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Sensory and motor maps in the mammalian superior colliculus

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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 (SC) is an important part of the neural substrate for the generation of orienting responses, involved in both the localization of sensory stimuli and the initiation of orienting responses¹.

The seven alternating cellular and fibrous layers of the mammalian SC form two major functional divisions: a superficial division and a deep division². Inputs to the superficial division are almost exclusively visual and originate from two major sources: the retina and the visual cortex. Most efferent projections of the superficial layers ascend in fiber tracts that terminate in the pulvinar or other thalamic nuclei that, in turn, project to cortical areas implicated in visual function³.

This review focuses upon the deep division of the SC, a site of convergence of sensory signals from several modalities and a source of efferent commands for the initiation of orienting movements. Many neurons residing in the deep division are responsive to auditory, somatosensory and/or visual stimuli⁴⁻¹⁰. Other cells in the deep division have motor properties,

discharging before saccadic eye movements¹¹⁻¹³; still other neurons may discharge before movements of the pinnae and/or head. Although the outputs of the deep division are both ascending and descending, collicular neurons can exert their most direct control over orienting movements through the descending pathways¹⁴. Brainstem nuclei receiving tectal inputs project, both directly and indirectly, to motor neurons innervating extraocular muscles, neck muscles and muscles controlling movements of the external ears¹⁵.

The intrinsic organization of the SC is poorly understood. The question of whether or not there is extensive communication between neurons in the superficial and deep divisions has not yet been resolved.

The deeper layers of the SC: a source of motor commands

Microstimulation studies

In alert monkeys with their heads fixed, collicular stimulation produces conjugate, contralateral saccades with latencies of approximately 20-30 ms (Ref. 16). The amplitude and direction of the saccades are a function of the site of stimulation in the SC and, within broad limits, are independent of the intensity or frequency of stimulation. Robinson¹⁶ developed a map of the amplitude and direction of saccades evoked by stimulation of different points of the SC (Fig. 1), and noted the alignment of this motor map with the retinotopic map in the overlying superficial layers (see below).

In monkeys free to move their heads, collicular stimulation rarely produces head movements¹⁷. The stimulation-induced head movements that do occur are variable in size and latency and do not have definite electrical thresholds. However, in animals with restricted ocular motility (such as cats), stimulation of the SC produces short latency movements of the eyes and head¹⁸ as well as movements of the external ears (pinnae) and vibrissae¹⁹. In general, the direction and amplitude of all stimulation-induced movements (eyes, head, pinnae, vibrissae) depend upon the site of stimulation. Medial stimulation produces movements with upward components and lateral stimulation produces movements with downward components. In the anterior SC, relatively small move-

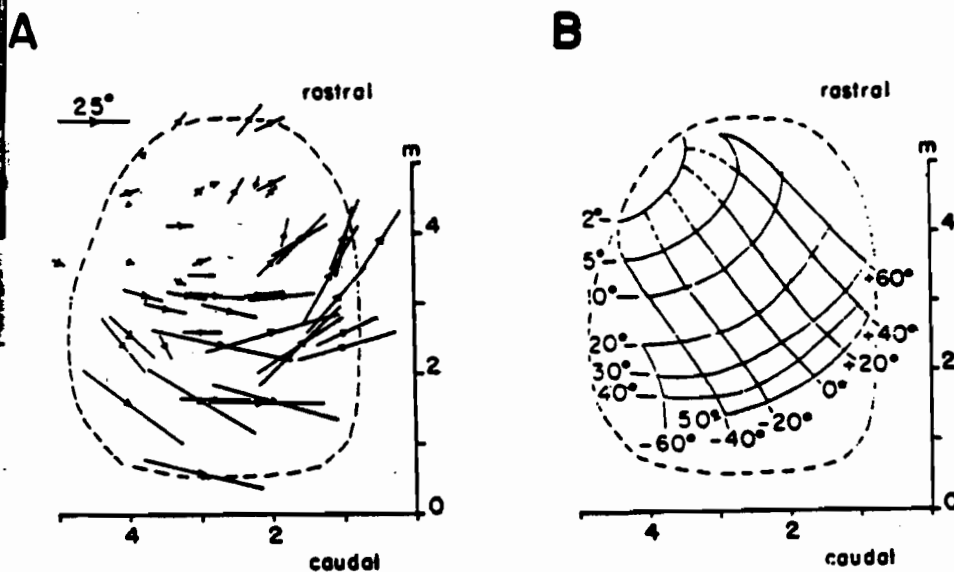
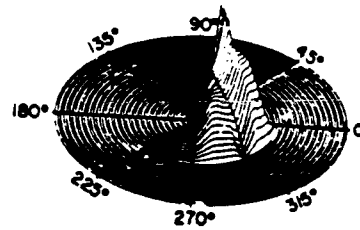
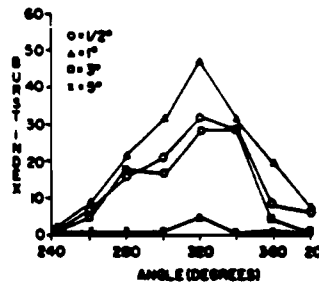
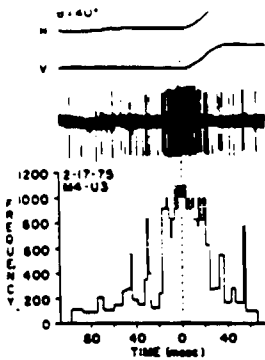


