EYE MOVEMENTS AND THE HIGHER PSYCHOLOGICAL FUNCTIONS

Edited by
John W. Senders, Dennis F. Fisher
and Richard A. Monty

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In any scientific endeavor,
You must have men who are clever
And men who are nice
As well, like John Weisz.
Without whose support and encouragement
it would have been impossible
to put this book together.

JOHN W. SENDERS

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Preface

This volume represents the edited proceedings of the second symposium on eye movements and behavior sponsored by the U. S. Army Human Engineering Laboratory. The conference was held at the Naval Postgraduate School in Monterey, California on February 6–9, 1977.

This volume is intended to serve as a complementary volume to R. A. Monty and J. W. Senders (Eds.), *Eye Movements and Psychological Processes,* published by Lawrence Erlbaum Associates (1976), rather than as a revision or update of it.

We wish to thank the U. S. Army Human Engineering Laboratory for sponsoring the symposium. In particular, we once again wish to express our deep appreciation to Dr. John D. Weisz, Director of the Human Engineering Laboratory, for his continued encouragement and support. It is to him that we have dedicated this volume.

We are also deeply indebted to Dr. Francis C. Volkmann for organizing and chairing the first session, and to the staff of the Naval Post Graduate School, especially Ms. Ruth Guthrie and Dr. J. Kenneth Arima, who made this one of the smoothest running symposia we have ever witnessed. We are grateful to Ms. Judy Weishampel for keeping the work of the first editor on an even keel and for maintaining liaison among us. Once again, special thanks go to B. Diane Eberly (now operating under the alias of Mrs. B. Diane Barnette), who since the last volume has advanced from the role of secretary to mathematics aide. She, nevertheless, was responsible for handling a myriad of details surrounding planning of the symposium and the resulting publication.

JOHN W. SENDERS
DENNIS F. FISHER
RICHARD A. MONTY

Introduction

This volume reflects the proceedings of a conference held in February 1977 at the Naval Postgraduate School at Monterey, California, and is the natural successor to an earlier volume of the proceedings of a conference in Princeton, New Jersey entitled *Eye Movements and Psychological Processes* (Monty & Senders, 1976). The earlier conference and book were organized with what we, as organizers and editors, hoped was a logical sequence, beginning with a common base of nomenclature, information, and understanding of the underlying mechanisms of oculomotor control, then progressing through a series of topics relating eye movements to processes that, at least conceptually, advanced from simple to more complex.

To quote from the preface of the earlier volume: "Our purpose was to bring together investigators representing different theoretical positions and methodological approaches to present their recent findings, to debate the theoretical points of view, and to identify and discuss the major research problems." That is, of course, an adequate statement of the purposes of the second conference as well. Parts of the first conference were devoted to search and scanning, to reading, and (Part 7) to eye movements and higher mental processes. The second conference was aimed at providing a greater opportunity for discussing these "higher mental processes." In view of the fact that there were many people at the second conference who had not attended the first or who may not have read the first proceedings, we thought it necessary to have one half day devoted to reviewing topics presented during two whole days at the first meeting.

Part I of this volume is devoted to an intensive review of the underlying processes and psychological functions of eye movements. It includes discussions of the relationships of cortical and subcortical visual areas to eye movements and visual processing associated with them; information about the position of the eye in the head and the perception of visual space; saccades and visual functioning; and masking. These four papers were essentially didactic in nature. All persons working in the area of eye movements must be aware of the status of knowledge relating to those topics in order to be able to design experiments appropriately and to interpret results accurately. Another session was devoted to methodology and models in order to update information since the earlier conference and published proceedings.

Beginning with the third session, questions of the effects of tasks on eye movements and the effects of eye movements on tasks were addressed. Here, out of necessity, higher mental processes include dealing with particular kinds of application: reading, watching television, flying aircraft, looking for objects, counting things, and the like. Although not all papers presented at the meeting are included in this volume, all were informative and made a contribution to the participants' understanding of the complex relationships between eye movements and behavior. Obviously, behavior and eye movements are the variables which could be compared and correlated. For most of the participants, of course, the behavior was then interpreted in terms of "higher mental processes." It seems appropriate once again to quote from the earlier volume:

> Now we are concerned with the question of what people do with eye movements.
>
> It is an important question. We spend our time, as Steinman has pointed out, sometimes voluntarily selecting places in the visual field to look at, and at other times allowing a process to go on that one is nearly unaware of, in which the eye successively fixates different parts of an apparently nicely stabilized visual field. From these "looks" we continually reconstruct, renew, and refresh some internal map of what is "out there."
>
> There has been continuing study over the last 25 years of how people look at dynamical things, for example, dials on an aircraft instruments panel [when one is flying], or faces if one is engaged in conversation or lecturing. They change when one is not looking at them; sometimes they change while one is looking at them. Certain rules can be established relating the content of dynamic displays to the distribution of visual attention across these displays.
>
> Another aspect of the visual world is the static aspect. We look at a landscape and things mostly stay where they are. Trees don't get up and walk around; paintings and cast-iron eagles, in particular, tend to stay exactly as they have been. Yet the eye does come back from time to time to look once again at a piece of the visual field which it has just recently visited and from which it has departed. A very interesting problem is that of the relationship between the content and structure of a [static] visual field, and the way in which one distributes visual attention over that field.

And further:

> The possibility of keeping physical records as aids to memory by the use of spatially organized materials must have occurred very early to ancient man. The

> particular ways in which these materials are specially organized, however, has varied through all possible arrangements. Languages may be written from left to right or right to left and top to bottom or bottom to top, in vertical lines and in horizontal lines, and there is no particular reason to assume that any one way of organizing material is better than any other. However, some serial arrangement in one sense or another must be imposed if the written material is to be interpreted correctly. The degree, however, to which positional structure within sentences is important depends upon the degree to which the language is inflected. English is a highly positional language in which the meanings of sentences are determined both by the words within the sentence and by the positions they hold relative to the other words. This is not necessarily true of all languages.

Even more interesting, of course, is the higher mental process involved in the extraction of meaning from written language. Much of the work in this area is related to the hypothetical internal representation of the material that is read and the relationship of that material to the eye movements made during the reading as well as subsequent to it, as was the case for some of the chapters in the earlier volume. Virtually all the chapters beyond the first set in this volume imply that there is "a strong direct link between the way in which the eye moves and the fact of its moving at all, and the kind of perceptual and memory structure which is being used by the observer to store and organize information."

