

Visual Functions of the Primate Superior Colliculus

Ziad M. Hafed,^{1,2} Klaus-Peter Hoffmann,³
Chih-Yang Chen,⁴ and Amarender R. Bogadhi⁵

¹Werner Reichardt Centre for Integrative Neuroscience, University of Tübingen, Tübingen, Germany; email: ziad.m.hafed@cin.uni-tuebingen.de

²Hertie Institute for Clinical Brain Research, University of Tübingen, Tübingen, Germany

³Faculty for Biology and Biotechnology, Ruhr University Bochum, Bochum, Germany; email: Klaus-Peter.Hoffmann@ruhr-uni-bochum.de

⁴Institute for the Advanced Study of Human Biology, Kyoto University, Kyoto, Japan; email: chen.chihyang.3a@gmail.com

⁵Central Nervous System Diseases Research, Boehringer Ingelheim Pharma GmbH & Co. KG, Biberach, Germany; email: bogadhi.amar@gmail.com

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Annu. Rev. Vis. Sci. 2023. 9:361–83

First published as a Review in Advance on
April 11, 2023

The *Annual Review of Vision Science* is online at
vision.annualreviews.org

<https://doi.org/10.1146/annurev-vision-111022-123817>

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Keywords

superior colliculus, vision, eye movements, orienting, active vision, primate

Abstract

The superior colliculus (SC) is a subcortical brain structure that is relevant for sensation, cognition, and action. In nonhuman primates, a rich history of studies has provided unprecedented detail about this structure's role in controlling orienting behaviors; as a result, the primate SC has become primarily regarded as a motor control structure. However, as in other species, the primate SC is also a highly visual structure: A fraction of its inputs is retinal and complemented by inputs from visual cortical areas, including the primary visual cortex. Motivated by this, recent investigations are revealing the rich visual pattern analysis capabilities of the primate SC, placing this structure in an ideal position to guide orienting movements. The anatomical proximity of the primate SC to both early visual inputs and final motor control apparatuses, as well as its ascending feedback projections to the cortex, affirms an important role for this structure in active perception.

INTRODUCTION

The superior colliculus (SC) is a layered midbrain structure that is anatomically well-connected to both the sensory and motor peripheries (May 2006). It is evolutionarily well-preserved and is labeled the optic tectum (OT) in nonmammalian vertebrates. In a variety of species, including fish (Bollmann 2019), frogs (Udin 2007), reptiles (Foster & Hall 1975), birds (Wylie et al. 2009), and mice (Cang et al. 2018), the OT/SC is a primary visual structure. For example, in the mouse, an increasingly popular model for visual neuroscience research (Bassett et al. 2020, Cang et al. 2018, Huberman & Niell 2011, Ito & Feldheim 2018), approximately 85–90% of all retinal ganglion cells project to the SC (Cang et al. 2018, Ellis et al. 2016). This makes the OT/SC in many species critical for visually guided behavior (Isa et al. 2021, Lettvin et al. 1959, Sprague 1966, Sprague & Meikle 1965).

In primates, the SC has also long been known to respond to visual stimuli. However, the diversity and functional roles of such responses are only now beginning to be investigated in more detail. In fact, the primary view of the primate SC in the wider neuroscience community is that it is predominantly a motor controller (Gandhi & Katnani 2011), and the prevalence of this view is partly due to the historical development of the field. This raises the important question of whether the primate SC, from the perspective of visual processing, is indeed fundamentally different from the OT/SC in other animals.

Because the nonhuman primate is an important animal model for linking detailed mechanistic investigations of the OT/SC in different animal species to functional studies of the human SC, which are primarily investigated with functional magnetic resonance imaging (Chang et al. 2016; Himmelbach et al. 2013; Katyal & Ress 2014; Katyal et al. 2010; Linzenbold & Himmelbach 2012; Linzenbold et al. 2011; Loureiro et al. 2017, 2018; Rahmati et al. 2020; Savjani et al. 2018; Schneider & Kastner 2005), it is necessary to understand the visual functions of the primate SC. We summarize this understanding in this review, and we argue that not only does the visual machinery in the primate SC support cognitive functions (Basso & May 2017), but it is also optimized for guiding orienting behaviors.

We first briefly review the historical progress of research on the primate SC, demonstrating that this structure's visual capabilities were recognized early on, before a somewhat drastic shift toward oculomotor control studies, followed by studies on cognitive processes (Basso & May 2017) related to working memory, target selection, decision making, perceptual learning, and covert visual attention. We then describe how recent investigations show that the primate SC has rich, feature-tuned visual responses, with direct consequences for active visually guided behavior. Taken together, these investigations demonstrate that rich SC visual functions not only are relevant in other animals, but also matter for primates, and in a functionally specialized manner.

IN THE BEGINNING, THERE WAS VISION

Early primate SC studies were decidedly dominated by exploration of this structure's visual properties (Cynader & Berman 1972, Goldberg & Wurtz 1972, Humphrey 1968, Kadoya et al. 1971b, Schiller & Koerner 1971, Updyke 1974). These studies were motivated by experiments in other mammalian species like cats (Marchiafava & Pepeu 1966, McIlwain & Buser 1968, Sprague 1966, Sprague et al. 1970, Sterling & Wickelgren 1969, Straschill & Hoffmann 1969, Wickelgren & Sterling 1969), ground squirrels (Michael 1970), and hamsters (Schneider 1967), which laid the foundation for recognizing a role for the SC in sensory-motor behavior. Interestingly, some research questions on primate SC visual functions that remain open today, such as the SC's role in foveal vision (Chen et al. 2019), were heavily discussed in these early studies. For example, anatomical tracing investigated whether the SC directly receives foveal inputs (Cowey & Perry

1980, Hendrickson et al. 1970, Hubel et al. 1975, Lund 1972, Perry & Cowey 1984, Wilson & Toyne 1970), and also whether each of the right or left SC receives monocular or binocular retinal projections (Hubel et al. 1975, Pollack & Hickey 1979). Moreover, the dependence of the SC's visual responses on the primary visual cortex (V1) and geniculostriate pathway was investigated by ablation or inactivation (Davidson et al. 1992; Schiller et al. 1974, 1979).

All of these studies highlighted the importance of vision in the primate SC. Besides receiving direct retinal inputs (Perry & Cowey 1984), the primate SC also has substantial binocular zones (Hubel et al. 1975, Pollack & Hickey 1979), suggesting that it can potentially sense visual disparities, as does V1. Neurons in the SC superficial layers are also not entirely dependent on V1 activity (Schiller et al. 1974), despite the SC being heavily anatomically connected to V1 (Cerkevich et al. 2014, Fries 1984, Kadoya et al. 1971a, Lock et al. 2003, Lui et al. 1995, Lund 1972, May 2006), whereas deeper-layer neurons are heavily dependent on such activity.

Physiologically, primate SC visual response properties were also studied early on, albeit primarily with anesthetized monkeys. It was found that SC neurons possessed visual receptive fields (RFs) (Cynader & Berman 1972, Goldberg & Wurtz 1972). Moreover, there was a lawful monotonically increasing relationship between RF size and retinotopic visual eccentricity (Cynader & Berman 1972, Goldberg & Wurtz 1972, Humphrey 1968, Updyke 1974). These results suggested a neural specialization for the central visual field (Chen et al. 2019, Ottes et al. 1986, Robinson 1972), which is a hallmark of many primate visual areas (Azzopardi & Cowey 1996, Dow et al. 1981).

