

Conceptual issues related to the role of the superior colliculus in the control of gaze

David L Sparks

Various conceptual issues have been brought into focus by recent experiments studying the role of the superior colliculus in the control of coordinated movements of the eyes and head, the interaction of saccadic and vergence movements, and cognitive processes influencing the initiation and execution of saccades.

Addresses

Division of Neuroscience, Baylor College of Medicine, One Baylor Plaza, Houston, Texas 77030, USA;
e-mail: sparks@saccade.neusc.bcm.tmc.edu

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Abbreviations

BN	burst neuron
EMG	electromyograph
GABA	γ -aminobutyric acid
IBN	inhibitory burst neuron
OPN	omnipause neuron
SC	superior colliculus
VOR	vestibulo-ocular reflex

Introduction

In primates, photoreceptor cones are concentrated in and around the fovea, and visual acuity falls off sharply as a function of the distance of the image from the fovea. Nonetheless, we rarely notice gradations in spatial resolution when perceiving our environment. The photoreceptors are mounted on a mobile platform, and coordinated movements of the eyes and head implement high spatial frequency samples of the visual environment by shifting the line-of-sight from one part of the visual scene to another. Understanding the strategies and mechanisms by which gaze shifts are used to sample the visual environment and the perceptual processes that integrate information obtained from successive samples is as critical to a complete description of visual perception as is an understanding of events taking place at the retina.

The superior colliculus (SC), a midbrain structure, plays an important role in triggering and organizing orienting movements and is a useful model system for studying the neural computations involved in the translation of sensory signals into motor commands. The body of this review focuses on conceptual issues emerging from a subset of recent papers [1*,2–12,13*,14,15**,16*,17*,18,19*,20–25,26**–28**,29,30*,31–37,38*–40*]. Recent work in other important areas (e.g. anatomical studies of the intrinsic and extrinsic connections of collicular neurons [41–43,44*,45,46,47*,48,49*,50*,51–58,59**,60*,61**], electrophysiological and lesion studies of collicular function [62*,63**,64,65,66*,67*,68–72,73*,74,75*,76–78,79*,80*,81–85,86*,87,88],

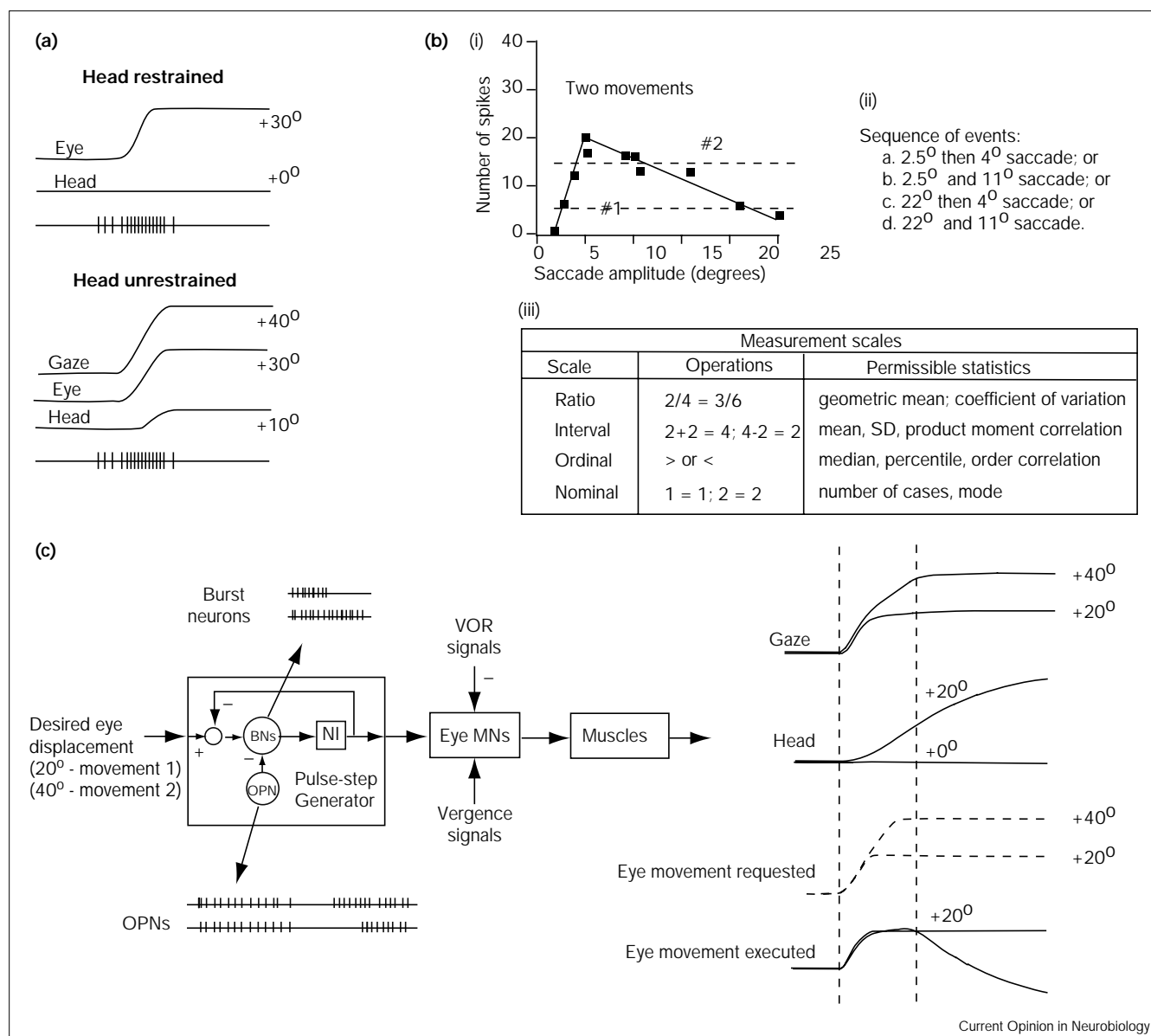
the signals carried over afferent and efferent pathways [89*,90*,91], and the development and testing of models of collicular function [92*–95*]) is listed in the bibliography. Research related to the development of the SC and the development and coordination of sensory and motor maps is periodically reviewed in the Development section of this journal, published every February.

The collicular motor map

What is represented in the collicular map? How is it represented? The SC (or optic tectum) contains a motor map for controlling orienting movements. Local electrical stimulation of the SC in a variety of animals, including primates, produces orienting responses that may involve coordinated movements of the eyes, head, and body (see [1*,2] and references therein). These stimulation experiments indicate that the SC is involved in the generation of eye, head and body movements, but they provide little information about how the movements are represented at the level of individual neurons. For example, microstimulation of rostral regions of the SC usually produces eye movements. When the head is unrestrained, microstimulation of intermediate regions usually evokes combined eye–head movements [3,4]. Microstimulation of the most caudal regions can produce movements of the eyes, head, and body. More than one interpretation of these observations is possible. Different types of motor signals may originate from different regions of the SC — for example, eye movement signals may originate from the rostral SC, whereas separate eye movement and head movement signals may originate from intermediate regions of SC. Alternatively, the activity of movement-related cells throughout the rostral–caudal extent of the colliculus could generate a signal requesting a change in gaze. Requests for small changes in gaze, originating in the rostral SC, are usually implemented by movements of the eyes, whereas requests for larger gaze shifts, originating in more caudal areas, are usually implemented by combined eye and head movements.

