The Primate Superior Colliculus and the Control of Saccadic Eye Movements

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The superior colliculus is a brainstem structure playing a critical role in orienting movements of the head, pinnae, and eyes. The superior colliculus acts as an important intermediary between sensory and motor signals, issuing motor commands that are translated into the appropriate temporal code required by the motoneuron pools. Collicular cells are broadly tuned with respect to the direction and amplitude of the movements they initiate, and a large population of collicular neurons is active before each movement. How information is extracted from the spatial and temporal profile of the active population and how the translation of the motor command progresses from the anatomically (spatially) organized map of saccade direction and amplitude found in the colliculus to the level of the temporally-coded motoneuron commands are important, but unsolved, problems. This review considers this spatial-to-temporal transformation, a prime motivating problem in oculomotor research. Recent findings have led to alterations of previously held views of the role of the primate superior colliculus in generating movements that orient our sense organs toward visual, auditory, and tactile stimuli. Some of these most current findings are presented in this review. NEUROSCIENTIST 2:284-292, 1996

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Orienting movements of the eyes and head usually follow the sudden appearance of a visual stimulus or the sudden onset of a loud sound. These responses enhance the quality of additional signals originating from the source of the stimulus and aid in the sensory guidance of appropriate limb and body movements. The superior colliculus, a midbrain structure (Box 1), plays a critical role in triggering and organizing the orienting movements of the eyes and head. Studies of the role of the superior colliculus in the control of orienting movements have provided important insights into one of the enduring problems of systems neuroscience-the question of how sensory signals are translated into commands to modify ongoing movements or initiate new ones. This sensorimotor integration issue has been thoroughly reviewed (1-4). This review focuses on the role of the superior colliculus in the control of saccadic (abrupt, high-velocity) eye movements with particular regard to two important issues: population coding and the spatial-to-temporal transformation problem.

Population Coding

Many neurons in the deeper layers of the superior colliculus (SC) discharge before saccadic eye movements. These neurons are usually silent but, at a variable time before the onset of a saccade, begin to discharge with a low (50-100 Hz) frequency. Then, approximately 18-20 ms before the onset of the movement, the cells generate a vigorous burst of activity, reaching instantaneous frequencies of 800-1200 spikes per second. The high-frequency burst of collicular cells probably serves as a trigger signal for the initiation of saccades (5). Collicular cells with saccade-related activity have movement fields: each cell discharges before saccades having a particular range of directions and amplitudes, regardless of the initial position of the eye in the orbit (5-7). Moreover, these cells are organized topographically within the SC to form a motor map. Neurons discharging before small saccades are found rostrally, and cells discharging before large saccades are found caudally in the superior colliculus. Upward movements are represented medially, and downward movements are represented laterally. Cells discharging before leftward movements are found in the right SC, and those discharging before rightward saccades are in the left SC.

The issue of population coding arises because the movement fields of collicular cells are large and coarsely tuned-i.e., each neuron fires before a broad range of saccades. Because each cell is active before many movements, a large population of neurons is active before each saccade (7, 8). How can premotor cells that discharge before and during a broad range of movements be responsible for the initiation and execution of accurate and precise movements? To restate the question,

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how are the signals needed to select, initiate, and control movements extracted from the spatial and temporal profiles of activity within a large population of coarsely tuned neurons?

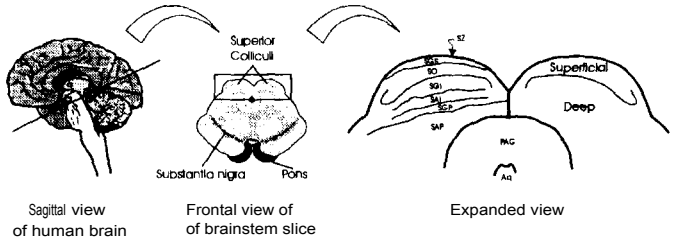
There have been several suggestions for how such broadly tuned neural activity might precisely control the direction and amplitude of a saccade (7, 9, 10). For example, Sparks et al. (7) suggested that the direction and amplitude of a saccade is the result of a weighted *average* of each neuron's vector contribution. As illustrated in Figure 2, this model predicts that deactivation of a small region of collicular neurons may produce saccades that are hypermetric or hypometric. The saccade metrics, in this case, depend upon the location of the deactivated neurons within the population of cells active before and during a saccade. For example, without the contribution of cells that code for relatively small amplitude movements, the remaining active neurons would produce a movement hypermetric to that coded by the full complement of cells within the population. van Gisbergen et al. (10) reported that simulation results for a vector-summation model of the population coding of superior colliculus neurons were encouraging, except for saccades with amplitudes beyond 50°. In this model, saccade amplitude and direction are based upon the vector sum of the individual cell contributions. Because the effect of the total population of cells is a simple addition of the contribution of individual cells, this model predicts that lesions that inactivate *any* members of the active population will cause saccades to be hypometric. Using a technique that reversibly deactivated a region of the superior colliculus, Lee et al. (11) tested the predictions of the weighted-average and the vector-summation models.

