

Neural Cartography: Sensory and Motor Maps in the Superior Colliculus¹

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Abstract. The sudden onset of a novel or behaviorally significant stimulus usually triggers responses that orient the eyes, external ears, head and/or body toward the source of the stimulus. As a consequence, the reception of additional signals originating from the source and the sensory guidance of appropriate limb and body movements are facilitated. Converging lines of evidence, derived from anatomical, electrophysiological and lesion experiments, indicate that the superior colliculus is an important part of the neural substrate responsible for the generation of orienting responses. This paper briefly reviews the functional organization of the mammalian superior colliculus and discusses possible linkages between the sensory and motor maps observed in this structure. The hypothesis is advanced that the sensory maps are organized in motor (not sensory) coordinates and that the maps of sensory space are dynamic, shifting with relative movements of the eyes, head and body.

Introduction

Many neurophysiological studies are concerned with the broad question of how the neural events initiated by physical stimuli are transformed into commands for the control of movements. Acute experiments have been used to examine the quantitative relationship between the physical properties of sensory stimuli and the pattern of neuronal activity observed at successive synaptic relays in the afferent pathways. More recently, chronic-microelectrode recording techniques have permitted a description of the relationship between neuronal activity and motor events. Although much has been learned about the coding of sensory information, the signals carried by neurons serving as inputs to motoneurons and the pattern of motoneuron activity that precedes specific move-

ments, the general question of how signals in sensory coordinates are translated into commands in a motor frame of reference has not been solved. Sensory signals must undergo a complex transformation since the spatial coordinates of afferent signals are usually different from the coordinates of the movements they guide.

In mammals, sensory signals initiating orienting movements converge in the deeper layers of the superior colliculus (SC). Cells responsive to sensory stimuli are arranged topographically according to the location of their receptive fields and, thereby, form maps of sensory space. The deeper layers of the SC also contain neurons involved in the generation of movements of the eyes, head, vibrissae and pinnae. Cells discharging before saccadic eye movements are also organized topographically according to the location of their movement fields (see below) and form a map of motor (saccadic) space. This paper contains a brief review of the functional organization of the

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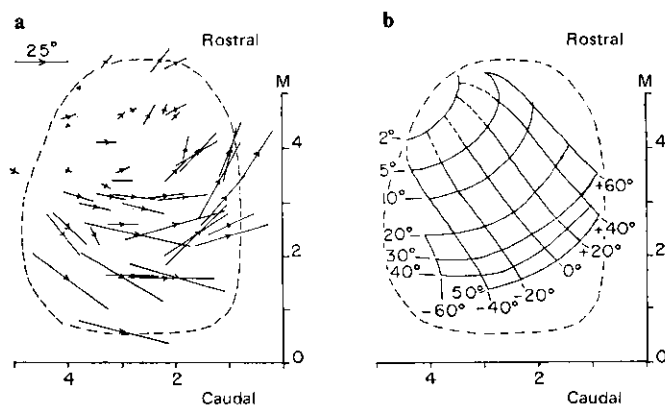


Fig. 1. Maps of the direction and amplitude of stimulation-induced saccades. **a** Dorsal view of the left SC of the monkey. Arrows indicate the direction and amplitude of saccades produced by stimulation. **b** Smoothed contours of the motor map of the SC. Isoamplitude lines (2–50°) run from medial to lateral and isodirection lines (–60° to +60°) run from anterior to posterior [from Robinson, 1972]. The motor map generated by stimulation experiments is an accurate predictor of the movement fields of cells encountered in the deeper layers of the SC.

mammalian SC and a discussion of the possible linkages between the sensory and motor maps [see Sparks, 1986, for a more comprehensive review].

