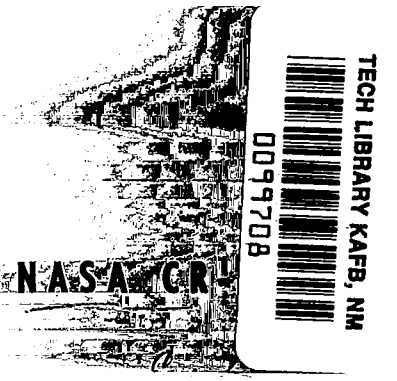


**NASA CONTRACTOR  
REPORT**

**NASA CR-238**



**PHYSIOLOGY OF THE  
VISUAL CONTROL SYSTEM**

*by Lawrence Stark, Carl Kupfer, and Laurence R. Young*

Prepared under Contract No. NAS 2-1328 by  
BIOSYSTEMS, INC.  
Cambridge, Mass.  
*for*

**NATIONAL AERONAUTICS AND SPACE ADMINISTRATION • WASHINGTON, D. C. • JUNE 1965**



NASA CR-238

PHYSIOLOGY OF THE VISUAL CONTROL SYSTEM

By Lawrence Stark, Carl Kupfer,  
and Laurence R. Young

Distribution of this report is provided in the interest of information exchange. Responsibility for the contents resides in the author or organization that prepared it.

Prepared under Contract No. NAS 2-1328 by  
BIOSYSTEMS, INC.  
Cambridge, Mass.

for

NATIONAL AERONAUTICS AND SPACE ADMINISTRATION



# PHYSIOLOGY OF VISUAL CONTROL SYSTEM

Contract No. NAS 2-1328

Biosystems, Inc.  
Cambridge, Mass.

## ABSTRACT

The neurological aspects of the eye movement control system are investigated using experimental and analytical techniques. Specifically, it is maintained that the basic difference between version and vergence rests with the intermittency operator and the discrete control of version. Control system analytical evidence supports a central processor location for the intermittency operator as opposed to a motor or sensory one. Neuroanatomical and physiological evidence also supports a central processor locus for the intermittency operator. Possible loci hypothesized are the accessory vestibular nuclei or contiguous pontine areas.



## TABLE OF CONTENTS

Summary	1
Introduction	2
Interaction Between Vergence and Versional Movement	4
Introduction	4
Algebraic Addition	5
Fatigue	<b>14</b>
Statics	14
Comparison of Control Characteristics	19
Dynamic Interactions	33
Summary	36
Bibliography	36
The Intermittency Operator in the Control System for Eye Movements	38
The Role of the Intermittency Operator	38
Possible Location of the Intermittency Operator at either the Sensory or the Motor End	50
Multi Input Analysis Method	55
Suggestions for Further Experiments	64
Bibliography	<b>68</b>
Control of Eye Movements: Neuroanatomical Considerations	70
Introduction	70
Purpose	73
The Visual System	74
Motor Output for Eye Movements	81
Location of the Intermittency Operator	85
Bibliography	87

# PHYSIOLOGY OF THE VISUAL CONTROL SYSTEM

Contract No. NAS 2-1328

Biosystems, Inc.  
Cambridge, Mass.

## SUMMARY

With the use of experimental and analytic techniques of control theory, the neurological mechanisms controlling eye position are investigated. It is concluded that the eye movement control system deals with a number of requirements by acting as a hybrid system. Complex tasks requiring much planning use "higher level" paths controlled in a discrete manner, while "lower level" tasks are controlled in a continuous fashion.

This report covers several important aspects of the eye movement control system. Among them are the comparative properties of the vergence and version systems; the evidence pertaining to intermittency; and the neurological pathways involved in eye movements as well as anatomical possibilities for the locus of an intermittency operator. There are, however, other significant aspects of this servomechanism which still remain to be investigated.

It is maintained that the basic difference between version and vergence rests with the intermittency operator and the discrete control of version. Control system analytic evidence supports a central processor locus for the intermittency operator as opposed to a motor or sensory one. Neuroanatomical and physiological evidence also supports a central processor locus for the intermittency operator. Possible loci hypothesized are the accessory vestibular nuclei or contiguous pontine areas.

## INTRODUCTION

The eye movement system is a classical type of servomechanism, exhibiting many of the characteristics common to both biological and mechanical control systems. This report represents the continuing effort to use the experimental and analytic techniques of control theory to expose and explain the underlying neurological mechanisms which control eye position. In addition, those characteristics of eye position control which may have bearing on the design of complex mechanical servomechanisms are considered.

The multi-input adaptive control system which directs the eyes may be introduced by a simple analogy to the control system for a radar tracking unit. The input is the angle of the target and the output is the angle of the optic axis. The task is to point the radar (line of sight) at the target of interest and track it through its motion; while remaining relatively unaffected by disturbances. The acquiring of the target is accomplished by a fast-slow rate on a radar system and by the rapid saccadic jumps of the eye. The tracking is through a velocity feedback loop in both cases, leading to the smooth pursuit eye movements. Evidence from eye tracking records shows that these stages use discrete sampled data control analogous to digital computer control of the radar. When the input is predictable this information is used by the eye to lock on to the target and overcome the delays inherent in the neuromuscular system. Such utilization of predictable characteristics of target motion can be programmed into a radar controller. Finally, the control systems must be able to maintain tracking accuracy despite disturbance forces which tend to introduce errors. Wind gusts constitute one of the most serious sources of disturbance on a tracking radar, while movement of the base on a ship borne system is also an important characteristic. The analogy to the eye movement system is primarily in terms of maintaining fixation on a target in the presence of head and body motion. This is accomplished through compensatory eye movements stimulated, at least in part, by the vestibular system which senses head motion. These compensatory movements are a "lower level" control system, performing a less sophisticated job than the acquisition (saccadic) and tracking (pursuit) subsystems, and appear to be controlled by a continuous analog process rather than the discrete digital form.

In addition to the eye movements mentioned above, there are miniature movements and vergence movements. The miniature eye movements consist of slow drifts, rapid corrective flicks and high frequency tremor, perhaps analogous to drift, discrete compensation with a dead zone, and dither in the radar system. The vergence movements involve motion of the two eyes in opposite directions in order to maintain binocular fixation, and provide a second major task for the overall control system to perform. The vergence control system will be shown to be essentially continuous.

To anticipate the results, we are led to the conclusion that the eye movement control system is able to deal with a number of requirements by acting as a hybrid system. Those tasks which are complex enough to require



much planning, and use "higher level" paths are controlled in a discrete manner, whereas those which are "lower level" in complexity or speed requirements are controlled in a continuous fashion. The implications of this tentative conclusion in terms of other biological systems and mechanization for automatic control systems remain to be explored.

The main body of this report consists of three major sections. In the first section the version (eyes moving together) control system characteristics are compared with the vergence (eyes moving oppositely) characteristics to conclude that the basic difference between them lies in the intermittency operator and discrete control of version. The next section examines in detail the evidence pertaining to this intermittency operator, gathered from a wide variety of transient response records and frequency spectra, and emphasizing the powerful technique of using multiple inputs. Various possibilities for the location of the intermittency operator are proposed, and it is concluded that the control evidence places it in the "central processor" (CNS) rather than at the sensor (retina) or motor (muscle) ends. The final section takes these conclusions and attempts to find neurological evidence for this location of the intermittency operator. The neurological pathways from various inputs to the eye muscles are described and possible sites of the intermittency operator are discussed.

This report explains the relationship between control system characteristics and physiological descriptions for several important aspects of the eye movement control system. Similar investigations remain to be done for several other interesting aspects of this servomechanism.

## CHAPTER I

### INTERACTION BETWEEN VERGENCE AND VERSIONAL MOVEMENTS

#### INTRODUCTION

At least two systems control eyeball position at any instant. These are the versional and the vergence control systems. The versional system is that which traces a target moving in a plane perpendicular to the visual axis; the vergence system controls the angle of the binocular system so that similar regions of the retina receive similar positions of the target image. The interaction of these two systems has been an area of concern as study of eye movements has progressed. Are they completely independent or do they interact as each contributes to the single position of the eyeball?

There have been several past and recent approaches to this question. Among them are:

- a) Analyses on the physiological level to suggest that the vergence system uses only the medial rectus (21), only the medial and lateral recti (1), only a poorly defined small fiber system of the medial rectus, or finally only a special, slow neural motor system, occasionally identified as a portion of the autonomic nervous system (3), thus evidencing a muscular disparity of the vergence system. The evidence is not especially clear, but some behavioral studies to be mentioned in this report support the concept of this disparity.
- b) Another set of experiments--those of Mueller, 1826 (13), relating to the transient response of the eye, have also stimulated discussion of this problem. His findings of independence of the two systems have been repeatedly confirmed and are reviewed in the first section of this report.
- c) Recently the cybernetic approach applying servo-analytic concepts to the study of eye movements adds yet another dimension to the question of interaction of the two systems.

It is known that interaction or independence of the two systems relates to the judgement of distance, target size, reading habits, and fatigue of eye muscles. All of these are of importance in human engineering problems of man-machine systems. This report is limited, however, to the purely scientific problems of the various properties of these two systems, and their manner of interaction.

## ALGEBRAIC ADDITION

In this first section experimental data about static additions, transient responses and dynamical sinusoidal inputs will be reviewed and evaluated for evidences of algebraic addition of the vergence and versional systems.

### Static Additions

A recent report by Drs. A. Troelsta and L. Stark (20) shows that in static interaction of accommodative convergence and horizontal versional movements there is evidence to indicate simple algebraic addition of the two systems.

Prior to a consideration of their work it is important to understand clearly the distinction between (1) fusional vergence movements following a binocular visual input and (2) accommodative vergence movements following a monocular visual input.

In the first case the versional input signal may be considered an oppositely polarized angular deviation of target image position with respect to the foveae. The eyes then have to move or correct in opposite directions in order to fuse the target images on each fovea. This is ordinary vergence movement.

In the second case, only one eye sees the target which moves near and far on the optical axis of the seeing eye. This eye remains fixed in position due to the fixation and pursuit control loops of the tracking control system. The accommodative system of the seeing eye, however, tracks the target as regards its near and far movements on the optical axis. The sensory signal here is a blur of target and other associated clues such as change in apparent size and intensity of the target. Primarily, the motor response signal of the accommodative system controls the dioptric strength of the lens in its maintenance of a focused target. In addition, however, motor signals reach two other ocular motor control systems-- the pupil and the extraocular eye muscles. The pupil responds by changing the aperture size; and the extraocular muscles, by changing the vergence state of the eyeball. (This pupillary constriction and convergence of the eyes plus lens accommodation in response to the inward movement of a target is called the near triad of accommodation.)