An injection of lidocaine reversibly anesthetizes a local region of the superior colliculus, effectively depressing neuronal activity for 5-20 min. According to the vector-summation model, such inactivation of a subset of an active population of neurons in the superior col-

Box 1: Basic Anatomy

The mammalian superior colliculi are found on the dorsal surface of the brainstem, one on each side of the midline. Each superior colliculus (SC) is laminar in structure (Fig. 1), and each layer can be crudely described as comprised of cells with activity related to sensory, sensory and motor, or purely motor events.

Under close anatomical and electrophysiological examination, the *superficial* layers are found to receive exclusively visual inputs (see chart in Fig. 1). The *deep* subdivision receives visual, auditory, somatosensory, and motor inputs from major cortical and subcortical regions, in addition to providing motor output signals to areas in the brainstem related to orienting movements of the eyes, head, and pinnae toward visual, auditory, and tactile stimuli. Ascending axons *(unfilled arrow)* from the deep layers are directed to nuclei of the dorsal thalamus, which, in turn, sends projections to most regions of the cerebral cortex. Descending axons *(filled arrow)* project to regions involved in controlling eye movements, such as the paramedian pontine reticular formation (PPRF), and the nucleus reticularis tegmenti pontis (NRTP). The SC also projects to regions subserving head and pinnae movements.



Inputs	Layer	Outputs
Exclusively Visual Retina Visual cortex	Superficial	Thalamus (pulvinar)
Visual, Auditory, Somatosensory, & Motor *Cortical* Frontal eye fields Prefrontal cortex Posterior parietal Temporal cortex Occipital cortex *Subcortical* Inferior colliculus Spinal cord Substantia nigra Deep cerebellar nuclei Thalamus Hypothalamus Pontine reticular nuclei	Deep	Thalamus Predorsal Bundle Tectobulbar tract Tectoreticular tract - projections to areas involved in orienting the eyes, head, and/or pinnae.

Fig. 1. A schematic representation of the anatomical location and structure of the mammalian superior colliculus (SC). The expanded view shows the multilayered structure of the SC, which can be simplified to two major subdivisions, the *superficial* and *deep* layers. The chart lists a few of the major sources and targets of inputs and outputs, respectively, to and from the superior colliculus. This is not an exhaustive list (32). SZ, stratum zonale; SGS, stratum griseum superficiale; SO, stratum opticum; SGI, stratum griseum intermedium; SAI, stratum album intermedium; SGP, stratum griseum profundum; SAP, stratum album profundum; PAG, periaqueductal gray; Aq, aqueductus cerebri. Frontal view of brainstem slice after Nieuwenhuys et al. (33). Expanded view after Ma et al. (34).

