

What Are the Functions of the Superior Colliculus and Its Involvement in Neurologic Disorders?

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The superior colliculus (SC) is an evolutionary conserved sensorimotor structure that is specialized for detecting, localizing, and orienting toward environmental events and has a critical role in orienting motor responses, visuospatial attention, and perceptual decision-making.¹⁻⁸ The SC consists of a superficial layer that receives visual inputs and intermediate and deep motor layers that initiate saccades and other orienting movements toward the contralateral hemispace. Modern molecular and genetic methods combined with behavioral assessments have provided further understanding of the cell types, circuits, and functions of the SC (reviewed in ref. 9,10). The SC is affected by α -synuclein and tau neuropathology in Lewy body dementia (LBD),¹¹ shows abnormal responses to visual stimuli in Parkinson disease (PD),^{12,13} may contribute to impaired saccades in progressive supranuclear palsy (PSP),¹⁴ and may be involved in the pathophysiology of cervical dystonia.^{15,16} This brief review will focus on recent concepts on the functional organization and connectivity of the SC that are relevant to understand the pathophysiology of these and other neurologic disorders.

Laminar Organization and Connections

The SC has a distinct laminar structure consisting of alternating layers of neurons and fibers. It can be divided into 3 major gray matter lamina or strata, superficial (stratum griseum superficiale), intermediate (stratum griseum intermediale), and deep (stratum griseum profundum), interspersed with predominantly fiber-rich layers^{3,17} (Figure). The superficial or visuosensory layer receives retinotopically organized afferents from the retina (primarily direction-sensitive ganglion cells), lateral geniculate nucleus (LGN), primary visual cortex (V1), and medial temporal visual area (MT) representing the contralateral visual field.¹⁸ The intermediate and deep layers receive inputs from virtually the entire neuraxis.^{19,20} Cortical excitatory inputs originate from the frontal eye field (FEF)^{21,22} and the intraparietal sulcus (parietal eye field, lateral intraparietal area in monkeys).^{23,24} The deep and middle layers also receive excitatory auditory input from the inferior colliculus¹⁹ and somatosensory input from the contralateral spinal cord and dorsal column nuclei.²⁵ By contrast, the substantia nigra pars reticulata (SNr) provides a tonic GABAergic inhibitory input to the SC.^{26,27} The SC also receives modulatory inputs from several brainstem areas, including the parabrachial nucleus,²⁸ parabrachial nucleus,^{29,30} pedunculopontine nucleus,³¹ locus ceruleus,³² and dorsal raphe.³³

The outputs of the SC target widespread areas of the neuraxis.¹⁷ The superficial layer projects to thalamic nuclei that project to cortical visual areas. A group of superficial layer neurons that receive primarily input from the visual cortex projects to the medial subnucleus of the inferior pulvinar.^{34,35} This portion of the pulvinar, in turn, projects to the medial temporal visual area (area V5/MT), which is a component of the dorsal visual stream.³⁶ Tectopulvinar neurons respond to moving visual stimuli and provide a major source of motion information for visuospatial attention that bypasses the pathway from the retina to the dorsal LGN (dLGN) and then V1. A second group of superficial layer SC neurons that receive primarily retinal input projects to the dLGN. The superficial layer of the SC also projects to the pretectal nucleus, which projects back to the SC.¹⁷