In the work by Troelsta and Stark (20), in which the target moves inward on the optical axis of the seeing eye, the occluded eye receives motor signals proportional to the accommodative response of the seeing eye. The vergence movement of the occluded eye can be measured and gives an indication of the accommodative vergence control system activity.

Experimental Method: Using an XY recorder they presented the subject with a target as shown in Fig. 1.1. Target movement is sinusoidal (0.3cps) or stepwise (0.1cps) and was seen only by the right eye. The path of the left eye was

blocked by an opaque screen. The subject was requested to fixate the target and to keep it in focus. The movements of the left, occluded eye were measured. (All references to the right eye are to the seeing eye and references to the left eye are to the occluded eye.)

As shown in Fig.1.1 the visual input to the right eye may be resolved into a depth perception and a target displacement.

Depth perception is a function of  $\cos \theta$ :

$$\text{Depth Perception} = \Delta S \cos \theta = \frac{\Delta S(S + \Delta S)}{\sqrt{(S + \Delta S)^2 + X^2}} \approx \Delta S$$

since  $(S + \Delta S)^2 \gg X^2$  for the experimental conditions used ( $S = 21\text{cm}$ ,  $\Delta S = 15\text{cm}$ ,  $X_{\text{max}} = 6\text{cm}$ ). Consequently the depth perception is more or less independent of the value of  $X$ .

Target displacement is a function of  $\sin \theta$ :

$$\text{Target Displacement} = \Delta S \sin \theta = \frac{(\Delta S)X}{\sqrt{(S + \Delta S)^2 + X^2}} \approx \frac{(\Delta S)X}{S + \Delta S}$$

Two types of associated movements of the left eye can result from the input to the right eye: (1) accommodative convergence (AC), and (2) associated tracking (AT).

(1) Accommodative convergence (or divergence) movements of the left eye are those occurring when the right eye changes its accommodation. For example, if the target is moved in the optical axis of the right eye, the left eye will roughly follow the target movement, even though the left eye receives no sensory visual information and the right eye is stationary. With reference to Fig.1.1 and the assumption of some gain for accommodative convergence, movement of the left eye which results from accommodative convergence will be:

$$AC = G_{AC} \frac{(\Delta S)P}{(S + \Delta S) \sqrt{S^2 + X^2}} \cdot \frac{360}{2\pi} \text{ degrees} \quad (1)$$

Gain will be frequency dependent, but in this experiment it is neglected because low frequencies are used. Furthermore, it will be assumed that  $G_{AC}$  is dependent only on the depth perception of the right eye and is independent of  $\theta$  and additional visual information (such as, target displacement).

$G_{AC}$  can be determined experimentally by measuring the movement of the covered and uncovered left eye when the target is moved along in the optical axis of the right eye.

(2) Associated tracking movements of the left eye result when the right eye moves while tracking the target. These movements are opposite in sign to the accommodative convergence movements and are assumed proportional to the target displacement seen by the right eye:

$$AT = -G_{AT} \cdot \frac{(\Delta S)X}{(S + \Delta S) \sqrt{S^2 + X^2}} \cdot \frac{360}{2\pi} \text{ degrees} \quad (2)$$

The definition of  $G_{AT}$  is similar to  $G_{AC}$  except that  $G_{AT}$  is assumed dependent only on target displacement.  $G_{AT}$  is measured experimentally by presenting only a target displacement to the right eye and measuring the movement of the left eye, covered and uncovered. For three values of  $\theta$  approximately 10 degrees apart the values of  $G_{AT}$  obtained are 1.25, 1.15 and 1.15.

(3) Combined associated movements. In general, the right eye will receive information that consists of both depth perception and target displacement. If these two kinds of information contribute independently to the associated movement of the left eye, equations (1) and (2) may be combined. In this experiment then, the net movement of the left eye may be represented by

$$AC + AT = \frac{\Delta S}{(S + \Delta S) \sqrt{S^2 + X^2}} \cdot \frac{360}{2\pi} (PG_{AC} - XG_{AT}) \text{ degrees} \quad (3)$$

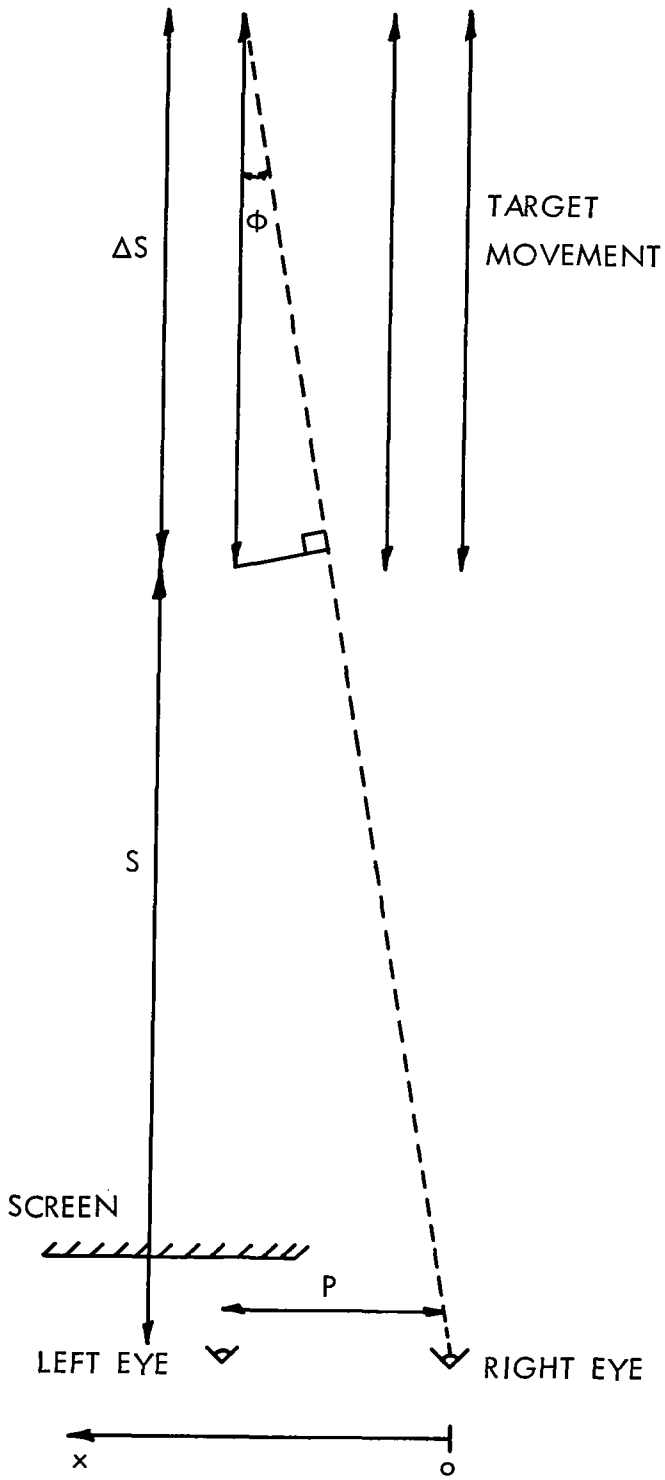
or

$$AC + AT = \frac{24}{\sqrt{440 + X^2}} (6G_{AC} - XG_{AT}) \text{ degrees} \quad (4)$$

From equation (4) it is clear that the value of X for which there will be no associated movement of the left eye is given by

$$6G_{AC} - XG_{AT} = 0 \quad (5)$$

Figure 1.1 Experimental arrangement for adding versional and vergence inputs. (20)



Key

- S=minimum axial distance of target.
- ΔS= target travel distance.
- φ= gaze angle, rt. eye.
- P= interpupillary distance.
- X= perpendicular distance of target from rt. eye.
- Broken Line indicates optical axis of rt. eye.

The value of  $X_{\text{zero}}$  crossing as predicted by equation (5) was compared with the experimentally measured value for three different conditions of the eyes. The results are shown in Table 1 and Fig.1.2.

The experimental results clearly indicate that  $G_{\text{AC}}$  and  $G_{\text{AT}}$  are independent of each other;  $G_{\text{AC}}$  is greatly influenced by fatigue of the eyes; and  $G_{\text{AT}}$  is relatively unchanged with fatigue.

### Transient Responses

From the days of Mueller (13) and Helmholtz (6) to the recent work of Alpern (2,3), physiologists have shown that eye movement transient responses also seem to summate as simple algebraic additions. When the input is a step input, however, the vergence and versional components of the movements can be distinguished by observing the different dynamical characteristics of these two systems. The response of the versional system to a step is a very rapid saccadic jump, whereas the convergence system with its continuous dynamical characteristics has a slower response in correction of a transient error.

The response shown in Fig.1.3 illustrates these features (5). A base-in prism equivalent to 4 degrees of convergence is intruded in front of the right eye thus requiring it alone to converge 4 degrees to produce zero fusional-vergence error-signal. Actually both eyes perform some quick initial versional movement, about 2 degrees in amplitude, to produce an equal but opposite error in each eye. This error is then corrected by means of slower fusional vergence movements of both eyes. A similar result is seen in Fig. 1.4 with the presence of both far and near fixation targets along the line of sight of the right eye (5). The subject switches fixation from one target to the other. The separateness of versional and vergence movements is again clearly seen: the initial rapid saccadic versional jump of both eyes to the right, and then the slower convergence movement of both eyes.

When one eye is occluded and two targets are in the line of sight of the seeing eye it has been suggested that only vergence movement occurs as shown in Fig. 1.5 (5). The general appearance of the record is a large convergence (accommodative vergence) movement of the left occluded eye and a stationary position of the right fixating eye. The right eye is kept still by the continued action of the tracking control system with its position (fixation) and velocity (pursuit) control systems. Since it is the sole viewing eye these control systems must be very active. However, a tendency of the fixated eye to converge can be noted even in this noisy record especially if one observes that all the small corrective fixation saccades are directed rightward in this eye. These interactions deserve further investigation.

However, the main part of Mueller's experiment (figs.1.3 and 1.4 is clearly established. Two separate and distinctive control systems together control eye position --the versional and vergence mechanisms.

Table 1. Values of predicted  $X_{\text{zero crossing}}$  for three different conditions of the eyes (left eye occluded).

