

Sensori-motor integration in the primate superior colliculus

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The sudden onset of a novel stimulus usually triggers orienting responses of the eyes, head and external ears (pinnae). These responses facilitate the reception of additional signals originating from the source of the stimulus and assist in the sensory guidance of appropriate limb and body movements. A midbrain structure, the superior colliculus, plays a critical role in triggering and organizing orienting movements and is a particularly interesting structure for studying the neural computations involved in the translation of sensory signals into motor commands. Auditory, somatosensory and visual signals converge in its deep layers, where neurons are found that generate motor commands for eye, head and pinna movements. This article focuses on the role of the superior colliculus in the control of saccadic (quick, high-velocity) eye movements with particular regard to three issues related to the functional properties of collicular neurons. First, how do neurons with large movement fields specify accurately the direction and amplitude of an eye movement? Second, how are signals converted from different sensory modalities into commands in a common motor frame of reference? Last, how are the motor command signals found in the superior colliculus transformed into those needed by the motor neuron pools innervating the extraocular muscles?

Key words: superior colliculus / saccadic eye movements / microstimulation / movement fields / sensory maps / motor maps

IN MAMMALS the superior colliculus is composed of seven alternating fibrous and cellular layers. On the basis of anatomical and behavioral data,^{1,2} these layers are grouped into two functionally and connectionally different units, the superficial and deep compartments (Figure 1). The superficial layers (stratum zonale, stratum griseum superficiale and stratum opticum) receive inputs devoted almost exclusively to vision. Cells in the superficial layers of each colliculus are activated by stimuli appearing in the contralateral visual field and are topographically organized according to the location of their receptive

fields. The visual signals observed are in retinal coordinates; cells respond to visual stimuli if, and only if, particular regions of the retina are activated. The outputs of the superficial layers are primarily ascending and terminate, for the most part, in various regions of the thalamus, including the pulvinar. In contrast, the deeper layers (stratum griseum intermedium, stratum album intermedium, stratum griseum profundum and stratum album profundum) receive inputs from several modalities (visual, auditory, and somatosensory) and contain neurons with motor properties. Visual responses are in motor coordinates: cells fire when a particular movement is appropriate, not when a particular region of the retina is activated. The deeper layers have both ascending and descending efferent projections. The intrinsic organization of the superior colliculus is poorly understood. Whether or not there is extensive communication between neurons in the superficial and deep divisions has not yet been resolved.

Orienting movements of the eyes, head and pinnae can be initiated by auditory, visual or somatosensory stimuli. This raises the interesting questions of how and where visual signals coding the locus of retinal stimulation, auditory signals coding information about interaural differences in the timing and intensity of incoming sound waves, and somatosensory signals coding the site of stimulation in a body-centered frame of reference are transformed into common coordinates so that they can share a common motor circuitry for generating orienting movements. Because of the convergence of sensory signals in the deep layers and the presence of cells with motor properties, many researchers believe that these signal transforms occur in the superior colliculus. The approach in my laboratory has been to consider the translation of sensory signals into motor commands from a motor perspective.

The superior colliculus contains a map of motor (saccadic) space

Although electrical stimulation studies suggest that the superior colliculus contains neurons related to

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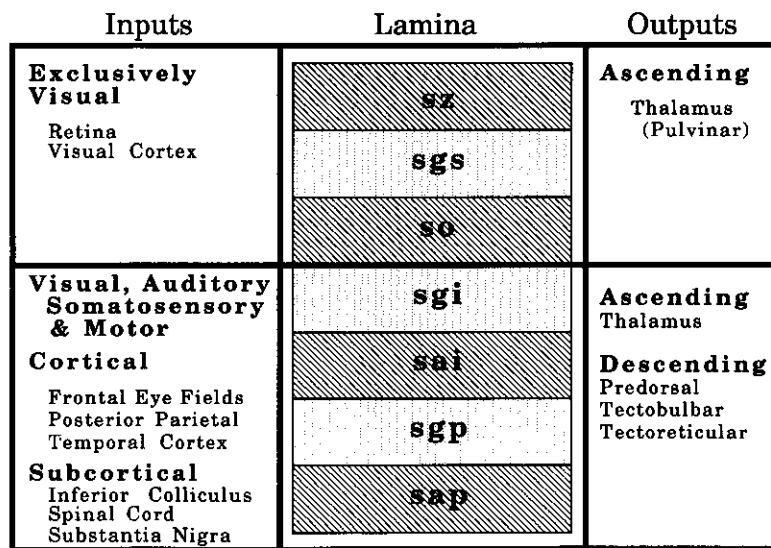