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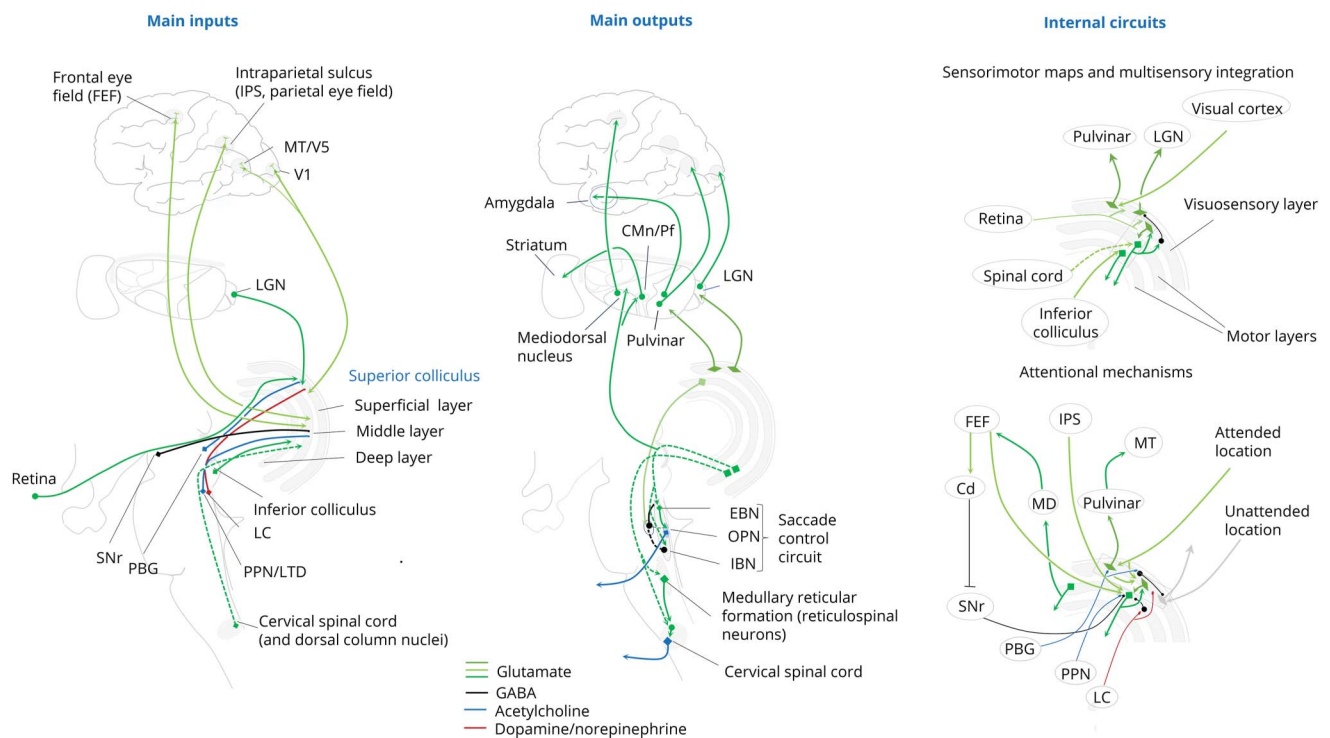
Glossary

dLGN = dorsal LGN; EBNs = excitatory burst neurons; FDG-PET = fluorodeoxyglucose PET; FEF = frontal eye field; fMRI = functional MRI; IBNs = inhibitory burst neurons; LGN = lateral geniculate nucleus; LBD = Lewy body dementia; OPNs = omnipause neurons; PD = Parkinson disease; PSP = progressive supranuclear palsy; V1 = primary visual cortex; V5/MT = medial temporal visual area; SC = superior colliculus; MT = medial temporal visual area; SNr = substantia nigra pars reticulata.

Neurons in the intermediate and deep layers provide crossed descending projections to the brainstem reticular formation and spinal cord and uncrossed projections to the midbrain and thalamus. The crossed descending projections innervate brainstem centers controlling saccadic eye movements.^{17,37,38} The brainstem saccade control circuit targeted by the SC includes excitatory burst neurons (EBNs) and inhibitory burst

neurons (IBNs) located within the paramedian pontine reticular formation for horizontal saccades and in the interstitial nucleus of the medial longitudinal fasciculus for vertical saccades and omnipause neurons (OPNs) located in the nucleus raphe interpositus.^{39,40} The rostral pole of the SC contains a map of the contralateral fovea and harbors fixation neurons that send a monosynaptic excitatory input to OPNs that

