

CHAPTER 11

The superior colliculus

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4 Abstract

5 The mammalian superior colliculus (SC) serves the crucial function of guiding and coordinating the
6 orienting response. Integrating multisensory, motor, and cognitive information, and sending motor
7 commands directly to the brainstem circuitry, the SC initiates a rapid orienting response that can
8 invoke much of the body. The phylogenetic preservation of this structure illustrates its ongoing signif-
9 icance for survival, but for higher mammals, evolutionary pressure for flexible control over orienting
10 behaviour coincided with development of a much more complex set of corticotectal projections. As a
11 result, orienting in higher mammals (e.g. primates) is controlled by a careful interplay between senso-
12 ry-driven and goal-driven processes that converge in the SC. This review focuses on the SC as a critical
13 locus for this interaction, whereby one compartment fits the role of a visual saliency map, and another
14 a priority map that represents the integration of salience and behavioural relevance.

15 Introduction

16 Located on the dorsal surface of the midbrain, the mammalian SC is ideally situated to guide and
17 coordinate orienting behaviour. By integrating multiple sources of sensory, motor, and cognitive
18 signals, and in turn sending motor commands directly to the brainstem circuitry, the SC initiates a
19 rapid orienting response that can invoke the eyes, neck, and shoulder muscles (Akert, 1949; Boehnke
20 and Munoz, 2008; Corneil et al., 2008; Dean et al., 1989; Hess et al., 1946; Ingle, 1983; Pruszyński
21 et al., 2010; Sokolov, 1963). For primates, the flexible control over orienting behaviour is essential,
22 and resulted in the development of a more complex set of corticotectal projections compared with
23 earlier mammals. In this review we highlight key findings that have emerged in predominantly
24 primate research since earlier reviews of the SC have appeared (Krauzlis, 2005; Munoz et al., 2000;
25 Robinson and McClurkin, 1989; Schiller, 1977; Sparks, 1986; Sparks and Hartwich-Young, 1989;
26 Wurtz and Albano, 1980). We build off an idea first developed by Edwards and others (Casagrande
27 et al., 1972; Edwards, 1980) that the mammalian SC represents two largely independent structures
28 with functionally distinct roles. One compartment is consistent with the role of a *saliency map*, where
29 saliency is defined as the sensory qualities that make a stimulus distinctive from its surroundings. The
30 other compartment is consistent with the role of a *priority map* (Boehnke and Munoz, 2008; Fecteau
31 and Munoz, 2006; Serences and Yantis, 2006), where priority is defined as the integration of visual
32 saliency and behavioural relevance, the relative importance of a stimulus for the goal of the observer.
33 We have two main aims: 1) we present an up-to-date summary of the intrinsic and extrinsic
34 circuitry of the SC, primarily but not exclusively as it relates to the monkey, focusing on key aspects
35 of laminar organization; 2) we outline the main functions of the SC, highlighting key findings that
36 are changing and expanding our view of the SC for the flexible control of orienting behaviour.

1 Superior colliculus structure

2 SC layers

3 The mammalian SC is a laminated structure consisting of seven anatomically distinct layers that have
 4 been traditionally grouped into two functional regions (Edwards, 1980; Sprague, 1975), a *superficial*
 5 region concerned exclusively with visual processing (Goldberg and Wurtz, 1972a), and a *deeper*
 6 region concerned with multisensory (Meredith and Stein, 1983, 1985; Stein and Meredith, 1993),
 7 motor (Robinson, 1972; Sparks, 1978; Wurtz and Goldberg, 1971), and higher-level cognitive proc-
 8 esses (Fig. 11.1A). The superficial layers consist of the three dorsal most laminae, residing within
 9 approximately the top 1 mm of the collicular surface: the *stratum zonale* (SZ), the *stratum griseum*
 10 *superficiale* (SGS), and the *stratum opticum* (SO). The deeper layers refer to the remaining four lower
 11 laminae: the *stratum griseum intermediale* (SGI), the *stratum album intermediale* (SAI), the *stratum*
 12 *griseum profundum* (SGP), and the *stratum album profundum* (SAP). The cytological and physiologi-
 13 cal characteristics of deeper layer SC cells are virtually indistinguishable from the underlying reticu-
 14 lum, and very different from superficial layer SC cells. So much so that the deeper layers have instead
 15 been considered to be part of the reticular core (Edwards, 1980), challenging the view of the SC as a
 16 unified structure. In this review we will highlight important functional differences between the
 17 superficial (SGS and SO) and intermediate (SGI and SAI) layers of the SC, which we henceforth refer
 18 to as the SCs and SCi, respectively.