Figure 1. Schematic diagram of the laminar organization of the mammalian superior colliculus. Hatching represents fibrous layers; stipple, cellular layers. The superficial layers (sz, stratum zonale; sgs, stratum griseum superficiale; so, stratum opticum) are exclusively visual in terms of function and connections. The deep compartment of the superior colliculus (sgi, stratum griseum intermediale; sai, stratum album intermediale; sgp, stratum griseum profundum; and sap, stratum album profundum) is, by virtue of anatomical connections and physiological properties of its neurons, uniquely suited for a central role in sensori-motor integration. It receives signals from sensory modalities (auditory, somatosensory, visual) used to guide orienting movements and conveys, via the descending pathways of the deep division, motor commands to premotor nuclei in the brainstem and spinal cord.

movements of the eyes, head and external ear, only the signals involved in initiating saccadic eye movements have been studied in detail. Saccades are quick, high velocity rotations of the eye, usually made in an attempt to bring the image of a target onto the fovea, the region of the retina with the greatest density of photoreceptors. The neural signals involved in the generation of saccadic eye movements have been studied using rhesus monkeys trained to look to visual targets for a liquid reward and chronic single unit recording techniques. Using these methods, the pattern of activity of a single neuron can be recorded while the animal generates a series of saccades that vary systematically in direction and amplitude.

Many neurons in the deep layers of the superior colliculus generate a high-frequency burst of spike activity (Figure 2A) that begins 18-20 ms before saccade onset.³ The activity of these neurons is tightly coupled to saccade onset⁴ and each burst neuron has a movement field—i.e. the cells discharge before a range of saccades (Figure 2B) that have particular directions and amplitudes.^{5,6} The burst is observed before saccades in the movement field

regardless of the initial position of the eye in the orbit. Therefore, the discharge of collicular cells is not related to moving the eye to a particular position in the orbit but to changes in eye position that have a certain direction and a certain amplitude.

Saccade-related burst neurons are arranged topographically within the superior colliculus, according to the motor map (Figure 2C) revealed first using microstimulation (passing small currents through a microelectrode). Microstimulation in the deeper layers of the primate superior colliculus produces contralateral saccadic movements of both eyes with a latency of approximately 20-30 ms.⁷ Within broad limits, the amplitude and direction of a stimulation-induced saccade are independent of stimulation parameters (frequency, current, duration) and depend primarily upon the site that is stimulated. Thus, information about the direction and amplitude of an impending saccade is assumed to be encoded anatomically; it is the location of the active neurons in the superior colliculus, not their frequency of firing, that determines the metrics, that is, direction and amplitude, of a saccade.

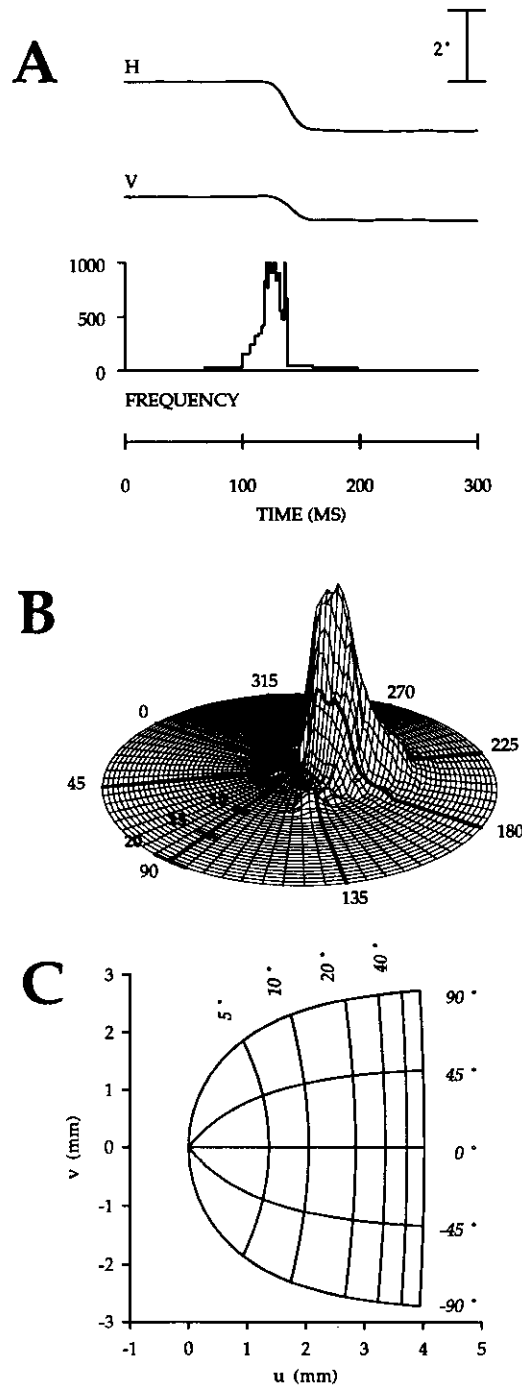


Figure 2. A. Discharge pattern recorded from a typical saccade-related burst neuron in the superior colliculus. H, horizontal eye position; V, vertical eye position; graph, instantaneous spike frequency. B. The movement field of a saccade-related burst neuron in the superior colliculus. Three-dimensional representation of the number of spikes as a function of the direction and amplitude of saccadic eye movements. For saccade direction (labeled 0°-315°), 0° = straight left; 180° = straight right, 90° = straight up and 270° = straight down. The polar plot has been rotated to reveal features of the movement field. The cell discharges before a range of eye movements having particular directions and amplitudes. C. The motor map of the superior colliculus (modified from ref 12). Isoamplitude lines (5° to 40°) run from medial to lateral and isodirection lines (-90° to +90°) run from anterior to posterior. u and v represent distance in mm in the superior colliculus.