Beyond RFs, visual response profiles to different types of stimuli were investigated. For example, Schiller & Koerner (1971) described what they called event detector neurons in the awake macaque monkey, as well as jerk detector neurons, which responded best to rapid stimulus displacements. Similar characterizations were also made in anesthetized monkeys (Cynader & Berman 1972; Marrocco & Li 1977; Moors & Vendrik 1979a,b). Influences of stimulus size (Cynader & Berman 1972, Schiller & Koerner 1971), polarity (i.e., dark versus light contrasts) (Cynader & Berman 1972, Humphrey 1968, Malevich et al. 2022, Updyke 1974), or novelty (Cynader & Berman 1972) were also alluded to, demonstrating, at least qualitatively, that the primate SC visual processing machinery shares general principles of visual processing with other brain areas. Such principles included center-surround interactions (Cynader & Berman 1972, Goldberg & Wurtz 1972, Marrocco & Li 1977, Schiller & Koerner 1971, Updyke 1974), relative motion (Bender & Davidson 1986, Davidson & Bender 1991, Davidson et al. 1992), and stimulus-onset and -offset responses (Cynader & Berman 1972, Goldberg & Wurtz 1972, Humphrey 1968, Schiller & Koerner 1971).

By the end of the twentieth century, it became customary to refer to primate SC neurons as being either visual (i.e., responding to the onset of a spot of light in their RFs), visual-motor (i.e., additionally responding at the time of a saccadic eye movement toward the RF location), or motor. However, this simple classification masks a large diversity of visual dependencies in the primate SC, even at the time of saccade generation (**Figure 1**), and it was a direct outcome of a shift in focus to study the primate SC from the perspective of motor control and cognition; that is, the diversity in visual dependencies of SC neurons became secondary with the advent of the field of cognitive neuroscience, and its merging with neurophysiological investigations in awake and behaving monkeys, by the 1980s.

VISUAL PATHWAYS TO THE PRIMATE SUPERIOR COLLICULUS

Approximately 10% of retinal ganglion cells directly project to the primate SC's superficial layers (Perry & Cowey 1984). In the most peripheral areas (at the monocular temporal crescent), contralateral eye input dominates, but the rest of the SC is largely binocular (Hubel et al. 1975,

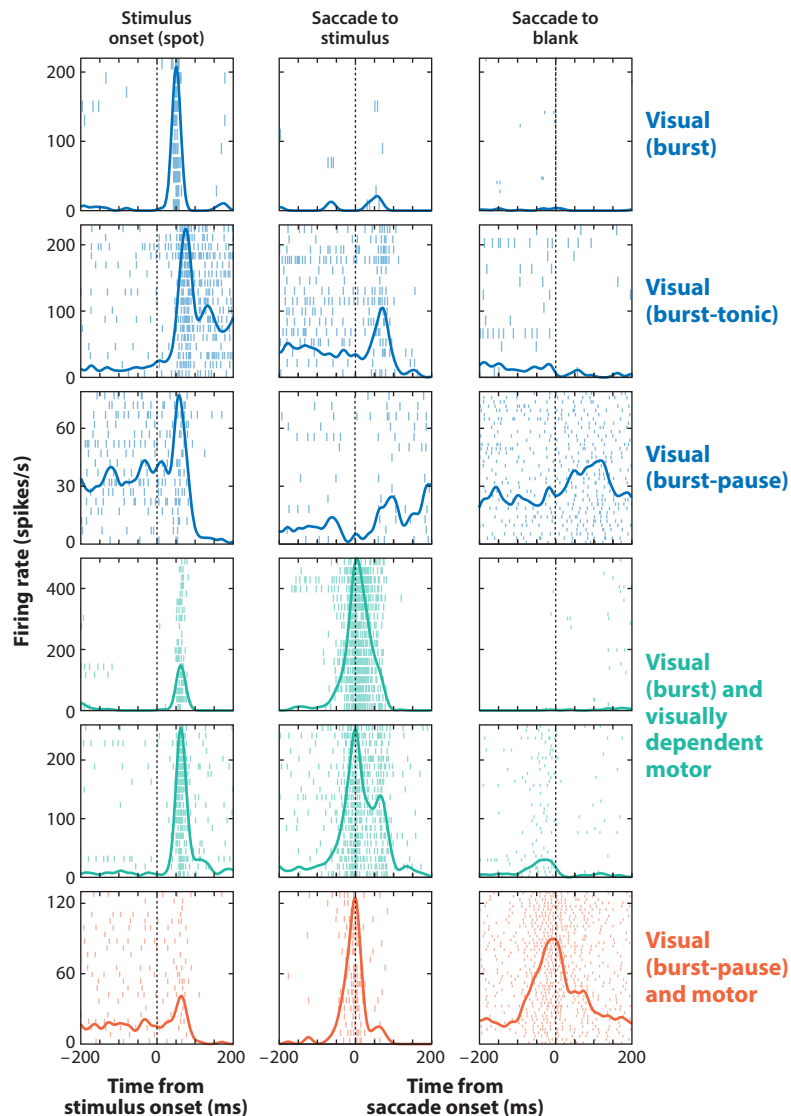


Figure 1

Diverse visual dependencies in the primate superior colliculus (SC), even in response to simple spot stimuli. Visual neurons can have no baseline discharge before stimulus onset (row 1, column 1) or possess some tonic discharge (rows 2 and 3, column 1). After stimulus onset, visual neurons can also either exhibit only a short-lived burst (row 1, column 1) or be burst-tonic, maintaining a postburst discharge for as long as the visual stimulus is in the receptive field (RF) (row 2, column 1). Still other visual-only neurons exhibit a postburst pause (row 3, column 1). Visual-motor neurons (rows 4–6) strongly discharge before and during saccadic eye movements to the RF location, in addition to their visual responses (column 2; note that in row 2, column 2, the neuron only discharged after saccades, indicating a potential reafferent response to the shifted retinal image). Remarkably, many SC visual-motor neurons are visual target dependent in their motor discharge (rows 4 and 5, columns 2 and 3): When an identical saccade is made to a blank, a neuron having strong saccade-related discharge with a visual target (column 2) is rendered virtually silent (column 3) (Edelman & Goldberg 2001, 2003; Mohler & Wurtz 1976; Willeke et al. 2019). The net result is that the primate SC likely has more visually related responses (at both stimulus and saccade onset) than saccade-related responses (see also **Figure 7** below).

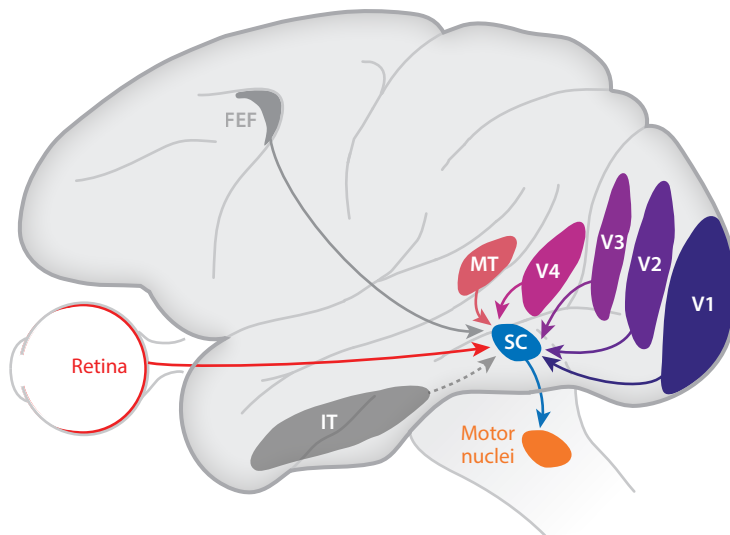


Figure 2

Diversity of visual inputs to the primate SC. The primate SC (shown schematically in blue on a rhesus macaque monkey's brain) receives direct retinal inputs, as well as inputs from most early visual cortical areas (V1, V2, V3, V4, and the MT cortex). There are also inputs from the IT cortex, where object representations (e.g., face patches) exist, and inputs from the FEF, which constitutes an important part of the dorsal cortical visual stream for aiding in visually guided behaviors. Note that parietal cortical areas with visual responses also project to the SC. A classic output pathway of the SC (in relation to its popular view as a gaze shift controller) is through a downward projection to the lower brainstem, containing premotor and motor nuclei for controlling eye and body movements. Note that other important outputs of the SC include ascending connections back to the cortex, which are not shown (Wurtz et al. 2005). These ascending projections suggest the existence of a visual loop between cortical areas that includes passage through the SC (see also **Figure 7** below). Thus, SC visual representations matter for more than just moving the eyes and body and can influence decision making, selective attention, and even object-based visual representations (see also **Figure 6** below). Abbreviations: FEF, frontal eye field; IT, inferior temporal; MT, middle temporal; SC, superior colliculus.

