

The Superior Colliculus: A Window For Viewing Issues In Integrative Neuroscience

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ABSTRACT The superior colliculus (SC) serves as a fruitful site for investigating a variety of interesting problems in integrative neuroscience. Situated at the interface between sensory and motor processing, the SC contains computational maps of cells responsive to visual, auditory and somatosensory stimuli as well as cells which fire before saccadic eye and head movements. In this chapter the computational issues of the coordination of different motor programs, population coding of saccades, target selection, derivation of eye position signals from corollary discharge, and coordinate transformations necessary for sensorimotor integration will be discussed with respect to the SC.

The intermediate and deeper layers of the superior colliculus (SC) are sites where auditory, visual, and somatosensory signals converge and an area where motor commands for orienting movements of the eyes and head are generated (see Sparks, 1986; Sparks and Mays, 1990 for recent reviews). Studies of the SC concerned with the translation of sensory signals into motor commands have been forced to address some of the most important and perplexing problems of integrative neuroscience. In the process, significant advances have been made in understanding: a) the role of computational maps in processing sensory and motor signals; b) the coordination of different motor programs; c) the extraction of information from the spatial and temporal pattern of activity in populations of neurons; d) the role of corollary discharge in guiding movements; and e) mechanisms for selecting a single response for execution from a large repertoire of potential responses. The experimental strategies developed for studying the SC have also been fruitful when applied to studies of other brain areas. In this chapter, we review the advances listed above, emphasizing studies related to the question of sensorimotor integration - the translation of sensory signals into motor commands.

Computational maps

Many neural computations are performed by computational maps in the brain (see Knudsen, du Lac, and Esterly, 1987, for a review). For example, sensory neurons may be organized in two- or three-dimensional arrays with systematic variations in the value of a computed parameter (e.g., the angle of orientation of a line segment, the direction or velocity of stimulus movement) across each dimension of the array. Neurons, as elements of the map, may be thought of as an array of preset processors or filters, each tuned slightly differently, and operating in parallel on incoming signals. Consequently, signals are transformed, almost instantaneously, into a distribution of neural activity within the computational map. The values of the stimulus parameters are represented as locations of peaks of activity within the map (Knudsen, du Lac, and Esterly 1987).

Computational maps may also be used for programming movements. Systematic variations in the direction, amplitude, or velocity of a movement can be represented topographically across a neural array. The most thoroughly studied motor map is the map of saccadic eye movements found in the SC, first described in detail using microstimulation techniques (Robinson, 1972). As illustrated in Figure 1, the amplitude and direction of stimulation-induced saccades are a function of the site of stimulation in the SC. The neuronal bases of this map and a discussion of how information about the metrics (direction and amplitude) of saccades is extracted from the computational map are described in other sections.

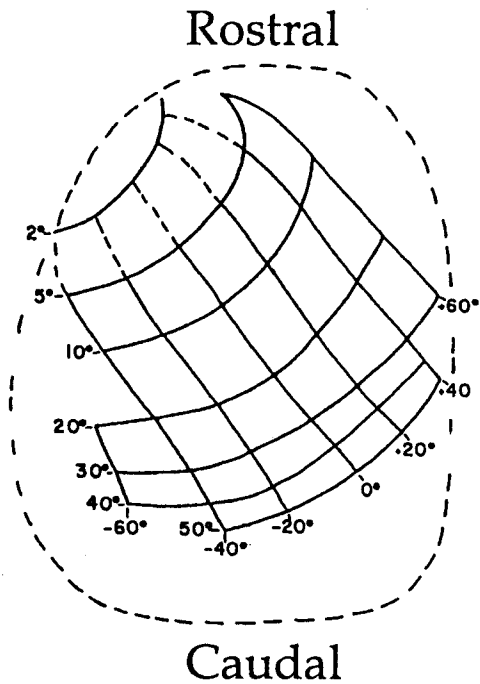


Fig. 36.1. Motor map of the SC. Isoamplitude lines (2-50) run from medial to lateral, and isodirection lines (-50 to +60) run from anterior to posterior. (From Robinson's [1972] microstimulation data.)

Coordination of motor programs

Combined movements of the eyes and head, made in response to external stimuli or produced by stimulation of the SC, have been studied extensively in attempts to understand how different motor programs are coordinated.

Note that the motor map illustrated in Figure 1 only extends to about 45°. But visual stimuli appearing at an eccentricity of 80° in the visual field can be detected. What happens when a sudden stimulus appears at 80°? Can an orienting movement of only 45° occur because the collicular motor map only extends to 45°? Note that the experiments upon which the map shown in Fig. 1 are based were performed in monkeys with restrained heads. That the collicular motor map extended beyond the oculomotor range was first demonstrated in experiments using cats as subjects (Roucoux, Crommelinck, and Guitton, 1980). Roucoux, Crommelinck, and Guitton (1980) found that stimulation in some regions of the SC produced large gaze shifts involving coordinated rotations of the eyes and head. Both the eyes and head began to move at about the same time and *in the same direction*. In many

cases, the amplitude of the stimulation-induced head movement was larger than the amplitude of the eye movement. But when gaze, the sum of eye and head positions, reached the angle coded by the site being stimulated in the motor map, the head continued to move but the vestibulo-ocular reflex (VOR) became active; the eye changed direction and moved in the opposite direction by an amount that compensated for the continued movement of the head. Gaze angle remained constant.

Results of early experiments (Stryker and Schiller, 1975) indicated that stimulation of the monkey SC did not produce coordinated movements of the eyes and head like that described in the cat. Also, in cats (Munoz, Guitton, and Pelisson, 1991) and barn owls (du Lac and Knudsen, 1990), the amplitude and velocity of gaze shifts depends on the duration, frequency and intensity of stimulation. But the metrics of movements produced by stimulation in the monkey SC were thought to be independent of stimulation parameters.

What is the current status of these apparent differences in the functional organization of cat and monkey SC? Recent experiments conducted by Freedman, Stanford and Sparks (1993) used a broader range of stimulation parameters than did early experiments studying the effects of microstimulation in the monkey. These newer studies indicate that there are no fundamental differences in the functional organization of the cat and monkey SC. Stimulation of the caudal SC in monkeys produces large gaze shifts that involve coordinated movements of the eyes and head (see Fig. 2). Moreover, the parameters of stimulation do influence the metrics of the movements in monkeys when the head is free to move (see Fig. 3).

The microstimulation experiments in the cat and monkey and behavioral studies using cats, monkeys and humans as subjects (Bizzi, Kalil, and Morasso, 1972; Morasso, Bizzi and Dichgans, 1973; Harris, 1980; Roucoux, Crommelinck, and Guitton, 1980; Munoz, Guitton, and Pelisson, 1991; Lauritis and Robinson, 1986; Guitton and Volle, 1987; Tomlinson and Bahra, 1986a, 1986b) indicate that eye-head coordination is not achieved by a single motor program. At least two major modes of operation are observed. When the desired gaze shift is small, this may be accomplished by movements of the eyes alone; voluntary or involuntary movements of the head are countered by the VOR. Very large gaze shifts (e.g., 80-

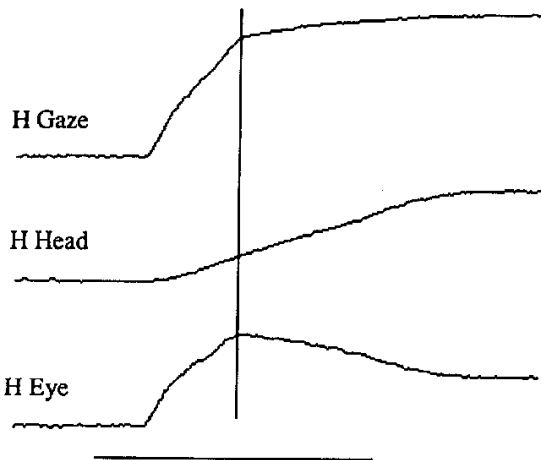


Fig. 36.2 Coordinated movement of eyes and head produced by stimulation of the monkey SC. A suprathreshold stimulation train delivered for 200 ms (horizontal calibration mark) produced a predominantly horizontal (H) gaze shift of 17 deg. The vestibulo-ocular reflex is apparent at the end of the high velocity gaze shift (vertical line) as the head continued moving. (Freedman, Stanford, and Sparks, unpublished)

90°) are accomplished by moving both the eyes and head in the same direction toward the target. During the initial phase of these movements, the VOR is switched off but later, after the line of sight is near the target, the VOR is reactivated. Strategies for achieving intermediate amplitude gaze shifts are not as clear, but the VOR may still be active with reduced gain.