Fig. 1. Maps of the direction and amplitude of stimulation-induced saccades. (A) Dorsal view of the left superior colliculus of a rhesus monkey. Arrows indicate the direction and amplitude of saccades produced by stimulation. (B) Smoothed contours of the motor map of the superior colliculus. Isoamplitude lines (2° to 50°) run from medial to lateral and isodirection lines (-60° to +60°) run from anterior to posterior. (Taken from Ref. 16.)



cell in the superior colliculus of monkey. H, horizontal eye position; V, vertical eye position. The middle trace is the spike discharge and the bottom graph shows instantaneous spike frequency as a function of time. The dotted line represents the onset of the eye movement. (B) Burst index (number of spikes) as a function of the direction and amplitude of saccadic eye movements for a single collicular cell. Each point represents the median value of three observations. (C) Three-dimensional representation of burst index as a function of saccade direction and amplitude. (Taken from Ref. 12.)

ments are produced, whereas caudal stimulation produces larger movements. Thus, based upon stimulation data, the SC may contain multiple motor maps as well as multiple sensory maps (see below). Since in most experiments, simultaneous measurements of the movements of the eyes, head, vibrissae and pinnae are not obtained, it is not clear whether the SC contains several completely independent motor maps or a single motor representation that coordinates the various subcomponents of an orienting response.

Chronic unit recording studies

The neuronal basis of movements produced by microstimulation has been examined by recording the activity of collicular neurons in alert, unanesthetized animals. In rhesus monkeys, many neurons in the deep division generate a high frequency burst of activity beginning 18–20 ms before saccadic eye movements (Fig. 2). Each of these cells discharges maximally before saccades of particular directions and particular amplitudes (the movement field of the cell), regardless of the initial position of the eye in the orbit^{13,20}. Movements to the center of the movement field are preceded by a vigorous discharge, but movements deviating from this optimal direction and amplitude are accompanied by less vigorous responses (Fig. 2). Neurons discharging prior to small saccades have small and sharply tuned movement fields; cells discharging before large amplitude saccades have large movement fields and tuning is relatively coarse¹². Cells generating saccade-related bursts of activity are organized topographically¹³, and correspond to the motor map revealed by microstimulation.

Although the vigor of discharge of a particular saccade-related burst cell varies for different movements within the movement field, information concerning saccade direction and amplitude is not contained within the discharge of a single cell. Except for the maximal discharge that precedes saccades to the center of the movement field, the discharge of SC neurons is ambiguous with respect to saccade direction or amplitude. Identical discharges may precede many saccades with different directions and amplitudes²⁰. Thus, 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.

Stimulation data suggest that the SC of some animals may also contain neurons discharging before movements of the pinnae, vibrissae and head²¹, but this possibility has not been explored extensively.

The deep layers of the SC: a site of sensory convergence

Responses to visual, somatosensory and auditory stimuli

The convergence of inputs from many brain areas representing a variety of sensory modalities is a striking feature of the organization of the deep division of the SC. Cortical inputs originate in the frontal and prefrontal cortex, parietal cortex, temporal lobe and occipital lobe¹⁵; more than 40 subcortical areas have been identified that project to the deep division of the SC²². Presumably, inputs from these areas provide the SC with both sensory and motor signals, but relatively little is known about the information conveyed to the SC from these sources (but see Ref. 1 for more details).

