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Context dependence of receptive field remapping in superior colliculus

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Churan J, Guitton D, Pack CC. Context dependence of receptive field remapping in superior colliculus. *J Neurophysiol* 106: 1862–1874, 2011. First published July 13, 2011; doi:10.1152/jn.00288.2011.—Our perception of the positions of objects in our surroundings is surprisingly unaffected by movements of the eyes, head, and body. This suggests that the brain has a mechanism for maintaining perceptual stability, based either on the spatial relationships among visible objects or internal copies of its own motor commands. Strong evidence for the latter mechanism comes from the remapping of visual receptive fields that occurs around the time of a saccade. Remapping occurs when a single neuron responds to visual stimuli placed presaccadically in the spatial location that will be occupied by its receptive field after the completion of a saccade. Although evidence for remapping has been found in many brain areas, relatively little is known about how it interacts with sensory context. This interaction is important for understanding perceptual stability more generally, as the brain may rely on extraretinal signals or visual signals to different degrees in different contexts. Here, we have studied the interaction between visual stimulation and remapping by recording from single neurons in the superior colliculus of the macaque monkey, using several different visual stimulus conditions. We find that remapping responses are highly sensitive to low-level visual signals, with the overall luminance of the visual background exerting a particularly powerful influence. Specifically, although remapping was fairly common in complete darkness, such responses were usually decreased or abolished in the presence of modest background illumination. Thus the brain might make use of a strategy that emphasizes visual landmarks over extraretinal signals whenever the former are available.

macaque; single unit; reverse correlation

HUMANS AND OTHER PRIMATES frequently make fast eye movements known as saccades, each of which introduces an abrupt shift of the retinal image. Despite these fast changes in retinal stimulation, the resulting perception remains continuously stable. This suggests the existence of neuronal mechanisms that are able to connect the presaccadic and the postsaccadic visual images to a percept of a stable world.

There are several mechanisms that might contribute to the maintenance of such perceptual stability. During naturalistic viewing conditions, the brain might maintain a representation of the positions of objects relative to one another, a metric that would be unaffected by eye movements. Alternatively, the visual system might keep track of impending eye movements by monitoring oculomotor commands known as corollary discharges (Sperry 1950). Such signals would duplicate those sent to the structures that move the eyes, and they could be used by visual structures to interpret the retinal stimulation caused by saccades.

One of the most dramatic examples of the influence of corollary discharge signals on visual processing is the remapping of visual space that occurs around the time of a saccade. During remapping, the positions of visual receptive fields (RFs) shift before the start of the saccade to the spatial location that they will occupy after the saccade. This mechanism is thought to provide a more continuous representation of the retinal scene in the face of the abrupt spatial and temporal changes brought about by each saccade. Remapping was first observed in the lateral intraparietal area (LIP) (Duhamel et al. 1992) and subsequently in other areas, including the superior colliculus (SC) (Dunn et al. 2010; Walker et al. 1995), the frontal eye field (FEF) (Sommer and Wurtz 2002; Umeno and Goldberg 1997, 2001), and the visual cortex (Nakamura and Colby 2002; Tolias et al. 2001).

Because remapping is triggered by a corollary discharge signal (Sommer and Wurtz 2002), one might expect it to occur in a manner that is largely independent of the details of the retinal stimulation. Indeed, this would seem to be a necessary condition for remapping to be useful for maintaining perceptual stability in natural environments. However, most studies of remapping have used a paradigm in which a stimulus consisting of a single probe is presented against a dark background. These studies have revealed the existence and time course of remapping, but it remains unclear how these results generalize across different visual conditions. In particular, the average luminance of the stimulus, as well as the contrast between the probes and the background, may be of relevance, as the influence of oculomotor signals on visual perception has been shown to be mediated by stimulus luminance and contrast (Georg et al. 2008; Michels and Lappe 2004; Richard et al. 2009). To address this issue, we have investigated perisaccadic remapping in the SC of the macaque monkey using two different manipulations of the visual stimulus. In the first, we presented many probes simultaneously as part of a sparse noise stimulus of the kind that is often used to map visual cortical RFs (e.g., Jones and Palmer 1987; Livingstone et al. 2001; Pack et al. 2006; Ringach 2004; Szulborski and Palmer 1990). A second stimulus manipulation involved variations of the standard remapping paradigm (Duhamel et al. 1992; Sommer and Wurtz 2002; Umeno and Goldberg 1997, 2001; Walker et al. 1995), in which we presented a single probe and varied the overall luminance of the visual scene.

Surprisingly, both manipulations led to sharp reductions in the frequency of remapping responses. Thus although we were able to replicate previous findings using the standard paradigm (Walker et al. 1995), we did not find that remapping generalized across variations in visual structure or background luminance. One possible explanation for our results is that remapping in the SC occurs only under conditions in which visual references are unavailable, suggesting that the brain uses different strategies to maintain visual stability under different conditions.

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MATERIALS AND METHODS

Physiological Procedures

Two adult male rhesus monkeys took part in the experiments. Each monkey underwent a sterile, surgical procedure to implant a headpost and recording cylinder over the SC, as described in detail elsewhere (Choi and Guitton 2006). The eye position was recorded by a video eye-tracker (EyeLink 1000, SR Research, Kanata, Ontario, Canada) for one monkey and by an implanted scleral eye coil (Robinson 1963) for the other monkey; the sampling rate for both systems was 1,000 Hz. After a postoperative recovery period, the monkeys were seated in a primate chair (Crist Instruments, Hagerstown, MD) and trained, head-fixed to keep fixation and make visually guided and delayed saccades toward stimuli presented on a screen. All procedures were approved by the Animal Care Committee of the Montreal Neurological Institute (McGill University, Montreal, Canada) and were in compliance with regulations established by the Canadian Council of Animal Care.

The SC was identified based on an anatomical, functional MRI scan, as well as the physiological pattern of visual and saccade-related neuronal responses. To obtain a substantial number of neurons from the deeper layers, where remapping neurons were observed to be more frequent (Walker et al. 1995), in ~40% of the penetrations, we pushed the electrode through all collicular layers until the typical visual and saccade-related activity disappeared. We then retracted the electrode until we reached visuomotor layers again, and from this deep position, we started the recordings.

Recordings were performed using tungsten microelectrodes (FHC, Bowdoin, ME) with a typical impedance of ~2 MΩ. The signal was sampled at 40 kHz. Single units were identified online and later re-sorted offline using spike-sorting software (Plexon, Dallas, TX).

Behavioral Paradigms

We studied the remapping phenomenon using two distinct experimental approaches: *1*) sparse visual noise in conjunction with a reverse correlation analysis and *2*) a variant of the standard remapping paradigm of Duhamel et al. (1992). In each case, the stimuli were generated using a Pentium III personal computer at a spatial resolution of 800 × 600 pixels and a presentation frame rate of 85 Hz. The frames were programmed in Matlab v7.0 using the Psychophysics Toolbox (Brainard 1997; Pelli 1997) and back-projected on a semi-transparent screen by a cathode ray tube video projector (Electrohome Marquee 8000). The screen covered an area of 80 × 50° of visual angle at a viewing distance of 78 cm.

In each paradigm, the monkey was required to direct gaze to within ±2.5° around the fixation point (FP) or saccade target (ST) to obtain a small amount of water or juice at the end of each trial.

Sparse noise-mapping task We initially used a sparse noise paradigm to map RFs during saccadic eye movements. In this paradigm, one delivers rapid sequences of visual stimuli, such that all relevant spatial and temporal positions can be explored during the course of a single experiment. Our adaptation of the stimulus included a ST that changed position often, so that RFs could be mapped at different time periods relative to each saccade. As detailed below, this paradigm differs from the standard one used to study remapping in that it probes many stimulus locations simultaneously, and it raises the overall luminance of the visual scene.

The sparse noise stimulus consisted of 50% black (<0.001 cd/m^2) and 50% white (30.5 cd/m^2) squares presented at random positions on a gray background (7.0 cd/m^2; Fig. 1*A*). The positions of the black and white squares were changed randomly at the frame rate of 85 Hz. The size of the squares and the percentage of the screen covered by the stimuli were adjusted individually for each neuron to obtain strong visual responses. Across recordings, the size of the squares varied between 1° and 5° (side length), and they covered between 2% and 5% of the screen area; typical values were a size of 3°, covering 4% of the screen. The monkey made visually guided saccades to small (~10-ft arc) red targets that appeared on the flickering background. For most neurons, the distribution of possible ST positions (Fig. 1*A*) was arranged as a square, with the next target appearing either at the adjacent horizontal or the adjacent vertical position to the current fixation (for an animated example of the stimulus, see Supplemental Video). In this way, the direction of the next saccade was not predictable before the ST appeared. We also tested a population of neurons on a task in which only two target locations were used. In this case, the direction (left or right) and amplitude of the next saccade were thus fully predictable.

The amplitude of the saccades in each recording was constant, but it varied between 10° and 20° in different recordings. There was a random 400- to 1,200-ms fixation period required after each saccade before the next ST was presented. Typically 2,000–3,000 trials were collected during each recording session.

Single-probe remapping task The task we used to probe spatial remapping around the time of saccades was very similar to the standard task used for the same purpose in the SC by Walker et al. (1995). The spatial and temporal layouts of the paradigm are described in Fig. 2. The monkey made 20° visually guided saccades directed to a ST located in the visual hemifield ipsilateral to the recorded neuron. This position had the advantage that SC motor activity did not interfere with visual responses. A visual probe (square size 30 arcmin, luminance 29 cd/m^2) was flashed for 59 ms (five frames) simultaneously with the onset of the ST. The probe was presented either in the visual RF of a neuron (RF condition) or in the future field (FF), the position where the RF would be after the saccade (FF condition). The spatial position of the FF probes was, in most cases, in the ipsilateral visual hemifield, whereas the RF was in the contralateral visual hemifield. This spatial arrangement has been described as "across remapping" (Dunn et al. 2010). To characterize visual responses that occurred independent of saccades, we also performed controls in which the visual probe was presented in either the RF or FF during fixation. To measure purely motor responses, we performed an additional control in which saccades were made to the ST without the presentation of a visual probe. All saccade conditions were randomly interleaved, and at least 15 trials were recorded for each condition.

