VISUAL-MOTOR FUNCTION OF THE PRIMATE SUPERIOR COLLICULUS¹

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INTRODUCTION

One of the major functions of the brain, and probably the original function of all nervous systems, is to produce movement in response to sensory stimulation. In recent years one case of such sensory-motor function, the visual initiation of eye movements, has been studied extensively. Much of this work has centered on the most obvious candidate for visual-motor guidance, the superior colliculus. There has long not been any doubt that the superior colliculus is involved in vision and eye movement—the structure receives direct projections from the retina and over a century ago stimulation of the colliculus was shown to produce eye movements (Adamük 1870). But it has only recently been possible to study the relation of single cell activity within this structure to both movement and vision.

This cellular approach, along with new anatomical, physiological, and behavioral methods, has enabled the investigation of the machinery whereby the visual stimulus initiates motor movement. It is these advances that we concentrate on in this review. We emphasize the primate superior colliculus because most of the work relating to movement has been done in the rhesus monkey, *Macaca mulatta*. At the same time we draw on work done on the cat and tree shrew to supplement areas as yet unexplored in the monkey, although many interesting facets of work on these and other species are not considered. Other recent reviews have considered many of these other aspects (Sprague et al 1970, Gordon 1975, Sprague 1972,

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Sprague et al 1972, Sprague 1975, Sparks & Pollack 1977, Goldberg & Robinson 1978).

The organization of this review follows the recent suggestions that the seven alternating fiber and cell layers of the superior colliculus can be functionally divided into two parts (Figure 1): 1. the superficial layers, consisting of stratum zonale, stratum griseum superficiale, and stratum opticum, and 2. the deep layers, consisting of stratum griseum and album intermediale, and stratum griseum and album profundum. This division is based upon behavioral, anatomical, and electrophysiological studies in several mammals.

The subdivision of the superior colliculus was first suggested by behavioral and anatomical studies in the tree shrew (Casagrande et al 1972, Harting et al 1973, Casagrande & Diamond 1974). When lesions were restricted to the superficial layers, tree shrews had deficits in the ability to perform a visual discrimination; larger lesions extending into the deep layers resulted in an additional failure to orient to stationary or moving objects. Harting et al (1973) found that the efferent connections of those layers also differ; the superficial layers that receive direct retinal input project to "visual," i.e. dorsal and ventral lateral geniculate and pulvinar, thalamic nuclei. In contrast, the deep layers project to thalamic nuclei that are not generally considered to be visual centers and to subthalamic and lower brainstem nuclei that are generally considered to be motor areas or reticular formation. Harting et al (1973) interpreted these results as evidence that the colliculus of the tree shrew consists of two divisions: a superficial division, concerned with visual processing, and a deeper division, concerned with orienting movements of the head and eyes in response to stimuli.



Figure 1 Alternating fiber and cell layers of monkey superior colliculus. A drawing of a coronal section through the colliculus is shown. The seven layers indicated on the right are divided into three layers designated as the superficial division and four layers designated as the deep division. I. C., inferior colliculus; C. G., central gray.

More recently, Edwards (in press) has argued that in the cat there is a complete anatomical segregation of the superficial layers from the deeper layers. First, he pointed out that the morphological features of cells found in the two zones are distinct; cell profiles in the superficial layers are similar to those in other primary sensory nuclei while cell profiles in deeper layers are like those found in other areas of the brainstem reticular core. Second, the afferent and efferent connections are consistent with a division into a sensory part and a reticular-like part. Third, receptive field properties indicate that the superficial cells are like other cells of the primary sensory pathways having limited fields while deep cells have diffuse and often multimodal sensory fields. Finally, repeated attempts to demonstrate connections between these layers have failed and so in the absence of unequivocal evidence Edwards was led to consider that such connections do not exist.

Electrophysiological experiments in the behaving monkey also emphasize the differences between the superficial and deep layers. As we shall see, even in the behaving animal the cells of the superficial layers are primarily visual while cells in the deeper layers discharge in relation to eye movements, although they may also have sensory responses. Moreover, activity between the parts is not necessarily coordinated; visual activity in the superficial layers does not necessarily lead to movement activity in deeper layers and, conversely, movement activity in deeper layers does not require visual activity in the superficial layers (Mohler & Wurtz 1976, Sparks et al 1977, Mays & Sparks 1979).

This review has four parts. In the first part we describe the visual responses of cells in the superficial layers, and in the second part the activity of cells in the intermediate and deep layers in relation to movement. In these two sections our primary goal is to describe the cellular elements within the superior colliculus based on the available physiological and anatomical observations. In the third part we attempt to derive a picture of intracollicular organization. Finally, in the fourth part we consider the functional relationship of the superior colliculus to current views of the oculomotor system. These last two sections concentrate on the functional organization of the colliculus and of necessity rely more on hypotheses than on verified observations.

VISUAL CELLS IN SUPERFICIAL LAYERS

The approach of the electrode tip to the surface of the superior colliculus is signaled by a roar of neuronal activity that is elicited by spots of light in the visual field. Superficial cells respond briskly to visual stimuli and are not fussy about stimulus size, shape, direction, or speed of movement. Some superficial cells also have a more subtle component to their response that is related to rapid eye movements (saccades) made by the animal. In this first section we examine properties of cells responding to passive visual stimulation, the behavioral modulation of the visual responses that occurs in some visual cells, and the afferent and efferent organization of the superficial layers.

Visual Responses

HORIZONTAL AND VERTICAL ORGANIZATION The contralateral visual field is mapped in an orderly way across the superficial layers of the primate superior colliculus (Cynader & Berman 1972). The central visual field is represented at the anterior pole and lateral margin, while the peripheral visual field is represented at the posterior pole. The upper fields are represented medially, the lower fields laterally. The visual field representation in the primate differs from other mammals in two ways (Lane et al 1971, Cynader & Berman 1972, Kaas et al 1974). First, there is minimal ipsilateral representation of the visual field so that the vertical meridian representation occurs at the anterolateral margin of the colliculus. Second, the magnification factor of the central representation is larger than in most mammals; the central 10° is expanded to include more than 30% of the surface of the colliculus.

This horizontal map is produced by input from the two retinae. The projection of the contralateral hemi-retina includes the entire colliculus while the projection of the ipsilateral hemi-retina is represented only in the anterior portion of the colliculus leaving a monocular representation of the crescent at the posterior pole (Hubel et al 1975).

With increasing depth in the superficial layers, cells have increasingly larger visual receptive fields (Humphrey 1968, Cynader & Berman 1972, Goldberg & Wurtz 1972a, Moors 1978). Cells near the surface have central activating regions with diameters smaller than a degree while cells encountered more ventrally (as well as those with more peripheral receptive fields) have central activating regions often larger than 10° across.

RESPONSE TO STATIONARY STIMULI The visual receptive fields of superficial layer cells consist of a central activating region surrounded by a zone capable of suppressing the response of the center (Humphrey 1968, Schiller & Koerner 1971, Cynader & Berman 1972, Goldberg & Wurtz 1972a, Updyke 1974, Marrocco & Li 1977, Moors 1978). The majority of these cells respond transiently to the onset and/or offset of spots of light with a latency of about 40–80 msec. There is a gradient of response strength across the activating center; responses to small flashes of light are greater toward the central portion of the field and are weaker toward the periphery (Goldberg & Wurtz 1972a). The activating center exhibits the property of internal summation, that is, a progressively greater number of spikes per burst are elicited as a function of increasing stimulus diameter. The summation effect has two components: there is an increase in response, reaching a maximum at some stimulus diameter smaller than the activating center, and the response latency is also reduced with larger stimuli (Moors 1978). When the diameter of the spot exceeds the boundaries of the central activating region and infringes upon the surround, the center response is suppressed. The relative strength of the center-surround interaction is variable; some surrounds are sufficiently weak as to allow diffuse flashes of light to activate the cells. We should emphasize that stimulation of the suppressive surround of colliculus cells alone evokes no cell discharge (Schiller & Koerner 1971, Goldberg & Wurtz 1972a, Cynader & Berman 1972), whereas the antagonistic surrounds of some retinal ganglion cells and lateral geniculate neurons can be independently excited by annuli (e.g. Dreher et al 1976). We therefore suggest that the term suppressive surround be used to describe receptive fields of superior colliculus cells to distinguish them from the antagonistic surrounds found in other parts of the visual pathways.