Pollack & Hickey 1979). Interestingly, each eye input may be patchy (i.e., containing segregations of either only ipsilateral or only contralateral eye projections). Physiologically, the SC is binocular (Cynader & Berman 1972, Schiller et al. 1974), with some indications that regions of ocular dominance may link to the patchiness of retinal projections (Hubel et al. 1975). Moreover, ipsilateral eye inputs terminate slightly deeper than contralateral eye inputs in the superficial layers (Hubel et al. 1975).

Beyond the retina, the SC receives a large array of cortical visual inputs (Cerkevich et al. 2014, Fries 1984, Kadoya et al. 1971a, Lock et al. 2003, Lui et al. 1995) (**Figure 2**). In all of the cortical source areas, cortical layer 5 projects to the SC; in V1, both layers 5 and 6 project to it (Cerkevich et al. 2014, Fries 1984). In early cortical visual areas, up to V4 and TEO, the projections to the SC are retinotopically organized such that there is approximate registration between the retinal visual maps in the SC and the source areas (Lock et al. 2003). In addition, the earliest visual areas and the frontal eye field project to the superficial and intermediate layers, whereas higher-order visual areas in the inferior temporal cortex only seem to project to the intermediate layers (Fries 1984). Therefore, both superficial and deeper SC layers act as places of strong integration of visual information. Indeed, it is now believed that visual responses can be found at all SC depths (Massot et al. 2019). This can inform studies on the functional role of the primate SC's visual apparatuses

A LACK OF VISION DOWNSTREAM OF THE SUPERIOR COLLICULUS?

An intriguing open question with respect to visual pathways has to do with areas downstream of the SC. Besides receiving visual input, the SC projects to brainstem motor nuclei for implementing orienting behaviors. This raises the question of whether there is sophisticated visual pattern analysis (such as orientation and spatial frequency tuning) taking place in SC-recipient brainstem circuits. Classic models of these circuits (Hafed 2016) do not show them performing any visual signal processing, which would represent a remarkable cutting off of all visual information in structures closely related to the SC. Emerging evidence suggests that this is not the case: Investigations (Buonocore et al. 2020) of premotor omnipause neurons (Keller 1974, 1977), acting as the final gate for triggering saccades, are revealing significant visual pattern analysis capabilities in these very late premotor neurons. The neurons exhibit various feature tuning properties, and it will be important in the future to understand why such properties exist and how they might arise in relation to the visually rich primate SC. One likely possibility is that such visual analysis in these neurons allows rapid coordination between external sensory events and internally planned actions. This is an interesting topic for future research on the brainstem's role in active vision.

and can lead to intriguing questions about possible visual pattern analysis capabilities downstream of the SC (see the sidebar titled A Lack of Vision Downstream of the Superior Colliculus?).

A VISION FOR ORIENTING IN THE PRIMATE SUPERIOR COLLICULUS

The results discussed above suggest that visual responses are pervasive across the entire primate SC. If this is the case, then SC neurons should be highly sensitive to patterned stimuli (Chen et al. 2018, Hafed et al. 2022). Consider, for example, the neuron of **Figure 3**. In one condition, its visual response is measured while a small spot of light is presented; in another, a visual pattern appears. Not only is the initial response stronger for the pattern, but it also occurs earlier. Moreover, the neuron maintains a strong sustained response of >50 spikes/s despite returning to almost-zero baseline activity with the spot. As discussed in more detail below, these response differences reflect feature tuning characteristics of SC neurons even with matched stimulus sizes (Chen et al. 2018). Therefore, the primate SC is highly sensitive to patterned visual stimuli, consistent with anatomy (**Figure 2**).

Such sensitivity may be exactly what is needed to endow the primate SC with an ability to optimize the accuracy and efficacy of orienting eye and body movements under naturalistic conditions. In other words, the primate SC need not simply mimic or inherit cortical visual processing. Rather, it possesses a functionally specialized visual machinery that is optimal for orienting responses, exploiting the SC's privileged access to the motor periphery. In the next section, we summarize evidence for this.

The Superior Colliculus as a Foveal Visual Structure

A hallmark of primate vision is foveation. Indeed, a large proportion of visual analysis by primates is performed using foveal vision. As a result, if the primate SC were to serve optimal orienting behaviors, then it should be possible to generate highly precise and small saccadic eye movements (Chen et al. 2019, Hafed et al. 2021, Ko et al. 2010, Willeke et al. 2019). Indeed, deeper SC layers are causally involved in microsaccade generation (Hafed et al. 2009), and these layers also represent tiny spatial displacements associated with the foveal goals of smooth eye movements (Hafed & Krauzlis 2008, Krauzlis et al. 1997). However, as part of the historical shift of perception of the primate SC as a gaze shifting machine, it became customary to assume that the SC is concerned

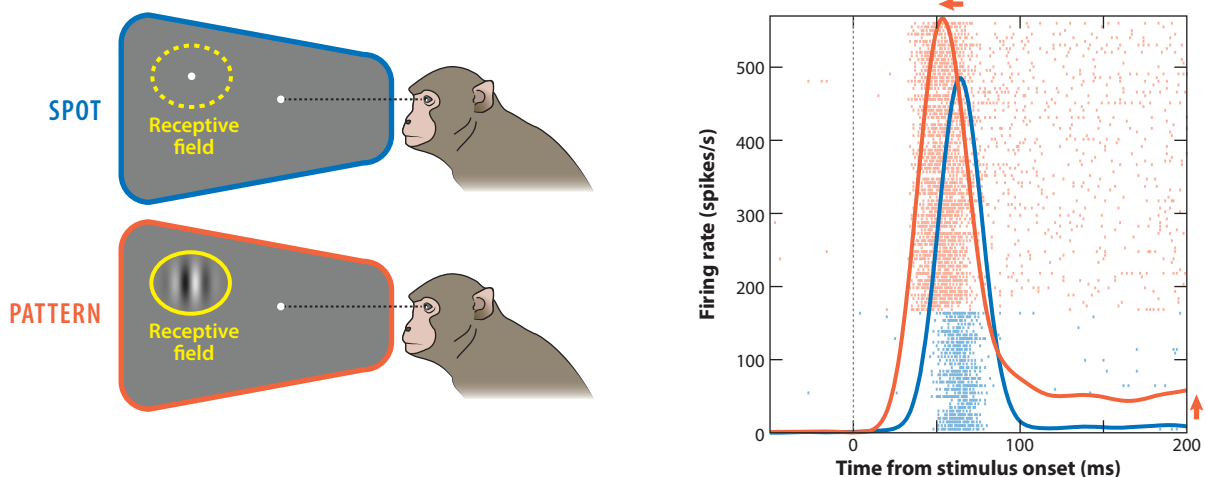


Figure 3

Superior colliculus neurons prefer patterned visual stimuli. Visual responses of an example neuron to either a spot that persisted in the receptive field, and that was also behaviorally relevant for a subsequent saccade (*blue; top*), or a visual pattern that was only passively viewed without any additional task requirements (*orange; bottom*) are shown. The neuron was highly sensitive for the spot, reaching a peak firing rate of almost 500 spikes/s (*blue curve*). Nonetheless, it became almost silent after the initial response. With a preferred visual pattern, the same neuron responded significantly earlier (and more strongly) than for the spot (*orange curve*), and it also maintained a subsequent sustained firing rate of > 50 spikes/s. Individual rasters in the background show individual trial spiking responses for the two conditions.

only with shifting gaze to targets away from the fovea (Munoz & Wurtz 1993), rather than with active foveal visual processing. This resulted in a long-lasting lack of characterization of foveal visual response properties in the primate SC, despite early suggestions that such responses might exist (Cowey & Perry 1980).