To explore the effects of background luminance on remapping, we carried out each of the single-probe experiments at one of three different levels of background screen illumination: *1*) white stimuli on a completely dark background (background luminance, <<0.01 cd/m^2); *2*) white stimuli on a low-luminance background (background luminance, ~0.03 cd/m^2); *3*) black stimuli on a white background (background luminance, ~29 cd/m^2). Room lights were extinguished for all experiments.

Delayed saccade task To determine the visual and motor responses of each neuron, we obtained data in a delayed saccade task. For this task, the monkey had to fixate a spot at the center of the screen, while a ST was presented at one of 32 randomly interleaved positions [four amplitudes (5°, 10°, 15°, and 20°) and eight directions covering the contralateral as well as the ipsilateral visual hemifield]. Following the appearance of the ST, the monkey had to maintain fixation for another 300–700 ms until the FP disappeared, after which, the saccade was executed. After the saccade, the monkey had to keep fixating on the ST for another 300–500 ms to get a reward.

Data Analysis

The procedures used for analysis of the remapping data as well as for the calculation of the kernels for reverse correlation were written in MATLAB (MathWorks, Natick, MA).

Sparse noise mapping. Kernels were calculated as the spike-triggered averages (STA) of stimuli consisting of probes presented at different spatial positions (x, y) and at different latencies (τ) relative to the spike

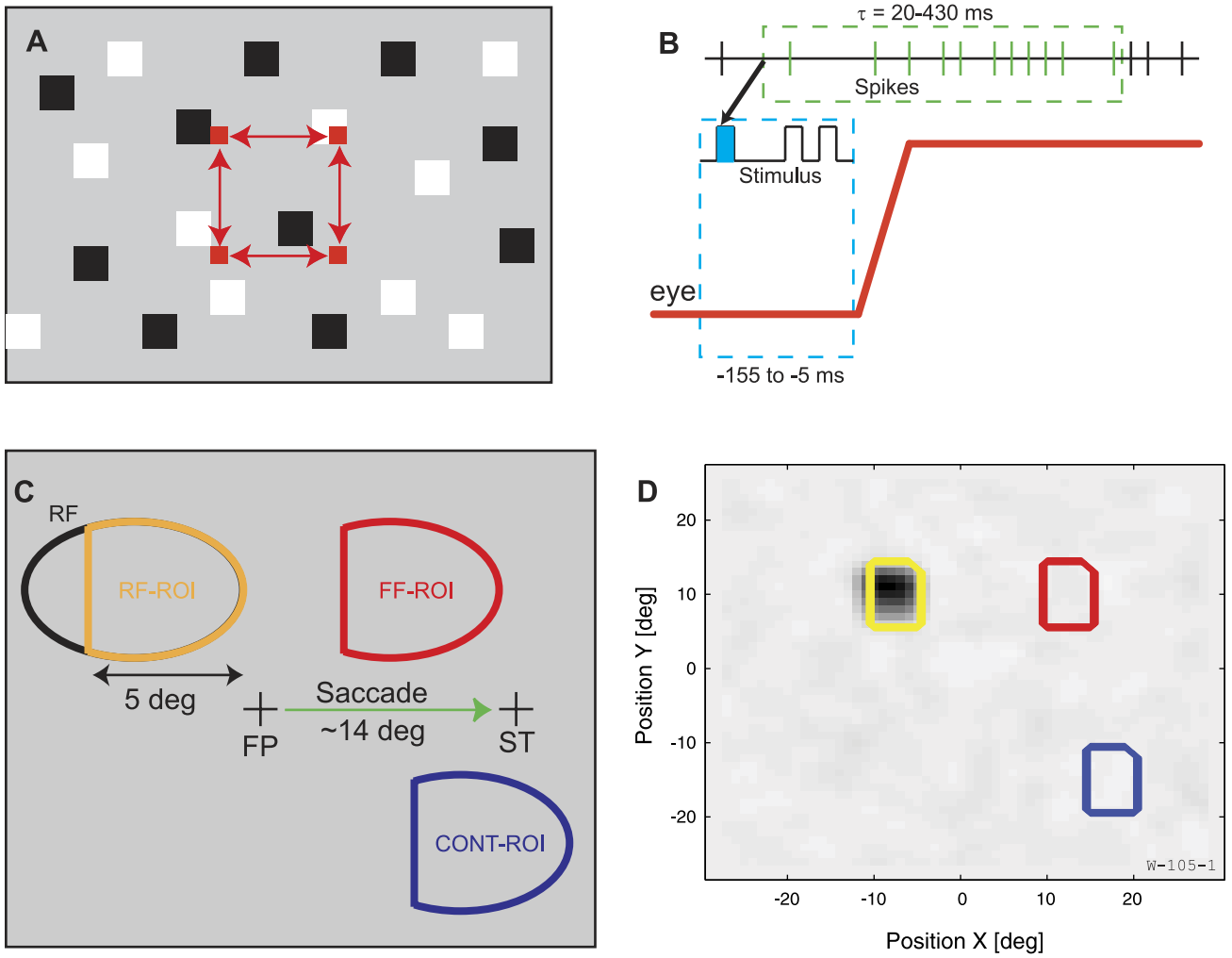

Fig. 1. *A*: spatial layout of the sparse noise-mapping task. The monkey made saccades (red arrows) to visual targets (red squares) presented over a flickering background, which consisted of a sparse pattern of black and white rectangles changing position randomly at 85 Hz. After a fixation period of 400–1,200 ms, the fixation point (FP) disappeared, and a new saccade target (ST) appeared to trigger either a horizontal or a vertical saccade. In some configurations, only 2 alternate STs were presented, triggering horizontal leftward and rightward saccades (not shown in this figure). *B*: stimuli presented in a time window between 155 ms and 5 ms before saccade onset were correlated with spikes that occurred with a latency (τ) of 20–430 ms after the stimulus. *C*: perisaccadic changes in visual responses were measured only for saccades directed into the visual hemifield ipsilateral to the recording site. Three regions of interest (ROIs) were defined: receptive field (RF)-ROI consists of the 5° of the RF positioned toward the direction of the saccade (orange). To obtain the future field (FF)-ROI (red), the RF-ROI was shifted by the vector of the saccade. As a control, the CONT-ROI (blue) was obtained by shifting the RF-ROI to a position far outside of RF and FF. *D*: positions of the different ROIs for 1 example neuron are shown as overlays on a spatial map of visual responses. The RF-ROI (yellow) is shifted according to the vector of the saccade (20° rightward) to obtain the FF-ROI (red). The control field (blue) is placed far from RF-ROI and FF-ROI. Strong responses to stimuli presented 155–5 ms before a saccade were found in RF-ROI but not in FF-ROI or in CONT-ROI.

$$STA(x, y, \tau) = \frac{\sum_{i=1}^{n} \left| s(x, y, t_i - \tau) \right|}{n} \quad (1)$$

Here, s is the sparse noise stimulus, and n represents the number of recorded spikes. The spatial position (x and y) was sampled at a resolution of 1°, and the τ was sampled in steps of 5 ms within the range 20–430 ms. The absolute value in the numerator indicates that we treated white and black stimuli as equal for the purposes of the analysis. This was based on our observation that the responses to black and white stimuli were generally very similar when the RFs were estimated separately for black or white stimuli.

The STA represents the average stimulus preceding each spike by a certain delay. This average, in turn, depends on the density of the sparse noise stimulus (Dayan and Abbott 2001), which as mentioned above, varied across recordings. Thus to compare this STA across neurons for which the density $\bar{s}$ of the sparse noise stimulus differed, we normalized the STA according to

$$STA_n(x, y, \tau) = \log_2\left(\frac{STA(x, y, \tau)}{\bar{s}}\right) \quad (2)$$

Here, a STA_n, at a certain position in space and time (x,y,τ) with a value of 0, represents a response that would be expected to occur randomly, whereas $STA_n(x,y,\tau) > 0$ indicates an activation of the neuron by the stimulus, and $STA_n(x,y,\tau) < 0$ indicates suppression by the stimulus.

We next estimated each neuron's RF by finding the parts of visual space in which visual stimuli elicited significant responses during fixation. This involved first estimating a baseline STA_n by calculating for each neuron a STA_n in which the order of visual inputs was shuffled randomly. This procedure was repeated 100 times, yielding a distribution of controls for the STA_n. We considered a pixel to be significantly activated if its STA_n value was above the mean + 2 SD of this baseline STA_n. As this statistical criterion is based on individual pixels, it is insufficient to determine the position of the RF. To determine the RF for each neuron, we used the size of clusters of

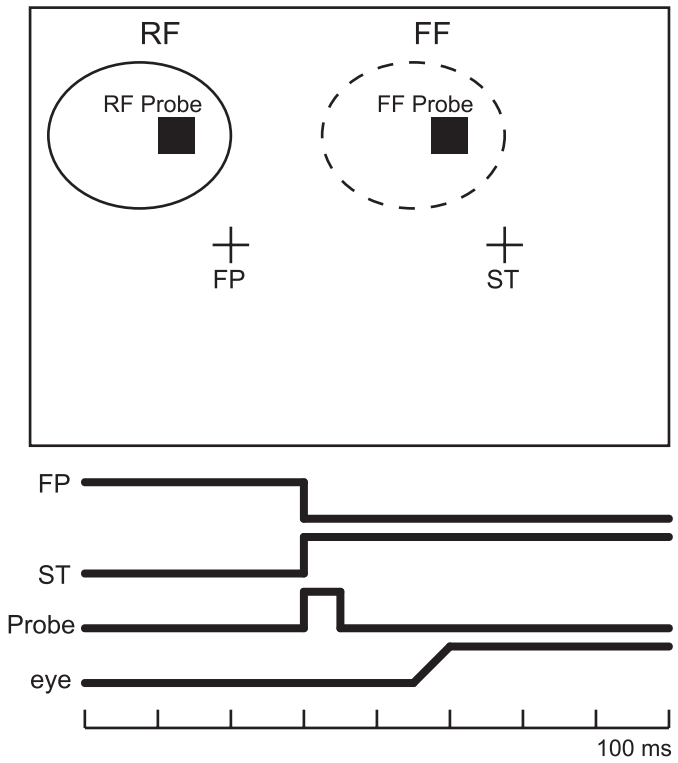

Fig. 2. Sketch of the different conditions in a saccade trial in the single-probe remapping task. After a random (300–700 ms) period of fixation, the FP disappeared, and a ST appeared, typically 20° in the periphery. A visual probe (luminance, 29 cd/m^2) was flashed at the same time for 59 ms either in the RF or in the FF of the neuron. In one control condition, saccades were performed without the presentation of a visual probe. In another control condition, probes were presented in RF or FF during fixation without saccades. Conditions were randomly interleaved.

adjacent, above-threshold, space-time data points as a second criterion. We calculated the sizes of these clusters using the real data and compared them with the cluster sizes obtained from the 100 random baseline samples of the STA$_n$. Clusters in real data with a size larger than 95% of the largest cluster sizes, found when baseline STA$_n$ were used, were considered to be RFs.