Where it has made a contribution to the reader's understanding of the content of a paper, we have preserved the discussion with only a few deletions. In some cases, the points raised during the discussions were as important to those present as the paper itself. Although all the papers presented at this meeting had been prepared in advance, unlike those of the first meeting, we have attempted to preserve, through the discussions, the spirit of intense involvement and serious give-and-take that pervaded the whole meeting. We hope that the chapters and comments presented here will encourage subsequent research efforts using eye movements, so that the state of the art and understanding of the processes are continually advanced.

* * * * *

WARREN H. TEICHNER, 1921-1978

Just before this book went to press, the editors learned of the death of Warren H. Teichner, who was a participant in the symposium and a contributor to this volume. We were saddened to lose a good friend and colleague who had contributed so much to Experimental and Engineering Psychology.

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Part I

BASIC PROCESSES

I.1

The Visual Substrate of Eye Movements

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Michael E. Goldberg
Armed Forces Radiobiology Research Institute

The visual system is continually bombarded with stimuli. Not all of these stimuli are of equal significance; some are ignored whereas others elicit a shift of attention and an eye movement. The visual processing preceding such a movement requires analysis of the visual stimulus in terms of three questions: where is it, what is it, and is it behaviorally significant? Recent work has attempted to analyze several cortical and subcortical visual areas in order to determine their contributions to the visual processing preceding eye movements. We will discuss these questions with reference to the superior colliculus, the striate cortex (area 17), the posterior parietal cortex (area 7), and the frontal visual area (area 8, "the frontal eye fields") of the rhesus monkey.

SUPERIOR COLLICULUS

The cells in the superficial grey and optic layers of the monkey superior colliculus respond to visual stimuli (Cynader & Berman, 1972; Goldberg & Wurtz, 1972a; Humphrey, 1968; Schiller & Koerner, 1971). Unlike cells in striate cortex (Hubel & Wiesel, 1968; Wurtz, 1969a), visual cells in the superior colliculus are not sensitive to the shape or orientation of stimuli. Instead, these respond to the onset of small spots of light within their receptive field, and also to stimuli moving over a wide range of directions and stimulus velocities (Goldberg & Wurtz, 1972a) as shown in Fig. 1. They have large receptive fields, and receptive field size increases with depth in the colliculus (Goldberg & Wurtz, 1972a; Humphrey, 1968). It is highly unlikely that cells in the colliculus can provide much qualitative information about visual stimuli, although ensembles of collicular neurons

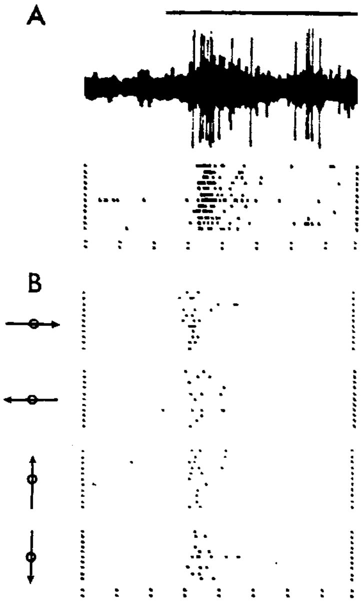

FIG. 1. Response of a pandirectional cell to both stationary and moving stimuli. The cell was recorded from the superficial layers of the superior colliculus of an awake monkey. (A) illustrates the discharge of the cell to a stationary spot of light flashed in its receptive field. The horizontal line above the trace indicates the time of stimulus onset. The raster in (A) shows the response of the same cell to repeated presentations of the same stimulus. Each dot represents either a discharge of the cell or the beginning or end of a line. Each horizontal line of dots indicates a single fixation by the monkey and a single presentation of the stimulus. (B) depicts the response of this cell to a spot of light swept across the receptive field while the monkey fixates. The interval between pairs of dots is 50 *msec.* (From Goldberg & Wurtz, 1972a. Reproduced with permission.)

could provide some information about the spatial localization of visual stimuli (McIlwain, 1975).

Collicular neurons do have several features that may be useful in analyzing the behavioral significance of stimuli. If a visual stimulus is going to be the target for a saccadic eye movement, cells in the superficial layers of the colliculus which ordinarily respond to that stimulus will have an enhanced response. This enhancement is selective; it does not occur before eye movements to stimuli that are not in the receptive field of the cell (Goldberg & Wurtz, 1972b; Wurtz & Mohler, 1976a), as shown in Fig. 2. This pre-eye movement activity is an enhancement of the visual response. It is time-locked to the onset of the visual stimulus and does not appear if the appropriate eye movement occurs in the absence of a visual stimulus. The enhanced activity in these neurons may signal that (1) there is a stimulus in a certain part of the visual field, and (2) the eye is going to (or should) move to fixate that stimulus.