Anatomical Organization of the Superior Colliculus

In mammals the SC is composed of 7 alternating fibrous and cellular layers. Based upon functional considerations [Casagrande et al., 1972] and the pattern of anatomical connections [Harting et al., 1973; Lund, 1964, 1972a, b] comparative neuroanatomists have divided the colliculus into two major divisions: superficial and deep. The superficial layers (stratum zonale, str. griseum superficiale and str. opticum) receive inputs devoted almost exclusively to vision. The outputs of the superficial layers are primarily ascending and terminate, for the most part, in various regions of the thalamus that project to cortical areas subserving visual functions [Huerta and Harting, 1984]. In contrast, the deeper layers (str. griseum intermedium, str. album intermedium, str. griseum profundum and str. album profundum) receive inputs from several modalities (visual, auditory and somatosensory), contain neurons with motor properties and have both ascending and descending efferent projections [Huerta and Harting, 1984]. Whether or not there is significant *direct* communication between

the superficial and deep divisions is an unresolved issue [Edwards, 1980].

Motor Maps and Properties of Neurons with Saccade-Related Discharges

Although, based upon data obtained from electrical stimulation studies, the SC may contain neurons related to movements of the head and external ears, only the signals involved in initiating saccadic eye movements have been studied in detail. One class of neuron in the SC generates a relatively discrete, high-frequency burst of spike activity beginning about 20 ms before saccade onset [Sparks, 1978]. It is important to note that these neurons discharge before saccades of a particular direction and amplitude, regardless of initial eye position, i.e., the saccade-related burst is not associated with a movement of the eye to a particular position in the orbit but to a certain *change* in eye position. The onset of the high-frequency burst is tightly coupled to saccade onset. In behavioral tasks in which a briefly presented visual target sometimes elicits a saccade and sometimes fails to do so, the probability of the high-frequency burst is almost perfectly correlated with the probability of saccade occurrence [Sparks, 1978].

Each collicular neuron discharging before saccadic eye movements has a movement field [Sparks et al., 1976; Sparks and Mays, 1980, Wurtz and Goldberg, 1972], i.e., each cell discharges before a range of saccades having particular directions and amplitudes. Neurons with motor properties are arranged topographically within the SC. Cells discharging prior to small saccades are located anteriorly and those firing before large saccades are found posteriorly. Cells near the midline discharge prior to movements with up components and cells located laterally discharge maximally before movements with down components (fig. 1).

Since each neuron fires before a broad range of saccades, it follows that a large population of collicular neurons discharges before any particular saccade. It is known that neurons in the center of the active population fire early and vigorously while cells on the fringe of the population fire less strongly and their activity may follow, rather than precede, saccade onset [Sparks and Mays, 1980]. Although the peak frequency, duration and other parameters of the saccade-related burst vary for different movements within a cell's movement field, information concern-

ing saccade direction and amplitude is not encoded by the discharge of a single neuron. Except for the maximal burst preceding saccades to the center of the movement field, the parameters of the discharge are ambiguous with respect to saccade direction or amplitude. Identical discharges precede saccades with different directions and amplitudes [see Heiligenberg, 1987, for discussion of a similar observation in the optic tectum of weakly electric fish]. Neither the magnitude, configuration or timing of the discharge of a single cell are related in any unique way to the direction of the saccade alone or the amplitude of the saccade alone. Nor is the discharge of different saccade-related burst units, some of which discharge maximally to small saccades and some of which discharge maximally to large saccades, distinguishable [Sparks and Mays, 1980]. Thus, motor error (the direction and amplitude of the movement required for target acquisition) is encoded anatomically. It is the location of active neurons within the topographical map of movement fields, not their frequency of firing, that specifies saccade direction and amplitude.

Sensory Maps

Neurons in the superficial layers respond almost exclusively to visual stimuli. The proportion of cells responding only to visual stimuli decreases and the number of cells responding to somatosensory and auditory stimuli increases as an electrode passes through the superficial layers and then through the deeper layers [Gordon, 1973; Stein and Arigbede, 1972]. Cells responsive to cutaneous and auditory stimuli are first encountered in the st. griseum intermedium [Drager and Hubel, 1975; Stein and Arigbede, 1972]. Units responsive to auditory stimuli are found most commonly in the posterior colliculus [Chalupa and Rhoades, 1977; Gordon, 1973; Stein and Arigbede, 1972].

