american physiological society

JNP JOURNAL OF NEUROPHYSIOLOGY

J Neurophysiol 125: 1121–1138, 2021.
First published February 3, 2021; doi:10.1152/jn.00724.2020

REVIEW

Society for the Neural Control of Movement

Active vision at the foveal scale in the primate superior colliculus

Ziad M. Hafed,[1,2] Chih-Yang Chen,[3] Xiaoguang Tian,[4] Matthias P. Baumann,[1,2] and Tong Zhang[1,2]

[1]*Werner Reichardt Centre for Integrative Neuroscience, Tübingen University, Tübingen, Germany;* [2]*Hertie Institute for Clinical Brain Research, Tübingen University, Tübingen, Germany;* [3]*Institute for the Advanced Study of Human Biology (WPI-ASHBi), Kyoto University, Kyoto, Japan; and* [4]*University of Pittsburgh Brain Institute, University of Pittsburgh, Pittsburgh, Pennsylvania*

Abstract

The primate superior colliculus (SC) has recently been shown to possess both a large foveal representation as well as a varied visual processing repertoire. This structure is also known to contribute to eye movement generation. Here, we describe our current understanding of how SC visual and movement-related signals interact within the realm of small eye movements associated with the foveal scale of visuomotor behavior. Within the SC's foveal representation, there is a full spectrum of visual, visual-motor, and motor-related discharge for fixational eye movements. Moreover, a substantial number of neurons only emit movement-related discharge when microsaccades are visually guided, but not when similar movements are generated toward a blank. This represents a particularly striking example of integrating vision and action at the foveal scale. Beyond that, SC visual responses themselves are strongly modulated, and in multiple ways, by the occurrence of small eye movements. Intriguingly, this impact can extend to eccentricities well beyond the fovea, causing both sensitivity enhancement and suppression in the periphery. Because of large foveal magnification of neural tissue, such long-range eccentricity effects are neurally warped into smaller differences in anatomical space, providing a structural means for linking peripheral and foveal visual modulations around fixational eye movements. Finally, even the retinal-image visual flows associated with tiny fixational eye movements are signaled fairly faithfully by peripheral SC neurons with relatively large receptive fields. These results demonstrate how studying active vision at the foveal scale represents an opportunity for understanding primate vision during natural behaviors involving ever-present foveating eye movements.

NEW & NOTEWORTHY The primate superior colliculus (SC) is ideally suited for active vision at the foveal scale: it enables detailed foveal visual analysis by accurately driving small eye movements, and it also possesses a visual processing machinery that is sensitive to active eye movement behavior. Studying active vision at the foveal scale in the primate SC is informative for broader aspects of active perception, including the overt and covert processing of peripheral extra-foveal visual scene locations.

active vision; fixational eye movements; foveal vision; microsaccades; superior colliculus

INTRODUCTION

Foveal visual processing and its associated motor behaviors are important to investigate to fully understand primate (including human) vision. Although a research focus on the neural mechanisms associated with active vision at the foveal scale had been somewhat neglected for some time in the past, recent efforts to understand eye movement control at the minute scale of fixational eye movements (frequently displacing visual retinal images by as little as one single retinal photoreceptor) have emerged (1–6). These efforts represent an important component of broader attempts to investigate the neural control of movement in general. Indeed, the field of neural movement control has a long and rich history of landmark studies of eye movements as representing a model control system in the brain (7–17). It is, therefore, natural to also consider the control of tiny eye movements within this broader scheme. This is particularly relevant nowadays, especially in light of a renewed interest in small eye movements and how they might influence visual and cognitive processing (3, 18–22).

Investigating the neural control of eye movements naturally includes studies of the superior colliculus (SC). The SC is known to contribute to eye movement generation, with a

Correspondence: Z. M. Hafed (ziad.m.hafed@cin.uni-tuebingen.de).
Submitted 29 December 2020 / Revised 1 February 2021 / Accepted 2 February 2021

well-known classic role in driving saccades (23–27), including large gaze shifts requiring a combination of both eye and head movements (28–32). This structure also supports smooth pursuit eye movements (33–36), which involve foveal movement goals. All of this points to the importance of the SC in orienting responses in general, whether they are overt or covert (2, 37–40). This is in addition to the SC's role in modulating pupil diameter (41–43). At the foveal scale, it is now known that the SC magnifies the representation of the central visual field much more than previously assumed (44), meaning that a role for the SC in active vision at the foveal scale also figures prominently.

An interaction between vision and eye movements at the level of the SC, whether in its foveal visual representation or outside, is also expected because the SC is very much a visual structure in addition to its motor contributions. The superficial SC layers receive direct retinal projections (45–48), and the SC also receives inputs from a number of cortical visual sensory areas (49–54). This means that the SC is fundamentally a sensory-motor structure, with the deeper layers also exhibiting multisensory responses (55–60). From the perspective of this article, its sensory-motor nature implies that the SC is a perfect candidate for studying the neural mechanisms of vision and action together. In fact, the SC contains anatomical loops within its layers, linking purely visual superficial layers with deeper visual-motor layers (37, 61–64) and vice versa (65–69). Moreover, these loops exhibit rich interactions showing both excitatory and suppressive influences (65, 68). This is in addition to equally rich lateral interactions within the layers (70), which likely help in mediating interactions between foveal and extra-foveal active vision that we summarize in this article. Given that the SC also projects to both downstream motor systems (71–73) and upstream cortical visual areas (74–85), the role of the SC in active vision also extends beyond the scope of intra-SC connections.

In line with all of the above, in addition to recent emerging attempts to study the role of the SC in the control of tiny eye movements, parallel investigations of visual modulations around the time of such eye movements were also made. The net result is that we now have a relatively rich recent description of active vision processes in the primate SC at the foveal scale of visuomotor behavior. In what follows, we provide an integrative view of these processes, and we describe their implications and consequences for future research. Reviews of other aspects of SC function are provided elsewhere (37, 40, 62, 86).

VISUAL AND NONVISUAL DRIVES FOR FIXATIONAL EYE MOVEMENTS

Fixational eye movements come in two primary flavors: microsaccades and the slow ocular position drifts that occur in between them (87, 88). We will address ocular position drifts in the section SMOOTH OCULAR MOVEMENTS AND FOVEAL SC GOAL-RELATED AND VISUAL REPRESENTATIONS; for the case of microsaccades, these are small saccades that are typically $<$30 min arc in amplitude (89–91), although the exact definition of what constitutes an upper limit on microsaccade size seems to vary between studies (1, 4, 92, 93). Here, we use the functional definition of these movements as being fixational eye movements; that is, they occur during the intended goal of maintaining gaze fixation on a foveal target. Functionally, they serve to sample the foveal visual environment (94–96), much like larger saccades sample different visual scene locations (97, 98).

It was found approximately one decade ago that microsaccades are associated with strong activity in the rostral region of the SC, which represents the most central portion of the visual field (91, 99). Whenever a microsaccade is generated, rostral SC neurons in the intermediate and deep layers exhibit a discharge characterized by a premovement buildup of neural activity, followed by a peak burst of action potentials before a return to baseline (91, 99). For every neuron, the preferred range of microsaccade amplitudes and directions that are associated with elevated perimovement discharge is different. This results in each neuron exhibiting a movement response field (RF), or the range of movement directions and amplitudes that a neuron represents. Such microsaccade-related SC activity is also causally relevant for microsaccade generation, as eliminating this activity also reduces microsaccade frequency (91, 100). As we also describe in the section SMOOTH OCULAR MOVEMENTS AND FOVEAL SC GOAL-RELATED AND VISUAL REPRESENTATIONS, such activity additionally represents goal locations for other active oculomotor behaviors at the foveal scale, such as with smooth pursuit eye movements (33, 35, 36, 101, 102) or even ocular position drifts.

For almost 10 years, the extent of knowledge about the role of the SC in microsaccade generation was limited to the description just provided. However, a lot remained to be learned. For example, there were no descriptions of different cell types in relation to microsaccades, as had been done before for larger saccades. Specifically, for the latter movements, there are mixtures of visual-only neurons, visual-motor neurons, and motor neurons associated with saccades in the SC (27, 103–106). However, historical investigations of the rostral SC, representing small visual eccentricities, were primarily focused on its motor roles, whether in fixation (107), smooth pursuit eye movements (36), or microsaccades (91, 99). Understanding the full diversity of microsaccade-related discharge in the SC became especially important, in light of these general SC properties, when considering the fact that microsaccades were becoming increasingly accepted as being purposeful eye movements (108), meaning that they actively optimize eye position at the fixated target in both humans (94, 95) and monkeys (20, 96, 109).

Two recent studies enabled the above-mentioned needed advances in the understanding of the broader role of the SC in microsaccade generation. In one study, it was found that the SC has a highly sensitive and high fidelity visual representation of foveal images in its rostral region (44). Thus, it is now known that the SC at its foveal end not only has microsaccade-related discharge in the intermediate and deep layers (91, 99), but that it also contains very sensitive visual neurons (in the superficial and intermediate layers) rapidly detecting tiny images appearing within the rod-sparse foveola region of the retinal image (44). As expected, the visual RFs of these neurons are much smaller than eccentric visual RFs, resulting in a remarkable continuity of RF sizes as a function of eccentricity from the smallest to largest RFs known to exist in the SC (44, 103, 110–112). As we

will also state when discussing fixational ocular position drifts, deeper layer SC activity that is involved in microsaccade generation also contributes to representing retinotopic foveal goal locations during fixation periods in between microsaccades (39, 100).

In the second study, the authors went even further by designing a behavioral task that explicitly dissociates visual sensory responses from movement-related discharge at the small scale of microsaccades (108). These authors specifically demonstrated that monkeys and humans can very naturally, and with remarkably minimal training, generate precise and accurate "memory-guided microsaccades" (108). The task consisted, first, of an onset of a brief tiny visual flash at a foveal location; then, a memory period ensued, and the subjects were only allowed to generate a spatially accurate memory-guided saccadic movement after the fixation spot disappeared. The authors deliberately picked foveal target eccentricities that resulted in saccade sizes similar to the sizes of microsaccades observed during simple gaze fixation, allowing them to explore potential nonvisual drives for microsaccades. An example trial from this task can be seen in Fig. 1*A*, and demo movies can also be viewed at: https://www.nature.com/articles/s41467-019-11711-x#Sec21. Success rate for memory-guided microsaccades was at least as good as, if not slightly better, than the success rate for similarly sized visually guided movements (108). Moreover, the reaction times after the "go" signal (Fig. 1*A*) were like those expected from task-instructed small eye movements (108, 113), and the directional errors were consistently minimal (Fig. 1*B*). Finally, the amplitudes of memory-guided microsaccades reflected the remembered target eccentricities well, and they also formed a continuum with larger memory-guided movements when extra-foveal memorized target eccentricities were tested (Fig. 1*C*).