RESPONSE TO MOVING STIMULI Most cells of the superficial layers also respond to moving stimuli. In contrast to the cat (e.g. Sterling & Wickelgren 1969), few sampled cells in the monkey are selective for the direction of movement. For the few directionally sensitive cells, tuning curves are broad, extending over 180° or more (Goldberg & Wurtz 1972a). Cells are also nonselective for stimulus velocities: the majority respond well to low stimulus velocities (as slow as 5°/sec), and many cells respond also to high stimulus velocities sometimes equivalent to saccadic velocities (600– 900°/sec) (Goldberg & Wurtz 1972a, Robinson & Wurtz 1976, Marrocco & Li 1977, Moors 1978).

Three types of response patterns to moving stimuli have been described (Marrocco & Li 1977). One type consists of two sets of leading and lagging edge responses resulting from the passage of the stimulus edge through the initial and final receptive field borders. A second response pattern consists of a single set of leading and lagging edge responses occurring only at the initial receptive field border; an inhibitory effect resulting from the initial discharge eliminates the leading and lagging edge response at the second receptive field border. A third type of pattern is a sustained response throughout the receptive field elicited by a small moving stimulus. This response type is more commonly encountered in the lower half of the superficial layers. There is possibly a fourth kind of visually responsive cell termed the "jerk" detector, but these cells are either quite deep in the superficial layers or in the intermediate layers and have only been seen in paralyzed preparations (Schiller & Koerner 1971, Cynader & Berman 1972).

Behavioral Modulation of Visual Responses

The use of awake behaving monkeys has allowed examination of the visual responses of these cells when the animal actively responds to the visual stimuli. Two types of modulation of the visual response have been found: one that leads to an enhanced visual response when the monkey uses the visual stimulus as a target for a saccade and another that reduces the response of the cell to stimuli falling on the retina during a saccadic eye movement.

VISUAL ENHANCEMENT Goldberg & Wurtz (1972b) noticed that for some cells the visual response was more vigorous when a trained monkey was required to make a rapid or saccadic eye movement from a fixation point to a visual stimulus lying within the central activating region. The enhancement took the form of either a more vigorous on-response to the visual stimulus or a prolonged on-response or both. The enhanced onresponse was not evident on initial trials when the monkey was first required to make a saccade to the visual stimulus, but it occurred on subsequent trials when the monkey could expect to make a saccade to the receptive field stimulus. Since the enhancement of the visual response occurred before the monkey actually made the saccade, the receptive field stimulus was equivalent in both fixation and saccade trials; only the behavioral significance of the stimulus changed. The enhancement was found more frequently in the more ventral cells of the superficial layers.

The visual enhancement is spatially specific, that is, the visual response of the cell is enhanced only when a saccade is made near the central activating region of a cell. Saccades made to stimuli remote from the receptive field fail to produce an enhanced response. The visual enhancement is therefore not a generalized arousal or alerting effect.

The enhancement phenomena is temporally specific, that is, visually enhanced responses are transient effects temporally related to the beginning of the saccade (Wurtz & Mohler 1976a). By presenting the receptive field stimulus at varying times before and after the initiation of the saccade, response enhancement could be seen in visual responses occurring as early as 200 msec before saccade onset and also in visual responses occurring after the end of the saccade. The enhancement does not occur when the monkey responds to a stimulus but does not make a saccade to it.

Goldberg & Wurtz (1972b) suggested that the enhancement of visual responses at the cellular level might be a correlate of the selective attention seen at the behavioral level. The subsequent experiments showing the spatial and temporal relation of visual enhancement to eye movement suggest that the enhancement should be regarded either as only one type of selective attention or as part of the process specifically related to the initiation of saccades (Wurtz & Mohler 1976a). The subsequent finding of a more generalized enhancement effect in parietal cortex (Robinson et al 1978, Bushnell et al 1978) reinforces the view that the enhancement in the colliculus is related specifically to saccades. The visual enhancement effect has been reviewed more extensively elsewhere (Wurtz et al, in press).

The enhancement effect is also different from the modification of the visual response of a cell due to a remote stimulus, which has been demonstrated in the cat (Rizzolatti et al 1974). This remote effect (at least in the monkey) can result from interaction between two stimuli rather than from the monkey's use of the stimulus (Richmond & Wurtz 1978).

VISUAL SUPPRESSION The second type of modulation found in some visual cells produces a suppression of their discharge rate following saccades (Goldberg & Wurtz 1972a). In these behavioral experiments, two paradigms were used. The monkey was first required to maintain fixation while a visual stimulus was swept at saccadic velocities across the receptive field. The monkey was then required to make a saccade to a second fixation point while a visual stimulus was appropriately positioned in the visual field so that the effect of the saccade was to sweep the visual stimulus across the receptive field. Robinson & Wurtz (1976) found that in this second condition a suppression of cell activity occurs that is appropriately timed and powerful enough to eliminate the response of the cell to visual stimuli even if the stimuli are 1 to 2 log units above background. The suppression occurs with saccades in many directions and is only slightly influenced by saccadic amplitude. The effect of the suppression is to reduce sensitivity to all visual input during an eye movement.

This reduction of sensitivity could not result from any visual input since the suppression persists in total darkness (Goldberg & Wurtz 1972a). Nor could it result from peripheral sensory feedback such as proprioception since Richmond & Wurtz (1977) found that the suppression persisted in the collicular cells even when the eye was paralyzed by a retrobulbar block. They concluded that the suppression, and by inference the reduced sensitivity to visual stimulation, was a result of a corollary discharge to saccadic eye movement impinging on these visually related cells in the colliculus. Some cells show both enhancement of response to a relevant stimulus before a saccade as well as reduced sensitivity to an irrelevant stimulus during the saccade. These cells showing either type of modulation will be referred to as *modulated visual cells* in contrast to other *unmodulated visual cells*.

Afferent Influences to Superficial Layers

The afferent influences that contribute to the visual responses of superficial layer cells and to their modulation are summarized in Table 1. The three

Afferent connections	Efferent connections
Retina	Thalam us:
Visual cortex:	Dorsal lateral geniculate (magnocellular, interlaminar)
Striate & Prestriate	Pregeniculate (Ventral lateral geniculate)
Other cortical areas: Frontal eye fields	Inferior pulvinar
Midbrain:	Midbrain:
*Parabigeminal *Pretectum	Parabigeminal Pretectum

Table 1 Connections of the superficial layers

anatomically identified sources are the retina, several cortical areas, and two midbrain nuclei. Projections from the midbrain are shown with asterisks since these have not yet been demonstrated in the primate.

RETINOTECTAL Axons of retinal ganglion cells enter the superior colliculus bilaterally to terminate chiefly within the upper portion of stratum griseum superficiale (Hendrickson et al 1970, Tigges & Tigges 1970, Lund 1972a,b, Tigges & O'Steen 1974, Hubel et al 1975). As seen with autoradiography, the termination zone is particularly dense in the upper 200 μ m except in the foveal region where retinotectal projection is sparse (Hubel et al 1975). In the parafoveal region receiving binocular input, terminals from the ipsilateral and contralateral eve appear as patches. Patches of contralateral eye inputs are concentrated in the upper 50–125 μ m while patches from the ipsilateral eye extend somewhat more ventrally. A similar organization has been seen in the cat (Graybiel 1975). These anatomical observations may account for the electrophysiological observation that within the superficial layers there are intercalated areas of ipsilateral and contralateral eve dominance (Hubel et al 1975, Marrocco & Li 1977). All cells within 0.8 mm of the surface could be consistently driven by optic chiasm stimulation, which suggests a direct (but not necessarily monosynaptic) connection from retina to colliculus. More ventral cells in stratum opticum and the upper portion of the intermediate layers are also driven but with longer latencies (Marrocco & Li 1977). For many cells the short latency responses persist after ablation of striate cortex (Marrocco 1978).