It is now known that the primate SC contains neurons highly sensitive to foveal visual images, and there are SC neurons with RFs entirely contained within the rod-sparse foveola region (Chen et al. 2019) (**Figure 4a–c**). Such neurons exhibit large responses (e.g., 500 spikes/s peak firing rates; see examples in **Figure 4a,d,e**). Interestingly, foveal RFs obey a strict rule of representing the contralateral side along the eccentricity dimension, such that RFs for the smallest retinal eccentricities become strongly skewed (**Figure 4b**). This is reminiscent of suggestions from studies of retinal projections to the SC (Cowey & Perry 1980). Moreover, in the superficial layers, containing retino-recipient neurons, visual response latencies are slightly longer for the smallest eccentricities (**Figure 4c**), potentially reflecting the slower temporal dynamics of cone photoreceptors. Therefore, the primate SC is a highly foveal visual structure.

The primate SC's foveal visual representation also encompasses the complete range of visual, visual-motor, and motor responses known to exist in this structure. For example, traversing the SC layers in the zone representing the foveal region, one first encounters purely visual neurons superficially, followed by visual-motor neurons in deeper layers (**Figure 4d**). Interestingly, visually dependent microsaccade-related neurons also exist (an example of which is shown on the right in **Figure 4f**): Such neurons (like the examples in **Figure 1** with larger eccentricities) exhibit classic microsaccade-related motor bursts when microsaccades are directed toward a visible spot but no activity when similar microsaccades are directed toward a blank (Willeke et al. 2019). Therefore, the SC's foveal representation has a complete visual-motor system (**Figure 4e,f**), enabling visual guidance of small, but accurate, gaze shifts (Hafed et al. 2021).

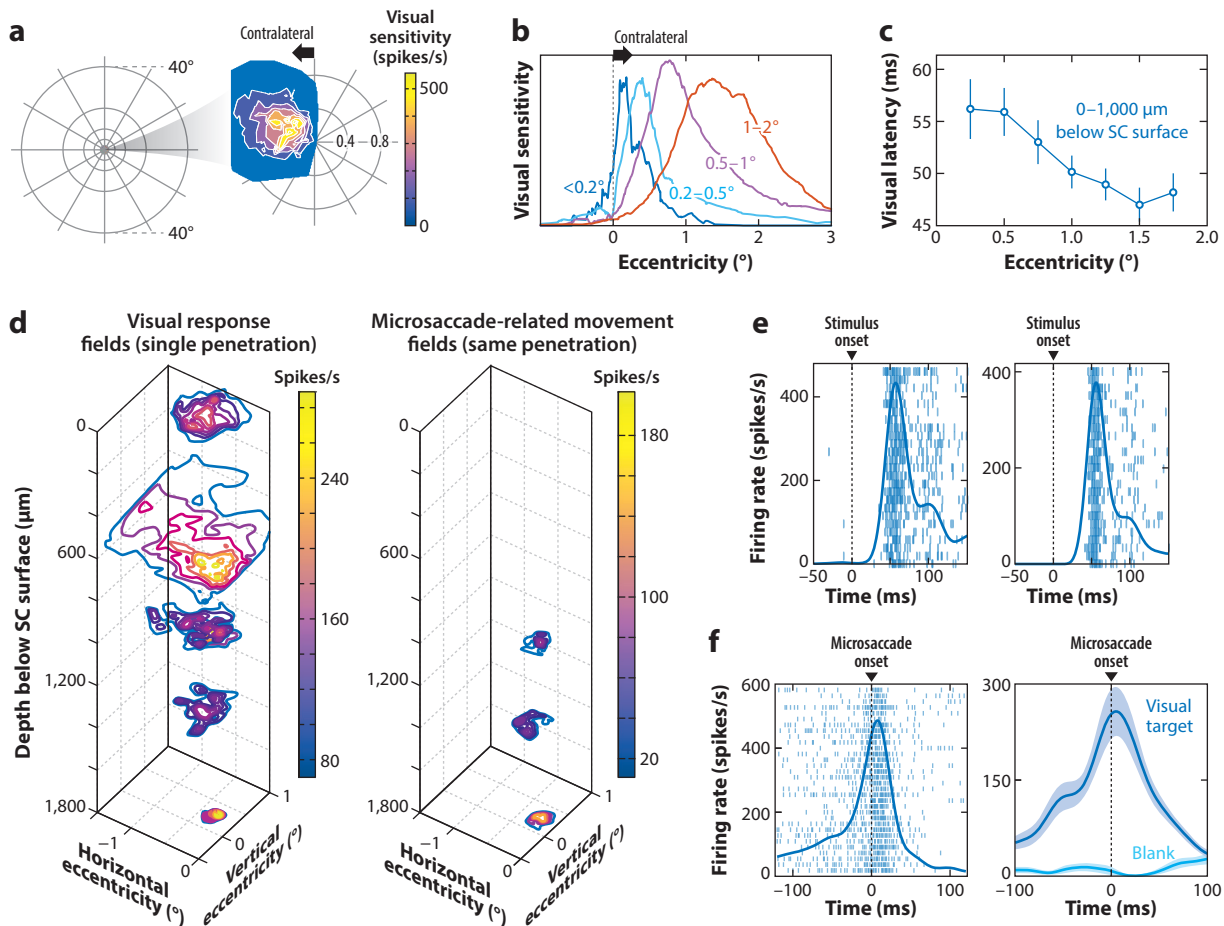


Figure 4

The primate superior colliculus (SC) as a foveal structure. (a) Foveal eccentricities (approximately central 2°) constitute a tiny portion of the visual field depicted on the left. The primate SC contains neurons with visual receptive fields (RFs) (right, showing an example neuron) that are fully contained within the primarily rod-free foveola region of the retinal image (i.e., eccentricities less than 0.5°). (b) SC neurons have RFs that not only fully tile the representation of the central visual field, but also do so through a strict contralateral cutoff along the eccentricity dimension. (c) Superficial SC neurons also show slower responses for smaller foveal eccentricities. (d) The SC's foveal visual representation contains visual neurons in superficial layers (left) and movement neurons (for microsaccades) in deeper layers (right). (e) Two example foveal SC neurons showing high visual sensitivity. (f) Two example deeper foveal SC neurons showing strong microsaccade-related discharge. The neuron on the right exhibits visually dependent microsaccade-related discharge, only firing when there was a visual target (spot of light) for the eye movements. Panels a–e adapted with permission from Chen et al. (2019); copyright Elsevier. Panel f (right) adapted from Willeke et al. (2019) (CC BY 4.0).

Importantly, the SC allocates more neural tissue in its topographic representation to the fovea than to the periphery. Indeed, the relative magnification of foveal versus peripheral visual representation in the primate SC is similar to that in V1 (Chen et al. 2019). Such foveal magnification implies that neural activations for tiny saccades are close, in anatomical coordinates, to visual eccentricities that are one or two orders of magnitude larger, potentially explaining the robust influences of microsaccades on peripheral visual sensitivity (Hafed 2013, Hafed et al. 2015).

An interesting future research direction with respect to the SC's foveal visual representation would be to investigate eye movements and SC functions under scotopic conditions, in which

retinal signals are rod- rather than cone-photoreceptor dominated. For example, there is evidence that monkey gaze reflexively shifts upward (and remains subsequently stable) in darkness (Barash et al. 1998), but the mechanisms for this are largely unexplored. It would also be interesting to better understand the detailed patterns of projections, whether from the retina or otherwise, to the SC's foveal region (Covey & Perry 1980, Hubel et al. 1975, Pollack & Hickey 1979, Wilson & Toyne 1970).