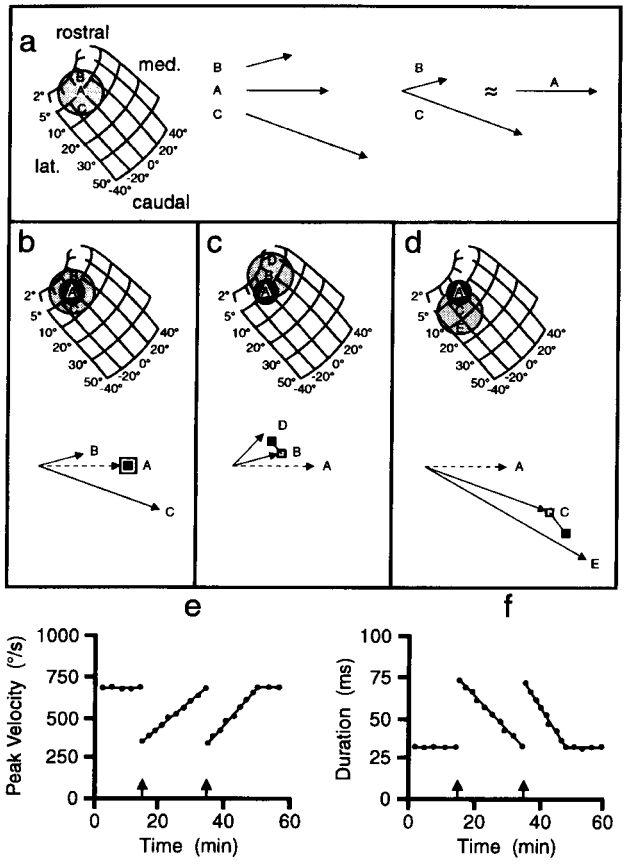


Fig. 2. Panel a, *left* depicts the motor map of the left superior colliculus (SC). Lines of isoamplitude *(2* to *50°)* run from the lateral edge to the medial aspect of the SC map. lsodirectional lines *(-40* to *40°)* run from the rostral to the caudal borders, with 0° and 90° representing straight right and straight up trajectories, respectively. The *lightly shaded region* represents the hypothetical population of cells active prior to saccades directed to a target *5°* to the right of the fixation stimulus. The active population is assumed to be symmetrical in shape, with the most vigorous activity found in the center of the population. *Middle:* the cells found at locations *A, B,* and C fire most vigorously for the movements shown in vector form. *Right:* the weighted average of the activities in sites *B* and C yields the same movement as activity in the center of the active population (A). Panels *b-d* show the predicted effect of deactivating a subset of the active population of collicular cells. The site deactivated with lidocaine *(darkly shaded circle)* is the same in each panel; however, the location of the active population *(lightly shaded circle) is* different because saccades to different targets *(open square; A* in panel *b, B in* panel c, and C in panel d) are required. Beneath each map are the saccade vectors representative of neural activity at the sites not deactivated *(solid line arrows).* The *open square* represents the endpoint of the intended saccade associated with the activity of the entire population of cells within the *lightly shaded circle.* The *dashed-line arrow* represents the vector of the movement elicited by neurons at site *A* prior to deactivation. The loss of otherwise contributing cells around site *A* leads to predictions that saccades to targets *B* or *C (open square,* panels c and d, respectively), would be made to the approximate location represented by the filled square. Panels e and f show, in a schematic form of the actual data, the effect of SC cell deactivation on saccadic peak velocity and duration, respectively, observed for similar amplitude saccades over a period during which two separate lidocaine injections were made at the same collicular site *(arrows* indicate time of injections). After Lee et al. (11).

liculus was predicted to invariably produce hypometric saccades. On the other hand, the averaging hypothesis predicted hypometric and hypermetric saccades to targets requiring movements smaller and larger, respectively, than the electrically elicited "best saccade" (saccade resulting from stimulation at the injection site) (Fig. 2, a-d).

Lee and co-workers observed the systematic pattern of errors predicted by the weighted-average hypothesis. Both hypo- and hypermetric movements were observed, and the upward and downward components were larger if targets required more upward or downward components than the "best saccade," respectively. Interestingly, after the injection, the velocity of visually-guided movements corresponding to the "best saccade" was slower, and the duration was prolonged (Fig. 2, e-f). These results provided the first conclusive experimental support for population coding of the parameters of a movement. With population coding, a large range of different movements can be generated by addressing different sets of cells centered at different locations in the motor map. Yet precise gradations in amplitude and direction are possible using relatively few coarsely tuned cells because small shifts in the locus of the active population produce small changes in direction and/or amplitude. The effects of "noise" or variability in the discharge frequency of individual neurons are greatly minimized as the contribution of each unit to the amplitude and direction of the movement is likely to be relatively small. As a result, large populations of broadly tuned neurons contributing to a saccadic eye movement may be responsible for the high degree of accuracy.

These results have broad implications. In general, sensory neurons providing signals used to select and guide movements are broadly tuned with respect to the attributes of the stimuli they encode, and cells discharging in association with movements are broadly tuned with respect to the parameters of the movements they produce. Thus, large populations of cells discharge in response to each stimulus, and large populations of cells must be active before and during each movement. Moreover, many large populations of sensory and motor cells in widely distributed areas of the nervous system may be active simultaneously both before and during the movement. How the signals needed to select, initiate, guide, and control movements are extracted from the spatial and temporal profiles of large populations of widely distributed and coarsely tuned neurons has emerged as one of the most fundamental questions in systems neuroscience. The experiments of Lee et al. are the first to address directly the question of how information is extracted from the profile of population activity, and it will be of interest to see if the strategy used by the superior colliculus is also used in other sensory and motor systems.

Spatial-to-Temporal Transformation

Microstimulation Studies-Evidence for a Collicular Place Code

It has long been known that stimulation of the superior colliculus produces conjugate (yoked) movements of the eyes (12, 13). However, Robinson (14) performed the first systematic microstimulation mapping study of the superior colliculus. Using constant current pulse trains that elicited saccade-like eye movements directed contralateral to the side stimulated in alert monkeys, Robinson found that the colliculus was arranged topographically in that saccade amplitude and direction depended upon the site of stimulation. Schiller and Stryker (15) demonstrated that this deep, motor-related map was in topographic register with a retinotopic visual map organized in the overlying, superficial layers of the superior colliculus. Both groups concluded that, within broad limits, the properties of electrically-elicited eye movements were independent of the parameters of the microstimulation and the initial eye position in the orbit.

The results of Robinson (14) and of Schiller and Stryker (15) have been interpreted as evidence for a pure spatial code of saccade amplitude and direction; it is the site of neural activity within the motor map alone, and not the level (vigor) or the duration of the activity, that determines the properties of a saccadic eye movement.

Motoneuron Activity-Temporal Coding

Saccades are produced by a precisely timed pattern of activity in the motoneuron pools innervating the extraocular muscles. Temporal precision is necessary because of the mechanical characteristics of the oculomotor plant (the eyeball, extraocular muscles, orbital suspensory tissues, and any other passive orbital tissues influencing rotation of the eye). The motoneurons generate a brief initial burst of activity (the pulse) that produces a phasic increase in muscle tension to overcome the viscous drag of the orbital tissues and move the eye at a high velocity. The brief pulse must be followed by lower-frequency but sustained neural activity (the step) to sustain the change in muscle tension required to overcome the elastic restoring forces of the orbital tissue and hold the eye in the new position. This temporal pattern of activity observed when recording from motoneurons is quite different from that observed in the superior colliculus.