The receptive fields of visually responsive neurons in the SC of rhesus monkeys are larger and less precisely tuned for stimulus features than the receptive fields of cells in the lateral geniculate nucleus or striate cortex. For example, cells in the striate cortex have small receptive fields (only a few degrees in diameter) and display precise tuning for the spatial orientation of edges of light, for stimulus wavelength and for the direction and velocity of stimulus movement. In contrast, the activity of collicular neurons appears to be more concerned with the location of the stimulus than with stimulus features. Collicular cells have large receptive fields, respond to the presence of a stimulus regardless of shape, size or orientation, are responsive to stimuli of all visible wavelengths, and have only poor tuning for the direction and velocity of stimulus movement (see Ref. 1 for references).

Cells in the superficial layers of the SC of each colliculus are activated by stimuli appearing in the contralateral visual field and are topographically organized according to receptive field location. Neurons with receptive fields in the upper visual field are located medially; those with receptive fields in the lower visual field are found laterally. Units with receptive fields near the center of the visual field reside anteriorly; those responsive to peripheral stimuli are located posteriorly.

Although cutaneous stimulation is most effective for activating somatosensory collicular cells, somatosensory inputs to the deeper layers of the colliculus arrive via both lemniscal and spinothalamic pathways. In acute experiments, vigorous neural activity is evoked by rapid movement of a tactile stimulus along a particular axis, light tapping of the skin and displacement of the hair and vibrissae¹⁰. Somatic receptive