Population coding of motor commands

In general, the movement fields of collicular cells are large and coarsely tuned.^{6,8} How can cells with large, poorly-tuned movement fields code precisely the metrics of a saccade? To state the problem differently, because each neuron fires before a broad range of saccades, a large population of neurons is active before each saccade. How are the signals needed to control saccade metrics extracted from the activity of this large population of coarsely tuned cells? One possibility is that the location of the most intense activity within the population is determined at a subsequent stage of neural processing. Another possibility^{6,9-12} is that each member of the active population contributes to the movement; the metrics of the saccade are determined by the average or sum of the population response.

Results of recent experiments,¹³ in which a small subset of the active population was reversibly deactivated, support the population averaging hypothesis outlined in panel 1 of Figure 3. The region of neurons active before a given saccade is assumed to occupy a symmetrical area within the motor map. Only those neurons in the center of the active population (A) discharge maximally before the programmed movement but there are also subsets of active neurons, such as those at sites B and C that tend to produce movements with directions and amplitudes other than the programmed movement; because these are symmetrically arranged, they produce opposing movement tendencies. The resultant will be a saccade of the programmed direction and amplitude. According to this hypothesis, each member of the active population contributes to the ensuing saccade. Neurons with sharply tuned movement fields are not necessary for the generation of accurate saccades.

This hypothesis predicts that if cells in a single region of the superior colliculus were inactivated, a predictable pattern of errors should result when the animal is required to make a series of saccades differing in amplitude and direction. The rationale of the experiment is outlined in panels 2-4 of Figure 3. Suppose a small subset of collicular neurons discharging maximally before straight right saccades 5° in amplitude were inactivated (shown as the darkly shaded area). If the animal were required to make a 5° rightward movement (panel 2), saccade direction and amplitude should be unaffected. The average of the movement tendencies produced by the unaffected neurons in the active population

(shown as the larger lightly shaded circle) should result in a saccade having the correct direction and amplitude. But, because the inactivated neurons in the center of the active zone normally discharge earlier than those on the fringe, the latency of the saccade should increase slightly (approximately 30-40 ms). Saccadic velocity might also be reduced as recent evidence suggests that the level of activity within the active population could determine the velocity of the movement (ref 14; Munoz and Guitton, unpublished report; Rohrer, White and Sparks, unpublished report).

With the same region of neurons inactivated, if the animal is now required to make an upward (20° angle) saccade 4° in amplitude (panel 3), the center of the population of cells that will be active shifts to a different region in the superior colliculus. For this movement, the inactivated cells are located on the periphery, rather than the center, of the active population. In this case, the silenced cells will not balance the activity of cells discharging maximally before saccades having a smaller amplitude and more of an upward component, so the animal should make a saccade that undershoots the target and has too much of an upward component. Similarly, if the animal attempts to make a downward (-20° direction) 9° amplitude saccade (panel 4), the resulting movement should overshoot the target and have too much of a downward component.

We trained rhesus monkeys (*Macaca mulatta*) on a saccadic eye movement task in which reinforcement was contingent on looking to a visual target. A glass pipette¹⁵ was used to record extracellular unit activity, for microstimulation and for pressure injection of various agents that affect neuronal activity into the superior colliculus. The location of the pipette tip in the collicular motor map was determined from plots of movement fields and measurements of the direction and amplitude of stimulation-induced saccades. The behavioral effects of the injections were assessed by comparing saccades to a selected set of visual targets before and after the injections.

Measurable modifications of saccadic eye movements lasting from 5-20 min were produced by injections of 50-200 nl of an anesthetic, 2% lidocaine. As predicted, the direction and amplitude of movements similar to the 'best saccade' (the movement produced by passing small current pulses through the recording/injection probe) were not altered noticeably after the injection. However, the velocity of movements similar to the best saccade