Of the three major categories of retinal ganglion cells (i.e. X, Y, W) only two have been shown to project to the colliculus (de Monasterio & Gouras 1975, Schiller & Malpeli 1977, de Monasterio 1978a,b). These groups are both nonspectrally selective and have been termed 1. broad-band cells and 2. "rarely encountered cells." Primate broad-band cells are similar to Y-cells found in the cat retina (see Rodieck 1979 for review). They respond with a transient burst to the onset or offset of stationary spots of light, have antagonistic on- or off-surrounds, and are rapidly conducting. The second group projecting to the colliculus is the "rarely encountered" group (also called atypical ganglion cells). This second group is characterized by slowly conducting axons and low spontaneous activity. Some cells have on-off centers with suppressive surrounds, others have either on- or off-centers and may lack surrounds altogether. It seems likely that these cells represent a heterogeneous group of primate W-like cells and may be the major source of retinal input to the primate superior colliculus (de Monasterio 1978a). This notion is consistent with the similarities in visual receptive field structure of rarely encountered retinal ganglion cells and superficial layer colliculus cells. Both groups of cells have on-off centers, suppressive surrounds, and lack spectral sensitivity. The generally larger sizes of colliculus activating centers compared to the receptive field centers of retinal ganglion cells suggest a substantial convergence of retinal inputs in the colliculus.

CORTICOTECTAL The projection of striate cortex to the superficial layers is well established in primate and numerous other species (Garey et al 1968, Wilson & Toyne 1970, Abplanalp 1970, Harting & Noback 1971, Kadoya et al 1971, Sterling 1971, Lund 1972b, Kawamura et al 1974, Robson & Hall 1975, Finlay et al 1976, Powell 1976). The projection of striate cortex arises from layer V and terminates for the most part ipsilaterally throughout the superficial layers (Lund et al 1975, Powell 1976). Slight degeneration is sometimes also found in the intermediate layers.

The receptive field properties of corticotectal cells are more specific for stimulus features than colliculus cells, yet they are less specific than nontectally projecting cells of striate cortex (Finlay et al 1976). When compared to cortical cells as a whole, corticotectal cells have somewhat larger receptive fields, have weak orientation specificity, and tend to have a weak directional preference for moving stimuli. They are binocular with complextype receptive fields and high spontaneous activity.

Surprisingly, removal of the striate input, either by ablation or by cooling, has little or no effect upon the visual responses of cells in the superficial layers of the primate colliculus (Schiller et al 1974). Observed changes are limited to "patchy" receptive fields having subareas of on- or off-responses and an increase in monocularly dominated receptive fields. The visual responses of cells in the anterior colliculus representing the central visual field, which appears to receive a relatively weak input from the retina, are not especially affected by interruption of striate-tectal inputs. These results taken together with the lack of similarity in the receptive field organization of corticotectal cells suggest that striate cortex does not make a significant contribution to the passive visual properties in the superficial layers of the superior colliculus. Nor is striate cortex likely to be an important source of input to modulated cells since the enhancement effect seen in striate cortex is not spatially selective as it is in the colliculus (Wurtz 1969, Wurtz & Mohler 1976b) and the suppression effect in striate cortex is at best weak and is often not seen (Wurtz 1969, Bartlett & Doty 1974, Duffy & Burchfiel 1975). The contribution of striate cortex to the activity in the superficial layers remains a puzzle in the primate.

The frontal eye fields (area 8) project to the superficial layers and stratum opticum, and also to the dorsal part of intermediate layers (Kuypers & Lawrence 1967, Astruc 1971, Kunzle & Akert 1974, Kunzle et al 1976). Nearly half of the sampled neurons in a restricted part of area 8 respond to visual stimuli, and their receptive field properties are similar to those of the superficial layers (Mohler et al 1973, Wurtz & Mohler 1976b). They respond transiently to small flashes of light with a latency of 70–110 msec, in general are not selective for stimulus orientation or direction of movement, and show enhancement similar to that seen in the colliculus. Unlike colliculus cells, their receptive fields are commonly 20° or more in diameter and may extend 10–20° into the ipsilateral visual field. While the exact contribution of these cells is unknown, it may be that visual neurons in the frontal eye fields provide facilitative input to colliculus cells showing visual enhancement.

In the cat, other cortical visual areas project to the superficial layers (Kawamura et al 1974). In general, projections of cortical areas more remote from area 17 are to increasingly deeper colliculus layers. In the monkey, regions of prestriate cortex have been shown to project to the superficial layers (Kuypers & Lawrence 1967, Benevento & Davis 1977), but the organization of connections within the superficial layers is unknown.

Reciprocal and Efferent Influences of the Superficial Layers

In keeping with the visual character of afferent connections to the superficial layers, the efferent connections also distribute to known visual nuclei of the thalamus and have reciprocal connections with two other visual structures found in the midbrain (Table 1).

THALAMUS The superficial layers project mainly to three visual thalamic nuclei: the dorsal lateral geniculate, the pregeniculate nucleus (ventral lateral geniculate), and the inferior pulvinar (Mathers 1971, Harting et al 1973, Benevento & Fallon 1975, Trojanowski & Jacobson 1975, Graham 1977, Harting et al 1978). In the tree shrew the cells giving rise to these

projections are stratified within the stratum griseum superficiale; cells projecting to the dorsal and ventral lateral geniculate arise primarily from the upper portion while cells projecting to pulvinar are located primarily in the lower half (Albano et al 1979). The nature of the tectal input to these visual structures has not been studied. However, some cells in the pregeniculate nucleus are modulated by saccadic eye movements in complete darkness (Büttner & Fuchs 1973). Projections to nonvisual thalamic nuclei have been described in monkey (Benevento & Fallon 1975) but have not been confirmed in other species (Harting et al 1973, Graham 1977). These nonvisual projections were found using anterograde degeneration and were only evident in cases where the lesions invaded the anterior colliculus where damage to fibers of passage and the pretectum is particularly likely.

MIDBRAIN In addition to these visual thalamic projections, the superficial layers receive from and send connections to two visual midbrain structures, the pretectal complex and the parabigeminal complex. In cat, the superficial layers receive connections from two pretectal nuclei: the nucleus of the optic tract and the posterior pretectal nucleus (Edwards et al 1979). Several other studies in cat, tree shrew, and monkey have reported reciprocal connections from the superficial layers back to the pretectum but do not agree upon which specific nuclei receive these connections (Harting et al 1973, Berman 1977, Benevento et al 1977, Graham 1977, Itoh 1977). Thus, these connections may be reciprocal only in a general sense since it is not yet clear whether the specific nuclei that project to the colliculus also receive the collicular projections.

In cat, the parabigeminal nucleus, a small midbrain nucleus lying in the lateral tegmental area adjoining the superior colliculus, also sends and receives connections to the superficial layers (Harting et al 1973, Benevento & Fallon 1975, Graham 1977, Harting 1977, Graybiel 1978a, Edwards et al 1979, Henkel & Edwards 1978). The responses of visual cells of the superficial layers and the parabigeminal cells are strikingly similar (Sherk 1978). Like cat colliculus cells, parabigeminal cells are frequently direction selective but are not selective for stimulus size or speed of movement. Receptive fields consist of a central activating region and a surround with diameters corresponding to the range encountered in the colliculus. The reciprocal connection of the parabigeminal nucleus led Graybiel (1978a) to consider the parabigeminal nucleus as a "satellite system" possibly modulating the visual responses in the superficial layers.

Function of Superficial Layers

What role the cells in the superficial layers play in behavior has not been investigated in the monkey. The prominent ascending projections through the thalamus suggest that the visual processing seen in the superior colliculus could contribute to the form discrimination functions usually attributed to cerebral cortex. While this may be true in other mammals (for example, tree shrew, see Casagrande & Diamond 1974; cat, see Berlucchi et al 1972, Sprague et al 1977, Tunkel & Berkley 1977), the role in form discrimination in primates appears to be slight (Rosvold et al 1958, Anderson & Symmes 1969, Butter 1974a,b) or simply not yet revealed with the tasks that have been tried. Human psychophysical studies suggest that a saccade to a part of the visual field may alter detection thresholds in that part of the field (Singer et al 1977); this type of perceptual modulation may be related to ascending effects of the colliculus in general and of visual enhancement in particular. The superficial layers also might have critical effects on activity in the deep layers, which we consider later.

MOVEMENT CELLS IN THE DEEP LAYERS

As a microelectrode passes from superficial layers into the deep layers of the superior colliculus, a dramatic change in the relation of collicular activity to visual-motor behavior occurs. The cells now discharge in close temporal relation to saccades in the dark as well as in the light. In this section we summarize the types of these cells, their relation to eye movements, and anatomical connections of the strata intermediale and profundum.