Parenthetically, note that the collicular motor maps currently being used in anatomical, physiological, pharmacological and computational studies [5,6] were defined using microstimulation in head-restrained subjects and are grossly distorted. Electrical stimulation of sites in the regions of the collicular motor map representing large gaze shifts drives the eye to approximately the same orbital position regardless of whether the head is restrained or unrestrained. The gaze shifts produced when the head is restrained are reduced in amplitude by approximately the amount that the head would have contributed if free to move [2,4]. Consequently, when the head is restrained, there may be a large dissociation between the ‘desired’ change in gaze specified by the

Figure 1



Complicating factors in determining which motor commands are generated by the activity of individual collicular neurons. (a) A hypothetical case in which the discharge of a cell associated with a 30° eye movement made when the head is restrained is identical to the discharge associated with a 40° gaze shift accomplished by a 10° head movement and a 30° eye movement. (b) Inadmissible statistical solutions. (i) The graph depicts a section through the movement field of a collicular cell. Number of spikes in the saccade-related burst is plotted as a function of the amplitude of the saccade for movements in the optimal direction. Note that the number of spikes (or peak frequency of the burst, or average frequency of the burst, or any other measure

that we have considered) is not linearly related to saccade amplitude; nor is it linearly related to saccade direction (not illustrated). (ii) With this plot available, if told that two saccades occurred and the cell generated 5 spikes before the first saccade and 15 spikes before the second saccade, we could conclude that one of four sequences of movements occurred: a,b,c or d. (iii) For cells with response/movement fields of this type, measures of spike activity do not meet the criteria for any useful scale of measurement of saccade amplitude and no useful statistics are permitted. (c) A schematic diagram illustrating the problem of interpreting neurophysiological recordings obtained in animals making combined eye-head gaze shifts. See text for additional details.

locus of collicular activity and the stimulation-induced movement that actually occurs.

Have chronic single-unit recording experiments answered the question of how coordinated eye-head movements are represented by neuronal activity in SC? Does one

population of neurons code for changes in eye position and another population code for changes in head position? Or do collicular neurons code for a change in gaze without specifying the relative contributions of eye and head movements? It is surprisingly difficult to determine whether the activity of a collicular neuron codes for movements of

the eyes, movements of the head, or changes in gaze. The fact that collicular neurons discharge maximally before eye movements with particular directions and amplitudes in head-restrained animals does not necessarily mean that the activity of the cells specifies a change in eye position. The activity of the cells could specify a change in gaze that is accomplished by a movement of the eyes when the head is fixed (or when the eyes are centered in the orbits), but accomplished by a combined eye and head movement if the head is free to move.

Comparing the activity of the same cell during combined eye-head movements with the activity observed during eye movements when the head is restrained can also be misleading. Figure 1a illustrates a hypothetical case in which the discharge of a cell associated with a 30° eye movement made when the head is restrained is identical to the discharge associated with a 40° gaze shift accomplished by a 10° head movement and a 30° eye movement. Therefore, the activity of the cell could specify a 30° eye movement, a 10° head movement which was not observed when the head was restrained, or a 40° gaze shift (which was not fully achieved when the head was restrained). None of these interpretations can be dismissed because, even in subjects that have been performing oculomotor tasks with the head restrained for several months, movements of the eyes are associated with vigorous neck muscle activity [7–9], indicating that commands to move the head are often generated even when head movement is restrained.

Multiple regression methods relating cell firing rate to the direction, amplitude, and speed of changes in eye, head, and gaze position cannot be used to determine whether the activity of a collicular neuron codes for changes in eye, head, or gaze position. Movements of the eyes, movements of the head, and changes in gaze are not independent, but highly correlated. Moreover, as illustrated in Figure 1b, when used as a measure of the parameters of the movements of the eyes, head, or gaze, the activity of individual collicular neurons does not meet the requirements for any useful scale of measurement. For example, their firing pattern does not meet the criteria for an interval scale: equal changes in number of spikes do not indicate that equal changes in saccade amplitude have occurred. Nor do measures of collicular activity meet the criteria for an ordinal scale of measurement. A larger (or smaller) number of spikes does not mean that a movement with a larger (or smaller) amplitude has occurred. Because measures of the activity of single collicular neurons do not meet the criteria for any useful scale of measurement, no useful statistics are permitted.

A recent study has provided evidence that motor-related activity in the SC is associated with the amplitude and direction of the gaze shift, and that it is only weakly related to eye or head movements [10]. Assuming that the level of neuronal activity is related to the relative location

of a cell within the active population, the authors generated statistics-free predictions about the patterns of neural activity expected for cells coding for changes in gaze, or eye, or head position during behavioral conditions that dissociate movements of the eyes and head. For all the cells tested, the pattern of activity observed matched the pattern expected for cells coding for a change in gaze. None of the cells studied generated the patterns of activity expected for cells specifying changes in eye or head position.

Can microstimulation experiments be used to test hypotheses about how changes in gaze, eye or head position are coded by the activity of collicular neurons? Stimulation trains that evoke combined movements of the eyes and head could activate one set of neurons generating requests to move the eyes and a second group of neurons producing requests to move the head. Alternatively, stimulation trains could activate a single functional type of cell generating requests for changes in gaze — requests that may be implemented by movements of the eyes or combined movements of the eyes and head. If combined eye and head movements occur because stimulation of a site in the collicular map activates two classes of cells, one producing an eye movement command and the other a command to move the head, then repeated stimulation of the same site using the same stimulation parameters should always produce approximately the same eye and head movements. This is not what is observed. Repeated microstimulation of a single collicular site with the same stimulation parameters produces gaze shifts of similar directions and amplitudes that are accomplished using many combinations of eye and head movements, depending on the initial positions of the eyes in their orbits (see [2]).

Whether neurons throughout the rostral-caudal extent of the SC generate a single unitary signal for the desired gaze displacement or generate eye movement commands in one region and commands for eye and head movements in other regions is an important issue that must be resolved. The design of experiments and the interpretation of the results of studies assessing the types of signals conveyed to the SC from other brain regions, the types of transformations the collicular signals must undergo, and the intrinsic organization of the SC are influenced by our views of which motor commands are found in the SC. Results of recent experiments investigating the disparity sensitivity of SC neurons [11,12,13•], studies of changes in gaze involving combined saccades and vergence movements [14,15•,16•], evidence that the SC is involved in reaching movements of the arm (see [17•] and references therein), and studies implicating the SC in avoidance behaviors (see [1] and references therein) have not been incorporated into general views of the function of the SC.

Transformation of collicular signals – a neural uncertainty problem?

Much remains to be learned about how the movement-related signals observed in the SC are transformed into

those required by the motoneuron pools innervating the extraocular and neck muscles. The physiological and morphological bases for synergistic movements of the eyes and head during orienting responses are well established (see [18,19] and references therein). For example, signals carried by reticulospinal neurons are related to both neck muscle activity and eye position, and they are distributed not only to the spinal cord but also to the abducens nucleus and other structures involved in the control of eye movements [20].

Two general types of models have been developed to account for the coordination of eye and head movements during large gaze shifts. Anatomical pathways allowing the same signals to be sent to neck and eye muscles justify the development of models (hereafter referred to as gaze comparator models) [21] in which a reference signal of desired gaze displacement serves as the input to a single gaze motor error comparator that controls both eye and head movements. A second type of model (to be referred to as separate comparator models) [22] assumes that the gaze displacement command is decomposed into separate eye and head displacement signals that use separate comparators, separate command generators, and separate feedback circuits to control the eye and head components of the gaze shift.