Condition of eyes	$G_{AC}$	$G_{AT}$	$X_{\text{zero crossing}}$ (cm)	$X_{\text{zero crossing}}$ (arbitrary abscissa of Fig. 1.2)
Normal	0.95	1.17	4.9	97
Highly Fatigued	0.62	1.20	3.1	170
Not Accommodating	0	—	0	300



Figure 1.2 Associated eye movements of occluded left eye as a function of angle of gaze of viewing right eye, with target moving in line of sight of right eye. Note control experiment with left eye. (20)

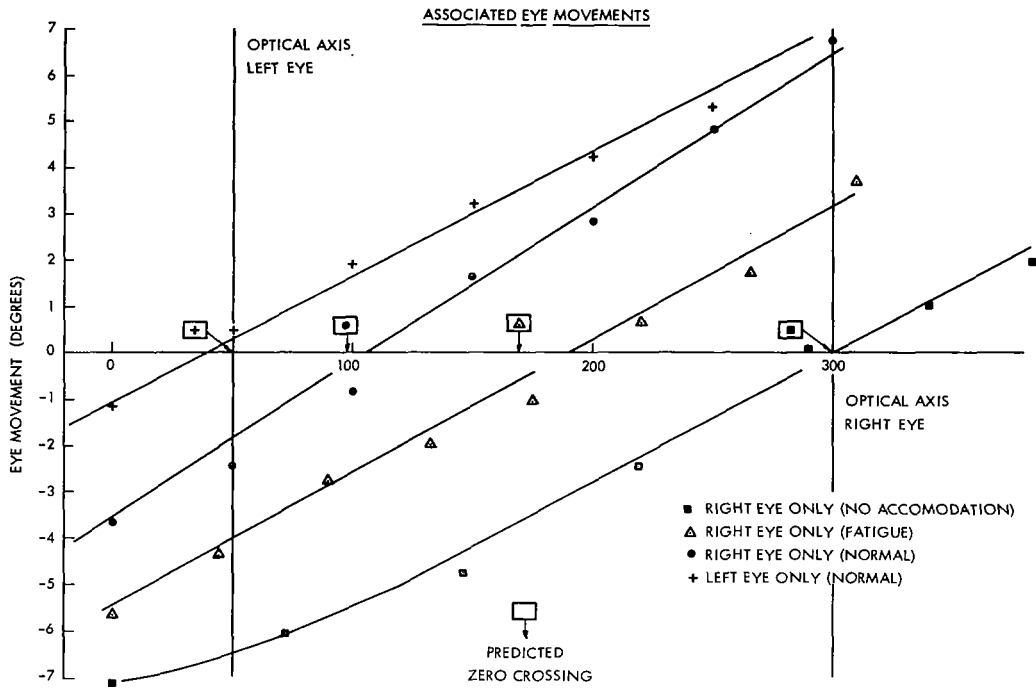


Figure 1.3 Electro-oculographic record of eye position with a base-in prism equivalent to 4 degrees of convergence intruded in front of the right eye. (5)

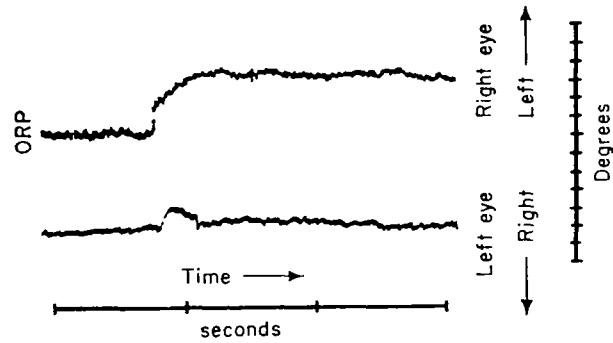


Figure 1.4 Record of eye position when fixation is changed from a far to a near target along the line of sight of the right eye, with binocular fixation. (5)

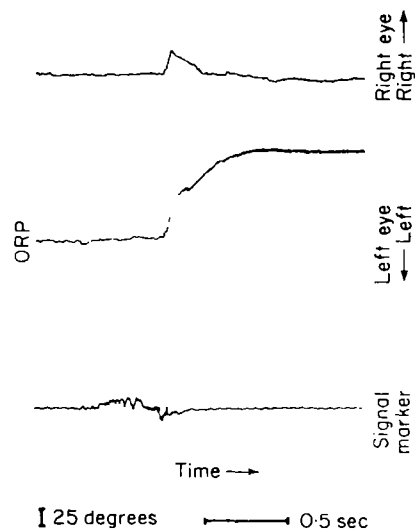


Figure 1.5 Record of the eye position when fixation of the right eye is changed from a far to a near target (along its line of sight) when the left eye is occluded. Note that only the occluded eye moves. (5)

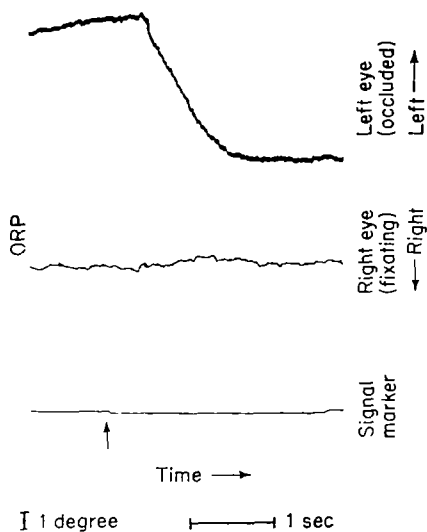
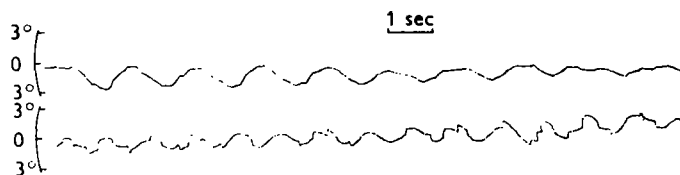


Figure 1.6 A recording of eye vergence (above) and mean lateral eye position (below) when independent simple harmonic changes are given to target vergence and mean lateral target position. (16)



## Dynamical Inputs: Sinusoids

Using sinusoidal inputs and illustrating both sum and difference of right and left eye positions Rashbass and Westheimer (16) have shown that two non-harmonically related sinusoids driving the vergence and versional systems separately result in responses which are also separate and independent. This experiment is illustrated in Fig.1.6 for a single time function. This figure shows a recording of eye vergence and mean lateral eye position when independent simple harmonic changes are given to target vergence and mean lateral target position.

It is important to note the different characteristics of the two control system outputs --the smooth vergence movements perhaps without saccades except as an error in the recording and display methods; and the mixed pursuit and saccadic versional movements. No quantitative study of the actual harmonic content of the two response curves has in fact been carried out.

### DIFFERENTIAL EFFECT OF FATIGUE

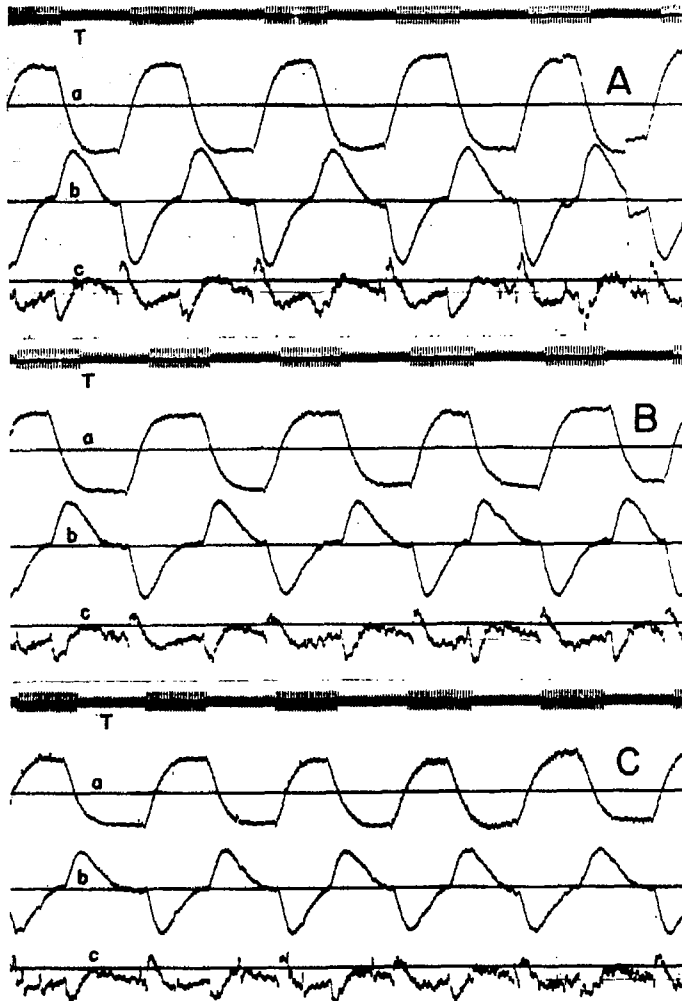
Fig.1.7, taken from a paper by Lion and Brockhurst (11), shows the eye movement system tracking a versional target, which jumps back and forth between two points in the horizontal plane. The three records of each trace are position, velocity, and acceleration of the eye movement following the target. The records, taken after various periods of tracking, show that there is no fatigue observed in the versional system. This finding is characteristic.

It can be seen in Fig.1.2 that as fatigue reduces the gain of accommodative convergence, the version and vergence systems continue to add algebraically with the vergence system giving only 0.6 of its former contribution. In all other aspects the systems remain completely independent. Fig.1.6, from Rashbass and Westheimer, also shows the same effect in a dynamical sinusoidal experiment, wherein the convergence system is fatiguing and reducing its gain while the version system continues to respond without fatigue. This differential effect of fatigue is further evidence in favor of the independence of these eye movement control systems, and reinforces the algebraic addition hypothesis developed in the previous section.

### STATICS

In this section comparative experimental data relating to limitation of range and intorsion and extorsion in the vergence and versional systems is reviewed.

Figure 1.7 Electro-oculographic record, taken after various periods of tracking, A at start of test, B after 5 minutes, C after 10 minutes, of (a) eye position, (b) velocity, and (c) acceleration as the eye follows a versinal target. Note the absence of fatigue in the versinal system. (11)



### Limitation of Range

An easily demonstrated phenomenon is the difference in limitation of range of the vergence and versional systems. First of all, in the fully diverged system the eyes remain with their visual axes nearly parallel or perhaps with some slight divergent angle. However, by moving the target horizontally the eye muscles clearly can produce further lateral rotation of the eyeball. Again the vergence system operates more effectively and is entirely restricted to the horizontal plane whereas versional tracking movements can occur vertically and obliquely quite readily.

Another experiment illustrating limitation of range is that of figure 1.8b & c. The target moves closer and closer to the subject until the limit of convergence is reached (fig.1.8b). Then with lateral movement of the target each eye can be shown separately capable of further adductive rotations (fig.1.8c). This has been suggested by Verhoef (21) as evidence that the convergence system has only the medial rectus at its disposal whereas the versional system can employ the superior and inferior oblique muscles to produce greater adductive movement. Electromyographic evidence suggests other explanations. Breinen (4) has shown that the medial rectus increases its firing rate when the versional eye movement produces adduction over and above the maximal convergence position.