In summary, the motor representation in the SC involves the coordination of at least two motor programs (eye and head). The motor command signals observed in the SC are abstract and quite different from those needed by motor neurons sending signals to individual muscles.

Population coding

To this point only the motor representations revealed by electrical stimulation of different regions of the SC have been considered. How are these higher order motor commands represented at the level of the activity of single neurons?

Many neurons in the SC discharge before saccadic eye movements. These cells have movement fields: i.e., each neuron discharges maximally prior to saccades having a particular direction and a particular amplitude, regardless of the initial position of the eye in the orbit (Wurtz and Goldberg, 1972; Sparks,

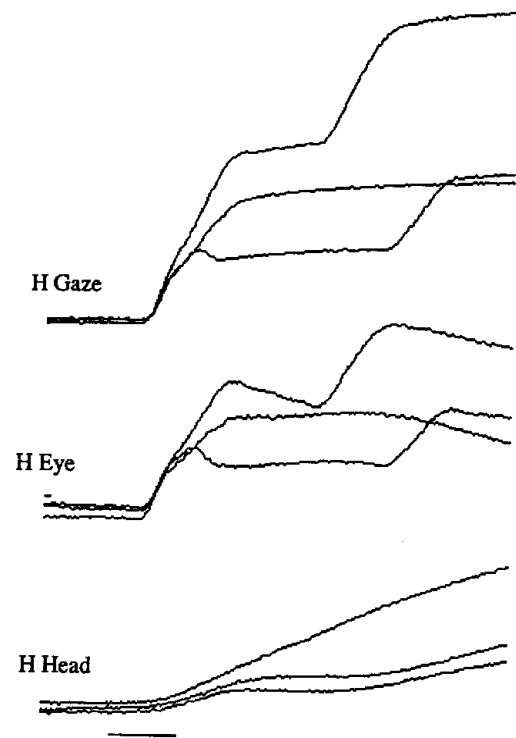


Fig. 36.3 Effects of varying train duration on gaze shifts produced by microstimulation of the monkey SC. Three traces of horizontal (H) gaze, horizontal eye, and horizontal head position are superimposed. The changes in eye, head, and gaze position were produced by suprathreshold stimulation trains 75, 100, or 200 ms in duration. The horizontal calibration line marks the time and duration of the 75-ms stimulation train. Note that the amplitude of the gaze shift increases as the duration of the stimulation train is increased. The 200-ms stimulation train produced a staircase of changes in gaze position: an initial change of 34° followed, after approximately 100 ms, by a second, smaller horizontal gaze shift. (Freedman, Stanford, and Sparks, unpublished)

Holland and Guthrie, 1976, Sparks and Mays, 1980). A gradient of response amplitude is observed across the movement field. Movements to the center of the movement field are preceded by a vigorous discharge, but movements deviating from this optimal direction and amplitude are accompanied by less vigorous activity. The size of the movement field is a function of the amplitude of the optimal movement. Neurons discharging prior to small saccades have small and sharply tuned fields, whereas neurons discharging prior to large saccades have large movement fields and relatively coarse tuning. The movement fields of SC

neurons are also characterized by a temporal gradient. Cells begin firing earlier for saccades near the center of the movement field than they do for movements to the periphery of the field (Sparks and Mays, 1980).

The topographical organization of movement fields within the SC forms the neuronal substrate of the

motor map revealed by microstimulation (Fig. 1). Neurons discharging prior to small saccades are located anteriorly, and neurons firing before large saccades are found posteriorly. Cells near the midline discharge prior to movements with up components, and cells laterally discharge maximally before movements with down components.

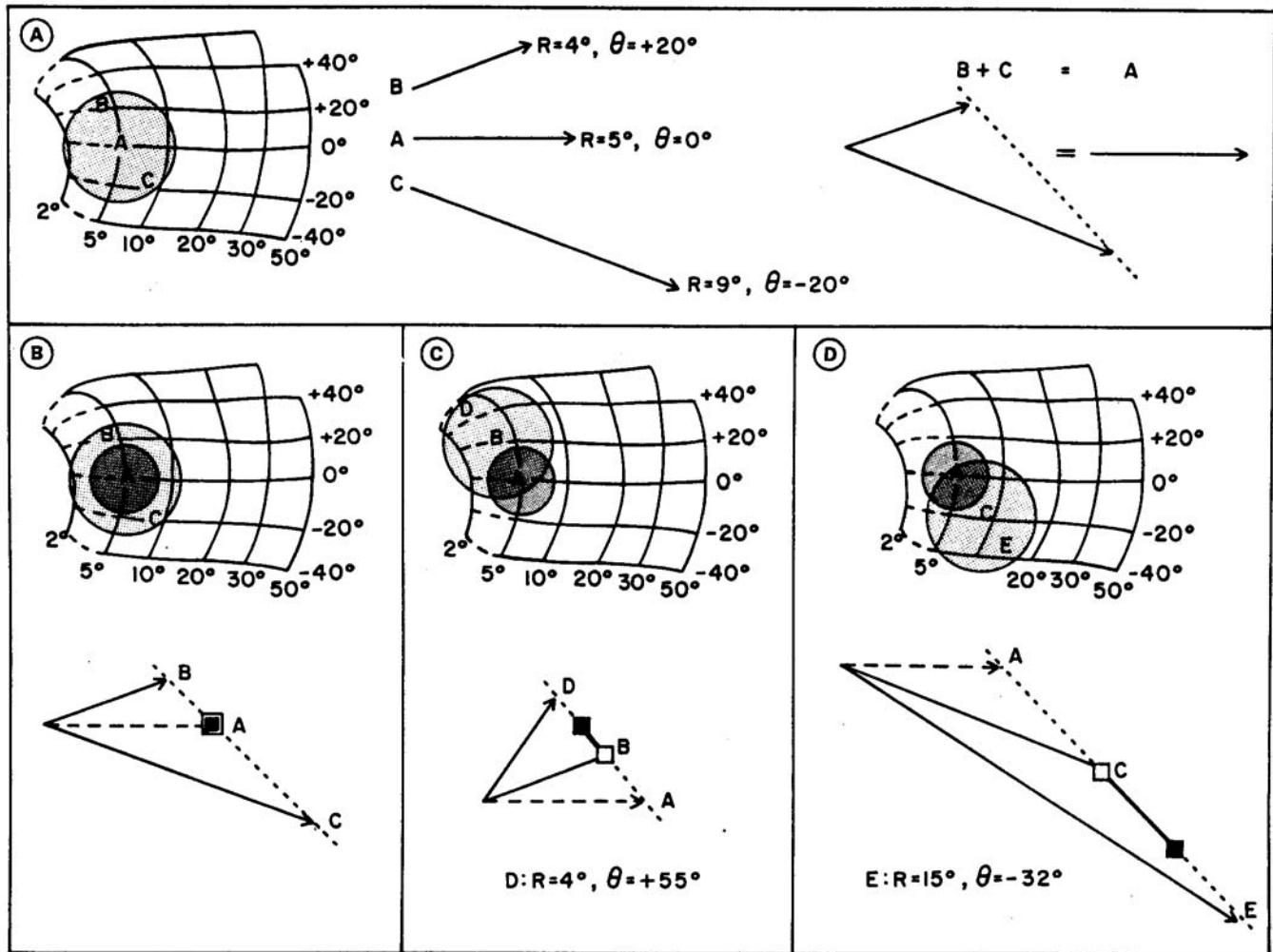


FIGURE 36.4 (A) The population-averaging scheme of Sparks, Holland, and Guthrie (1976). (Left) Motor map of the left SC. The stippled area represents the hypothetical extent of cells active before saccades to a target located 5° to the right of the fixation stimulus. The active population is assumed to be symmetrical in shape. (Middle) Cells at locations A, B, and C fire most vigorously for the movements shown. (Right) Weighted averaging of activity at points B and C yields the same movement as activity at the center of the active population (A). (B-D) The predicted effect of deactivating a subset of cells in the active population. The site of deactivation (darkly stippled circle) remains the same in each panel, but the location of the active population (lightly stippled area) is different in each panel because saccades to three different targets are required. Beneath each map are the saccade vectors associated with neural activity at each of the locations, illustrated. The open square represents the vector of the intended, or programmed, saccade associated with activity in the lightly stippled area. The dashed line represents the vector of the movement tendency produced by neurons at the deactivated site. These neurons will not contribute to the metrics of the saccade, and a saccade to the approximate location of the filled square is predicted. (Reprinted from Lee, Rohrer, and Sparks, 1988, by permission.)