Properties of Cells Related to Movement

Cells related to movement discharge before saccadic eye movements made to visual targets. Most cells also discharge before saccades made spontaneously in the light or the dark (Wurtz & Goldberg 1971, Schiller & Koerner 1971, Wurtz & Goldberg 1972a) and before the quick phase of optokinetic (Schiller & Koerner 1971) and vestibular nystagmus (Schiller & Koerner 1971, Wurtz & Goldberg 1972a). These cells were first studied in the monkey (Schiller & Koerner 1971, Wurtz & Goldberg 1971), although such cells had been reported previously in the cat superior colliculus (Straschill & Hoffmann 1969). In the monkey there is considerable agreement on most of the characteristics of these cells (Schiller & Koerner 1971, Wurtz & Goldberg 1971, Schiller 1972, Schiller & Stryker 1972, Wurtz & Goldberg 1972a,c, Robinson & Jarvis 1974, Wurtz & Mohler 1974, Sparks 1975, Mohler & Wurtz 1976, Sparks et al 1976, Sparks & Pollack 1977, Sparks et al 1977, Sparks 1978, Wurtz 1978, Mays & Sparks 1979) so that we cite references in this section only when specific or conflicting findings are involved.

Cells related to movement have three salient characteristics: 1. They discharge before saccadic eye movements, usually leading the onset of eye

movement by about 50 to nearly 150 msec. 2. The cells only discharge before an eye movement to one area of the visual field, an area referred to as the movement field of the cell (Wurtz & Goldberg 1972a) in analogy to the visual field of visual neurons. 3. The movement fields are organized in retinotopic coordinates rather than in spatial coordinates. That is, if the movement field of a cell is located 20° to the right as the monkey looks straight ahead, the cell will discharge before a 20° rightward saccade. The cell will also discharge in a similar manner before a 20° rightward saccade starting from any other orbital position. We consider each of these characteristics in turn.

TIMING OF DISCHARGE The time of onset of movement cell discharge varies with depth within the colliculus (Mohler & Wurtz 1976). The most dorsal movement cells, found at the junction of stratum opicum and stratum griseum intermediale, show the shortest lead time before onset of saccades, usually about 40-50 msec. The burst of activity is superimposed on a low background rate. Other cells deeper in the colliculus have an earlier but more gradual onset in their rate of discharge before a saccade, which is superimposed on a higher background rate of discharge. The increase in discharge rate of these cells begins at least 100-150 msec before the onset of the saccade. The slow rate of onset of the early discharge and the typically high background rate of these cells probably account for several larger estimates of their lead before saccades (200-300 msec, see Wurtz & Goldberg 1972a; 70-500 msec, see Schiller & Koerner 1971). Variation in the lead time among these movement cells suggests a continuum, but further work might well reveal a series of discrete cell types. For ease of reference, we refer to the cells discharging close to the onset of the saccade as short-lead cells and to the other cells as long-lead cells.

Another distinction between cells related to movement is based on the presence or absence of a burst of action potentials preceding the eye movement (Sparks et al 1976, Sparks et al 1977). Saccade-related burst cells have a relatively discrete burst of high frequency discharge beginning about 20 msec before saccade onset even though the earliest increase in activity may occur 80–100 msec before a saccade. Other cells show a gradual buildup of activity starting 80–100 msec before the saccade but have no such burst of activity. The depth of the cell types has not been determined. It seems clear, however, that the short-lead cells are all burst-type cells; the long-lead cells may or may not be burst-type cells. This overlap of the short-lead type and the burst-type neuron will be important since these cells are probably output cells of the colliculus, and we consider them again later.

The relation of the cell discharge to the end of the eye movement also varies, occasionally ending with the end of the saccade, but frequently continuing beyond the end of the saccade. In general, the deeper the cell within the colliculus, the longer the discharge continues after the end of the saccade (Mohler & Wurtz 1976), but no systematic study has been devoted to this relationship.

MOVEMENT FIELDS A movement field is determined by having the monkey saccade to one point in the visual field on a series of trials, then to other points, until the discharge of the cell preceding a series of points is obtained. While the cell discharge may increase before saccades to a large area of the visual field, there is a gradient in the vigor of response across the field. Saccades to points in the center of the movement field are preceded by a more vigorous discharge than saccades to the edge of the movement field. The gradient within a movement field declines more sharply towards the fovea (Sparks et al 1976) as does the gradient of the visual receptive fields in the superficial layers (Goldberg & Wurtz 1972a). The onset of the discharge has also been reported to start earlier in the central area of the movement field in some cases (Sparks et al 1976) but not in others (Mohler & Wurtz 1976).

HORIZONTAL AND VERTICAL ORGANIZATION Within the superior colliculus there is an orderly horizontal organization of movement fields. This map of the movement fields is in register with the retinotopic map of the superficial layers, but the detailed topography of this movement map is even less well known than that of the visual map. A difference between the visual and movement fields is that while visual fields have not been shown to cross the vertical meridian into the ipsilateral field (Cynader & Berman 1972), movement fields definitely cross into the ipsilateral field especially when the movement fields include the vertical meridian. The size of the movement fields varies with location on the retinotopic map. Fields near the fovea are smaller in overall size (5° across) and have steeper gradients of cell discharge to given points within the field while fields further from the fovea are larger (20–30° across) with rather gradual response gradients.

Neither the duration nor the vigor of cell discharge is related to location of the movement field in the visual field (Sparks et al 1976). Thus a cell with a movement field 5° from the fovea discharges just as vigorously as a cell with a movement field 20° away. This is in contrast to cells in the pontine reticular formation whose duration of discharge varies with saccade amplitude. The organizational principle in the colliculus is based on which cell discharges, not how much it discharges.

Movement cells are first encountered at the junction of the superficial and intermediate gray layers. As movement cells are located farther within the deep layers the size of the movement fields gradually increases (Mohler & Wurtz 1976). The movement fields of the most dorsal cells (at the dorsal border of stratum griseum intermediale) are about the same size as the visual receptive fields of the superficial layer cells just above. Movement field size increases with depth until the field can easily cover a quadrant of the visual field. Exactly how deep within the colliculus movement cells are found has surprisingly never been determined.

Visual-Motor Integration

SENSORY RESPONSES Many of these cells related to movement also respond to visual stimulation as first reported by Schiller & Koerner (1971), and this sensory response is all that is evident in the paralyzed monkey (Cynader & Berman 1972, Updyke 1974). In the awake monkey the visual response is very slight compared to the movement related discharge of such cells, often being only a few spikes even to an optimal stimulus. The visual receptive fields of these cells always overlap the movement fields but are seldom coterminous with them. These visual responses probably do not result from the visual activity in the superficial layers since following ablation or cooling of striate cortex these cells of the deep layers lose their visual responses (Schiller et al 1974). In addition, the enhanced visual response, prominent in the deeper parts of the superficial layers, has not been found in these deep layer cells (Goldberg & Wurtz 1972b, Mohler & Wurtz 1976).

Another visually related movement cell is the "quasi-visual cell" reported by Sparks et al (1977), and Mays & Sparks (1979). These cells have a fixed latency response to the onset of a visual target and continue to discharge until a saccade of appropriate amplitude and direction occurs. Because the quasi-visual cells continue to discharge even after the saccade target has been removed, Mays & Sparks (1979) point out that these cells "hold" the information of eye position error. Since these cells begin their discharge long before the onset of a saccade, usually without a discrete burst of activity, we think they could be regarded as a new variety of long-lead cell. Like long-lead cells, quasi-visual cells are usually below the first movement cells encountered in a microelectrode penetration and like some long-lead cells, quasi-visual cells have visual responses.

Some cells in the deep layers of the colliculus also respond to auditory and somatosensory stimuli (Updyke 1974) and this has been studied most extensively in the cat and mouse (Wickelgren 1971, Stein & Arigbede 1972, Gordon 1973, Stein et al 1976b, Drager & Hubel 1975, 1976). The relation of such multisensory input has not been studied in awake animals, but since eye movements can obviously be initiated by other than visual stimuli, the possible function of these inputs is intriguing. VISUALLY TRIGGERED MOVEMENT CELLS The visually triggered movement cells identified by Mohler & Wurtz (1976) discharge before saccades into the movement field of that cell but only when the saccade is triggered by a visual target. Spontaneous eye movements in light or dark are not accompanied by such a discharge as would be the case with the movement cells considered thus far. These visually triggered movement cells are located at the dorsal border of the stratum griseum intermediale and are identical to the short-lead neurons except for the added requirement of a visual trigger. These cells usually also show a slight response to visual stimulation. But it must be emphasized that this visual response is not necessary for the "gating" of such cells since the movement part of its discharge can be elicited without a visual response. Similar cells have recently been reported by Mays & Sparks (1979).