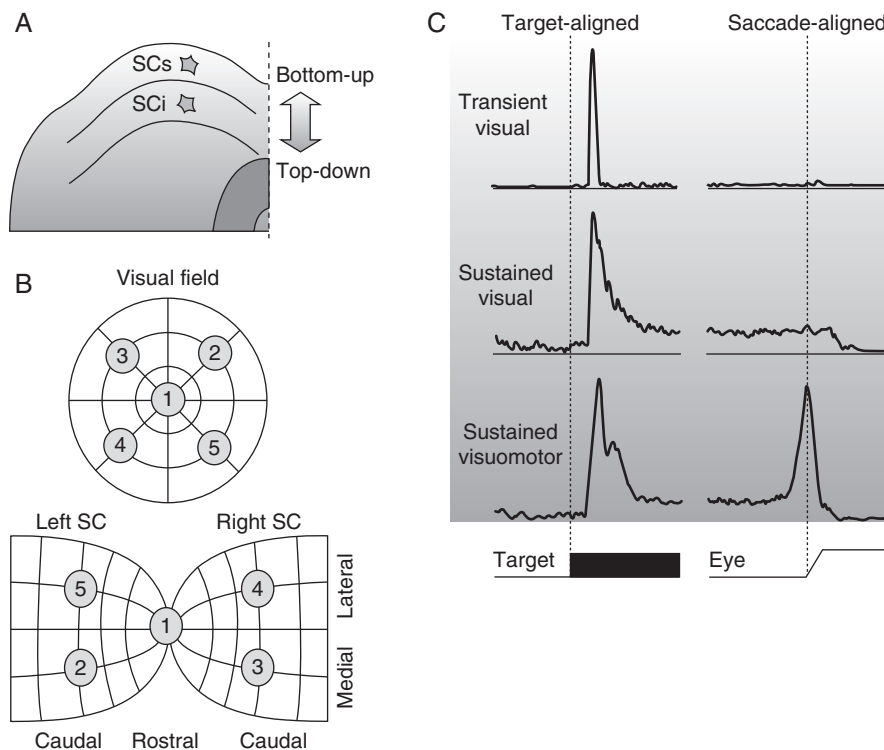


Fig. 11.1 The primate SC. A) Transverse view of the SC highlighting the superficial (SCs) and intermediate (SCi) layers. The progression from top to bottom represents a shift from mostly bottom-up towards increasing top-down processes. B) Topography of the correspondence between visual space (top) and SC space (bottom). C) Common response properties of SC neurons along the progression from the superficial to intermediate SC layers.

1 SC maps

2 Topographic maps are a central organizing principle of the brain, and play a crucial role in spatially-
 3 guided behaviour. It has long been known that neurons within the SC are organized into well-defined
 4 topographic maps, whereby each colliculus contains multisensory (Groh and Sparks, 1996; Jay and
 5 Sparks, 1987; Meredith and Stein, 1983, 1985; Stein and Meredith, 1993), and motor (Robinson,
 6 1972; Sparks, 1978; Wurtz and Goldberg, 1971) representations of contralateral space (Fig. 11.1B).
 7 For example, the SCs contains a visual map such that a given neuron at a specific location on the map
 8 responds to stimuli presented in a restricted region of the contralateral visual field, which defines a
 9 receptive field (Cynader and Berman, 1972). The SCi on the other hand has both multisensory and
 10 motor representations, such that local stimulation of neurons at a given location on the map causes
 11 the eyes to move with a fixed vector of a specific direction and amplitude (Robinson, 1972). In terms
 12 of the visual and motor representations, the rostral, caudal, medial, and lateral SC represent the
 13 fovea, periphery, upper, and lower visual fields, respectively (Fig. 11.1B). As a general principle, the
 14 central region of vision defining the high acuity fovea has a much greater neural representation than
 15 the periphery (Van Essen et al., 1984). The same is true for the SC in which about one-third of its
 16 surface is devoted to the central 10° of visual angle (Cynader and Berman, 1972; Robinson, 1972;
 17 Schiller and Stryker, 1972). As such, the size of response fields in the SC increase as one moves from
 18 the rostral pole (representing the fovea) caudally (representing the periphery). The transformation of
 19 two-dimensional (2D) visual space into SC space is well understood (Cynader and Berman, 1972;
 20 Marino et al., 2008; Robinson, 1972; Schiller and Stryker, 1972), and can be best described by a loga-
 21 rithmic scaling factor (Ottus et al., 1986; Van Gisbergen et al., 1987). Furthermore, there is close spatial
 22 correspondence between the visual and motor representations in the SC (Marino et al., 2008).

23 SCs inputs and outputs

24 The SCs receives visual inputs from two primary sources (Fig. 11.2): 1) a direct projection from the
 25 retina (the retinotectal pathway) (Covey and Perry, 1980; Hubel et al., 1975; Pollack and Hickey,
 26 1979); and 2) direct projections from visual cortex, specifically primary visual cortex (V1), V2, V3,
 27 V4, and middle temporal area (MT) (Cusick, 1988; Fries, 1984; Graham, 1982; Lock et al., 2003;
 28 Tigges and Tigges, 1981; see Harting et al., 1992 for a detailed anatomical study of corticotectal
 29 projections in the cat). The retinotectal projection is most dense in the upper 200 µm (Hubel et al.,
 30 1975), and there is evidence that the progression from earlier to later cortical visual areas is repre-
 31 sented by increasing depth in the SCs, with the V1 projection overlapping the retinotectal in the
 32 upper part of the SCs, and higher cortical visual areas projecting progressively deeper (Kawamura
 33 et al., 1974; Shipp, 2004; Sprague, 1975; Tigges and Tigges, 1981).

34 While visual activity in the primate SCs has been shown to persist after a temporary 'lesion' of
 35 visual cortex via cortical-cooling (Schiller et al., 1974), the retinotectal pathway has been somewhat
 36 superseded by a growing reliance on visual cortex in higher mammals. For example, the relative
 37 number of retinotectal fibres has systematically decreased with the increasing evolutionary elaboration
 38 of the geniculostriate system, with ratios of retinal fibres projecting to the SCs and LGN (lateral
 39 geniculate nucleus) that range from 3:1 in hamsters, to 2:1 in rats, and 1:8 in rhesus monkeys (Schiller,
 40 1977). In short, for phylogenetically older mammals, the SC acted as the primary centre for visual
 41 analyses, a role that has been increasingly assigned to new areas of extrastriate visual cortex that have
 42 evolved in higher mammals, especially primates.

43 The primate SCs has three dominant outputs: the pulvinar complex (Berman and Wurtz, 2010;
 44 Casanova, 2004; Stepniewska et al., 2000), the LGN (Harting et al., 1978; Mathers, 1971), and intrinsic
 45 vertical connections with the SCi (Behan and Appell, 1992; Helms et al., 2004; Isa, 2002; Isa et al.,
 46 1998; Isa and Saito, 2001). The SCs projects to all layers of the pulvinar, and the magnocellular and
 47 interlaminar layers of the LGN, but the exact nature of these projections is not completely under-
 48 stood. Via such pathways, however, the SCs has substantial projections back into most of the extras-
 49 triate visual cortex, which places it in an ideal position to influence incoming visual signals as they
 50 enter the rest of the brain. The intrinsic vertical connection between the SCs and the premotor layers