Figure Organization, Extrinsic Connections, and Internal Circuits in the Superior Colliculus



The superior colliculus (SC) has a laminar structure consisting of superficial, middle, and deep layers. The superficial (visuosensory) layer receives afferents from the retina, lateral geniculate nucleus (LGN), primary visual cortex (V1), and medial temporal visual area (MT/V5). The intermediate and deep layers receive inputs from the frontal eye field (FEF), intraparietal sulcus (IPS, parietal eye field), substantia nigra pars reticulata (SNr), inferior colliculus, and contralateral spinal cord. Brainstem modulatory inputs to the SC originate from the parabigeminal nucleus (PBG), pedunculopontine nucleus (PPN), laterodorsal tegmental nucleus (LTD), locus ceruleus (LC), and dorsal raphe (not shown). Superficial layer neurons project to the medial subnucleus of the inferior pulvinar, which in turn targets area MT/V5, and to the dorsal LGN, which targets V1. Neurons in the intermediate and deep layers provide a crossed descending projection (dotted lines) to innervate the saccadic control circuit, which includes excitatory burst neurons (EBNs) and inhibitory burst neurons (IBNs) targeted by the caudal pole of the SC and omnipause neurons (OPN) targeted by the rostral pole. The crossed descending axons from the SC descend areas of the reticular formation containing reticulospinal neurons and then reach the cervical spinal cord targeting primarily interneurons. Ascending projections from the middle and deep layers include collateral projections from saccadic neurons to the mediodorsal (MD) nucleus of the thalamus, which in turn projects to the FEF; projections to the centromedian/parafascicular (CMn/Pf) nuclei, which target the caudate nucleus (Cd); and projections to the medial pulvinar, which projects to the amygdala. The SC also sends inputs to the substantia nigra pars compacta, ventral tegmental area, subthalamic nucleus, PPN/LDT, and periaqueductal gray (not shown). Local circuits in the SC are critical for multisensory integration for orienting responses, visuospatial attention, and perceptual decision-making. Neurons in the intermediate and deep layers receive inputs from the visuosensory neurons of the superficial layer, are organized into a motor map in register with the visual map, and integrate visual with auditory inputs from the inferior colliculus and somatosensory inputs from the cervical spinal cord and dorsal column nuclei. Recurrent collaterals from the intermediate to the superficial layer may either excite superficial layer neurons projecting to the deep layers or, through GABAergic interneurons, suppress the activity of superficial layer neurons projecting to the pulvinar and dLGN. The SC receives input from the FEF and IPS, which are components of the dorsal attention network involved in goal-oriented visuospatial attention. These inputs trigger voluntary and reflex saccades. The FEF also projects to the Cd, which inhibits GABAergic neurons of the SNr projecting to the SC. Reciprocally, saccadic neurons of the SC send signals to the FEF through the MD. A signal from the deep layers of the SC modulates the sensory responsiveness of neurons in the superficial layers. Cholinergic input from the PBG and PPN/LDT may create focal excitation and global surround inhibition mediated by local GABAergic neurons within the SC. Dopaminergic projections from the LC modulate visual threat processing through GABAergic neurons at the intermediate layers of the SC.

tonically inhibit the saccadic burst neurons.^{37,38} The caudal portion of the SC harbors neurons that discharge before both reflex and voluntary saccades and project to burst neurons that in turn activate EBNs and IBNs. Projections from these neurons to ocular motor nuclei mediate the visual grasp reflex, which is a component of an orienting response to salient stimuli.⁸ Inhibitory burst neurons also inhibit contralateral OPNs, thereby providing a disynaptic pathway that triggers saccades.^{37,38} Topographic connections involving excitatory and inhibitory commissural neurons in the SC may have an important role in conjugate upward and downward vertical saccades.⁴¹ Neurons in the intermediate layer of the SC also discharge during orienting responses linked to movements of the head⁴² and upper limb.⁴³ The middle and deep layers of the SC provide crossed descending projections to areas of the reticular formation such as the gigantocellular nucleus harboring reticulospinal neurons⁴⁴ and to the upper cervical spinal cord (tectospinal tract) where they target primarily interneurons to control coordinated head-eye movements.⁴⁵⁻⁴⁸