Visual Map

Visual signals reaching the superficial layers are organized retinotopically and arise both directly from the retina and from the visual cortex. These inputs are maintained in register, i.e., a region of the SC that receives input from a specific retinal area will also receive input from regions of the visual cortex processing information about the same retinal locus. Neurons in each colliculus are responsive to visual stimuli presented in the contralateral visual field. Cells with

receptive fields in the upper visual field are located medially; those with receptive fields in the lower visual field are located laterally. Units responsive to stimuli near the center of the visual field are located rostrally; those with peripheral receptive fields are found caudally.

Visually responsive cells in the deeper layers also appear to be arranged according to a retinotopic map although the activity of at least one class of these cells does not depend upon activation of a particular region of the retina (see below).

Somatosensory Map

Cutaneous stimuli applied to the contralateral body surface elicit the most vigorous responses from collicular cells sensitive to somatosensory stimuli [Clemo and Stein, 1982; Gordon, 1973; Nagata and Kruger, 1979; Stein et al., 1976]. Neurons with tactile receptive fields are organized topographically. The representation of body regions innervated by the trigeminal nerve and the representation of the forelimb occupies most of the available space. Consequently, the representation of the large cutaneous surface area of the trunk and hindlimb is small.

Auditory Map

Early studies using qualitative methods obtained evidence for a topographical representation of auditory space in the deeper layers of the SC [Chalupa and Rhoades, 1977; Drager and Hubel, 1975; Gordon, 1973; Harris et al., 1980; Tiao and Blakemore, 1976; Wickelgren, 1971]. For example, Gordon [1973] reported that in paralyzed cats the position of the auditory receptive fields of collicular neurons was highly correlated with the location of the visual receptive fields of the same or nearby neurons. She inferred a topographical map of auditory space by referring the location of auditory receptive fields to the location of visual receptive fields, known to be topographically arranged.

Knudsen's [1982] discovery of a precise map of auditory space in the optic tectum of barn owls was the stimulus for reexamining the auditory responsiveness of collicular neurons in cats. Wise and Irvine [1983] used calibrated probe microphone assemblies attached to each ear of anesthetized cats to study the responses of neurons in the deeper layers of the SC. Most acoustically responsive cells discharged maximally for a range of interaural intensity differences (IIDs) in which the contralateral intensity was greater

and responses were suppressed for IIDs in which the ipsilateral intensity was greater. The position of the cutoff between excitatory and suppressive IIDs varied for different neurons. The IID functions of collicular neurons would be expected, under free-field stimulation conditions, to produce large contralateral spatial receptive fields, and acoustically responsive neurons were topographically organized according to the IID function [Irvine and Wise, 1983a, b].

Middlebrooks and Knudsen [1984] also looked for a map of spatial receptive fields in the SC of anesthetized cats. Auditory stimuli were presented using a moveable speaker. In their study, the response of all auditory units was selective for sound locations and, although many cells had large receptive fields, each cell displayed peak responses to stimuli presented in a limited range of locations. The centers of the 'best areas' (the locations of sound stimuli eliciting responses greater than 75% of maximum) varied systematically with their location in the SC and formed a map of auditory space that closely resembled the map of the visual field.

Apparent Alignment of Auditory, Somatosensory and Visual Maps

Using the visuotopic organization of superficial layer neurons as a reference for plotting the receptive fields of underlying tactile cells, Stein et al. [1976] developed schematic diagrams of the SC to illustrate a registration of the visuotopic and somatotopic maps. Similarly, Drager and Hubel [1975, 1976] observed in the mouse a relationship between somatosensory receptive fields, especially those involving the whiskers, and the visual receptive fields of overlying cells. Whenever visual receptive fields of the superficial tectal cells were located in regions of the visual field usually crossed by whiskers, somatosensory responses of neurons encountered in the same electrode penetration were evoked only from whiskers or immediately adjacent fur, but never from more distant parts of the body. In general, several workers using anesthetized or paralyzed preparations and a variety of animals [mouse: Drager and Hubel, 1975, 1976; cats: Stein et al., 1976; cebus monkey: Updyke, 1974; guinea pigs: King and Palmer, 1983; hamsters: Chalupa and Rhoades, 1977; Finlay et al., 1978; barn owls: Knudsen, 1982; iguanas: Gaither and Stein, 1979; Stein and Gaither, 1981] have observed a correspondence between visual, somatosensory and/or auditory receptive fields.