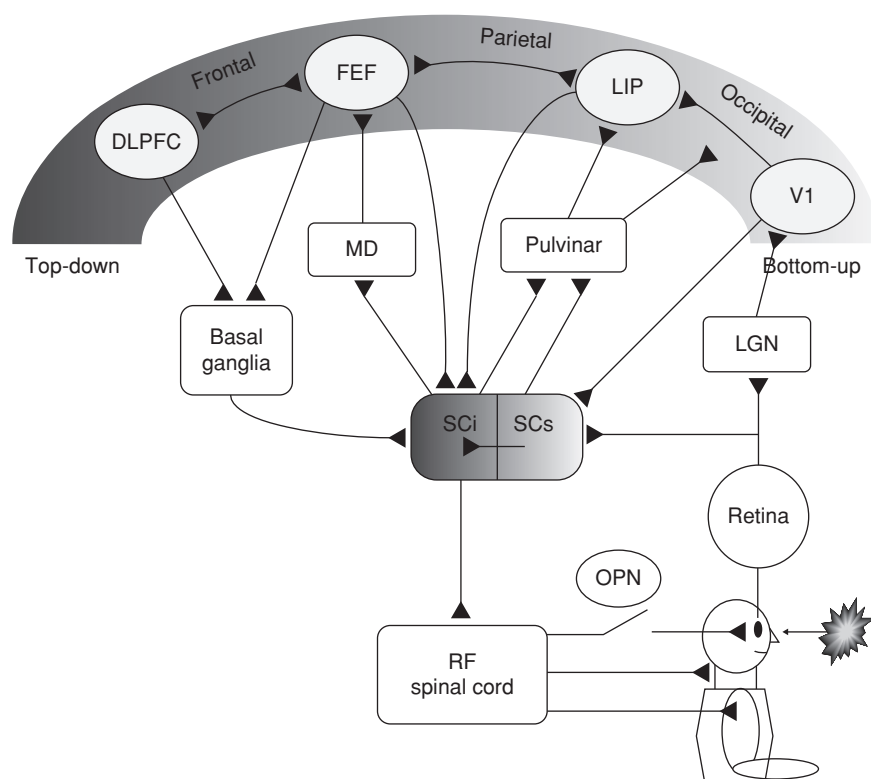


Fig. 11.2 Dominant extrinsic and intrinsic circuitry of the primate SC. Shading from light to dark represents the gradual shift from bottom-up to top-down processes respectively. DLPFC, dorsal lateral prefrontal cortex; FEF, frontal eye field; LIP, lateral intraparietal area; V1, primary visual cortex; MD, medial dorsal nucleus of the thalamus; LGN, lateral geniculate nucleus; RF, reticular formation; OPN, brainstem omnipause neuron region; SCs, superior colliculus superficial layers; SCi, superior colliculus intermediate layers.

- 1 of the SCi (Behan and Appell, 1992; Helms et al., 2004; Isa, 2002; Isa et al., 1998; Isa and Saito, 2001)
- 2 has been proposed to mediate visually-guided orienting, and might act as an important locus for the
- 3 interaction between sensory (bottom-up) and goal-related (top-down) processes (Dorris et al., 2007;
- 4 Fecteau and Munoz, 2006; Olivier et al., 1999; Trappenberg et al., 2001).

5 SCi inputs and outputs

- 6 Compared to the SCs, the primate SCi receives a broader set of corticotectal projections (Fig. 11.2)
- 7 from occipital, temporal, parietal, and frontal cortices (Cusick, 1988; Fries, 1984; Kunzle and Akert,
- 8 1977; Kunzle et al., 1976; Lock et al., 2003; see Harting et al., 1992 for corticotectal projections in the
- 9 cat). These include lateral intraparietal area (LIP) (Lynch et al., 1985), the frontal eye fields (FEFs)
- 10 (Kunzle and Akert, 1977; Kunzle et al., 1976; Stanton et al., 1995; Stanton et al., 1988), supplement-
- 11 tary eye fields (SEFs) (Huerta and Kaas, 1990; Shook et al., 1990), dorsolateral prefrontal cortex
- 12 (DLPFC) (Goldman and Nauta, 1976), and anterior cingulate cortex (ACC) (Leichnetz et al., 1981).
- 13 The LIP-SCi projection carries both visual and motor-related information (Pare and Wurtz, 1997,
- 14 2001), and given LIP's role in covert spatial attention (Bisley and Goldberg, 2003, 2006; Goldberg
- 15 et al., 2002, 2006; Ipata et al., 2006), it likely carries important signals in this regard as well. In terms

1 of frontal projections, these may be thought of as representing the highest level top-down control to
 2 the SCi, and these inputs are critical for the flexible control of oculomotor behaviour (Everling and
 3 Munoz, 2000; Hanes and Wurtz, 2001; Johnston and Everling, 2006a, 2006b, 2008; Johnston et al.,
 4 2007; Segraves and Goldberg, 1987). A large proportion of SCi neurons have visual responses, but it
 5 is not absolutely clear whether these arise from direct projections from visual cortex, and/or the
 6 SCs, and/or through areas LIP or FEF. Nonetheless, corticotectal inputs appear to be crucial for
 7 visual activity in the SCi because visual responses are abolished when visual cortex is temporarily
 8 inactivated via cortical cooling (Schiller et al., 1974).

9 The SCi also receives important subcortical projections from the basal ganglia (Kunzle and Akert,
 10 1977), cerebellum and brainstem (Edwards et al., 1979). The basal ganglia represent a group of
 11 substrates involved in the control of purposive motor behaviour, learning, and reward (Hikosaka
 12 et al., 2000, 2006). The primary means through which the basal ganglia influence the SCi is through
 13 direct inhibitory projections from the substantia nigra pars reticulata (SNr), an important output
 14 node of the basal ganglia (Jayaraman et al., 1977). The nigrotectal projection is believed to regulate
 15 saccadic burst initiation by imposing a blanket of tonic GABAergic inhibition over the SCi (Hikosaka,
 16 1989; Hikosaka et al., 2000, 2006; Wurtz and Hikosaka, 1986), the release of which allows the SCi to
 17 trigger downstream premotor circuitry to drive the appropriate orienting response.