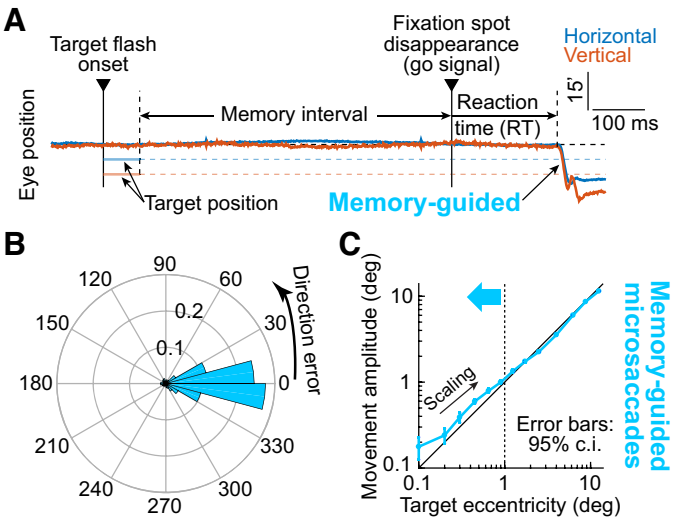

Figure 1. Memory-guided microsaccades as a means to study nonvisual drives for microsaccade generation. *A*: example trial from a monkey successfully triggering a directionally accurate small saccade to a remembered foveal target flash, and within a short reaction time from an abstract go signal. The target was only briefly flashed at trial onset, and the monkey had to remember its location until the go signal. *B*: memory-guided microsaccade directions were highly congruent with the directions of the remembered foveal targets. Results from an example monkey are shown. Two other monkeys and seven human subjects exhibited very similar results. *C*: memory-guided microsaccade amplitudes also reflected the remembered target eccentricities well, and they formed a continuum with larger eye movements toward more eccentric targets (the shown data are from the same monkey as in *B*). Note that the smallest movements (e.g., <1° in amplitude) slightly overshot the target, but this was also true in manual response versions of the task not requiring small eye movements (108). This suggests a distortion of foveal space in short-term working memory. Adapted with permission from Willeke et al. (108).

Besides clarifying a long-standing misconception that microsaccades are involuntary eye movements, the task of Fig. 1 now allowed studying the different components of SC neural activity in association with the small scale of microsaccades. For example, the neuron in Fig. 2*A* exhibited a discharge for memory-guided microsaccades that was very similar to the classic microsaccade-related activity characterized earlier (91, 99). The movement RF of the neuron (shown in the right half of Fig. 2*A*) was also almost entirely foveal; the radial dimension is plotted in the figure on a logarithmic scale to magnify small-amplitude ranges (99). Using the different epochs in this task, Willeke et al. (108) then classified SC neurons into one of five different types (Fig. 2, *B*–*E*) based on their activity in relation to visual onsets, memory-guided microsaccades, or visually guided microsaccades. Remarkably, it was found that the SC contains the entire spectrum of possible neural discharge variants, suggesting that all of the ingredients for active vision at the foveal scale exist in this structure (108).

More specifically, the authors first confirmed that the foveal representation in the rostral SC contains all three most well-known saccade-related neuron types: visual-only neurons, visual-motor neurons, and motor neurons. Visual-only neurons exhibit a short-latency visual response after the onset of the flashed cue indicating the upcoming microsaccade target location (Fig. 2*B*; V-neurons); however, they do not exhibit any movement-related discharge for microsaccades directed toward the RF, whether the microsaccades are memory-guided or visually guided (Fig. 2*C*; V-neurons). Visual-motor neurons show both visual responses (Fig. 2*B*; VM-neurons) as well as perimovement activity elevations like those in Fig. 2*A* (Fig. 2*C*; VM-neurons). Note how the motor discharge in these neurons is similar whether the microsaccades are visually guided or memory-guided. Finally, motor neurons do not show visual responsiveness (Fig. 2*B*; M-neurons), but they show movement-related discharge regardless of visual guidance of microsaccades (Fig. 2*C*; M-neurons).

Remarkably, two additional cell types were discovered using the memory-guided microsaccade task (108). The first type is that of "visually dependent saccade-related neurons" (VDSR-neurons). These neurons are either visual-motor or motor (i.e., with or without a visual response), but they only exhibit movement-related discharge if the microsaccade is visually guided (Fig. 2, *B* and *C*; VDSR-neurons). If a similar microsaccade is directed toward a blank, as in the case of memory-guided microsaccades, then the neurons do not exhibit any movement-related discharge at all, as if they are not contributing to the movement. Only three prior studies with large saccades have reported an occasional observation of these visually dependent saccade-related neurons (104, 114, 115), with the general assumption being that these neurons are extremely rare. However, with larger and less biased sampling obtained using multi-electrode array recordings, Willeke et al. (108) demonstrated that these types of neurons

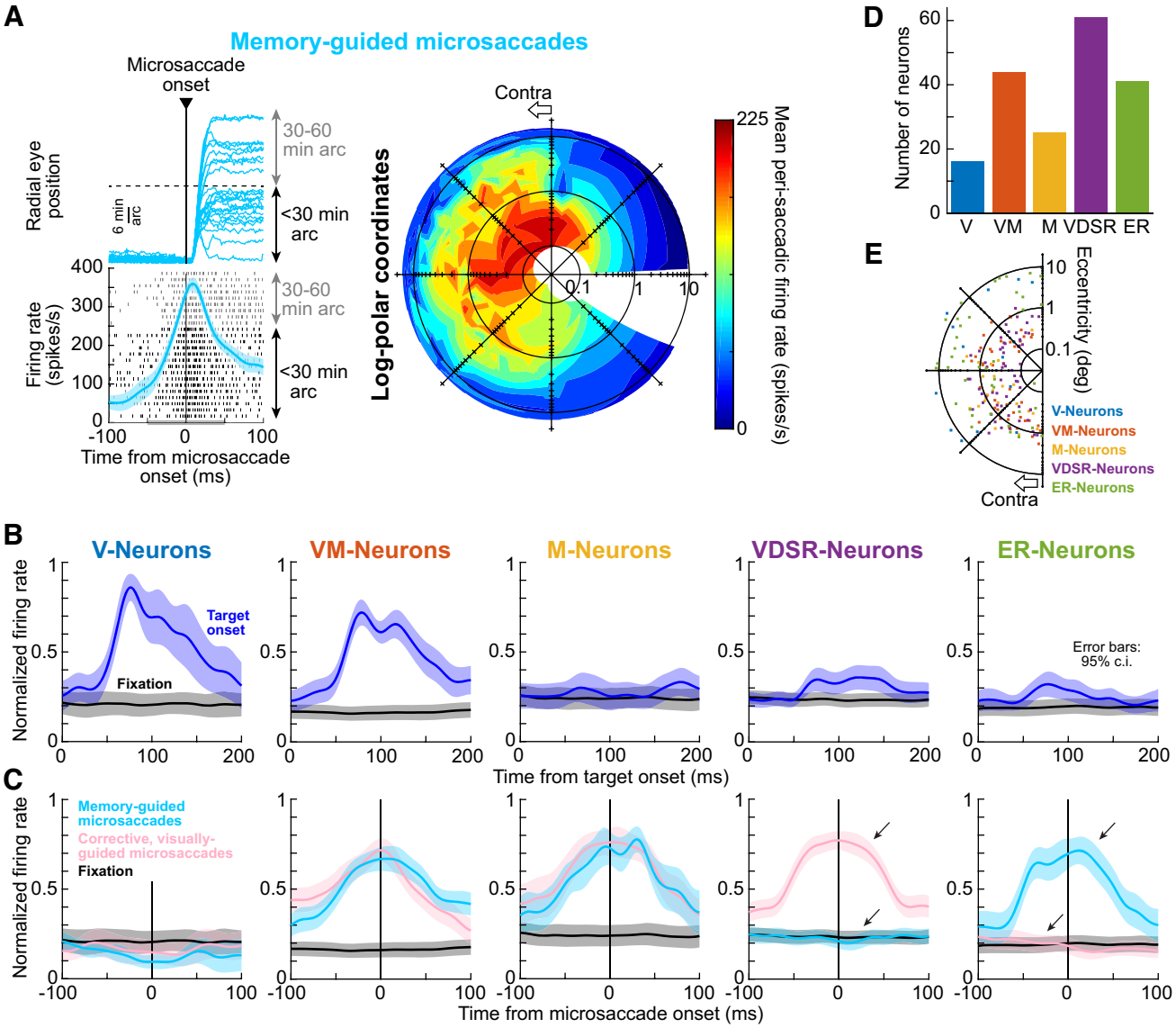

Figure 2. Full gamut of visual and saccade-related neural modulations within the foveal visual representation of the primate SC. *A*: the *left* panel shows eye position (*top*) and neural discharge (*bottom*) for contraversive microsaccades that are memory-guided, in the absence of any visual target (108). The right panel shows the movement response field (RF) of the same neuron. The neuron exhibits microsaccade-related activity even with memory-guided microsaccades. *B* and *C*: the foveal SC representation contains all combinations of visual and movement-related discharge. V stands for "visual-only neurons"; VM stands for "visual-motor neurons"; M stands for "motor neurons"; VDSR stands for "visually-dependent saccade-related neurons"; and ER stands for "exclusively responding" neurons for memory-guided microsaccades (108). Examples of neural discharge for all of these types are shown either after visual stimulus onset (*B*) or around microsaccade generation (*C*). Note how V neurons only discharge for stimulus onsets but not for eye movements (whether visually guided or memory-guided), whereas M neurons only discharge for eye movements (whether visually guided or memory-guided) but not for visual stimulus onsets. Of note, VDSR neurons show robust neural discharge for microsaccades, but only when these movements are visually guided; the neurons are otherwise silent for the same movement sizes and directions triggered toward a blank. *D*: distribution of cell types encountered in the foveal SC representation. VDSR neurons are much more common than might be assumed based on the sparse literature on these neurons with large saccades. *E*: all of the neuron types have RF hotspot locations that fully cover the foveal visual representation; the only exception is ER neurons, which tend to be more eccentric, suggesting an inward expansion of RF extents with memory-guided movements (108). Adapted with permission from Willeke et al. (108).

are actually much more common than previously assumed. For example, Fig. 2*D* plots the distribution of these neurons relative to the other types, and VDSR neurons are at least as likely as the sum of VM and M neurons combined. This suggests that VDSR neurons are a key component of SC neural discharge, and they warrant much deeper investigation. For one, these neurons cast strong doubt on a current hypothesis that intrasaccadic SC bursts dictate the moment-to-moment kinematics of an ongoing saccade (116–118); indeed, a significant fraction of neurons completely stop bursting for memory-guided movements whose kinematics are only mildly different from those of visually guided saccades (114). We argue that the functional role of SC movement-related bursts, whether for microsaccades or larger saccades, remains to be an open and intriguing question, especially in light of the prevalence of VDSR neurons (Fig. 2*D*).