Significance of Map Alignment

Alignment of Sensory Maps

Although considerable effort has been devoted to demonstrating the alignment of sensory maps, less experimental attention has been devoted to the functional significance of the observed correspondence. Most investigators have assumed that the alignment of the maps is biologically relevant and that the maps are static. Some investigators have made assumptions about the basis of the alignment. Even though data supporting these assumptions are sparse, we can consider the possible advantages of maintaining an alignment between the various sensory maps. One possibility is that the independent maps of sensory space facilitate the generation of a modality-independent map in which stimuli originating from a particular region of the external world, regardless of sensory modality, activate a particular subset of topographically organized multimodal neurons. The finding that many cells in the deeper layers respond to more than one modality is consistent with this hypothesis. There is, however, no direct evidence that the site of convergence is in the SC or that independent maps of visual, auditory and somatosensory space are necessary for the multimodal responses of collicular neurons. The multimodal responses observed in the SC could be generated in cortical or subcortical regions projecting to the colliculus. A second reason for maintaining alignment of the sensory maps is to permit cues from all sensory modalities to access shared maps of motor space. This possibility is discussed in more detail below.

Still assuming that the maps are static and that the alignment of the sensory maps is functionally relevant, what is the basis of map alignment? One view is that the topography of the visual map is imposed upon the other modalities. Drager and Hubel [1975, 1976] suggest that the somatosensory map is determined by the way body parts are seen from the eye and that the other sensory maps are all arranged so as to be in registration with the visual map. This implies that auditory and somatosensory signals, originally encoded in different coordinates than visual signals, have been transformed into retinal coordinates. Also problematic for this view is the fact that independent movements of the eyes, head, external ears, limbs and body would alter the relationship between static maps of visual, auditory and somatosensory space. In mammals, experimental evidence supporting the as-

assumption that the topography of the visual map is imposed upon the other modalities is lacking. Indeed, in cats, visually guided behavior first appears around 14 days after birth [Fox, 1970; Norton, 1974], a few days *after* acoustically guided and tactually guided behaviors have developed. Thus, in the cat, auditory, somatosensory and motor maps appear to be present and functioning prior to the development of visually guided behavior and prior to the development of normal receptive-field properties by visual neurons in the SC.

Alignment of Sensory and Motor Maps

As discussed elsewhere in this volume [Finger, 1987], a direct solution to the problem of sensorimotor coupling might be a rigidly linked, point-to-point relationship between sensory maps and a topographically organized motor output system. Such a point-to-point linkage between the retinotopic map of visual space found in the superficial layers of the SC and the subjacent motor (saccadic) map has been proposed [Schiller and Koerner, 1971]. According to this foveation hypothesis, the SC codes the location of a visual target relative to the fovea and initiates a saccade that produces foveal acquisition of the target. Retinal error (the distance and direction of the target image from the fovea) is represented by the site of visually triggered activity in the retinotopically organized superficial layers of the SC. Visually triggered discharges in the superficial layers are assumed to relatively directly activate underlying regions of the colliculus containing neurons that discharge before saccadic eye movements. Since the map of the movement fields of the deeper neurons corresponds to the retinotopic map of the overlying superficial neurons, a saccade would be produced that brings the foveal projection onto the region of the visual field containing the target.