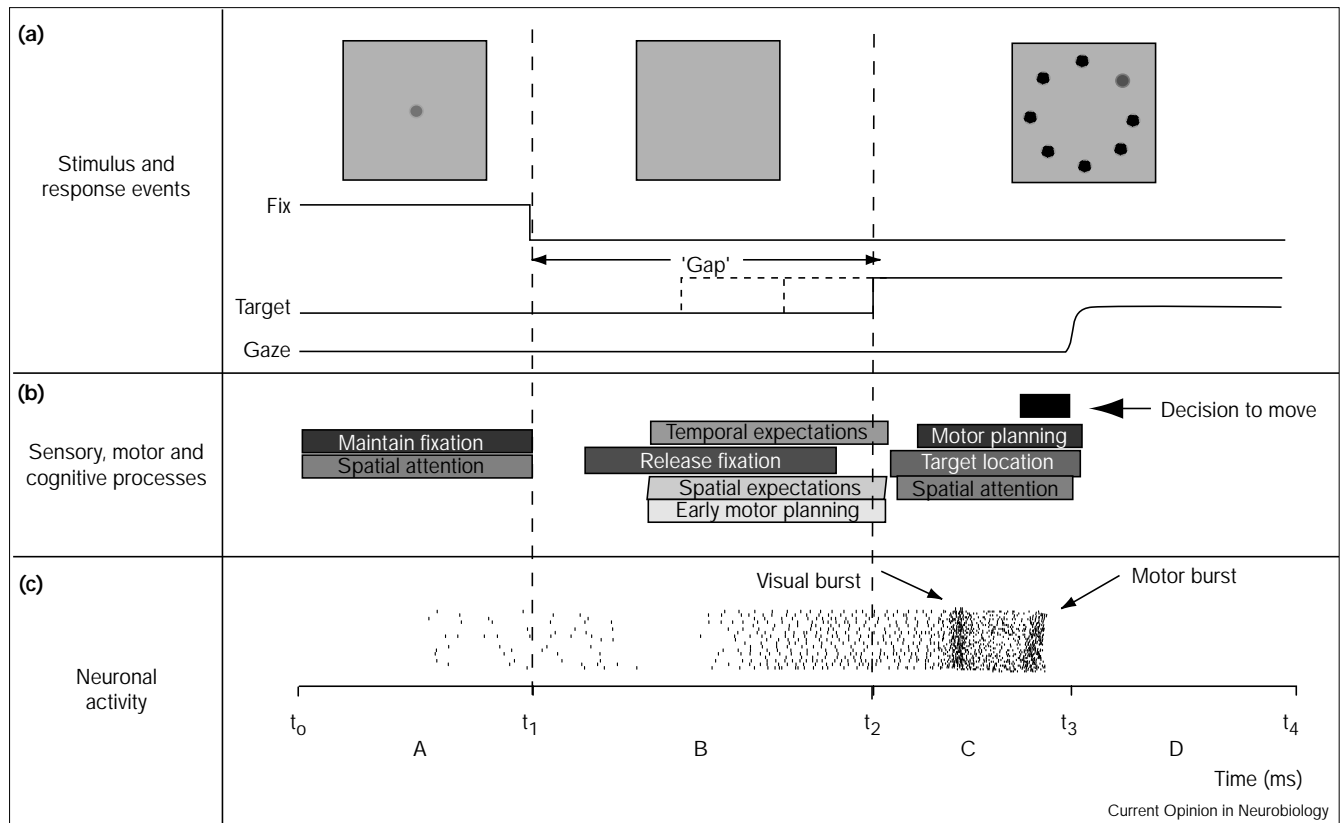
Experimental findings used to support either class of model are equivocal. For example, the finding that subjects compensate for electrical stimulation-induced perturbations to ongoing gaze shifts [23] has been cited as evidence for gaze comparator models, but models with separate eye and head comparators can also account for the findings. The findings that the activity of inhibitory burst neurons (IBNs), previously thought to be related to eye velocity, is best correlated with gaze velocity [24,25] and that the activity of pontine omnipause neurons (OPNs) in the cat is better correlated with gaze duration than the duration of the eye component of the gaze shift [26] have been interpreted as support for gaze comparator models. Similarly, the finding that the activity of OPNs in the monkey is better correlated with the duration of eye movements than the duration of gaze shifts [27] has been interpreted as support for the separate comparator model. The results of experiments recording the activity of various types of cells in the brainstem during combined eye-head gaze shifts, however, have no unambiguous interpretation for reasons related to the vestibulo-ocular reflex (VOR) and other reflexes that affect movements of the eyes.

The VOR provides an automatic mechanism for controlling the interaction between eye and head movements. Images of the visual scene are stabilized on the retina by vestibularly induced rotations of the eye that are equal and opposite to head movements. But large gaze shifts are often accomplished by movements of the head and the eyes in the same direction. Numerous studies have shown

that the gain of the VOR is reduced during gaze shifts and that the amount of the attenuation increases as the amplitude of the gaze shift increases (see [28] and references therein). Consistent with these behavioral results, Roy and Cullen [28] observed an amplitude-dependent reduction in the head-velocity signal being conveyed to the motoneurons when recording the activity of neurons in the VOR pathway during combined eye-head gaze shifts. The exact time course of the changes in VOR gain is still being studied, and proposals found in the literature range from a discrete on/off switch of VOR (where the VOR may be 'switched off' during voluntary head movements), to an exponential decrease in VOR gain beginning at the onset of the gaze shift (see [28] for references).

Early experiments relating the activity of cortical and subcortical neurons to the amplitude, direction, and speed of saccadic eye movements were performed in head-restrained animals, and, usually, saccade targets were presented in a single depth plane. These conditions minimize the contributions of the vestibular, vergence, pursuit, and optokinetic subsystems to the movements made to acquire saccade targets. However, when the head is free to move, oculomotor subsystems other than the saccadic system are active and may make important contributions to gaze shifts. For example, if the gain of the VOR is not reduced to zero during the entire time course of a combined eye-head gaze shift, then the eye movement that is executed will be different from the eye movement requested by a putative saccadic command circuit. This will happen because, downstream from the saccadic command circuit and feedback loop, the vestibular signal will modify the output of the motoneuron pools, a resource shared by the saccadic and vestibular systems. These points are illustrated in Figure 1c. The right panels plot the eye and head movements associated with two hypothetical gaze shifts of 20° and 40° that are initiated when the eyes are in the center of their orbits for the 20° gaze shift, or 20° in the direction of impending gaze shift. With these initial conditions, large differences in the head contribution to the gaze shifts will be obtained (see [2]). For the hypothetical gaze shifts illustrated, the desired eye displacement was 20° and 40°, and the head contribution was 0° and 20°. The eye contribution, determined by the difference between the desired eye displacement command and the eye movement produced by the VOR, was 20° for both gaze shifts. As illustrated, if the VOR is active, the eye movement that is executed is not the movement requested by the saccadic pulse-step generator. Note that in this hypothetical example, the number of spikes generated by burst neurons (BNs) and the duration of the pause in activity of OPNs are unrelated to the amplitude of the eye contribution to gaze. Instead, the activity of these neurons appears to be correlated with gaze amplitude even though, for the model illustrated, both BNs and OPNs are explicitly involved in generating an eye movement signal.

Figure 2



Complicating factors encountered in studying the neural correlates of cognitive factors related to the control of gaze. (a) Stimulus and response events during a 'gap' task used to study saccade initiation (see e.g. [38]). A central fixation target (Fix) appears in time interval A. The offset of the fixation target is followed by an interval (B) in which no targets are present. During interval C, one of several possible targets (gray dot amongst black dots) appears and is followed after a saccadic reaction time by a change in the direction of gaze (D). (b) The hypothetical time course of a few putative sensory, motor, and covert cognitive processes that may be associated with the stimulus and response events. (c) The activity of a hypothetical neuron in the SC recorded when a rhesus monkey was performing this task. Each tick mark represents an action potential and each row of tick marks represents a single trial. The cell displays a low rate of activity during interval A, a decrease and then an increase in activity during interval B, and two bursts of activity during interval C. The first of these bursts is tightly coupled to the onset of the visual target and probably represents

sensory events. The second burst is tightly linked to saccade onset and may represent a signal to initiate a saccade. The sustained activity observed between the visual and motor burst is difficult to interpret because it could be associated with visual processes, spatial attention, or motor planning. The changes in activity observed during interval B are especially difficult to interpret. These changes in activity occur in the interval before the visual stimulus is presented and before information about which movement will be required is available. Based upon the animal's past experience performing this task, this activity could be related to expectations about when (dependent upon the range of gap intervals) and where (dependent upon the range of target locations) the target will occur. Or it could be related to planning a movement to the expected location of the target. It has also been proposed that neural activity of this type is related to the disengagement of fixation. Also, this is an interval in which postural adjustments preparing for impending head movements could occur.

Thus, even if separate comparators for the eye and head components of gaze exist, the activity of cells in the saccadic pulse-step generator circuit may be poorly correlated with the observed movements of the eyes, and appear to be correlated with the change in gaze. This situation arises because copies of the motor command signal, not visual or proprioceptive signals of the actual movement, are used in the feedback circuit. Consequently, in the absence of independent information about the desired eye displacement signal or the status of the VOR, the patterns of spike activity generated by brainstem neurons involved in combined eye-head movements have no unequivocal interpretation, and correlations between

measures of spike activity and various parameters of eye, head and gaze movements may be misleading (see [29,30] for a discussion of similar issues).