The ascending projections from the intermediate and deep layers of the SC are denser than the descending projections and contribute to higher aspects of visual function, such as attention and perceptual decision-making.⁶ For example, SC neurons projecting to the brainstem saccade generator send collateral projections to the mediodorsal nucleus of the thalamus, which in turn targets the FEF, thus providing a feed-forward information (corollary discharge) about impending eye movements.⁴⁹ Outputs of the SC to the thalamus also affect basal ganglia and limbic circuits.⁵⁰ The SC projects to the centromedian and parafascicular nuclei, which provide output to the caudate nucleus,⁵⁰ thus affecting goal-driven actions. The SC also projects to areas of the pulvinar that target the basolateral amygdala, thus providing a subcortical circuit for orienting responses to threat stimuli.^{51,52} The SC also sends direct excitatory projection to dopaminergic neurons of the substantia nigra pars compacta,⁵³ to the subthalamic nucleus,⁵⁴ and to cholinergic neurons in the pedunculopontine and laterodorsal tegmental nucleus,⁵⁵ which are involved in attention and action selection.

Local Circuits

The SC contains maps of the sensory space and actions that are topographically arranged and in register with each other through a direct link between the visuosensory superficial layer and the motor intermediate and deep layers⁵⁶⁻⁶² (Figure). The retinal map of the space serves as a template for aligning sensory and motor maps.⁶³ The superficial layer projects to the motor layers and provides a disynaptic excitatory pathway from the retina to neurons generating saccades and other orienting movements.⁶⁴⁻⁶⁷ The map of saccadic eye movements is organized according to the spatial motor error computed from the position of the eyes relative to the position of the visual target of interest.^{68,69} Neurons in the deep layers of the SC also receive auditory and somatosensory inputs that match the retinotopy.^{19,25} This indicates that these neurons constitute multisensory functional units,⁷⁰⁻⁷² which are able to generate

amplified responses to spatiotemporally concordant visual and auditory stimuli.⁷³

Local GABAergic neurons in the superficial layer allow visuosensory neurons to function as salience detectors controlling bursting activity in neurons in the intermediate layer.⁷⁴ Neurons in the intermediate layer provide 2 recurrent collateral pathways of the superficial layer⁶; one of them excites neurons in the superficial layers projecting to the deep layers enhancing their response to visual stimuli,⁶⁸ whereas the other terminates on local GABAergic interneurons that suppress the activity of superficial layer neurons projecting the pulvinar and dLGN and contributes to suppression of retinal motion perception during eye movements.⁷⁵ The disynaptic intralaminar pathway from the retina to the middle through the superficial layer of the LC triggers short latency express saccades,⁷⁶ whereas the cortical input from the FEF and intraparietal sulcus to the middle layer is necessary for conventional voluntary and reflex saccades.⁶ The FEF, through inputs to the caudate nucleus, also promotes saccadic eye movements by releasing the SC from the tonic GABAergic inhibition by the SNr.²⁷ This nigrotectal connection not only regulates burst initiation but also modulates the spatiotemporal properties of premotor neurons through connections to local GABAergic neurons.⁷⁷