To estimate the perisaccadic responses, we calculated the STA$_n$, including only stimuli that were presented in a time window between 155 ms and 5 ms before a saccade (Fig. 1*B*), a time period for which strong remapping was observed in previous studies (e.g., Kusunoki and Goldberg 2003; Walker et al. 1995). Note that intervals (τ) between stimulus presentation and response ranged between 20 ms and 430 ms, which included spikes in the epochs during and after the saccade, when the majority of remapping responses was found (see Fig. 5*E*). We then defined the perisaccadic spatial RF map using the maximal STA$_n$ at each spatial position over the whole range of τ (20–430 ms). We did this to account for the large variability of latencies that has been reported for remapping responses (Nakamura and Colby 2002; Umeno and Goldberg 1997; Walker et al. 1995; see Fig. 5*E*).

To generate predictions about RF remapping, we used data from the fixation condition to compute spatial region-of-interest (ROI) masks. These were used to examine perisaccadic activity at different spatial positions in the visual field (Fig. 1*C*). Three different ROIs were used: *1*) RF-ROI represents the RF location obtained during fixation. We restricted this region to the 5° on the side of the RF facing the direction of the saccade to ensure that the RF-ROI and the FF-ROI did not overlap, even for the smallest saccades used in the experiment (10°); *2*) FF-ROI is the RF-ROI area shifted in the ipsilateral direction by the saccade vector; *3*) CONT-ROI, used as a control, is the RF-ROI area shifted to a visual field position outside of the RF, as well as outside of the FF area.

Within each ROI, we expressed the response as the average of all of the corresponding pixel values.

The spatial arrangement of the different ROIs is shown in Fig. 1*D* for one example neuron. These ROIs were calculated for rightward saccades 20° in amplitude. For this analysis, we used only ipsiversive saccades to minimize the influence of motor signals on the visual responses.

Single-probe remapping task. We calculated the baseline activity from all different trial types in one experimental block in a time window between 200 ms before and 20 ms after the onset of the visual probe and/or the ST. The peristimulus time histogram (PSTH) was calculated in a time window between 30 ms and 550 ms after the onset of the probe by convolving each spike with a one-half Gaussian (SD, 30 ms) and averaging the sum of these one-half Gaussians across all trials. A one-half Gaussian rather than a full Gaussian was chosen to provide a veridical estimate of the response latency (Seth 2008). A significant response was defined by a significant ($P < 0.05$, *t*-test) increase of activity above baseline in a time window of at least 30 ms duration. As a measure of the strength of response to the visual probe, we calculated a continuous sensitivity index (d') value

$$d'(t) = \frac{act_{PSTH}(t) - act_{Base}}{\sqrt{\frac{std^2_{PSTH}(t) + std^2_{Base}}{2}}} \quad (3)$$

where $act_{PSTH}(t)$ is the continuous peristimulus activity, act_{Base} is the baseline activity, and $std_{PSTH}(t)$ and std_{Base} are the intertrial SDs of the peristimulus activity and the baseline activity, respectively.

The maximal d' in a time window between 30 ms and 550 ms after onset of the probe was used as an indicator of the detectability of the visual probe in the different experimental conditions. The latency of the neuronal response was defined as the onset of a significant response as described above.

Classification of neurons. After excluding neurons that lacked visual responses, we performed further analysis on 216 neurons (136 from *monkey 1*; 80 from *monkey 2*), recorded using the sparse noise paradigm, and 140 neurons (59 from *monkey 1*; 81 from *monkey 2*), tested with the single-probe paradigm. For comparison with previous literature, these neurons were then further categorized qualitatively as being either purely visual or visuomotor, the latter having distinct visual and motor responses in the delayed saccade paradigm. For some of the neurons, we lacked sufficient data to perform the categorization. A breakdown of the cell types used in each experiment is provided in Table 1.

Although we have not attempted to reconstruct our electrode tracks, it is likely that most of our recordings came from the intermediate layers of the SC. As mentioned above, we targeted these layers in most penetrations, and most of the neurons for which classification is possible were visuomotor (Table 1). The few purely visual cells included in the analysis were generally found at roughly the same depth as these visuomotor neurons, despite the fact that most purely visual neurons are located in the superficial layers (Goldberg and Wurtz 1972). It is possible that some or all of these visual neurons were "quasivisual" cells (Mays and Sparks 1980), which only reveal their motor contributions in a double-saccade task.

Table 1. *Classification of cell types and numbers of remapping neurons found in each cell type using the two paradigms*

	Sparse Noise	Single Probe
Visual	0/17 (0%)	7/14 (50%)
Visuomotor	0/151 (0%)	21/83 (25%)
Visual or Visuomotor	0/48 (0%)	8/43 (19%)
Total	0/216 (0%)	36/140 (26%)

RESULTS

Our goal in these experiments was to examine the sensitivity of RF remapping in the SC to visual conditions. We first studied remapping using a sparse noise paradigm, in which many probes were presented simultaneously as the monkeys made visually guided saccades. We then tested the effects of overall luminance and stimulus contrast in the context of a more standard, single-probe paradigm.

Sparse Noise-Mapping Paradigm

In the sparse noise-mapping paradigm, monkeys executed saccades to follow a sequence of targets, while random visual stimuli were presented in the background (Fig. 1*A*). Saccades were interspersed with periods of fixation, during which, the statistics of the random noise stimulus were identical to those used to probe RFs during saccades.

We recorded from 216 SC neurons, in which the visual responses were strong enough to allow the calculation of visual RFs during fixation (see MATERIALS AND METHODS, *Sparse noise mapping* for details). Of these neurons, 22 had responses that were too low to permit calculation of perisaccadic RFs. Data from the remaining 194 neurons (120 in *monkey 1*; 74 in *monkey 2*) were used to estimate RFs during fixation and around the times of saccades. Of these 194 neurons, 75 were recorded under conditions in which the location of each ST was unpredictable (randomly chosen between vertical and horizontal). For the remaining 119 neurons, saccades were made back and forth between two targets, so that the location of each target was always predictable.

For each neuron, we compared the maximal visual responses in the fixation RF and the FF, defined as the position of the RF shifted by the vector of the saccade. The FF thus represents the RF location, which would be expected if remapping occurred. We also examined responses at a control position placed outside of the RF and FF areas in the ipsilateral visual hemifield (CONT-ROI in Fig. 1, *C* and *D*).

Figure 3*A* shows the results of the sparse noise-mapping procedure for one example SC neuron. Each panel shows the spatial responses to stimuli presented in a particular 50-ms time bin relative to saccade onset. The maximal visual responses occurred in a discrete spatial area, which we used to define ROI for the fixation RF (RF-ROI) and the FF (FF-ROI). For this neuron, the responses in the RF-ROI were stable across the different time windows, and importantly, we found no evidence of an increase in activity in the FF-ROI in any of these windows.

To summarize these results across the population, we compared the responses to stimuli presented in the RF-ROI and FF-ROI with those presented in a control spatial region (CONT-ROI defined in MATERIALS AND METHODS, *Sparse noise mapping*). As a measure of the strength of the response to stimuli in each ROI, we first calculated the average STA_n in the three ROIs for each time interval between spike and stimulus (τ between 20 and 430 ms). Then, we chose the maximal activity at any τ to represent the strength of the response. We first analyzed 75 neurons recorded under conditions in which the direction of the saccade was not predictable from one trial to the next. For our analysis, we used stimuli presented in a time window between 155 ms and 5 ms before the saccade, where previous work (e.g., Kusunoki and Goldberg 2003; Walker et al. 1995) has demonstrated strong RF remapping. Figure 3, *B* and *C*, shows the results for the RF-ROI and the FF-ROI. Whereas 39% (29/75) of the neurons showed RF responses that were significantly above the control responses ($P < 0.01$), none of the neurons showed significantly elevated FF responses. For the population, responses to stimuli in the RF were significantly higher than controls ($P < 0.001$), whereas responses to FF stimuli were not significantly different from the control position ($P = 0.43$).

The lack of remapping in these data may have been due to any number of reasons, as our experiment differed substantially from previous approaches. One obvious possibility is the ST location, which is entirely predictable in the single-probe paradigm but randomly chosen from two possibilities in our experiments. To test this possibility, we examined the responses of 119 neurons recorded using a variation on the sparse mapping procedure, in which the location of a ST was completely predictable. In this condition, 37/119 (31%) of the neurons showed significantly ($P < 0.01$) higher responses in the RF-ROI than in the CONT-ROI (Fig. 3*D*), whereas again, none of the neurons showed increased FF responses (Fig. 3*E*). The responses in FF-ROI are not significantly different between the predictable and nonpredictable conditions ($P = 0.54$, *t*-test), suggesting that ST predictability was not a key factor in the lack of remapping observed here (see also Nakamura and Colby 2002). Thus we found no evidence for presaccadic remapping during sparse noise stimulation, although as we show below, there was remapping in some of these neurons in the single-probe remapping task.