18 In terms of outputs, the SCi projects to the paramedian pontine reticular formation (PPRF) and
 19 rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) where the horizontal and
 20 vertical saccade premotor circuitry is located (Moschovakis et al., 1988; Rodgers et al., 2006; Sparks,
 21 2002). The SCi also projects to the substantia nigra pars compacta (SNc) (Comoli et al., 2003;
 22 McHaffie et al., 2006). This projection carries transient visual activity to the basal ganglia dopamin-
 23 ergic system (Comoli et al., 2003), and is critical for reinforcing the context/actions that immediately
 24 precedes biologically relevant visual events (Dommett et al., 2005; Redgrave and Gurney, 2006). The
 25 SCi also projects to the FEF via the mediodorsal thalamus, MDN (Lynch et al., 1994; Sommer and
 26 Wurtz, 2004a). This projection serves to relay an internal copy (i.e. corollary discharge) of the
 27 saccadic motor command back to cortex immediately prior to movement onset to provide warning
 28 of an impending eye movement so that visual representations may be updated (Sommer and Wurtz,
 29 2004b, 2006). This is thought to be responsible for maintaining our stable view of the world in the
 30 face of the rapid shifts of the visual axis caused by rapid eye movements (Sommer and Wurtz, 2006,
 31 2008a, 2008b).

32 Finally, there is anatomical evidence of long-range connections within the SCi (Behan and Kime,
 33 1996). There is also pharmacological (Meredith and Ramoa, 1998) and electrophysiological (Munoz
 34 and Istvan, 1998) evidence for a lateral inhibitory network across the SCi (see, however, Lee and Hall
 35 (2006)), whereby neurons with different spatial tuning functions are interconnected and compete in
 36 a push-pull relationship (Munoz and Istvan, 1998; Saito and Isa, 2004). Lateral inhibition is key to a
 37 winner-take-all mechanism that has been central to theories of visual attention and visual search (Itti
 38 and Koch, 2001; Treisman and Gelade, 1980; Wolfe et al., 1989; Wolfe and Horowitz, 2004), by
 39 controlling the allocation of overt/covert spatial attention via restricting all but one spatial location
 40 from reaching threshold. We elaborate on these important functions in the next section.

41 **Superior colliculus function**

42 **SCs response properties**

43 SCs neurons have been described as exclusively visual, with a characteristic transient visual response
 44 (Cynader and Berman, 1972; Goldberg and Wurtz, 1972a; Schiller and Koerner, 1971). That is, these
 45 neurons show a short, high-frequency, burst of action potentials as early as 40 ms following the
 46 appearance of a visual stimulus in their response field (a region of space in which the presence of a
 47 stimulus affects the firing of that neuron) (Fig. 11.1C). Other visual neurons typically found deeper in
 48 the SCs are the quasi-visual neurons described by Mays and Sparks (1980), and the tonic- or sustained-
 49 visual neurons described by McPeck and others (Li and Basso, 2008; McPeck and Keller, 2002;

1 White et al., 2009) (Fig. 11.1C). These neurons show an initial transient burst of action potentials
 2 followed by a lower frequency sustained firing pattern while a stimulus is present in the neuron's
 3 response field. They do not however show a burst of action potentials associated with a saccade that
 4 is characteristic of SCi neurons (Mays and Sparks, 1980; McPeck and Keller, 2002). It is not abso-
 5 lutely clear whether these neurons belong to the lower region of the SCs or the upper region of the
 6 SCi, but they are typically found above neurons with saccade-related activity (Li and Basso, 2008;
 7 Mays and Sparks, 1980; McPeck and Keller, 2002).

8 Like neurons throughout many areas of the visual system, SCs neurons are highly sensitive to
 9 stimulus intensity (Bell et al., 2006; Li and Basso, 2008). Despite large projections from visual cortex
 10 (Fries, 1984; Lock et al., 2003), SCs neurons show little preference for specific visual features, but
 11 there is evidence of some broad direction-of-motion tuning (Goldberg and Wurtz, 1972a), possibly
 12 arising from convergent projections from visual area MT (Fries, 1984; Lock et al., 2003), which is
 13 highly selective for visual motion (Born and Bradley, 2005). Similarly, SCs neurons show little pref-
 14 erence for specific colours (Marrocco and Li, 1977; Schiller and Malpeli, 1977), and were thought to
 15 be driven exclusively from the broadband, achromatic visual pathway in early vision (the magnocel-
 16 lular path) (Schiller et al., 1979). However, recently we (White et al., 2009) found that the sustained-
 17 type of SC visual neurons are highly sensitive to luminant and isoluminant colour stimuli (i.e.
 18 isoluminant with the background). This suggests that they receive converging signals originating
 19 from both the broadband (magnocellular) and colour-opponent divisions of the geniculostriate
 20 pathway.

21 **SCi response properties**

22 SCi neurons have a much broader range of response properties than SCs neurons, owing to the fact
 23 that they integrate multisensory, motor, and cognitive signals from multiple cortical and subcortical
 24 brain areas (Fig. 11.2). Many SCi neurons (i.e. visuomotor neurons) discharge a burst of action
 25 potentials approximately 50 ms following the appearance of a visual stimulus in the neuron's response
 26 field, and a separate burst of action potentials associated with the occurrence of a saccade (Mohler
 27 and Wurtz, 1976) (Fig. 11.1C). The visual response of SCi neurons are also similar to SCs neurons in
 28 that they are highly sensitive to variations in stimulus luminance (Bell et al., 2006; Li and Basso,
 29 2008), and often respond equally well to isoluminant colour stimuli (White et al., 2009). Saccade-
 30 related neurons in the SCi discharge action potentials for a range of saccade amplitudes and direc-
 31 tions that define a movement field, the region of space to which a directed saccade affects the firing
 32 of that neuron (Munoz and Wurtz, 1995a; Sparks, 1978; Sparks and Mays, 1980; Wurtz and Goldberg,
 33 1972a). Many neurons in the SCi have clearly defined closed movements fields. However, some
 34 saccade neurons discharge action potentials for all saccades equal to or greater in amplitude than
 35 their optimal, and these have been referred to as open-ended movement fields because they lack a
 36 distal border (Munoz et al., 1991a, 1991b; Munoz and Wurtz, 1995a, 1995b). A consequence of these
 37 open ended fields is that activity may move across the SC during the saccade as a hill or wave. This
 38 hypothesis generated vigorous debate and experimentation in the field and much follow-up work
 39 has failed to support the hypothesis (Anderson et al., 1998; Moschovakis et al., 2001; Soetedjo et al.,
 40 2002). However, experiments conducted on animals with head unrestrained have yielded the most
 41 convincing evidence to support this hypothesis (Choi and Guitton, 2006, 2009; Munoz et al., 1991a,
 42 1991b; but see Freedman and Sparks, 1997).