Collicular Relation to Saccade Metrics

STIMULATION In the awake monkey, Robinson (1972) and Schiller & Stryker (1972) (Stryker & Schiller 1975) found that stimulating the superior colliculus produced results paralleling those found with single cell recording. Stimulation produced saccades whose amplitude was related to the point stimulated, even with suprathreshold currents. The shortest latency for a saccade following stimulation was 20 msec—a time equal to the lead time of burst neurons before a saccade. Thresholds for eliciting saccades were lowest in the intermediate layers.

Schiller & Stryker (1972) also compared the direction and amplitude of saccades evoked by micro-stimulation at one point in the colliculus with the movement fields of cells recorded at the same point. After stimulation with the same microelectrode the eyes moved to the same part of the visual field represented by the movement fields of adjacent cells. The map of eye movement directions corresponded to the retinotopic map found in superficial layers (Cynader & Berman 1972). This retinotopically organized movement map in the primate may differ from areas of the cat colliculus where stimulation has been reported to be related to the position of the eye in the orbit (Straschill & Rieger 1973, Roucoux & Crommelinck 1976, Crommelinck et al 1977) although others have not found this (Stryker & Blakemore 1972, Stein et al 1976a, Harris 1979).

EYE-HEAD In monkeys free to move their heads, eye and head movements usually occur together (Bizzi et al 1971) so that the movement cells in the superior colliculus might be related not only to saccades but also to attempted head movement. Robinson & Jarvis (1974) allowed the monkey to make horizontal head movements as well as eye movements but found that the colliculus cells still discharged in close temporal relation to eye movement, not to head movement. By stimulating the colliculus, Stryker & Schiller (1975) found that eye movements were elicited with short latency, with fixed threshold, and with the same amplitude regardless of the initial position of the eye in the orbit. Head movements following stimulation had variable latency (> 90 msec), variable threshold, and usually occurred when the eye had deviated to one side of the orbit. Both studies reach the conclusion that the monkey superior colliculus does not determine the occurrence of head movement. This may be species dependent since stimulation and recording experiments in the cat colliculus suggest that this structure might be related to head movement (Harris 1979, Roucoux et al, in press).

If a head movement occurs along with an eye movement, the amplitude of the eye movement is shortened primarily by feedback from the vestibular system, called the vestibular ocular reflex (Bizzi et al 1971). The shift in gaze (eye plus head movement) remains the same regardless of the occurrence of the head movement. When reduction of saccade amplitude occurs, the discharge of collicular movement-related cells in the colliculus is appropriate for the saccade that would have occurred if the head had not moved (Robinson & Jarvis 1974). The discharge of the movement cells can therefore be regarded as related to the retinal error, which leads to a shift in gaze regardless of whether the error is reduced by a saccade or not.

SACCADE METRICS Another indication that the colliculus cells are not necessarily tied to the metrics of the executed saccade is the observation that a movement cell that discharged before 40° long saccades also discharged when the monkey executed two serial 20° saccades (Mohler & Wurtz 1976). The cell did not discharge preceding ordinary 20° saccades since such a saccade did not fall into the movement field of the cell. The cell discharged in relation to the size of the error, not necessarily the amplitude of the saccades accomplishing the movement.

Mohler & Wurtz (1976) concluded that the discharge of the movement cells (including short-lead cells) could be decoupled from the saccade since they observed cells in a monkey that discharged before saccades and continued to discharge at the appropriate time even when the monkey stopped making the saccades. Sparks (1978), using a more elaborate paradigm, rarely observed such decoupling in the burst neurons and concluded that these neurons are more tightly coupled to saccades than Mohler & Wurtz (1976) thought. Unfortunately, no one has compared systematically the tightness of coupling with the type of cell, long-lead or short-lead. The short and consistent interval between the discharge of short-lead cells and the onset of the saccade is probably the best argument that short-lead cells are the output neurons of the superior colliculus; decoupling, like the occurrence of head movements along with saccades or the execution of two saccades instead of one, may occur between the colliculus and the site of saccade generation.

SMOOTH PURSUIT Those movement cells that discharge before saccades to targets outside the foveal region do not discharge before smooth pursuit eye movements except before the catch-up saccades during pursuit movements (Wurtz & Goldberg 1972a). Cells within the foveal region of the superior colliculus do discharge during tracking eye movements, but it seems likely that this discharge relates to the movement of the target stimulus rather than the eye movement itself (Schiller & Koerner 1971, Goldberg & Wurtz 1971). The relation of colliculus cells to the slow phase of nystagmus or vergence eye movements has not been investigated.

Afferent and Efferent Connections

The characteristics of the movement cells and their influence on other brain areas is dependent upon the afferent and efferent connections of the deep layers summarized in Table 2. Quite unlike the simpler patterns of connections of the superficial layers, the number of structures projecting to the deep layers is overwhelming; subcortical projections involve nearly all regions of the brainstem and corticotectal projections include regions from prefrontal to occipital cortex. With the exception of certain sensory areas of cerebral cortex, these connections do not generally involve structures associated with primary sensory pathways.

AFFERENT CONNECTIONS For purposes of simplification, the afferent connections may be organized into seven groups (Table 2). Many connections are indicated with asterisks since most of the data is derived from cat and few of these connections have been established in the primate.

Cortical afferents to the deep layers arise from numerous areas including striate, prestriate, auditory, and somesthetic cortex, parietal and temporal cortical areas, prefrontal cortex and frontal eye fields (Kuypers & Lawrence 1967, Garey et al 1968, Paula-Barbosa & Sousa-Pinto 1973, Kawamura et al 1974, Kunzle & Akert 1974, Kunzle et al 1976, Goldman & Nauta 1976, Benevento & Davis 1977, Jones & Wise 1977, Wise & Jones 1977, Hartmann-von Monakow et al 1979). These corticotectal projections are diffuse and do not terminate within a single lamina although there is some evidence of stratification since striate and prestriate areas tend to terminate more dorsally than more remote cortical areas (Kawamura et al 1974). Actually the projections from striate and prestriate regions have two terminal foci, one in the superficial layers, which appears discrete, and a second in the

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Afferent connections	Efferent connections
Cortex	Ascending
Striate & Prestriate cortex Auditory, Somesthetic, Motor cortex Regions of Parietal, Temporal cortex Prefrontal cortex Frontal eye fields Diencephalon * Zona incerta * Reticular n.	Subthalamus & thalamus Zona incerta Fields of forel Reticular, Limitans n. Reunions n. Intralaminar n. (Parafascicular, Centromedian) Mediodorsal n. (rim)
* Pregeniculate	Suprageniculate Medial geniculate (magnocellular)
(Ventral lateral geniculate) Pretectum * n. Posterior commissure * Anterior, Posterior pretectal n.	Midbrain Anterior, Posterior pretectal n. n. Posterior commissure
* n. Optic tract	Descending ipsilateral
Midbrain * Cuneiform, Subcuneiform * Substantia nigra (pars reticularis) * Parabigeminal, Peri-parabigeminal * Paralemniscal * n. Brachium inferior colliculus * External n. inferior colliculus * Pericentral n. * n. Sagulum * Locus coeruleus * Raphe dorsalis * Lateral parabrachial n. Pons and medulla	(Tectopontine/Tectobulbar) <i>Midbrain</i> Parabigeminal, Peri-parabigeminal Paralemniscal Subcuneiform, Cuneiform Inferior colliculus External capsule <i>Pons</i> Reticularis tegmenti pontis Reticularis pontis oralis Dorsolateral pontine n. Facial motor n.
 * n. Pontis caudalis, oralis * Reticularis tegmenti pontis * Ventral n. lateral lemniscus * Dorsomedial periolivary n. * Medial n. trapezoid body (medial) * Sensory, Spinal trigeminal Cerebellum * n. Gigantocellularis * n. Paragigantocellularis lateralis * Medial vestibular n. * Perihypoglossal * Cuneate, Gracile n. Cervical spinal cord 	Descending contralateral (Tectospinal/Predorsal Bundle) Pons Reticularis tegmenti pontis Reticularis pontis oralis, caudalis Abducens, perioculomotor regions Facial n. Medulla Subnucleus B Medial accessory n. inferior olive Raphé Cervical spinal cord Commissural pathway

Table 2 Connections of the intermediate and deep layers

deep layers, which appears diffuse. Areas 19, 21, 7 and Clare-Bishop project diffusely and only to the deeper layers (Kawamura et al 1974); projections from other cortical areas have a similar pattern (Kuypers & Lawrence 1967, Garey et al 1968, Goldman & Nauta 1976).