### Intorsion and Extorsion

Careful studies have noted the slight wheeling motion of the eye with horizontal, vertical, and oblique movements in versional tracking. Some of these studies have utilized the method of after-image estimation of wheel angular rotations (15), while others have employed objective photographic methods exploiting a particular feature of the iris to mark the vertical meridian of the eye (18). Wheel rotation occurs as a function of target position in the XY plane, but normal subjects generally show almost completely vertical orientation when looking at targets in horizontal and vertical directions. Wheeling rotations are most noted when the subject looks at targets in oblique directions. Figure 1.9 (14) illustrates the horizontality of the horizontal meridian of the eye in the primary (straight-ahead gaze) and secondary (gaze along either the horizontal or vertical meridian but not both) positions of gaze. The apparent wheeling motion of the eyeball in the tertiary positions (oblique directions of gaze) is mostly due to a false torsion dependent upon spherical geometry. That is, the horizontal retinal meridian is horizontal but its projection upon a tangent screen is oblique.

True torsion only occurs to a minor degree in extreme positions of upward and downward temporal gaze. The nasal quadrants are too restricted for this slight distortion to be present on nasalward oblique gaze.

Figure 1.8 A set of photographs of a normal subject illustrating (a) the eyes in the rest position; (b) the limited adductive movement possible in full convergence; and (c) the further adduction possible in versinal tracking movement.



(a) primary position



(b) maximum convergence



(c) maximum version

Figure 1.9 Projection of retinal horizon for various directions of gaze. Note the horizontality of the horizontal meridian of the eye in the primary, secondary and tertiary positions of gaze. (14)





Verhoef (21) has pointed out that the degree of intorsion and extorsion depends on whether the visual axis arrives at a particular oblique point as the result of a vergence or versional movement. This is a most interesting and acute observation and would clearly indicate that different muscles or portions of muscles are employed for these two systems. It is suggested that experiments be performed in this area to study the effect more carefully. A related area of study is that in which Knoll (7)(17) has shown that various eso- and exophorias are altered by varying the elevation of the plane of regard.

The actions of the six extraocular muscles have been studied as a function of the angle of gaze. Figures 1.10a & b show some of Krewson's results (8). The portions of these graphs most relevant to our present purposes are the short dashed lines showing strong inward rotation action for the superior rectus and the inferior rectus when the eyeball is already somewhat inwardly rotated. This evidence supports the possibility of versional movements performing further adduction by means of other muscles, i.e. the vertical recti, than the medial rectus available, and possibly alone available, to the vergence control system.

#### COMPARISON OF CONTROL CHARACTERISTICS

We shall now attempt to review and compare the servoanalytic characteristics of the versional and vergence control system.

##### Frequency Response Curves

Frequency response curves have been obtained for the versional system in horizontal tracking movements with both predictable and unpredictable inputs (Fig. 1.11a & b)(22). It is important to note the peak in the frequency response curve for unpredictable inputs (bottom curve, fig. 1.11a) which is partial evidence for a sampled data (or intermittent) model of the eye movement system. The phase portion of the Bode diagram (Fig. 1.11b) illustrates the difference in phase characteristics between predictable and unpredictable signals. The prediction operator can be seen to effectively reduce phase lag. Here then, two important servo-characteristics, the intermittency operator and the prediction operator, are clearly noted.

Frequency response curves for the vergence system are shown in Fig. 1.12a and b (27). The gain portion show no peak (Fig.1.12a) a fact that is consistent with the time function data curves which show no intermittency. Comparison of the frequency response curves in the phase portion of the diagram (Fig. 1.12b) for predictable and unpredictable inputs illustrates the relatively small effect of the prediction operator in the vergence system. Only

Figure 1.10a Action of extraocular muscles in various positions of gaze. (8)

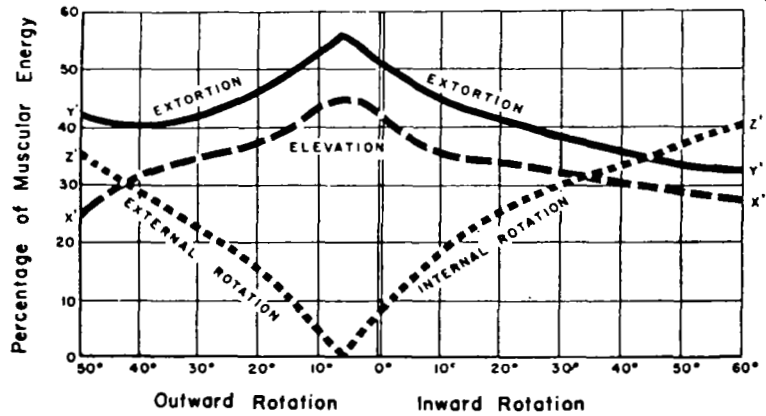
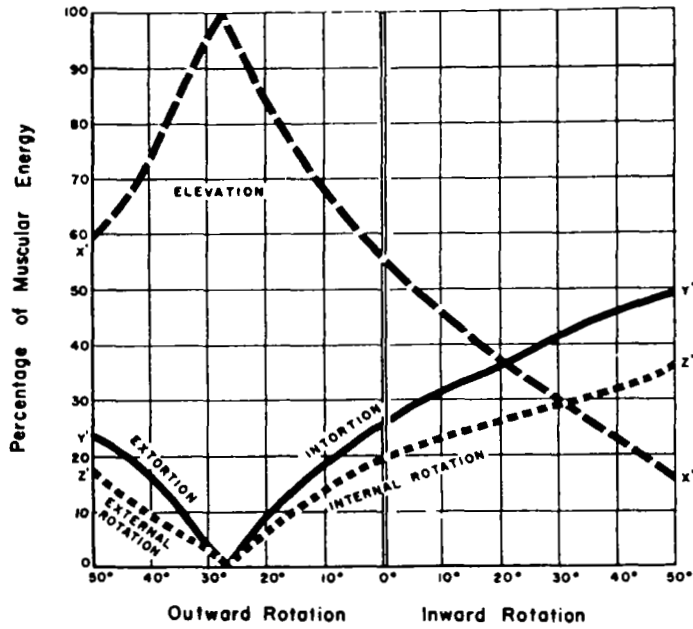


Figure 1.10b Action of extraocular muscles in various positions of gaze. (8)

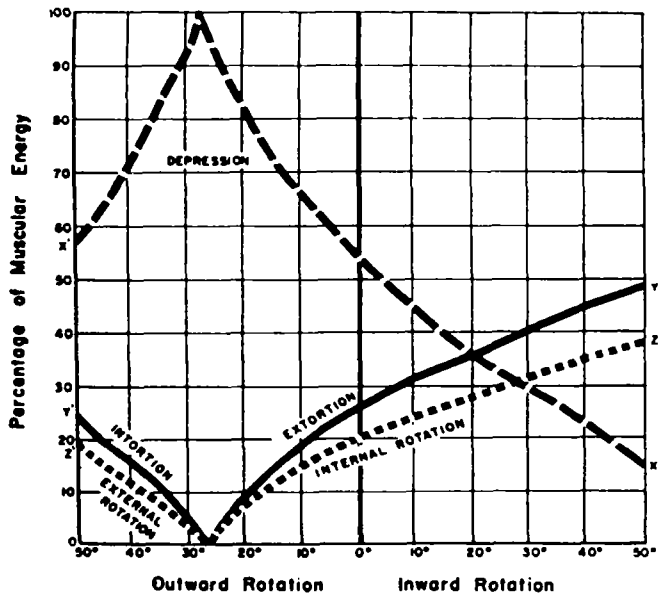
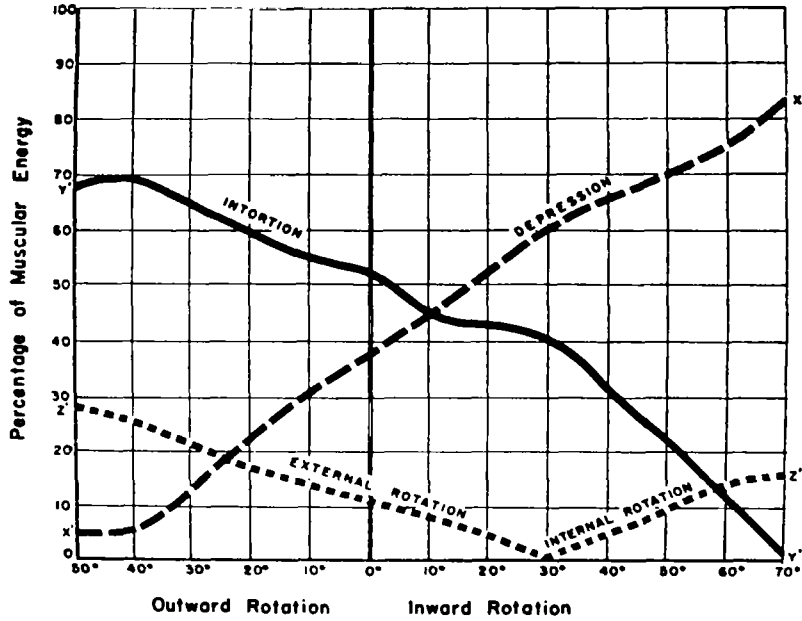


Figure 1.11a Gain portion of frequency response plot of versional system, with predictable and unpredictable inputs.

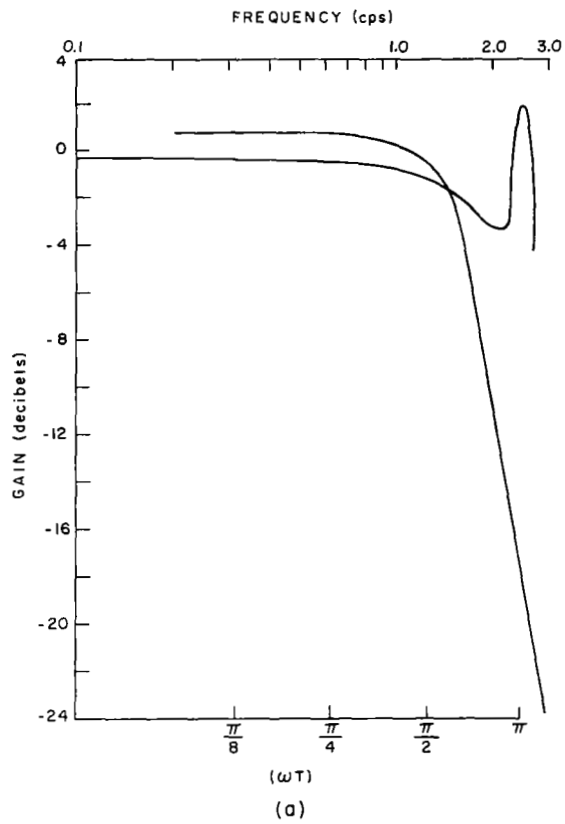


Figure 1.11b Phase portion of frequency response plot of versional system, with predictable and unpredictable inputs.