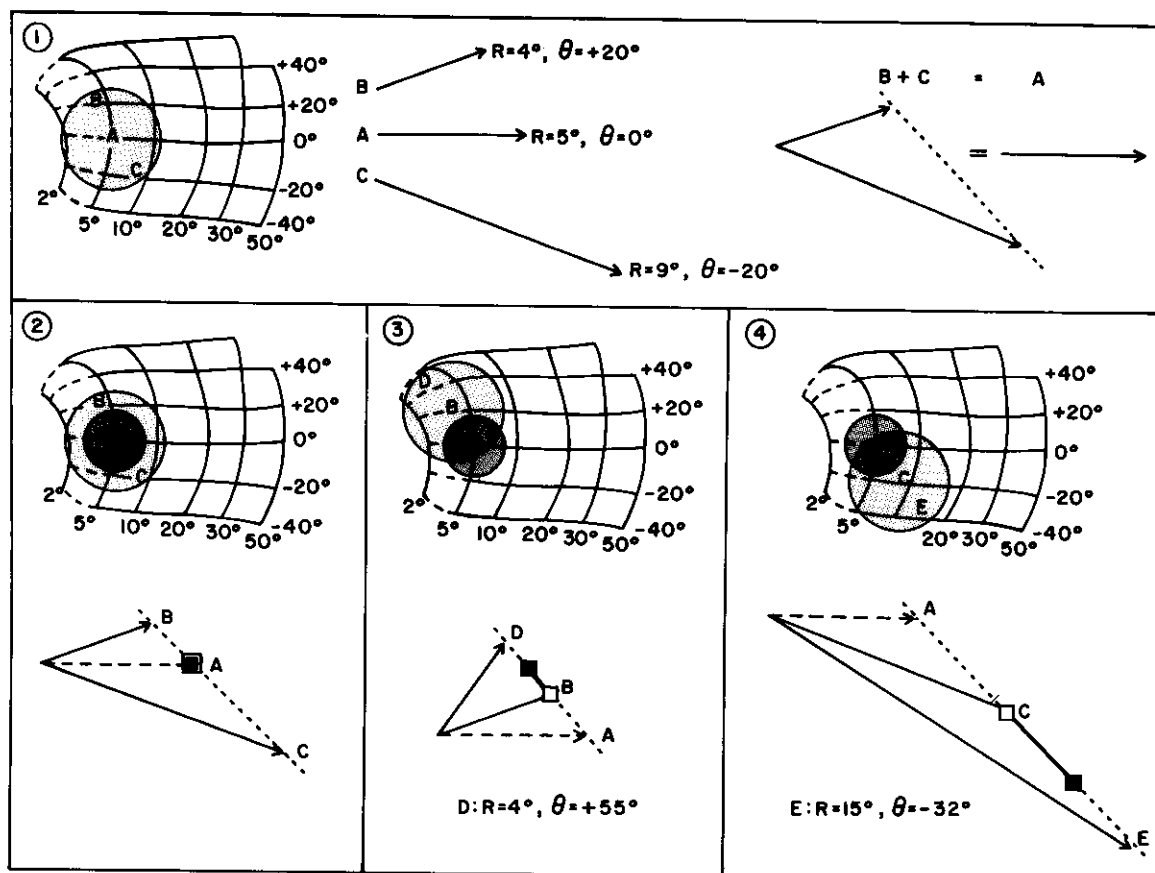


Figure 3. The population-averaging scheme of Sparks, Holland and Guthrie.⁶ Left, the motor map of the left superior colliculus. The stippled area represents the hypothetical extent of neurons active before saccades to a target located 5° to the right of the fixation stimulus. The active cell population is assumed to be symmetrical in shape. Middle, cells at locations A, B and C fire most vigorously for the movements shown. Right, weighted averaging of activity at points B and C yields the same movement as activity at the center of the active population (A). 2-4. The predicted effect of deactivating a subset of cells in the active population. The site of deactivation (darkly stippled circle) remains the same in each panel but the location of the active population (lightly stippled area) is different in each panel because saccades to three different targets are required. Beneath each map are the saccade vectors associated with neural activity at each of the locations illustrated. The open square represents the vector of the intended, or programmed, saccade associated with activity in the lightly stippled area. The dashed line represents the vector of the movement tendency produced by neurons at the deactivated site. These neurons will not contribute to the metrics of the saccade, so a saccade to the approximate location of the filled square is predicted. From ref 13.

was dramatically reduced and was accompanied by increases in duration, such that saccadic amplitude remained relatively constant (not illustrated, see ref 13).

As predicted by the population-averaging hypothesis, a systematic pattern of errors in direction and amplitude was observed (Figure 4). Saccades to targets requiring more of an upward component than the best saccade had too much of an upward component, and saccades to targets requiring movements with more of a downward component than the best saccade had too much of a downward component.

Also as predicted, movements to targets requiring a saccade smaller in amplitude than the best saccade were hypometric; saccades to targets requiring a movement larger than the best saccade were hypermetric.

