Title: Context dependence of receptive field remapping in superior colliculus

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Abstract

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 presaccadically to visual stimuli placed in the spatial location that will be occupied 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 (SC) 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.

Keywords: Superior colliculus, remapping, macaque
Introduction

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 postasaccadic 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 shift before the start of the saccade to the spatial location 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 parietal cortex (LIP, Duhamel et al. 1992), and subsequently in other areas, including the superior colliculus (SC, Walker et al. 1995, Dunn et al. 2010), frontal cortex (FEF, Umeno and Goldberg 1997, 2001; Sommer and Wurtz 2002), and the visual cortex (Tolias et al. 2001; Nakamura and Colby, 2002).

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 (Michels and Lappe 2004; Georg et al. 2008; Richard et al. 2009). To address this issue, we have investigated peri-saccadic remapping in the superior colliculus (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 receptive fields (e.g. Jones and Palmer 1987; Szulborski and Palmer 1990; Livingstone et al. 2001; Ringach 2004; Pack et al. 2006). A second stimulus manipulation involved variations of the standard remapping paradigm (Duhamel et al. 1992, Walker et al. 1995, Umeno and Goldberg 1997, 2001; Sommer and Wurtz 2002) 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.
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) for one monkey and by an implanted scleral eye coil (Robinson 1963) for the other monkey; the sampling rate for both systems was 1000 Hz. After a post-operative recovery period the monkeys were seated in a primate chair (Crist Instruments) and trained, head-fixed, to keep fixation and make visually-guided and delayed saccades towards stimuli presented on a screen. All procedures were approved by the Animal Care Committee of the Montreal Neurological Institute, and were in compliance with regulations established by the Canadian Council of Animal Care.

The superior colliculus was identified based on an anatomical fMRI 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 visuo-motor layers again, and from this deep position we started the recordings.

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

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 PC computer at a spatial resolution of 800x600 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 CRT video projector (Electrohome 8000). The screen covered an area of 80x50 degrees 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 or saccade target 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 receptive fields during saccadic eye movements. In this paradigm one delivers rapid sequences of visual stimuli, such that all relevant spatial and temporal position can be explored during the course of a single experiment. Our adaptation of the stimulus included a saccade target that changed position often, so that receptive fields 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/m²) and 50% white (30.5 cd/m²) squares presented at random positions on a gray background (7.0 cd/m²) (Figure 1A). 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' arc) red targets that appeared on the flickering background. For most neurons the distribution of possible saccade target positions (Figure 1A) 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 saccade target 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 400-1200 ms fixation period required after each saccade before the next saccade target was presented. Typically 2000-3000 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 saccade target (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', luminance 29 cd/m²) was flashed for 59 ms (5 frames) simultaneously with the onset of the saccade target. The probe was presented either in the visual receptive field of a neuron (RF-condition) or in the future field, the position where the receptive field 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 3 different levels of background screen illumination: 1) white stimuli on a completely dark background (background luminance << 0.01 cd/m²); 2) white stimuli on a low-luminance background (background luminance ~0.03 cd/m²); 3) black stimuli on a white background (background luminance ~29 cd/m²). 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 saccade target was presented at one of 32 randomly interleaved positions (4 amplitudes (5, 10, 15 and 20 deg.) and 8 directions, covering the contralateral as well as the ipsilateral visual hemifield). Following the appearance of the saccade target, the monkey had to maintain fixation for another 300-700 ms until the fixation point disappeared, after which the saccade was executed. After the saccade the monkey had to keep fixating on the saccade target 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 (The MathWorks Inc.).
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 \((\tau)\) relative to the spike:

\[
STA(x, y, \tau) = \frac{\sum_{i=1}^{n} |s(x, y, t_i - \tau)|}{n}
\]

Here \(s\) is the sparse noise stimulus and \(n\) represents the number of recorded spikes. The spatial position \((x \text{ and } y)\) was sampled at a resolution of 1 degree, and the latency \(\tau\) 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 receptive fields 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 in order to compare this STA across neurons for which the density \(\tilde{s}\) of the sparse noise stimulus differed, we normalized the STA according to:

\[
STA_n(x, y, \tau) = \log_2 \left( \frac{STA(x, y, \tau)}{\tilde{s}} \right)
\]

Here an \(STA_n\) at a certain position in space and time \((x,y,\tau)\) with a value of 0 represents a response that would be expected to occur randomly, while \(STA_n(x,y,\tau) > 0\) 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 receptive field 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 plus two standard deviations 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 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 to 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 receptive fields.