Figure 3*F* shows the discharge of the example neuron shown in Fig. 3*A* in the standard, single-probe paradigm. The neuron responded well to stimuli flashed in its RF during fixation and around the time of a saccade. There was no response in the FF during fixation, but a probe flashed in the FF just before saccade onset elicited a consistent, albeit weak, postsaccadic response. This response was not due to the saccade per se, as no response was observed in the absence of a visual probe. Of the 41 neurons, which we were able to hold long enough to test in both paradigms, we observed remapping in five in the standard paradigm but none in the sparse noise-mapping paradigm.

A potentially important difference between the sparse noise and standard remapping paradigms is the overall luminance of the stimulus. Whereas in the single-probe paradigm, white visual probes were presented on a dark background, in the sparse noise experiments, black and white probes were flashed on a gray background. This changes the average luminance of the stimulus, as well as the contrast between the probes and the background, and the influence of these factors on remapping has not been studied. However, they may be important, as the influence of oculomotor signals on visual perception has been shown to be mediated by stimulus luminance and contrast (Georg et al. 2008; Michels and Lappe 2004; Richard et al. 2009). Thus to further investigate the importance of these parameters, we performed additional experiments using the single-probe remapping paradigm. This approach allowed us to examine the influence of luminance and contrast on remapping responses in the SC.

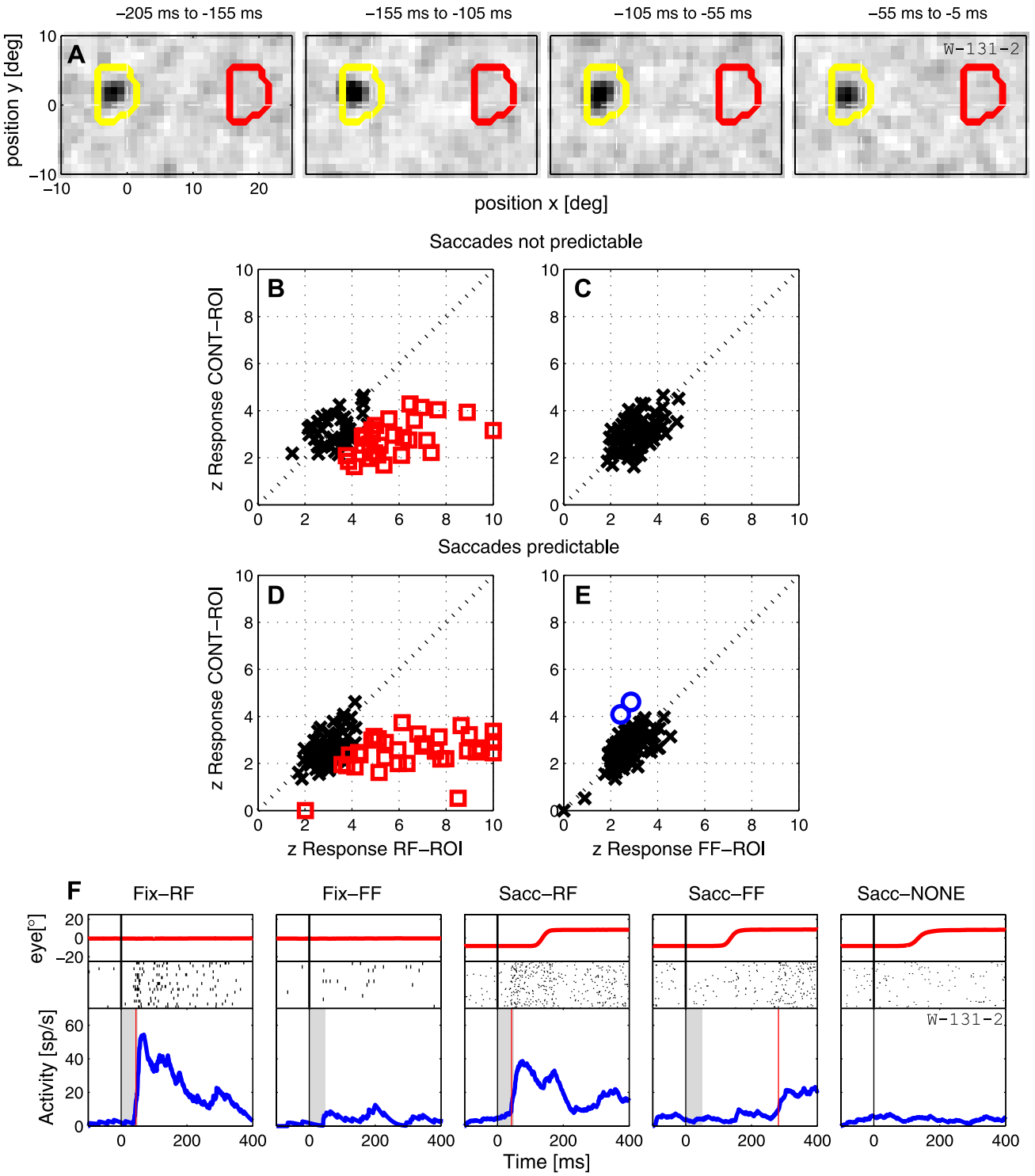

Fig. 3. *A*: maximal responses (over time) of 1 example neuron to sparse noise stimuli in 50 ms time windows before the onset of ipsiversive saccades (amplitude 20°). The position of the RF-ROI is shown in yellow; the position of the FF-ROI (which is the RF-ROI shifted by the vector of the saccade) in red. The neuron shows strong responses (indicated by dark shades of gray) to stimuli presented in the RF-ROI in all time windows, whereas there are no presaccadic responses in the FF-ROI. *B*: comparison of maximal responses of 75 neurons to sparse noise stimuli presented in the RF-ROI with stimuli presented in the CONT-ROI in a time window from 155 ms to 5 ms before saccade onset. The neurons were recorded under a condition in which the next saccade was not predictable. Neurons with significantly ($P < 0.01$) higher RF-ROI responses compared with the CONT-responses (29 of 75, 39%) are marked as red squares. *C*: comparison of maximal responses to stimuli presented in FF-ROI with stimuli presented in CONT-ROI for the same 75 neurons shown in *B*. No significant differences were found between FF-ROI and CONT-ROI responses for any of the neurons. *D* and *E*: comparison of maximal responses of 119 neurons recorded under conditions in which the next saccade was fully predictable. Neurons (37/119, 31%) showed significant RF responses (red squares), whereas no neuron showed significant responses to stimuli in the FF-ROI. Two neurons showing significantly higher CONT-ROI responses compared with their FF-ROI responses are marked as blue circles. *F*: activity of the same neuron as shown in *A* during the single-probe remapping task. The neuron shows significant responses to probes presented in its RF during fixation (Fix; *panel 1*), as well as before a saccade (Sacc; *panel 3*). More importantly, it shows significant responses to a FF probe presented before a saccade (*panel 4*) but no response to a probe presented at the same position during fixation (*panel 2*).

Single-Probe Remapping Paradigm

We recorded the responses of 221 SC neurons in the single-probe remapping paradigm. We excluded 81 neurons that lacked visual responses, that responded to an ipsiversive saccade in the absence of a visual probe, or that showed significant responses to a FF probe during fixation. The responses of the remaining 140 neurons were analyzed in detail.

The activity for one example neuron is shown in Fig. 4. During fixation trials, this neuron responded strongly to a probe presented in the RF but not to a probe presented in the FF. In saccade trials, when a visual probe was flashed more than 100 ms before saccade onset, the RF response remained, but in addition, the neuron responded to a probe at the FF position. When no probe was presented, no increase in activity was observed in either the fixation or saccade conditions.

To determine the prevalence of remapping under these conditions, we calculated the frequency with which FF activity was significantly ($P < 0.05$, t-test) above baseline for at least 30 ms in a time interval between 20 ms and 550 ms after the onset of the probe. With the use of this criterion, 36 out of 140 neurons (26%) showed remapping, which is comparable with the 30% reported by Walker et al. (1995). Thus our results are generally consistent with previous work (Walker et al. 1995), documenting the existence of RF remapping in the SC.

To measure the strength of neuronal responses in the different conditions, we first estimated the continuous signal-to-noise ratio of the response (defined by the d' value; see MATERIALS AND METHODS, *Single-probe remapping task*, for details) in a time range between 20 ms and 550 ms after the