Similar problems are encountered when interpreting results of vergence-saccade interactions [15,16]. Advances in understanding the neuronal bases of eye-head coordination and saccadic-vergence interactions will be impeded until we find a way to cope with this neural uncertainty problem — namely, the problem of not being able to determine whether or not the eye movement that was executed is the one that was requested by the subsystem under investigation.

This general problem of interpreting electrophysiological findings when more than one oculomotor subsystem (e.g. saccadic, pursuit, vergence, and/or vestibular) is active may be magnified because brainstem neurons other than the motoneurons (e.g. the pontine burst neurons and the cells that make up the neural integrator) may also be shared by oculomotor subsystems. Models will perform differently depending upon whether these interactions occur before or after feedback signals are formed.

Coping with cognition

Several cognitive processes influence the probability of occurrence, latency, accuracy and speed of saccadic eye movements (see [31,32] for reviews). Many of these processes probably alter the excitability of neurons (including those in the SC) involved in controlling saccadic movements. Indeed, variations in the discharge pattern of collicular neurons have been ascribed to a number of 'cognitive' states: such as spatial attention [33,34], motor memory [35], response selection [36], motor preparation [37,38*], motor set [39*], and target selection [40*]. As illustrated in Figure 2, during most behavioral tasks, several cognitive processes may be active simultaneously, and the activity of collicular neurons may be influenced by more than one process. Because collicular neurons may be resources shared by other processes, it does not follow that changes in the activity of collicular neurons is evidence that a particular covert process is ongoing or that the neurons being recorded are an integral part of that covert process. Indeed, at the level of the SC, isomorphic relationships between the activity of single neurons or classes of neurons and particular cognitive processes may not exist. In theory, in carefully designed experiments (such as holding other important cognitive processes constant), the activity of collicular neurons could serve as an index of the status of particular cognitive states or events. But, in practice, neither the number of covert processes affecting cellular activity nor the methods for controlling their onset, offset, intensity or duration are known. Thus, in general, it is difficult to ascribe changes in neuronal activity to a particular cognitive process, especially if the neurons reside in brain regions where the output of many simultaneously active sensorimotor and cognitive processes are likely to converge.

To date, most studies of cognitive influences on neuronal activity and saccadic performance can be described as single-factor/single-level studies. The activity of neurons is examined under conditions in which one cognitive factor of special interest to the investigators (e.g. spatial attention, response selection, or motor preparation) is thought to be invoked or not invoked. Only rarely (see [38*,39*] for exceptions) have experimenters tried to manipulate the level of the factor (e.g. the degree of spatial attention or amount of motor preparation). In many experiments, independent behavioral measures ensuring that the experimental manipulation was effective in producing the expected behavioral consequence are not obtained. Formal

operational definitions of the cognitive factors being manipulated are noticeably absent in this area of research, and the operational definition of one cognitive state (implied from the experimental procedures used) may be identical to the operational definition of a 'different' cognitive process. For example, the antecedent conditions used to invoke the covert process of spatial attention — using pre-cues to indicate a region of visual space in which an important stimulus is likely to appear or the use of blocks of trials in which the important stimulus appears in the same region of visual space — are also antecedent conditions that may invoke the process of motor preparation. Motor preparation can begin early during blocks of trials in which the same movement is required or if the location of the goal of the movement is pre-cued. The expected consequences (implied from the experimental procedures) of invoking spatial attention or motor preparation are also similar. Both cognitive states are expected to produce changes in reaction time, response accuracy, and neuronal activity. Clearly, we need non-identical operational definitions for the various cognitive states implicated in the neural control of orienting movements.

Conclusions

Although it has been known for more than 50 years that microstimulation of the SC produces coordinated movements of the eyes and head, it is surprisingly difficult, for technical reasons, to learn how these movements are represented at the level of individual collicular neurons. At this point, the limited pertinent data suggest that the activity of individual collicular neurons specifies a change in gaze. There is no unequivocal evidence that cellular activity specifies movements of the eyes or movements of the head.

Advances in understanding the neural bases of eye-head coordination and saccadic-vergence interactions will be impeded until it is possible to know whether or not the eye movements that are executed are the ones requested by the neural circuit being studied.

Current attempts to demonstrate isomorphic relationships between the activity of single collicular neurons (or classes of neurons) and particular cognitive processes may be misguided. It may be more fruitful to focus on descriptions of the behavioral and cognitive manipulations that produce reliable changes in the excitability of collicular neurons and the behavioral consequences of these changes.

Acknowledgements

Most of the concepts considered in this review have been discussed extensively during weekly journal club meetings in my laboratory. It would be difficult to know the actual source of some of the ideas, but Jamie Nichols would probably receive credit for the notion of motor equivalence classes or 'motomeres', and Ed Freedman and I have had extensive discussions about 'neural uncertainty'. Ellen Barton, Raj Gandhi, Paul Glimcher, Laurent Goffart, Jenni Groh, Rimas Kalesnykas, and Terry Stanford were all important contributors to the weekly discussions. John Maunsell made many helpful comments on an earlier version of the paper. Research in my laboratory is supported by National Institutes of Health grant EY01189-27.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Herrero L, Rodriguez F, Salas C, Torres B: **Tail and eye movements evoked by electrical microstimulation of the optic tectum in goldfish.** *Exp Brain Res* 1998, **120**:291-305.
This paper describes orienting and escape-like responses to electrical microstimulation that are dependent on stimulus parameters. The interesting discussion of the microstimulation data obtained from various animals has a neuroethological perspective.
2. Freedman EG, Stanford TR, Sparks DL: **Combined eye-head gaze shifts produced by electrical stimulation of the superior colliculus in rhesus monkeys.** *J Neurophysiol* 1996, **76**:927-952.
3. Guitton D, Crommelinck M, Roucoux A: **Stimulation of the superior colliculus in the alert cat. I. Eye movements and neck EMG activity evoked when the head is restrained.** *Exp Brain Res* 1980, **39**:63-73.
4. Roucoux A, Crommelinck M, Guitton D: **Stimulation of the superior colliculus in the alert cat. II. Eye and head movements evoked when the head is unrestrained.** *Exp Brain Res* 1980, **39**:75-85.
5. Robinson DA: **Eye movements evoked by collicular stimulation in the alert monkey.** *Vision Res* 1972, **12**:1795-1808.
6. McIlwain JT: **Effects of eye position on saccades evoked electrically from the superior colliculus of alert cats.** *J Neurophysiol* 1986, **55**:97-112.
7. Lestienne E, Vidal PP, Berthoz A: **Gaze changing behaviour in head restrained monkey.** *Exp Brain Res* 1984, **53**:349-356.
8. Roucoux A, Vidal P, Veraart C, Crommelinck M, Berthoz A: **The relation of neck muscle activity to horizontal eye position in the alert cat. I. Head fixed.** In *Physiological and Pathological Aspects of Eye Movements*. Edited by Roucoux A, Crommelinck M. The Hague: W Junk; 1982:371-378.
9. Vidal PP, Roucoux A, Berthoz A: **Horizontal eye-position related activity in neck muscles of the alert cat.** *Exp Brain Res* 1982, **46**:448-453.
10. Freedman EG, Sparks DL: **Activity of cells in the deeper layers of the superior colliculus of the rhesus monkey: evidence for a gaze displacement command.** *J Neurophysiol* 1997, **78**:1669-1690.
11. Bacon BA, Lepore F, Guillemot JP: **Striate, extrastriate and collicular processing of spatial disparity cues.** *Arch Physiol Biochem* 1998, **106**:236-244.
12. Bacon BA, Lepore F, Guillemot JP: **Binocular interactions and spatial disparity sensitivity in the superior colliculus of the Siamese cat.** *Exp Brain Res* 1999, **124**:181-192.
13. Bacon BA, Villemagne J, Bergeron A, Lepore F, Guillemot JP: **Spatial disparity coding in the superior colliculus of the cat.** *Exp Brain Res* 1998, **119**:333-344.
Recordings of neuronal activity in the superficial layers of the SC in adult paralyzed and anesthetized cats revealed four groups of cells sensitive to spatial disparities: cells with excitatory interactions; cells with inhibitory interactions; and cells showing sensitivity to crossed or uncrossed disparities. The selectivity of SC cells was coarser than cells in areas 17 and 18.
14. Chaturvedi V, Van Gisbergen JAM: **Shared target selection for combined version-vergence eye movements.** *J Neurophysiol* 1998, **80**:849-862.
15. Chaturvedi V, Van Gisbergen JAM: **Perturbation of combined saccade-vergence movements by microstimulation in monkey superior colliculus.** *J Neurophysiol* 1999, **81**:2279-2296.
Interesting interactions were observed when saccades were evoked by electrical stimulation of the SC while monkeys prepared for a visually guided saccadic-vergence movement from a far to a near target. Under these conditions, the stimulation-evoked movement had both saccadic and vergence components, whereas control stimulation-evoked movements lacked a vergence component. The pattern of interactions observed can be accounted for by the authors' hypothesis that saccades evoked by collicular stimulation do not merely lack a vergence component, but result from a command that specifically specifies a zero-vergence component. The authors speculate that cells at each SC site may be tuned for depth as well as for amplitude and direction.