The second new cell type revealed by the memory-guided microsaccade task is the functional opposite of VDSR neurons. In this type, the neurons only exhibit movement bursts for memory-guided microsaccades rather than for visually guided microsaccades (Fig. 2, *B* and *C*; ER-neurons). In their study, the authors labeled these neurons as "exclusively responding" neurons (108), meaning "exclusively responding for memory-guided microsaccades." This property of the neurons likely reflects an expansion of movement RFs associated with the increased spatial uncertainty of movement goal location. Indeed, within the central visual field representation in the rostral SC, the RF hotspots of ER neurons are more eccentric than for other types of neurons (Fig. 2*E*). That is, these neurons normally represent larger eye movements. However, with increased target location uncertainty due to a lack of visual guidance, the RFs of these neurons expand inward toward the fovea; as a result, the neurons respond exclusively for memory-guided microsaccades (with expanded RFs) but not for similarly sized visually guided movements (108). An RF alteration is known to exist with caudal neurons for larger memory-guided saccades (119, 120), and even foveal goal representations recruit larger populations of neurons when the foveal target for fixation (100) or smooth pursuit eye movements has larger spatial uncertainty associated with it (101, 102).

Therefore, the foveal region of the SC contains the full gamut of neuron types for linking vision and eye movements, and the neuron RF hotspots also tile the entire visual field representation (Fig. 2*E*). Moreover, nonvisual drives for microsaccades (and larger saccades) can dramatically alter SC activity, as in the case of VDSR neurons. This diversity of neural response types leaves open important additional questions, which have the potential to further clarify behavioral properties of orienting eye movements at the foveal scale. Consider, for example, the specific case of visual targets in the upper versus lower retinotopic visual fields. With extrafoveal SC recordings, it was found that the SC has significantly stronger and faster visual responses in neurons representing the upper visual field than in neurons representing the lower visual field (Fig. 3*A*) (111). That is, a stimulus within a neuron's preferred RF hotspot location elicits a significantly stronger and earlier visual response if the neuron's RF hotspot location is above the horizontal meridian; if the neuron represents a lower visual field location, a stimulus at its preferred RF hotspot location evokes weaker and later responses. In terms of behavioral consequences, the significance of visual burst strength and latency in the SC for saccadic reaction times is well established (111, 121–123). As a result, one might expect that saccades toward the upper visual field have faster reaction times than saccades toward the lower visual field. This is indeed true (Fig. 3*C*) (111, 113, 124, 125). For microsaccades, a recent study explicitly asked whether these small movements would still exhibit a similar asymmetry in reaction times (113). This was again the case (Fig. 3*C*, *right*; the *left* panel replicates findings from other studies). Therefore, visually guided microsaccades are triggered faster for foveal visual targets in the upper visual field than for foveal visual targets in the lower visual field, and this reaction time asymmetry persists even for delayed visually guided and memory-guided microsaccades (113). This leads to a strong prediction that visual response properties

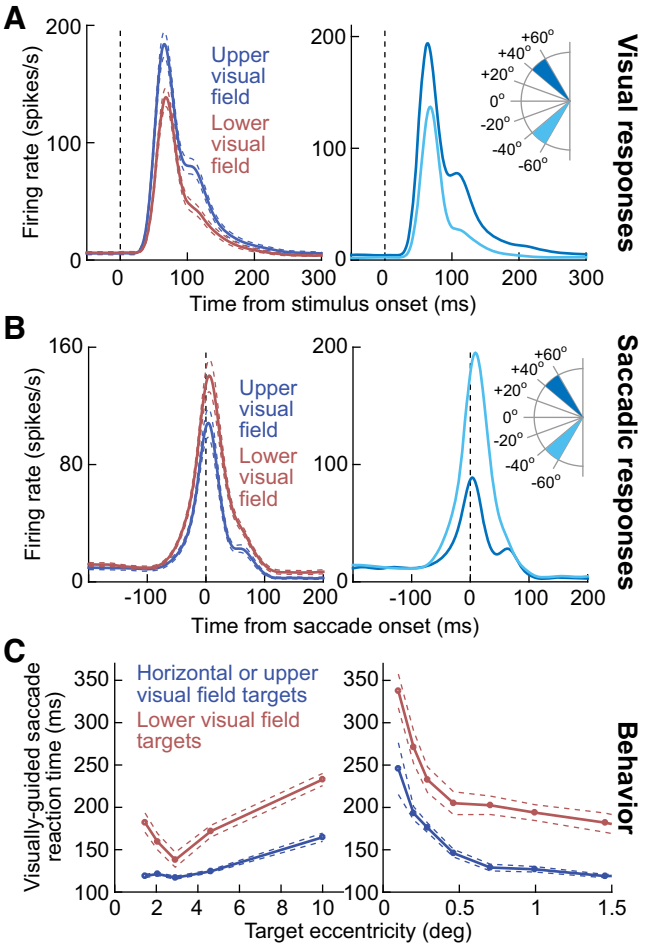

Figure 3. Asymmetric representation of upper and lower visual field locations, in both visual and saccade-related superior colliculus (SC) discharge, and with direct consequences for active vision at the foveal scale. *A*: visual responses in the primate SC are earlier and stronger in neurons representing the upper visual field (blue) than in neurons representing the lower visual field (red). This holds even when neurons are matched for eccentricity and depth within the SC. The *left* panel shows a population summary, and the *right* panel focuses on neurons representing 40°–60° directions from the horizontal meridian as an example direction range. *B*: saccade-related discharge is also asymmetric with respect to saccades directed toward the upper vs. lower visual field. However, surprisingly, the motor bursts are stronger for lower visual field saccades than for upper visual field saccades. The functional implications of this reversal in movement-related discharge (relative to visual responses) remain to be investigated. *C*: consistent with SC visual response properties, saccadic reaction times are significantly faster for upper visual field saccades than for lower visual field saccades. The *right* panel shows that this effect still holds for microsaccades within the foveal visual representation. This makes it likely that the neural results in *A* and *B* would still be observed within the foveal region of the primate SC. *A* and *B* were adapted with permission from Hafed and Chen (111); *C* was adapted with permission from Hafed and Goffart (113).

like those shown in Fig. 3*A* in extrafoveal SC neurons might also still exist for foveal visual neurons. Future research should test for this possibility. It is also interesting to note from Fig. 3*C* that whenever target eccentricity decreases below ~2°, saccadic reaction times strongly increase in general (and more so for lower visual field targets). The persistence of this increase independent of visual guidance of the movements (113) suggests that it is not purely sensory in origin. Rather, it reflects the idea that gaze fixation is an

outcome of a distributed balance of many competing small movement tendencies, represented by small-eccentricity RFs in the rostral SC, that cancel each other out (39, 100, 113).

Surprisingly, saccade-related bursts in the SC show the exact opposite visual field asymmetry from visual responses: neurons representing saccade target locations in the lower visual field emit stronger motor bursts (for their preferred saccades) than neurons with movement RFs in the upper visual field (Fig. 3*B*) (111). Even though the functional significance of this asymmetry is not yet clear, one can also predict, based on all of the aforementioned evidence, that microsaccade-related bursts in the rostral SC would be stronger in neurons preferring downward microsaccades than in neurons preferring upward microsaccades. This remains to be seen. Interestingly, such an asymmetry of saccade motor bursts between upper and lower visual field saccades (Fig. 3*B*) (111) presents another opportunity related to our discussion of VDSR neurons in Fig. 2. Specifically, if it turns out that saccade kinematics for upper and lower visual field target locations are not different from each other, then the difference in saccade-related motor bursts (Fig. 3*B*) provides further evidence against the idea that intrasaccadic SC motor bursts dictate the moment-to-moment kinematics of eye movements. A detailed kinematic analysis of upper versus lower visual field saccades and microsaccades is, therefore, warranted.

In all, we now know that combined with an enlarged representation of the fovea (44), the primate SC has all of the ingredients that are necessary for successfully engaging in active vision at the foveal scale (Fig. 2). This is functionally important because eye movements allow remote sensing of the far environment by vision (Fig. 3) (111, 126). From that perspective, the need for active vision at the foveal scale becomes immediately obvious. A simple example of this is the size of the full moon in the night sky on the retina; the moon subtends $\sim$0.5° (30 min arc) of visual angle, which is a very small value; yet, we can still scan the individual features on the face of the moon with small eye movements and high fidelity visual analysis. In that sense, microsaccades during fixation are essentially no different from small saccades scanning a small region of the visual image (94, 95, 97, 98). The fact that we can also engage memory at such a foveal scale (108) is also worthy of note, and it provides a means for linking microsaccade-related SC discharge to discharge representing "imaginary" foveal goals during smooth pursuit eye movements (101, 102). As we will describe later, this also has the potential for extending the role of the rostral SC to representations associated with smaller and slower ocular position drifts during fixation, which continuously occur in between microsaccades and saccades. This extension will be highly useful for at least two reasons. First, it will reconcile our current take on the rostral SC's role in active vision at the foveal scale with its historically hypothesized function in maintaining gaze fixation and preventing saccades (107, 127). Second, it can relate rostral SC activity for scanning a foveal target using microsaccades (and other small eye movements) with foveal object recognition processes in ventral cortical visual areas. Indeed, studying the detailed functional similarities and differences between SC visual processing capabilities and those of cortical visual areas is an important area of future research.