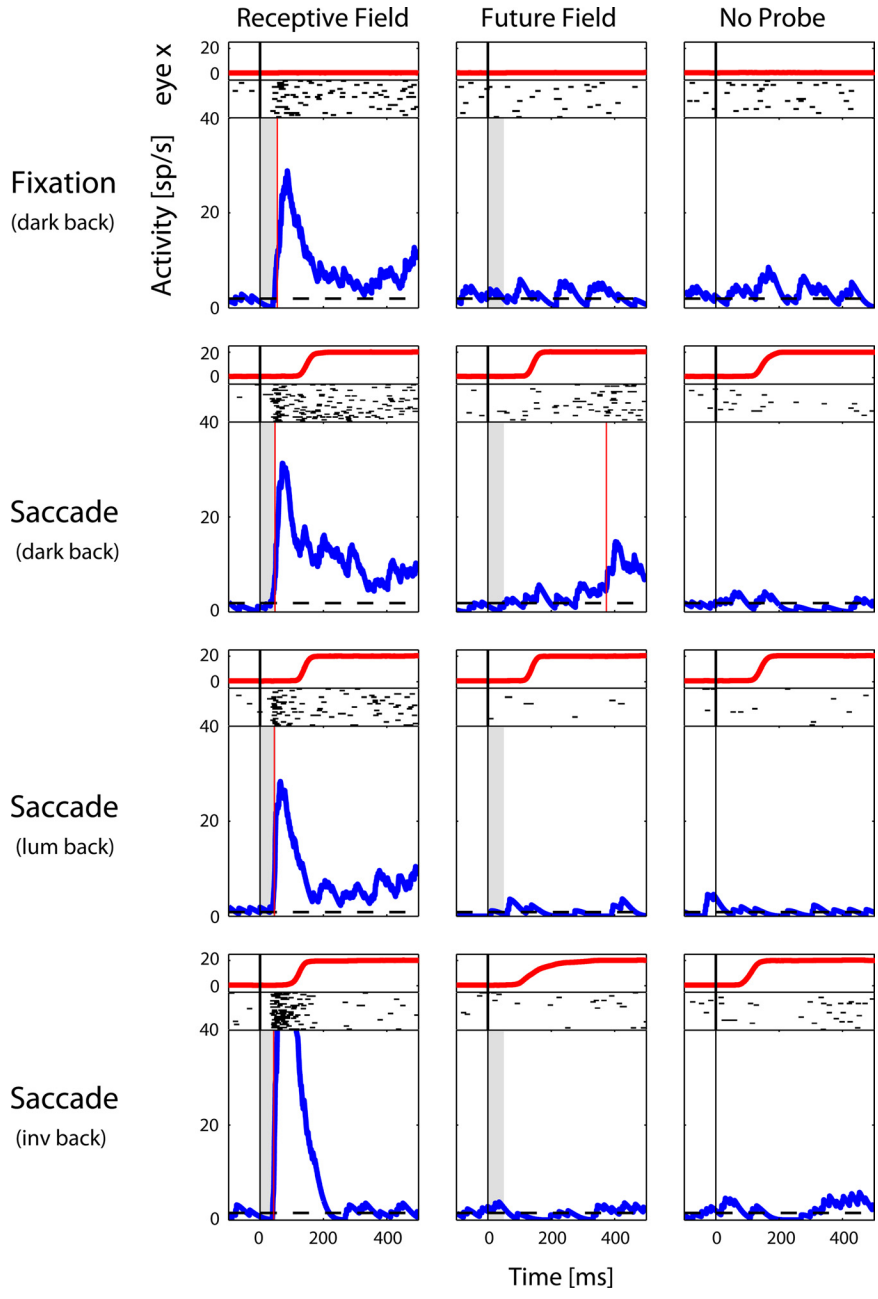

Fig. 4. Average eye traces, raster plots, and peristimulus time histograms obtained during different conditions in 1 example experiment. The *1st row* shows responses to probes presented during continuous fixation. In *rows 2–4*, the monkey made visually guided, horizontal saccades (amplitude 20°) into the ipsilateral visual hemifield. The mean saccadic latency was 117 ms. The shaded areas represent the duration of the visual probe; the dashed horizontal lines show the baseline activity; the red vertical lines show the latency of the neuronal response, which was 40 ms for probes in the RF and 348 ms for the FF position. The *1st* and *2nd rows* show responses to probes presented on a dark visual background (back; <0.01 cd/m^2); in the *3rd row*, the luminance (lum) of the background was raised slightly to $\sim$0.03 cd/m^2, and in the *4th row*, black visual probes were presented on a white background [inverted (inv); 29 cd/m^2]. Whereas the responses to probes in the RF are very similar for all conditions, the neuron only responded to FF probes when they were presented on a dark background.

onset of the probe. Because the latency of remapping responses varied substantially across neurons, we took the amplitude of the remapped response to be the maximal d' across the whole time range. Figure 5 shows the maximal d' for RF and FF probes presented during fixation and before a saccade. The 36 neurons showing significant responses to FF probes, presented before a saccade (but not during fixation), are marked as red squares. This analysis shows that responses in the RF were, on average, unchanged ($P = 0.96$; Fig. 5*A*) between the fixation and saccade conditions and that perisaccadic responses to FF probes (although significant) were quite weak, with a maximal $d' > 1$ for only 12/36 (33%) of the remapping neurons (Fig. 5*B*).

A recent study (Zirnsak et al. 2010) has made very specific predictions regarding the RF locations of remapping neurons. Under the conditions of our experiments (ipsiversive 20° sac-

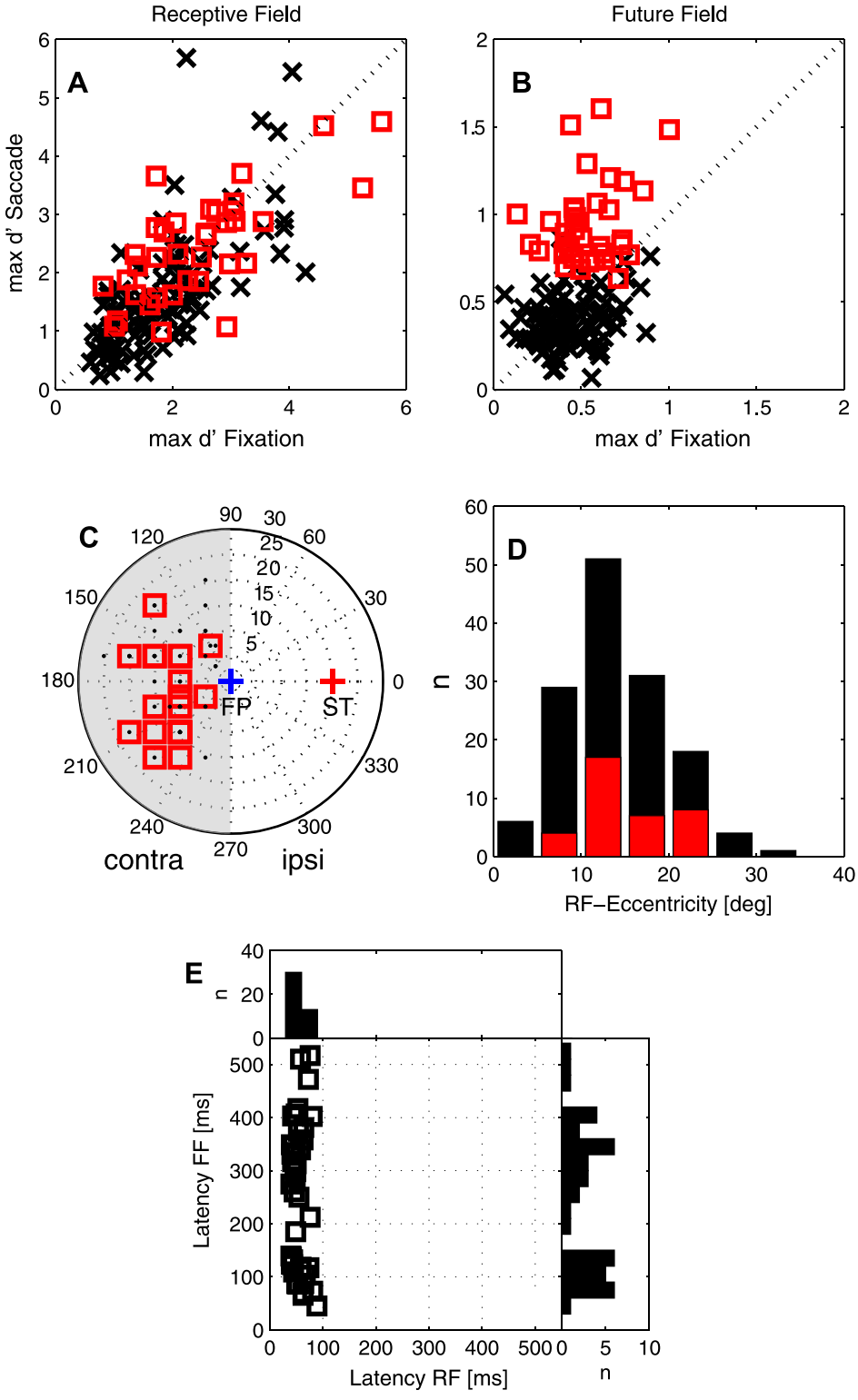

Fig. 5. *A* and *B*: comparison of maximal responses to RF probes (*A*) and to FF probes (*B*) presented during continuous fixation and before saccades. Thirty-six neurons showed significant responses to FF probes presented before saccades but not during fixation. These remapping neurons are marked as red squares in both panels. d′, sensitivity index. *C*: retinal position of the RF centers of remapping neurons (red squares) and nonremapping neurons (black dots) relative to the vector of the saccade (ST is marked as a red cross). contra, contralateral; ipsi, ipsilateral. *D*: comparison of eccentricities of RF centers of remapping (red) and nonremapping (black) neurons. The average RF eccentricities of the 2 groups is not significantly different ($P = 0.12$). *E*: latencies of responses of remapping neurons to probes presented at the RF and FF positions relative to the onset of the visual probe.

cades), this model predicts that remapping should be found only for RFs near the vertical meridian and away from the fovea (see Fig. 6*B* of Zirnsak et al. 2010). Although we found relatively few neurons with RFs in this region of visual space, we generally found that the remapping cells were distributed evenly across the region that we sampled, including points far from the vertical meridian (Fig. 5*C*). The RF eccentricities did not differ significantly between remapping and nonremapping neurons ($P = 0.12$; Fig. 5*D*). It remains possible, however, that we would have found stronger remapping responses if we had aimed our recordings specifically at neurons with RFs located in the positions indicated by the model.

Effect of Increased Background Luminance

We next investigated the possible reasons for the discrepant remapping results obtained in the sparse noise and single-probe paradigms. As mentioned above, one of the differences between these paradigms was the luminance of the visual background. In the sparse noise-mapping paradigm, visual stimuli were presented on a gray background, whereas in the single-probe paradigm, the probes were presented in complete darkness on a screen with a very low background luminance ($<<0.01$ cd/m^2). To investigate the effect of background luminance on remapping, we introduced a variation on the standard paradigms, in which we increased the luminance of the background slightly to $\sim$0.03 cd/m^2.