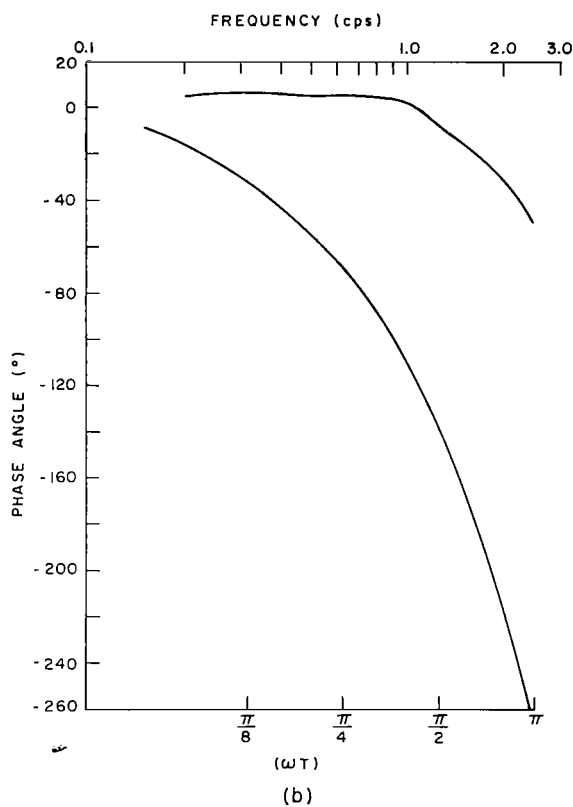


Figure 1.12a Gain portion of frequency response plot of vergence system. Note lack of a peak in the response curve to non-predictable inputs, indicating a lack of intermittency. (27)

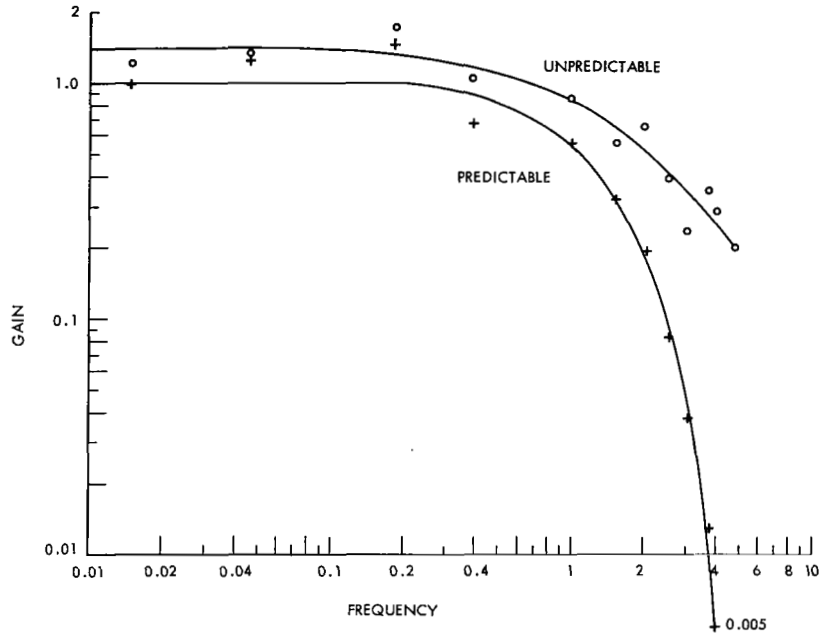
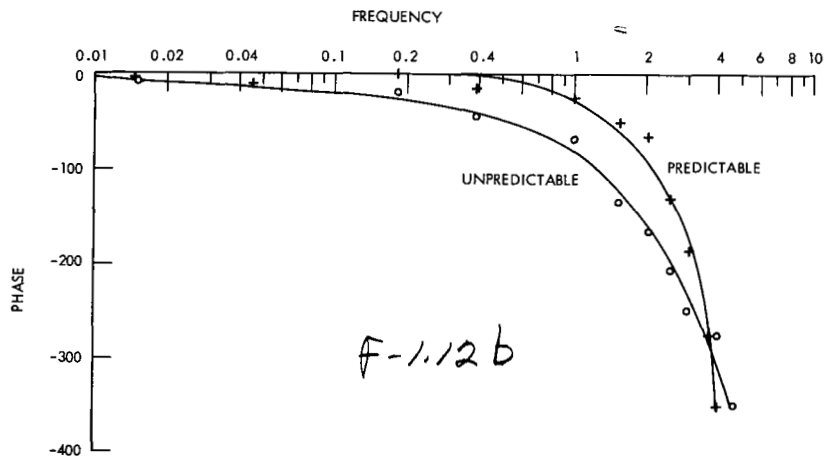


Figure 1.12b. Phase portion of frequency response plot of vergence system. Note the relatively small effect of the prediction operator. (27)



a relative increase in phase margin (for stability) results as an effect of the prediction operator in this system.

### Transient Experiments, Ramps, Parabolas

The versional system shows a relatively accurate position and velocity control system as indicated in the ramp-parabola experiment of Fig. 1.13 (23). Changes in position and velocity are compensated for by the intermittent double position and velocity control system as discussed in Young and Stark (24).

Response to the parabolic portion of the input evidences the lack of an acceleration control loop in the versional system. The saccadic corrections, while alternate or irregular in direction during the ramp portion of the trace, become unidirectional during the parabolic portion of the trace. This indicates that the sampled data versional control system approximates a parabola (or other irregular curves) with a series of constant velocity segments. In the case of the parabolas these constant velocity segments are estimated from the preceding portion of the input curve and are always too low in velocity to compensate for the latter portion of the input --that particular 0.2 sec. intersaccadic segment. Thus a correction in the direction of a larger velocity segment at the next sampled data correction time is necessary.

Ramp and parabola experiments with the vergence control system are shown in Fig. 1.14 and 1.15 (26). From other transient studies of the convergence system it may be predicted that continuous response with larger errors will be seen because of the lower frequency response.

### Pulse Experiments

Pulse experiments for versional movements clearly show the high frequency response of this system. Furthermore, as shown on Fig. 1.16a & b (23) the response to an input pulse of short duration is an output pulse of at least 200 msec. duration. This proves that the system has a refractory period rather than a simple delay. The sampled data intermittency operator in the versional control system is also consistent with the refractory period.

Step experiments with the vergence system are shown in Fig. 1.17 (26). The convergence system shows no refractory period similar to the sampled data versional system, but does show another phenomenon sometimes noted in biological systems; i.e. that sometimes a small error signal lasting only a short time is ignored rather than allowed to produce a delayed response correcting an error that is no longer present.

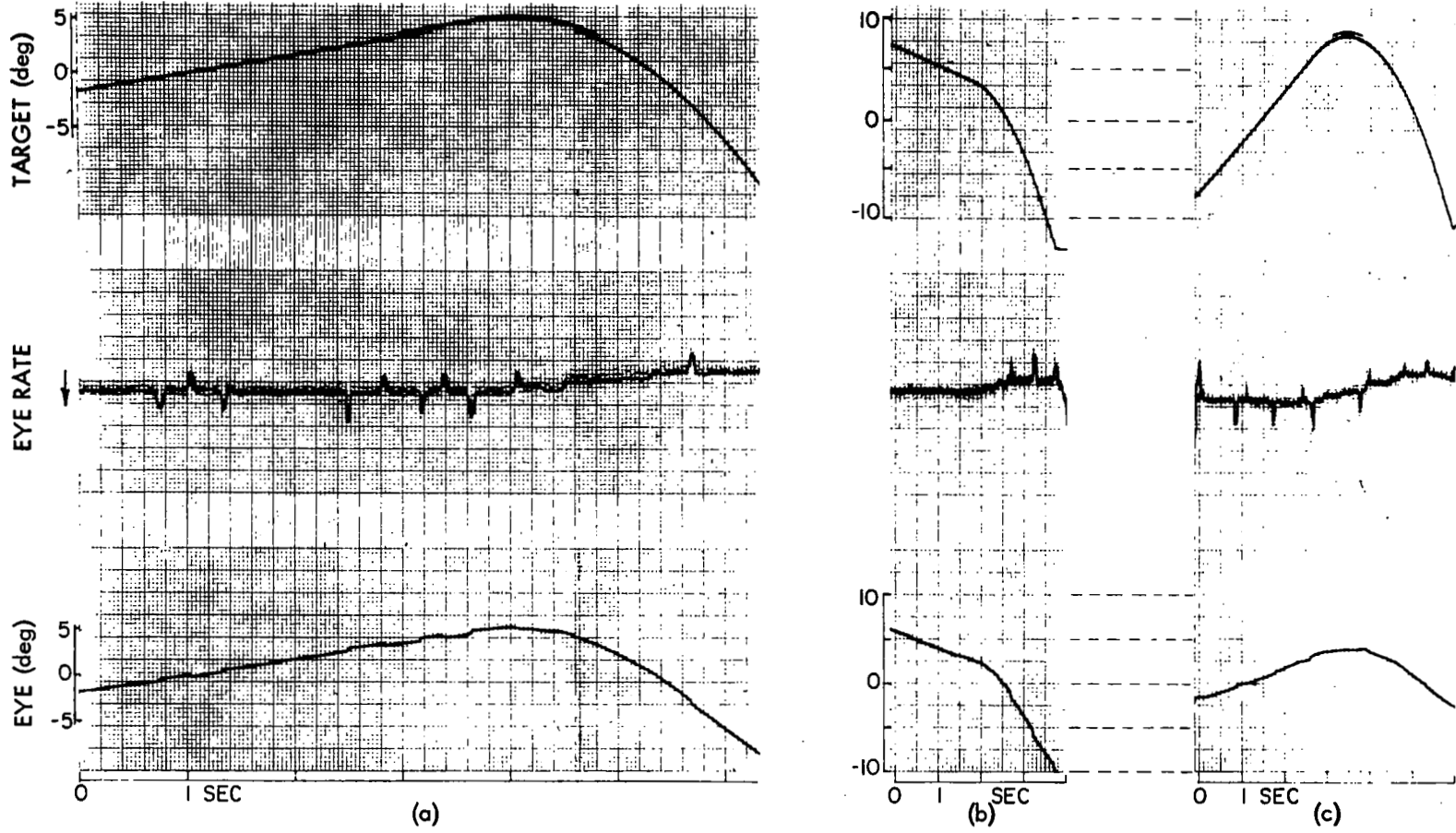


Figure 1.13 Parabolic input responses. (23)