MICROSACCADES AND ENHANCED VISUAL SENSITIVITY

The fact that the SC has a rich diversity of visual and oculomotor signals at the foveal scale (44, 108) also provides an opportunity for investigating how visual sensitivity, whether at the level of perception (18) or neurons (128), can be modulated during active foveal visuomotor behavior. The motivation here dates to some of the earliest studies on vision and eye movements in the primate SC with large saccades (112, 129). There, it was found that the onset of a visual stimulus elicits an enhanced visual response by SC neurons if the stimulus is behaviorally relevant as opposed to when the same stimulus is just passively viewed. By behavioral relevance, it is meant that the stimulus was to become the target of a foveating saccade. This work was then extended further by presenting visual sine wave gratings of different contrasts within the visual RFs of SC neurons, allowing the authors to construct contrast sensitivity curves (130). It was found that the preparation to make a saccade toward an RF stimulus increases a neuron's visual contrast sensitivity (130). These SC neural studies were interesting because they represented a neural correlate of perceptual active vision studies that have emerged and became popular over the past three or four decades. A hallmark of all of these studies is that visual sensitivity and other perceptual properties of human subjects are probed using stimulus onsets occurring near the time of saccades (131–135).

The similarity of SC neural discharge for microsaccades and larger saccades (91, 99, 108) led, in light of these (neural and perceptual) findings with large saccades, to a new hypothesis that perimicrosaccadic modulations in vision might still happen at the foveal scale (1). When this idea was tested perceptually in humans, not only was it validated, but another highly interesting revelation also occurred (18): perimicrosaccadic changes in vision can still happen when microsaccades occur in tasks requiring peripheral covert visual attention, meaning that performance changes in covert visual attention tasks are periodically punctuated by perimicrosaccadic effects. As a result, enhancement or suppression of attentional performance, known to happen at different times in covert visual attention tasks, might be strictly time-locked to the occurrence of microsaccades in these tasks (i.e., they might be mediated by perimicrosaccadic changes in vision). More specifically, it was found (2, 18, 20, 90) that peripheral attentional performance (a measure of visual sensitivity in SC neurons and neurons in other relevant visual areas) is enhanced whenever a discrimination stimulus appears right before the onset of a microsaccade with a congruent direction (i.e., with a vector direction aligned with the vector connecting the fovea to the peripheral stimulus location); performance is reduced for a microsaccade in the opposite direction (18). Thus, perceptually, visual sensitivity can indeed be enhanced before individual microsaccades, in a manner similar to presaccadic enhancement for large saccades (130). The interesting difference here is that such enhancement can happen even at peripheral eccentricities far away from the microsaccade movement end points.

Directly motivated by these observations, SC recordings were made in neurons representing different eccentricities. Sine wave gratings of different contrasts were presented at different times relative to microsaccade onset. Remarkably, the authors found that visual responses are enhanced if stimulus onsets occur immediately before the onset of microsaccades made toward the locations of the peripheral stimuli (128). Besides being a direct correlate of perceptual effects in covert visual attention tasks in humans (18), these results were a clear example of how active vision at the foveal scale can be relevant for peripheral visual sensitivity farther away from the saccade movement goal. Therefore, previous results of SC visual enhancement before saccades (112, 129, 130) extend to microsaccades, and with the added insight that the enhancement can spread to the periphery.

The analyses in Chen et al. (128) also revealed interesting differences in the properties of sensitivity enhancement between visual-only and visual-movement SC neurons. Specifically, although the contrast sensitivity curves of both visual-only and visual-movement SC neurons can be gain modulated (in a primarily multiplicative fashion) before microsaccade onset, enhanced sensitivity for directionally congruent microsaccades is only eccentricity-dependent in visual-motor neurons but not in visual-only neurons. In other words, for stimuli appearing before microsaccades directed toward the stimuli, visual-only neurons show enhanced visual responses regardless of stimulus (and neural preferred) eccentricity. Enhanced visual responses in deeper visual-motor neurons are, instead, restricted to eccentricities of up to ~5°–10°; more eccentric neurons are suppressed (128). It would be interesting to explore the functional consequences of these differences between visual-only and visual-movement neurons in behavior, as was done more exhaustively for suppression, a topic that we discuss in detail shortly.

Enhanced visual sensitivity before microsaccades is additionally interesting from the perspective of intra-SC connections alluded to earlier. Ghitani et al. (65) identified an excitatory pathway from the motor layers of the SC back toward the superficial visual layers. This confirms the richness of visual modulations around eye movements that exist in the SC, including sensitivity enhancement (112, 128–130). However, important questions still remain. For example, Tian and colleagues used the results in Chen et al. (128) to argue that only perimicrosaccadic changes in visual sensitivity may be, at least in principle, sufficient to fully account for one of the most classic results in covert visual cueing paradigms (2, 18, 20). These authors argued that if microsaccades occur systematically in covert cueing tasks (90, 136, 137), and if perimicrosaccadic changes in visual sensitivity do happen (18, 128), then a model that only knows about these two properties (without the need to invoke a separate entity called "attention") fully replicates classic notions of "attentional capture" (enhanced visual performance in covert attentional cueing tasks) or "inhibition of return" (suppressed visual performance at cued locations). Because this may be viewed as a controversial idea, a critical further test of their hypothesis would be to devise a means to causally trigger microsaccades (in the absence of attentional cueing) and then measure peripheral visual sensitivity for stimuli that are completely irrelevant to behavioral performance. If microsaccades do play a causal role in modulating peripheral SC visual sensitivity (and behavior), then SC visual responses should be modulated with such a causal manipulation. The latest findings from the same authors, using this approach, strongly support this hypothesis (138).

In all, from the perspective of enhanced SC visual sensitivity around the time of microsaccades, studying active vision at the foveal scale in the SC can now bridge very diverse fields such as microsaccade control and perceptual selection and enhancement, and in an intriguing manner (2). We next turn to an equally intriguing topic associated with visual sensitivity in the SC, this time concerning the effects of tiny eye movements on visual suppression.

MICROSACCADES AND SUPPRESSED VISUAL SENSITIVITY

Another classic example of perisaccadic modulation of vision from the large saccade literature is that of saccadic suppression (131, 139–143). In this phenomenon, presentation of visual stimuli at locations other than the saccade target results in a strong reduction in visual sensitivity (and perceptual detectability), if the stimuli appear in the immediate temporal vicinity of saccades. This phenomenon is thought to underlie perceptual stability of vision in the face of continuous eye movements (135, 144). In the SC, Wurtz and colleagues studied mechanisms of saccadic suppression with large saccades in great detail, but primarily in the superficial visual-only layers (106, 145–148). They described two related phenomena. In one, the background activity of SC neurons is momentarily suppressed if the image of a stimulus is swept across a visual RF by saccades. This also happens when saccades occur in complete darkness, suggesting an extraretinal source signal acting to actively reduce neural activity (147). Interestingly, experimental blockage of proprioceptive feedback from the eyeball muscle periphery did not eliminate this reduction in SC activity (146), leading the authors to propose that the reduction represents an impact of a corollary of the outgoing motor command on visual neural responses (146). In the second phenomenon, the authors presented stimulus onsets (e.g., a bar that was swept through the RF) around the time of saccade onset. They found that visual sensitivity of superficial SC neurons is also decreased in such a case (145, 147). In other words, the visual response to a stimulus is weakened if the stimulus appears in the temporal vicinity of a saccade. This latter phenomenon is what we label as saccadic suppression here, because it relates most closely to the experimental paradigms used in human perceptual experiments to study visual sensitivity around the time of saccades (135); in these paradigms, a sudden (and usually very brief) stimulus onset is presented near saccade onset to probe the instantaneous state of visual system sensitivity, as was done in the SC (145).

For microsaccades, there have been no clear correlates, yet, of the early experiments by Wurtz and colleagues, exploring reductions of background activity when retinal images are swept around by eye movements. Recently, Khademi et al. (149) recorded visual neural activity when a stimulus was inside the RF of an SC neuron; if a microsaccade swept the image of the stimulus (by a small amount) in the RF, there was no strong evidence of suppressed background activity.

This could be due to the fact that the stimulus during the microsaccades is always inside the excitatory central part of the visual RF. Indeed, visual-visual interactions for suppressed visual activity with large saccades seem to play an important role, and visual stimulation (by saccades) of both the center and surround region of an RF is an important prerequisite for reduced activity (148). In any case, this does not mean that microsaccades are not associated with suppressed visual sensitivity when stimuli appear near the time of microsaccade onset. To the contrary, there is very strong suppression of sensitivity (150, 151). Therefore, suppressed visual sensitivity may or may not be directly linked to suppression of background activity due to saccade-induced image displacements.

The basic phenomenon of microsaccadic suppression (of visual sensitivity) in the SC looks remarkably similar to perceptual measures of microsaccadic suppression with brief stimulus onsets (141, 143, 151). Briefly, if a stimulus appears within ~70 ms before or after microsaccade onset, then the response of a visual-motor SC neuron to the stimulus is strongly suppressed relative to when the very same stimulus appears without any temporally coincident microsaccades (151). Suppression starts before microsaccade onset, is strongest immediately after such onset, and recovers again <100 ms later (151). Therefore, this time course looks very similar to the time course of microsaccade-related discharge (e.g., Fig. 2*A*, *left*)—in one case, movement-related activity is elevated, and in the other, visual sensitivity is suppressed, but with similar temporal progression. Even in the studies of microsaccade-related enhancement of visual sensitivity mentioned in the previous section (128), if the microsaccade was not directed toward the peripheral stimulus, or if the stimulus appeared right after a microsaccade, suppression occurred instead of enhancement. As also stated in the previous section, for far peripheral visual-motor neurons, suppression also occurred before microsaccades made in the direction of the test stimulus.

Therefore, complementing neural enhancement, microsaccadic suppression of visual sensitivity of SC neurons represents yet another example of how foveal action can have an impact on extrafoveal vision, since suppression occurs extrafoveally (151). However, after the initial characterizations of SC microsaccadic suppression approximately one decade ago (151), important questions remained. In particular, there was no characterization of microsaccadic suppression of the activity of visual-only (superficial) SC neurons, and there remained an interest in relating SC visual suppression to behavioral effects. Most importantly, with large saccades, perceptual saccadic suppression was discovered to exhibit very intriguing dependencies on the image properties of the visual stimuli appearing around the time of saccades (131), and it was, therefore, important to attempt to search for a neural correlate of these dependencies.