The issue of population coding arises because the movement fields of collicular neurons are large and coarsely tuned (Sparks, Holland and Guthrie, 1976; Sparks and Mays, 1980). Because each neuron fires before a broad range of saccades, a large population of neurons is active before each saccade. How are the signals needed to precisely control the direction and amplitude of a saccade extracted from the activity of this large population of coarsely tuned cells? One possibility is that the location of the most intense activity within the population is determined at a subsequent stage of neural processing (Knudsen, du Lac and Esterly, 1987). Another possibility (McIlwain, 1976; Sparks, Holland and Guthrie, 1976; Tweed and Vilis, 1985; van Gisbergen, van Opstal and Tax, 1987; van Opstal and van Gisbergen, 1989) is that each member of the active population contributes to the movement and the exact trajectory of a saccade is determined by the average or sum of the population response. Results of recent experiments (Lee, Rohrer and Sparks, 1988; Sparks, Lee and Rohrer, 1990), in which small subsets of the active population were reversibly deactivated, support the population averaging hypothesis.

The population averaging model (see Fig. 4) assumes that the region of collicular neurons active before a given saccade occupies a symmetrical area within the motor map. Only the neurons in the center of the active population discharge maximally before the programmed movement. But, for each subset of active neurons (B) producing a movement tendency with a direction and amplitude other than the programmed movement, there will be a second subset of active neurons (C) producing an opposing movement tendency such that the resultant of the two movements will have the programmed direction and amplitude. According to this hypothesis, each member of the active population contributes to the ensuing saccade; there is no need to sharpen the population response in order to generate an accurate saccade. Thus, as illustrated in Fig. 4, with the same region of colliculus inactivated, requiring the animal to make different saccades should result in a predictable pattern of errors.

Rhesus monkeys were trained on a saccadic eye movement task. A glass pipette (Malpeli and Schiller, 1979) was used for recording extracellular unit activity, microstimulation, and pressure injection of various agents into the SC that affect neuronal activity.

The location of the pipette tip in the collicular motor map was determined from plots of movement fields and measurements of the direction and amplitude of stimulation-induced saccades. The behavioral effects of the injections were assessed by comparing saccades to a selected set of visual targets before and after the injections.

As predicted by the population-averaging hypothesis, a systematic pattern of errors in direction and amplitude was observed after small injections of lidocaine (see Fig. 5). Saccades to targets requiring more of an upward component than the “best saccade” had too much of an upward component, and saccades to targets requiring movements with more of a downward component than the “best saccade” had too much of a downward component. Also as predicted,

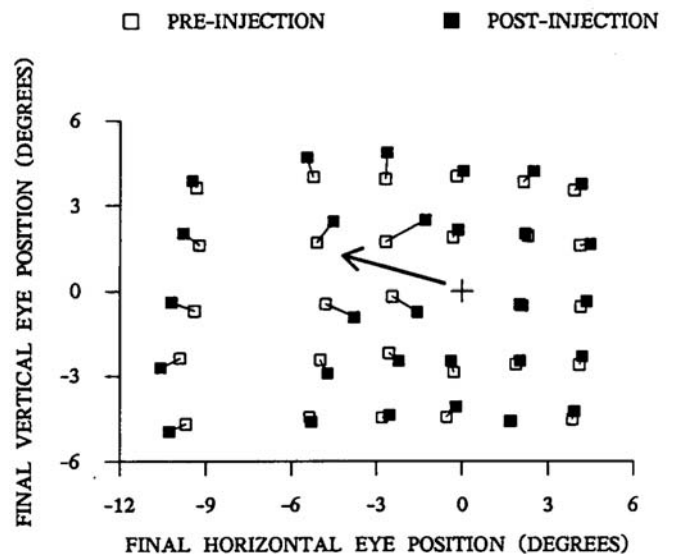


FIGURE 36.5 The plot shows the position of the initial fixation (+) and the endpoint (arrowhead) of the best saccade. Each symbol represents the average endpoint of three to five visually guided saccades. Unfilled symbols represent movements occurring before the injections; filled symbols represent postinjection trials for matching targets. Lines connecting the squares represent the average error introduced by modifying the spatial and temporal pattern of neuronal activity within the SC. Effects of a single 200-nl injection of lidocaine. (From Lee, Rohrer, and Sparks, 1988.)

movements to targets requiring a saccade smaller in amplitude than the “best saccade” were hypometric; saccades to targets requiring a movement larger than the “best saccade” were hypermetric.

Results of these experiments support the major predictions of the vector-averaging model. According to this model, saccadic accuracy results from the averaging of the movement tendencies produced by the entire active population rather than the discharge of a small number of finely tuned cells. Small changes in the direction and amplitude of saccades are produced by slight shifts in the location of the large population of active cells. Moreover, since the contribution of each neuron to the direction and amplitude of the movement is relatively small, the effects of variability or “noise” in the discharge frequency of a particular neuron are minimized. Thus, the large movement fields (resulting in a large population of neurons being active during a specific movement) may contribute to, rather than detract from, saccadic accuracy.

Our findings may generalize to other sensory and motor systems. Georgopoulos, Schwartz and Kettner (1986) described a distributed population code in the motor cortex for the control of reaching movements of the arm. Vogels (1990) developed a population coding model of visual orientation discrimination in which the orientation of the stimulus is represented by an ensemble of broadly tuned units in a distributed manner. Heiligenberg (1991) has shown that jamming avoidance response of weakly electric fish is driven by a distributed system of contributions resulting from the evaluation of inputs from pairs of points within a somatotopic map.

Spatial attention: Target and response selection

Do the sensory and motor maps in the SC represent all potential saccade targets and all potential movements or only those targets that have been selected as a saccade goal and only those responses that are chosen for execution? Neural signals related to the metrics of a movement, or to the onset of potential targets, are readily observed. Isolation of neural signals related to the process of target or movement selection is difficult because selection is a covert process. Glimcher and Sparks (1992) designed experiments to test whether neural activity in the SC is related to saccade selection. Their tasks used a cue to specify which of two physically identical visual stimuli was the goal of an impending saccade. This cue was

spatially and temporally isolated from the potential targets as well as from visual cues signalling movement initiation. Response selection output elements must be differentially sensitive to target and distractor stimuli and changes in their activity must be linked to the time at which sufficient information is available for response selection, as is the case for prelude bursters. They studied the low frequency activity (prelude) that precedes the vigorous saccade-related burst in one class of collicular neurons (prelude burster). The low frequency activity begins shortly after information become available for correct saccade selection and that this activity was predictive of saccade choice.

One of the trial types used to separate the effects of movement selection and visual stimulation on neural activity is illustrated in Fig. 6. Trials were initiated when a fixation stimulus was illuminated yellow. After a variable interval two potential targets appeared. Which was the target and which was the distractor was unknown until the fixation LED later changed color to red or green. Red indicated that the upper stimulus would serve as the target and the lower stimulus as the distractor. Green indicated the opposite. The informative change in color of the fixation stimulus was separated by an additional delay from the cue that signalled saccade initiation (offset of the fixation stimulus).

By using relatively long delay intervals in the behavioral task, we noted that the onset of prelude activity can precede burst onset by up to seven seconds. This early responding occurred only after sufficient information became available to permit accurate response selection. We found that prelude bursters responded differentially to distractors and targets presented at the same location in their response field (see Fig. 7). These data are consistent with the hypothesis that the low-frequency activity of the prelude burst cells reflects the output of the covert process of response selection. For these cells, responses to distractor stimuli are heavily filtered but not completely eliminated. Further studies will be required to determine if the SC actively participates in the selection process or if collicular neurons are merely passively reflecting the results of processing occurring at other levels.

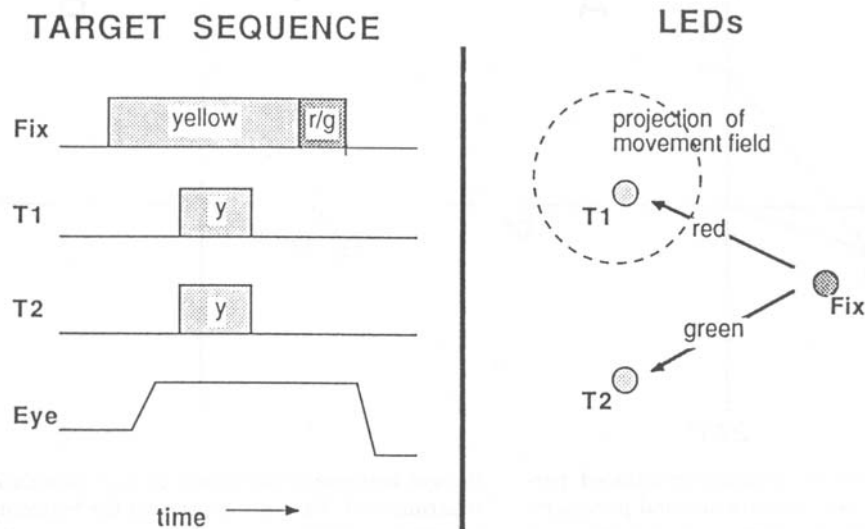


FIGURE 36.6 Schematic diagram of one trial type used to separate the effects of movement selection and visual stimulation on prelude burster activity. Animals first fixated a central yellow LED (Fix). After a variable delay, two yellow LEDs were illuminated briefly at eccentric locations (T1, T2). After another variable delay, the color of the fixation LED changed to red or green and signaled which of the two eccentric stimuli would be the endpoint of a rewarded saccade (the target) and which served as a distractor. After another variable interval, the fixation LED was extinguished and the animal made a saccade to the target's location. The last delay temporally isolated target specification from response initiation.