Natural-Scene Statistical Regularities and the Superior Colliculus

Beyond foveal analysis, the SC also supports larger gaze shifts. In this case, statistical regularities in natural visual scenes ought to be reflected in the SC's visual functional organization. One such regularity is related to the retinal image locations of peripersonal (near) space versus extrapersonal (far) space.

Consider, for example, **Figure 5a**. Relative to the fovea, an apple on a tree occupies the upper retinotopic visual field, whereas an apple in the hand occupies the lower visual field; the apple's retinal image is thus bigger in the lower visual field due to its proximity to the eye (Previc 1990). Indeed, retinal image disparities (and other distance-related image properties) confirm this: Far retinal disparities between the images of the two eyes (i.e., disparities reflecting the presence of objects farther than the line of sight) occupy the upper visual field, whereas near retinal disparities primarily appear in the lower visual field (Gibaldi & Banks 2019, Sprague et al. 2016). This implies that a saccade to foveate the far apple (i.e., an upward saccade) occurs under different visual guidance from an identically sized saccade toward the near apple (i.e., a downward saccade).

Because eye movements enable remote sensing, primate SC visual responses should be particularly sensitive to upper or lower visual field location. Indeed, there is a large difference in visual (and motor) RF size between the SC's upper and lower visual field representations (Hafed & Chen 2016) (**Figure 5a**), with upper visual field RFs being significantly smaller than lower visual field RFs. Interestingly, visual responses in the upper visual field are also stronger and occur earlier (**Figure 5b**, which shows two example eccentricity-matched neurons). More generally, in experiments using patterned sine wave gratings (Chen et al. 2015, Li & Basso 2008), contrast sensitivity curves (**Figure 5c**) are sharper and reach higher saturation levels in the upper visual field. These effects are not gradual across the visual field; instead, there is a sharp transition across the horizontal meridian, suggesting a functional discontinuity (Hafed & Chen 2016). Such a discontinuity might reflect structural discontinuities in cortical visual areas that project to the SC. For example, each of the right or left V1 (and subsequent extrastriate visual areas) has segregated neural tissue for representing the upper and lower visual fields.

Interestingly, orienting behaviors robustly reflect these findings. Saccadic reaction times are faster for upper than for lower visual field locations (Hafed & Chen 2016, Hafed & Goffart 2020) (**Figure 5d**). Moreover, normal visually guided saccades become express saccades (having reaction times <100 ms) significantly more often if a target appears in the upper visual field (Hafed & Chen 2016) (**Figure 5d**). Consistent with **Figure 5a**, saccade landing accuracy is also better in the upper visual field (Hafed & Chen 2016). Ecologically, this makes sense because natural behaviors often rely on upward saccades to explore the environment. For example, hiking on a slightly rough terrain almost exclusively involves upward saccades (Matthis et al. 2018): Hikers first direct their gaze onto a rock a few steps ahead of their current position; as they walk toward the rock, they maintain gaze on this rock by slowly rotating the eye downward; at some point, they make an upward saccade toward the next rock location, and they repeat the procedure as they walk forward (Matthis et al. 2018). It would be interesting in the future to extend the results shown in **Figure 5a-d** to investigate whether primate SC neurons representing the upper visual field are

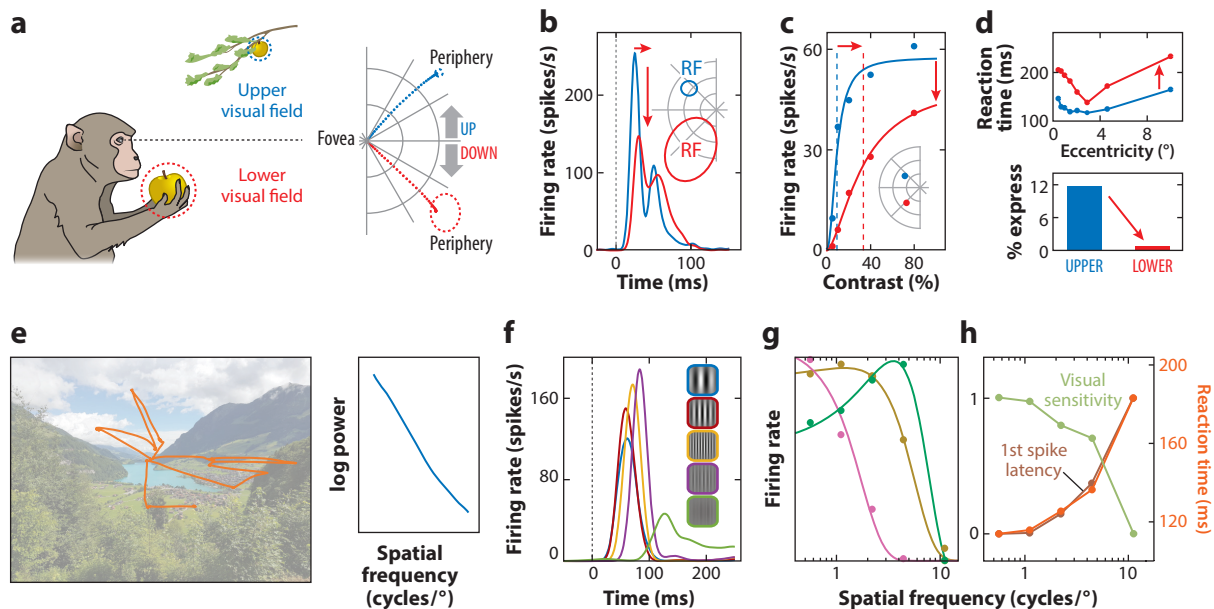


Figure 5

Visual properties of the primate superior colliculus (SC) are consistent with a role of eye movements in optimally scanning our natural environment. (a) Relative to the line of sight, objects in the upper visual field tend to be far and therefore project smaller retinal images. In the example on the left, an apple in a tree (blue) is visually smaller than an apple in the hand (red). SC receptive field (RF) sizes reflect this asymmetry (right). (b) SC visual responses to spot stimuli are stronger and earlier for upper visual field locations than for lower visual field locations, as shown by the example pair of eccentricity-matched neurons. The visual RFs of the neurons are also different in size (inset). (c) A pair of eccentricity-matched SC neurons also demonstrates how image contrast sensitivity (with grating stimuli) is higher for upper visual field neurons. (d) The visual properties in panels a–c directly translate into faster saccadic reaction times to target stimuli in the upper visual field (top), as well as a much larger likelihood of express saccades, with latencies <100 ms (bottom). (e) Another property of natural scenes is that their spectral content is dominated by low spatial frequencies (right), and we use eye movements to scan natural scenes (an example scan path is shown in orange on the left). (f) Primate SC neurons exhibit spatial frequency tuning, showing a difference in both visual sensitivity (peak firing rate) and latency (first spike latency after grating onset) for different spatial frequencies. The example neuron prefers a relatively high spatial frequency (purple), but it still responds earlier to low spatial frequencies. (g) Three example spatial frequency tuning curves. (h) Across the population, there is a preference for low spatial frequencies (as in the image content of panel e), and visual latency is also faster for low than for high spatial frequencies. As a result, saccades have faster reaction times (orange) in response to low spatial frequency stimuli. Panels a–c and d (bottom) adapted with permission from Hafed & Chen (2016); copyright Elsevier. Panel d (top) adapted with permission from Hafed & Goffart (2020); copyright the American Physiological Society. Panels f–h adapted from Chen et al. (2018) (CC BY 4.0).

primarily tuned to far binocular disparities, as might be expected from natural scene statistics (Gibaldi & Banks 2019, Sprague et al. 2016).