These findings support the hypothesis that saccadic accuracy results from the averaging of the movement tendencies produced by the entire active population. Small changes in the direction or amplitude of saccades are produced by slight shifts in the location of the large population of active cells. Interestingly, the large movement fields of collicular neurons may

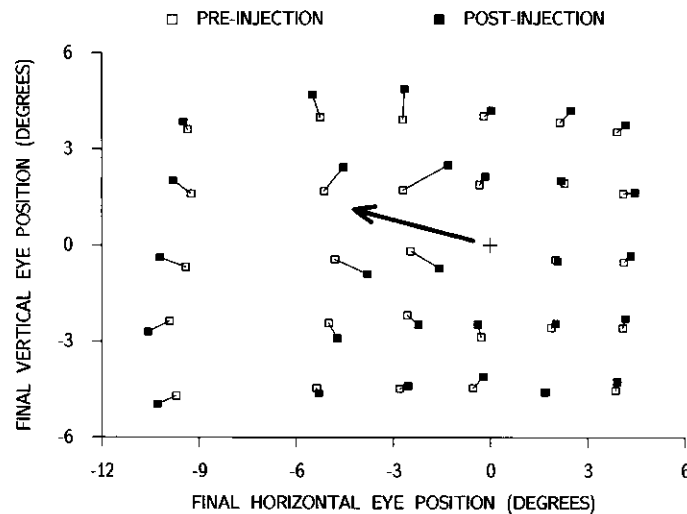


Figure 4. Plot of the position of the initial fixation (+) and the endpoint (tip of arrow) of the 'best saccade', derived from the experiment shown in Figure 3. Each symbol represents the average endpoint of 3-5 visually guided saccades. Lines connecting the squares represent the average error introduced by modifying the spatial and temporal pattern of neuronal activity in the superior colliculus. The effects of a single 200 nl injection of lidocaine are shown. From ref 13.

contribute to, rather than detract from, the accuracy of saccadic eye movements. The simulations of Baldi and Heiligenberg¹⁶ produced the apparently paradoxical result that, over a fairly large range, the wider the tuning curve of individual elements, i.e. the less precise they are, the more robust and precise the overall computation. Because the contribution of each neuron to the direction and amplitude of the movement is relatively small, the effects of variability or 'noise' in the discharge frequency of a particular neuron are minimized. The lack of sensitivity to noise in the response of individual elements is a general characteristic of coarse population coding.^{17,18} Distributed population codes are not restricted to eye movement control but have also been reported for the control of reaching movements of the arm (see Kalaska, this issue¹⁹; ref 20) and for the control of the jamming avoidance response in weakly electric fish (see Heiligenberg, this issue²¹). Ordered arrays of broadly tuned sensory neurons coding a computed parameter such as the angle of orientation of a line segment or the direction of velocity of stimulus movement also characterize neural maps of several modalities.²²

Dynamic sensory maps in the superior colliculus

As an electrode is lowered through the superior colliculus, many cells responsive to sensory stimuli

are encountered. Neurons in the superficial layers respond almost exclusively to visual stimuli but as the electrode passes through the deeper layers, the proportion of cells responding only to visual stimuli decreases and cells responding to somatosensory and auditory stimuli are encountered. Many cells in the deeper layers are multimodal, responding to visual, auditory, and/or somatosensory stimuli.³ The cells of each modality form a topographic map but the question arises whether these maps are coded in sensory or motor coordinates.

In anesthetized or paralysed preparations, a fixed correspondence between visual, somatosensory and auditory maps is observed,²³⁻²⁶ implying that the sensory signals have been translated into a common coordinate system. It is usually assumed that this alignment facilitates the formation of a general, modality independent map of the external environment. In such a map, stimuli originating from a particular region of the external world, regardless of sensory modality, would activate a particular subset of topographically organized multimodal neurons. The activation of these sensory neurons could, in turn, initiate orienting responses by exciting adjacent cells with movement-related activity organized in a motor map aligned with the multimodal map of sensory space.

Unfortunately, this hypothesis cannot be tested in anesthetized animals because under anesthesia the

axes of the head-centered auditory map, the retinotopic visual map and the body-centered somatosensory system maintain a fixed relationship to each other. To answer the question of what happens to the correspondence of sensory maps or the alignment of the sensory and motor maps during voluntary movements of the eyes, head or body, experiments with unanesthetized animals are needed (see ref 3 for further discussion).

An alternative hypothesis²⁷⁻³⁰ is that the signals of collicular neurons responsive to sensory stimuli are encoded in motor, rather than sensory, coordinates. This hypothesis is based on several considerations. Because the discharge of saccade-related motor cells in the superior colliculus is related to movements of a certain direction and amplitude regardless of the original position of the eye in the orbit, sensory signals that initiate saccades must specify the change in eye position required to look to the target, not the location of the target in head, body or retinal coordinates. Moreover, a specific subset of collicular neurons must be activated to initiate a particular saccade because it is the location of active neurons within the topographical map of movement fields that specifies the metrics of the movement. Consider, for example, a monkey with the head and gaze directed 'straight ahead' and the right hand held at 10° to the right of the point of fixation. Looking to the

location of a tactile stimulus applied to the right hand requires a 10° rightward saccade and neurons in the left superior colliculus must be activated to produce this movement. But a saccade to a similar tactile stimulus when the animal's right hand is 10° to the left of the fixation point must be initiated by the activity of cells in the right superior colliculus.