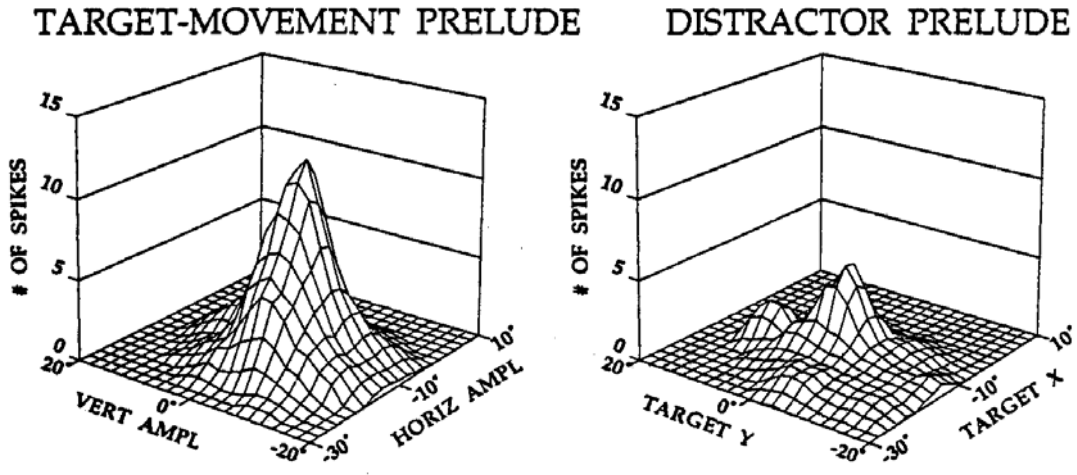


FIGURE 36.7 Four hundred movement trials were used to construct these plots of the sensitivity of one neuron to targets and distractors. (Left) Target-movement prelude field. For each of the 400 trials, the number of spikes in the 200 ms before the movement initiation cue was plotted against the horizontal and vertical amplitude of the movement. Prelude activity occurring well in advance of the movement is spatially tuned. (Right) Distractor-nonmovement prelude field. Here the same unit activity for each of the 400 trials is plotted against the X, Y coordinates of the distractor. (From Glimcher and Sparks, 1992.)

Corollary discharge

Precise information about the position of the eyes in the orbits is required for the spatial localization of visual targets (see next section). The question of whether eye position signals originate from a central

copy of the oculomotor command or arise peripherally from extraocular muscle proprioceptors has been a central issue in oculomotor physiology.

Porter, Guthrie and Sparks, (1983) localized cell bodies innervating extraocular muscle sensory receptors using the technique of retrograde transport of

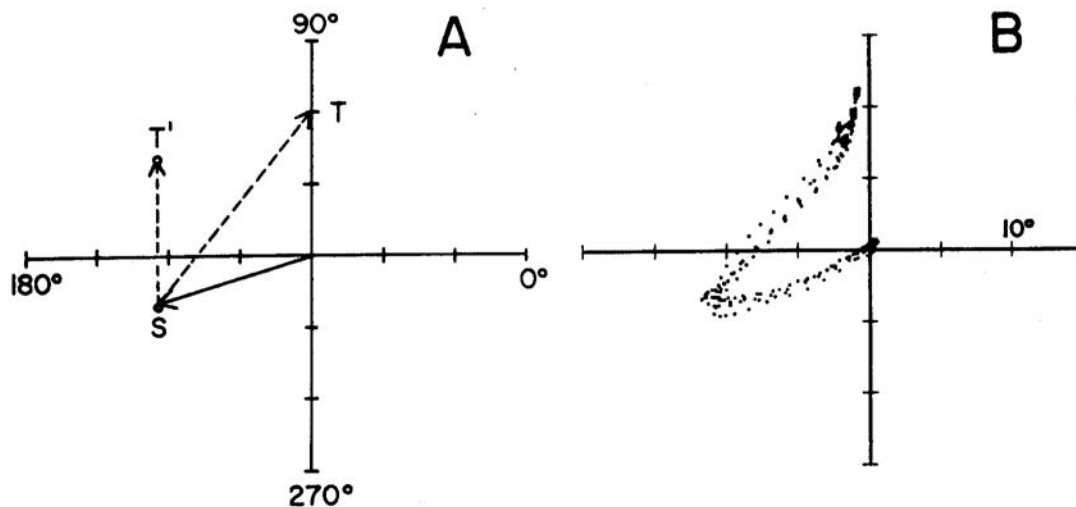


FIGURE 36.8 Compensation for stimulation-induced perturbations in eye position. (A) The experimental paradigm. In complete darkness, while monkeys were fixating on a center target represented by the intersection of the axes, an eccentric target (T) was flashed for 60-100 ms. After the offset of T but before the animal initiated a saccade, electrical stimulation of the SC drove the eyes to another position in the orbit (S). Retinocentric models predict that the animal will look to position T'; spatial models predict that the animal will look to T. (B) Typical results. The trajectories of the eye movements occurring on four stimulation trials are superimposed. Each dot represents the horizontal and vertical position of the eye sampled at 2-ms intervals. The target was flashed 20° above the fixation point. Stimulation drove the eyes downward and leftward. After a brief delay, the animal compensated for the stimulation-induced movement by making a saccade that directed gaze to the approximate position of the target in space. See text and Sparks and Mays (1983) for more detail.

horseradish peroxidase (HRP) after its injection into the muscles. The oculomotor nerves proper, trigeminal ganglia and the brainstem of three species of macaque were examined but labelled sensory cells were found only within the ipsilateral trigeminal ganglia. Section of the ophthalmic nerve at its junction with the trigeminal ganglion prior to injection of HRP into ipsilateral extraocular muscles eliminated all labeling of trigeminal sensory neurons. Thus, in rhesus monkeys, extraocular muscle proprioceptive fibers are anatomically isolated along their peripheral course from axons carrying motor commands. At this site, they can be transected without damaging the motor fibers.

Mays and Sparks (1980a) and Sparks and Mays (1983) developed a behavioral task requiring eye position information, a stimulate and compensate behavioral task. While maintaining central fixation, an eccentric target was flashed briefly. Randomly, on 30% of the trials, after the offset of the target, but before a visually-guided saccade began, microstimulation of the SC drove the eyes to a different orbital position. Monkeys compensated for this

stimulation-induced perturbation in eye position by generating a saccade to the approximate position of the now absent target. Note that the compensatory movement was not a passive rotation to a preset orbital position (Sparks and Mays 1983; Sparks and Porter, 1983). Nor could saccades to the position of the target on stimulation trials be based upon a visual update of target location; the eccentric target was extinguished before the onset of the stimulation-induced saccade. Since the occurrence of stimulation was unpredictable, compensation for stimulation-induced saccades could not be programmed in advance. Because trials were run in total darkness, targets could not be localized with respect to an external visual frame of reference. Therefore, saccades to the targets must have been directed by signals combining information about the retinal locus of stimulation and precise information about the change in eye position produced by stimulation of the SC.

Guthrie, Porter and Sparks (1983) tested the performance of animals with bilateral ophthalmic nerve transections on the stimulate and compensate behavioral task. Animals with bilateral nerve sections

compensated for stimulation-induced perturbations of eye position (Guthrie, Porter and Sparks 1983). This compensation is possible only if information about the stimulation-induced eye movement is still available. Because transection of ophthalmic nerves eliminated extraocular muscle proprioception, eye position information must have been provided by a centrally generated copy of the motor command.