The *spatial-to-temporal transform problem* relates to the question of how the anatomical or spatial code of saccade direction and amplitude found in the superior colliculus is transformed into the temporal pattern of activity required by motoneurons for the generation of saccades. Despite the recognized importance of the spatial-to-temporal transform problem and the fact that much experimental attention has been devoted to it (Box 2), how this process is accomplished is unresolved. We consider two possible reasons for the intractability of this problem. First, the spatial-to-temporal question may be ill-posed; recent evidence challenges the notion of a purely topographic motor representation in the SC. Second, the design of experiments uncovering details about the signal transformation has been impeded by uncertainty about exactly which signal transformations occur.

Challenges to Traditional Views of Collicular Function

The statement of the spatial-to-temporal transform problem is based upon two major conclusions reached in early influential papers (14, 15) about the role of the SC in the control of saccadic eye movements: 1) it is *only the site of collicular activity,* not its level or time course, that determines the direction and amplitude of a saccade; and 2) the SC plays no role in the control of the velocity or duration of a saccade. However, studies in animals other than primates and recent primate investigations challenge these long-standing concepts. Profound and systematic effects of varying the microstimulation parameters on elicited orienting movements have been observed in various non-primate species, including the cat-eye/head movements (16-18), barn owl-head movements (19), and rat head/body movements (20, 21). Moreover, incidental observations in recent primate studies are consistent with the findings reported for non-primate species and are not consistent with the hypothesis that the SC plays no role in the control of saccade velocity or duration. Schiller and Sandell (22) and Sparks and Mays (23) varied the stimulation current in the monkey superior colliculus and observed changes in the amplitude of the elicited eye movement, and van Opstal et al. (24) reported changes in velocity. Furthermore, collicular injections of lidocaine (11, 25) or muscimol (26) resulted in saccades of significantly slower velocities and prolonged durations.

It appears that other factors, not solely the site of collicular activity, can have an impact on the properties of the ensuing orienting movement. To resolve the conflict between earlier primate studies and the different results obtained from primate/non-primate species, Stanford et al. (27) repeated the early microstimulation studies of the primate superior colliculus but systematically varied, over a wider range than used in the early experiments, the duration and frequency of the stimulation trains. In contrast to the reports of the early studies, they observed dramatic effects of variations in the duration and frequency of the stimulation train (Fig. 4). Saccadic peak velocity could be slowed, duration shortened, and amplitude significantly diminished (Fig. 4A) if the stimulation train durations were too brief to produce the site-specific maximal amplitude. A comparison between low- (100-200 pulses per second) and high-frequency (500-800 pulses per second) stimulus trains showed that saccadic peak velocity was slower for the low- relative to the high-frequency stimulus trains (Fig. 4B).

Stanford and co-workers not only confirmed the importance of the site of collicular stimulation but further extended our understanding of the functional properties

Box 2: Factors To Consider Regarding the Spatial-to-Temporal Transformation Problem

Traditionally, it has long been held that the location of the cell in the collicular map codes the direction and amplitude of the *change* in eye position in the orbit (14, 15). The cells of the superior colliculus exhibit ragged prelude activity punctuated with a high-frequency burst beginning about 20 ms prior to saccade onset (see Fig. 3A), but unlike the excitatory burst neurons (EBNs), the temporal profile of the burst of individual SC cells is not related, in any obvious way, to the parameters of the saccadic movement. The collicular activity is conveyed to the pons, where it directly or indirectly influences the EBNs.

The temporal nature of the EBN output signals, from the brainstem saccade generators in the paramedian pontine reticular formation (PPRF; horizontal component) and mesencephalic reticular formation (MRF; vertical component) downstream of the superior colliculus, affects oculomotor behavior in three important ways (35, 36). First, the frequency of the explosive burst of cell activity is correlated with the peak velocity of the saccadic eye movement. Second, the number of spikes or the integral of the burst is correlated with the amplitude of the saccade (37-39). Third, the duration of the EBN burst is correlated with the duration of the saccade. The temporal features of the EBN burst, but not the activity of individual collicular cells, code the major properties of a saccade.

The rate of firing activity of tonic neurons (TN), another type of cell found in the PPRF, is correlated with eye position and may represent the output of the neural integrator (see below). The pulse and step activities of the EBNs and TNs are conveyed to the motoneurons (MN) that innervate the extraocular muscles to abruptly move the eye (the pulse) and maintain its position (the step) once the eyes stop moving (Fig. 3A).

Robinson (28) developed a position model of saccadic control (Fig. 3B) that made use of the physiological properties of the EBNs and TNs to reproduce the pulse/step profile of MN activity. Since then, many additions and modifications have been made, e.g., a displacement model (Fig. 3B) reported by Jurgens et al. (29). Models such as these are able to simulate eye movements with the properties of naturally-occurring saccades, and many experiments have been designed to test their assumptions and predictions. However, the mechanisms used by the oculomotor system to translate the spatial code of saccade direction and amplitude, found in the superior colliculus, into the temporal pattern of activity required by motoneurons remain unknown.