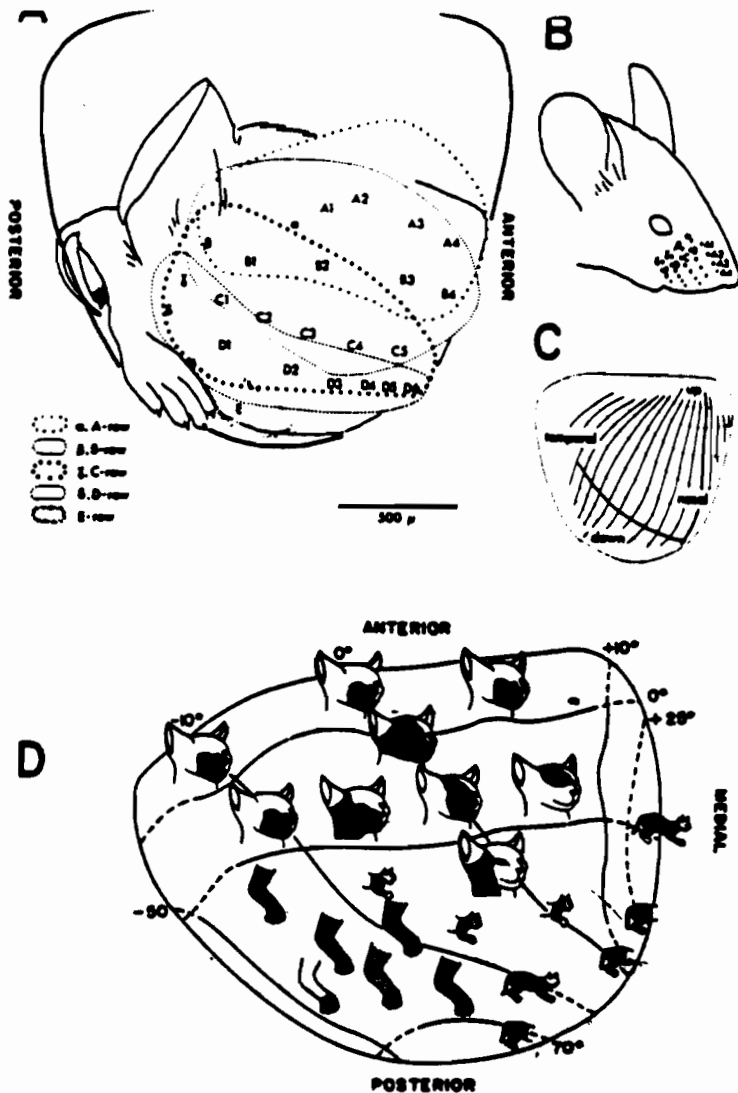


Fig. 3. Maps of the tactile and visual projection onto the tectum of mouse (A-C) and cat (D). (A) Somatosensory projection onto the superior colliculus of the mouse. Letters refer to whiskers (see B) and indicate the site of neural activity evoked by stimulation of the whiskers. The overlapping ovals represent regions activated by the five rows of whiskers. (C) Retinotopic representation of the visual receptive fields for the mouse. (D) Schematic illustration of how different body sectors are represented in the cat superior colliculus. Coordinates are shown for the topographical map of visual receptive fields. Note that the disproportionately large representation of the head and forelimb corresponds to the large area devoted to the representations of central and inferior-temporal visual receptive fields. (A-C taken from Ref. 5; D from Ref. 10.)

fields of collicular neurons range from 2 mm diameter to the entire dorsal surface of the body¹⁰.

Tactile receptive fields are also organized topographically in the SC^{5,10}. In each colliculus, representation of the contralateral forelimb and body regions innervated by the trigeminal nerve is extensive. Consequently, only a small part of the colliculus is allocated to representation of the large cutaneous surface area of the trunk and hindlimb¹⁰.

Acoustically responsive cells in the SC have fairly non-specific frequency sensitivity. Complex sounds such as hisses, whistles, finger snaps, or jangling keys

and even early studies using qualitative methods suggested a topographical representation of auditory space in the deep division of the SC⁶. Recent studies^{8,23} indicate that although acoustically responsive cells have large receptive fields, the response of these neurons is selective for the location of the sound. Each cell has a 'best area', a range of stimulus locations that elicit responses greater than 75% of maximum. The best areas of cells vary systematically with cell location, forming a map of auditory space in the SC²³.

Alignment of sensory maps in the SC

In experiments using anesthetized or paralyzed preparations, the auditory, somatosensory, and visual maps are found to be aligned. For example, in paralyzed cats, collicular neurons responding to both auditory and visual stimuli have visual and auditory receptive fields that overlap spatially⁶. For cells responding to auditory but not to visual stimuli, the location of the auditory receptive field is correlated with the spatial location of the receptive fields of nearby visually responsive neurons. Thus, Gordon⁶ 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. Similarly, the visuotopic organization of superficial layer neurons can be used as a reference for plotting the receptive fields of underlying cells responsive to tactile stimuli^{4,5,10} (Fig. 3).

Multimodal neurons and sensory-sensory interactions

Neurons responding to sensory stimuli from more than one modality have been identified in the optic tectum of fish, reptiles, birds and the SC (the mammalian homologue of the optic tectum) of mammals. For example, in pit vipers, many tectal cells respond to both visual and infrared stimuli; in the weakly electric fish, tectal cells respond to both visual and electrosensory stimuli. In mammals, many cells are responsive to visual, auditory and/or somatosensory stimuli.

When combinations of visual, somatic and auditory stimuli are presented to cats⁹ and guinea-pigs⁸, dramatic enhancement effects and inhibitory effects can be observed in the response of collicular neurons. These interaction effects depend upon the spatial and temporal overlap of the multimodal stimuli. Enhancement usually occurs if each stimulus is in the center of its receptive field and if the two stimuli are temporally contiguous. Response depression occurs most commonly when one of the two stimuli is outside or on the fringe of the cell's receptive field or if there is a large temporal disparity in the onset of the two stimuli^{8,24}.

Functional significance of multimodal interactions and map alignment

Multimodal interactions

That the responsiveness of collicular neurons to one sensory stimulus can be dramatically altered by simultaneous presentation of stimuli from other modalities is a recent observation. Therefore, neither the actual site of convergence nor the functional consequences of multimodal interactions are well understood. Although the site of convergence may be in the SC, there is no direct evidence for this hypothesis. The multimodal responses observed in collicular neurons could origin-