Sensorimotor integration

How do sensory signals elicit orienting movements of the eyes? In order to produce a saccadic eye movement, the brain must determine the target's location in a sensory coordinate framework, compute the position of the target with respect to the eyes, and execute a saccade to bring the target onto the fovea. Saccades can be generated to visual, auditory and somatosensory targets, but the sensory coordinate frameworks for each of these modalities are different. The signals must be transformed into a common eye-centered motor coordinate framework before the motor circuitry in the SC for generating the movement can be accessed. The issues of spatial localization of sensory targets and coordinate transformations for generating motor commands to targets of different modalities will be discussed in succeeding sections.

LOCALIZATION OF VISUAL TARGETS Visual targets excite a particular region of the retina. Neural representations of these targets are presumably encoded in retinal coordinates at least through the early stages of visual processing. If the eyes have not moved since presentation of a brief visual stimulus, then the retinal error vector corresponds to the saccade vector necessary to bring the target's position onto the fovea. However, saccades can be made to the remembered location of a briefly flashed target despite the occurrence of an intervening eye movement, either one induced by stimulation as described above or one directed to a visual target (Mays and Sparks, 1980b). Retinal information is insufficient for generating eye movements to brief visual targets under these conditions: eye position information is necessary as well. How are eye position and retinal visual signals combined?

Evidence for a neural map of visual space in non-retinal coordinates in the SC came from the double-saccade experiment of Mays and Sparks (1980b, Fig. 9). In this experiment, monkeys were presented with two targets flashed briefly in sequence. Monkeys made

saccades to first one and then the other. The saccade to the second target was made accurately, despite the fact that its vector differed from the original retinal error vector. The intermediate layers of the SC were found to contain visually-responsive cells which would fire if the remembered location of the target lay in its receptive field, even though that region of the retina had never been stimulated. Similar quasi-visual or QV cells have since been found in the frontal eye fields (Bruce and Goldberg, 1990) and parietal cortex (Gnadt and Andersen, 1988; Duhamel, Colby and Goldberg, 1992).

The existence of these QV cells encoding the position of the target relative to the current position of the eyes indicates that a coordinate transformation has taken place. Information about the position of the eyes in the orbit has been combined with the retinal image of the target. The resulting coordinate framework was termed motor error by Mays and Sparks, referring to the difference or error between the current position of the eyes and the position of the target. Other authors have used the term updated retinal coordinates to describe similar kinds of cells (Duhamel, Colby and Goldberg, 1992).

This coordinate transformation may occur through any of several different mechanisms. Absolute eye position information (the position of the eyes in the orbit) could be used to transform the visual signals into a head-centered coordinate frame. Mathematically this could be done by adding the retinal error vector and the eye position vector. After an eye movement, subtraction of the new eye position vector would yield the current motor error of the remembered target. If movements of the head in space are included, then a similar addition and subtraction of head position (either with respect to the body or with respect to inertial space) would be required as well. For the sake of simplicity, we will assume the head to be fixed in space.

Such a mechanism suggests the existence of a head-centered (or, if head movements are included, body-centered or spatial) visual map. Such a map is not necessary, however. The subtraction of a vector representing change in eye position from the retinal signal is mathematically equivalent to the addition and subtraction of absolute eye position vectors. This mechanism would produce the eye-centered motor error coordinate framework directly.

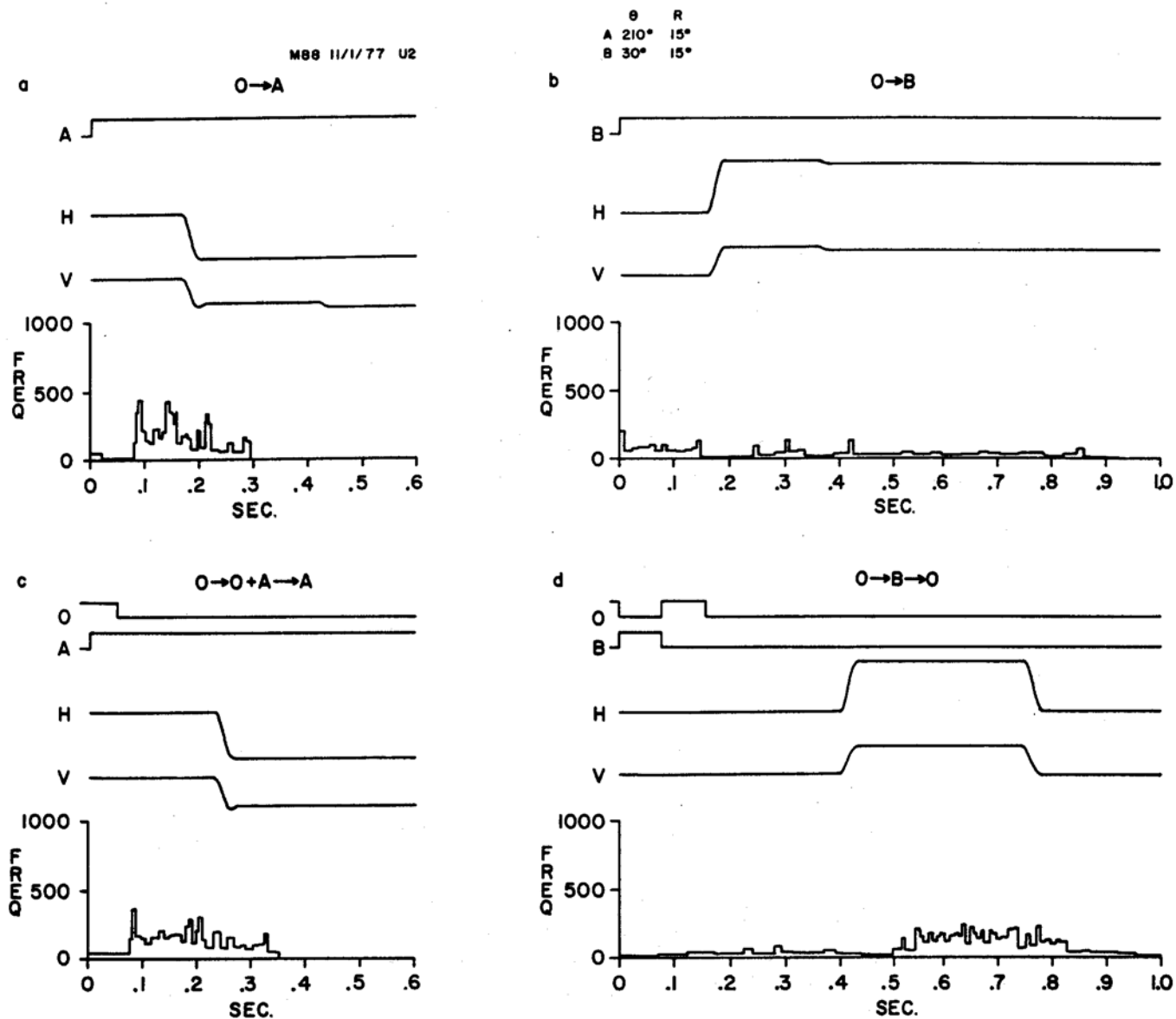


Figure 9. Discharge pattern of a quasi-visual (QV) cell. Panel A shows the response of the cell to a target (A) presented in the receptive field of the cell. Panel B shows the response of the cell to a target (B) presented in the opposite direction. Panel C shows the response of the cell to the target A in the receptive field on a delayed-saccade trial, in which target onset and saccade onset were separated by a longer interval. The cell's activity was temporally coupled with the onset of the target, and no saccade-related burst occurred. Panel D shows the activity of the cell on a double-saccade trial, in which saccades to B and then back to the fixation 0 were required in sequence. The B to 0 saccade was the same as the 0 to A saccade. The cell began firing after the saccade to B and before the saccade back to 0, though target 0 was no longer illuminated.

No head-centered, body-centered, or spatial map of visual space has ever been found, perhaps due to the paucity of experiments which could potentially have discovered such a representation. Although such a representation might facilitate integration of information across saccades and/or the perception of visual stability as the eyes move, it is worth noting that except for saccades and pursuit movements, the eyes move less with respect to the visual scene than do

either the head or body, thanks to the vestibular and optokinetic mechanisms for stabilizing retinal images. That the location of visual targets may be stored in an updated eye-centered frame of reference is therefore also plausible.