To estimate the peri-saccadic 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 (Figure 1B) – a time period for which strong remapping was observed in previous studies (e.g. Walker et al. 1995; Kusunoki and Goldberg 2003). Note that intervals \((\tau)\) between stimulus presentation response ranged between 20 ms and 430 ms, which included the epochs during and after the saccade, when the majority of remapping responses was found (s. Fig. 5E). We then defined the peri-saccadic spatial receptive field map using the maximal \(STA_n\) at each spatial position over the whole range of \(\tau\) (20 ms – 430 ms). We did this to account for the large variability of latencies that has been reported for remapping responses (Walker et al. 1995; Umeno and Goldberg 1997; Nakamura and Colby 2002; Fig. 5E).

In order to generate predictions about receptive field remapping, we used data from the fixation condition to compute spatial region of interest (ROI) masks. These were used to examine peri-saccadic activity at different spatial positions in the visual field (Fig. 1C). Three different ROI were used:
1) RF-ROI represents the receptive field location obtained during fixation. We restricted this region to the 5 degrees on the side of the RF facing the direction of the saccade in order 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 Figure 1D for one example neuron.  

These ROIs were calculated for rightward saccades 20 degrees in amplitude. The yellow line shows the position of the RF-ROI; the red line shows the FF-ROI; and the blue line shows the CONT-ROI. For this analysis we used only ipsiversive saccades, in order 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 saccade target. The peri-stimulus 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 half-Gaussian (std 30 ms) and averaging the sum of these half-Gaussians across all trials. A 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 (t-test, p<0.05) 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 d' value:  

\[ d'(t) = \frac{act_{PSTH}(t) - act_{base}}{\sqrt{std^2_{PSTH}(t) + std^2_{base}}} \]  

where \( act_{PSTH}(t) \) is the continuous peri-stimulus activity, \( act_{base} \) is the baseline activity, and \( std_{PSTH}(t) \) and \( std_{base} \) are the inter-trial standard deviations of the peri-stimulus activity and the baseline activity.  

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 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 visuo-motor, 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 superior colliculus. As mentioned above, we targeted these layers in most penetrations, and most of the neurons for which classification is possible were visuo-motor (Table 1). The few purely visual cells included in the analysis were generally found at roughly the same depth as these visuo-motor 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.

Results
Our goal in these experiments was to examine the sensitivity of receptive field remapping in the superior colliculus (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. 1A). Saccades were interspersed with periods of fixation, during which the statistics of the random noise stimulus were identical to those used to probe receptive fields during saccades.

We recorded from 216 SC neurons in which the visual responses were strong enough to allow the calculation of visual receptive fields during fixation (see Methods for details). Of these neurons, 22 had responses that were too low to permit calculation of peri-saccadic receptive fields. Data from the remaining 194 neurons (120 in monkey 1, 74 in monkey 2) were used to estimate receptive fields during fixation and around the times of saccades. Of these 194 neurons, 75 were recorded under conditions in which the location of each saccade target 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 receptive field (RF) and the future field (FF), defined as the position of the RF shifted by the vector of the saccade. The FF thus represents the receptive field location that would be expected if remapping occurred. We also examined responses at a control position placed outside the RF and FF areas in the ipsilateral visual hemifield (Figure 1C, D, CONT-ROI).

Figure 3A 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, with strong responses being represented by dark grey tones and weak or absent responses by light grey. The maximal visual responses occurred in a discrete spatial area, which we used to define regions of interest for the fixation receptive field (RF-ROI; yellow) and the future field (FF-ROI; red). 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 to those presented in a control spatial region (CONT-ROI defined in Methods). As a measure of the strength of the response to stimuli in each ROI, we first calculated the average STAₙ 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. Walker et al. 1995; Kusunoki and Goldberg 2003) has demonstrated strong receptive field remapping. Figures 3B and 3C show the results for the RF-ROI and the FF-ROI. While 39% (29/75) of the neurons showed RF responses that were significantly above the control responses (p<0.01; red rectangles), 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), while 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 saccade target 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 saccade target 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 (red squares in Fig. 3D), while again none of the neurons showed increased FF-responses (Fig. 3E). The responses in FF-ROI are not significantly different between the predictable and non-predictable conditions (p=0.54, t-test), suggesting that saccade target 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 pre-saccadic 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 3F shows the discharge of the example neuron shown in Figure 3A in the standard, single-probe paradigm. The neuron responded well to stimuli flashed in its receptive field during fixation (Panel 1) and around the time of a saccade (Panel 3). There was no response in the FF during fixation (Panel 2), but a probe flashed in the FF just before saccade onset (Panel 4) elicited a consistent, albeit weak, post-saccadic response. This response was not due to the saccade per se, as no response was observed in the absence of a visual probe (panel 5). Of the 41 neurons that we were able to hold long enough to test in both paradigms, we observed remapping in 5 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 (Michels and Lappe 2004; Georg et al. 2008; 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 superior colliculus.