43 There is also a close spatial correspondence between the visual and motor response fields of SCi
 44 neurons (Marino et al., 2008). This ensures that a visual response is mapped directly onto the appro-
 45 priate SCi output neurons projecting to the brainstem premotor circuitry to trigger a saccade
 46 (Rodgers, Munoz, Scott, and Pare, 2006) and/or orienting head movement (Corneil et al., 2007;
 47 Corneil et al., 2002, 2004) to the visual stimulus.

48 Finally, a distinctive characteristic of many SCi neurons is 'prelude' or 'build-up' activity that
 49 precedes the saccade (Glimcher and Sparks, 1992; Munoz and Wurtz, 1995a). This low-frequency
 50 activity can begin well in advance of the movement itself and is associated with motor preparation

1 (Corneil et al., 2007; Dorris et al., 1997; Dorris and Munoz, 1998; Li and Basso, 2008; Munoz and
 2 Wurtz, 1995a), as well as various high-level processes such as a covert shift of attention (Ignashchenkova
 3 et al., 2004; Kustov and Robinson, 1996), expectation (Basso and Wurtz, 1997, 1998; Thevarajah
 4 et al., 2009), and target selection (Basso and Wurtz, 1997, 1998; Glimcher and Sparks, 1992; Horwitz
 5 and Newsome, 1999, 2001; McPeck and Keller, 2002).

6 Rostral SC responses

7 The rostralateral pole of the SC contains the foveal and parafoveal representation of visual space
 8 (Fig. 11.1B) (Cynader and Berman, 1972; Robinson, 1972; Schiller and Stryker, 1972). Within the
 9 SCs, there are neurons with very small visual receptive fields that include the fovea. Within the SCi
 10 there is a continuation of the motor map (Hafed et al., 2009; Krauzlis et al., 1997), and at the rostral
 11 pole of the SCi there are neurons that discharge tonically during fixation and pause for most
 12 saccades, except very small contraversive saccades (Krauzlis, 2003; Munoz and Wurtz, 1993a,
 13 1993b). These neurons have been labelled fixation neurons because of their tonic discharge recorded
 14 during periods of active fixation that persists without a visual stimulus (Dorris and Munoz, 1995;
 15 Munoz and Wurtz, 1993b). This tonic fixation-related activity is enhanced in an antisaccade task
 16 (Everling et al., 1999), when strong saccade suppression is necessary prior to target appearance.
 17 Most fixation neurons also increase their discharge for small contraversive saccades (Krauzlis, 2003;
 18 Munoz and Wurtz, 1993a) and neurons in the rostral SCi have now been shown to discharge for
 19 microsaccades (Hafed et al., 2009). Microstimulation of the extreme rostral SC has been shown to
 20 delay saccade initiation (Munoz and Wurtz, 1993b) and even interrupt ongoing saccades (Munoz
 21 et al., 1996). In addition, microinjection of the GABAA agonist muscimol into the rostral SC impairs
 22 the ability to delay saccades to suddenly appearing visual stimuli (Munoz and Wurtz, 1993b) (imply-
 23 ing a critical role in saccade suppression), but it also impairs the ability to generate microsaccades
 24 (Hafed et al., 2009).

25 Recent findings suggest the rostral SC also plays a role in pursuit eye movements (Basso et al.,
 26 2000; Krauzlis and Dill, 2002; Krauzlis, 2001, 2003, 2004a, 2004b; Krauzlis et al., 2000), the smooth
 27 continuous movements of the eyes as they track a moving stimulus to keep it fixed on the fovea.
 28 Unlike saccades which can be guided by a range of visual and non-visual signals, pursuit eye move-
 29 ments are traditionally believed to be driven by visual motion signals mediated via substrates that
 30 are selective for motion (e.g. area MT and MST; Ilg (2008), Ilg and Thier (2003)), which then
 31 project to the motor nuclei via the cerebellum to initiate the movement (Krauzlis, 2004b). While
 32 the rostral SC lacks the motion tuning necessary to guide pursuit, recent findings suggest the
 33 pursuit system relies on much of the same circuitry as the saccade system (Krauzlis, 2004a), of
 34 which the rostral SC is an important component. One potential role of the rostral SC for pursuit is
 35 that the tonic activity associated with these neurons convey information about the position error
 36 between the tracked stimulus and the currently foveated position (Krauzlis et al., 2000), which is
 37 corroborated by microstimulation and inactivation experiments of the rostral SC during pursuit
 38 (Basso et al., 2000).

39 Finally, there is some evidence that the rostral SC is also involved in vergence eye movements
 40 (Chaturvedi and van Gisbergen, 1999, 2000; Suzuki et al., 2004; Van Horn et al., 2008), which serve
 41 to move the eyes in opposite directions in order to foveate stimuli at different depths.

42 SC and express saccades

43 Express saccades represent the fastest visually triggered eye movements with saccadic reaction times
 44 (SRT) that approach the minimal afferent (~50 ms) and efferent (~20 ms) limits (Fischer and Boch,
 45 1983; Fischer and Ramsperger, 1984). They are believed to be produced when the incoming visual
 46 signal to the SCi is transformed directly into the saccade motor command (Dorris et al., 1997;
 47 Edelman and Keller, 1996). Express saccades are facilitated during a 'gap' paradigm (Saslow, 1967),
 48 in which a fixation spot is removed a few hundred milliseconds before the onset of a saccade target.