16. Zhou W, King WM: **Premotor commands encode monocular eye movements.** *Nature* 1998, **393**:692-695.
Recordings obtained during eye movements that involve saccadic, pursuit, and vergence oculomotor subsystems are used to argue that premotor neurons in the pons generate monocular commands for either right or left eye saccades. The authors' interpretation of the data does not consider the possibility that, because of downstream convergence of signals from different subsystems, the movement that is executed may differ from the command that was issued.
17. Stuphorn V, Hoffmann K-P, Miller LE: **Correlation of primate superior colliculus and reticular formation discharge with proximal limb muscle activity.** *J Neurophysiol* 1999, **81**:1978-1982.
This laboratory has previously described neurons in the SC that discharge in relation to limb movement. Results of long-time-span cross-correlation functions between single-cell activity and signals obtained from chronically implanted EMG electrodes are described in this paper. The discharge of many cells in the SC and the underlying reticular formation is significantly correlated with the temporal pattern of muscle activity. On average, cellular activity preceded correlated muscle activity by 52 ms. Neural discharge was most often correlated with the EMG activity of shoulder muscles and less frequently with EMG activity of axial and distal arm muscles.
18. Sparks DL: **The neural control of orienting eye and head movements.** In *Motor Control: Concepts and Issues*. Edited by Humphrey DR, Freund H-J. Chichester: John Wiley & Sons Ltd; 1991:263-275.
19. Petit J, Klam F, Grantyn A, Berthoz A: **Saccades and multisaccadic gaze shifts are gated by different pontine omnipause neurons in head-fixed cats.** *Exp Brain Res* 1999, **125**:287-301.
Recordings from pontine omnipause neurons (OPNs) during self-initiated saccades and during tracking of a moving target in head-restrained cats revealed two subgroups of omnipause cells: saccade (S-OPNs) and complex (C-OPNs) OPNs. S-OPNs are those that have been described previously by other researchers and are characterized by a number of properties, including a high correlation between pause duration and saccade duration. During tracking, S-OPNs cease firing during saccades, but resume their discharge during perisaccadic 'drifts'. The pause duration of C-OPNs is not correlated with the duration of saccades, and, during tracking, activity is interrupted for the total duration of gaze shifts, including both saccades and perisaccadic 'drifts'. Recordings from C-OPNs during coordinated movements of eyes and head will be of special interest because the authors predict that when the head is unrestrained, these cells will pause for the total duration of gaze shifts.
20. Grantyn A, Berthoz A: **Burst activity of identified tectoreticulo-spinal neurons in the alert cat.** *Exp Brain Res* 1985, **57**:417-421.
21. Galiana HL, Guitton D: **Central organization and modeling of eye-head coordination during orienting gaze shifts.** *Ann NY Acad Sci* 1992, **656**:452-470.
22. Phillips JO, Ling L, Fuchs AF, Siebold C, Plorde JJ: **Rapid horizontal gaze movement in the monkey.** *J Neurophysiol* 1995, **73**:1632-1652.
23. Pelisson D, Guitton D, Goffart L: **On-line compensation of gaze shifts perturbed by micro-stimulation of the superior colliculus in the head-free cat.** *Exp Brain Res* 1995, **106**:196-204.
24. Cullen KE, Guitton D, Rey CG, Jiang W: **Gaze-related activity of putative inhibitory burst neurons in the head-free cat.** *J Neurophysiol* 1993, **70**:2678-2683.
25. Cullen KE, Guitton D: **Analysis of primate IBN spike trains using system identification techniques. II. Relationship to gaze, eye, and head movement dynamics during head-free gaze shifts.** *J Neurophysiol* 1997, **78**:3283-3306.
26. Pare M, Guitton D: **Brain stem omnipause neurons and the control of combined eye-head gaze saccades in the alert cat.** *J Neurophysiol* 1998, **79**:3060-3076.
This important study reports a number of interesting observations concerning the relationship between the activity of omnipause neurons (OPNs) during eye saccades and combined eye-head gaze shifts. The authors recorded activity in OPNs and found that these neurons cease to be active for the duration of all gaze shifts studied: active combined eye-head movements; passive movements evoked by whole-body rotations or by head rotation about a stationary body; and movements evoked by electrical stimulation of the caudal superior colliculus. These results are interpreted as supporting the hypothesis that OPNs participate in gaze control. The authors dismiss the arguments made in the text (about a mismatch between the movement command and the movement that is executed) and Figure 1c of this review by stating that "there is no supporting evidence for the vestibuloocular reflex being active during large gaze shifts"; a statement that is no longer accurate [28]. The authors found that brief trains of electrical stimulation delivered to the OPNs during a gaze shift produced perturbations in gaze that affected

both eye and head components. This was interpreted as an effect mediated through brainstem burst neurons and, therefore, as evidence that the brainstem burst neurons are involved in both eye and head movements. However, OPN stimulation also causes a cessation of activity of burst neurons in the SC [96]. Thus, there are alternative routes by which OPN stimulation can affect head motion. The alternative route allows other interpretations of this perturbation effect.

27. Phillips JO, Ling L, Fuchs AF: **Action of the brain stem saccade generator during horizontal gaze shifts. I. Discharge patterns of omnidirectional pause neurons.** *J Neurophysiol* 1999, **81**:1284-1295.

This paper describes recordings from OPNs in the rhesus monkey during combined eye-head gaze shifts. Pause duration was highly correlated with the duration of either eye or gaze movements but poorly correlated with the duration of head movements. The end of the pause could be better correlated with the end of the eye contribution to gaze (usually demarcated by an eye counter-rotation associated with the VOR) than with the end of the gaze movement. In cases where eye counter-rotation was delayed, pause offset was also delayed. These and other findings are used to argue that OPN neurons control only the portion of the gaze movement commanded by the eye burst generator. It should be noted that the correlation between pause duration and gaze duration would have been as high as the correlation with eye duration if a distinction had been made between fast and slow components of the gaze shift. The authors' definition of gaze duration included a slow component that may not be attributable to the output of the putative gaze burst generator. This slow component may not be part of the active gaze shift and may occur because, after the gaze shift is completed, the head continues to move and the gain of the VOR is less than 1.

28. Roy JE, Cullen KE: **A neural correlate for vestibulo-ocular reflex suppression during voluntary eye-head gaze shifts.** *Nat Neurosci* 1998, **1**:404-410.

This paper describes a technically difficult experiment recording the activity of neurons involved in mediating the vestibulo-ocular reflex (VOR) while animals were generating large combined eye-head gaze shifts. The authors report that the head-velocity signal carried by VOR pathways is reduced during gaze shifts in an amplitude-dependent manner, as suggested by earlier behavioral studies in monkeys and humans.