Role in Visuospatial Attention and Perceptual Decision-Making

Spatial attention enhances sensory signals to facilitate the processing of sensory information for goal-oriented behaviors.^{8,78} Studies in monkeys indicate that the SC has an important role in visuospatial attention.⁹ Saccadic neurons of the SC use a population vector average for single targets and use a winner-takes-all code for multiple possible targets according to their behavioral relevance.^{1,79} The SC receives inputs from the FEF and intraparietal sulcus,²¹⁻²⁴ which are core components of the dorsal attention network involved in goal-oriented visuospatial attention.⁸⁰⁻⁸² This circuit can modulate the gain of incoming retinal signals reaching cortical and subcortical structures and thus affect visual processing.⁸³⁻⁸⁷ Most of the FEF projections to the SC signal cognitive operations preceding the onset of saccades,⁸⁸ whereas input from the intraparietal sulcus provides online visuospatial information for triggering of reflexive saccades.⁸⁹ Attention modulates the influence of sensory inputs to the SC in the selection of saccades⁹⁰; motor commands, in turn, influence the sensory responses in the SC independently of the execution of the eye movements.^{68,91} This indicates that the SC is involved in the shift in the focus of attention to the target location.⁹²⁻⁹⁴ Although the SC, through the pulvinar, connects to cortical visual areas involved in spatial attention such as area MT and superior temporal sulcus,^{95,96} inactivation studies show that the SC can modulate spatial attention independently of the cerebral cortex,⁹⁷ for example, through the basal ganglia.²⁷ Brainstem cholinergic and GABAergic inputs, through interactions with forebrain inputs, may create a priority map within the SC by a mechanism of focal excitation and global surround inhibition; this establishes the spatial location of interest and drives an orienting movement toward the selected target.^{98,99} Cholinergic inputs from the

parabigeminal nucleus^{29,30} to the superficial layers of the SC may enhance the visual responsiveness and spatial selectivity of visuosensory neurons through nicotinic receptors in retinal axon terminals and local GABAergic neurons, whereas GABAergic inputs from this nucleus may suppress activity to unattended regions in the SC map.⁹⁹⁻¹⁰² Cholinergic inputs from the pedunculopontine nucleus may contribute to selective attention and generation of saccades through nicotinic receptor activation of neurons in intermediate and deep layers of the SC projecting the brainstem.¹⁰³⁻¹⁰⁵ The SC is also activated during REM sleep; cholinergic and GABAergic modulation of the SC may thus also affect REM sleep and may be associated with visuospatial learning and memory consolidation.¹⁰⁶

Role in Emotional Responses

Studies in rodents show that the SC influences innate or reflexive actions through 2 segregated pathways originating from its intermediate layer, a crossed tectobulbar pathway that targets the contralateral brainstem and spinal cord and mediates approach behaviors and an uncrossed tectopontine pathway that targets the ipsilateral pons and mediates avoidance behaviors.^{64,107} Neurons in the superficial layers project to the amygdala both through the pulvinar and through the parabigeminal nucleus. The deep layers of the SC provide excitatory projection areas required for the initiation of threat-evoked escaped responses, including the dorsal periaqueductal gray¹⁰⁸ and ventral tegmental area.¹⁰⁹ Stress enhances escape behavior through projections of the locus ceruleus to the SC.¹¹⁰ These projections provide dopaminergic inputs that modulate visual threat processing through D2 receptors in GABAergic neurons at the intermediate and deep layers.¹¹¹ The context-dependent innate behaviors initiated by SC neurons are accompanied by stereotypical cardiovascular and respiratory responses, which are mediated by projections of the SC to neurons in the medullary gigantocellular reticular nucleus projecting to the spinal cord.¹¹²

Clinical Correlations

Functional MRI neuroimaging studies have allowed the detection of SC activation in response to visual stimuli in both normal and pathologic conditions. One such study showed that the activity of the SC increases linearly with increasing luminance contrast in normal individuals and that luminance contrast processing in the SC is affected by normal aging.¹¹³ These studies also show that the SC-pulvinar-amygdala pathway is activated on exposure to threat and may underlie the ability of humans with blindsight to recognize fearful emotion in facial expressions.¹¹⁴⁻¹¹⁷ Diffusion tensor imaging confirmed the presence of a pathway connecting the FEF to the superior colliculus in humans.²² Consistent with studies in monkeys,^{83,92-94} transcranial magnetic stimulation studies show that the preparatory activity of the FEF before onset of a saccade toward a target modulates the visual detection threshold in humans.^{118,119}