The subcortical afferents to the intermediate and deep layers of the cat have been surveyed recently by Edwards and his colleagues (1979). They found over 40 sources of afferent input, which are also summarized in Table 2. These nuclei include reticular nuclei of the thalamus, midbrain, pons and medulla, several pretectal nuclei, the deep cerebellar nuclei and inputs from the sensory and spinal trigeminal, the cuneate and gracile nucleus and cervical spinal cord (Grofová et al 1978, Edwards et al 1979). In addition, the intermediate and deep layers receive a "patchy" projection from substantia nigra (Graybiel 1978b).

EFFERENT CONNECTIONS Efferent fibers of the intermediate and deep tectal pathways are organized in Table 2 into four pathways: ascending, descending ipsilateral, descending contralateral, and commissural. These pathways have been established in a diverse group of species including the primate (Harting et al 1973, Benevento & Fallon 1975, Kuypers & Maisky 1975, Graham 1977, Edwards 1977, Edwards & Henkel 1978, Edwards et al 1979, Kawamura & Hashikawa 1978, Holcombe & Hall 1978). The ascending pathway takes a route through the stratum opticum and the brachium of the superior colliculus to connect with regions of the thalamus and subthalamus such as the medial and inferior pulvinar, the magnocellular division of the medial geniculate, fields of Forel, certain nuclei of the intralaminar complex, zona incerta, and the reticular nucleus of the thalamus (Harting et al 1973, Benevento & Fallon 1975, Graham 1977).

The target structures of the ipsilateral descending pathway are primarily located in the midbrain and pons (Harting et al 1973, Graham 1977, Harting 1977, Baleydier & Magnin 1979). In the midbrain region, fibers distribute to the parabigeminal-lateral tegmental area, the mesencephalic reticular formation (nucleus cuneiformis and subcuneiformis) and the external nucleus of the inferior colliculus. In the pons, target structures involve the pontine reticular formation (nucleus reticularis pontis) and the so-called dorsolateral pontine nuclei (Harting et al 1973, Frankfurter et al 1976, Graham 1977, Harting 1977). The descending contralateral pathway, also called the tectospinal tract or the predorsal bundle, has more extensive regions of termination including regions of the pontine and medullary reticular formation, regions near and possibly within the abducens nucleus, subnucleus B of the medial accessory nuclei of the inferior olive, and cervical spinal cord (Harting et al 1973, Frankfurter et al 1976, Harting 1977, Castiglioni et al 1978, Weber et al 1978).

Now that we have emphasized the number and diversity of these efferent connections, we can begin to notice several patterns. First, several of the structures listed in Table 2 project to the cerebellum and may therefore provide pathways linking the superior colliculus with visual-oculomotor regions of the cerebellar cortex (Frankfurter et al 1976, Harting 1977, Weber et al 1978). These nuclei include the dorsolateral pontine nuclei, regions of the pontine reticular formation, and subnucleus B of the medial accessory nuclei of the inferior olive. Second, other projections involve structures concerned with movements involved in orienting responses. In cat, the descending colliculus connections from paralemniscal nuclei to the facial nucleus have been implicated in the control of pinnae movements, and in tree shrew, section of the predorsal bundle results in a loss of visual orienting responses (Henkel & Edwards 1978, Raczkowski et al 1976). Third, these layers project to regions in and about the abducens and oculomotor nuclei (Harting 1977, Edwards & Henkel 1978). This pathway provides for disynaptic, sometimes monosynaptic, excitation directly to oculomotor neurons in addition to less direct pathways through the pontine reticular formation (Grantyn & Grantyn 1976). Finally, many of the same structures we have discussed also project back to the superior colliculus.

Whether there is a laminar organization of cells that give rise to specific efferent projections is not yet certain. In cat, cells involved in the commissural pathway are located primarily in the stratum griseum intermediale (Edwards 1977, Magalhaes-Castro et al 1978). Axons coarsing in the predorsal bundle appear to arise from cell bodies located in the intermediate layer in squirrel (Holcombe & Hall 1978) and in the deep layers in galago (Raczkowski & Diamond 1978). Projections to the paralemiscal region arise from the deep layers while the projections to the parabigeminal nucleus arise from cells in the intermediate layers (Henkel & Edwards 1976). Projections to perioculomotor areas of the abducens arise primarily from the intermediate layer (Edwards & Henkel 1978). There is also disagreement concerning the laminar distribution of cells of origin that project to brainstem reticular regions. Graham (1977), using autoradiographic technique, found the greatest amount of transport in cases with the deepest injections. However, studies using retrograde tracing techniques find that after brainstem injections of reticular nuclei and spinal cord most labeled cells are located in both the intermediate and deep layers (Kuypers & Maisky 1975, Hashikawa & Kawamura 1977, Kawamura & Hashikawa 1978, Castiglioni et al 1978). The only tentative conclusion that may be made at this point is that each layer appears to give rise to somewhat different efferent connections. We suspect that future anatomical studies will reveal that each colliculus target structure will have its own laminar pattern such as has been already revealed in the superficial layers.

INTRACOLLICULAR ORGANIZATION

We have thus far considered five elements within the superior colliculus. Two elements, modulated and unmodulated visual cells, are found within the superficial layers and three elements, visually-triggered, short-lead, and long-lead movement cells, are found within the deep layers. Anatomical studies have provided no clues concerning the functional connections between these cells. Electrophysiological studies indicate, however, a temporal order of cell discharge to the onset of a visual target and the onset of a saccade, which provides a clue about the sequence of processing occurring within the superficial and deeper layers. The timing of discharge of each of the five elements is summarized in Figure 2A, the hypothetical relationships between cells derived from this temporal order is illustrated in Figure 2B, and the possible output signal conveyed by each cell type is shown in Figure 2C. This list of cell types, drawing of possible connections, and identification of possible functions is made explicit not to imply certainty but to make specific the hypotheses to be tested and modified.

Superficial Layers

UNMODULATED VISUAL CELLS Based on the latency of response to a visual stimulus, the temporal sequence of cell discharge in the superficial layers is from top down. As we have previously noted, unmodulated visual cells tend to have shorter response latencies and also tend to be located more dorsally in the superficial layers. Unmodulated visual cells could be regarded as conveying a retinal error signal; that is, the population of cells that discharge in the retinotopically organized map can indicate the difference between where the monkey is currently looking and where a saccade target is located. It appears that these cells derive their visual properties primarily from the retina and so may be considered as neurons of the primary visual pathways.

MODULATED VISUAL CELLS The discharge of the modulated visual cells that show enhancement could convey a selected retinal error signal; one visual error signal selected from many to be used as a target for a saccadic eye movement. Since the visually enhanced response incorporates information that an eye movement is about to occur, it can hardly be regarded as an early stage in the decision to make a visually guided eye movement; it is more accurately viewed as the result of this process. One function of the enhancement may be to prolong the visual response which then more easily overlaps in time with the discharge of the movementrelated cells in the deep layers.



Figure 2 Temporal sequence of cell discharge in monkey superior colliculus (A), hypothetical intracollicular organization based on this sequence (B), and possible signal conveyed by each of these elements.

The drawing at the top of A indicates the onset of a visual target on the top line with the subsequent saccade from a fixation point to that target 200 msec later shown on the second line. Subsequent lines show schematic representations of the discharge of each type of cell in relation to stimulus onset and the subsequent saccade. The dashed horizontal line indicates the division between the superficial and intermediate-deep layers. The discharge of the visually triggered movement cell is similar to that of the short-lead cell but the cell would not show such a discharge if the saccade were not to a visual target. Two examples of the discharge leads the onset of the saccade target in a series of trials in which the monkey can anticipate the temporal sequence.

B shows a hypothetical sequence of these cells. Small arrows between boxes emphasize that the intracollicular connections drawn are based on timing of discharge, not known anatomical connections. No afferents are shown; arrows on the right emphasize the possibility of outputs from every layer even though only certain outputs (visually triggered movement cells and short-lead movement cells) are emphasized in the text. It is obvious that the temporal sequence shown only eliminates some alternatives but does not require the connections shown. The connections drawn are derived from the temporal relation of cell discharge to visually initiated saccades but other nonsaccadic functions of the colliculus might produce different temporal relations implying different intracollicular connections.