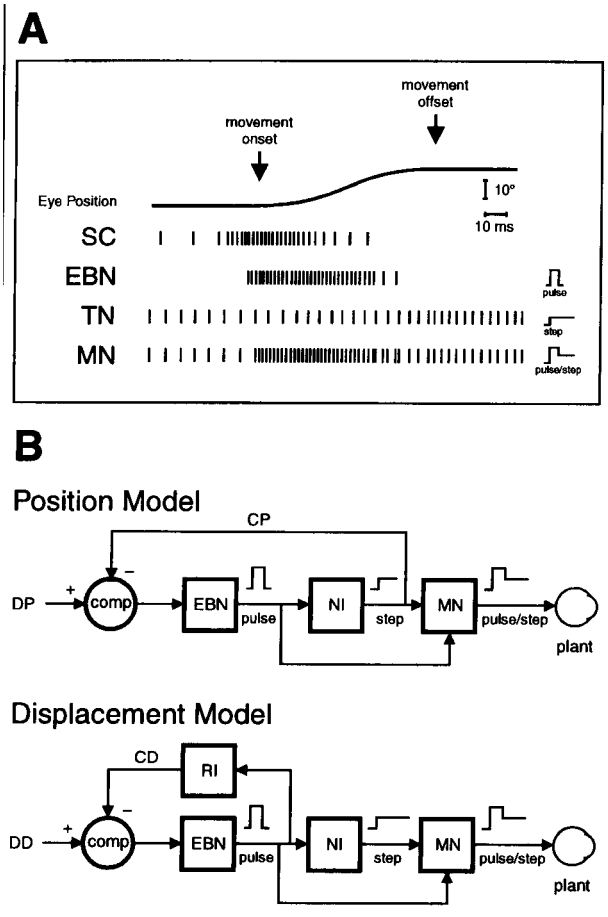


Fig. 3. A: A schematic representation of the temporal pattern of activity for cells involved in the generation of saccadic eye movements. Each *short vertical line* represents an action potential. A high-frequency burst of activity is exhibited by collicular cells, excitatory burst neurons (EBNs), and motoneurons (MNs). However, it is the activity of the EBNs that codes many of the properties of saccadic eye movements, not the collicular cells (see text). As the eye position in the orbit changes, the rate of tonic activity changes *(TN* and *MN)* to hold the eye steady at its new position (see below). SC, superior colliculus; *EBN,* excitatory burst neuron; *TN,* tonic neuron; *MN,* motoneuron. After Fuchs et al. (36). B: Simplified schematic representations of the position and displacement models of saccadic control. In the position model, a signal of desired eye position *(DP)* is compared *(comp,* comparator) with the signal of current eye position *(CP)* received from the neural integrator *(NJ)* to derive a motor error signal that drives the excitatory burst neurons *(EBN).* The DP signal is formed by combining the desired displacement (the desired change in eye position) command observed in the SC and frontal eye fields with a signal of the current positions of the eyes in the orbits. The displacement model avoids the need to construct a DP command by replacing the DP command with desired displacement (DD), and the current displacement *(CD)* input to the comparator comes from a "leaky," resettable displacement integrator (RI). After each saccade, the RI must reset to zero before the next intended displacement command arrives, or the resultant saccade would not have the desired amplitude. The position model, however, contains elements that are prepared for the next movement immediately following saccade offset. Present in both models is the *pulse* of activity originating from the explosive burst of the EBN population. The integration of this pulse *(NQ* yields the tonic or *step* activity that maintains the eye *(plant)* in a particular orbital position. The *pulse/step* activity, conveyed to the motoneurons that innervate the extraocular muscles, initiates an abrupt displacement of the eye to a new position within the orbit and then holds it there.