Upper versus lower visual field primate SC anisotropies may also be relevant for behaviors beyond saccades. Specifically, in addition to gaze shifts, deeper SC layers help control goal-directed reaching arm movements (Nagy et al. 2006, Philipp & Hoffmann 2014, Werner et al. 1997). Interestingly, neurons involved in such movements reside in the lateral side of the SC map (i.e., in the side representing the lower visual field). This is consistent with the near versus far visual field dichotomy of Figure 5a (Previc 1990), and it could aid in eye–hand coordination.

It is also important to consider potential implications of SC visual field asymmetries for orienting in darkness or with large stimuli, for which greater uncertainty about target location may give rise to an upward shift in gaze position (Barash et al. 1998, Malevich et al. 2020). Similarly, it is known that visual attentional performance is better in the lower visual field (He et al. 1996,

Rubin et al. 1996), opposite to the SC anisotropy. This is intriguing because the SC contributes to visual attentional mechanisms (Krauzlis et al. 2013). One way to reconcile this difference is to posit that larger SC RFs in the lower visual field provide cortical areas with a mechanism for binding disparate features or objects together. This can facilitate selecting these features or objects for enhanced attentional processing even when they individually occupy different cortical RFs. In this case, the larger SC RFs could be a way to encompass multiple smaller cortical RFs in a single spotlight for visual selection.

Perhaps the biggest implication of the observations in **Figure 5a–d** relates to the SC's anatomical organization. If upper visual field RFs are smaller than lower visual field RFs (**Figure 5a**), and if there is full coverage of the visual field by the SC, then more neural tissue (assuming a constant cellular density in a given layer) should be dedicated to the upper visual field. There is physiological evidence supporting this (Cynader & Berman 1972, Hafed & Chen 2016, Updyke 1974), and it is also in agreement with results for the rodent SC, for which a majority of the SC represents the upper visual field (Drager & Hubel 1976). Therefore, the primate SC likely has both upper visual field and foveal magnification.

Beyond upper versus lower visual field differences, another statistical regularity of natural scenes is related to spectral content (**Figure 5e**). Natural scenes are dominated by low spatial frequencies (Ruderman & Bialek 1994, Tolhurst et al. 1992) (**Figure 5e**), and saccadic reaction times are facilitated by natural scene statistics (White et al. 2008). Therefore, one can ask whether primate SC neurons are sensitive to different spatial frequencies (Chen et al. 2018, Hafed et al. 2022, Tailby et al. 2012). Indeed, individual SC neurons exhibit differential responses to different spatial frequencies, in terms of both visual sensitivity and response latency (Chen et al. 2018) (**Figure 5f,g**). Moreover, upper visual field neurons prefer higher spatial frequencies than do lower visual field neurons (Hafed & Chen 2016), consistent with their smaller RFs. Nonetheless, across the population (Chen et al. 2018), the SC clearly prefers low spatial frequencies (population visual sensitivity curve in **Figure 5b**), consistent with natural scene statistics (**Figure 5e**).

Interestingly, SC neurons respond earlier to low than to high spatial frequencies even if an individual neuron prefers high spatial frequencies. That is, there is a dissociation between response sensitivity and response latency (**Figure 5f**). This property is well mimicked by saccadic reaction times, which are faster for low spatial frequencies (**Figure 5b**), and one can model a given monkey's overall saccadic reaction time profile remarkably well by a simple linear model of both SC response sensitivity and latency (Chen et al. 2018), even before any target selection has taken place. Therefore, coarse-to-fine image analysis, common in V1 (Bredfeldt & Ringach 2002, Mazer et al. 2002, Purushothaman et al. 2014) and other early visual areas, is particularly relevant for the SC, especially for efficiently driving rapid orienting eye movements. It would be interesting and important in the future to compare the dynamics of such coarse-to-fine image analysis between the SC and V1.

A final statistical regularity in natural scenes that may be reflected in primate SC visual responses is the incidence of dark contrasts. Dark contrasts tend to occur in natural scene patches associated with low spatial frequency, high contrast, and far binocular disparities (Cooper & Norcia 2015). Consistent with this, primate SC neurons detect dark contrasts faster than light contrasts, and this faster detection is amplified in upper visual field neurons (Malevich et al. 2022). Moreover, as with spatial frequency tuning, SC neurons can detect dark contrasts faster than bright ones even if they are more sensitive to bright contrasts, and saccadic reaction times can be faster for dark contrasts (Malevich et al. 2022).

In all of the above examples of potential natural-scene statistical regularities, primate SC visual processing is functionally distinct from cortical visual processing. Indeed, there is no evidence that V1 preferentially processes the upper visual field, and V1 is likely more band-pass in spatial

frequency tuning than the SC. Even the likelihood of preferring dark contrasts is different between V1 (Yeh et al. 2009) and the SC (Malevich et al. 2022). Thus, the large integration of visual information by the primate SC (**Figure 2**) suggests that its sensitivity to visual patterns (**Figure 3**) is an outcome of optimizing visual information to best exploit the SC's privileged access to driving orienting behaviors, rather than of simply mimicking cortical visual processing.

Visual Feature Tuning by Superior Colliculus Neurons

The above results suggest a privileged role for the SC in detecting stimuli, whether in the upper visual field or with low spatial frequencies and/or dark contrasts. However, the primate SC is also involved in more varied visual pattern analysis processes.

In the early days, primate SC studies observed visual feature tuning to simple stimuli like discs. As mentioned above, these investigations primarily focused on SC spatial RF structures, demonstrating response dependence on stimulus size. For example, neural responses were suppressed for stimuli bigger than a given RF, suggesting surround inhibition (Chen & Hafed 2018, Cynader & Berman 1972, Goldberg & Wurtz 1972, Marrocco & Li 1977, Schiller & Koerner 1971, Updyke 1974). These observations were early seeds for seminal ideas on how the SC mediates orienting responses. Indeed, the concept of population coding (Lee et al. 1988), as a means for specifying accurate saccade sizes despite large and diffuse individual RFs, reflects earlier investigations of SC visual and motor RF properties.

More recently, Churan et al. (2012) used reverse correlation to explore spatiotemporal RF structure in detail. They presented rapidly flickering patterns of sparse black and white targets. They then performed spike-triggered averaging of the stimulus pattern that was on the display at different times before any given SC spike. Consistent with earlier RF analyses, it was likely that an SC neuron would emit a spike approximately 50 ms after stimulus onset (they did not differentiate between white and black stimuli in their analyses, although this would matter; Malevich et al. 2022, Updyke 1974). They then identified times and/or spatial regions for which stimulus onsets exerted a suppressive, rather than excitatory, influence. Approximately half of the neurons were only excitatory. The rest exhibited suppressive influences, often arising after the initial excitatory drive. This could account, for example, for short-lived SC visual bursts after static stimulus onset (e.g., first row in **Figure 1**). Moreover, suppressive influences also arose spatially in the form of a region surrounding the excitatory RF component. Interestingly, regions around an excitatory RF component that were closer to the fovea were more likely to suppress neural activity than regions that were more eccentric. This suggests a global organizational pattern of visual RFs across the SC's topographic map, analogous to global patterns for certain visual features (like orientation) in the mouse SC (Ahmadlou & Heimel 2015, Feinberg & Meister 2015).

The existence of excitatory and suppressive spatial RF components also helps support the notion that visual patterns are particularly effective stimuli for the primate SC (Updyke 1974) (**Figure 3**). Indeed, visually responsive SC neurons in awake monkeys were found to also be orientation tuned (Baumann et al. 2022, Chen & Hafed 2018). These results expanded on earlier observations of rare orientation-tuned SC neurons (Cynader & Berman 1972, Updyke 1974). Moreover, gratings oriented parallel to the line connecting the RF center to the fovea tended to elicit weaker responses than orientations that were orthogonal (Chen & Hafed 2018). This property needs to be investigated further, especially because it can represent a homology with the mouse SC, in which orientation tuning domains might exist (Ahmadlou & Heimel 2015, Feinberg & Meister 2015). This property would also be related to the more foveal suppressive surround of RFs described above (Churan et al. 2012).