**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 Figure 4. During fixation trials this neuron responded strongly to a probe presented in the RF (row 1, left panel) but not to a probe presented in the FF (row 1, middle panel). In saccade trials (row 2), when a visual probe was flashed more than 100 ms before saccade onset, the RF response remained (left panel), but in addition the neuron responded to a probe at the FF position (center panel). When no probe was presented, no increase in activity was observed in either the fixation or saccade conditions (rows 1 and 2, right panels).
To determine the prevalence of remapping under these conditions, we calculated the frequency with which FF activity was significantly (t-test, p<0.05) above baseline for at least 30 ms in a time interval between 20 ms and 550 ms after the onset of the probe. Using this criterion, 36 out of 140 neurons (26%) showed remapping, which is comparable to 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 receptive field remapping in the superior colliculus.

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 Methods for details) in a time range between 20 ms and 550 ms after the 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, Figure 5A) 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 (Figure 5B).

A recent study (Zirnsak et al. 2010) has made very specific predictions regarding the receptive field locations of remapping neurons. Under the conditions of our experiments (ipsiversive 20° saccades), this model predicts that remapping should be found only for RFs near the vertical meridian and away from the fovea (see Figure 6B 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 (Figure 5C). The RF eccentricities did not differ significantly between remapping and non-remapping neurons (p=0.12; Figure 5D). 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, while in the single-probe paradigm the probes were presented in complete darkness on a screen with a very low background luminance (<<0.01 cd/m²). 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 ~0.03 cd/m².

The results of increasing the background luminance are shown for the example neuron in Fig.4, 3rd row. Recall that this neuron showed clear remapping responses when probes were presented against a dark background (second row, middle panel). Surprisingly this remapping disappeared in the presence of slight background illumination (third row, middle panel). As shown in the 3rd row, left panel, responses in the RF were virtually unaffected by this experimental manipulation.

The result shown in Figure 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 (Figure 6A), the responses did not differ significantly between the backgrounds (p=0.75, paired t-test). In contrast, when the background was dimly lit (Figure 6B), the majority of responses to FF-probes were significantly reduced (p<0.001, paired t-test) (Fig. 6B), with only 6 of 26 (23%) of the neurons maintaining significant responses to FF-probes. These neurons are marked as squares in Figure 6B.
Increasing the background luminance makes the probe slightly less salient relative to the background. Thus one explanation for the results shown in Figure 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 Figure 4 did not exhibit remapping responses under this condition (Figure 4, bottom row), 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. 7A) were not significantly different between inverted and standard conditions (p=0.92, paired t-test). Responses to FF-probes (Fig. 7B), however, were significantly reduced (p<0.001) by inversion of the stimulus. Only 4 neurons retained significant remapping for the inverted stimulus, and these are marked as squares in Fig. 7B. Thus our results show that receptive field remapping in the superior colliculus 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 peri-saccadic receptive field remapping in the macaque superior colliculus. Our results confirm a previous report (Walker et al. 1995) that remapping occurs when the receptive field 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 exhibit remapping. These results suggest that remapping responses in the superior colliculus 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 (Walker et al. 1995; Dunn et al. 2010), 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 (our Figure 5B; also compare Figure 8 in Walker et al. 1995 and Figure 4D in Dunn et al. 2010) compared to 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 approximately ~50% of the neurons tested, under background illumination conditions similar to those that largely abolished remapping in the current study (Nakamura & 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 has been suggested as a source 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 transsaccadic perceptual stability (reviewed in Wurtz 2008; Sommer and Wurtz 2008). Secondly, remapping may provide information for calculation of an accurate transsaccadic spatial representation of the targets of subsequent eye movements (Vaziri et al. 2006; Sommer and Wurtz 2002).

In principle the SC could participate in both functions, as neurons in this area have visual, motor and attention responses. However, while the visual information provided by SC can be used to perform
visual discrimination tasks (e.g. Pasik and Pasik 1971; Schilder et al. 1972; Lovejoy and Krauzlis 2010) this perception occurs without conscious awareness ('blindsight', Weiskrantz et al. 1974; Weiskrantz 1996; Cowey and Stoerig 1995), 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 (Wurtz and Goldberg 1971; Robinson 1972), 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 the updating of pre-computed motor plans, not on the updating of 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 saccade targets 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 (Dassonville et al. 1992; Cai et al. 1997; Honda 1989; Bridgeman 2007). Indeed in experiments in which visual information and corollary discharge information are both present, the percept tends to be dominated by the visual input (Matin et al. 1982; Magne and Coello 2002). 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 ms long (Figure 5E; 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 receptive field remapping. Indeed in our data (Figure 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/m² to ~0.03 cd/m², 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 (Figure 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; Chan and Tyler 1992; Kontsevich and Tyler 1999) 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 (Gottlieb et al. 1998; Cavanagh et
al. 2010; Rolfs et al. 2011). This is supported by a recent study (Joiner et al. 2009; reviewed in Wurtz et
al. 2011) that showed a reduction of remapping responses in the FEF when the future field probe was
presented together with distractors that were placed outside the receptive and future fields.
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 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 (Segraves and Goldberg 1987; Leichnetz and Goldberg 1988; Sommer and Wurtz 2000, 2001 for
FEF, Lynch et al. 1985; Ferraina et al. 2002; 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 (Figure 5E) 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 are 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., Meredith and Ramoa 1998; Munoz and Istvan 1998; McHaffie et al. 2005; Takahashi et
al., JNP 2010), might have a powerful effect on remapping responses, which are usually rather weak
compared to responses in the classic receptive field. 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 grey background, that even before the first saccade begins, attention is drawn to the specific retinotopic location where the second target will land after the first saccade occurs. They proposed that this phenomenon can be driven by a remapping of the focus of attention rather than by remapping of objects in the visual field (Rolfs et al. 2011; Krauzlis and Nummela 2011). If this is the case, it would be interesting to examine these results, as well as other studies of perceptual remapping (Melcher 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 receptive fields.