Recent SC studies with microsaccades explored all of these questions. First, the cell-type dependence of visual sensitivity suppression in the SC was investigated. Remarkably, it was found that microsaccadic suppression of visual sensitivity in the SC is much weaker in visual-only neurons than in visual-motor neurons (150). This effect is clearly seen in Fig. 4, *A* and *C* with two example neurons. Consider, for example, the *leftmost* panels. In the visual-only neuron (Fig. 4*A*), a

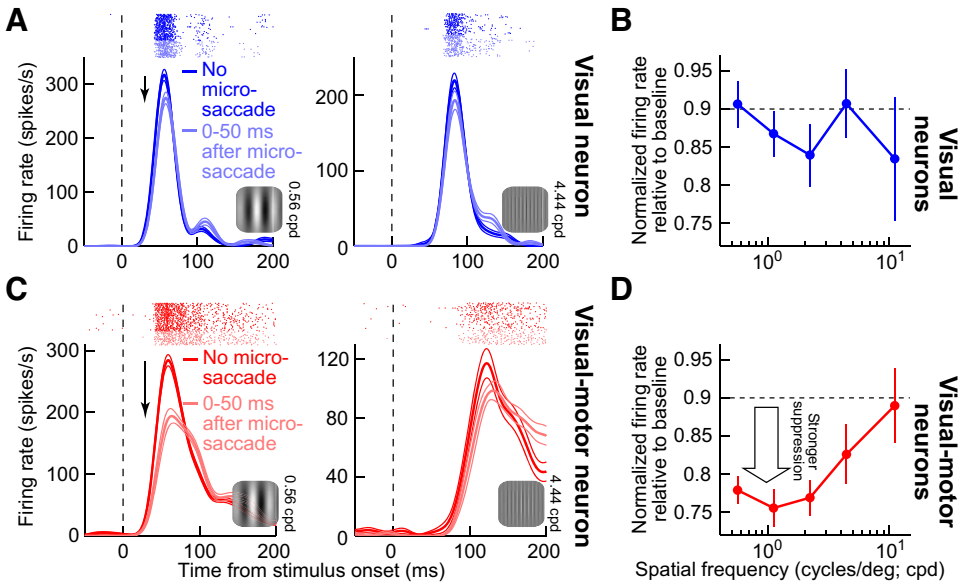

Figure 4. A neural locus for spatial-frequency specific microsaccadic suppression in visual-motor neurons of the primate superior colliculus (SC). *A*: example visual responses from a visual-only neuron in the superficial SC. The *left* panel shows responses to a low spatial frequency grating, and the *right* panel shows responses to a higher spatial frequency grating. If the grating appears immediately after a microsaccade, visual responses for both gratings are only mildly suppressed (faint colors) relative to baseline visual responses (saturated colors). *B*: across spatial frequencies, suppression of visual responses by microsaccades (relative to visual responses for identical gratings without microsaccades) is only mild and not dependent on spatial frequency. *C*: example visual responses from a visual-motor SC neuron. Unlike in *A*, visual responses are strongly suppressed by microsaccades (relative to baseline), but only for the low spatial frequency grating. Visual responses are virtually unaltered by microsaccades for the higher spatial frequency grating. *D*: across spatial frequencies, it is clear that visual-motor SC neurons show strong suppression that is dependent on spatial frequency, demonstrating a neural correlate for a classic and well-known human perceptual phenomenon in association with large saccades (131). Adapted with permission from Chen and Hafed (150).

stimulus appeared immediately after microsaccade end and the neuron's visual response was only mildly suppressed. On the other hand, in the deeper visual-motor neuron (Fig. 4*C*, *left*), the same stimulus evoked a very strong visual response in baseline but the response was strongly reduced after microsaccades (150). This is consistent with a study by Hafed and Krauzlis (151), in which it was found that there could be up to ~50% suppression in visual-motor neurons by microsaccades. This dichotomy between visual-only and visual-motor neurons in terms of suppression is very interesting because it suggests that with large saccades, stronger suppression would also still be seen in the deeper visual-motor layers. As described at the beginning of this section, the bulk of early work with large saccades in the past was in exploring suppressed visual sensitivity in only superficial neurons (146–148), so this is an area of interesting future research. In fact, and consistent with our hypothesis, it was recently found that reversible inactivation of the superficial SC layers did not alter the influences of saccadic suppression on visual responses of MT neurons (normally receiving input from the SC through the pulvinar), whereas inactivation of the deeper SC layers did. Thus, saccadic suppression in cortical areas may be mediated more strongly by ascending pathways from the deeper layers to the frontal cortex (82, 83), rather than by ascending pathways from the superficial layers to MT (77).

Another outcome of the study of Fig. 4 (150) is that it explored the impacts of different stimulus properties (in particular, spatial frequencies) on microsaccadic suppression. Each neuron (two examples are shown in Fig. 4, *A* and *C*) was visually stimulated with a grating onset of different spatial frequencies immediately after microsaccade end. It was found that in the visual-only neurons, the mild suppression is constant as a function of spatial frequency; that is, suppression is unselective for spatial frequency (Fig. 4*B*). On the other hand, in visual-motor neurons, suppression strongly depends on spatial frequency. For low spatial frequency stimuli appearing after microsaccades, suppression is strong (Fig. 4*C*, *left*), but it is much weaker for high spatial frequencies (Fig. 4*C*, *right*; note how the visual response with and without microsaccades is almost the same in the case of the high spatial frequency stimulus). This effect is also seen in the population summary of suppression strength as a function of spatial frequency in Fig. 4*D*. This result is interesting because it was the first direct neural correlate of the same perceptual effect (selectivity of suppression) observed in humans with large saccades more than two decades earlier (131). This result also motivated very intriguing and surprising follow-up questions regarding why the spatial frequency dependence of saccadic suppression may or may not emerge, as we describe shortly (152). From the perspective of SC visual functions per se, this result is additionally very interesting because it motivates investigating these functions in relation to cortical visual processes. Specifically, the difference in suppression "tuning" between visual-only and visual-motor neurons precludes a simple model of visual-motor neurons, simply reflecting descending intralaminar connections from the more superficial visual-only layers. Rather, there are rich bidirectional dependencies between the SC and several cortical visual areas that are very important to investigate in more detail in the future (70, 78, 79, 153–155).

As in the case of sensitivity enhancement effects mentioned in the previous section, the microsaccadic suppression results made in the SC (Fig. 4) were all extending much farther into the periphery than the microsaccadic movement end points themselves (150, 151). Therefore, these results represent yet another example of the potential impacts that foveal active vision can have on broader visual and motor modulations in the brain. Indeed, consistent with this, direct behavioral correlates of Fig. 4 were investigated. Specifically, because SC visual responses are particularly relevant for saccadic reaction times (112, 122–124), it was hypothesized that suppressed visual bursts (in association with microsaccades) should translate into slower reaction times for saccade targets at the (extrafoveal) visual burst locations (151). To test this, trials with microsaccades occurring near target onset in a visually guided saccade task were analyzed. It was indeed found that reaction time elevations do consistently occur for stimulus onsets time-locked to microsaccade generation, and with remarkable similarity of time course between such a behavioral cost and the neural visual suppression time course (Fig. 5*A*) (151). These results were recently replicated and extended with human subjects, and also using either saccadic or manual responses (156). Most interestingly, it became necessary to also ask whether such a strong relationship between visual suppression and behavioral costs also existed for visual-only SC neurons, especially given the past work with large saccades in the superficial layers that we alluded to above (145, 147). Therefore, Chen and colleagues exploited the diversity of effects in Fig. 4 to investigate behavioral correlates. They again trained monkeys to generate a visually guided saccade, but this time to a specific spatial frequency grating. In visual-motor neurons, they confirmed that the stronger the neural suppression is, the greater the behavioral reaction time cost that is observed (150). This effect is seen in Fig. 5*B* for stimulus onsets right after microsaccades, a reaction time cost is clear for low spatial frequencies (black), just like visual responses in the SC (visual-motor neurons) are most strongly suppressed (red). The authors then correlated, for all spatial frequencies and all stimulus onset times after microsaccades, reaction time with visual response strength. In visual-motor neurons (Fig. 5*C*), the effects were unequivocal: the weaker the visual response strength, the stronger the increase in reaction time. It is important to note here that this correlation still held even though the visual bursts were measured in a pure fixation task and the saccadic reaction times were measured in a completely different "overt" task, and in completely different behavioral sessions (150). This strongly validates similar observations of how behavioral reaction times can be predicted from visual responses in the SC collected during simple fixation and in separate sessions (122). It is also testimony to the importance of SC visual bursts for visual orienting (121). Remarkably, visual-only neurons showed much weaker relationships to the behavioral effects (Fig. 5*D*). This, again, calls for a reevaluation of the hypothesized (145) role of the superficial SC in mediating saccadic suppression signals to the cortex via a pulvinar pathway.

Another reevaluation is also warranted with respect to perceptual selectivity of saccadic suppression for low spatial frequencies (131). Specifically, Fig. 4 shows that visual-only neurons do not show selective microsaccadic suppression, whereas visual-motor neurons do. Given that visual-only SC