The results of increasing the background luminance are shown for the example neuron in Fig. 4. Recall that this neuron showed clear remapping responses when probes were presented against a dark background. Surprisingly, this remapping disappeared in the presence of slight background illumination, and as shown, responses in the RF were virtually unaffected by this experimental manipulation.

The result shown in Fig. 4 was typical of the SC neurons that showed remapping. Figure 6 shows the effects of changing background luminance for 26 neurons that showed remapping with a dark background. When the probe was presented in the RF (Fig. 6*A*), the responses did not differ significantly between the backgrounds ($P = 0.75$, paired *t*-test). In contrast, when the background was dimly lit (Fig. 6*B*), the majority of responses to FF probes was reduced significantly ($P < 0.001$, paired *t*-test; Fig. 6*B*), with only six of 26 (23%) of the neurons maintaining significant responses to FF probes. These neurons are marked as squares in Fig. 6*B*.

Increasing the background luminance makes the probe slightly less salient relative to the background. Thus one explanation for the results shown in Fig. 6 is that the change in probe contrast, rather than the overall luminance, was responsible for the decrease in remapping responses. To test this possibility, we interleaved additional blocks of trials in which black probes were presented against a high-luminance, white background. Such stimuli are extremely potent cues for the primate visual system (Yeh et al. 2009). Nevertheless, the example neuron shown in Fig. 4 did not exhibit remapping responses under this condition (Fig. 4), suggesting that probe saliency was not the determining factor in remapping for this neuron.

We tested the effect of this inverted stimulus for 19 neurons showing significant remapping at the FF position under standard conditions (black background, white probe). Figure 7 shows the effect of the inversion. The responses to RF probes (Fig. 7*A*) were not significantly different between inverted and standard conditions ($P = 0.92$, paired *t*-test). Responses to FF probes (Fig. 7*B*), however, were significantly reduced ($P < 0.001$) by inversion of the stimulus. Only four neurons retained significant remapping for the inverted stimulus, and these are marked as squares in Fig. 7*B*. Thus our results show that RF remapping in the SC is highly sensitive to the luminance of the background against which probes are presented.

DISCUSSION

In this work, we have examined the influence of visual stimulus parameters on perisaccadic RF remapping in the macaque SC. Our results confirm a previous report (Walker et al. 1995) that remapping occurs when the RF is probed with an isolated stimulus presented against a dark background. However, we also found that even modest deviations from these visual conditions reduced or abolished remapping responses in most cells. In particular, in a condition involving the simultaneous presentation of multiple probes (sparse-mapping paradigm), we found no remapping in a large population of neurons. For cells that demonstrated clear remapping in the standard paradigm, small changes in the luminance of the visual background diminished the frequency and strength of remapping substantially. This effect was not due to changes in the contrast of the visual probe, as conditions involving a black stimulus presented against a white background also failed to

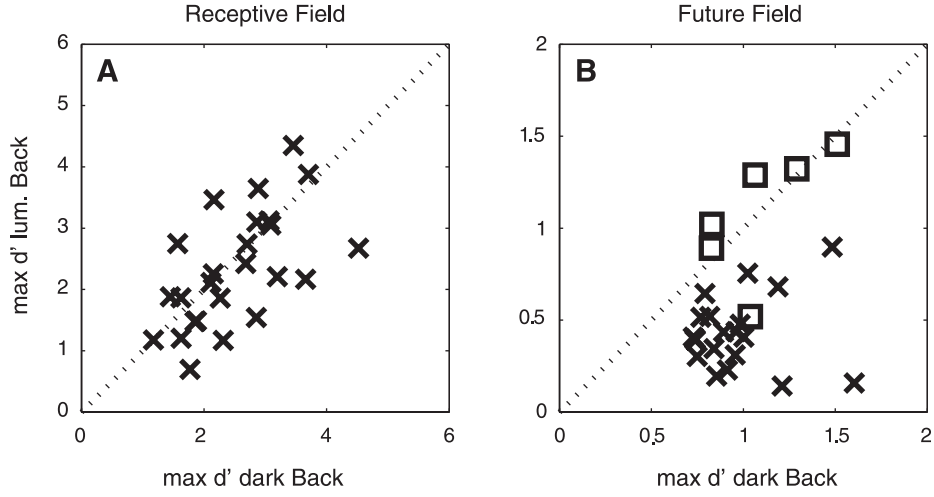

Fig. 6. Effect of background luminance on the maximal responses to visual probes at RF (*A*) and FF (*B*) positions. Neurons showing significant responses to FF probes on a luminance background are marked as squares in *B*.

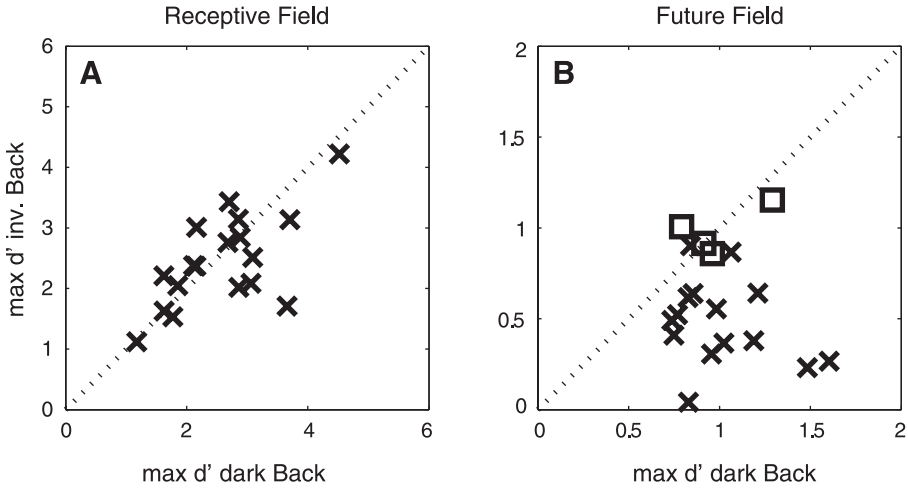

Fig. 7. Influence of stimulus inversion on the maximal responses to visual probes at RF (*A*) and FF (*B*) positions. Neurons showing significant responses to FF probes on an inverted background are marked as squares in *B*.

exhibit remapping. These results suggest that remapping responses in the SC are highly sensitive to the overall luminance of the visual scene, such that SC remapping is likely to be weak or absent under naturalistic lighting conditions.

Comparison with Previous Work

Our results in the single-probe paradigm (black background) are generally consistent with those from the two previous studies on SC (Dunn et al. 2010; Walker et al. 1995), which have shown remapping in the SC for isolated probe stimuli presented on a dark background. The remapping responses found in all three studies, however, were quite weak (Fig. 5*B*; also Fig. 8 in Walker et al. 1995 and Fig. 4*D* in Dunn et al. 2010) compared with those reported from the FEF (Sommer and Wurtz 2006) and LIP (Kusunoki and Goldberg 2003). These weak responses are likely to be influenced by the specific methods used in the different studies, and so, the differences in percentage of remapping neurons reported in the different studies in SC (26% here; 30% in Walker et al. 1995; 50% in Dunn et al. 2010) can be explained by the differences in the physical properties of the paradigms and the statistical criteria used to determine whether a neuron was remapping.

A survey of the existing literature on remapping suggests that remapping likely occurs in other brain regions, even when lighting conditions more closely approximate a natural setting. In area V3A, remapping was found in ~50% of the neurons tested, under background illumination conditions similar to those that largely abolished remapping in the current study (Nakamura and Colby 2002). In the FEF, Sommer and Wurtz (2006) found remapping in 61% of the neurons using an experimental setup that was described as "dimly lit". Although the effect of background luminance on the strength of the remapping response was not investigated systematically in these cortical areas, the large fraction of remapping responses found suggests that remapping in the cortex is more robust to changes in the visual stimulus conditions. Nevertheless, it would be of interest to explore this issue systematically in FEF and LIP, which have been suggested as sources for the remapping signals in the SC (Dunn et al. 2010).

Remapping Responses in SC: Relation to Saccade Sequences

Remapping is likely to serve at least two functions that have been discussed extensively in previous publications. The first is primarily a visual function, whereby remapping contributes to trans-saccadic perceptual stability (reviewed in Sommer and Wurtz 2008; Wurtz 2008). Secondly, remapping may provide information for calculation of an accurate trans-saccadic spatial representation of the targets of subsequent eye movements (Sommer and Wurtz 2002; Vaziri et al. 2006).

In principle, the SC could participate in both functions, as neurons in this area have visual, motor, and attention responses. However, whereas the visual information provided by SC can be used to perform visual discrimination tasks (e.g., Lovejoy and Krauzlis 2010; Pasik and Pasik 1971; Schilder et al. 1972), this perception occurs without conscious awareness ("blindsight"; Cowey and Stoerig 1995; Weiskrantz 1996; Weiskrantz et al. 1974), so the role of SC remapping in generating perceptual stability is likely to be indirect. In contrast, the SC is closely linked to the planning and execution of saccadic eye movements (Robinson 1972; Wurtz and Goldberg 1971), and in this domain, remapping in the SC can provide information necessary for the execution of complex movements involving several targets. A classic example is the double-step saccade task (Becker and Jürgens 1979).

In double-step saccades, the subject is instructed to make saccades to two targets in quick succession. Recent evidence indicates that the generation of the second saccade in a sequence is based on updating precomputed motor plans, not updating visual vectors (Quaia et al. 2010). This is consistent with the idea that the SC motor map controls the second saccade by remapping the representation of the second target around the time that the first saccade is executed (Mays and Sparks 1980). Behavioral correlates of this idea come from a recent study, in which greater remapping activity in the intermediate layers of the SC was correlated with decreasing error of the second saccade in a double-step task (Dunn et al. 2010). Furthermore, it has been shown that a decrease of remapping activity in FEF, due to blocking the SC-thalamus-FEF corollary discharge, causes a systematic error in the second saccade in the double-step saccade task (Sommer and Wurtz 2002). All of these results are consistent with a role for remapping in controlling sequences of saccades.