C shows for each variety of cell the type of signal it could convey to the rest of the nervous system since the superior colliculus must be part of an extended system for the initiation of saccades.

The function of the suppressive input to some of these active cells might be to ensure that no new retinal error signal is generated during a saccade; the retinal error signal would not only be selected but it would usually not be updated until the saccade is over. The source of the suppression seen in many of the active cells in the superficial layers is unknown.

Deep Layers

LONG-LEAD CELLS In contrast to the top down sequence shown for the superficial layers and in traditional notions of collicular function, the order of the onset of the saccade-related discharge in the intermediate and deep layers is from the bottom up (Mohler & Wurtz 1976). Long-lead movement cells deep in the colliculus start to discharge earlier, before the onset of saccades, than the more dorsal cells. In fact, the discharge of long-lead cells occurs as early as any other demonstrated saccade-related neurons in the brain. For example, long-lead movement cells in the colliculus precede a saccade by 150 msec or more while long-lead burst neurons in the pontine reticular formation may lead the eye movement by about 100–125 msec (Fuchs & Luschei 1972, Keller 1974).

The discharge of these long-lead cells could be regarded as a selected movement field signal since their discharge indicates that one part of the field has been selected as opposed to another. This selection is not necessarily dependent upon visual information present at the moment of saccade onset since the discharge of these cells can anticipate the visual signal to make a saccade and can occur before saccades made in total darkness. One wonders whether the slow and irregular start of the cell may reflect a tentativeness of the selection and whether the large movement fields of these cells reflect a lack of spatial specificity in the selection process. Certainly, the movement fields of these cells taken individually would seem too large to accurately define a selected eye movement. This selected movement field signal presumably arrives at the colliculus rather than being generated by it, but the source of this signal may be any of the myriad possibilities listed in Table 2.

SHORT-LEAD CELLS The transition from long-lead to short-lead cells involves both a temporal change, trimming the prolonged discharge on a high background rate to a final burst on a near silent background, and a spatial change, narrowing the size of the movement field from broad to narrow. This latter step might result if short-lead movement fields are derived from the overlap of subjacent fields in a way comparable to that suggested by McIlwain (1976) for visual fields. Alternatively, these fields might be spatially refined by an extracollicular input. Because of the smaller size of their movement fields, short-lead movement cells are most closely related to the amplitude of the saccade. For this reason and because the discrete and vigorous saccade-related discharge of these cells precedes the eye movement by the same latency (20 msec) as a saccade elicited by stimulation, these cells appear to be a likely output element of the colliculus.

The discharge of the short-lead movement cells may be considered as a delayed error signal—a delayed signal because the discharge occurs just before the saccade rather than after the visual stimulus, and an error signal because their discharge is associated with a particular saccadic amplitude that reduces the error between where the eye is now and where it will soon be.

VISUALLY TRIGGERED CELLS The visually triggered movement cell is shown in Figure 2 as successive stage in the processing sequence because it incorporates both movement-related activity and activity resulting from the appearance of a visual target. The visual target for these cells is a necessary condition for the movement-related discharge to occur: the movement discharge may be viewed as "gated" by the presence of the visual stimulus. This gating effect [or partial gating in some cells (Mohler & Wurtz 1976, Mays & Sparks 1979)] is independent of any discrete visual response the cell may have to the visual stimulus. Thus these cells suggest a sequence of processing that involves not only an upward flow of movement activity within deep cells, but also a downward flow of visual processing from the superficial layers. Since the visually triggered movement cells are encountered in the most dorsal part of the movement layers, an input from visual cells could be quite direct, perhaps involving dendro-dendritic connections. Although there is no anatomical evidence on this point, Golgi material indicates considerable overlap in the distribution of superficial and intermediate layer cells (Valverde 1973, Langer & Lund 1974, Tokunaga & Otani 1976) and electron micrographs show that dendro-dendritic connections are frequent (Sterling 1971). Alternatively this connection may be indirect and may involve an extracollicular source such as the frontal eye fields and other extra-striate visual areas. The close functional relationship between the visually triggered movement cells and the active cells with enhanced responses is emphasized by the difficulty in distinguishing in some cases one cell type from the other (Wurtz & Mohler 1976a).

Visually triggered cells might be regarded as transmitting a delayed retinal error signal since these cells add the requirement of a visual gating signal to the delayed error signal. Like the short-lead cells, these cells probably also represent an important collicular output to the oculomotor system. A second possible connection that crosses the boundaries of the two divisions of the colliculus is also suggested by the temporal sequence of discharge. This connection might provide the input producing the visual enhancement effect in the active visual cells and is shown as a dashed line in Figure 2B from the long-lead movement cells to the active visual cells. Long-lead movement cells discharge during the time that a stimulus target for a saccade still falls on the receptive field of a cell and, when these long-lead cells show an anticipatory response during a series of trials to the same target, their discharge would overlap even the onset of the visual stimulus. Since there is no evidence that the deep cells connect to the superficial cells directly (Edwards, in press), this connection might be indirect, perhaps via the parabigeminal-lateral tegmental region. Alternatively, the input to the superficial layers could arise from the same source that activates the long-lead cells.

This summary indicates how our thinking about the organization of the superior colliculus has come full circle. The original ideas of collicular organization centered on a transition from visual activity in the superficial layers to movement activity in the intermediate and deep layers (Schiller & Koerner 1971, Robinson 1972, Wurtz & Goldberg 1972b, Sprague 1975). This view was made compelling by the registration between the visual and movement maps, but the subsequent view emphasizing the separation of the colliculus into superficial and deeper layers (summarized in the introduction) left little reason for the visual-motor convergence. The present emphasis on the convergent flow of visual and motor processing provides a new rationale for the registration but maintains the fundamental separation between superficial and deeper layers.

RELATION TO OCULOMOTOR SYSTEM

In the previous section we identified five cell elements within the colliculus. We now consider the relation of these elements to the oculomotor system and specifically to visually guided eye movements. Initiation of visually guided saccades must depend on at least three events: the selection of the visual target, the determination of retinal error, and the triggering of the saccade.

Selection

Target selection within the visual field is usually taken for granted in analyses of oculomotor control since reference is made to *the* target or *the* retinal error, but even in rarified laboratory experiments more than one visual target is usually present, and some type of selection process must precede the initiation of the saccade. While it would be premature to argue that the selection process is complete within the colliculus, several cell types already considered are appropriate for this function: long-lead cells show an early discharge related to one part of the visual field; visual responses are enhanced before saccades to one area of the field; visually triggered movement cells discharge only before saccades to a visual target in one part of the visual field. This spatial selection function is essentially the shift of visual attention view applied specifically to eye movements (Goldberg & Wurtz 1972b, Wurtz & Goldberg 1972c), which subsequent experiments have shown is an appropriate restriction (Wurtz & Mohler 1976a).

Retinal Error

This factor, essentially the visual guidance of the saccade, has been the factor most thoroughly considered by control theory models of saccade generation (see Robinson 1973 for review). The basis of these control theory models is that the eye musculature requires a pulse and a step of activity in the oculomotor neurons to move the eye to a new position and hold it there. Neural elements that could provide this input to the oculomotor neurons have been identified in the paramedian pontine reticular formation. These are the medium-lead burst cells, which discharge in a vigorous burst of activity 15 msec prior to the saccade, and the tonic cells, which have a discharge rate related to eye position. Thus both components of the oculomotor discharge are coded in the temporal domain: the pulse, a transient change in discharge frequency, and a step, a steady state change in frequency. Any scheme concerning the connection of the superior colliculus to the brainstem occulomotor system must therefore involve a translation from "which" cell is firing to the "frequency" of cell discharge. This translation is frequently referred to as a spatial to temporal transformation. The result of this transformation is that larger saccade amplitudes are represented by higher frequencies of cell discharge.