Another feature that primate SC neurons are sensitive to is color. Early work investigating retinotectal projections suggested that such projections may not carry color-opponent information

(Schiller & Malpeli 1977). Similarly, SC inputs from the geniculostriate pathway were investigated by inactivating the lateral geniculate nucleus, and it was again suggested that the SC does not receive color-opponent information (Schiller et al. 1979). Physiologically, SC neurons did not appear to be color opponent (Marrocco & Li 1977). Such evidence, all from anesthetized animals, was exploited by psychophysicists designing experiments with stimuli isolating short-wavelength-cone (S-cone) signals to bypass SC involvement. However, White et al. (2009) demonstrated in awake monkeys that intermediate-layer SC neurons can be very sensitive to color. Moreover, Hall & Colby (2014) found that virtually all visually responsive SC neurons (also in the most superficial layers) respond to S-cone isolating stimuli, and with similar latencies to luminance stimuli when S-cone isolating stimulus contrast is high. In both cases, clear influences on eye movement behavior were also observed (Hall & Colby 2016, White et al. 2009). When hue information is behaviorally relevant, intermediate-layer SC neurons can detect even subtle changes in color (Herman & Krauzlis 2017). Therefore, color is an important visual feature in the SC.

Many primate SC neurons, particularly in the superficial layers, are also strongly sensitive to motion (Bender & Davidson 1986, Cynader & Berman 1972, Davidson & Bender 1991, Marrocco & Li 1977, Schiller & Koerner 1971, Updyke 1974). A minority of neurons are even selective for motion direction (Cynader & Berman 1972, Marrocco & Li 1977, Updyke 1974), and speed tuning is fairly broad (with deeper neurons having narrower speed tuning) (Updyke 1974). SC neurons can also detect images moving at saccadic speeds (Robinson & Wurtz 1976), and some will respond to relative motion between an object and a background (Bender & Davidson 1986, Davidson & Bender 1991, Davidson et al. 1992). Even deeper neurons in the foveal SC zone respond to motion in a nondirectionally sensitive way (Krauzlis 2004). All of this evidence makes sense since motion is a salient feature, and the SC is relevant for salience computation (White et al. 2017). Related to motion, 10–20-Hz flicker rates increase overall SC firing rates, and flicker fusion occurs at >20 Hz (Chen & Hafeed 2018). This finding could be informative for understanding the perceptual flicker performance of patients with lesions in V1 (Trevethan & Sahraie 2003), who might rely on visual pathways involving the SC (Isa & Yoshida 2021, Kinoshita et al. 2019).

Taken together, these results show that the primate SC responds very well to many visual features that are relevant for scene representation. In some cases, the implications of such visual feature tuning for orienting behaviors are obvious. For example, one can (rapidly) generate saccades to hue-defined forms. For other observations, like the more foveal suppressive RF surrounds (Churan et al. 2012) or the potentially global patterns of orientation tuning preferences across the SC topographic map, further behavioral investigations are needed.

Visual Object Detection and Discrimination by the Superior Colliculus

Moving from simple visual features to patterned stimuli (**Figure 3**) allows one to further ask how the SC visual machinery can support higher-level vision. After all, we orient toward real objects most of the time. As early as 1974, Updyke (1974) observed that half of intermediate-layer SC neurons in the anesthetized Cebus monkey, and a substantial fraction of superficial neurons, responded robustly to real, three-dimensional objects. This suggests that the SC might have access to mechanisms associated with the perception of high-level visual forms. More recently, SC responses to faces and face-like stimuli were reported (Le et al. 2020, Nguyen et al. 2014, Soares et al. 2017), and it was suggested that these responses are early enough to allow the SC to act as a fast object detector. Indeed, tests exploring the influences of task-irrelevant visual forms on target selection for saccades and manual responses revealed that there was an express influence of visual forms, versus scrambled but spectrally equivalent visual scenes, on reaction times (Bogadhi et al. 2020).

These results suggest a generalized mechanism for peripheral object detection, which may exploit the privileged access of the SC to the motor control periphery. Indeed, it may take too long

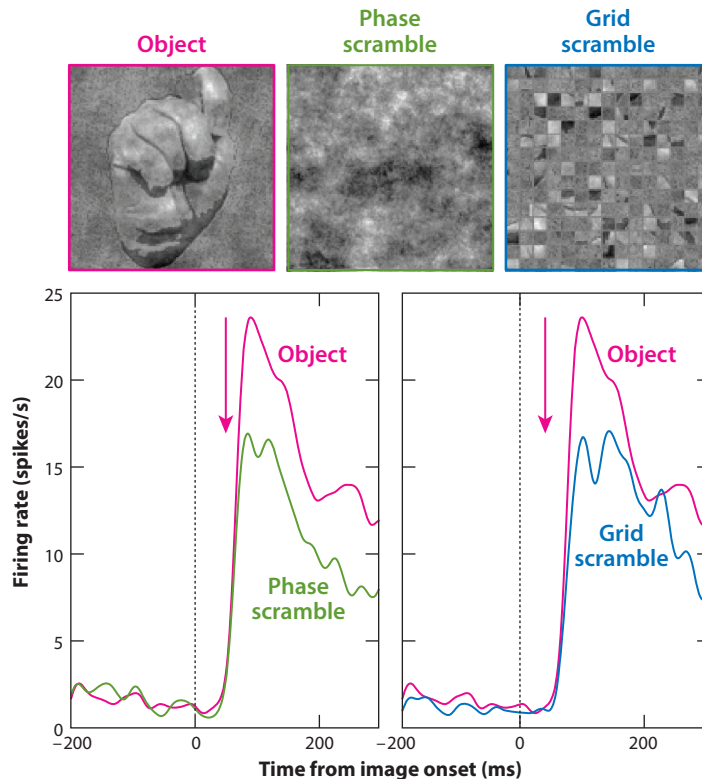


Figure 6

Rapid object detection by primate superior colliculus (SC) neurons. When images of real objects (*top left*; shown example: hand) are placed in the visual receptive fields (RFs) of some SC neurons, the initial visual responses of the neurons are significantly stronger than when different scrambles of the same objects' images, maintaining luminance and either spectral (phase scramble) or local-feature (grid scramble) information, are displayed. Thus, the SC is part of the mechanisms for express orienting responses to visual forms. Figure adapted from Bogadhi & Hafed (2022) (CC BY 4.0).

for the ventral cortical visual processing stream to discriminate visual objects and then relay this information to generate express saccades. In contrast, early object detection and discrimination in the SC's initial visual bursts are sufficient for express saccade generation. Consistent with this, when comparing real versus scrambled visual forms, Bogadhi & Hafed (2022) found that initial SC visual bursts were indeed different (**Figure 6**).

These results are consistent with a causal role for primate SC activity in maintaining object selectivity in the temporal cortex (Bogadhi et al. 2021), as demonstrated via SC inactivation. Thus, not only may the primate SC be capable of quickly detecting visual forms (**Figure 6**), but such detection can also influence these forms' cortical processing. These results may represent a homology with the mouse SC's collicular visual cortex (Beltramo & Scanziani 2019), and they promise to motivate interesting future research. For example, an approach using neural networks could explore the image properties that maximally excite SC neurons, as has been done in the cortex (Bashivan et al. 2019). Moreover, as we describe below, visual object information is also present in the SC even at the time of saccade motor execution, which can allow the SC to relay peripheral visual object information to the rest of the visual system in anticipation of the retinal-image consequences of rapid eyeball rotation.