29. Stanford TR, Sparks DL: **Systematic errors for saccades to remembered targets: evidence for a dissociation between saccade metrics and activity in the superior colliculus.** *Vision Res* 1994, **34**:93-106.
30. Frens MA, Suzuki Y, Scherberger H, Hepp K, Henn V: **The collicular code of saccade direction depends on the roll orientation of the head relative to gravity.** *Exp Brain Res* 1998, **120**:283-290.
- Single-unit recordings and electrical microstimulation were used to study the influence of static head tilt on the oculomotor output of the superior colliculus (SC). Limited conclusions can be reached on the basis of the exceedingly noisy recording data, but large effects on the direction of electrically evoked saccades were observed. The conclusion that the collicular oculocentric map rotates relative to the head during ocular counter rolls seems inconsistent with the authors' argument that modifications in stimulation-evoked trajectories result from processes that are present downstream of or parallel to the output of the SC. An alternative interpretation is that the collicular map is fixed but the movement that is executed is not the movement that was requested because of visual- and otolith-mediated alterations in the activity of neural elements shared by the vestibular and saccadic systems.
31. Kowler E: **The role of visual and cognitive processes in the control of eye movement.** In *Reviews of Oculomotor Research*, vol 4. *Eye Movements and Their Role in Visual and Cognitive Processes*. Edited by Kowler E. Amsterdam: Elsevier; 1990:1-70.
32. Schall JD, Thompson KG: **Neural selection and control of visually guided eye movements.** *Annu Rev Neurosci* 1999, **22**:241-259.
33. Goldberg ME, Wurtz RH: **Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses.** *J Neurophysiol* 1972, **35**:560-574.
34. Kustov AA, Robinson DL: **Shared neural control of attentional shifts and eye movements.** *Nature* 1996, **384**:74-77.
35. Mays LE, Sparks DL: **Dissociation of visual and saccade-related responses in superior colliculus.** *J Neurophysiol* 1980, **43**:207-232.
36. Glimcher P, Sparks DL: **Movement selection in advance of action: saccade-related bursters of the superior colliculus.** *Nature* 1992, **355**:542-545.
37. Dorris MC, Pare M, Munoz DP: **Neuronal activity in monkey superior colliculus related to the initiation of saccadic eye movements.** *J Neurosci* 1997, **17**:8566-8579.

38. Dorris MC, Munoz DP: **Saccadic probability influences motor preparation signals and time to saccadic initiation.** *J Neurosci* 1998, **18**:7015-7026.

In this experiment, the probability of the required saccade being directed into the response field of a neuron was varied between blocks of trials. The level of activity increased as the probability of the required saccade being in the response field of the cell increased. As neuronal activity increased, saccadic reaction time decreased. This paper is noteworthy because of the authors' effort to define a cognitive process (motor preparation) and as a demonstration of the complexity of this task. Because the changes in neuronal activity met three operational criteria, they were attributed to the advanced preparation of motor programs. Logically, this attribution is not permitted. Meeting the criteria, necessary for activity to be attributed to motor preparation, is not sufficient to ascribe neural activity to motor preparation. The criteria are not exclusive; other cognitive processes could also meet these criteria. See [39*] for a different interpretation of similar findings.

39. Basso MA, Wurtz RH: **Modulation of neuronal activity in superior colliculus by changes in target probability.** *J Neurosci* 1998, **18**:7519-7534.

In this experiment, the number of possible saccade targets was systematically varied while recording the activity of SC neurons. The activity of one class of cells was systematically related to the number of possible saccade targets in two different tasks, one a condition in which the number of saccade targets was varied while keeping the visual display constant (see authors description of experimental methods). These variations in activity level were correlated with saccadic latency. The authors suggest that this predictive activity is involved in establishing a motor set, a loosely defined behavioral state related to a subject's 'preparedness' to make a particular movement. Attention, target and response selection, and movement preparation are all subsumed under this broader term. See [38*] for a different interpretation of similar findings.

40. Horwitz GD, Newsome WT: **Separate signals for target selection and movement specification in the superior colliculus.** *Science* 1999, **284**:1158-1161.

This paper describes an investigation of the role of SC neurons in target selection. Cells generating a 'prelude' of activity before saccade onset were examined while monkeys performed a task that involved selection of one of two possible saccade targets contingent upon the direction of motion of dots appearing on a visual display. On the basis of different constellations of functional properties, the authors hypothesize that the activity of one group of neurons may be involved in decision formation and target selection, whereas the activity of a second group of cells is related to saccade execution.

41. Beck PD, Kaas JH: **Thalamic connections of the dorsomedial visual area in primates.** *J Comp Neurol* 1998, **396**:381-398.
42. Farid Ahmed AK, Dong K, Hanna GF, Yamadori T: **Retrograde double-labeling study of retinal ganglion cells from the ipsilateral vLGN and SC in the albino rat.** *Neurosci Lett* 1998, **244**:47-51.
43. Ichinohe N, Shoumura K: **A di-synaptic projection from the superior colliculus to the head of the caudate nucleus via the centromedian-parafascicular complex in the cat: an anterograde and retrograde labeling study.** *Neurosci Res* 1998, **32**:295-303.
44. Isa T, Endo T, Saito Y: **The visuo-motor pathway in the local circuit of the rat superior colliculus.** *J Neurosci* 1998, **18**:8496-8504.
- This whole-cell patch-clamp recording study in slice preparations obtained from young rats in response to stimulation of the optic tract or superficial gray layer provides important information about intrinsic pathways in the SC. The results also provide evidence for a glutamatergic excitatory pathway from the optic tract to the intermediate layers via superficial gray and optic layers - pathways that appear to be under strong suppression by the GABAergic system.
45. Kolmac CI, Power BD, Mitrofanis J: **Patterns of connections between zona incerta and brainstem in rats.** *J Comp Neurol* 1998, **396**:544-555.
46. Kolmac CI, Mitrofanis J: **Patterns of brainstem projection to the thalamic reticular nucleus.** *J Comp Neurol* 1998, **396**:531-543.
47. Meredith MA, Ramoa AS: **Intrinsic circuitry of the superior colliculus: pharmacophysiological identification of horizontally oriented inhibitory interneurons.** *J Neurophysiol* 1998, **79**:1597-1602.

This is a study of the intrinsic circuitry of the SC. Parasagittal slices from young adult ferrets were used to examine the responses of intermediate/deep layer neurons to electrical stimulation applied rostral or caudal to the recording site. Many neurons displayed a prolonged period of poststimulus suppression of spontaneous activity following either rostral or caudal electrical stimulation. Suppressing responses were attributed to a stimulation-evoked excitatory synapse on an inhibitory interneuron because application of excitatory neurotransmitter antagonists or GABA antagonists both decreased or eliminated the response.