If remapping in the SC is useful for controlling multiple saccades, why would such a mechanism be active only in conditions of near-total darkness? One alternative means of maintaining a stable spatial representation of STs is to measure

spatial position relative to visual landmarks (Deubel et al. 2010). Under appropriate circumstances, this strategy may provide better accuracy than a purely oculomotor one, as the corollary discharge has been suggested to be rather imprecise and sluggish (Bridgeman 2007; Cai et al. 1997; Dassonville et al. 1992; Honda 1989). Indeed, in experiments in which visual information and corollary discharge information are both present, the percept tends to be dominated by the visual input (Magne and Coello 2002; Matin et al. 1982). Therefore, remapping signals that are driven by corollary discharges may be less relevant for guiding saccades when the visual background is illuminated, and this may provide a functional rationale for our findings in the SC.

In general, despite the evidence for the involvement of FEF, LIP, and SC in remapping and the involvement of this phenomenon in double-step tasks, we note that for many neurons, the latencies of remapping responses are several hundred milliseconds long (Fig. 5*E*; Dunn et al. 2010; Umeno and Goldberg 1997, 2001). It is difficult to imagine what behavioral purpose these very late responses could serve.

Remapping Responses in SC: Effects of Salience and Attention

One possible explanation for our results is that the increased background luminance effectively decreases the bottom-up salience of the stimuli used to probe RF remapping. Indeed, in our data (Fig. 4), remapped responses were rather weak, and so, they might be disproportionately affected by changes in stimulus salience. We consider this explanation to be unlikely, as the manipulation of background luminance in our experiment involved a change from ~0.001 cd/m^2 to ~0.03 cd/m^2, which resulted in a reduction of stimulus contrast from 99.99% to 99.80%. We are not aware of any mechanism in the visual system that would discriminate reliably between such fine changes in contrast. Second, when we held contrast constant while changing background luminance (using inverted stimuli consisting of black probes on a white background), we again observed reduced remapping (Fig. 7). This manipulation also argues against an effect of bottom-up salience, as both electrophysiological (Yeh et al. 2009) and psychophysical (e.g., Blackwell 1946; Kontsevich and Tyler 1999; Tyler et al. 1992) studies have shown that inverted stimuli are actually more salient than white stimuli on a black background.

On the other hand, even minor changes in the luminance of the visual background do have large effects on the surrounding context. Specifically, they render parts of the experimental apparatus (such as the borders of the screen) visible, and these could serve to distract attention. Recent studies of the relationship between attentional processes and remapping (Cavanagh et al. 2010; Mayo and Sommer 2010; Rolfs et al. 2011) have led to the proposal that the brain does not remap all visual objects but rather, only the salient or behaviorally relevant parts of a visual scene (Cavanagh et al. 2010; Gottlieb et al. 1998; Rolfs et al. 2011). This is supported by a recent study (Joiner et al. 2009; reviewed in Wurtz et al. 2011), which showed a reduction of remapping responses in the FEF when the FF probe was presented together with distractors that were placed outside of the RF and FF. Consequently, the reduction of remapping in our experiments can be partly caused by distractors in the visual field. On the other hand, in our setting, the abrupt appearance of the probe should draw bottom-up attention in a fairly automatic fashion (Theeuwes 1995; Yantis and Jonides 1990), which could account for the residual remapping responses that we observed when the background was illuminated. One direction for future experiments on background effects would be to increase the behavioral relevance of the FF probe, for instance, by requiring a second saccade to its remembered position (similar to Walker et al. 1995) to investigate whether this could counteract the effect of the luminance background.

Integration of Signals in SC

The brain circuitry associated with remapping appears to include various cortical and subcortical areas that are linked through reciprocal connections. Specifically, the SC is known to be essential for transmitting a signal related to saccade onset to the FEF via the thalamus. Inactivation of this pathway abolishes remapping at the level of single FEF neurons (Sommer and Wurtz 2006) and partially impairs its presumptive behavioral correlate in the double saccade task (Sommer and Wurtz 2002). Thus signals from the SC appear to be crucial for initiating remapping responses in the cortex.

Whether remapping in the SC is a cause or a consequence of cortical remapping is less clear. Cortical areas that exhibit strong remapping have monosynaptic connections to the intermediate layers of SC (Leichnetz and Goldberg 1988; Segraves and Goldberg 1987; Sommer and Wurtz 2000, 2001, for FEF; Ferraina et al. 2002; Lynch et al. 1985; Lynch and Tian 2006; Pare and Wurtz 1997, 2001, for LIP), and these could be the source of the remapping observed in the SC. Evidence consistent with this idea comes from a study by Dunn et al. (2010), in which the commissures joining the two cortices were cut. The results showed a reduction in across-hemifield remapping in both LIP and intermediate layers of the SC, suggesting that the latter might receive remapping signals from the former. The fact that remapping responses are often found at relatively long latencies (Fig. 5*E*) is also generally consistent with the idea that remapping signals reach the SC after they have been computed in the cortex. The lack of remapping in the intermediate collicular layers in the presence of background illumination might then reflect an intracortical process that emphasizes visual landmarks when they are available (Deubel 2004; Deubel et al. 2010).

Alternatively, remapping responses could be generated within the SC, as visual and motor information is already present within the intermediate layers. This would explain why the across-hemifield remapping in the superficial layers of the SC remains, even when forebrain commissures are cut (Dunn et al. 2010). The effects of luminance on remapping in the SC might then involve an increase of the influence of inhibitory surrounds with increasing background luminance (Westheimer 1967). These inhibitory inputs, as well as others that are known to be associated more generally with SC circuitry (e.g., McHaffie et al. 2005; Meredith and Ramoa 1998; Munoz and Istvan 1998; Takahashi et al. 2010), might have a powerful effect on remapping responses, which are usually rather weak compared with responses in the classic RF. Indeed, inhibitory, visual mechanisms might explain, in part, our failure to find remapping responses during the sparse mapping paradigm, in which multiple stimuli were presented simultaneously on each

monitor frame. However, we have little evidence for such a general process, since the background luminance does not significantly change the baseline activity (results not shown) or the RF responses in our data.

Remapping and Visual Perception

Rolfs et al. (2011) have shown in subjects making double-step saccades to continuously present visual objects on a gray background that even before the first saccade begins, attention is drawn to the specific retinoptopic location where the second target will land after the first saccade occurs. They proposed that this phenomenon can be driven by remapping the focus of attention rather than by remapping objects in the visual field (Krauzlis and Nummela 2011; Rolfs et al. 2011). If this is the case, it would be interesting to examine these results, as well as other studies of perceptual remapping (Melcher and Morrone 2003), under different luminance conditions. An alternative possibility is that as mentioned above, the double-step saccade task involves updating motor plans rather than visual RFs.

A related phenomenon is the perceptual compression of visual space that occurs around the time of a saccade (Ross et al. 1997). Some models (Binda et al. 2009) have claimed that remapping is responsible for this compression phenomenon, whereas other models (Hamker et al. 2008; Richard et al. 2009) do not require remapping to explain compression. Our results showing a reduction of remapping in the presence of visual markers suggest that remapping and compression are not necessarily related, since compression is actually stronger in the presence of visual landmarks (Lappe et al. 2000). This possibility could be explored further by testing the effects of landmarks on remapping in cortical areas that are more involved in perception (e.g., LIP and FEF).

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DISCLOSURES

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

REFERENCES

Becker W, Jürgens R. An analysis of the saccadic system by means of double step stimuli. *Vision Res* 19: 967–983, 1979.

Binda P, Cicchini GM, Burr DC, Morrone MC. Spatiotemporal distortions of visual perception at the time of saccades. *J Neurosci* 29: 13147–13157, 2009.

Blackwell HR. Contrast thresholds of the human eye. *J Opt Soc Am* 36: 624–643, 1946.

Brainard DH. The Psychophysics Toolbox. *Spat Vis* 10: 433–436, 1997.

Bridgeman B. Efference copy and its limitations. *Comput Biol Med* 37: 924–929, 2007.

Cai RH, Pouget A, Schlag-Rey M, Schlag J. Perceived geometrical relationships affected by eye-movement signals. *Nature* 386: 601–604, 1997.

Cavanagh P, Hunt AR, Afraz A, Rolfs M. Visual stability based on remapping of attention pointers. *Trends Cogn Sci* 14: 147–153, 2010.

Choi WY, Guitton D. Responses of collicular fixation neurons to gaze shift perturbations in head-unrestrained monkey reveal gaze feedback control. *Neuron* 50: 491–505, 2006.

Cowey A, Stoerig P. Blindsight in monkeys. *Nature* 373: 247–249, 1995.

Dassonville P, Schlag J, Schlag-Rey M. Oculomotor localization relies on a damped representation of saccadic eye displacement in human and nonhuman primates. *Vis Neurosci* 9: 261–269, 1992.

Dayan P, Abbott LF. *Theoretical Neuroscience—Computational and Mathematical Modeling of Neural Systems*. Cambridge, MA: The MIT Press, 2001.

Deubel H. Localization of targets across saccades: role of landmark objects. *Vis Cogn* 11: 173–202, 2004.

Deubel H, Koch C, Bridgeman B. Landmarks facilitate visual space constancy across saccades and during fixation. *Vision Res* 50: 249–259, 2010.

Duhamel JR, Colby CL, Goldberg ME. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255: 90–92, 1992.

Dunn CA, Hall NJ, Colby CL. Spatial updating in monkey superior colliculus in the absence of the forebrain commissures: dissociation between superficial and intermediate layers. *J Neurophysiol* 104: 1267–1285, 2010.

Ferraina S, Pare M, Wurtz RH. Comparison of cortico-cortical and cortico-collicular signals for the generation of saccadic eye movements. *J Neurophysiol* 87: 845–858, 2002.