A simple version of the foveation hypothesis encounters several difficulties [Sparks, 1986] although only two are considered here. First, the timing of neuronal activity in the superficial and deeper division is not consistent with the proposed hypothesis. The onset of visual activity in the superficial layers typically begins at least 100 ms before the onset of the saccade-related burst of neurons in the deep division. Since direct superficial-to-deep connections would require less than 10 ms, the transmission of signals between these divisions can be neither simple nor direct. Second, the presumed coupling between the activity of

neurons in the superficial and deep divisions has not received experimental support. Under some experimental conditions, superficial neurons display vigorous visual responses that do not result in the activation of underlying saccade-related neurons [Mays and Sparks, 1980]. Conversely, saccade-related neurons may produce vigorous bursts of activity in the absence of changes in the activity of overlying cells in the superficial layers. Thus, for most saccade-related neurons, the discharge of overlying visual cells is neither necessary nor sufficient to activate most cells generating saccade-related bursts. For these and other reasons, the alignment of the visual and motor maps in the monkey SC cannot be accounted for by the foveation hypothesis.

Motor Organization Hypothesis

An alternative hypothesis concerning the functional organization of the SC is that the signals of collicular neurons responsive to sensory stimuli are encoded in motor, rather than sensory, coordinates. This hypothesis is based upon a number of considerations. The initiation of a saccadic eye movement toward a target requires that sensory systems specify the change in eye position required to look to the target, not merely the location of the target in head, body or retinal coordinates. Moreover, since collicular neurons with saccade-related activity are organized topographically and it is the location of active neurons within the topographical map of movement fields that specifies the metrics of the movement, a specific subset of collicular neurons must be activated in order to initiate a particular saccade. Consider, for example, a monkey with both the head directed 'straight ahead' and gaze directed 24° to the left of center (fig. 2a). When an auditory stimulus is presented 10° to the left of center, interaural cues will be used to localize the target in head coordinates: 'target is 10° left'. However, since the eyes are directed 24° left, looking to the target requires a 14° rightward saccade and neurons in the left SC must be activated to produce this movement. If, on another trial, an auditory target is presented in the same location while gaze is directed straight ahead (fig. 2b), cells in the right SC must be activated to produce the 10° leftward saccade required to look to stimulus.

Recent experiments conducted in this laboratory support the hypothesis that sensory signals observed in the SC are organized in motor coordinates. Rhesus monkeys, trained to look to either visual or auditory

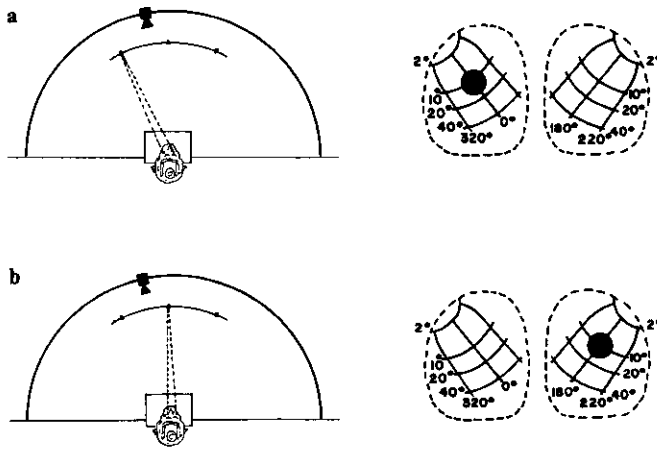


Fig. 2. The shift in the active population of auditory cells in the SC with changes in eye position. **a** Monkey viewing the left fixation light, with the speaker to the right of the fixation position. Auditory cells in the left colliculus are activated. **b** When gaze is shifted to the center fixation light (to the right of the speaker), the auditory cells in the right colliculus are now active and code the trajectory of the movement required to look to the target [from Jay and Sparks, 1987].

targets in a completely darkened room, were placed with their heads fixed in the center of a semicircular track [Jay and Sparks, 1984, 1987]. Movement of a speaker (with a light-emitting diode attached) along the track and rotation of the track allowed targets to be presented at most locations on an imaginary sphere surrounding the animal. Three fixation lights separated by 24° were placed along the horizontal meridian. At the beginning of each trial, one of the three fixation lights was randomly activated. After a variable interval, an auditory (broad-band noise burst) or visual target was presented and the animal was required to look to the target location in order to receive a liquid reward. A delayed saccade task was used to separate, temporally, sensory and motor activity.