Involvement of the SC may contribute to impaired visuospatial attention and orienting responses in neurodegenerative disorders

such as DLB. A neuropathologic study showed substantial reductions in neuronal density and accumulation of α -synuclein and tau inclusions primarily involving the intermediate and deep layers of the SC.¹¹ As these layers receive inputs from brainstem areas vulnerable to α -synuclein and tau neuropathology,¹²⁰ these findings can be interpreted as consistent with a prion-like disease propagation as occurs in neurodegenerative disorders.¹¹ The intermediate and deep layers of the SC are also vulnerable to tau pathology in chronic traumatic encephalopathy.¹²¹ The neuropathologic changes in the SC may contribute to some of the clinical manifestations of neurodegenerative disorders such as LBD. Dysfunction of the dorsal attention network connected with the SC has been implicated in visual hallucinations.¹²² Neuropathologic studies showed that the degree of neuronal loss and tau accumulation (but not the brunt of α -synuclein pathology) in the SC was related to the severity and frequency of visual hallucinations in LBD.¹¹ The SC is also affected in PD. An fMRI study showed a lack of modulation of SC activation in response to luminance contrast in de novo patients with PD compared with controls, suggesting that abnormal visual processing in the SC occurs early in the disease course.¹² Patients with PD may show short-latency saccades and difficult to inhibit reflexive saccades toward visual stimuli.^{123,124} These findings have been interpreted as in part reflecting neuroadaptation in the SC to compensate for excessive inhibition from the SNr, as shown in experimental models of PD.¹²⁵ It has been suggested that levodopa may modulate the balance between voluntary and reflex saccades in PD by facilitating planning movements in the FEF and suppressing the release of reflexive saccades originating in the SC.¹²³ The superior colliculus is also involved by tau pathology in PSP.¹⁴ In patients with this disorder, the progressively reduced accuracy of horizontal saccades suggests a brainstem oculomotor pathology that includes the SC and/or paramedian pontine reticular formation, whereas the functioning of the oculomotor system above the brainstem was found to be similar between patients with PSP and PD.¹²⁶ In PSP, saccade disturbances reflect paucity in burst generation by EBNs and imprecise timing and premature discharge of IBNs, reflecting maladaptive SC activity leading to a change in the intended trajectory of the ongoing saccade.¹²⁷ Functional MRI studies also suggest SC dysfunction in cervical dystonia.¹⁵ One such study showed slower SC activation in response to both luminant and chromatic visual stimuli in these patients compared with controls.¹⁶ It has been proposed that cervical dystonia may reflect an alteration in the SC circuitry resulting from impaired GABAergic activity and manifested by abnormal temporal discrimination in visuosensory neurons of the superficial layer and disinhibited burst activity of the tectospinal neurons in deeper layers.¹²⁸ An fMRI study using causal connectivity modeling showed that the modulation of the strength of functional connection from the striatum to the SC in response to a looming visual stimulus was greater in patients with cervical dystonia than that in controls.¹²⁹

Perspective

The evidence briefly discussed in this review indicates that the SC, like the thalamus, striatum, and brainstem, should be

considered as an important contributor to network dysfunction underlying cognitive and motor abnormalities in neurodegenerative disorders. Unfortunately, although SC activation can be identified on fMRI, the SC is too small to be identified with fluorodeoxyglucose PET (FDG-PET). Higher sensitivity imaging procedures and neuropathologic studies with careful clinical correlations may provide further insight on the contribution of the SC in these and other disorders.

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Appendix Author

Name	Location	Contribution
Eduardo Benarroch, MD	Mayo Clinic, Rochester, MN	Drafting/revision of the manuscript for content, including medical writing for content; major role in the acquisition of data; study concept or design; and analysis or interpretation of data

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