Experiments conducted in my laboratory support the hypothesis that sensory signals in the deep layers of the superior colliculus are organized in motor coordinates. In one experiment²⁷ monkeys were required to look to the locations previously occupied by two visual targets briefly presented in succession. The total duration of the two presentations was less than the reaction time of the monkey. In these experiments, one type of neuron (quasi-visual cell) in the deep layers of the superior colliculus seemed to be visually responsive, to have a receptive field and to respond to targets in its receptive field whether or not a saccade was made toward the target (see Figure 5B). But on trials requiring a change in fixation (Figure 5C), quasi-visual cells began to fire after the eye had reached the position of the first target and continued to fire until after the second saccade. The receptive fields of these cells did not contain the original target but contained the position where the target would be if, after the first saccade, the second target were flashed again in the same

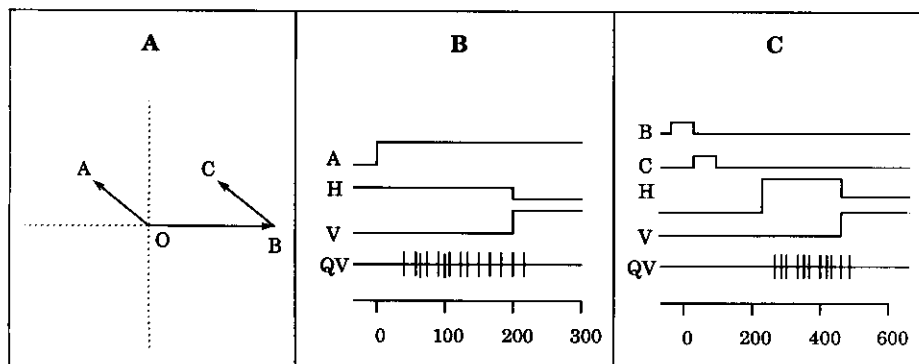


Figure 5. Discharge pattern of a hypothetical quasi-visual (QV) cell. A. Trajectories of the saccades occurring on single (O-A) and double (O-B and B-C) saccade trials. B. The quasi-visual cell seems to display a sustained response to visual targets presented in the upper left visual field. On O-A trials, the onset of the quasi-visual cell is tightly coupled to the onset of a visual target in the cell's response field and the activity continues until a saccade to the target occurs. A, time of onset of target A; H, horizontal eye position; V, vertical eye position; X axis = time in ms. C. Typical response on double-saccade trials. No observable alteration in discharge rate is related to the onset of targets B or C but after the eyes reach position B, an increase in discharge frequency begins and continues until after the second (B-C) saccade (see ref 27 for actual data). This demonstrates that the activity of the cell is not dependent on stimulation of a particular region of the retina, but on the direction and amplitude of the movement required to look to a current target or to the remembered location of a target presented earlier.

spatial location. We interpret the results of this experiment as supporting the hypothesis that the activity of quasi-visual cells reflects motor error, the direction and amplitude of a saccade required to look to a target. Quasi-visual 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 because of an eye movement occurring when the target disappears.

This was confirmed in a separate experiment²⁸ by recording the activity of quasi-visual cells during trials in which the monkey compensated for stimulation-induced perturbations in eye position: quasi-visual cells increase their discharge rate whenever there is a certain difference between present and desired eye position, regardless of whether this motor error is 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 quasi-visual 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 quasi-visual cell activity shifts to a location that represents the new motor error.

Results of other experiments^{29,30} support this view. Using a delayed saccade task to produce temporal separation of sensory and motor activity, the receptive fields of sound-sensitive cells in the superior colliculus of alert monkeys were plotted while varying the direction of visual fixation. If the receptive fields of auditory neurons in the superior colliculus are organized in head-centered coordinates, the direction of fixation should have no effect. But, if the response of auditory neurons is organized in motor coordinates, then the response should depend upon both sound source and fixation direction.

For every sound-sensitive cell encountered in the superior colliculus, the position of the eyes in the orbits has a distinct effect on the response to an auditory stimulus. Plots of the average number of spikes evoked by the auditory stimulus as a function of the position of the loud speaker indicated that the receptive field of the neuron shifted with the position of the eyes in the orbits. But, when the average number of spikes in the response was plotted as a function of the movement required to look to the target, the data obtained with the different fixation positions were 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, that is, the position of the eyes in the orbits relative to target position. The map of auditory space found in the monkey superior colliculus is not a static representation. With each movement of the eyes in the orbits, the population of neurons responsive to an auditory stimulus in a particular spatial location changes to a new site within the superior colliculus, a site that specifies the metrics of the movement that would direct gaze to the target location.