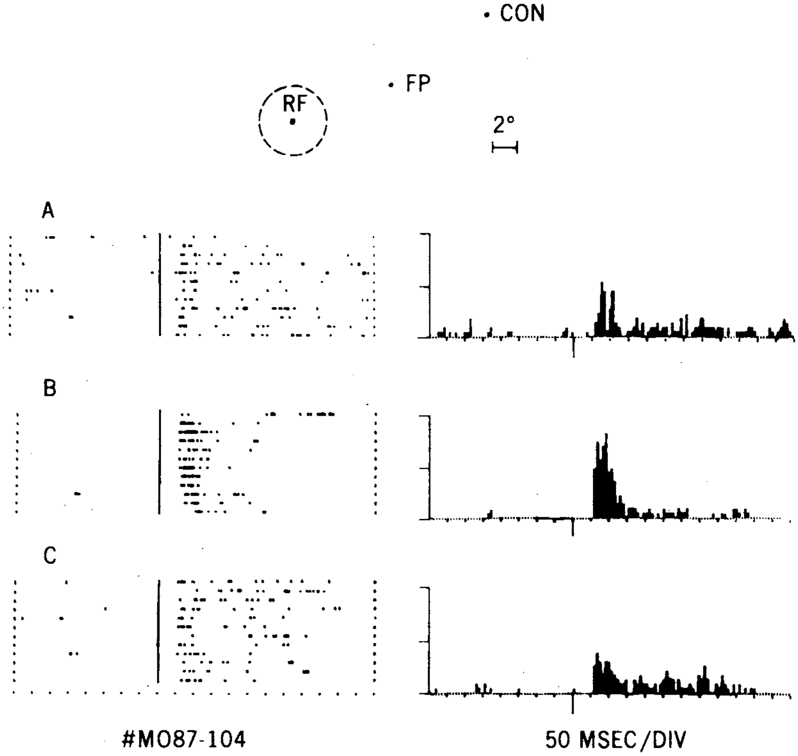

FIG. 2. Enhancement specificity for a collicular neuron. (A) shows the response of the neuron to a spot of light flashed in the receptive field (RF) while the monkey fixates. (B) illustrates the discharge of the same cell to the same stimulus when the monkey uses that light as the target for an eye movement from the fixation point (FP) to the RF stimulus. (C) presents the response of this cell to the RF stimulus on the trials when the animal makes an eye movement to the control point (CON). Histograms sum the data in the adjacent raster; full scale of the vertical axis, 250 spikes/sec per trial. (From Wurtz & Mohler, 1976a. Reproduced with permission.)

Moving objects are powerful stimuli for collicular neurons. During an eye movement the entire visual field moves across the retina allowing stimuli that would not have been salient when the eye was stationary to become so. The brain must have a system that can differentiate between real stimulus movement in the environment and artifactually salient stimulus movement caused by movement of the eye across a stationary field. Many cells in the superficial layers of the superior colliculus that respond to real stimulus movement do not respond to self-induced stimulus movement (Robinson & Wurtz, 1976) as shown in Fig. 3. These results are in contrast to data from the striate cortex, where cells do not distinguish between these two types of stimulus movement (Wurtz, 1969b). The ability of collicular neurons to distinguish real from self-induced

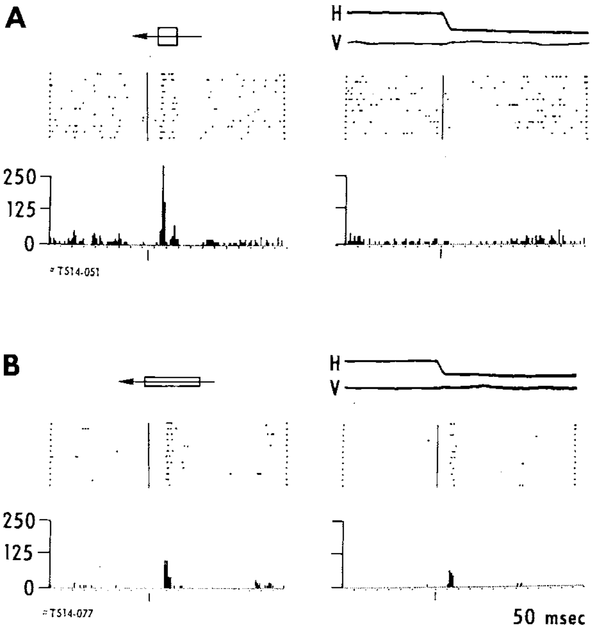

FIG. 3. Activity of cells which do and do not distinguish real from self-induced stimulus movement. (A) left: shows the response of a collicular neuron to a stimulus swept across the receptive field at 900°/sec while the animal fixates. (A) right: shows the lack of response of the same cell to comparable stimulus movement generated by a 20° eye movement. Representative electrooculogram traces are illustrated above the raster. Raster and histograms for eye movement experiments are triggered on the beginning of the eye movement. (B) illustrates the results of similar experiments conducted on a cell which does not distinguish between these types of stimulus movement. (From Robinson & Wurtz, 1976. Reproduced with permission.)

stimulus movement is accomplished by a threshold elevation of at least one log unit that is present over a wide range of stimulus directions. It is unlikely that collicular cells fail to respond to self-induced stimulus movement because of movement of the visual background, since the differentiation is seen when peripheral visual factors are drastically reduced, as illustrated in Fig. 4. This lack of response is due to an extraretinal input. When the monkey is placed in total darkness, one can see a suppression of background activity after eye movements, noted in Fig. 5. This suppression indicates the presence of the extraretinal input. Collicular neurons which do not differentiate between real and self-induced stimulus movement do not show this background suppression in total darkness. The suppression begins at roughly the time that visual stimuli resulting from an eye movement would reach the colliculus.

The source of extraretinal suppression is not yet known. It is not proprioceptive from the extraocular muscles, since it is present when the monkey

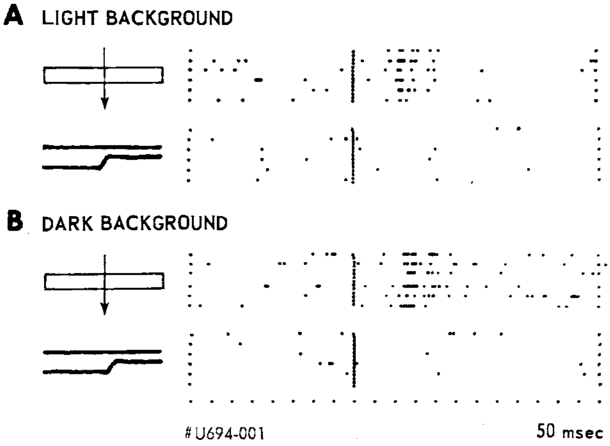

FIG. 4. Reduction of visual factors with persistence of the differentiation between real and self-induced stimulus movement. (A) illustrates the response of a cell to rapid stimulus movement while the monkey fixates, and lack of response to stimulus movement caused by an eye movement in the light. (B) shows comparable results when these experiments are conducted after a large reduction in background illumination. (From Robinson & Wurtz, 1976. Reproduced with permission.)