1 The early removal of the fixation spot is associated with a decrease in fixation-related activity at the
 2 rostral pole of the SC (Dorris and Munoz, 1995; Munoz and Wurtz, 1993b). Simultaneously, there is
 3 disinhibition of saccade-related neurons elsewhere in the SC, leading to an increase in low frequency
 4 build-up activity at loci that may drive the next saccade (Dorris and Munoz, 1998; Munoz and Wurtz,
 5 1995a). This elevates the system closer to response threshold which when coupled with the target-
 6 evoked visual response can trigger express saccades.

7 SC lateral interactions

8 The saccade system is believed to be governed by a winner-take-all mechanism, which serves to
 9 restrict only one spatial location as the locus of visual attention/eye movements at any given moment.
 10 Such a mechanism has been central for theories of visual attention and visual search (Itti and Koch,
 11 2001; Treisman and Gelade, 1980; Wolfe et al., 1989; Wolfe and Horowitz, 2004). A key component
 12 of a winner-take-all mechanism is a lateral inhibitory network that operates across the visual field
 13 (e.g. the maps in the SC, Fig. 11.1). At a given moment, two or more regions of distally represented
 14 activity on the SC map (generated by two or more discrete stimuli) are believed to compete in a
 15 winner-take-all manner, only one of which reaches the threshold necessary to evoke a saccade
 16 (Trappenberg et al., 2001). However, if the regions of activity are in close proximity on the SC map,
 17 their activity is mutually excitatory, pushing the saccade system closer to response threshold (Dorris
 18 et al., 2007; Trappenberg et al., 2001), and evoking even faster responses that are sometimes directed
 19 towards the centre-of-gravity of the two stimuli (Edelman and Keller, 1998; Findlay, 1982).

20 There is anatomical evidence for long-range connections within the SCi (Behan and Kime, 1996).
 21 There is also neurophysiological (Dorris et al., 2007; Munoz and Istvan, 1998) and pharmacological
 22 (Meredith and Ramoa, 1998) support for the existence of lateral inhibitory mechanisms in the SCi.
 23 However, a major criticism of these studies is that electrical stimulation can evoke inhibitory
 24 responses by activating axons of passage from GABAergic cell populations that project to the SC, e.g.
 25 nigrotectal projections, which are believed to impose a blanket of tonic GABAergic inhibition over
 26 the SCi (Hikosaka, 1989; Hikosaka et al., 2000, 2006; Wurtz and Hikosaka, 1986). A study using slice
 27 preparations failed to find support for the long-range inhibition hypothesized to exist across the SCi
 28 (Lee and Hall, 2006). However, slice preparations can damage long-range intracollicular fibres, and
 29 more recent slice work did find strong evidence for lateral inhibition across both the SCs
 30 (Phongphanphane et al., 2009) and SCi (Isa et al., 2009).

31 An extrinsic source of inhibition that can support a winner-take-all mechanism is the nigrotectal
 32 projection. This projection is believed to regulate saccadic burst initiation by imposing a blanket of
 33 tonic GABAergic inhibition over the SCi (Hikosaka, 1989; Hikosaka et al., 2000, 2006; Wurtz and
 34 Hikosaka, 1986). The release of this inhibition allows the SCi to trigger the brainstem saccade genera-
 35 tor. Recently, Jiang and colleagues (Jiang et al., 2003) described characteristics of the ipsilateral and
 36 contralateral nigrotectal pathway. Neurons comprising the ipsilateral projection may deliver spatially
 37 specific disinhibition to the SCi because they are tonically active (~100 Hz), and there is a discrete
 38 pause in their discharge for voluntary contraversive saccades to a restricted region of the visual field
 39 (Hikosaka and Wurtz, 1983). The function of the projection from the SNr to the contralateral SCi is
 40 less clear because it has only been studied in anesthetized animals (Jiang et al., 2003). Neurons that
 41 comprise the contralateral projection have tonic activity that increases following visual stimulation
 42 anywhere in the contralateral visual hemifield, and they have large termination fields in the contralat-
 43 eral SCi (Jiang et al., 2003). This suggests that these neurons may produce spatially global inhibition of
 44 the contralateral SCi. This type of global suppression signal is hypothesized to be required for success-
 45 ful suppression of the automatic prosaccade in the antisaccade task (Munoz and Everling, 2004).

46 SCs and salience

47 Salience refers to the sensory qualities that make a stimulus distinctive or conspicuous from its
 48 surroundings (e.g. a rapidly flickering bright red light against a dim stationary background). The
 49 concept of a visual salience map, a 2D representation of salience across the visual field, has been

1 central to theories of visual attention and visual search (Itti and Koch, 2000, 2001; Treisman and
 2 Gelade, 1980; Wolfe et al., 1989). The salience map is believed to integrate the outputs of various
 3 visual feature maps, each representing a unique visual attribute such as intensity, motion, flicker,
 4 colour, orientation, etc. (Itti and Koch, 2001). The more salient the stimulus, the more likely it is to
 5 capture our attention (Theeuwes, 2004).