Georg K, Hamker FH, Lappe M. Influence of adaptation state and stimulus luminance on peri-saccadic localization. *J Vis* 8: 15 11–11, 2008.

Goldberg ME, Wurtz RH. Activity of superior colliculus in behaving monkey. I. Visual receptive fields of single neurons. *J Neurophysiol* 35: 542–559, 1972.

Gottlieb JP, Kusunoki M, Goldberg ME. The representation of visual salience in monkey parietal cortex. *Nature* 391: 481–484, 1998.

Hamker FH, Zirnsak M, Calow D, Lappe M. The peri-saccadic perception of objects and space. *PLoS Comput Biol* 4: e31, 2008.

Honda H. Perceptual localization of visual stimuli flashed during saccades. *Percept Psychophys* 45: 162–174, 1989.

Joiner WM, Cavanaugh J, Wurtz RH. Effect of onset attention on shifting receptive field activity in monkey frontal eye field. In: *Society* for Neuroscience. Chicago, IL: 2009.

Jones JP, Palmer LA. The two-dimensional spatial structure of simple receptive fields in cat striate cortex. *J Neurophysiol* 58: 1187–1211, 1987.

Kontsevich LL, Tyler CW. Nonlinearities of near-threshold contrast transduction. *Vision Res* 39: 1869–1880, 1999.

Krauzlis RJ, Nummela SU. Attention points to the future. *Nat Neurosci* 14: 130–131, 2011.

Kusunoki M, Goldberg ME. The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. *J Neurophysiol* 89: 1519–1527, 2003.

Lappe M, Awater H, Krekelberg B. Postsaccadic visual references generate presaccadic compression of space. *Nature* 403: 892–895, 2000.

Leichnetz GR, Goldberg ME. Higher centers concerned with eye movement and visual attention: cerebral cortex and thalamus. *Rev Oculomot Res* 2: 365–429, 1988.

Livingstone MS, Pack CC, Born RT. Two-dimensional substructure of MT receptive fields. *Neuron* 30: 781–793, 2001.

Lovejoy LP, Krauzlis RJ. Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nat Neurosci* 13: 261–266, 2010.

Lynch JC, Graybiel AM, Lobeck LJ. The differential projection of two cytoarchitectonic subregions of the inferior parietal lobule of macaque upon the deep layers of the superior colliculus. *J Comp Neurol* 235: 241–254, 1985.

Lynch JC, Tian JR. Cortico-cortical networks and cortico-subcortical loops for the higher control of eye movements. *Prog Brain Res* 151: 461–501, 2006.

Magne P, Coello Y. Retinal and extra-retinal contribution to position coding. *Behav Brain Res* 136: 277–287, 2002.

Matin L, Picoult E, Stevens JK, Edwards MW Jr, Young D, MacArthur R. Oculoparalytic illusion: visual-field dependent spatial mislocalizations by humans partially paralyzed with curare. *Science* 216: 198–201, 1982.

Mayo JP, Sommer MA. Shifting attention to neurons. *Trends Cogn Sci* 14: 389, 2010.

Mays LE, Sparks DL. Saccades are spatially, not retinocentrically, coded. *Science* 208: 1163–1165, 1980.

McHaffie JG, Stanford TR, Stein BE, Coizet V, Redgrave P. Subcortical loops through the basal ganglia. *Trends Neurosci* 28: 401–407, 2005.

Melcher D, Morrone MC. Spatiotopic temporal integration of visual motion across saccadic eye movements. *Nat Neurosci* 6: 877–881, 2003.

Meredith MA, Ramoa AS. Intrinsic circuitry of the superior colliculus: pharmacophysiological identification of horizontally oriented inhibitory interneurons. *J Neurophysiol* 79: 1597–1602, 1998.

Michels L, Lappe M. Contrast dependency of sacadic compression and suppression. *Vision Res* 44: 2327–2336, 2004.

Munoz DP, Istvan PJ. Lateral inhibitory interactions in the intermediate layers of the monkey superior colliculus. *J Neurophysiol* 79: 1193–1209, 1998.

Nakamura K, Colby CL. Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proc Natl Acad Sci USA* 99: 4026–4031, 2002.

Pack CC, Conway BR, Born RT, Livingstone MS. Spatiotemporal structure of nonlinear subunits in macaque visual cortex. *J Neurosci* 26: 893–907, 2006.

Pare M, Wurtz RH. Monkey posterior parietal cortex neurons antidromically activated from superior colliculus. *J Neurophysiol* 78: 3493–3497, 1997.

Pare M, Wurtz RH. Progression in neuronal processing for saccadic eye movements from parietal cortex area lip to superior colliculus. *J Neurophysiol* 85: 2545–2562, 2001.

Pasik T, Pasik P. The visual world of monkeys deprived of striate cortex: effective stimulus parameters and the importance of the accessory optic system. *Vision Res*, *Suppl* 3: 419–435, 1971.

Pelli DG. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat Vis* 10: 437–442, 1997.

Quaia C, Joiner WM, Fitzgibbon EJ, Optican LM, Smith MA. Eye movement sequence generation in humans: motor or goal updating? *J Vis* 10: 2010.

Richard A, Churan J, Guitton DE, Pack CC. The geometry of perisaccadic visual perception. *J Neurosci* 29: 10160–10170, 2009.

Ringach DL. Mapping receptive fields in primary visual cortex. *J Physiol* 558: 717–728, 2004.

Robinson DA. A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans Biomed Eng* 10: 137–145, 1963.

Robinson DA. Eye movements evoked by collicular stimulation in the alert monkey. *Vision Res* 12: 1795–1808, 1972.

Rolfs M, Jonikaitis D, Deubel H, Cavanagh P. Predictive remapping of attention across eye movements. *Nat Neurosci* 14: 252–256, 2011.

Ross J, Morrone MC, Burr DC. Compression of visual space before saccades. *Nature* 386: 598–601, 1997.

Schilder P, Pasik P, Pasik T. Extrageniculostriate vision in the monkey. 3. Circle vs triangle and "red vs green" discrimination. *Exp Brain Res* 14: 436–448, 1972.

Segraves MA, Goldberg ME. Functional properties of corticotectal neurons in the monkey's frontal eye field. *J Neurophysiol* 58: 1387–1419, 1987.

Seth AK. Causal networks in simulated neural systems. *Cogn Neurodyn* 2: 49–64, 2008.

Sommer MA, Wurtz RH. A pathway in primate brain for internal monitoring of movements. *Science* 296: 1480–1482, 2002.

Sommer MA, Wurtz RH. Composition and topographic organization of signals sent from the frontal eye field to the superior colliculus. *J Neurophysiol* 83: 1979–2001, 2000.

Sommer MA, Wurtz RH. Frontal eye field sends delay activity related to movement, memory, and vision to the superior colliculus. *J Neurophysiol* 85: 1673–1685, 2001.

Sommer MA, Wurtz RH. Influence of the thalamus on spatial visual processing in frontal cortex. *Nature* 444: 374–377, 2006.

Sommer MA, Wurtz RH. Visual perception and corollary discharge. *Perception* 37: 408–418, 2008.

Sperry RW. Neural basis of the spontaneous optokinetic response produced by visual inversion. *J Comp Physiol Psychol* 43: 482–489, 1950.

Szulborski RG, Palmer LA. The two-dimensional spatial structure of nonlinear subunits in the receptive fields of complex cells. *Vision Res* 30: 249–254, 1990.

Takahashi M, Sugiuchi Y, Shinoda Y. Topographic organization of excitatory and inhibitory commissural connections in the superior colliculi and their functional roles in saccade generation. *J Neurophysiol* 104: 3146–3167, 2010.

Theeuwes J. Abrupt luminance change pops out; abrupt color change does not. *Percept Psychophys* 57: 637–644, 1995.

Tolias AS, Moore T, Smirnakis SM, Tehovnik EJ, Siapas AG, Schiller PH. Eye movements modulate visual receptive fields of V4 neurons. *Neuron* 29: 757–767, 2001.

Tyler CW, Chan H, Liu L. Different spatial tunings for on and off pathway stimulation. *Ophthalmic Physiol Opt* 12: 233–240, 1992.

Umeno MM, Goldberg ME. Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *J Neurophysiol* 78: 1373–1383, 1997.

Umeno MM, Goldberg ME. Spatial processing in the monkey frontal eye field. II. Memory responses. *J Neurophysiol* 86: 2344–2352, 2001.

Vaziri S, Diedrichsen J, Shadmehr R. Why does the brain predict sensory consequences of oculomotor commands? Optimal integration of the predicted and the actual sensory feedback. *J Neurosci* 26: 4188–4197, 2006.

Walker MF, Fitzgibbon EJ, Goldberg ME. Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *J Neurophysiol* 73: 1988–2003, 1995.

Weiskrantz L. Blindsight revisited. *Curr Opin Neurobiol* 6: 215–220, 1996.

Weiskrantz L, Warrington EK, Sanders MD, Marshall J. Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain* 97: 709–728, 1974.

Westheimer G. Spatial interaction in human cone vision. *J Physiol* 190: 139–154, 1967.

Wurtz RH. Neuronal mechanisms of visual stability. *Vision Res* 48: 2070–2089, 2008.

Wurtz RH, Goldberg ME. Superior colliculus cell responses related to eye movements in awake monkeys. *Science* 171: 82–84, 1971.

Wurtz RH, Joiner WM, Berman RA. Neuronal mechanisms for visual stability: progress and problems. *Philos Trans R Soc Lond B Biol Sci* 366: 492–503, 2011.

Yantis S, Jonides J. Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *J Exp Psychol Hum Percept Perform* 16: 121–134, 1990.

Yeh CI, Xing D, Shapley RM. "Black" responses dominate macaque primary visual cortex v1. *J Neurosci* 29: 11753–11760, 2009.

Zirnsak M, Lappe M, Hamker FH. The spatial distribution of receptive field changes in a model of peri-saccadic perception: predictive remapping and shifts towards the saccade target. *Vision Res* 50: 1328–1337, 2010.