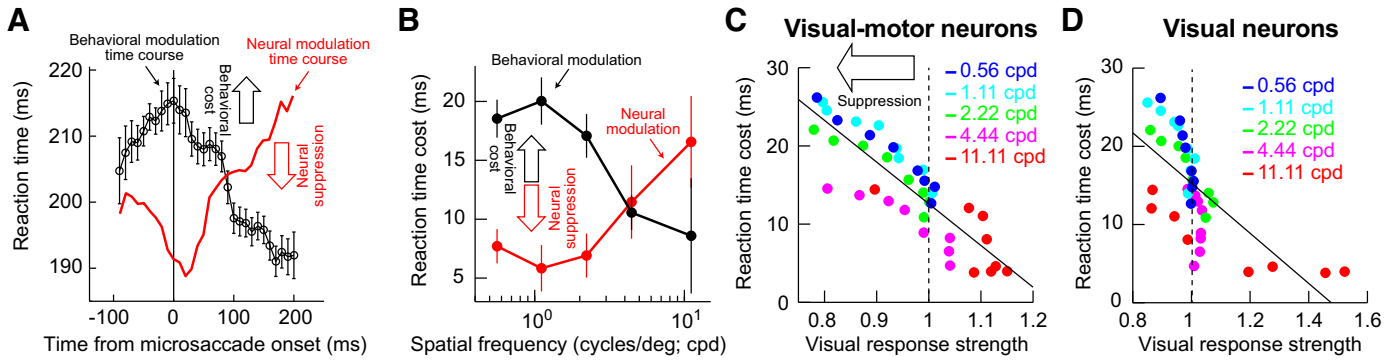

Figure 5. Relevance of superior colliculus (SC) microsaccadic suppression of visual neural responses to active behavior, but only in visual-motor SC neurons. *A*: if a peripheral visual stimulus appears at a time near microsaccade onset, suppression of visual responses (in visual-motor neurons) shows a characteristic time course shown in red (the *y*-axis is not shown for simplicity): peak suppression occurs around microsaccade onset, with premovement and postmovement suppression also occurring. If the subject decides to look at the appearing stimulus, the reaction time of saccades (black) exhibits a significant increase (i.e., a behavioral cost) that has the same time course as the neural suppression time course. Thus, suppression of SC visual responses by microsaccades (red) has direct consequences even for large saccades to the peripheral stimuli. *B*: the same relationship also emerges as a function of the spatial frequency of the appearing stimulus. In visual-motor neurons, the neural suppression of visual sensitivity is strongest for low spatial frequencies (red and Fig. 4; the *y*-axis for the red curve is omitted for simplicity); here, we show measures of visual sensitivity for stimulus onsets appearing immediately after microsaccades (as in Fig. 4). The reaction time cost, or the difference in saccadic reaction time between trials with and without microsaccades (black), is also highest for low spatial frequencies. *C*: across all spatial frequencies and all stimulus times after microsaccade onset (until neural recovery by approximately 100 ms), modulation of visual responses (*x*-axis) is a clear predictor of behavioral efficacy to the peripherally appearing stimulus (*y*-axis). *D*: this relationship is not the same for SC visual-only neurons in the superficial layers, suggesting that the relevance of microsaccadic suppression of visual sensitivity in the SC for behavior is restricted to the visual-motor layers. Indeed, visual-only neurons do not show selective suppression for low spatial frequencies (Fig. 4). *A* was adapted with permission from Hafed and Krauzlis (151). *B–D* were adapted with permission from Chen and Hafed (150).

layers exhibit different forms of lateral interactions relative to visual-motor SC layers (70), this leads to a very intriguing question: is it possible that perceptual saccadic suppression (131) can be rendered unselective for low spatial frequencies simply by changing the far peripheral visual context (putatively activating different kinds of lateral interactions from those involved with the classic experiment)? Remarkably, the answer turned out to be a resounding yes (152). Specifically, Idrees, Baumann, and colleagues performed perceptual saccadic suppression experiments, in which they changed the peripheral visual context that was swept across the retina by saccades (Fig. 6*A*) (152). They then presented perisaccadic flashes of Gabor gratings having different spatial frequencies. With one kind of peripheral visual context (the one shown in the example scenario of Fig. 6*A*), they replicated the classic selectivity of perceptual saccadic suppression for low spatial frequencies (Fig. 6*B*). However, and surprisingly, when they changed the peripheral visual context (but kept all other experimental conditions identical), they obtained suppression that was not selective for low spatial frequencies (152); suppression was equal in strength for all spatial frequencies (Fig. 6*C*). The profile in Fig. 6*B* looks similar to the profile of visual-motor SC neural suppression (Fig. 4*D*), whereas the profile in Fig. 6*C* looks similar to the profile of visual-only SC neural suppression (Fig. 4*B*). These intriguing results will motivate many future experiments further exploring the mechanisms of suppression, whether for microsaccades or larger saccades.

In all, this aspect of active vision at the foveal scale in the SC (i.e., suppression of visual neural sensitivity due to microsaccades) demonstrates, such as with sensitivity enhancement in the previous section, that neural suppression can extend well into the periphery (Figs. 4 and 5), meaning that the effects go beyond the microsaccadic movement endpoints themselves. Thus, investigating microsaccadic suppression can illuminate and motivate very intriguing broader results in active vision in general, and with novel implications for perception (Fig. 6).

VISUAL UPDATING AND MICROSACCADES

The results in the previous two sections were mainly concerned with visual sensitivity modulations around microsaccades. However, microsaccades are still eye movements. As a result, they do change the position of the eye and shift retinal images (albeit by only a small amount). Such shifts are expected to require updating of spatial representations, whether through simple visual image flows on the retina or through additional active mechanisms. Perceptually, a correlate of active updating mechanisms was long believed to emerge when subjects are asked to localize very brief visual flashes that are presented perisaccadically (134, 157–161). In this case, robust mislocalization of the flashes occurs. For microsaccades, this was also found to be the case (18). Interestingly, the direction of mislocalization depends on the eccentricity of the brief flash relative to the microsaccade. Foveal flashes are mislocalized in the direction of the movement, whereas extra-foveal flashes are mislocalized in the opposite direction (18). This, thus, looks like a kind of "compression" toward the foveal movement goal of the microsaccade, as in the case of larger saccadic compression. There are currently no exhaustive neural correlates of this microsaccadic mislocalization effect, save for an analysis of RF positions in the foveal SC representations right before microsaccade onset (44). It was found that foveal RFs are shifted relative to microsaccades, and in a manner that might be related to the directions observed in perceptual effects (18, 44). Future experiments are needed to further elaborate on these findings (44), and particularly in peripheral SC neurons.

In terms of the retinal image visual flows caused by microsaccadic image shifts, this issue was investigated in more detail in the SC recently (149). If a stimulus exists inside the RF

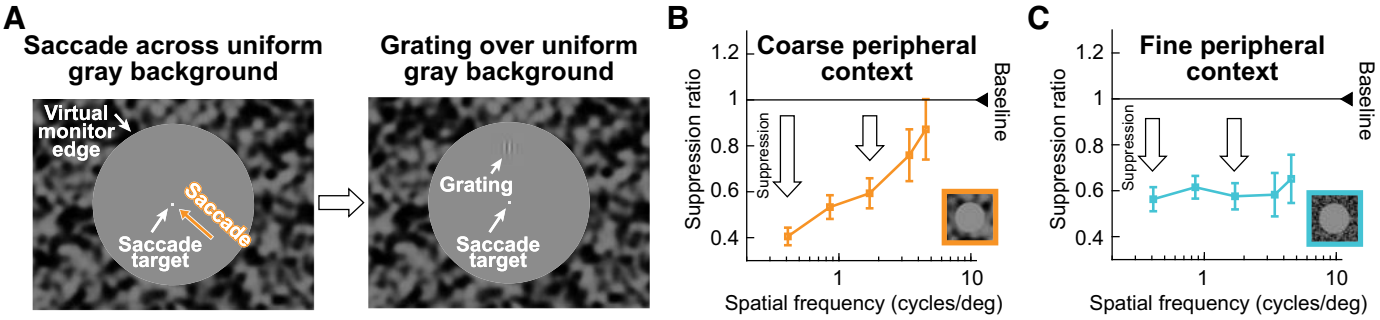

Figure 6. Discovery of a possibility of nonselective perceptual saccadic suppression as a function of peripheral visual context. *A*: in human perceptual experiments, gratings of different spatial frequencies are flashed at different times relative to a saccadic eye movement. *B*: when the texture around the gray background in *A* is coarse (as in the example of *A*), strong suppression for low spatial frequencies is obvious, consistent with the classic report of the phenomenon (131), and also consistent with the reaction time measure of suppression demonstrated in Fig. 5, *A*–*C*. *C*: however, surprisingly, if the peripheral visual context is a fine texture, the suppression becomes nonselective for low spatial frequencies. This means that lateral interactions of visual context matter a great deal for the selectivity of saccadic suppression; saccadic suppression may or may not be selective for low spatial frequencies, depending on visual context (152). As a result, the fact that visual-only neurons in Fig. 4 do not show selective saccadic suppression might suggest that they have different patterns of lateral interactions from deeper visual-motor neurons. Evidence for this exists in the rodent SC (70). Adapted from Idrees et al. (152).

of a visually responsive SC neuron (Fig. 7*A*), then the occurrence of a microsaccade shifts this image by a small amount (e.g., by a few minutes of arc). The net result is that SC neurons exhibit a postmovement visual reafferent response (Fig. 7*B*, *right*) (149). Note that this response generally follows the feature tuning of the neuron to the presented visual stimulus; for example, in the example neuron shown in Fig. 7*B*, the stimulus-evoked response (when the stimulus first appears inside the RF as a visual onset event) favors the low spatial frequency stimulus (Fig. 7*B*, *left*), and this is also true in the reafferent response after microsaccades (Fig. 7*B*, *right*). However, it turns out that this reafferent response reflects more than simply a

