in the SC mirrored these results. We found that 50% of neurons had sharper tuning curve widths with saccade cues, whereas 43% of neurons had wider tuning curve widths in the saccade cue condition. Even with this lack of consistent sharpening of tuning curves, the information about the stimulus location conveyed by SC neurons was higher in trials with saccade cues compared with trials without saccade cues. The improved ability of SC neurons to identify the target arises from a mechanism that may be different from that reported previously in the cortex. Results from the V4 cortex showed that increases in discharge rate occur with attention, i.e., attention results in increases in signal discharge. The influence of attention on response variability ranges between 5% and 10% (McAdams and Maunsell 1999b; Mitchell et al. 2007). We find that a better ability to discriminate the target in SC neurons results from decreases in noise. Specifically, the decreases in noise occur along the flanks of the tuning curves. This indicates that a cue to make a saccade increases the certainty of the saccade target by increasing the reliability of the signals arising from nearby neurons consistent with more recent findings in extrastriate cortex (Cohen and Maunsell 2009). This change would have an effect on the identification of the saccade target, particularly when there are multiple possible targets activating overlapping neuronal populations. Future experiments in which we record from multiple neurons while monkeys make saccades in cluttered visual fields will be required to test this hypothesis definitively. Experiments using multiple neuron recording will also allow us to measure the covariance between neurons (Series et al. 2004) to test these ideas definitively.

Our equation for Fisher information (see MATERIALS AND METHODS) was adopted from Pouget et al. (1999). Fisher information is inversely proportional to the square of the discriminability. In the cortex, the increase in discriminability is attributed to the increases in discharge associated with the preferred stimulus. Variability is not altered with attention (McAdams and Maunsell 1999b). When assessing variability by comparing spike count to spike variance relationships in the cued and uncued conditions, we also found no change in neuronal discharge reliability (see Fig. 8A), suggesting this measure is insufficiently sensitive. A pairwise comparison of the Fano factors is more sensitive (Fig. 8B) and revealed that the Fano factors were decreased in the Go condition. The additional benefit of using Fisher information is that it provides a measure of discriminability for each point along the tuning curve, something that is missed by comparing the count versus variance relationship. It is unclear whether the differences in the SC and V4 result from true differences in how top-down signals influence activity in sensory areas versus motor areas or whether the differences arise from differences in the measurement of information. Regardless, the modulation of variability in discharge rate along the flanks of tuning curves is an important way for top-down signals to influence the representation of targets for saccades.

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DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author(s).

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