6 Several brain areas have been allocated the role of a visual salience map, for example visual area V1
 7 (Koene and Zhaoping, 2007; Li, 2002; Zhaoping and May, 2007), V4 (Mazer and Gallant, 2003), LIP
 8 (Goldberg et al., 2006; Gottlieb, 2007; Gottlieb et al., 1998; Kusunoki et al., 2000), FEF (Thompson
 9 and Bichot, 2005; Thompson et al., 2005), and pulvinar (Robinson and Petersen, 1992). Several lines
 10 of evidence implicate the SCs as a particularly crucial component in this regard (Fecteau and Munoz,
 11 2006). First, a visual salience map should be mostly concerned with the low-level visual attributes of
 12 a visual scene. Of course, top-down expectations can modulate early sensory responses of SCs
 13 neurons (Goldberg and Wurtz, 1972b; Li and Basso, 2008; Robinson and Kertzman, 1995; Wurtz
 14 and Goldberg, 1972b; Wurtz and Mohler, 1976), and even neurons as early as LGN (McAlonan et al.,
 15 2008), but not typically to the same degree as is observed in the SCi. Second, a visual salience map
 16 should have well defined spatial selectivity, but no significant feature selectivity, because it is thought
 17 to integrate inputs from feature maps tuned to various visual dimensions (Itti and Koch, 2000, 2001;
 18 Treisman and Gelade, 1980; Wolfe et al., 1989). In this way, visual cortical areas such as V1 (Koene
 19 and Zhaoping, 2007) or V4 (Mazer and Gallant, 2003) might better fit the role of feature maps
 20 because neurons in these areas show a high degree of tuning for specific visual properties
 21 (Gegenfurtner, 2003; Johnson et al., 2008; Sincich and Horton, 2005; Solomon and Lennie, 2007).
 22 Third, a salience map should have direct access to all feature selective areas. The SCs receives direct
 23 projections from visual cortical areas V1, V2, V3, and MT (Fries, 1984; Lock et al., 2003; Tigges and
 24 Tigges, 1981), and the progression from earlier to later areas is represented by increasing depth in the
 25 SCs (Kawamura et al., 1974; Sprague, 1975; Tigges and Tigges, 1981). Higher visual, motor and
 26 cognitive areas (e.g. V4, LIP, FEF) project to the SCi (Lock et al., 2003). This suggests a more gradual
 27 shift from mostly bottom-up to mostly top-down processes with increasing depth in the SC (which
 28 is emphasized by the shading in Figs. 11.1 and 11.2). Finally, a structure coding salience should have
 29 extensive feedback to higher levels of visual processing, and the SCs has substantial projections to
 30 pulvinar which then projects to multiple extrastriate visual areas.

31 SCi and priority

32 Earlier we referred to the idea of a winner-take-all mechanism that is important for the control of
 33 competing sources of information during the process of selection (see section ‘SC lateral interac-
 34 tions’). For the flexible control of behaviour, such a mechanism ought to integrate sensory signals
 35 with the top-down signals related to the goals of the organism. Neurons in the SCi reflect both
 36 sensory *salience* and behavioural *relevance* (the relative importance of a stimulus for the goal of the
 37 observer) (Fecteau and Munoz, 2006), and the combined representation has been termed *priority*
 38 (Serences and Yantis, 2006, 2007). As such, the SCi has been functionally described as a *priority map*
 39 (Fecteau and Munoz, 2006). Below we describe some recent research that has implicated the SCi in
 40 this role.

41 SCi and target selection

42 In cluttered visual environments, the brain has the difficult task of selecting desired objects from
 43 undesired distractor information, the process of which has been termed target selection. Neurons
 44 throughout the network of visuosaccadic brain areas show neural activity reflecting this process (e.g.
 45 visual area V4 (Ogawa and Komatsu, 2004), LIP (Thomas and Pare, 2007), FEF (Schall, 1995, 2002),
 46 and the SC (Horwitz and Newsome, 1999, 2001; Kim and Basso, 2008; Krauzlis et al., 2004; Li and
 47 Basso, 2005; McPeck and Keller, 2002; Shen and Pare, 2007)).

48 Target selection processes provide a good example of the combined representation of bottom-up
 49 salience and top-down relevance. Target selection has been typically studied using simple visual

1 search tasks in which the observer has to find a target amongst a set of distractors. In its most simple
2 form, a target might differ from distractors along only one visual dimension (e.g. find the green
3 target amongst the red distractors). Immediately following the onset of the visual search array,
4 neurons that reflect target selection initially respond unselectively to the appearance of the target or
5 distractor in the neuron's response field (reflecting the bottom-up component). Shortly thereafter
6 the neuron begins to discriminate the two via a suppression of distractor-related activity, and an
7 enhancement of target-related activity (reflecting the top-down goal-related component). This
8 neural discrimination process typically begins before the eye is launched towards the target, demon-
9 strating that the selection process is not simply motor-activity associated with launching a saccade
10 into versus out of a neuron's movement field. Target selection processes have been observed in the
11 activity of visuomotor neurons from the SCi (Horwitz and Newsome, 1999, 2001; Kim and Basso,
12 2008; Krauzlis et al., 2004; Li and Basso, 2005; McPeck and Keller, 2002; Shen and Pare, 2007).
13 Furthermore, SCi inactivation (McPeck and Keller, 2004) impairs target selection, and SCi micro-
14 stimulation (Carello and Krauzlis, 2004) can bias selection processes in favour of stimuli contralateral
15 to the stimulation site. Visual neurons, which are located in the SCs, do not typically discriminate
16 targets from distractors (McPeck and Keller, 2002). These results support the direct involvement of
17 the SCi in target selection.

18 SCi and visuospatial attention

19 Because the brain cannot process all incoming sensory information at any given moment, it selects
20 only certain objects/locations over others by a filtering mechanism that has been termed attention.
21 In general, visuospatial attention is thought to follow eye movements, but a covert shift in visu-
22 ospatial attention can be achieved without moving the eyes (Ignashchenkova et al., 2004; Posner,
23 1980; Robinson and Kertzman, 1995). Attention is also thought to be controlled either involuntar-
24 ily by the salient properties of the stimulus itself (sometimes referred to as exogenous or 'stimulus-
25 driven' attention), or voluntarily by prioritizing the selection of objects/locations relevant to the
26 internal goals of the observer (sometimes referred to as endogenous or 'goal-driven' attention)
27 (Klein, 1994; Theeuwes, 1994). There is now extensive literature showing that neurons within the
28 SCi have discharges that correlate with both exogenous and endogenous shifts of visuospatial
29 attention (Bell et al., 2004; Dorris et al., 2002, 2007; Fecteau and Munoz, 2005, 2006; Fecteau et al.,
30 2004; Gattass and Desimone, 1996; Ignashchenkova et al., 2004; Kustov and Robinson, 1996;
31 Lovejoy and Krauzlis, 2010; Lovejoy et al., 2009; Muller et al., 2005; Robinson and Kertzman,
32 1995). For example, visuomotor neurons in the SCi show enhanced activity during an endogenous
33 shift of attention into their response fields, even in the absence of a visual stimulus (Ignashchenkova
34 et al., 2004). Microstimulation of the SCi can facilitate visual discrimination performance at the
35 spatially selective location represented by the stimulated site, which is indicative of a covert shift of
36 visual attention (Muller et al., 2005). Also, inactivation of a selective region of the SC with musci-
37 mol caused monkeys to ignore critical spatial cues that appeared in the affected region of visual
38 space, suggesting that the SC may act as a bottleneck for covert attention (Lovejoy and Krauzlis,
39 2010). Thus, the SCi can influence voluntary shifts of covert attention independent of eye
40 movements.