Figure 1.14 Response of the vergence system to ramp input. (26)

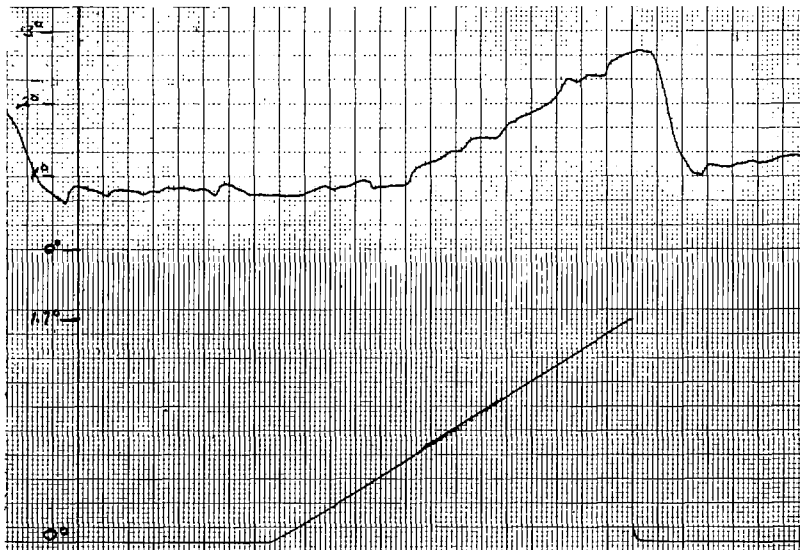
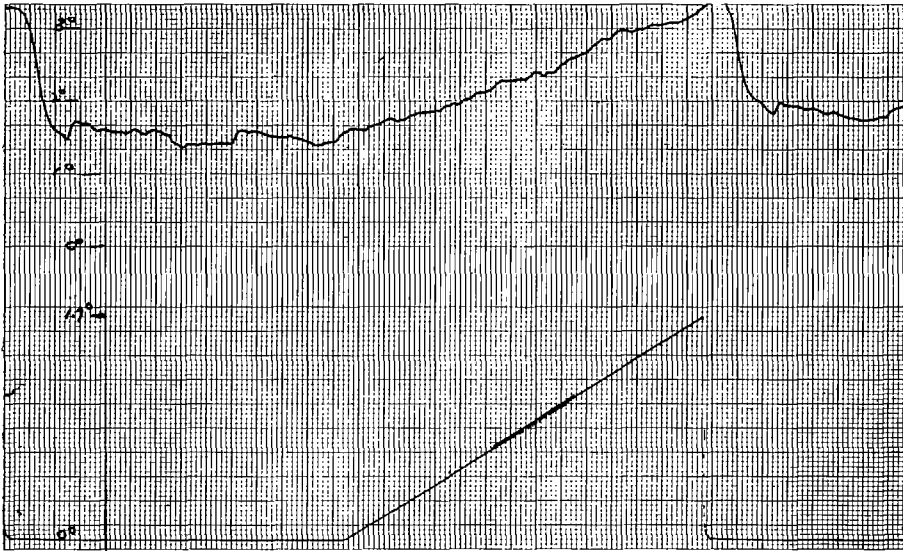


Figure 1.15 Response of the vergence system to parabolic input. (26)

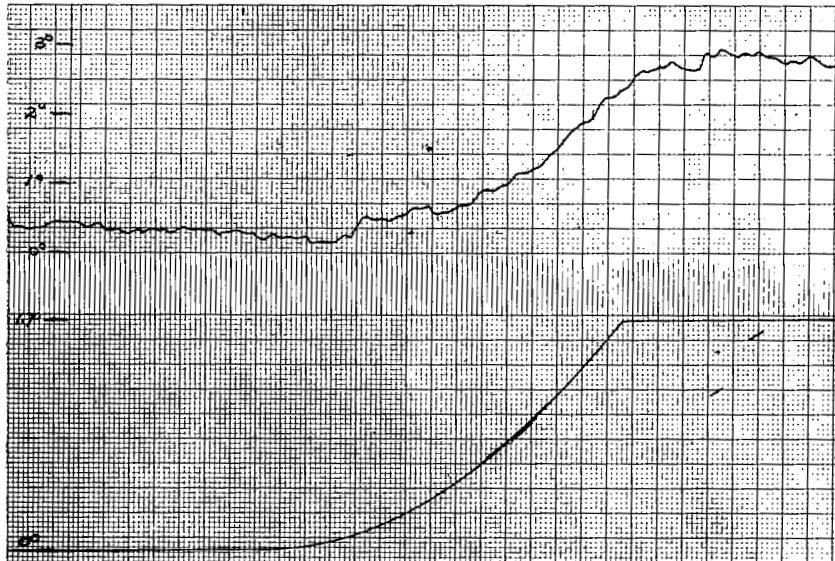
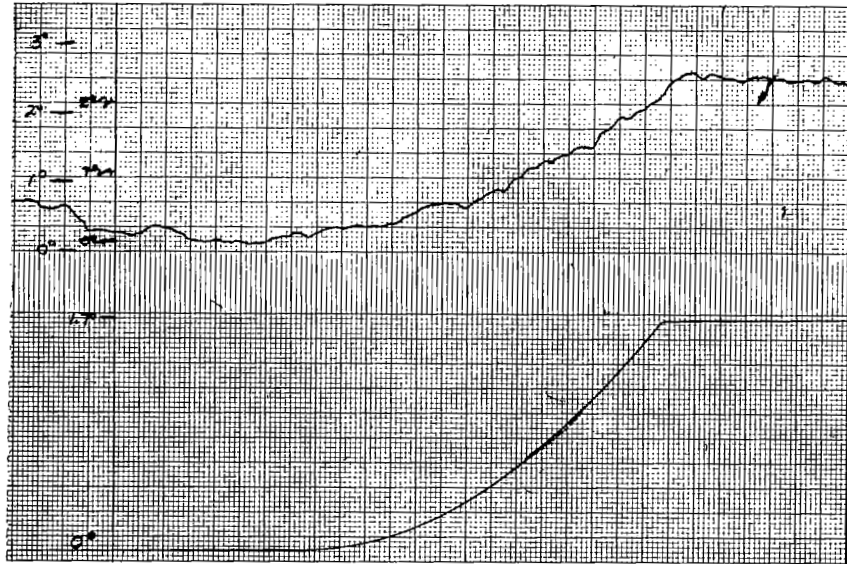


Figure 1.16a & b Pulse experiments for the versional system showing high frequency response. (23)

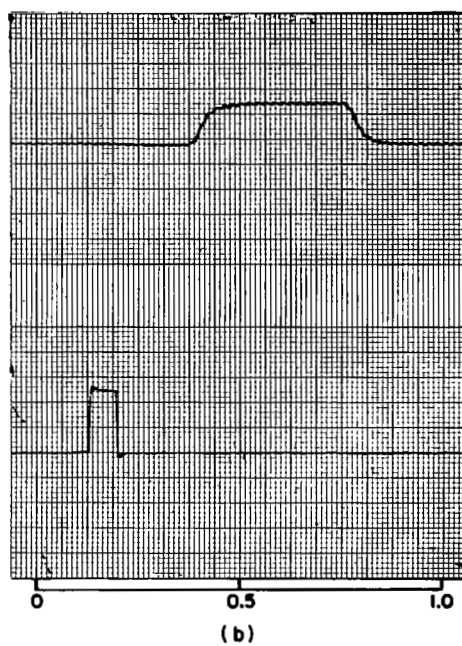
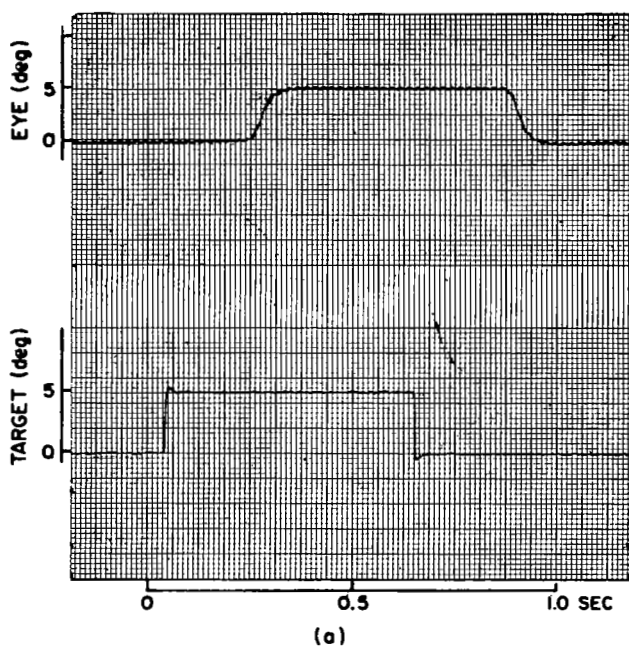


Figure 1.17 Response of the vergence system to step input.  
Note the lack of a refractory period. (26)



## Environmental Clamping

Environmental clamping of biological control systems has been stressed as one method of exploiting and exposing their interesting servoanalytical properties. An example of this technique is to feed the response of the versional system back through an operational amplifier to the input so that the gain of the feedback element is increased enough to produce instability (23). Instability oscillations such as those illustrated in Fig. 1.18c (23) are the result of this feedback technique. Examination of this curve shows the square waves (slightly rounded by the dynamics of the eyeball) which are a typical behavioral characteristic of a sampled data feedback control system under conditions of instability. Figs. 1.18a and b (23) show open loop behavior of the system wherein the system without feedback control swings to extreme boundary conditions. The series of steps that occur are again characteristic of the sampled data system.

On the other hand, instability oscillations of the convergence system, as shown in Fig. 1.19 (26), while irregular, are a continuous function and show quasi-sinusoidal curves. This oscillation is characteristic of a continuous control system under conditions of instability. The lower frequency of these oscillations is another indication of the lower frequency response of the vergence control system.

## Monocular and Binocular Inputs

The versional control system operates quite well in a qualitative sense with either monocular or binocular target inputs. No careful studies are available to compare system performance under these two behavioral conditions.

The vergence control system ordinarily requires a binocular input in order to obtain convergence or divergence. Satisfactory arrangements of inputs are of three types: (1) relay targets moving in the Z-axis, (2) continuous components moving in the Z-axis, or (3) artificially constructed inputs composed of similar targets presented separately to each eye and cohered by means of the fusional illustration, to obtain apparent Z-axis movement. All of these provide adequate stimuli for vergence movement.