Models for interactions between retinal and eye position signals fall into two classes, those which produce head-centered visual signals, and those which

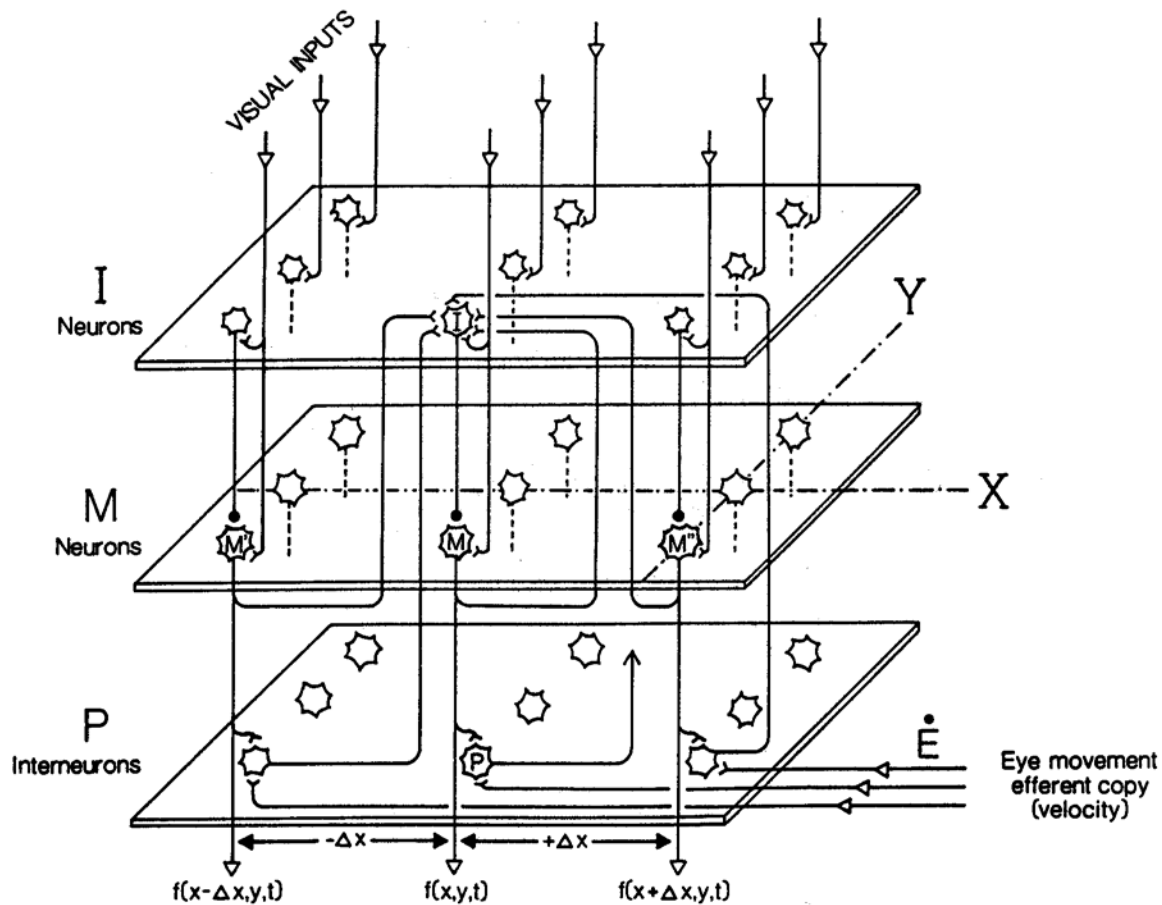


Figure 10. Architecture of the Droulez and Berthoz neural network model. The model has three layers of units: input (I) neurons, main (M) neurons, and interneurons (P). The input neurons receive weighted inputs from the main and interneurons of neighboring modules as well as direct excitatory retinal visual inputs. The main output neurons M also receives visual input. The interneurons receive a velocity signal (E). When an eye movement occurs, feedback from these interneurons shifts activity across the map.

produce updated eye-centered visual signals without employing explicit head-centered coordinates. The models also fall into two classes in terms of the coding format of the visual information. While eye position signals are generally agreed to exist in the form of a firing rate code, visual signals are place-coded topographic maps in some models (Zipser and Andersen, 1988; Droulez and Berthoz, 1991; Groh and Sparks, 1992a) and firing rate codes in others (Zipser and Andersen, 1988; single value per channel, Mittelstaedt, 1990).

Droulez and Berthoz (1991) proposed a model (Fig 10) which used eye velocity information to shift visual activity on an eye-centered map analogous to the QV map in the SC or FEF. The visual signals were encoded topographically, while eye velocity signals were encoded in firing rates. The site of activity for a

remembered visual target was shifted across the map when a non-zero eye velocity signal was received. The site of activity was stationary when the eyes were stationary. No head-centered visual signals were present in the model.

Mittelstaedt (1990) proposed a variety of classes of models which would transform visual signals from retinal to head-centered coordinates. These basic solutions differ in the source of the eye position information (proprioception or efference copy) and the circuitry for combining eye position and retinal signals. These solutions employ channels representing single values of a parameter (similar to rate coding) for both retinal and head-centered visual signals as well as for the eye position signals.

Zipser and Andersen (1988, Fig. 11) proposed two

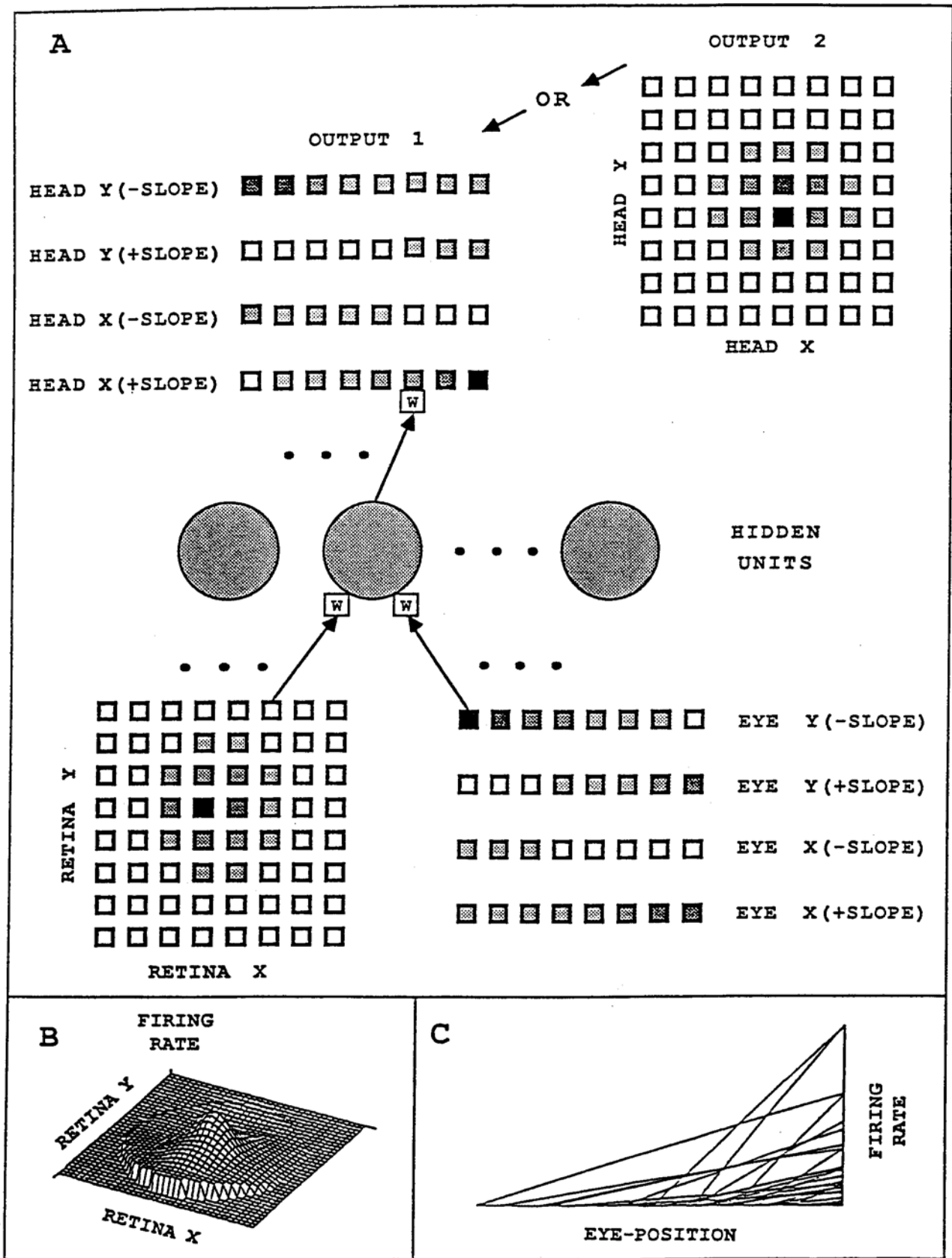


Figure 11. The Zipser and Andersen back-propagation network. (A) Inputs to the model consist of retinal visual signals and rate-coded eye position signals (horizontal and vertical, positive and negative slopes). These units project to a layer of hidden units, which in turn project to the output layer of head-centered visual signals. Two versions of the model were implemented, one using rate coded output units, the other using an array of place coded output units with gaussian receptive fields. (B, C) Activity patterns of the input units.

variations for a retinal-to-head coordinates model. The model consists of a three layer neural network. In one version, the head-centered output was encoded in a topographical map; in the other, the output was encoded in the firing rate. Both versions received place coded retinal input and rate coded eye position signals. Back propagation was used to modify the synaptic weights of the intermediate layer. Cells in parietal cortex which exhibited combinations of retinal visual and eye position dependent activity served as the inspiration for this model.