41 Neural correlates of two conceptual mechanisms believed to be central to the control of reflexive
42 visuospatial orienting, attentional capture (AC) and inhibition of return (IOR), are also found in
43 the SC. Following an abrupt appearance of a visual stimulus, visuospatial attention is believed to be
44 initially *captured* by the salient novel event (AC), but then subsequently *inhibited* from returning to
45 that object/location (IOR). These concepts have been central to cognitive theories of attention, and
46 are thought to facilitate visual search in complex scenes (Itti and Koch, 2001; Klein, 1988; Macinnes
47 and Klein, 2003; Najemnik and Geisler, 2005; Posner, 1980).

48 AC and IOR are typically studied using the Posner cueing paradigm in which a cue stimulus
49 precedes a target stimulus at the same spatial location (Posner, 1980). Saccadic reaction times (SRTs)
50 to the target are shorter when the delay between the cue and target is short (~100 ms), but are

1 prolonged when it is sufficiently long (~500 ms), reflecting AC and IOR respectively. When the delay
 2 is short, visual activity of SCi neurons in response to the cue and target combine to produce a greater
 3 response, which subsequently drives the faster SRTs reflected in AC (Fecteau and Munoz, 2005).
 4 Conversely, when the delay is long visually responsive neurons in the SCs and SCi display an attenu-
 5 ated target-related visual response that correlates with the slower SRTs reflected in IOR (Dorris et al.,
 6 2002). It is not entirely known whether these effects are driven directly from the intrinsic circuitry of
 7 the SC, but it is important to note that there is no evidence of actual inhibition of covert attention in
 8 the SCi during IOR (Dorris et al., 2002). Both these effects (AC and IOR) have neural correlates with
 9 *sensory* responses in the SC (Dorris et al., 2002; Fecteau and Munoz, 2005), and are therefore more
 10 closely related to modulations of bottom-up sensory processes (at least for these variants of AC and
 11 IOR as measured with saccades). In fact, some evidence suggests IOR may be explicable in terms of
 12 a simple low-level sensory adaptation/habituation mechanism, which might exist at various levels of
 13 visuomotor processing that include the SCs and SCi (Boehnke and Munoz, 2008).

14 SCi and reward expectancy

15 The expectation of reward has a significant effect on the top-down goals of the observer. This has
 16 been most clearly reflected in the responses of neurons in the SCi, most likely because the SCi receives
 17 direct inputs from brain areas that encode reward information including pre-frontal cortex and the
 18 basal ganglia (Ikeda and Hikosaka, 2007). When a visual stimulus signals an upcoming reward, both
 19 visual and preparatory activity of SCi neurons is enhanced (Ikeda and Hikosaka, 2003). The neurons
 20 encoding this enhanced signal tend to be the build-up or prelude-type neurons (Glimcher and
 21 Sparks, 1992; Munoz and Wurtz, 1995a). Similarly, the gain of SCi neurons is modulated by target
 22 spatial predictability, because predictable targets are associated with reward. That is, the activity of
 23 SCi neurons is modulated by the prior expectation that a target will appear in its response field: activ-
 24 ity is enhanced if the probability is high, and suppressed if the probability is low (Basso and Wurtz,
 25 1997, 1998; Dorris and Munoz, 1998; Glimcher and Sparks, 1992).

26 While reward-related gain modulation is observed in the SCi, it is not believed to be the cause
 27 (Ikeda and Hikosaka, 2003). There is, however, evidence that the SC itself plays an active role in
 28 encoding reward information during reinforcement learning via its projection to the SNc (Comoli
 29 et al., 2003). This projection carries transient visual activity to the basal ganglia dopaminergic system,
 30 which is critical for reinforcing the context/actions that immediately precede unpredicted, biologi-
 31 cally relevant visual events (Dommett et al., 2005; Redgrave and Gurney, 2006). Also, subthreshold
 32 stimulation of the SCi can bias choice probability towards the stimulated site of two equally rewarded
 33 stimulus locations, implicating the SCi as an important part of the circuit that actively chooses stra-
 34 tegic actions that produce positive rewards (Thevarajah et al., 2009).

35 Conclusion

36 The SC is arguably one of the most studied structures in the brain, yet there is still much to learn
 37 about its precise afferent and efferent circuitry to fully understand its role in the flexible control of
 38 the orienting response. Moreover, the SC contains many neurons with complex response properties
 39 that we know little about because they are either not modulated by the types of tasks used, or are
 40 modulated in ways that are difficult to interpret. In this review we highlighted recent research on the
 41 dominant functions of the SC that have led to insightful theoretical and computational models (e.g.
 42 Dean et al., 1989; Fecteau and Munoz, 2006; Haged et al., 2009; Krauzlis, 2005; Krauzlis et al., 2004;
 43 Moschovakis et al., 1998; Trappenberg et al., 2001). We highlighted functional differences between
 44 the SC layers, emphasizing the SCs as a critical sensory node for bottom-up processes, and the SCi as
 45 a critical sensorimotor node for integrating bottom-up and top-down signals for the flexible control
 46 of orienting behaviour. With an expanding role of the SC in higher-level functioning (e.g. target
 47 selection, reward-expectation, covert visuospatial orienting, etc.), it continues to be a critical area of
 48 research in sensorimotor neuroscience.

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