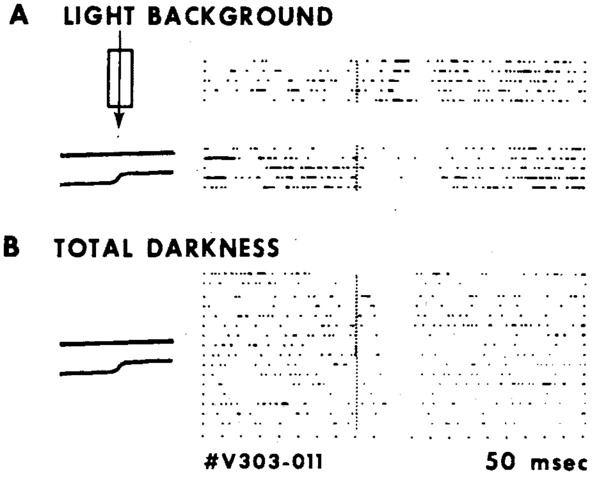

FIG. 5. Demonstration of an extraretinal suppression for collicular neuron which distinguished between types of stimulus movement. (A) shows the response of a cell with externally generated and self-induced stimulus movement. (B) illustrates a period of suppression of background firing after eye movements made spontaneously in total darkness, indicating the presence of the extraretinal input. (From Robinson & Wurtz, 1976. Reproduced with permission.)

attempts to make an eye movement after paralysis of its extraocular muscles (Richmond & Wurtz, 1977). It must be a corollary discharge originating from some system that discharges with eye movements. One attractive candidate for such a system is the small set of cells in the frontal eye fields that discharge after eye movements (Bizzi, 1968; Bizzi & Schiller, 1970; Mohler, Goldberg, & Wurtz, 1973), since it has been shown that the frontal eye fields project to the superficial layers of the superior colliculus (Astruc, 1971; Künzle, Akert, & Wurtz, 1976). Furthermore, stimulation of the frontal eye fields of the cat produces a reduced responsiveness of collicular neurons to visual stimuli (Guitton & Mandl, 1974).

The neurons in the superior colliculus that differentiate between real stimulus movement and self-induced stimulus movement seem to be those which show enhancement of their visual response before eye movements (Robinson & Wurtz, 1976) as shown in Fig. 6. The physiology of these neurons would, therefore, lead one to postulate that they have nothing to do with qualitative analysis of the visual field, something to do with spatial localization, and a great deal to do with identifying significant stimuli as targets for eye movements. These postulates are supported by the results of ablation studies that have shown a large increase in the latency of onset of the eye movements to fixate a peripheral target (Wurtz & Goldberg, 1972), illustrated in Fig. 7, and a small decrease in the accuracy of eye movements, as indicated by an increase in the number of corrective saccades following large saccades to fixate peripheral objects (Mohler &

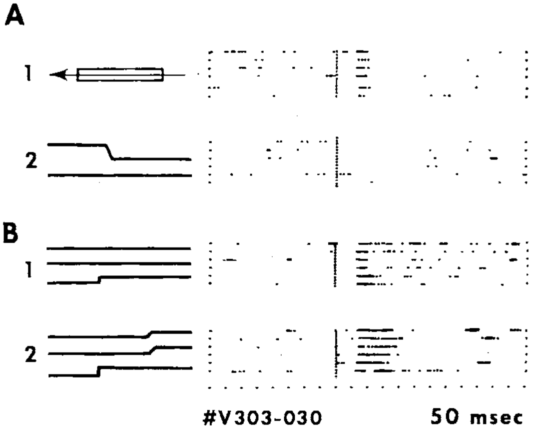

FIG. 6. Stimulus movement differentiation and response enhancement in the same collicular neuron. (A1) documents the discharge of this cell to real stimulus movement and lack of response (A2) with self-generated movement. (B1) shows the response of this cell to a stationary spot of light flashed in the receptive field while the monkey fixates. (B2) presents the enhanced response to this cell to the same stimulus when it is to be the target for a saccadic eye movement. (From Robinson & Wurtz, 1976. Reproduced with permission.)

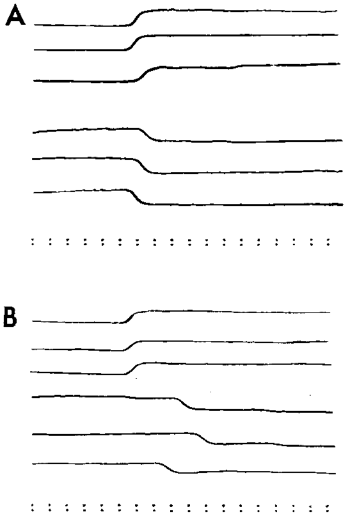

FIG. 7. Eye movements before and after a focal lesion in the superior colliculus. (A) shows a monkey's eye movements to targets 10° to the left (first three traces) and 10° to the right (second three traces). Each sweep is triggered by the saccade target onset. A microelectrode was used to find the area in the superior colliculus with neurons with visual receptive fields that included the target point, and then a focal electrolytic lesion was made through the microelectrode. (B) shows the eye movements to the same points as in (A) 24 hours after the lesion. The latency of eye movements to the target contralateral to the lesion is lengthened. (From Wurtz & Goldberg, 1972. Reproduced with permission.)

Wurtz, 1977). These data suggest that the stimulus selection process is impaired, whereas the mechanism for programming the eye movement is largely undisturbed.

STRIATE CORTEX

The work of Hubel and Wiesel (1968), among others, has shown that neurons in the striate cortex are extremely sensitive to the orientation and shape of visual stimuli. Some striate cortical neurons show presaccadic enhancement, but it is nonselective, occurring with eye movements to many points of the visual field (Wurtz & Mohler, 1976b). Although some striate neurons show a slight decrement in activity associated with eye movements in the dark when subjected to computer averaging (Duffy & Burchfiel, 1975), they do not exhibit the dramatic differentiation between real and self-induced stimulus movement that is shown by neurons in the superior colliculus (Wurtz, 1969b).

Immediately after striate cortical lesions, monkeys have a hemianopia. Within several weeks they can be trained to detect flashed stimuli in the contralateral field, and to make eye movements to them (Mohler & Wurtz, 1977). These eye movements and detections are presumably subsumed by the superior colliculus, since immediately after a subsequent collicular ablation these animals cannot perform either task and can never be trained to perform them. Neurons in the superior colliculus of animals with striate ablations still show specific presaccadic enhancement. Neurons in the striate cortex therefore contribute to eye movements by telling the brain what is in the contralateral visual field, and where it is, but they do not provide information about the behavioral significance of the target. Two other cortical areas provide information about behavioral significance of stimuli: the frontal eye fields (area 8) and the posterior parietal cortex (area 7).