The Superior Colliculus and Visual Threat Detection

If the SC can rapidly detect visual objects, then this places it within a pathway for rapid threat detection and avoidance. Indeed, SC lesions in infant monkeys impair these monkeys' responsiveness to toy snakes (Maior et al. 2011, 2012). Moreover, defensive behavior in reaction to snakes in marmoset monkeys is partly mediated by intermediate SC layers (Montardy et al. 2021). Looming stimuli could also reflect impending threats, and classic studies demonstrated primate SC responses to such stimuli (Updyke 1974). Therefore, both visual feature tuning and visual form detection by SC neurons can be exploited by this structure's proximity to the motor periphery to allow for rapid reaction to visual threats. Further studies could elucidate this role and relate it to emotional fear in humans.

LINKING PERCEPTION AND ACTION VIA THE PRIMATE SUPERIOR COLLICULUS

The research discussed above characterized primate SC visual functions primarily in the absence of eye movements. However, if the primate SC integrates a large amount of visual information (Figure 2), then it can also internally relay, to the rest of the visual system, its instantaneous accumulated evidence about the visual environment at the time of eye movement generation. This would allow it to bridge the period of sensory uncertainty associated with saccades, since rapid eyeball rotations cause gray-out in retinal images (Wurtz 2008), and since visual reafference arrives too late after movement onset. An intriguing possibility, given that saccade-related SC motor bursts are relayed virtually unchanged to the cortex (Sommer & Wurtz 2004), and given that these bursts are not necessarily directly relevant for saccade kinematic control (Zhang et al. 2022), is that these motor bursts actually encode sensory evidence about the visual appearance of the saccade target. Consistent with this, saccade-related motor bursts of individual SC neurons

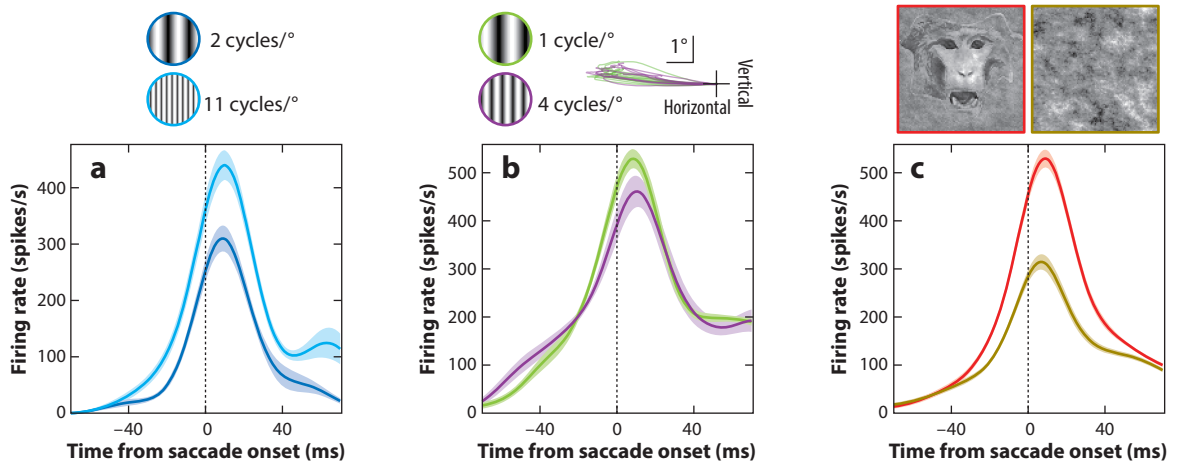


Figure 7

Visual feature tuning in primate superior colliculus (SC) neuronal movement commands. (a,b) Saccade-related motor bursts of two example SC neurons when grating images of different spatial frequencies are placed, to serve as the saccade targets, at the neurons' movement-related receptive field (RF) centers. Despite matched saccades (example eye position traces are shown in the inset for one of the neurons), the saccade-related motor bursts of the neurons are different for different target images. This effect is not explained by differences in saccade vectors or kinematics across the images (Baumann et al. 2022). (c) Saccade-related motor bursts of a third example neuron when object images (e.g., monkey face) or their phase-scrambled versions (as in Figure 6) are tested instead of gratings. SC neurons differentiate between real and scrambled object images in their saccade-related motor bursts (Baumann et al. 2022). Colored shaded background fields indicate ranges for standard error of the mean.

exhibit highly robust visual sensory tuning, much like the feature tuning properties described throughout this review (Baumann et al. 2022). That is, for similar saccade vectors and kinematics, individual SC neurons show significantly different strengths in their saccade-related motor bursts for different images as the saccade targets (**Figure 7a,b**). Intriguingly, SC saccade-related motor bursts also differentiate between real and scrambled visual object images (**Figure 7c**), and these effects robustly emerge in all saccade-related SC neurons (Baumann et al. 2022).

Thus, at the time of saccade generation, the SC internally relays at least two pieces of information to the rest of the visual system. First, the topographic site of active SC neurons informs the cortex of the upcoming saccade vector, allowing spatial remapping of retinotopic visual representations in anticipation of the retinal image shifts caused by eyeball rotation (Sommer & Wurtz 2002, 2006). Second, the spike rates in the active neurons provide a feature-tuned peripheral preview of the appearance of the saccade target that is about to be foveated. This makes the SC an important structure for integrating perception and action and for explaining a large range of perisaccadic perceptual and neural phenomena (Kroell & Rolfs 2021, 2022; Moore et al. 1998). Indeed, peripheral previews are critical for successful visually guided behavior (Nuthmann et al. 2021), and the results shown in **Figure 7** promise to lead to interesting future insights about active perception in natural behavior.

CONCLUSION

The primate SC is as rich a visual structure as it is a cognitive and motor control structure. This idea is important for the wider neuroscience community, in which the primate SC may be perceived as simply a saccade controller and not as an important visual node. Moreover, inclusion of ecological constraints on behavior can act as a powerful aid in discovering new phenomena related to visual-motor interactions in many animal species, including primates. This opens the door for many new and interesting questions that will undoubtedly advance our understanding of the visual, cognitive, and motor functions of the primate SC.

SUMMARY POINTS

1. The primate superior colliculus (SC) integrates visual information from multiple sources, including the retina.
2. There is a substantial diversity of visual dependencies in primate SC responses, even at the time of eye movement generation.
3. The primate SC contains neurons that are strongly sensitive to foveal visual inputs and magnifies representation of foveal visual image regions in its topographic map.
4. Visual feature tuning properties in primate SC neurons support orienting behaviors by reflecting certain statistical regularities in the environment, such as the difference in retinal image sizes between the upper and lower visual fields or the preponderance of low spatial frequency spectral energy in natural images.
5. The primate SC is endowed with the means to rapidly detect high-level visual forms, such as faces, potentially facilitating express behavioral responses to real-life objects, including threatening ones.
6. Visual feature and form information are embedded within primate SC saccade-related motor bursts, potentially allowing the SC's integrated evidence about eye movement target appearance to be internally relayed back to the visual system as a re-entrant signal during eyeball rotation.

FUTURE ISSUES

1. What are the implications of monocular and binocular retinal recipient zones in the primate SC topographic map? Is there disparity tuning in visually responsive neurons?
2. Are there primate SC feature maps that are multiplexed with the topographic spatial map?
3. What are the functional implications of visual sensory tuning in the SC saccade-related movement commands (**Figure 7**)?
4. Is there sophisticated visual pattern analysis that takes place downstream of the primate SC in the motor control brainstem? If not, how and why is visual information abruptly truncated downstream of the SC? If so, what is its functional importance?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We were supported by the Werner Reichardt Centre for Integrative Neuroscience, an Excellence Cluster (EXC307) funded by the Deutsche Forschungsgemeinschaft (DFG). We were also funded by the Hertie Institute for Clinical Brain Research and by the following DFG-funded grants: (a) SFB1233 Robust Vision (TP11; project number 276693517) and (b) BO5681/1-1. Support was also received as a Grant-in-Aid for Research Activity Start-up (project number 20K22684) from JSPS, Japan.

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Errata

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