Transformations of collicular signals to motor commands

The saccadic command signals observed in the superior colliculus are quite different from the control signals needed by the extraocular muscles. Thus, the collicular signals must be transformed in a number of ways before they reach the motor neurons³¹ (see also van Gisbergen, this issue³²). Transformations of collicular signals are required, in part, because of the properties of the oculomotor plant, which is the eye ball, extraocular muscles, orbital suspensory

Figure 6. A. Examples of nine saccades all having 8° right-ward horizontal components but differing in the magnitude and/or direction of the vertical component. B. The velocity profiles associated with three of the saccades illustrated in A. Note the reduction in peak velocity and the increase in duration of the horizontal component of movements having larger vertical components. H VEL, horizontal velocity. C. The locations of collicular neurons (on the left) discharging maximally before each of the nine saccades illustrated in A. By appropriate synaptic weighting, some neurons receiving tectal input in the central mesencephalic reticular formation (cMRF, on the right) could display a frequency of firing proportional to the velocity of the horizontal (or vertical) component of oblique saccades. Neurons discharging maximally before saccades with small vertical components (e.g. E) would provide large excitatory drive, while those discharging maximally before saccades with larger vertical components would provide proportionally smaller excitatory drive. D. A plot (filled squares) of the peak velocity of the horizontal component of the nine saccades shown in A as a function of the direction of the saccade (0 = straight right). The firing rate (solid line), displayed as percentage of maximum, of a hypothetical neuron receiving inputs from all collicular neurons discharging maximally before saccades having an 8° horizontal component. Strength of synaptic input is weighted according to the cosine of the angle of the movement. From ref 47.

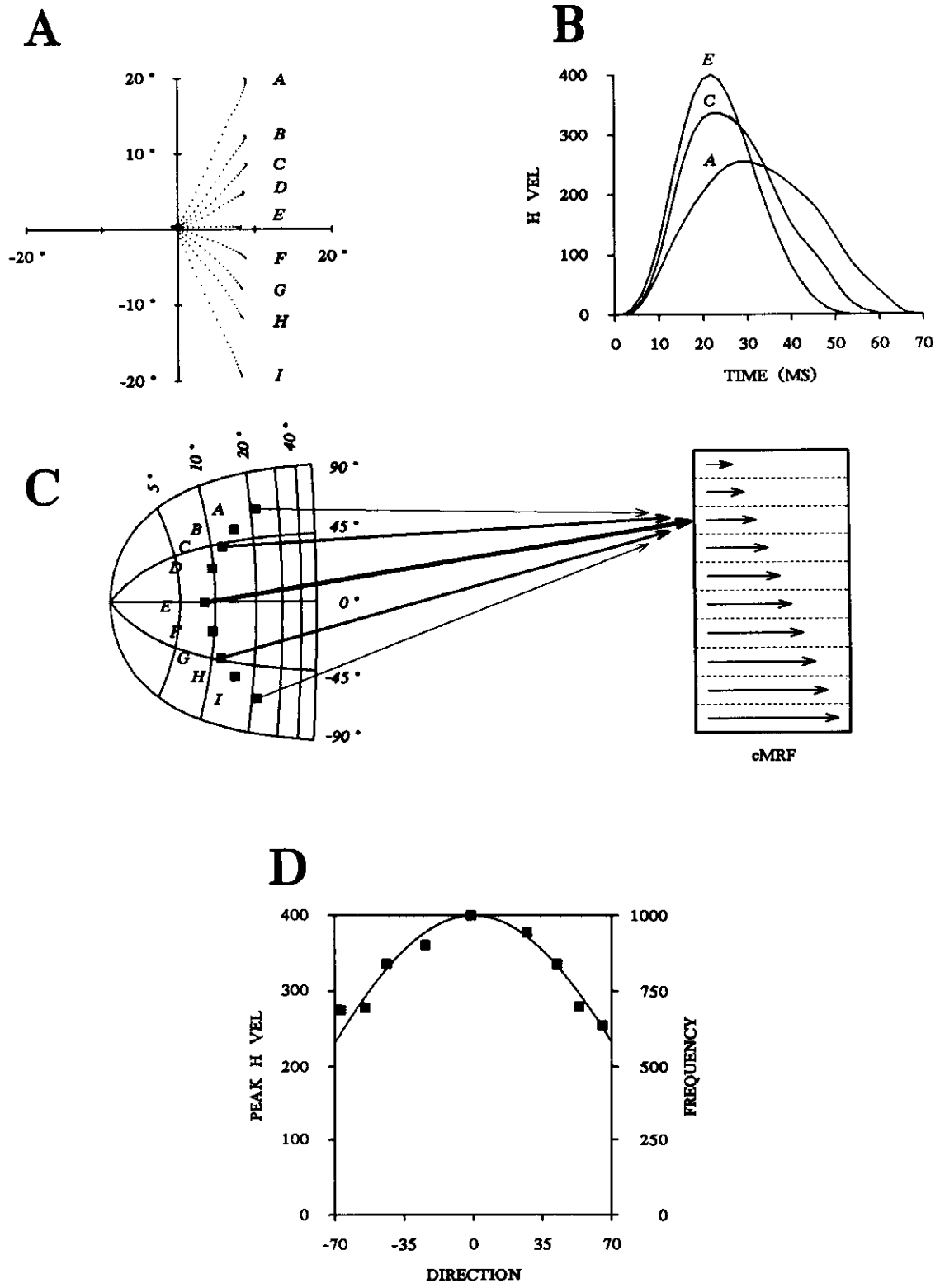


Figure 6.

tissues and any other passive orbital tissues influencing rotation of the eye. The highly overdamped characteristics of the plant impose constraints on the motor signals needed to produce a saccade. An initial burst of pulses is required to generate the phasic increase in muscle tension that overcomes the viscous drag of the orbital tissues and moves the eye at a high velocity. This must be followed by a step increase in firing rate to produce the sustained change in muscle tension required to hold the eye in the new position and to overcome the elastic restoring forces of the orbital tissue.