FRONTAL AND PARIETAL CORTEX

Since the early stimulation experiments of Ferrier (1874), it has been assumed that the frontal eye fields functioned as a motor cortex for eye movements. Bizzi (1968) studied the relationship of frontal cortical neurons to eye movements in untrained awake monkeys and found only a few neurons which discharged after, but not before, eye movements. Bizzi and Schiller (1970) found neurons that discharged with head position, but not before eye movements. In a careful study using electrical stimulation, Robinson and Fuchs (1969) found that excitation of the frontal eye fields resulted in saccades to the contralateral visual field. These data were difficult to interpret in the absence of preoculomotor single unit activity. The relationship of the frontal eye fields to visually guided eye movements became clearer when Mohler, Goldberg, and Wurtz (1973) found that over half of the neurons they studied had visual receptive fields. Again, like the colliculus and unlike the striate cortex, neurons in the frontal eye fields have large receptive fields, as shown in Fig. 8, that are not fastidious about the qualities of the visual stimuli that excite the neurons. Many of the frontal visual neurons had presaccadic enhancement, and this enhancement is specific: like that found in the superior colliculus, it occurs only with eye movements into the receptive field (Wurtz & Mohler, 1976b). The activity responsible for the saccades induced by electrical stimulation may be the enhanced response to the target of the eye movement. No lesion studies in monkeys have tested the hypothesis that the frontal eye field's contribution to saccadic eye movements involves target selection. However, there exists a large body of clinical literature to suggest that frontal lesions in humans that seem to cause contralateral oculomotor paresis do so by inducing visual neglect (Heilman & Valenstein, 1972).

Posterior parietal cortex (area 7) has also been implicated in the control eye movements. Using untrained monkeys, Hyvärinen and Poranen (1974) found neurons that discharged before eye movements, and others that discharged in relation to the monkey's looking at his hand or at other significant visual phenomena. Mountcastle and his associates (Mountcastle, Lynch, Georgopoulos,

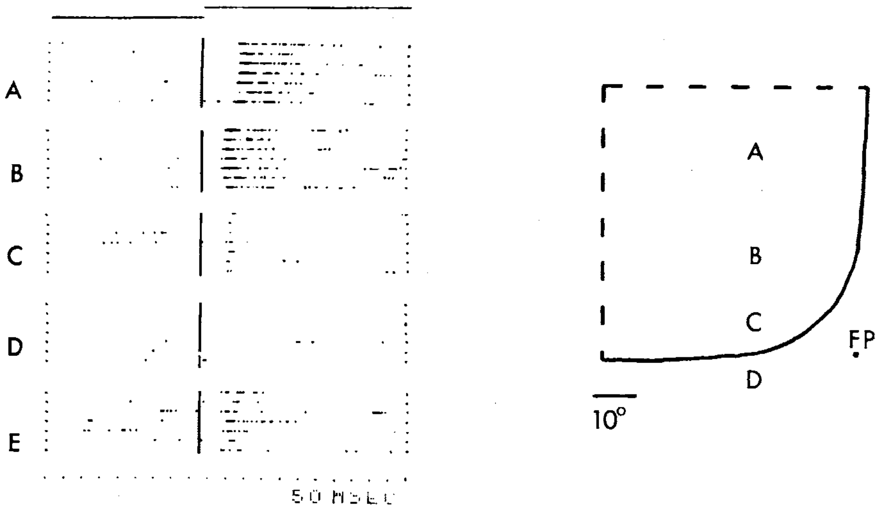

FIG. 8. Visual response of a neuron in area 8. The drawing outlines the area of the left upper quadrant of visual field where 1° spots of light produced excitatory bursts. FP indicates the location of the fixation point. The dot patterns A–D show the responses of the neuron to stimuli at points A–D in the field. Dot pattern E shows the response of the neuron to a 20° x 20° spot centered in the receptive field. (From Mohler, Goldberg, & Wurtz, 1973. Reproduced with permission.)

Sakata, & Acuna, 1975; Mountcastle, 1976) have studied this area in more detail using trained monkeys and have found that when the animals performed a task that required them to make saccadic eye movements, neurons in area 7 discharged before the eye movements, whereas others discharged when gaze had been accomplished.

We have analyzed the visual properties of parietal neurons in some detail (Goldberg & Robinson, 1977; Robinson & Goldberg, 1977). They, like neurons in the superior colliculus and the frontal eye fields, have large visual receptive fields without significant stimulus requirements, as illustrated in Fig. 9. Few if any of these neurons have inhibitory surrounds. The response of some of these neurons is enhanced before eye movements, shown in Fig. 10. Their enhancement makes the cells appear to have a premovement discharge, an activity that is actually a stimulus-locked response similar to that in the superior colliculus. Neurons in this area which discharge during visual fixation seem to do so because the fixation involves positioning the retina in an area that stimulates the tonically responding receptive field of the neurons. A fixation response can usually be exaggerated by obliterating the animal's fixation point with a large, bright stimulus. When the animal is presented with a raisin or some other interesting stimulus, the discharge of many neurons in this area becomes quite dramatic. However, this "raisin response" can usually be duplicated by finding the proper visual stimulus.

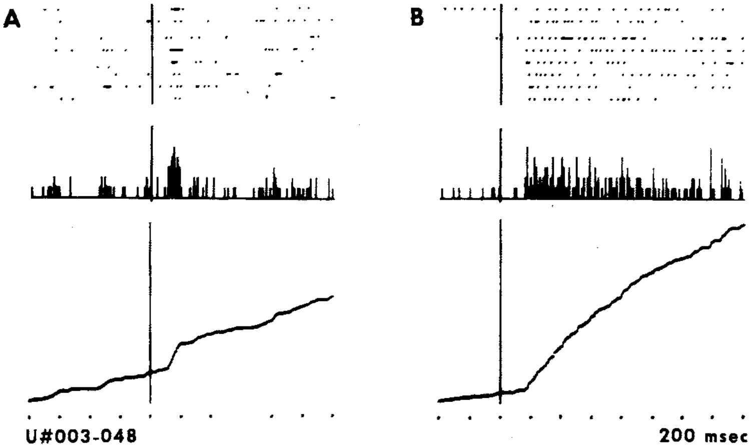

FIG. 9. Visual response of a parietal neuron to small and large stimuli. Data in (A) illustrate the response of this cell to a 0.5° x 0.5° spot of light centered on the vertical meridian 1° above the fixation point. (B) shows that a large stimulus (5° x 5°) centered at the same point still elicits a response indicating some summation within the visual receptive field and the lack of an inhibitory surround smaller than 5° x 5°. The trace at the bottom is a cumulative histogram calculated by summing the accumulated discharges in bins moving rightward. (Robinson & Goldberg, unpublished observations.)