48. Morin LP, Blanchard JH: **Interconnections among nuclei of the subcortical visual shell: the intergeniculate leaflet is a major constituent of the hamster subcortical visual system.** *J Comp Neurol* 1998, **396**:288-309.
49. Moschovakis AK, Kitama T, Dalezios Y, Petit J, Brandt AM, Grantyn AA: **An anatomical substrate for the spatiotemporal transformation.** *J Neurosci* 1998, **18**:10219-10229.
This anatomical study addresses the oculomotor 'spatiotemporal transformation' problem – that is, the question of how information encoded anatomically in the SC is transformed into the temporal pattern of motoneuron activity required for accurate saccades. The experiments revealed a significant positive correlation between the number of boutons of collicular neurons deployed in the paramedian pontine reticular formation and the amplitude of the horizontal component of saccades evoked by stimulation at the site where anatomical tracers were injected.
50. Munoz DP, Istvan PJ: **Lateral inhibitory interactions in the intermediate layers of the monkey superior colliculus.** *J Neurophysiol* 1998, **79**:1193-1209.
Extracellular recordings and collicular microstimulation were used to examine local network properties of cells in the intermediate layers of the monkey SC. Results are indicative of a local network of inhibitory interneurons permitting interactions between all regions of the ipsilateral and contralateral SC.
51. Olivier E, Porter JD, May PJ: **Comparison of the distribution and somatodendritic morphology of tectotectal neurons in the cat and monkey.** *Vis Neurosci* 1998, **15**:903-922.
52. Rivera N, Lugo N: **Four retinal ganglion cell types that project to the superior colliculus in the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*).** *J Comp Neurol* 1998, **396**:105-120.
53. Shipp S, Blanton M, Zeki S: **A visuo-somatomotor pathway through superior parietal cortex in the macaque monkey: cortical connections of areas V6 and V6A.** *Eur J Neurosci* 1998, **10**:3171-3193.
54. Stepniewska I, Qi HX, Kaas JH: **Do superior colliculus projection zones in the inferior pulvinar project to MT in primates?** *Eur J Neurosci* 1999, **11**:469-480.
55. Yasui Y, Ono K, Tsumori T, Yokota S, Kishi T: **Tectal projections to the parvicellular reticular formation and the upper cervical spinal cord in the rat, with special reference to axon collateral innervation.** *Brain Res* 1998, **804**:149-154.
56. Zhu JJ, Lo FS: **Control of recurrent inhibition of the lateral posterior-pulvinar complex by afferents from the deep layers of the superior colliculus of the rabbit.** *J Neurophysiol* 1998, **80**:1122-1131.
57. Linke R: **Differential projection patterns of superior and inferior collicular neurons onto posterior paralamina nuclei of the thalamus surrounding the medial geniculate body in the rat.** *Eur J Neurosci* 1999, **11**:187-203.
58. Linke R, De Lima AD, Schwegler H, Pape HC: **Direct synaptic connections of axons from superior colliculus with identified thalamo-amygdaloid projection neurons in the rat: possible substrates of a subcortical visual pathway to the amygdala.** *J Comp Neurol* 1999, **403**:158-170.
59. Pettit DL, Helms MC, Lee P, Augustine GJ, Hall WC: **Local excitatory circuits in the intermediate gray layer of the superior colliculus.** *J Neurophysiol* 1999, **81**:1424-1427.
This is the first application of the powerful techniques of whole-cell patch-clamp recording in slices, intracellular dye injection, and laser photolysis of 'caged' compounds to investigate the neural architecture of the superior colliculus. Uncaging glutamate 10–75 μm from the soma of cells in the intermediate gray layer elicited long-lasting inward currents as a result of direct activation of glutamate receptors on the neurons and brief inward currents arising from activation of presynaptic cells. Synaptic responses took place in clusters lasting up to several hundred milliseconds, suggesting the presence of extensive local excitatory circuits in the intermediate layer of the SC, which may be mediated, in part, by the recurrent collaterals described in earlier anatomical studies. The results also support conclusions reached in other studies [50*] using microstimulation and extracellular recording, studies contaminated by the problem of stimulation of fibers of passage. (i.e. axons which travel through the nucleus, without making any synapses on terminals of cells in the nucleus, may also be activated.)
60. Izawa Y, Sugiuchi Y, Shinoda Y: **Neural organization from the superior colliculus to motoneurons in the horizontal oculomotor system of the cat.** *J Neurophysiol* 1999, **81**:2597-2611.
This paper describes elegant experiments using a combination of electrophysiological and anatomical methods to further delineate the anatomical route by which neuronal activity in the SC mediates its effect on the motoneuron pools involved in movements of the eyes and head. Neurons in the pons and medulla having monosynaptic connections on motoneurons were identified by transneuronal labeling after injections of wheat germ agglutinin-conjugated horseradish peroxidase into the abducens nerve. Tectoreticular axon terminals were labeled by injecting dextran-biotin into the ipsilateral or contralateral SC in the same animals. Approximately 30% of the transneuronally labeled neurons received direct contacts by tectoreticular axon terminals. The latency of intracellular responses of lateral rectus and medial rectus motoneurons to SC stimulation was consistent with the anatomically defined disynaptic pathway.
61. Saito Y, Isa T: **Electrophysiological and morphological properties of neurons in the rat superior colliculus. I. Neurons in the intermediate layer.** *J Neurophysiol* 1999, **82**:754-767.
Whole-cell patch-clamp recording and intracellular staining with biocytin in slice preparations from young and adult rats were used to characterize the anatomical connectivity and membrane properties of individual neurons in local circuits of the SC. Six subclasses of cells were described on the basis of voltage responses to depolarizing current pulses. The authors observed two different types of inward rectification in response to hyperpolarizing current pulses.
62. Aizawa H, Wurtz RH: **Reversible inactivation of monkey superior colliculus. I. Curvature of saccadic trajectory.** *J Neurophysiol* 1998, **79**:2082-2096.
This paper reports the results of an experiment designed to test predictions of a model of the saccadic system in which the spread of neural activity within the SC during a saccade serves as the neural integrator used in feedback control models of saccade generation. The trajectories of saccades and the pattern of errors observed following reversible inactivation of SC neurons with large injections of a GABA agonist (muscimol) were not those predicted by the model.
63. Anderson RW, Keller EL, Gandhi NJ, Das S: **Two-dimensional saccade-related population activity in superior colliculus in monkey.** *J Neurophysiol* 1998, **80**:798-817.
This paper describes a careful reconstruction of the two-dimensional, spatiotemporal activity of neural activity in the intermediate layers of the SC during oblique and horizontal saccades. The methods developed for estimating the spatiotemporal pattern of collicular activity may be usefully applied to the study of other topologically organized brain regions. The results do not support the hypothesis that a rostrally directed spread of activity in the SC serves as a dynamic control mechanism for saccade generation.
64. Brecht M, Singer W, Engel AK: **Correlation analysis of corticotectal interactions in the cat visual system.** *J Neurophysiol* 1998, **79**:2394-2407.
65. Buchel C, Josephs O, Rees G, Turner R, Frith CD, Friston KJ: **The functional anatomy of attention to visual motion. A functional MRI study.** *Brain* 1998, **121**:1281-1294.
66. Edelman JA, Keller EL: **Dependence on target configuration of express saccade-related activity in the primate superior colliculus.** *J Neurophysiol* 1998, **80**:1407-1426.
The authors present recordings of the activity of neurons in the SC during express saccades generated after two spatially separated targets were presented simultaneously. For most neurons, responses were 'scaled versions of the visual response to two spatially separate targets' rather than the activity that normally accompanies a saccade to a single target. These data (in combination with the results of earlier two-point microstimulation experiments [5] and studies of the interaction of visual and stimulation-evoked saccades) indicate that many different patterns of collicular activity may be involved in the generation of a movement having the same direction, amplitude, and velocity profile. This constitutes a motor equivalence class that could be called a 'motomere'. (In color vision, two physically distinct stimuli that evoke the same perceptual response are known as metemeres.)
67. Everling S, Pare M, Dorris MC, Munoz D: **Comparison of the discharge characteristics of brain stem omnipause neurons and superior colliculus fixation neurons in monkey: implications for control of fixation and saccade behavior.** *J Neurophysiol* 1998, **79**:511-528.
This paper contains an extensive comparison of the functional properties of brainstem OPNs and fixation neurons in the superior colliculus (SC). The major conclusion is that the observed differences in the discharge properties of the two types of cells "are irreconcilable with the hypothesis that the discharge pattern of OPNs reflects simply the excitatory input from SCFNs (SC fixation neurons)".
68. Everling S, Dorris MC, Munoz DP: **Reflex suppression in the anti-saccade task is dependent on prestimulus neural processes.** *J Neurophysiol* 1998, **80**:1584-1589.
69. Everling S, Dorris MC, Klein RM, Munoz DP: **Role of primate superior colliculus in preparation and execution of anti-saccades and pro-saccades.** *J Neurosci* 1999, **19**:2740-2754.