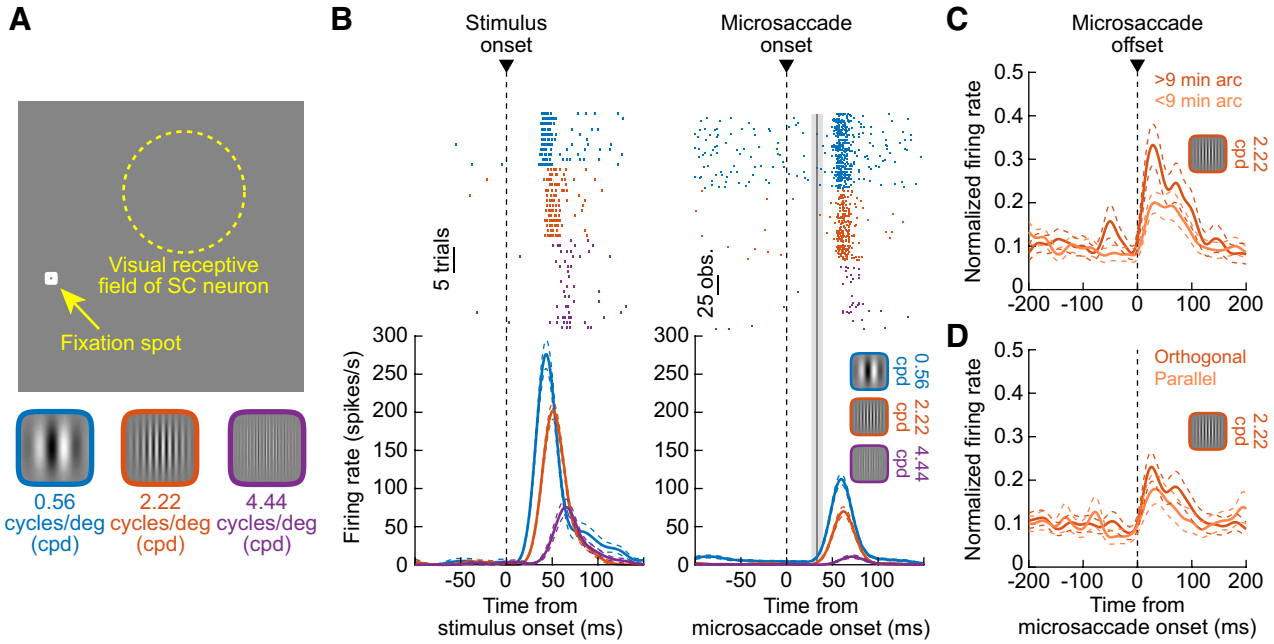

Figure 7. Visual reafferent responses in the superior colliculus (SC) after microsaccades. *A*: a stimulus of a given visual feature (e.g., a vertical grating and with some spatial frequency) can be present during fixation for a prolonged period inside a visual response field (RF) of a visually responsive SC neuron. *B*: if the stimulus first appears inside the RF (*left*), SC neurons detect the stimulus, and they are feature-tuned (they prefer a given variant of the image; in this case, it is the lowest spatial frequency grating) (122). With the stimulus already inside the RF, a microsaccade is associated with a visual reafferent response (*right*), reflecting the (tiny) image shift of the stimulus that is caused on the retina (149). The reafferent response shows similar feature tuning to the *left* panel. *C*: however, not all microsaccade-induced image shifts cause the same reafferent response. The size of the response depends on the amount of luminance modulation that the eye movement vector causes relative to the RF. In this case, a horizontal microsaccade that is big (>9 min arc) results in stronger luminance modulation on the retina and stronger reafferent response than a horizontal microsaccade that is small (<9 min arc). *D*: similarly, a predominantly vertical microsaccade (parallel to the grating orientation) causes weaker luminance image modulation over the RF than a predominantly horizontal microsaccade (orthogonal), and this is reflected in the SC visual reafferent response. Therefore, microsaccades are associated with visual updating of SC representations, with the updating done in a way to format the image representation as a function of how the movement vector is related to the underlying visual image over RFs. Adapted with permission from Khademi et al. (149).

new "event" of fixation onset. Rather, the properties of the visual reafferent response reflect the spatiotemporal luminance modulation that is experienced by the RF as a result of the microsaccadic image shift. Consider, for example, the situation shown in Fig. 7*C*. The RF stimulus consists of a vertical grating of 2.22 cycles/° (cpd) spatial frequency. If a predominantly horizontal microsaccade shifts this image across a given visual RF by some amount, then the RF should experience a luminance modulation of a specific amplitude for the duration of the microsaccade. Given a spatial frequency of 2.22 cycles/°, a small shift of <9 min arc (e.g., a microsaccade that is <9 min arc in amplitude) should cause a smaller intrasaccadic luminance modulation than a bigger shift (e.g., by a microsaccade that is >9 min arc in amplitude). It turns out that SC RFs, even though they are much bigger in diameter than 9 min arc (103, 110, 111), are indeed sensitive to such subtle image modulations (Fig. 7*C*) (149). This is remarkable given the general perception in the literature, to date, of the primate SC as being a motor control structure that is not sensitive to visual image features. Similarly, one can use the same logic to argue that if the microsaccade is now predominantly vertical in direction, as opposed to being predominantly horizontal, then a small retinal image shift in the vertical grating would not cause as strong a luminance modulation over the SC RF (there is now a parallel shift of the RF image relative to the grating orientation). As a result, predominantly horizontal microsaccades (orthogonal in direction to the grating orientation) should result in stronger visual reafferent responses than predominantly vertical (parallel) microsaccades, and this is what is observed (Fig. 7*D*) (149).

Therefore, the visual flow on the retinal image that is associated with microsaccades is sensed quite faithfully by extrafoveal SC neurons (149). This implies that microsaccades not only cause a temporal flagging of events (through visual reafferent bursts in general; Fig. 7), but they also modulate the representation of images, essentially enhancing the SC representation of orthogonal edges of appropriate spatial frequencies (Fig. 7, *C* and *D*). A strong future follow-up for these results is to ask whether SC neurons can be sensitive to even smaller images shifts, in association with ocular position drifts, which represent the lower limit of image shift sizes on the retinal image that are caused by active foveal visuomotor behavior. Another future research direction would be to explore whether a suppression of neural activity before the visual reafferent response can be observed. As noted in the previous section, it was suggested with large saccades (147) that intrasaccadic image shifts are associated with suppressed background activity. However, Fig. 7*B* shows that for microsaccades, there is no clear suppression of background activity before the visual reafferent responses. In the future, whether such a lack of reduction is general or only specific to the experimental condition should be investigated (e.g., due to the relatively bright gray background shown in Fig. 7).

SMOOTH OCULAR MOVEMENTS AND FOVEAL SC GOAL-RELATED AND VISUAL REPRESENTATIONS

We have so far focused on microsaccades. However, active vision at the foveal scale necessarily also involves slow ocular position drifts during fixation. These slow eye movements, which are much smaller than microsaccades, have received much less neurophysiological investigation. They thus represent an important frontier for future research on active vision, whether in the SC or beyond. However, the existing evidence in the literature so far already supports the idea that the SC might still represent, and even drive, slow ocular position drifts in a precise manner (71).

For example, if a monkey is trained to smoothly track the instantaneous invisible midpoint of two moving visual bars (Fig. 8*A*), then there is a foveal goal (the invisible midpoint) that needs to be continuously represented in the SC for as long as tracking is to proceed. This is because the SC is known to represent behaviorally relevant target locations (162). It turns out that the foveal region of the SC topographic map can indeed represent the real-time location of the invisible goal quite faithfully. Specifically, in the intermediate SC layers where visual-motor neurons exist, the neurons show continuous modulations during invisible target tracking, and for as long as such tracking takes place (up to $>3{,}000$ ms; Fig. 8*B*). Analysis of the "tuning" of such neural modulations reveals that the neurons elevate their activity whenever the instantaneous foveal movement goal enters their movement RF (similar to the movement RF shown in Fig. 2*A*), and they reduce their activity whenever the instantaneous foveal movement goal exits their movement RF (101, 102). With ocular position drifts during fixation, a similar result should be expected. Specifically, the foveal goal in this case would be the retinotopic location of the stationary fixated target. Whenever the eye drifts in such a way that the fixated target position (even if it is only inferred through non-visual guidance) enters into a neuron's movement-related RF, then the neuron should elevate its activity; similarly, when the fixated target leaves the neuron's RF, then the neuron should reduce its activity. Indeed, inspecting Fig. 1*A* of Hafed et al. (91) shows clearly how tonic SC activity in between microsaccades changes significantly as a function of intermicrosaccadic eye position, and in a manner that is consistent with the movement RF location inferred from the microsaccadic bursts of the neuron. This issue of real-time representation of goal position during ocular position drifts should be investigated in more detail in future studies. At the very least, it will relate rostral SC activity during ocular position drifts to early classic hypotheses about the role of such activity in maintaining gaze fixation in the absence of saccades (107, 127).

More interestingly, we also know that the potential modulation of activity in the deeper SC layers by ocular position drifts can work in tandem with visual modulations in the more superficial layers; these latter modulations would reflect the visual consequences of subtle eye position deviations (44). Specifically, in Fig. 8, *C–E*, an example of how SC foveal visual responses are sensitive to tiny ocular position drifts is shown. In Fig. 8*C*, a scenario is shown in which a foveal visual RF of an SC neuron is just slightly to the right of the line of sight, with an inner edge sharply ending in the contralateral (*right*) visual field (44). If eye position now drifts to the left (opposite from the RF location) by a very small amount, then the retinotopic image of the fixation spot shifts rightward and enters into the neuron's visual RF. Therefore, when eye position drifts ever so slightly away from the fixation spot, and in a direction that is opposite from the RF location, the neuron should be more active since it is visually activated by the

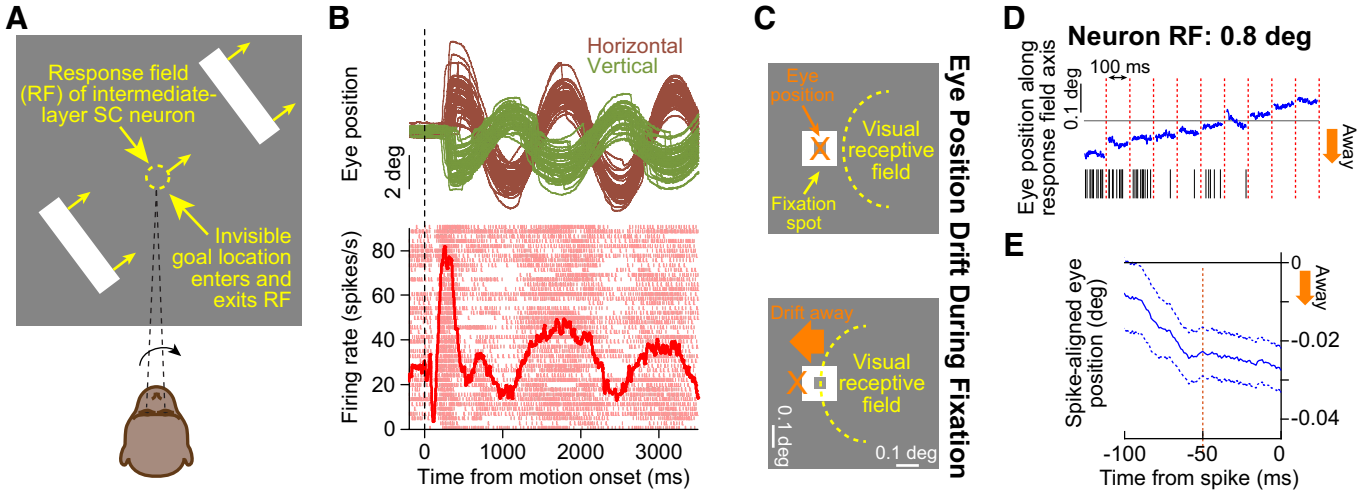

Figure 8. Real-time representation by superior colliculus (SC) neurons of instantaneous foveal goals and visual stimuli during slow ocular movements. *A*: smooth pursuit of an invisible target (the midpoint between two moving bars). Due to imperfections in smooth pursuit gain, the intended goal of the movement can occupy different retinotopic positions during tracking. It can therefore enter or exit a given neuron's RF. *B*: this gives rise to modulations in neural activity during tracking. Analysis of the modulation reveals that it is explained by the instantaneous retinotopic position of the intended movement goal relative to the RF location (101, 102). *C*: even for visual-only neurons, a foveal neuron's visual RF can experience the movement of the visual fixation spot (white) into its inner border (*bottom*) as the eye drifts in a direction opposite from the RF location during maintained fixation. Therefore, the neuron might increase or decrease its activity during ocular position drifts (44). *D*: an example demonstration of foveal visual neuron activity (spikes in the bottom) as a function of where the eye happens to be fixating relative to the fixation spot. For epochs in which the eye happens to be drifted away from the RF location (as in *C*), the neuron experiences the fixation spot as a visual stimulus and increases its spiking activity. *E*: spike-aligned average eye position of the neuron in *D*. The neuron emits a spike when the eye drifts, by a small amount, opposite to the RF direction (such that the visual fixation spot enters into the inner edge of the RF). *A* and *B* modified with permission from Hafed et al. (101). *C–E* modified with permission from Chen et al. (44).