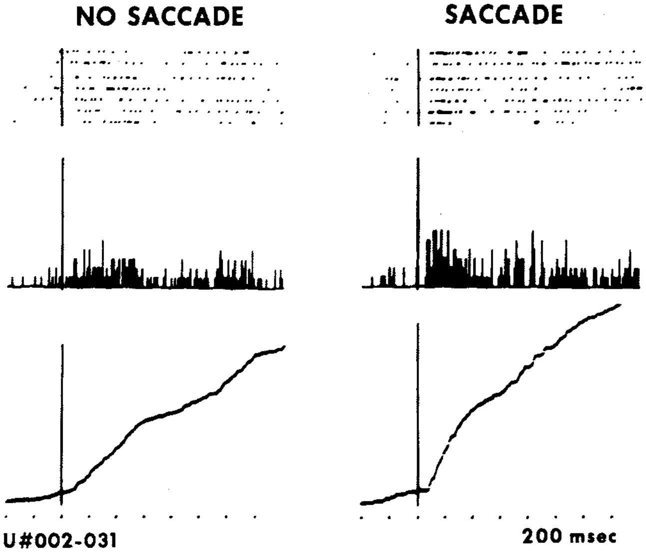

FIG. 10. Visual response enhancement for a neuron in parietal cortex. Data on the left show the response of the cell to a spot of light flashed on the screen 2° in the contralateral visual field, 2° above the horizontal meridian. The animal fixatés throughout these trials. Data on the right illustrate the enhanced response to the identical stimulus when the animal is going to use it as the target for a saccadic eye movement. (Robinson & Goldberg, unpublished observations.)

CONCLUSIONS

The visual substrate of saccadic eye movements can be discussed in terms of the properties of the neurons which provide the answers to the questions *what?* and *why?* for eye movements. If one looks at a saccadic eye movement to the onset of a visual stimulus, it is clear that the striate cortex receives the information first, and then analyzes it in exceedingly fine grain, without adding any behavioral data. At the level of the superior colliculus, neurons extract less information about the qualitative aspects of the visual stimulus, but information clarifying whether the stimulus will be the target for an eye movement or whether the seemingly salient stimulus is merely the result of an eye movement is already implicit in the discharge pattern of the neuron. As the visual response appears in the frontal eye fields and in the posterior parietal cortex, this behavioral information becomes more dominant. However, at all of these levels it is apparent that the neuronal discharge is strongly locked to the visual stimulus and, at best, only modified by the behavioral input.

DISCUSSION

LEISMAN: One factor that could affect activity in the receptive field would be contrast sensitivity. First, I wonder if you made any attempt to control for the space average luminance of the stimulus array?; second, you mentioned that pupillary dilation was a possible factor. Did you make any attempt to instill a cycloplegic?; and third, you were studying the superior colliculus while the animals were involved in a search task. Do you have any data on the interaction between the animals in the type of situation they were in and reticular mechanisms as well?

GOLDBERG: We did not look particularly carefully at the fine grain receptive field properties like space luminance and contrast gradations, because once we found a stimulus that could drive a cell we were more interested in changes in response to that stimulus when the animal behaved differently towards it. We did not use cycloplegics because we doubted that a cycloplegic monkey either could do or would want to do the task. We also felt that the specific enhancement control experiment obviated the need to use a cycloplegic: if pupillary dilation were important, the cell should be enhanced when the animal fixates a spot outside of the receptive field as well as one in the receptive field. I think that reticular mechanisms would be important; reticular lesions cause visual neglect, and there are anatomical connections between the superior colliculus and the reticular formation. We didn't study the reticular system.

STARK: It seems as if the neurophysiologists' recording techniques haven't been able to find motor neurons except in the brain stem; that is, if you stimulate areas aa and so on, you do get eye movements.

GOLDBERG: If you stimulate any visual area, even striate cortex, you can get eye movements. If you think about this question evolutionarily, and therefore teleogically, the oculomotor system of animals without a particularly well developed forebrain is well developed compared to that of primates. This is in contradistinction to the hand area; the hand in primates is significantly different from that of lower animals, and we have evolved a cortex to control the hand that is new. For example, there are direct monosynaptic connections from motor neurons, but no one has ever demonstrated a cortical connection to oculomotor neurons. If the job of the cerebral cortex is to analyze the visual world in a retinotopic fashion, to identify important objects and localize them, the cortex could transmit that information to the brain stem, which would then determine the motor parameters of the eye movement. It would not be necessary for the cortex to discharge in a way predictive of the exact parameters of the movement, but it would be necessary for the cortex to discharge in a way descriptive of the stimulus.

STARK: You mean because you can't record the appropriate neurons that are firing, you feel there are no upper motor neurons?

GOLDBERG: Because neither we nor anyone else has recorded from a cortical upper motor neuron for eye movements, I made a rationalization that enables me to feel comfortable with that fact.

I.2

Role of Eye Position Information in Visual Space Perception[1]

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In *Alice's Adventures in Wonderland* Alice asks, "Cheshire puss – Would you tell me, please, which way I ought to go from here?" To help Alice decide where to go the cat offered, "In that direction, lives a Hatter, and in that direction, lives a March Hare. Visit either you like: they're both mad." After deliberation Alice walked in the direction of the March Hare. Exactly how she could do that is a subject of some interest to us all.

Often we must feel a bit like Alice, especially when we find ourselves in new and strange environments. One of our problems is movement. The body moves, the head moves on the body, the eyes move with respect to the head. Consequently the position of a retinal image is not uniquely related to the position of an object in space but is continuously changing. Some accounting for these movements must be made and it is our task to describe what we know about the mechanism that accounts for movements of the eye.