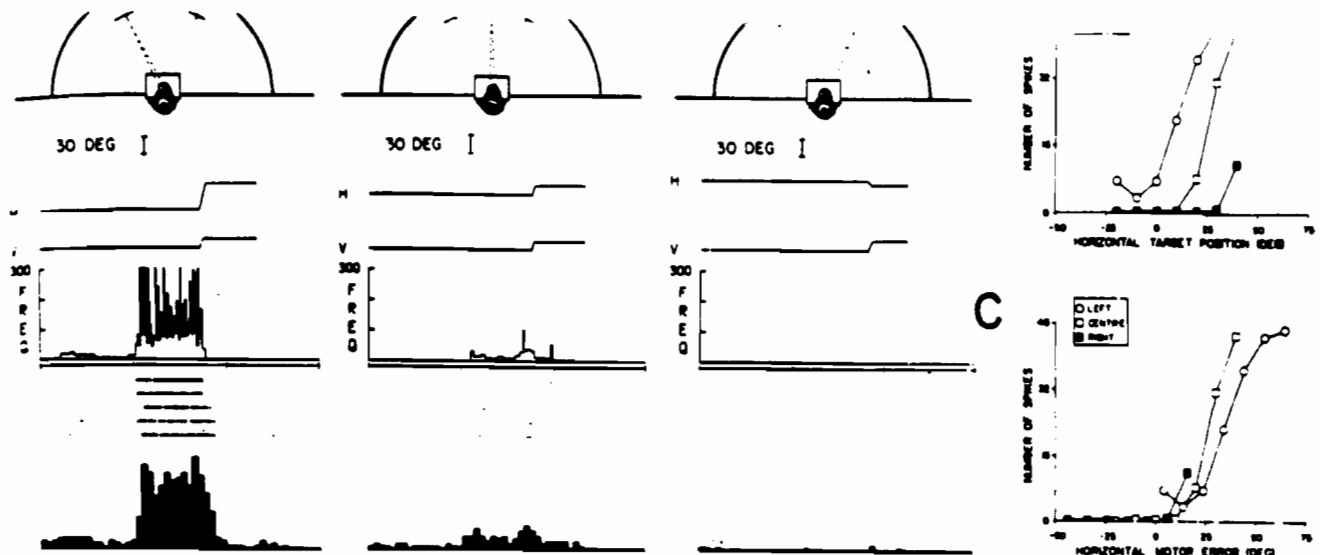


Fig. 4. The effects of eye position upon the response of a single cell in the superior colliculus of rhesus monkeys to an auditory stimulus. (A) Speaker was placed 20° right, 6° up from center while the fixation position was varied between 24° left (left), center (center) and 24° right (right). The time base represents 3 s; target presentation occurred at 1 s. Horizontal (up = right) and vertical eye position traces are shown in the top row; instantaneous firing rate for single trials are shown in the second row followed by rasters illustrating unit activity for five trials. The bottom row is a cumulative histogram for these trials. (B) A summary plot of the auditory receptive fields for this one cell as a function of horizontal target position (top) showing the shift in the position of the receptive fields as eye position was varied. The data are replotted in motor error (the difference between current eye position and saccade target location) coordinates in (C). The plots are better aligned in motor error coordinates. (Taken from Ref. 30.)

ate in cortical or subcortical areas sending signals to the colliculus.

The question of the functional consequences of sensory-sensory interactions also needs further study. It has been hypothesized^{24,25} that multimodal convergence onto neurons triggering orienting responses would allow cues from any of several sensory modalities to initiate orienting responses. Another conjecture is that the potency of different stimuli might depend upon environmental conditions. For example, auditory stimuli could be more effective in dim illumination while visual cues would be prepotent in higher light levels. Also, summation of signals from several modalities could function to enhance signal-to-noise ratios. Weak stimuli that cannot, alone, be used to identify or locate targets might increase the responsiveness of collicular cells to other types of sensory stimuli (see Refs 24 and 25 for further discussion of the functional role of multimodal interactions). Several of these hypotheses could be tested, explicitly, in experiments using alert, behaviorally trained animals. In such experiments it should be possible to vary the relative intensity, timing and location of paired auditory, visual and/or somatosensory stimuli while obtaining, simultaneously, behavioral reports of stimulus detectability, measures of the probability, magnitude and vigor of orienting responses, as well as concomitant records of neuronal activity.

Alignment of visual and motor maps

The foveation hypothesis of collicular organization proposes a specific functional role for the alignment of the retinotopic map of visual space found in the superficial division and the subjacent motor (saccadic) map^{11,16}. According to this 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 activate, relatively directly, 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 will be produced that brings the foveal projection onto the region of the visual field containing the target.