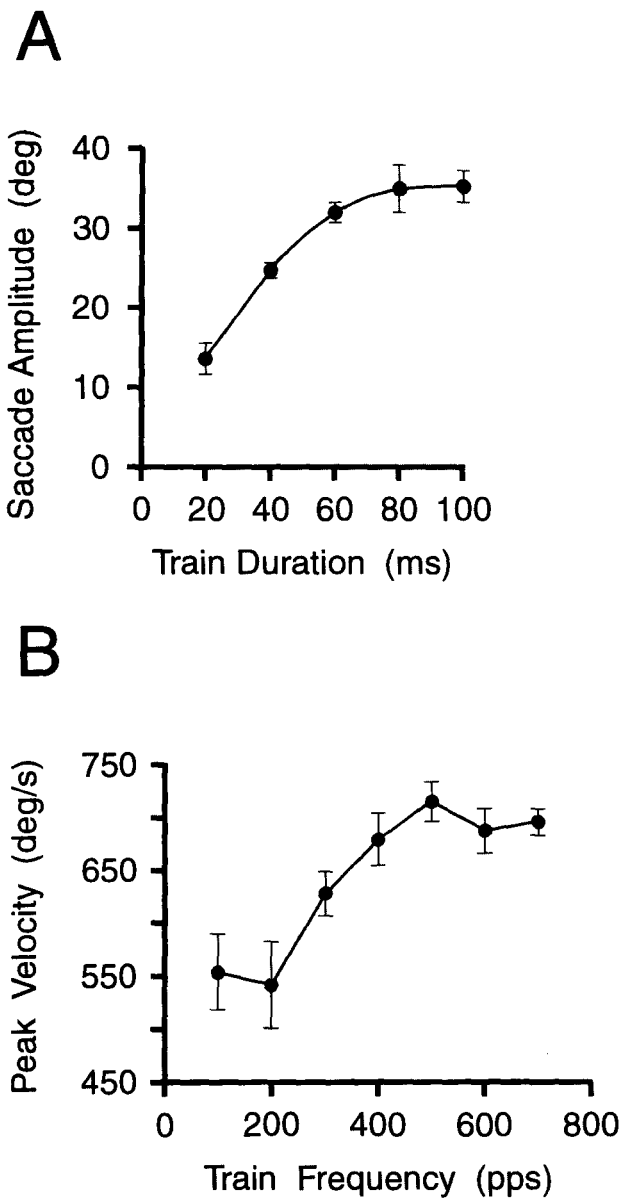


Fig. 4. Effect of varying stimulus train duration and frequency on stimulation-induced saccadic eye movements. A: Horizontal component amplitudes for saccades evoked by various train durations applied to a single collicular site. Stimulation parameters: frequency-500 pulses per second (pps); current-50 μA. *B:* Peak velocity for saccades evoked using various train frequencies (data from a different stimulation site). Plotted (A) and redrawn *(B)* from Stanford et al. (27). In both A and *B,* mean ± so points are shown.

of the primate superior colliculus by demonstrating that the amplitude, direction, duration, and velocity of an evoked eye movement can be modulated by varying the duration and/or frequency of the stimulation train, and hence, the collicular activity. Besides reconciling the apparent inconsistencies between non-primate and primate studies discussed earlier, this study has revealed that the collicular signals intrinsically contain information regarding saccade velocity and duration, in addition to well-established characteristics that code amplitude and direction.

Required Transformations of Collicular Signals

Crucial to the understanding of the transformation of collicular command signals into those required by motoneuron pools is a knowledge of the inputs required by the downstream circuits that generate the pulse and step of innervation. Most current models of the pulse/step generator circuits fall into two categories: position models or displacement models (Box 2). Position models, such as Robinson's (28), which inspired much of the research into saccadic eye movement control, assume that the reference signal for the feedback control circuit generating the pulse and step command is the desired position of the eye in the orbit. Displacement models, usually modifications of Robinson's model, assume that the reference signal for the pulse-step feedback circuitry is the desired displacement of the eye, i.e., a signal of the desired change in eye position rather than a signal of the absolute position of the eye in the orbit.

The model of Jurgens et al. (29) is one such alternative to the Robinson saccadic control model. It employs a desired eye displacement as the input signal and adds a resettable displacement integrator (RI) providing the feedback to the comparator. In this model, the displacement integrator "charges" to a value representing current eye displacement throughout the trajectory of the saccade, and the value must decay to zero before the next desired displacement command arrives at the comparator. Failing to rezero, the burst generator will not produce a saccade of the desired amplitude because a residual value on the RI will be subtracted from the desired displacement command and result in an other-than-intended initial motor error signal sent to the EBNs. The postsaccadic rezeroing may be the result of an active and immediate process, or the integrator may discharge passively over some measurable time course. As long as the displacement integrator is reset to zero during the intersaccadic interval, the amplitude of the saccade should match the desired displacement.

Experimental data provide no compelling reasons to favor position or displacement models. It is not known if collicular signals are translated into signals of desired displacement or signals of desired orbital position. But, these two models yield interesting and dramatically different predictions (30), given the assumption that the displacement integrator discharges gradually after having been charged during the execution of the previous saccade. Suppose that, in the case of the Jurgens et al. displacement model, a new displacement command was artificially introduced by electrically stimulating the superior colliculus at the time of completion of a naturally-occurring saccade, before the displacement integrator has had time to decay its signal to zero. The prediction would be that the stimulation-induced movement would