The major objective of the experiment was to plot the receptive fields of sound-sensitive cells in the SC of alert monkeys while varying the direction of visual fixation. If the receptive fields of auditory neurons in the SC are organized in head-centered coordinates, the direction of fixation would have no effect. But, if as hypothesized, the response of auditory neurons is organized in motor coordinates, then the response should depend upon both speaker position and fixation direction.

For every sound-sensitive cell encountered in the SC, the position of the eyes in the orbit had a distinct effect upon the response to an auditory stimulus. Plots of the average number of spikes evoked by the noise burst as a function of the horizontal position of the speaker show that the receptive field of the neuron shifts with the position of the eyes in the orbit. When these same data are reanalyzed, plotting the average number of spikes in the response as a function of the movement required to look to the target, the data obtained with the different fixation positions are closely aligned. Thus, the discharge of auditory neurons is not determined solely by the position of the auditory stimulus in space, but depends upon motor error, the position of the eyes in the orbit relative to target position. The map of auditory space found in the monkey SC is not a static representation. With each movement of the eyes in the orbit, the population of neurons responsive to an auditory stimulus in a particular spatial location changes to a new site within the SC, a site representing the new motor error signal.

A second experiment [Mays and Sparks, 1980] also supports the motor organization hypothesis. Monkeys were trained to perform a task in which, after fixation of an initial center target for a variable period, the offset of the center fixation target was followed by successive presentations of two targets (B and C). Although the total duration of targets B and C was less than the reaction time of the monkey, reward was contingent upon the animal making a saccade to position B within 300 ms and a second saccade from B to C before an additional 500 ms elapsed. Thus, two saccades were made in succession; the first to B and the second from B to C. In these experiments, we isolated one type of neuron (quasi-visual or QV cell) in the intermediate layers of the SC that signals motor error. These neurons appear to be visually responsive, to have receptive fields and to respond to targets in their receptive field whether or not a saccade is made toward the target. Moreover, QV cells discharge just before the B-to-C saccade. The cells firing in this case are not those whose receptive field contained the original target C, but cells whose receptive field would contain target C if the target were flashed again in the same spatial location after the eyes reached position B. In other words, the activity of QV cells reflects motor error. QV cells discharge whenever a saccade with a particular direction and amplitude is appropriate regardless of whether the movement becomes appropriate because of the onset of a visual stimulus or be-

cause of an eye movement occurring after the disappearance of the target. The hypothesis that the activity of QV cells encodes motor error was tested in a separate experiment [Sparks and Porter, 1983] by recording their activity during trials in which the monkey compensated for stimulation-induced perturbations in eye position. The hypothesis was confirmed by the finding that QV cells increased their discharge rate whenever there was a certain difference between current and desired eye position regardless of whether this motor error was produced by the sudden appearance of a visual target or by a stimulation-induced change in eye position after target offset. The neural representation of the visual target formed by QV cell activity is a dynamic one. If a target is displaced or if the eyes move after a brief target has disappeared, the site of QV cell activity shifts to a location that represents the new motor error.

Summary and Conclusions

The deeper layers of the SC contain separate representations of auditory, somatosensory and visual space as well as a map of motor (saccadic eye movements) space. In acute experiments the sensory and motor maps are aligned and it has been commonly assumed that the retinotopic map of visual space is the basis for the alignment. An alternative hypothesis states that the sensory maps are organized in motor (not sensory) coordinates. The sensory maps are viewed as dynamic and the receptive fields of collicular neurons are expected to shift with relative movements of the eyes, head and body. Sensory-induced collicular activity represents the trajectory of the movement required to look to the target rather than its location in space. Conceptual and empirical work is needed to develop and test models of the generation of the dynamic visual and auditory maps observed in the SC.

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