Recent models developed by Groh and Sparks (1992a) to address auditory coordinate transformations are also applicable to the visual system. These models can be used to transform retinal signals into head-centered coordinates. In the vector addition model (Fig. 12), the place coded retinal signal was decomposed into rate coded horizontal and vertical components. Rate coded horizontal and vertical eye position signals were added through excitatory synaptic connections. The resulting rate coded head-centered visual signal was then converted into a place code using a graded synaptic weighting pattern and inhibitory interneurons.

A second model proposed by Groh and Sparks employed local dendritic circuitry to execute a different neural algorithm (Fig. 13). A pattern of local connections at each dendrite involving excitation from a retinal visual input and inhibition from eye position units and interneurons resulted in dendrites that would selectively excite the soma if and only if the target was in that unit's head-centered receptive field. This model produced a place code of head-centered space without using a rate coded intermediate stage.

The use of rate coded visual signals in some of the above models limits their ability to encode multiple targets. A rate coded visual signal can only encode one target at a time (unless the targets are multiplexed). The Droulez and Berthoz model does not employ rate coded visual signals, and was shown to be capable of shifting multiple visual targets simultaneously. The dendrite model of Groh and Sparks can also transform the coordinates of multiple visual targets. The version of the Zipser and Andersen model producing place coded output was not tested with multiple targets. The limitation imposed by rate coding does not eliminate the other models from contention, however. Eye movements occur serially, so single stimuli may be chosen as targets of eye movements before they are

transformed into the appropriate coordinate framework for generating an eye movement. Models that can only represent single visual targets cannot account for another of the proposed uses for a head-centered representation of visual space, namely the perception of visual stability when the eyes move, since this percept presumably requires the encoding of the entire visual scene.

LOCALIZATION OF AUDITORY TARGETS Unlike the visual system, the receptotopic organization of the auditory system does not yield spatial information about the stimulus. The cochlea produces a neural representation of the component frequencies of a sound. The sound's location must be derived from the differences in sound arrival time at the two ears, the differences in sound intensity at the two ears, and the spectral cues produced by the folds of the pinnae. These cues provide a measure of the sound's position with respect to the ears and head.

Much of the data on neural maps of sound location has come from barn owls (see Konishi et al, 1988, for review). The brain stem of the barn owl contains a variety of signals related to sound position, culminating in a map of auditory space in the optic tectum, the avian homologue of the SC. This map is in register with the visual map in the same structure. However, the barn owl differs from cats and primates in that its eyes do not move with respect to the head. Therefore, the head-centered coordinates of the barn owl's auditory map can maintain a constant registry with the retinal coordinates of its visual map.

Early work in the SC of the cat revealed both auditory and visual spatial receptive fields (Wickelgren, 1971). However, these experiments were conducted in the anesthetized preparation, so no dissociation between head- and eye-centered coordinate frames occurred. Jay and Sparks (1984, 1987b) trained monkeys to make saccades to auditory targets. They found that the auditory receptive fields in the primate SC shifted with changes in eye position (Fig 14). The auditory map was encoded in an eye-centered coordinate framework that remained in register with the visual map encoded in the same coordinates.

Thus a coordinate transformation for auditory signals is also known to occur. This transform is from head-centered to eye-centered coordinates. Unlike the visual system, the coding format of the input to this

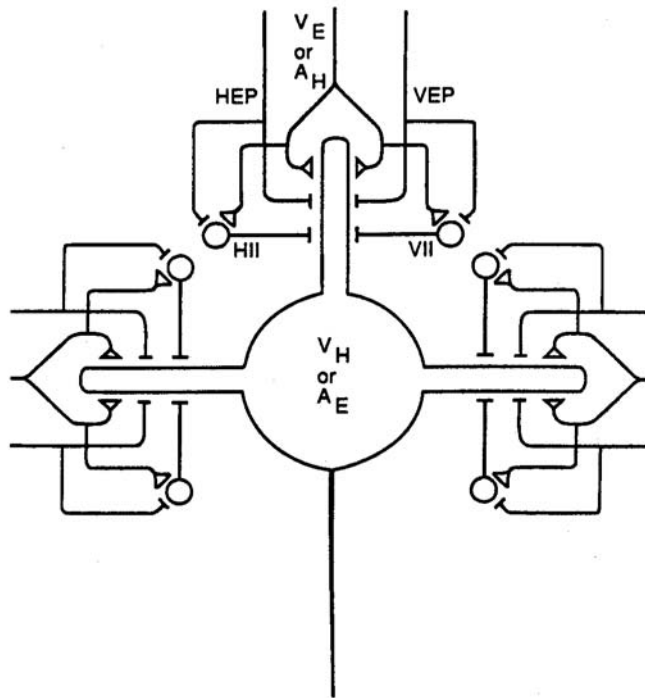


Figure 13. The dendrite model of Groh and Sparks. This unit is part of a map of units encoding head-centered visual target position, and has a receptive field in head-centered coordinates. Each dendrite receives input from one particular retinal location, as well as eye position signals. The pattern of synaptic weights permits the dendrite to compare retinal location and eye position, exciting the soma if the right combination is detected. Different dendrites monitor different retinal locations and require different eye positions to activate the soma, but produce selectivity for the same head-centered location as the other dendrites on a given unit. For the auditory system, the dendrites receive inputs from head-centered auditory units. Combining with eye position signals produces eye-centered receptive fields. A_H , auditory input, head coordinates; V_E , vertical eye position; HEP, horizontal eye position; VEP, vertical eye position; HII, horizontal inhibitory interneuron; VII, vertical inhibitory interneuron; V_H , visual signal, head-centered coordinates; A_E , auditory signal, eye-centered coordinates.

position of the auditory target with respect to the eyes (or visual target with respect to the head) but it need not be a linear one.

The rate coded intermediate stage imposes the same limitation on number of targets for the auditory system as it did for the visual system. However, it is possible that the head-centered auditory signals serving as input to the coordinate transformation are encoded in a firing rate rather than a map. If this is the case, the system may already be limited to single

targets, and the most parsimonious algorithm is the simple subtraction of firing rates through inhibitory synapses.

The dendrite model for the auditory transformation is like that described for the visual transformation, with local dendritic circuitry selecting appropriate target-eye position combinations. Multiple auditory targets can be represented, at a cost of a much larger network of units.

Which of these various models for visual and auditory coordinate transformations most closely approximates the brain itself depends on the format of head-centered auditory signals. In the cat, visual and auditory signals are both present in the region around the anterior ectosylvian sulcus, which projects heavily to the SC (Clarey and Irvine, 1986, Meredith and Clemo, 1989). The spatial selectivity and coordinate framework of these auditory signals is as yet unknown. The SC is probably not the only place in the brain where sensory signals are encoded in a coordinate framework different from that in which they arise, and it may well receive its sensory input from other dynamic maps.

Coding of sensory signals in a common coordinate framework is thought to be necessary not only for coordination of motor programs but also for sensory and perceptual processes such as binding of signals from the same source. Sounds tend to be localized in space to visual objects that are deemed likely to have emitted the sound. This allows us to watch movies and perceive the dialogue as coming from the images of characters on the screen, despite the fact that the sounds are usually emitted by speakers on the sides of the theatre. Ventriloquists perform a similar trick.

Sensory modalities interact with one another for the purpose of calibration as well. The optic tectum of the barn owl has served as a model system for studying the calibration of spatial audition by visual signals. Blind-reared owls have distorted, stretched and even upside down maps of auditory space in the tectum. (Knudsen, Esterly and du Lac, 1991). Ocular prisms affect the owl's orienting behavior to sound as well (Knudsen and Knudsen, 1989).