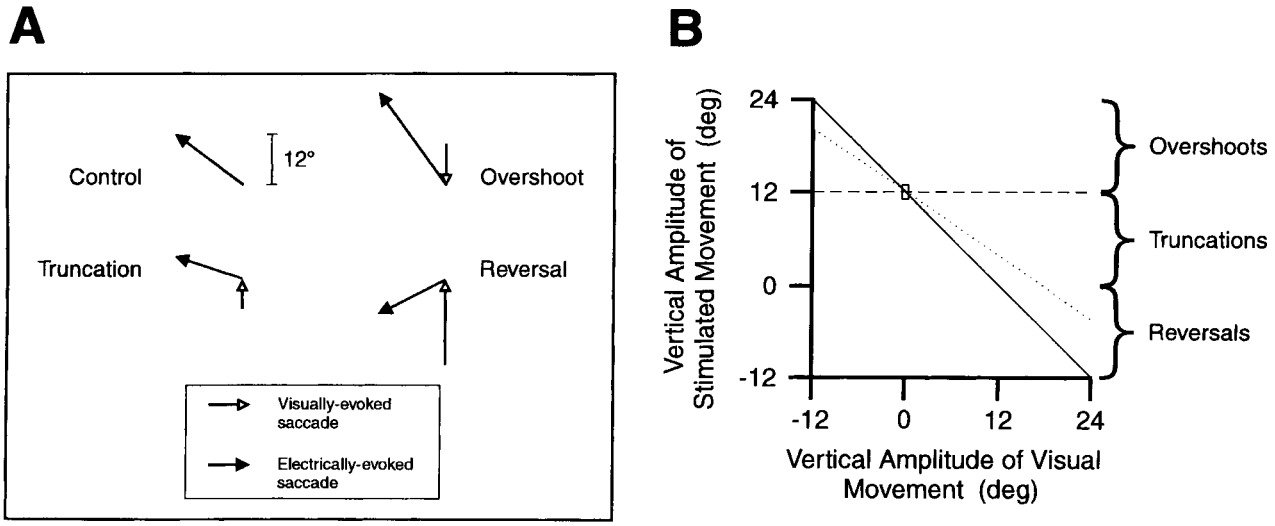


Fig. 5. A schematic representation of the predictions obtained from the simplified position and displacement models of saccadic control. A: Predictions regarding saccade amplitude and direction given examples of preceding visually-guided saccades *(open arrow)*. The EBN activity "charges" the putative RI throughout the duration of the saccade. The instantaneous and coincident inputs to the comparator from the "discharging" RI and the desired displacement command from the SC are hypothesized to affect the amplitude and direction of the ensuing saccade, resulting in a saccadic displacement *(solid arrow)* other than that requested *(control)*. If a 6° upward, visually-guided saccade were followed by a stimulation at an SC site specifying a movement with a 12° upward component (the control), then the burst generator is predicted to produce a saccade with only a 6° upward component (a truncation). The RI would be signaling the comparator that the eyes have already moved 6° up, which would result in a difference of 6° remaining to be moved. Overshooting saccades result from a preceding visual saccade that moved in the direction opposite to the control. Reversal saccades would result when the preceding visual saccade was larger and in the same direction as the control movement. B: An idealized representation of the predictions, from each of the models, in graphic form. Ideally, the predicted displacement model data should fall along the line of negative unity slope *(solid line)* if no discharge of the RI occurred prior to the onset of the stimulated saccade. However, the amplitude function of the data may more realistically reflect a slope less than negative unity *(dotted line)* because of some discharge of the RI. The position model predicts that visually-guided saccades will not influence the amplitude of stimulated saccades, so the data would fall along a line of zero slope *(long-dashed line)*. After Nichols and Sparks (30).

be modified by an amount dependent upon the amplitude of the visually-guided movement and the extent of the decay of the previously charged displacement integrator (Fig. 5A and B). In the Robinson model, the elements are fully prepared for the next movement immediately after saccade completion, and the electrically-elicited saccade trajectory would remain unaltered, independent of the time it is elicited relative to the offset of the preceding saccadic eye movement.

The above predictions were tested, and Nichols and Sparks (30) recently reported the results. At the outset, stimulation of the superior colliculus at the beginning and end of a block of trials would serve to provide control values for the stimulated saccade and to define the desired displacement command emerging from the superior colliculus and reaching the burst generator. Visually-guided saccades were initiated from various initial orbital positions along either the horizontal or vertical meridians within each block, so that the effects on only one component of the usually oblique stimulation-induced saccade were examined at a time. These visually-guided saccades were always directed to a fixed central location, thereby minimizing orbital effects on the stimulated eye movement. Once the visual saccade was within ± 2° of the target location, an electrically-stimulated saccade was initiated to probe the state of the displacement integrator a short time after the completion of the preceding saccade.

Illustrated in Figure 5B, a plot of the predicted component amplitudes of the stimulated movements would fall along a unity line of negative slope if the value of the charged displacement integrator had no chance to decay. If some decay had occurred, a slope slightly less than -1 would be observed. In other blocks of trials, the stimulated saccade could be initiated at varied times after the completion of the preceding saccade to uncover the time course of the decay of the displacement integrator. If, instead, the burst generator functions as Robinson modeled it, then visually-guided preceding saccades will not influence the amplitude of the electrically-stimulated saccade. The data in this case would fall along a line of zero slope positioned to match the component amplitude of the control saccade.