Alternatively, with one eye occluded, a target moving in-and-out on the Z-axis (or line of sight of the viewing eye), or having a component moving on the Z-axis will produce "accommodative convergence". That is, the occluded eye performs a vergence according to the level of effort transmitted to the ciliary muscle for accommodation. This vergence is part of the near triad wherein accommodation of the lens, convergence of the eyeball, and constriction of the pupil all occur in response to a near movement of the target. In addition it has been shown by opening the accommodation loop with atropine (19), that the level of command signal increases and that the amount of accommodative convergence also increases. The frequency response of fusional and accommodative convergence appear to be closely related.

Figure 1.18. Versional control system --instability oscillations. (24)

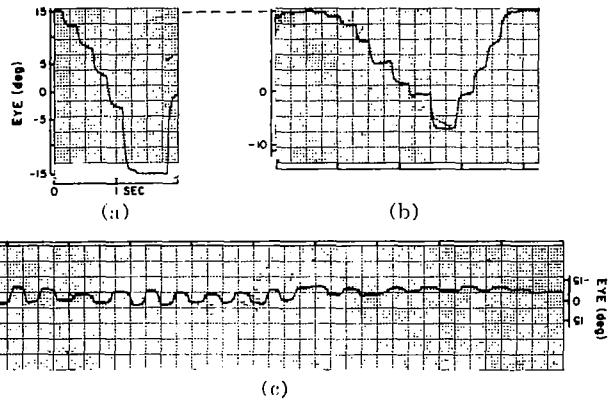
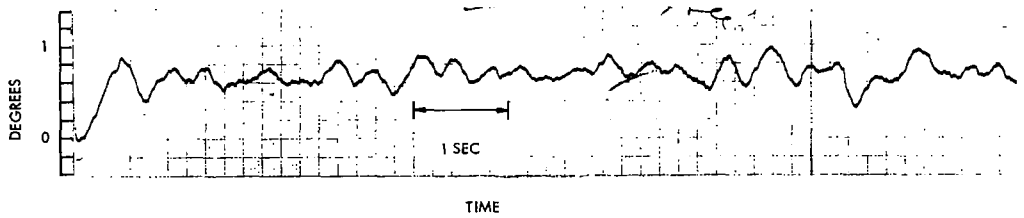


Figure 1.19. Vergence control system --instability oscillations. (27)



## DYNAMICAL INTERACTIONS

Although the two systems are relatively independent it is possible that some type of interaction occurs under special conditions. Apparent evidence in favor of this view is presented in Fig. 1.20 (12). In this experiment, as the horizontal versional movement tracks a special change-of-position target, the two eyes diverge during the saccadic jump and then converge during the period following the saccadic jump. Evidently this convergence is unaffected by a second saccadic jump which occurs shortly after the first one. Although this type of experimental result has not often been reported, Zoethout (25) states: "Divergence movement takes place during fixation (by this he means positional saccadic jumps) and convergence between fixation periods".

Two related explanations may account for this phenomenon in such a manner that interdependence of the vergence and versional systems is not required. The first explanation depends on the degree of sensitivity of the retina which occurs with a saccadic eye movement. Experiments of this sort have been done by Lettvin (10), Volkman (22), Latour (19) and J. Davis (4). Latour's result is shown in Fig. 1.21 which illustrates that the probability of seeing another light decreases greatly although not absolutely during a saccadic eye movement. Thus it is possible that if a target were not too bright or if it were moving rapidly (which increases the threshold as shown in Fig. 1.21), or both, the subject may lose fusion. If the target is near, underlying divergence tone might cause rapid divergence during the saccadic jump as shown in Fig. 1.20. With the re-establishment of retinal sensitivity, fusion occurs and shortly following that, fusional convergence. It would be interesting to experiment on an esophore with the target at some distance so that there would be relatively more convergence tone than divergence tone. Then, when the fusion is lost, especially if the subject were somewhat fatigued, one might see the occurrence of convergence during the saccadic movement.

In the second explanation, the versional system, when computing command signals to both eyeballs, might be expected to take into account the amount of convergence or divergence tone present in each eyeball. For example, when the subject is converging, the medial recti are only providing some oppositional divergence tone. The versional command signals to the right eye and to the left eye then have to take the underlying tone into account. Otherwise nonlinearities in the addition process may cause the subject to lose fusion. Corrections for these nonlinearities have to be made in all states of target position with respect to convergence and divergence tone. It would be interesting to study the discrepancy in vergence which occurs during saccadic movement as a function of target distance with respect to vergence rest distance. It might be possible to observe a convergence movement during a saccade. In fact, the whole relationship of this experiment to the definition of rest distance and to the efficacy of eye movement in reading is of interest.

Figure 1.20. Tracking response of the left and right eye to a special change-of-position target. Interaction of versinal and vergence control systems. (12)

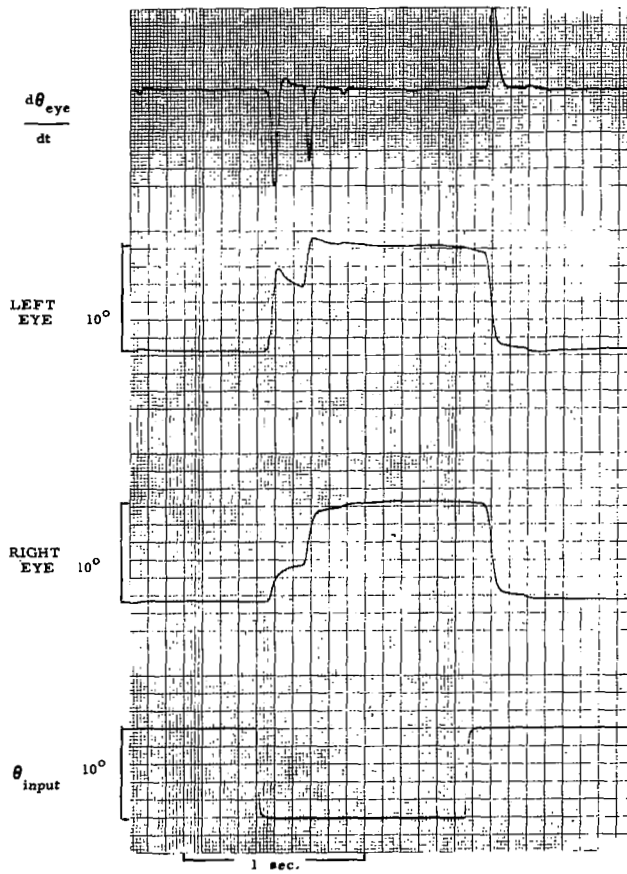
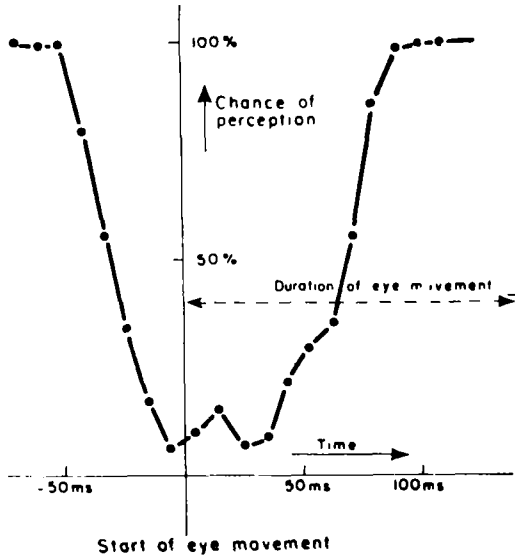




Figure 1.21 Latour's experiment. Suppression of visual sensitivity with a saccadic eye movement, illustrating that interdependence of the vergence and versional systems may not be required for interaction (9)



## SUMMARY

The preceding discussion outlines an important problem area in eye movement physiology which utilizes servoanalytic concepts integrated with other physiological information. When a clear understanding of these and other basic biological communication mechanisms is achieved, it shall no longer be necessary to resort to ad hoc studies in determining human engineering requirements for optimum visual performance.

## BIBLIOGRAPHY

1. Adler, F.H. Pathologic physiology of strabismus. Arch. Ophth., 50:19, 1953.
2. Alpern, M. and P. Ellen. A quantitative analysis of the horizontal movements of the eyes in the experiment of Johannes Mueller. Am.J. Ophth., 42:289, 1956.
3. Alpern, M. and J.R. Wolter. The relation of horizontal saccadic and vergence movements. Arch. Ophth., 56:685, 1956.
4. Breinen, G.M. The nature of vergence revealed by electromyography. Arch. Ophth., 54:407, 1955.
5. Davson, H., ed., The Eye, Vol. 3, Academic Press, N.Y., 1962.
6. Helmholtz, H. Uber die Accommodation des Auges. G. Arch. Ophth., 1:1-74, 1855.
7. Knoll, H.A. The relationship between accommodation and convergence and the elevation of the plane of regard. Am. J. Opt. and Arch. Am. Acad. Opt., March, 1962.
8. Krewson, W. Action of the extraocular muscles. Tr. Am. Ophth. Soc., 48:443, 1950.
9. Latour, P.L. Visual threshold during eye movements. Vision Res., Vol. 2:261, 1962.
10. Lettvin, J.Y. Student research. QPR 58, Res. Lab. Elec., M.I.T., pp. 254-258, July, 1960.
11. Lion, K.S. and R.J. Brockhurst. Study of ocular movements under stress. Arch. Ophth., 46:315, 1951.
12. Merrill, G. Unpublished data, Res. Lab. Elec., M.I.T.

13. Mueller, J. Elements of Physiology. Trans. by Taylor and Walton, London, 1842, p.1147.
14. Quereau, J.V.D. Rolling of the eye around its visual axis during normal ocular movements. Arch. Ophth., 53:807, 1955.
15. Quereau, J.V.D. Some aspects of torsion. Arch. Ophth., 51:783, 1954.
16. Rashbass, C. and G. Westheimer. Independence of conjugate and disjunctive eye movements. J. Physiol., 159:361, 1961.
17. Scobee, R.G. The Ocularotary Muscles. C.V. Mosby Co., St. Louis, 1952, p.157.
18. Simpson, J. Kinematics and muscles of the human iris. S.M. Thesis, Dept. of Mech. Engineering, M.I.T., 1963.
19. Stark, L and Y. Takahashi. QPR 67, Res. Lab. Elec., M.I.T., p. 205, 1962.
20. Troelstra, A. and L. Stark. Associated eye movements, QPR 70, Res. Lab. Elec., M.I.T., pp. 342-345, July 1963.
21. Verhoef, F. Problems concerning convergence. Tr. Am. Acad. Ophth., 52:15, 1947.
22. Volkman, F.C. Vision during voluntary saccadic eye movements. J. Opt. Soc. Am., 52:571, 1962.
23. Young, L.R. A sampled data model for eye tracking movements. Sc.D. Thesis, M.I.T., 1962.
24. Young, L.R. and L. Stark. Variable feedback experiments testing a sampled data model for eye tracking movement. IEEE Trans. on Human Factors in Electronics, HFE-4:38-51, 1963.
25. Zoethout, W.D. Physiological optics, 4th ed., Professional Press, Chicago, 1947, p. 277.
26. Zuber, B.L. Unpublished data. Res. Lab. Elec., M.I.T., 1963.
27. Zuber, B.L., A. Troelstra and L. Stark. Eye Convergence. QPR 70, Res. Lab. Elec., M.I.T., pp. 339-341, July, 1963.