LOCALIZATION OF SOMATOSENSORY TARGETS A tactile stimulus is detected by cutaneous receptors on the body. Like the visual system, the receptotopic organization of the somatosensory system encodes spatial information regarding the position of the

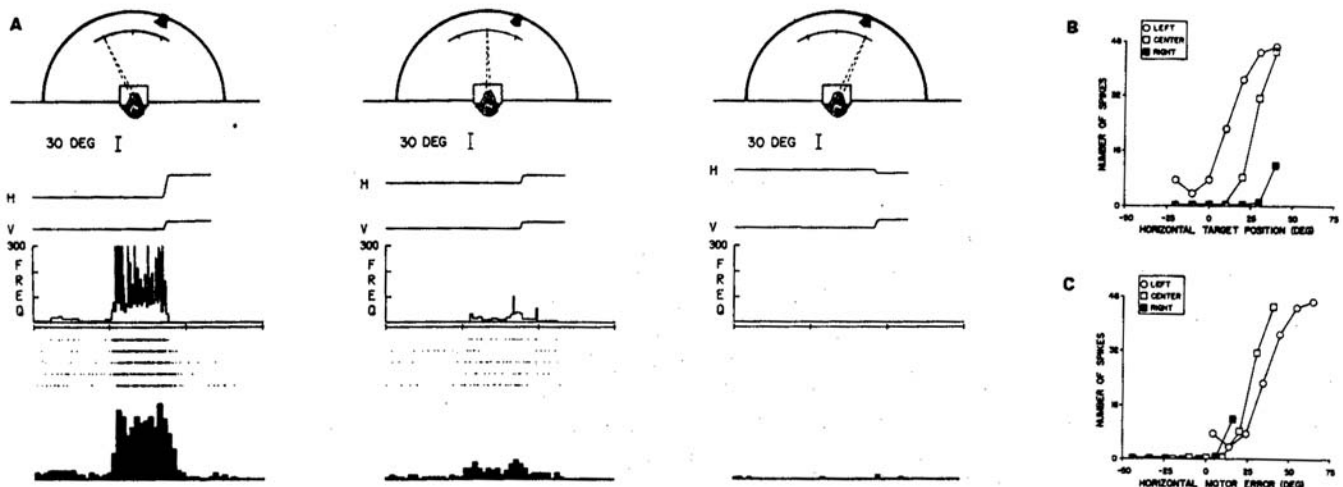


Figure 14. Auditory receptive fields shift with eye position. The monkey was trained to perform saccades to auditory targets. The top row in panel A shows a top view of the monkey and apparatus. The auditory stimulus was delivered by a moveable speaker mounted on a hoop. Visual fixation lights could be illuminated at various locations. The lower panels show the activity of an auditory cell in the SC. When the animal fixated to the left, the cell fired vigorously in response to an auditory stimulus delivered by the speaker positioned to the right. When the animal fixated straight ahead, the discharge was much weaker, and when the animal fixated to the right of the speaker, the cell was silent. Panel B summarizes the response of the cell as a function of the horizontal position of the target for the three different fixation positions. When the same data are plotted as a function of the horizontal component of the saccade to the target, the curves are more closely aligned (panel C).

stimulus on the body surface. However, the spatial information from the receptors directly activated by the stimulus is incomplete. Joint receptors, Golgi tendon organs and muscles spindles also provide information regarding the position of the limb receiving the tactile stimulus. The brain must compute the spatial position of the stimulus with respect to some body axis using the somatotopic information from the cutaneous receptors and the kinesthetic information regarding joint position.

The process of localizing somatosensory targets, then, is a combination of body position sense and stimulus location on the body surface. The resulting coordinate framework is body-centered. In order to generate a saccade to a tactile stimulus, the position of the stimulus with respect to the eyes must be determined, requiring yet another kind of coordinate transformation. How this might be accomplished by the brain is not known.

The SC of the anesthetized cat (Stein, Magalhaes-Castro and Kruger, 1975) and mouse (Drager and Hubel, 1975a, b, 1976) has been found to contain sensory responses to somatosensory stimuli. These responses show a rough topography and registry with visual responses, but in the anesthetized preparation, the visual and body axes do not move with respect to

one another, so the coordinate framework of the responses cannot be determined. The coordinate framework of somatosensory responses in the SC of the awake primate is as yet unknown.

Just as vision affects the localization of auditory targets, so too does it affect the localization of the body in space. Visual input strongly influences the perceived position of the limbs (e.g. Shimojo, 1987). The converse is also true: position sense can affect perception of the location of auditory and visual targets in contact with the body. Lackner and Shenker (1985) used vibration of arm muscles to induce the illusion of limb motion and limb displacement in human subjects sitting in the dark. This phenomenon is known as the vibratory myesthetic illusion. Subjects could make smooth pursuit movements tracking the illusory motion of the hand. If subjects held a single light source such as a fiber optic strand in their hands, they perceived concurrent motion and displacement of the visual stimulus corresponding to the motion and displacement of the hand. The subjects perceived that they were tracking the visual target so that there was no retinal slip. However, eye position measurements revealed that the eyes were stationary. A similar phenomenon occurred when subjects held an auditory speaker in their hands.

Once targets of different sensory modalities have been translated into a common coordinate framework, they can access a common motor circuitry for generating a saccade. All eye movements are generated by the same extraocular muscles. Above this level lies brain stem circuitry specific to all saccadic eye movements. Input to this saccade generator is provided by the SC and FEF, which represent saccade vectors in topographic motor maps. Two questions regarding the activity of these motor maps with respect to the generation of saccades are of interest: 1) Are the same cells active for saccades of all types? 2) If so, what differences in the activity profile of these cells might account for differences in the dynamics of saccades to targets of different modalities?

Motor activity in the SC is found in two classes of cells: saccade-related burst cells, which fire a high frequency burst shortly before a movement into the movement field of the cell, and visuomotor cells, which have a response coupled with the onset of the visual stimulus as well (Wurtz and Goldberg, 1972; Sparks, 1978; Mays and Sparks, 1980b). The majority of burst cells discharge before saccades to auditory stimuli (Jay and Sparks 1987a). Most visuomotor cells exhibit motor but not sensory activity for auditory saccades as well. Recent work by Groh and Sparks (1993) suggests that somatosensory saccades are also represented by the same population of motor cells.

Saccades to auditory (Jay and Sparks, 1990) and somatosensory (Groh and Sparks, 1992b) stimuli have a lower peak velocity than saccades of comparable amplitude to visual targets. This velocity difference suggests a difference in the manner in which sensory signals access common motor circuitry. Jay and Sparks (1987a) proposed that the lower velocity of auditory saccades was due to the slightly smaller population of motor cells active for such saccades. An alternative is that the discharge of motor cells is less vigorous for auditory and somatosensory saccades than for visual saccades. That activity patterns in the SC can influence saccade velocity is supported by several experiments. In the cat, the activity of premotor cells was correlated with the velocity of the movement (Berthoz, Grantyn and Droulez, 1986; Munoz and Guitton, 1987, 1991). Lee, Rohrer and Sparks (1988) reported that saccade velocity was reduced following lidocaine injections. Frequency of stimulation in the SC was correlated with saccade velocity (Stanford, Freedman, Levine and

Sparks, 1993). Whether differences in collicular activity produce the sensory modality dependent velocity profile differences has yet to be determined. Since discharge rate is spatially tuned for the movement vector, and since the spatial tuning of motor cells can vary under different conditions (Stanford and Sparks, 1993), this possibility can only be tested by a thorough sampling of the movement field for both visual and auditory or somatosensory saccades, which has yet to be done.

Conclusions

Studies of the SC have led to considerable progress in understanding a number of important and perplexing problems in integrative neuroscience. The experimental strategies developed for studying neurons in the SC have been used to advantage in other areas. The tasks developed for studying coordinate frameworks of visual and auditory signals have been extended to parietal (Gnadt and Andersen, 1988), frontal (Bruce and Goldberg, 1990; Russo and Bruce, 1989), and prefrontal (Bruce and Goldman-Rakic) cortical areas. The idea that sensory and motor signals are encoded by the spatial and temporal pattern of activity within large populations of neurons has a long history. The detailed map of saccade direction and amplitude found in the SC and the recent advent of methods for reversibly deactivating small populations of neurons permit explicit tests of hypotheses about the extraction of information from population responses. These methods could be extended to other candidate population codes. Tasks developed for studying neuronal correlates of target and response selection in the SC may allow a more direct approach to studies of this important historical problem. Coordination of the eye and head components of gaze saccades may serve as a useful model for more complex cases such as eye-hand coordination. Recent investigations (Schlag, Schlag-Rey and Dassonville, 1989) into the timing and nature of corollary discharge signals of eye position in the oculomotor system continue to add to the rich history of psychophysical experiments on such signals.

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