How this transformation comes about is unknown, but we think that there may be two mechanisms by which the colliculus translates its neuronal discharge, coded by location, to an oculomotor discharge, coded in frequency. First, the spatial to temporal transformation may result from the density of connections from different parts of the movement map. In cat, Precht et al (1974) found that the thresholds for producing EPSP's in the cat abducens nucleus was higher from stimulating electrodes in the anterior colliculus than in the posterior colliculus. Later, Edwards & Henkel (1978) found that the number of cells labeled by HRP injection of the pontine oculomotor area of the cat was sparse in the intermediate layers of the anterior colliculus and more dense in the posterior colliculus. They suggested that the greater density of neurons in the posterior colliculus might be the anatomical mechanisms by which the posterior colliculus exerts a stronger effect upon the abducens nucleus and thereby produces saccades of greater amplitude. If we assume that synaptic drive is related to discharge frequency in brainstem oculomotor neurons, then the result of activating more posterior regions of the colliculus, which represent more peripheral regions of the visual field, is to produce a greater frequency of discharge. However, the evidence for this mechanism for the spatial to temporal transformation is not suggested by the experiments of Raybourn & Keller (1977), who stimulated the superior colliculus and found responses in the eye movement-related cells of the pontine reticular formation, but did not find any lower threshold for the stimulation effects in the anterior than in the posterior colliculus (for long-lead burst cells). Instead, they found that monosynaptic connections were more common in the anterior than in the posterior colliculus.

A second mechanism which may contribute to this spatial to temporal transformation is the size of the movement fields within the colliculus. In general, the greater the amplitude of the saccade, the larger the movement field. Larger movement fields imply that any given saccade will have more cells discharging before the saccade and therefore greater synaptic drive to the brainstem oculomotor areas. Again, larger saccades would produce greater synaptic drive, which would lead to higher frequency in oculomotor areas.

An implication of this type of transformation is that any damage to the colliculus should produce a shortening of saccades, never a lengthening. Following partial ablation of the colliculus, saccades do fall short of the target as indicated by an increased frequency of small corrective saccades that move the eye farther away from the original starting position (Mohler & Wurtz 1977). This shortening of saccades has been studied only in the central 25° of the visual field. The hypothesis suggests that the damage would be more striking in the periphery.

Another transformation of the error signal that would be required by a recent model of the oculomotor system (Robinson 1975, Zee et al 1976) is a shift from a retinotopic coordinate system to a spatial coordinate system. This new model of the oculomotor system has several conceptual advantages for producing the appropriate burst of neural activity required to initiate a saccade. One advantage of the model is that since the error signal is in spatial coordinates, this signal would be available to guide head, hand, and body movements as well as eye movements, a particularly perspicacious parsimony. The disadvantage as far as analysis of the colliculus is concerned is that the model requires the error signal to be in spatial coordinates at least a hundred msecs before the onset of the saccade. As we have seen, the movement-related colliculus cells that discharge as late as 20 msec before saccade onset are in a retinotopic coordinate system, not a spatial one. At this point one can neither expect cells with position-related signals to be found, and preliminary reports have suggested that such signals might exist (Sparks et al 1977, Peck & Schlag-Rey 1978), or one can modify the model. The modification needed to fit the characteristics of the cells described would require a shift into spatial coordinates much later in the processing sequence, preferably just before the control of burst duration. The visual cells or enhanced visual cells in the colliculus could then provide the retinal error signal and, more important, the visually triggered movement cells could provide a delayed selected retinal error signal. The cellular activity within the colliculus would then be incorporated into a logical visual-motor sequence instead of being excluded as in the model formulated by Robinson and his colleagues (Robinson 1975, Zee et al 1976).

Trigger

It is necessary for the oculomotor system to know when a saccade should be initiated as well as where it should be directed, hence recent models of the oculomotor system incorporate a trigger in the model for initiation of the saccade (Robinson 1975, Zee et al 1976). This trigger closes a switch that enables the burst generator. The cells that might correspond to this switch have been identified as the pause cells (Keller 1974) lying near the midline of the pons; when they pause, it is suggested that they release the medium-lead burst neurons from inhibition. Initiation of this pause, and therefore the saccade, could be another function of the output cells of the superior colliculus, one of triggering saccades, not necessarily one of guiding them.

Tests of Oculomotor Relations

While the superior colliculus could logically be related to the oculomotor system in any of the ways described, that it is so related remains to be established. The close relationship of the superior colliculus to the initiation of saccadic eye movements demonstrated by electrical stimulation has already been considered, but electrophysiological and ablation experiments have also evaluated this relationship.

The best established output from the superior colliculus to the oculomotor system is to the pontine reticular formation. "Burst" type movement cells are most frequently activated antidromically by stimulation of the pontine area (Keller 1980), which is consistent with the emphasis on the short-lead movement cells as important output cells of the colliculus, as "burst" cells are quite similar (see Figure 2). The relation of the types of pontine cells to the colliculus has been investigated (Raybourn & Keller 1977) by stimulating the superior colliculus and recording the response of pontine neurons. Stimulation of the colliculus had the most direct and powerful effect on the pontine long-lead burst neurons and medium-lead burst cells. Thus, if the output of the colliculus contributes to the frequency of discharge related to the amplitude of saccades, it must do so indirectly through the long-lead burst cells. Collicular stimulation also produced short latency excitation in pause neurons, which suggests that the colliculus contributes to the background discharge which, when removed, may be a trigger for saccadic eye movements.

One would expect ablation of the superior colliculus to be devastating to the generation of saccadic eye movements but this has not been the case. One earlier report did suggest difficulty in moving the eyes following ablation of the monkey superior colliculus (Denny-Brown 1962) but another study found no such deficit (Pasik et al 1966). When eye movements were recorded (Wurtz & Goldberg 1972b, Mohler & Wurtz 1977), the deficit in saccades following large but incomplete unilateral collicular ablation was clear but circumscribed. The monkeys with ablations continued to make visually guided saccades into the visual field related to the ablated superior colliculus, but they tended to do so with longer (by 50–250 msec) latencies to initiate saccades, and they showed an increased frequency of small corrective saccades. The longer latency to make saccades might result from a deficit in any of the three necessary processes from the use of a less efficient pathway for selecting the saccadic target, determining retinal error, or triggering the saccade.

The lack of a substantial visual guidance deficit must indicate either that the colliculus does not perform the stimulus selection and retinal error processes or that it performs them in parallel with another source. The other source of this visual input must be dependent upon the striate cortex since ablation of this area along with the colliculus eliminates visually guided saccades (Mohler & Wurtz 1977). On the other hand, ablation of striate cortex also leaves the monkey able to make saccades to a visual target once his recovery is sufficient for him to detect the target, which indicates that the colliculus can indeed function without cortex. The remaining pathway for this visual guidance may involve the frontal eye fields since stimulation of this area elicits saccades even following collicular ablation (Schiller 1977). The ability of humans to make visually guided saccades and pointing movements even with extensive occipital brain damage (and a lack of perception of the target) has been reported (Pöppel et al 1973, Perenin & Jeannerod 1975, Weiskrantz et al 1974).

The frequency of spontaneous saccades is also reduced following ablation of the colliculus in monkey (Rosvold et al 1958, Denny-Brown 1962, Pasik et al 1966, Albano & Wurtz 1978) and in man (Heywood & Ratcliff 1975). This deficit in spontaneous saccades might indicate a decoupling of the ability of a stimulus to initiate a saccade. This is consistent with the reduction in distractibility during a fixation task as judged by the number of saccades made to a suddenly appearing peripheral stimulus in the monkey (Albano & Wurtz 1978). An analogous reduction in distractibility was reported earlier for the rat (Goodale & Murison 1975). These deficits might well be related to the stimulus selection or trigger functions of the colliculus we have already discussed.

Additional ablation studies in monkeys have found deficits in reaching tasks, particularly in the peripheral visual field (Keating 1974, 1976, Butter 1974a,b, Butter et al 1978) and more complex tasks (Rosvold et al 1958, Anderson & Symmes 1969, Kurtz 1977, Latto 1978), but whether these deficits relate to the initiation of saccades is unknown.

CONCLUSION

We have concentrated on one function of the superior colliculus, the initiation of saccadic eye movements, because the evidence on this particular function allows us to begin to outline how sensory information might lead to movement. Rather than a direct visual to motor transition within the colliculus, we find several steps, which are part of a sequence required in executing visually guided saccadic eye movements. The colliculus in turn is part of a more extended system, which probably includes the cerebral cortex and certainly connects to the pontine areas related to saccadic eye movement.

Saccadic eye movements, moreover, are only one part of a more general mechanism of gaze shift or orientation that involves head and body as well as eyes. Other animals rely more heavily on head and body movements than do primates and the organization of the superior colliculus or optic tectum in these animals may be related to such differences in behavior. For example, the cat has a tendency to use its head proportionately more than its eyes for orienting and the superior colliculus in the cat is more clearly related to head movements than is the colliculus in the monkey. The primate superior colliculus may represent a specialization of a more general function —that of orientation.

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