The plots of representative samples of the results in Figure 6A dramatically illustrate that the stimulated saccadic movement is dependent upon the metrics of the preceding visually-guided saccade. Speculatively, the metrics of the stimulated saccade may be interpreted to

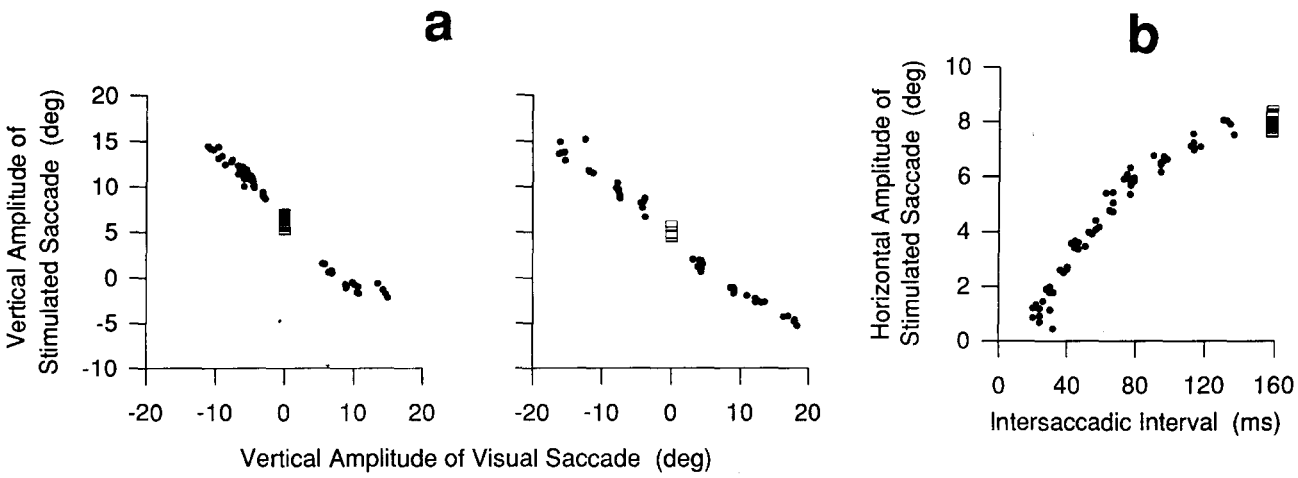


Fig. 6. Electrical stimulation of a single collicular site, using fixed parameters shortly after visually-evoked saccades, results in movements with a variety of amplitudes and directions. A: Plots of the amplitude of the stimulation-evoked saccade against the amplitude of the preceding visual movement show a linear relationship over much of the function. *Filled circles* represent the data of stimulated saccade amplitude following a visually-guided saccade. *Open squares* represent the control saccade data, evoked by electrical stimulation without a preceding visual saccade. The data function in the left panel shows that there is a transition region, encompassing the predicted reversal data points, which exhibits a shallower slope than that depicted by the truncation and overshoot data. There seems to be greater variability in this portion of the relationship, which is not evident in the right panel data set. The left panel shows the results from a site different from that of the right panel. 8: As the intersaccadic interval increases, the amplitude of the stimulation-evoked saccades *(filled circles)* increases to approach that of the control saccades not preceded by a horizontal visually-guided movement *(open squares;* arbitrarily plotted at ISI of 160 ms, which is beyond 3 time constants of this exponential function). Only the amplitude of the vertical component is plotted in *a,* and the horizontal component in b.

be dependent on the state of a putative displacement integrator. The results are consistent with the predictions of the displacement model and clearly not consistent with the position model. It is reasoned that the slope is less than -1 because the resettable displacement integrator has discharged some of its signal during the latent period between stimulation onset and the onset of the burst neurons. In fact, the time constant of the exponential decay has been determined to be 45 ± 8 ms for the sample of superior colliculus sites studied (see Fig. 6B). Similar results were recently reported by Kustov and Robinson (31).

The results of this study suggest the presence of a "leaky" displacement integrator that decays exponentially during the intersaccadic interval. These findings add an important new constraint on models of the saccadic system. Any successful model must incorporate an amplitude-dependent, non-stationarity that follows the observed exponential decay.

Sensory Signals and Motor Commands: Some Challenges

Most sensory signals and motor commands are represented by the spatial and temporal patterns of neural activity in large populations of neurons. Testing predictions of population-coding hypotheses for extracting signals and/or commands from the spatial and temporal profiles of the ensemble activity are often difficult. The difficulty lies in the need for perturbations of activity within specific regions of a map, or selective activation or inactivation of specific neurons with known functional properties. We have summarized evidence supporting the vector-averaging hypothesis of population coding in the primate superior colliculus, but it is not known if other sensory and motor systems employ the collicular population-coding scheme.

This review has also considered the question of how the activity of neurons distributed within the collicular motor map is used to generate the temporal pattern of activity required by separate motoneuronal pools. Earlier efforts to solve this problem may have been based upon incorrect assumptions about the function of the SC. Indeed, the review of recent work provides compelling reasons to revise our views of the role of the primate SC in the control of saccadic eye movements. Progress has also been slowed by uncertainty about exactly which signal transformations occur. Recent experiments testing the differential predictions of models of the saccadic system seem to exclude some from future consideration. Taken together, recent findings have narrowed our attention to a more limited number of unanswered questions concerning the transformation of collicular signals into those required by the motoneurons. This should facilitate the design of experiments addressing this important problem.

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