Actually, when Carroll was writing the Alice story, Helmholtz (see Helmholtz, 1909/1962) recognized the problem and proposed a source for the eye position information used in this accounting. At that time the muscle spindle had been found but it would be nearly a half of a century before its sensory

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[1] Much of the research in this chapter as well as the manuscript itself were supported by Research Grants EY 01049 from the National Eye Institute and BMS75-18181 from the National Science Foundation to the first author. Early work on control in the dark was supported by Grant EY 325 from the National Eye Institute to R.M. Steinman.

nature was discovered.[2] Thus, Helmholtz as early as 1862, and others before him were disposed to think that the relative positions of the eye as well as all parts of the body were known, in part, from the motor commands sent to the various muscles. Helmholtz called this the *effort of will.* Support came from his observations of the effect of oculomotor activity on *perception of direction.* Specifically, when the eye was passively displaced, images of objects in the environment appeared to move. This failure of the brain to account for externally produced eye movements has since been replicated by Irvine and Ludvigh (1936), by Brindley and Merton (1960), and by others on countless informal occasions. Helmholtz further noted that objects were perceived to move if the subject attempted to make an eye movement, but the eye itself was prevented from moving. This observation too has been replicated in several ways by Mach (1959), Kornmuller (1930), and others (see Matin, 1976, for a recent review and reinterpretation of the results of this procedure). Together, these observations led Helmholtz to conclude that, for *visual direction,* eye movements were accounted for by the effort of will put forth in moving the eye.

Three decades later histological evidence led Sherrington (1894) to deduce the sensory role of the muscle spindle. When he found these receptors in extraocular muscles (Sherrington, 1898), he speculated that they provided the eye position information used in perception of direction. Over the next three quarters of a century this speculation stimulated numerous qualitative tests of whether the eye position information arose from spindles or from the motor commands as Helmholtz (1909/1962) proposed. The bulk of evidence supported Helmholtz. None of these experiments challenged the notion that *eye position information* was needed.

The first formal proposal of a mechanism in which eye position signals were used to compensate for retinal image movement came from the work of Sperry (1950) and von Holst (1954). They attempted to account for the forced circling observed in animals whose visual systems were surgically inverted. A model of visual space perception that partially includes their suggestion is shown in Fig. 1.[3]

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[2] According to Dickinson (1974), some controversy exists about the identity of the investigator who first discovered the muscle spindle. Various accounts credit Hassal with the discovery in 1851, Wiesman in 1861, and Kühne in 1863. However, none of these investigators were correct in their speculations about the function of these structures they found in the muscle.

[3] The model shows the oculomotor control systems using solely retinally-based signals to control eye position and thus departs from the suggestion of von Holst (1954) and Sperry (1950) who maintained that it was the perceived location and motion of objects with respect to the head ("$\Theta_{T/H}$" in Fig. 1) that served as inputs to these motor systems. This modification was made solely on the basis that it makes the models of space perception included in this manuscript more comprehensible. The reader is referred to Robinson (1975) for a discussion of the relative strengths of models of eye movement control based on perceived object location as opposed to retinal error signals.

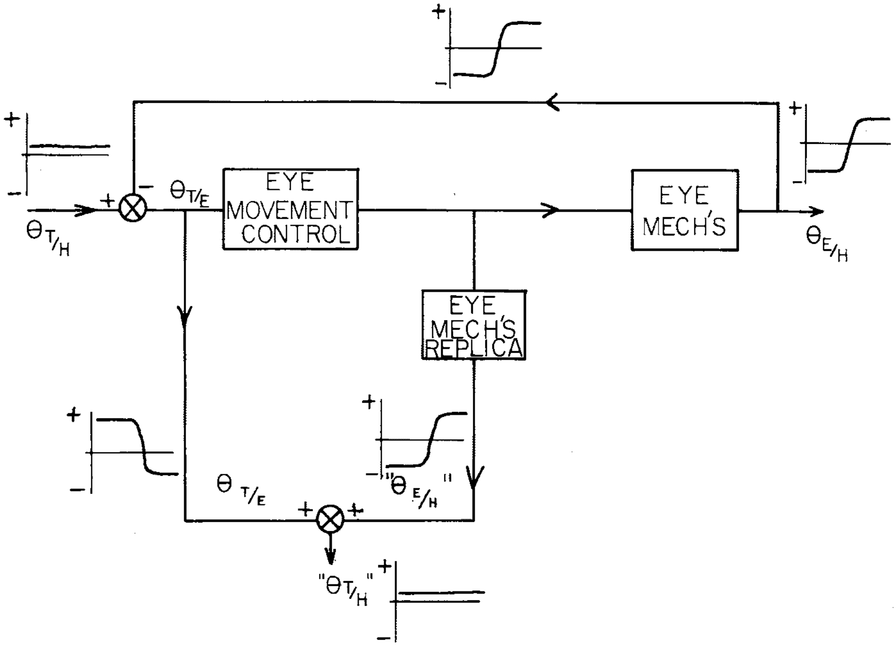

FIG. 1. A block diagram schematizing one way the nervous system could determine the location of a seen object with respect to the head. At the top left, the position of the target with respect to the head ($\Theta_{T/H}$) is shown combining with the position of the eye in the head ($\Theta_{E/H}$) to produce retinal image position (target position with respect to eye, $\Theta_{T/E}$). This happens because the retina is mechanically attached to the eye. Retinal image position ($\Theta_{T/E}$) is used by various *Eye Movement Control* systems to produce commanded eye position: (*Command* "$\Theta_{E/H}$"), a neural pattern that will produce $\Theta_{E/H}$ when passed through mechanical characteristics of the eye muscles and supporting tissues of the globe (*Eye Mech's*). The lower paths show that neural analogues of target position on the retina ("$\Theta_{T/E}$") and position of the eye in the head ("$\Theta_{E/H}$") are added to produce a neural representation of the position of the target with respect to the head ("$\Theta_{T/H}$"). This mechanism is often described as "subtractive" for reasons one can see by examining small graphs near signal lines. The plot in the upper left shows stable target position as a function of time. When the eye executes a spontaneous saccade as shown on the right, the retinal image changes position as though the object was moved in the direction opposite to the eye movement, as shown in the bottom left plot. If this signal is added to the analogue of eye position (on the right) then stable target position is reconstructed as shown at the bottom.