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, while 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 are declared by the authors.
References


Figure legends

Figure 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 400-1200 ms the fixation point disappeared and a new saccade target appeared to trigger either a horizontal or a vertical saccade. In some configurations only two alternate saccade targets 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 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: RF-ROI consists of the 5° of the RF positioned towards the direction of the saccade (orange). To obtain the 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 one 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 CONT-ROI (blue) is placed far from RF-ROI and FF-ROI. Strong responses to stimuli presented 155 ms – 5 ms before a saccade were found in RF-ROI, but not in FF-ROI or in CONT-ROI.

Figure 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 fixation point (FP) disappeared and a saccade target (ST) appeared, typically 20° in the periphery. A visual probe (luminance 29 cd/m²) was flashed at the same time for 59 ms either in the receptive field (RF) or in the future field (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.

Figure 3 A: Maximal responses (over time) of one 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, while there are no pre-saccadic responses in the FF-ROI. B: Comparison of maximal responses of 75 neurons to sparse noise stimuli presented in the RF-ROI to 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 to the CONT-responses (29 of 75, 39%) are marked as red squares. C: Comparison of maximal responses to stimuli presented in FF-ROI to 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, E: Comparison of maximal responses of 119 neurons recorded under conditions in which the next saccade was fully predictable. 37/119 (31%) neurons showed significant RF responses (red squares), while no neuron showed significant responses to stimuli in the FF-ROI. Two neurons showing significantly higher CONT-ROI responses compared to 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 (panel 1) as well as before a saccade (panel 3). More importantly, it shows significant responses to an FF-probe presented before a saccade (panel 4) but no response to a probe presented at the same position during fixation (panel 2).

Figure 4: Average eye traces, raster plots and PSTHs obtained during different conditions in one example experiment. The first row shows responses to probes presented during continuous fixation. In the 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 area represents the duration of the visual probe; the dashed horizontal line shows the baseline activity; the red vertical line shows the latency of the neuronal response, which was 40 ms for probes in the RF and 137 ms for FF position. The first and second rows show responses to probes presented on a dark visual background (<0.01 cd/m²); in the third row the luminance of the background was raised slightly to ~0.03 cd/m² and in the fourth row black visual probes were presented on a white background (29 cd/m²). While 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.
Figure 5 A and B: Comparison of maximal responses to RF-probes (A) and to FF-probes (B) presented during continuous fixation and before saccades. 36 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. C: Retinal position of the RF centers of remapping neurons (red squares) and non-remapping neurons (black dots) relative to the vector of the saccade (saccade target is marked as a red cross). D: Comparison of eccentricities of RF-centers of remapping (red) and non-remapping (black) neurons. The average RF-eccentricities of the two groups are 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.

Figure 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 panel B.

Figure 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 panel B.

Table 1: Classification of cell types and numbers of remapping neurons found in each cell type using the two paradigms.
<table>
<thead>
<tr>
<th></th>
<th>sparse noise</th>
<th>single probe</th>
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<tbody>
<tr>
<td>Visual</td>
<td>0/17 (0%)</td>
<td>7/14 (50%)</td>
</tr>
<tr>
<td>visuo-motor</td>
<td>0/151 (0%)</td>
<td>21/83 (25%)</td>
</tr>
<tr>
<td>visual or visuo-motor</td>
<td>0/48 (0%)</td>
<td>8/43 (19%)</td>
</tr>
<tr>
<td>Total</td>
<td>0/216 (0%)</td>
<td>36/140 (26%)</td>
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</tbody>
</table>
Fig. 1

A: 

B: 

C: 

D: 

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Fig. 1
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Fig.2
Saccades predictable

Saccades not predictable

Fig. 3
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Fig.5
Receptive Field

Future Field

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Fig.6
Fig. 7

Receptive Field

Future Field

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