The foveation hypothesis encounters several difficulties. Two problems are cited (see Ref. 1 for additional discussion). First, the timing of neuronal activity in the superficial and deep division is not consistent with the proposed hypothesis. The onset of visual activity in the superficial layers begins 100–120 ms before the onset of the saccade-related burst of neurons in the deep division. Since 100 ms is not required for direct superficial-to-deep connections, the transmission of signals between these divisions must 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 neurons²⁶. 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 neurons is neither necessary nor sufficient to activate most cells generating saccade-related bursts²⁶. The reason for the alignment of the visual map in the superficial layers and motor maps in the deep layers is unknown.

Alignment of sensory maps

Considerable effort has been devoted to demonstrating an alignment of auditory, somatosensory, and visual maps in the SC, but the functional significance of the observed correspondence remains obscure. One possibility is that the alignment of the sensory maps observed in the colliculus has little functional relevance. The separate representations of visual, somatosensory and acoustic space could be completely independent, with each sensory system using its allocated space to map the environment with a particular magnification factor. The observed correspondence between the visual and auditory maps, for example, might be an epiphenomenon resulting from the fortuitous alignment of retinal and head coordinates occurring, in acute experiments, when the head and eyes are in the primary position. Indeed, the observed correspondence between sensory maps in the SC of anesthetized and/or paralyzed subjects is curious because the spatial location of a stimulus is encoded differently for each of these sensory systems. The neural code for the location of a visual stimulus must be based upon information about the locus of retinal stimulation and the position of the eyes in the orbits. In contrast, the location of sound sources is encoded using head-centered cues such as interaural differences in the timing and intensity of incoming sound waves. Tactile stimuli are localized in a third, body-centered, reference system. The apparent alignment of auditory, visual and somatosensory maps in the SC implies that these sensory signals have been translated into a common coordinate system, but this hypothesis cannot be tested in the anesthetized animal²⁷ because, under these conditions, the axes of the head-centered auditory system, the retinotopic visual system and body-centered somatosensory system are aligned.

Nonetheless, most researchers assume that the alignment of the sensory maps observed in the deep division of the SC is functionally significant. It is commonly assumed that the deep division of the SC contains a topographical map of sensory space such that a point in the space surrounding the animal is represented by neurons residing at a particular location in the SC. Furthermore, it is assumed that sensory signals from different modalities originating from the same point in space activate a common pool of collicular neurons located within this representation. Similar to the foveation hypothesis, the activation of these sensory neurons, in turn, is hypothesized to initiate motor responses resulting in orienting movements toward the source of the stimuli.

These hypotheses have not yet been formalized into a model of collicular function and many of the assumptions remain implicit and untested. For example, if the alignment of the maps is functionally significant, what is the basis of the alignment? Is the topography of the visual map imposed upon the other modalities, or have visual, auditory and somatosensory signals all been translated into common (other than visual) coordinates? What happens to the correspondence of sensory

or body?

If the sensory maps are static, what is the basis of the correspondence between sensory maps? One view is that the topography of the visual map is imposed upon the other modalities. Dräger and Hubel⁵ are the strongest proponents of this view. They noted that a major part of the visual field of the mouse is crossed by whiskers, and described a topographical relationship between somatosensory receptive fields, especially those involving the whiskers, and the visual receptive fields of overlying cells. They suggested that '... the somatosensory projection in the tectum is thus determined by the way in which particular tactile body parts are seen from the eye . . .' and 'At deeper levels other systems are represented, all arranged so as to be in registration with the visual world coded above . . .' However, there is no experimental evidence to support the assumption that in mammals, the alignment of the maps is imposed by the visual system. Would, for example, the somatosensory and auditory maps be modified in dark-reared animals in which tactile and acoustic stimuli were never associated with visual stimuli? Also, it is known that in cats, visually guided behavior appears around 14 days after birth, a few days after acoustically guided and tactually guided behaviors have developed²⁸. Thus, auditory, somatosensory and motor maps are 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 SC²⁹.