fixation spot. This is what is seen in Fig. 8*D*, which demonstrates different microsaccade-free eye position epochs that are sorted by where the eye was relative to the RF location. As can be seen, only eye positions opposite from the RF direction were associated with elevated neural activity (more spikes). Moreover, the relative timing between eye position drifts and spiking is quantified in Fig. 8*E*. In this figure, averaged eye position before every spike was quantified; a spike was most likely to be triggered within less than ~50 ms (consistent with visual response latencies of neurons), if eye position was at some distance (which depended on RF preferred eccentricity) away from the RF hotspot (44). Therefore, visual representations in the foveal SC do also provide a real-time estimate of foveal visual target location during ocular position drifts. It remains to be seen how peripheral (and larger) SC visual RFs can be modulated by ocular position drifts.

In all, the existing evidence supports the idea that the SC is involved in the control and representation of foveal goals associated with ocular position drifts during fixation. One future important experiment to perform is to causally modulate rostral SC activity and look for changes in ocular position drifts. It is known that reversible inactivation of a portion of the rostral SC reduces microsaccades and alters average eye position (91, 100). It would, next, be interesting to see whether the dynamics and trajectories of ocular position drifts are also affected by such inactivation.

FOVEAL MAGNIFICATION AS A MEANS OF LINKING ACTIVE VISION AT THE FOVEAL AND EXTRA-FOVEAL SCALES

Finally, it is important to discuss how the SC structurally represents foveal eccentricities, because this can clarify a variety of observations alluded to in the previous sections. Historically, the rostral end of the SC was perceived to be largely nonspecific for eccentricity, particularly because of a hypothesized role for the rostral SC in maintaining gaze fixation, as opposed to moving the eyes saccadically (107). However, the ability to drive small microsaccades precisely suggests otherwise (91). This has prompted a detailed mapping of SC topography, revealing a foveal magnification factor (Fig. 9*A*) that is much larger than previously assumed (44). Specifically, the only model of SC topography that was accepted for the SC for a long time before the new mappings was that in Ottes et al. (163), which was itself based on the experiments of Robinson (23). This model was motivated by models of primary visual cortex topography, in which foveal magnification was previously observed. The model therefore represented retinotopic eccentricity with a logarithmic warping function that compressed large eccentricities in neural tissue and expanded small eccentricities. However, because most of the data for fitting the logarithmic function was eccentric (23), and because many logarithmic functions can fit the compressed periphery relatively well, while still diverging foveally, the model that was fit in this manner only represented the foveal visual representation using extrapolation from (sparse) peripheral measurements. With the new dense mappings, it turned out that the real foveal magnification factor, with many foveal mapping samples, is much stronger than the extrapolated magnification factor (Fig. 9*A*). This means that the SC surface topographic map of the contralateral visual field has a surprisingly large representation of the central visual field (Fig. 9, *B* and *C*) (44). For reference, the surface topographic map shown in Fig. 9, *B* and *C* is modeled using the same equations as in Ottes et al. (163), but with magnification parameters directly derived from dense foveal mapping (44), as follows:

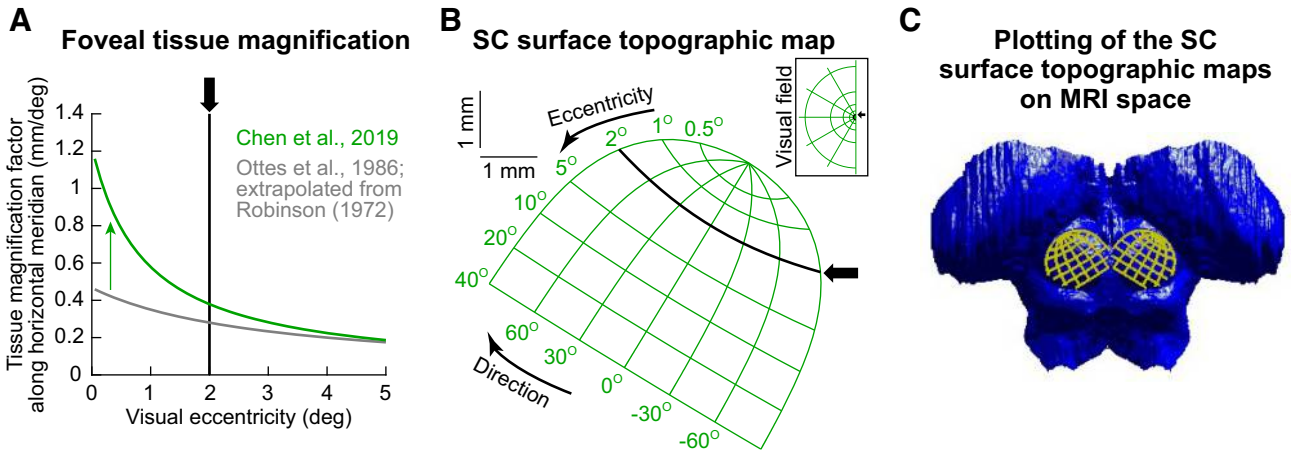

Figure 9. Magnified representation of the foveal visual representation in superior colliculus (SC) neural tissue. *A*: tissue magnification factor in the SC as a function of visual eccentricity. Gray shows the classically accepted model of SC topography (163), which was fitted based on sparse, and predominantly extrafoveal, data from Robinson (23). Green shows the fit based on dense sampling of both foveal and extrafoveal eccentricities (44). Because of logarithmic compression, both fits approach each other with increasing eccentricity. However, the fit based on the early sparse data severely underestimates foveal magnification factor when extrapolated to small visual eccentricities. *B*: full mapping of the contralateral retinotopic visual hemifield on the SC surface, demonstrating large foveal magnification. The magnification factor in *A* (green) was obtained from the shown map (along the horizontal meridian), and the 2° eccentricity line is marked in black in both panels. The *inset* shows the visual field coordinates with the 2° eccentricity line again marked in black. *C*: mapping of the entire visual field by the surface of the two SC's as viewed in three dimensions on an anatomical MRI reconstruction. The foveal representation is easily accessible with appropriate electrode trajectories. Based on the green curve in *A* and the surface topographic maps in *B* and *C*, it can be seen that neural activations in the foveal SC representation occupy a large fraction of SC tissue, which can help explain interactions between foveal and extrafoveal eccentricities in some of the modulations that we described in this article. Adapted with permission from Chen et al. (44).

$$X = B_x \log_e\left(\frac{\sqrt{R^2 + 2AR\cos(\theta) + A^2}}{A}\right), \quad (1)$$

$$Y = B_y \arctan\left(\frac{R\sin(\theta)}{R\cos(\theta) + A}\right), \quad (2)$$

where X and Y are anatomical distances along the SC axis (X being along the axis of the horizontal meridian and Y being along the orthogonal axis), R and θ are visual coordinates in eccentricity (R) and direction from horizontal (θ), and B_x, B_y, and A are model magnification parameters: 1.1 (B_x), 1.8 (B_y), and 0.9 (A).

One interesting consequence of the large foveal magnification in Fig. 9 is that a link between foveal and extrafoveal visual sensitivity modulations (such as those that we alluded to above with sensitivity enhancement before microsaccades) become neurally more proximal to each other than in retinotopic visual coordinates. In that sense, given that a large fraction of SC neurons can be simultaneously active at any one moment in time for representing a stimulus location (164), then a large foveal magnification factor might explain why visual-motor SC neurons only show premicrosaccadic enhancement only up to ~5°–10° eccentricity and suppression otherwise (128). An interesting future research direction in this regard would be, again, to link these modulations to slow ocular position drifts, since these latter movements are the least studied component of foveal visuomotor behavior at the neurophysiological level right now.

CONCLUDING REMARKS

Active vision at the foveal scale in the SC represents an important opportunity for clarifying the neural mechanisms of fixational eye movements. These eye movements represent the lower limit of neural control abilities of the brain. Moreover, the image shift consequences of these eye movements also represent the lower limit of self-generated visual flows on the retina. Therefore, understanding the perceptual implications of these visual flows is very important. In this article, we reviewed our current understanding of active vision at the foveal scale in the primate SC. We presented recent developments, and we also clarified the remaining open questions and intriguing possibilities. We anticipate that the next few years will witness important new developments not only at the level of the SC, but also at the level of both downstream brainstem motor nuclei as well as at the level of cortical visual and visual-motor areas.

GRANTS

Z.M.H., M.P.B., and T.Z. were funded by the Deutsche Forschungsgemeinschaft (DFG) through the following project ID's: 276693517 - SFB 1233 (Robust Vision), BO5681/1-1, and HA6749/4-1. C.Y.C. was funded by a Grant-in-Aid for Research Activity Start-up (project number: 20K22684) from JSPS, Japan.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Z.M.H. conceived and designed research; Z.M.H., C.-Y.C., X.T., M.P.B., and T.Z. prepared figures; Z.M.H., C.-Y.C., X.T., M.P.B., and T.Z. drafted manuscript; Z.M.H., C.-Y.C., X.T., M.P.B., and T.Z. edited and revised manuscript; Z.M.H., C.-Y.C., X.T., M.P.B., and T.Z. approved final version of manuscript.

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