The main implication of the model is that space perception depends critically on eye position signals and, primative as it appears, this model seemed consistent with perception data until only recently. To illustrate, eye position information is shown arising from the motor commands sent to the eye muscles. The most recent support for this came from quantitative replications of Helmholtz's observations done by Skavenski, Haddad, and Steinman (1972). They were led to do this experiment because Skavenski (1972) had earlier shown that subjects could use sensory information from orbital mechanoreceptors to control eye position in total darkness. Furthermore, these subjects could accurately report time and direction of passive displacement of their eyes when a forced choice psychophysical procedure was used (Skavenski, 1972). This result raised a serious question: Was it possible that proprioception made a *partial contribution* to the eye position information used in perceiving direction in Helmholtz's experiments? No one had measured the correspondence between changes in oculomotor commands and shifts in perceived direction to rule out a proprioceptive contribution. Skavenski et al. (1972) made these measurements in two experiments. First, oculomotor commands were varied while eye position was kept constant by applying known forces to a subject's right eye, while requiring him to fixate a target. The left eye was occluded. In this experiment the target remained on the same retinal locus so its perceived direction depended only on nonvisual eye position information. The diagram in Fig. 2 shows how this experiment indicates whether proprioception makes a contribution.

Figure 2 shows that a proprioceptive source of the eye position signals leads to the prediction that the target would be perceived to not change position or to move *in* the direction of the load when it was applied, while eye position information based on the effort of will predicts that the target would be perceived to move *opposite* to the direction of the load. The results shown in Fig. 3 support the "effort of will" prediction, because shifts in perceived direction were always opposite to the load.

Figure 3 shows mean shifts in the perceived direction of the fixation target for various loads applied to the left and right of the subject's right eye. In this experiment, subjects indicated shifts in the perceived direction of the fixation target by placing a second moveable target in their subjective straight ahead position. Perceived shifts were calculated from the *difference* between the mean straight position when the eye was not loaded and when it was loaded. Data points in Fig. 3 show that perceived shifts were always opposite to the direction of the load on the eye and the amplitude of the shift increased monotonically with load magnitude. In fact, the results do not depart in any systematic way from the predicted shifts in perceived direction based on the "effort of will." Essentially the same result was obtained from a second subject leading Skavenski et al. (1972) to conclude that perceived target direction was proportional to the magnitude of the command sent to the eye muscles.

In a second experiment Skavenski et al. (1972) found that systematic changes in proprioception from one eye had no effect on perceived target direction. Combined, the results of these two experiments were interpreted as indicating that the eye position signals of particular importance to perception of visual direction were based on the "effort of will."

The data shown in Fig. 3 also strongly indicate that a non-visual eye position signal is involved in visual space perception. It must be stressed that Skavenski et al. (1972) affected a change in the eye position information and measured a closely comparable change in the perceived direction of a target. Consequently,

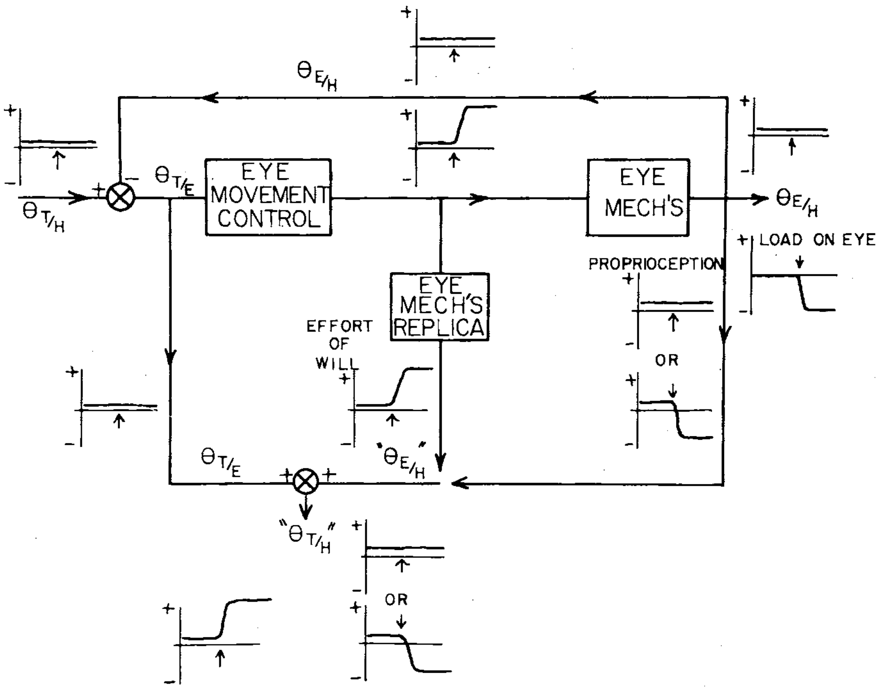

FIG. 2. A block diagram schematizing the changes in various oculomotor signals and their consequences on the perceived direction of a fixation target when an external *load* is applied to the eye. This diagram is organized like the one in Fig. 1, except that a proprioceptive path for eye position information has been added and now small plots show the changes in signals when an external load was applied to the eye at the time indicated by arrows near the plots. When the load was applied, the subject had to change the motor commands to increase the force on the eye by an amount exactly equal to the load, but in the opposite direction, to continue fixating the target. Eye position signals based on these motor commands would indicate the eye rotated opposite to the load as shown in the *effort of will* plot. If perceived target position depended solely on the effort of will, then adding that function to retinal image position ($\Theta_{T/E}$) yields the prediction that the target should be perceived to move *opposite* to the direction of the load. Predictions for a *proprioception* source of the eye position signals are complicated, but it can be shown that proprioceptor activity would indicate that the eye did not change position if the nervous system accounted for its bias of the muscle spindle by the gamma efferent system as shown in the top *proprioception* plot (Skavenski, 1976). If the nervous system ignored its bias of the spindle, then proprioception would indicate the eye rotated in the direction of the load in the bottom proprioception plot. If the proprioceptive path were connected to perception and the effort of will is not, the predictions are that the target should be perceived to not change position or move in the direction of the load as shown in the lowest plot.

under the somewhat static conditions of fixation eye movements, eye position information has a profound influence on where seen objects are localized in visual space. It is tempting to conclude that a combination of retinal signals with eye position information, as shown in Fig. 1, completely explains how we localize objects with respect to our heads.