70. Frens MA, Van Opstal AJ: **Visual-auditory interactions modulate saccade-related activity in monkey superior colliculus.** *Brain Res Bull* 1998, **46**:211-224.
71. Keller EL, Edelman JA: **Use of interrupted saccade paradigm to study spatial and temporal dynamics of saccadic burst cells in superior colliculus in monkey.** *J Neurophysiol* 1994, **72**:2754-2770.
72. King AJ, Jiang ZD, Moore DR: **Auditory brainstem projections to the ferret superior colliculus: anatomical contribution to the neural coding of sound azimuth.** *J Comp Neurol* 1998, **390**:342-365.
73. Gnadt JW, Beyer J: **Eye movements in depth: what does the monkey's parietal cortex tell the superior colliculus?** *Neuroreport* 1998, **9**:233-238.
- Recordings from identified cortico-tectal neurons in primate parietal cortex provide evidence that neurons in posterior parietal cortex transmit information about the depth of a stimulus to neurons in the SC.
74. Li JL, Xiao Q, Fu YX, Wang SR: **Centrifugal innervation modulates visual activity of tectal cells in pigeons.** *Vis Neurosci* 1998, **15**:411-415.
75. Lo FS, Cork RJ, Mize RR: **Physiological properties of neurons in the optic layer of the rat's superior colliculus.** *J Neurophysiol* 1998, **80**:331-343.
- This paper provides a description of the biophysical properties of cells in the optic layer of the SC of rats based upon intracellular recordings from 74 neurons. The authors report that most optic layer neurons behave as intrinsically bursting cells. Whereas optic layer neurons receive direct retinal excitation mediated by both NMDA and non-NMDA receptors, optic tract stimulation also produces GABA_A-receptor-mediated inhibition. This inhibition curtails the excitatory responses to retinal inputs by shunting the excitatory postsynaptic current.
76. Luksch H, Cox K, Karten H: **Bottlebrush dendritic endings and large dendritic fields: motion-detecting neurons in the tectofugal pathway.** *J Comp Neurol* 1998, **396**:399-414.
77. Maissonnette S, Huston JP, Brandao M, Schwarting RK: **Behavioral asymmetries and neurochemical changes after unilateral lesions of tuberomammillary nucleus or substantia nigra.** *Exp Brain Res* 1998, **120**:273-282.
78. Miller AM, Obermeyer WH, Behan M, Benca RM: **The superior colliculus-pretectum mediates the direct effects of light on sleep.** *Proc Natl Acad Sci USA* 1998, **95**:8957-8962.
79. Moschovakis AK, Dalezios Y, Petit J, Grantyn AA: **New mechanism that accounts for position sensitivity of saccades evoked in response to stimulation of superior colliculus.** *J Neurophysiol* 1998, **80**:3373-3379.
- The paper presents data interpreted as providing support for the hypothesis that slow post-saccadic eye movements (often observed with prolonged microstimulation of the SC) result from direct or indirect activation of motoneurons via a pathway that does not involve the saccadic burst generator.
80. Niemi-Junkola UJ, Westby GW: **Spatial variation in the effects of inactivation of substantia nigra on neuronal activity in rat superior colliculus.** *Neurosci Lett* 1998, **241**:175-179.
- This paper reports the effects of intranigral GABA microinjections on cells in the rat SC. Suppression of the tonic activity of SNr resulted in either facilitation or paradoxical inhibition of SC target neurons. These different effects mapped differentially onto spatially segregated regions of the SC containing output neurons with axons travelling in the descending projections involved in approach or avoidance/defensive behaviors. The authors suggest that this organization promotes selection of one behavior and simultaneous suppression of competing motor programs.
81. Patton P, Grobstein P: **The effects of telencephalic lesions on visually mediated prey orienting behavior in the leopard frog (*Rana pipiens*). I. The effects of complete removal of one telencephalic lobe, with a comparison to the effects of unilateral tectal lobe lesions.** *Brain Behav Evol* 1998, **51**:123-143.
82. Platt B, Withington DJ: **GABA-induced long-term potentiation in the guinea-pig superior colliculus.** *Neuropharmacology* 1998, **37**:1111-1122.
83. Porro CA, Biral GP, Benassi C, Cavazzuti M, Baraldi P, Lui F, Corazza CR: **Neural circuits underlying ketamine-induced oculomotor behavior in the rat: 2-deoxyglucose studies.** *Exp Brain Res* 1999, **124**:8-16.
84. Quaia C, Aizawa H, Optican LM, Wurtz RH: **Reversible inactivation of monkey superior colliculus. II. Maps of saccadic deficits.** *J Neurophysiol* 1998, **79**:2097-2110.
85. Rumberger A, Schmidt M, Lohmann H, Hoffmann KP: **Correlation of electrophysiology, morphology, and functions in corticotectal and corticopretectal projection neurons in rat visual cortex.** *Exp Brain Res* 1998, **119**:375-390.
86. Sasaki S, Isa T, Naito K: **Effects of lesion of pontomedullary reticular formation on visually triggered vertical and oblique head orienting movements in alert cats.** *Neurosci Lett* 1999, **265**:13-16.
- This paper contains evidence supporting earlier suggestions that the horizontal and vertical components of head movements are controlled separately. The authors report that pontine lesions that impair horizontal movements also produce adaptive changes in the vertical component of oblique gaze shifts.
87. Stein BE: **Neural mechanisms for synthesizing sensory information and producing adaptive behaviors.** *Exp Brain Res* 1998, **123**:124-135.
88. Wallace MT, Meredith MA, Stein BE: **Multisensory integration in the superior colliculus of the alert cat.** *J Neurophysiol* 1998, **80**:1006-1010.
89. Sommer MA, Wurtz RH: **Frontal eye field neurons orthodromically activated from the superior colliculus.** *J Neurophysiol* 1998, **80**:3331-3335.
- This is an important demonstration that the frontal eye fields (FEFs), a major source of inputs to the deep layers of the SC, also receive visual and saccade-related signals from the SC. As the authors suggest, bidirectional signal flow between the FEFs and the SC could be important in the initiation and execution of saccades. Unfortunately, current methods may not allow us to examine the functional consequences of removing the collicular input to FEFs. Perturbations to collicular neurons sending signals to FEFs are also likely to affect the activity of cells receiving input from FEFs and cells sending commands to downstream neurons.
90. Tate AK, Malpeli JG: **Effects of focal inactivation of dorsal or ventral layers of the lateral geniculate nucleus on cats' ability to see and fixate small targets.** *J Neurophysiol* 1998, **80**:2206-2209.
- This paper provides evidence that signals conveyed by neurons in layer A of the lateral geniculate nucleus, but not the signals carried by neurons in layer C, are critical for programming accurate saccadic eye movements. Corticotectal pathways are implicated in the deficits observed after layer A inactivation. Inactivation of C layers has little effect on visual responses of corticotectal cells, whereas visually-driven activity of many, but not all, corticotectal cells is dependent on layer A input.
91. Weyand TG, Gafka AC: **Corticostratial and corticotectal neurons in area 6 of the cat during fixation and eye movements.** *Vis Neurosci* 1998, **15**:141-151.
92. Bozis A, Moschovakis A: **Neural network simulations of the primate oculomotor system. III. An one-dimensional, one-directional model of the superior colliculus.** *Biol Cybern* 1998, **79**:215-230.
- A neural network model of the saccadic system specifically designed to be consistent with what is known about the anatomy and physiology of the SC is presented and discussed in this paper. The model accounts for the accuracy of saccades in double step experiments, the effects of focal SC lesions, and the properties of saccades evoked by electrical stimulation of the SC.
93. Krommenhoek KP, Wiegerinck WA: **A neural network study of precollicular saccadic averaging.** *Biol Cybern* 1998, **78**:465-477.
- The authors present a (somewhat complicated) analysis of what happens in the hidden layers of a neural network model that generates activity in the output layers representing a single motor error when two retinal targets with different intensities are simultaneously presented to the network.
94. Schlag J, Pouget A, Sadeghpour S, Schlag-Rey M: **Interactions between natural and electrically evoked saccades. III. Is the nonstationarity the result of an integrator not instantaneously reset?** *J Neurophysiol* 1998, **79**:903-910.
- This paper concludes that the results of previous experiments examining the interactions between natural and electrically evoked saccades do not test the properties of a feedback integrator. However, whether or not the data presented in the paper support this conclusion is questionable (send e-mail to sparks@saccade.neusc.bcm.tmc.edu to obtain a more detailed technical argument).
95. Quaia C, Lefevre P, Optican LM: **Model of the control of saccades by superior colliculus and cerebellum.** *J Neurophysiol* 1999, **82**:999-1018.
- This paper describes a model in which the cerebellum and SC are jointly involved in the initiation and execution of saccades. In this model, collicular neurons initiate saccades by disfacilitating pontine OPNs and provide directional drive to the brainstem circuitry. In terms of saccade amplitude, the SC generates signals that would always produce hypermetric saccades. The model assumes that the cerebellum can modify the directional signal, track the progress of the saccade toward the target (i.e. serve as a resettable displacement integrator) and terminate saccades by turning off collicular signals. The model makes a number of interesting predictions that are testable using available methods.
96. Keller EL, Edelman JA: **Use of interrupted saccade paradigm to study spatial and temporal dynamics of saccadic burst cells in superior colliculus in monkey.** *J Neurophysiol* 1994, **72**:2754-2770.