In one model of the oculomotor plant,³³ the signal required is a pulse, followed by an exponential slide to a final plateau in the firing frequency: this is the pattern of activity observed when recording from motor neurons innervating extraocular muscles. A high frequency burst of motor neuron activity precedes, by about 8 ms, the onset of saccades in the on-direction.³⁴⁻³⁷ The pulse of activity decays with a short and a long time constant to the steady-state level of activity associated with the new position.^{34,38} Two neural circuits located in the brainstem are assumed to generate the pulse/slide/step waveform observed in the activity of motor neurons: one in the pontine and medullary reticular formation is responsible for the horizontal component of saccadic eye movements (see below); the other in the rostral midbrain generates similar signals for controlling the vertical components.³⁹⁻⁴²

One of the required transforms of collicular signals is described here to illustrate possible mechanisms for performing the necessary computations. The discharge of burst neurons in the superior colliculus precedes saccades with particular directions and amplitudes. The burst observed in most collicular neurons occurs before saccades that have both horizontal and vertical components. But the burst is not uniquely related to the amplitudes of either the horizontal or the vertical component of the movement which are the signals needed by the horizontal and vertical pulse/slide/step generator circuits. Thus, separate signals for horizontal and vertical motor error must be extracted from the motor map found in the superior colliculus. Moreover, the separate signals of horizontal and vertical motor error must be coordinated to produce oblique saccades. Oblique saccades usually have relatively straight (rather than curved) trajectories (Figure 6A) because the onsets of the horizontal and vertical pulses are synchronized and the durations of the horizontal and vertical displacements are approximately equal.⁴³⁻⁴⁵

When the amplitudes of the horizontal and vertical components of an oblique saccade are unequal, the duration of the smaller component is greater than that of a pure horizontal or vertical saccade of the same amplitude (Figure 6B).

A possible mechanism for extracting a signal of horizontal motor error from the anatomically coded signal observed in the superior colliculus is illustrated in Figure 6. The axons of all the collicular neurons residing along an iso- ΔH curve (same change in horizontal position) are assumed to converge on neurons at a specific depth (see Figure 6D) in the central midbrain reticular formation, an area implicated in the control of horizontal saccades.⁴⁶ Neurons at that depth would discharge maximally before any saccade having a particular horizontal component, regardless of the vertical component of the movement. Similarly, the axons of neurons residing along other iso- ΔH curves are assumed to converge on neurons in the reticular formation at other depths. Other neurons receiving tectal output are hypothesized to extract information about the vertical component of oblique saccades.

The hypothesis presented in Figure 6 can be extended to suggest a mechanism by which the velocity of the horizontal and vertical components could be scaled according to saccadic direction. Neurons encoding the velocity of the horizontal component of oblique saccades by their frequency of firing could be formed by allowing cells in the reticular formation to receive excitatory synaptic inputs from all members of an iso- ΔH curve, but scaling the strength of the excitation by the location of collicular cells along the curve (Figure 6C). For example, those members of the 5° iso- ΔH curve that are located rostrally and near the middle of the colliculus (cells associated with 5° horizontal movements having no vertical component) would provide greater excitatory drive than members located more caudally and medially or laterally, i.e. cells associated with 5° horizontal movements and large vertical components. Appropriate scaling of synaptic strength according to the location of neurons in the superior colliculus would permit cells to fire at frequencies proportional to the velocity of the horizontal component of oblique saccades (Figure 6D). What is needed are anatomical experiments to test the hypothesis that the outputs of collicular neurons residing along an iso- ΔH curve converge at a common anatomical locus and electrophysiological experiments that describe the functional properties of the cells that receive the tectal output.

Conclusion

An exciting aspect of research related to the function of the superior colliculus is that the anatomical methods, neurophysiological tools and experimental preparations required to test specific computational models of sensorimotor integration are currently available. The superior colliculus is a site where sensory and motor signals are represented by the activity of populations of neurons and a site where computations are performed, in part, by the pattern of anatomical connections. As the goals of the computations and the destinations of the signals are known, it is possible to develop realistic, testable models of specific neural computations.

Experiments related to collicular function complement the work of other investigators tracing saccade command signals centrally from the motor neurons and those studying the structure and connectivity of brainstem neurons with saccade-related activity. Ultimately, studies from these various laboratories should yield a precise description of the neural network generating saccadic eye movements. In a broader sense, these studies will allow a description of the neural events that intervene between the central processing of sensory information and the central programming of motor commands.

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