A possibility less frequently considered is that the maps of sensory space observed in the deep division of the SC are dynamic and that they are encoded in motor, rather than sensory, coordinates. Recently, Jay and Sparks^{30,31} conducted experiments to test this hypothesis. The experiments were based upon the observation that collicular neurons with saccade-related activity are organized topographically and that it is the location of active neurons within the topographical map of movement fields, not their frequency of firing, that specifies the change in eye position required to direct gaze to the target location. Thus, they reasoned that the task of sensory systems is to specify, by activating a particular subset of collicular neurons, the *change* in eye position required to look to a target, not merely the location of the target in head, body or retinal coordinates. Consider, for example, a monkey with the head positioned 'straight ahead' but with gaze directed 24° to the left of center. When an auditory stimulus is presented 10° to the right of center, interaural cues will be used to localize the target in head coordinates ('target is 10° right'). However, since the eyes are directed 24° left of center, looking to the target requires a 34° rightward saccade, and neurons in caudal regions of the left SC must be activated to produce this movement. If an auditory target is presented in the same location on another trial with gaze directed 24° to the right of center, cells in the right SC must be activated to produce the 14° leftward saccade required to look to stimulus.

Jay and Sparks^{30,31} plotted the receptive fields of neurons responsive to auditory and visual stimuli while the eye position of trained, alert monkeys was systematically varied. If auditory signals are organized in head coordinates, then in these experiments in which

sive neurons should be independent of visual location, position and depend entirely upon the azimuth and elevation of the sound source. However, if auditory signals have been translated into motor error coordinates, then the response of collicular neurons to acoustic stimuli should depend upon the trajectory of the movement required to look to the stimulus and, therefore, be sensitive to both the position of the speaker in space and the position of the eyes in the orbits. They found that the auditory receptive fields shifted with changes in eye position and that, in rhesus monkeys, the map auditory space in the deep layers of the SC is not static. With each change in eye position, the site of neural activity induced by a fixed auditory stimulus shifts to a new location – a location that specifies the metrics of the movement that would direct gaze to the target location. Harris *et al.*⁷ conducted a similar experiment in cats and concluded that the sensory maps were not dynamic. Noting that eye movements in cats are usually accompanied by head movements, they suggested that sensory maps will only be out of alignment for brief periods of time. Although the functional properties of neurons in the SC of cats and monkeys may differ, there are several problems with the Harris *et al.* study (see Ref. 31 for a critique), and the conclusion that sensory maps in the SC of cats are not dynamic is premature.

Concluding remarks

The deep layers of the SC contain separate representations of auditory, somatosensory, and visual space as well as maps of motor space. In acute experiments, the sensory and motor maps appear to be aligned and it is commonly assumed that the retinotopic map of visual space is the basis for the alignment. However, recent data suggest that, in rhesus monkeys, the sensory maps in the deep division of the SC are organized in motor coordinates. According to this view, the sensory maps are dynamic and the receptive fields of collicular neurons shift with relative movements of the eyes, head and body. A dynamic mapping of sensory space is required because of constraints imposed by the organization of the motor map.

Future or ongoing experiments should provide needed information about the intrinsic organization of the SC as well as information concerning the functional significance of multimodal interactions. Other studies are needed to determine whether or not the sensory maps in the SC of animals with restricted ocular mobility are static or dynamic. Collectively, these studies will contribute much to our understanding of the complex transformations of signals required for the sensory guidance of coordinated movements.

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Errata

In the article 'Patterns of cell loss in Huntington's disease' by Neil W. Kowall, Robert J. Ferrante and Joseph B. Martin (Jan. 1987, Vol. 10, pp. 24–29) there were two minor errors. In Table I the neurochemical profile for substance P was deleted. Substance P is depleted in HD and is also depleted by KA/IBO and QUIN injections. Also, Ref. 18 was partially deleted in the reference list. It should read:

- 18 Graybiel, A. M. and Ragsdale, C. W. (1983) in *Chemical Neuroanatomy* (Emson, P. C., ed.) pp. 427–504, Raven Press

In the article 'Axonal bifurcation on the visual system' by Jean Bullier and Henry Kennedy (May 1987, Vol. 10, pp. 205–210) the proportions of doubly labelled cells were omitted in Fig. 3. The bifurcated bars linking the circles and boxes representing visual structures correspond to the following proportions: the thin dark bars correspond to proportions of doubly labelled cells below 5%, the medium-size stippled ones represent proportions between 5 and 30% and the large hatched bars correspond to percentages above 30%.

We apologize for these errors.