## CHAPTER II

### THE INTERMITTENCY OPERATOR IN THE CONTROL SYSTEM FOR EYE MOVEMENTS

#### THE ROLE OF INTERMITTENCY IN EYE TRACKING MOVEMENTS

##### The Sampled Data Model

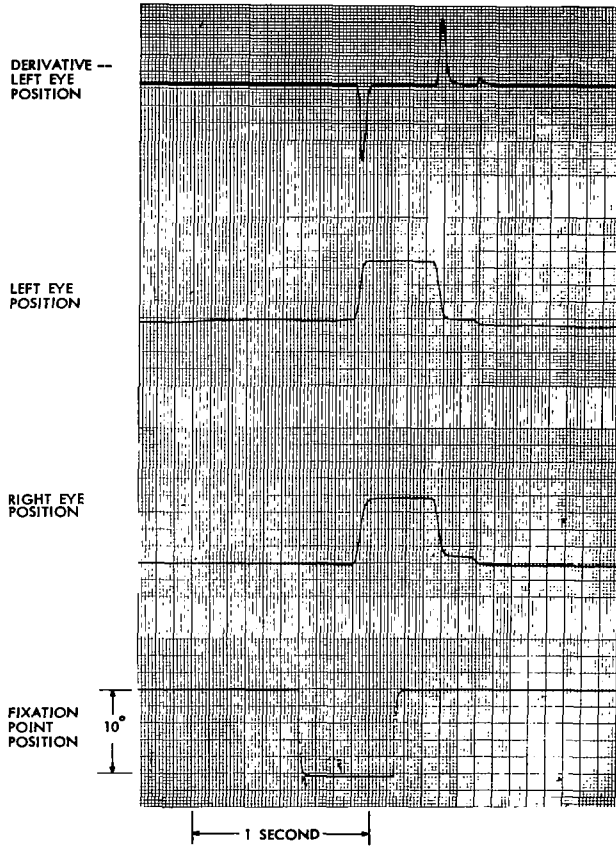
A sampled data model has been developed (20) to describe an important biological servomechanism --the control system for human eye tracking movements. A series of experiments were conducted wherein a subject attempted to maintain fixation of a horizontally moving target while the position of his head remained fixed. Study of the eye movement records led to the principles which form the foundation of the model. The discrete nature of the tracking in the non-predictable mode required a sampled data model for adequate description.

The evidence leading to a discontinuous control model stemmed from five important experimental results: 1) the system response to a target pulse of less than 0.2 seconds duration is a pair of equal and opposite saccadic jumps, separated by a refractory period of at least 0.2 second; 2) under open loop conditions in which the effective visual feedback is eliminated by addition of an external path from measured eye position to a target position, the system step response is a staircase of equal amplitude saccades spaced approximately 0.2 second apart; 3) during constant target acceleration the eye velocity changes in rather discrete jumps at 0.2 second intervals with position errors corrected by saccades in the direction of target motion; 4) the frequency response was calculated by an on-line digital computer which performed a Fourier analysis of the eye movement response to random continuous input; the resultant marked peak gain near 2.5 cycles per second is consistent with the sampling data system operating with a 0.2 second sampling period; and 5) inaccuracy of saccades associated with anticipation of square wave target motion indicates that such saccadic movements are based on previously remembered position, and for 0.2 second preceding the saccade no visual information can modify its course.

These defining experiments help to make precise the meanings of intermittency, sampling, and refractory period. Intermittency means the property of stopping or ceasing behavior for a time. Sampling implies that the system is connected only at discrete times. The refractory period is a concept that after a response the system cannot respond again. The periodicity of a sampler may be regular or irregular; it may be clock synchronized or input synchronized as in the case of the eye tracking movement control system.

The first few figures will illustrate certain of the sampled data properties of the eye tracking movement system. The general servoanalytic aspects of this system were reviewed in the previous chapter of this report. Figure 2.1, which demonstrates the pulse response of the eye tracking system, shows a target motion of 10 degrees from right to left and then back again

Figure 2.1 Pulse response of the eye tracking system.



from left to right. Approximately 0.2 second following the initial target movement both the left and right eye moved to follow the target. These movements were rapid saccadic jumps which in the model are considered as discrete position-error corrections. The slight rounding of these saccades are a consequence of the finite power of the eye muscles, the inertia of the eyeball, and the resisting force of the antagonistic muscles. Approximately 0.2 second following the return of the target to its initial position the eyes made a second jump back toward their original position. In this case, however, an error of approximately two degrees persisted, and 0.2 second following the second saccade a third corrective saccade occurred, again in both eyes. The top trace shows the derivative of left eye position. This indicates the rapid velocity of the position-correcting saccade in the first and second movements and the rather lower velocity which occurred in the third small corrective saccade.

Figure 2.2 shows the impulse response of the eye tracking system. Here the target jumped rapidly from right to left and then within 50 milliseconds jumped back to its original position. The eyes waited their 0.2 second or more refractory delay period before making the initial movement to follow the target. At the time this movement had been completed there already had ensued a long enough period for the control system to realize that the target had returned to its baseline position. However, a period of at least 0.2 second was required before the eyes could return to their original position with a second position-error correcting saccade. The requirement that the control system wait a minimum of 0.2 second to finish its response to an impulse of target position is a crucial experiment in proving the sampled data model. This indicates that there is not just a transport delay in the eye movement system but that there is an actual refractory period before a second command can be acted upon.

Figure 2.3 shows another set of results similar to Figures 2.1 and 2.2. Here we see the response of the eye movement system to a pulse and to an impulse showing the general features described above. In addition, the appearance of a divergence with the initial saccade and a slow correction for convergence during the next second is characteristic of many subjects especially when they are fatigued.

Figure 2.4 again shows an impulse response of the eye tracking movement system. An interesting feature of this response is the decreased gain of the system. Here the eyes have not fully made a 10 degree movement in response to the 10 degree impulse of target position. By the time a correction would have been possible the second saccade returning the eyes to the baseline position had already occurred. It is also possible to see some divergence and convergence type movement in this trace. Figure 2.4 also shows a spontaneous right and left movement of the eye. This is a common type of searching movement which often occurs when subjects are looking about in the experimental apparatus. Of interest is the fact that these two movements which quickly followed one another are spaced 0.2 second apart.

Figure 2.5 shows the response of the eye movement system to a parabolic input. Initially the eyes make a large saccade and then remain relatively

Figure 2.2 Impulse response of the eye tracking system.

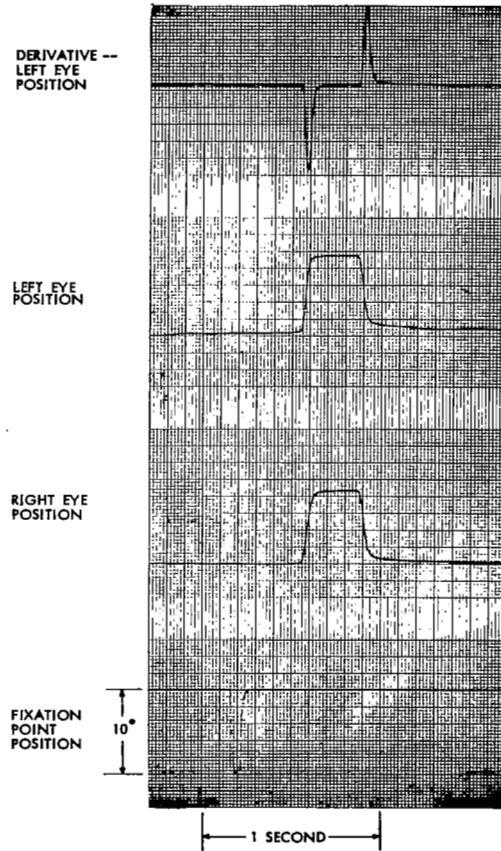


Figure 2.3 Pulse and impulse response of the eye tracking system compared.

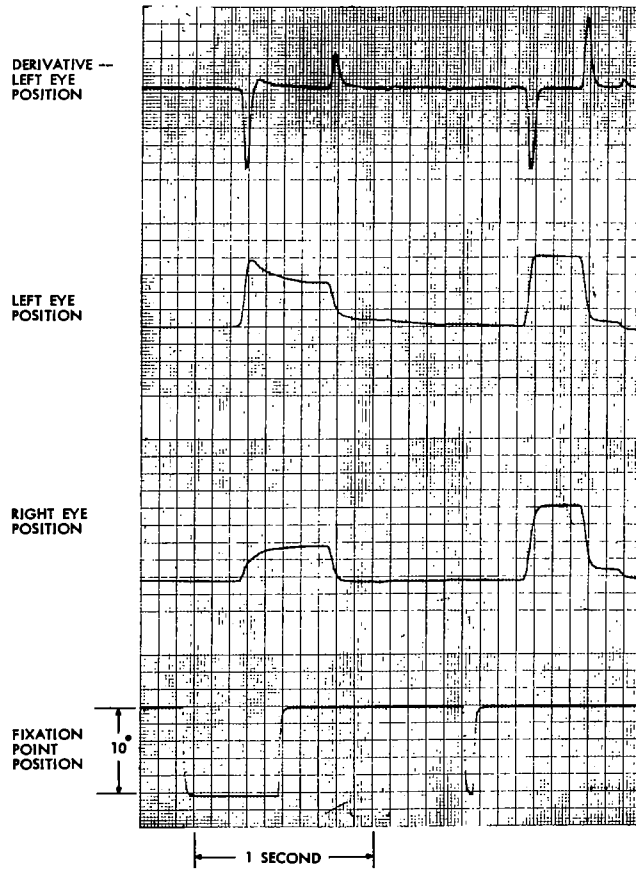




Figure 2.4 Pulse response of the eye tracking system together with a spontaneous movement.

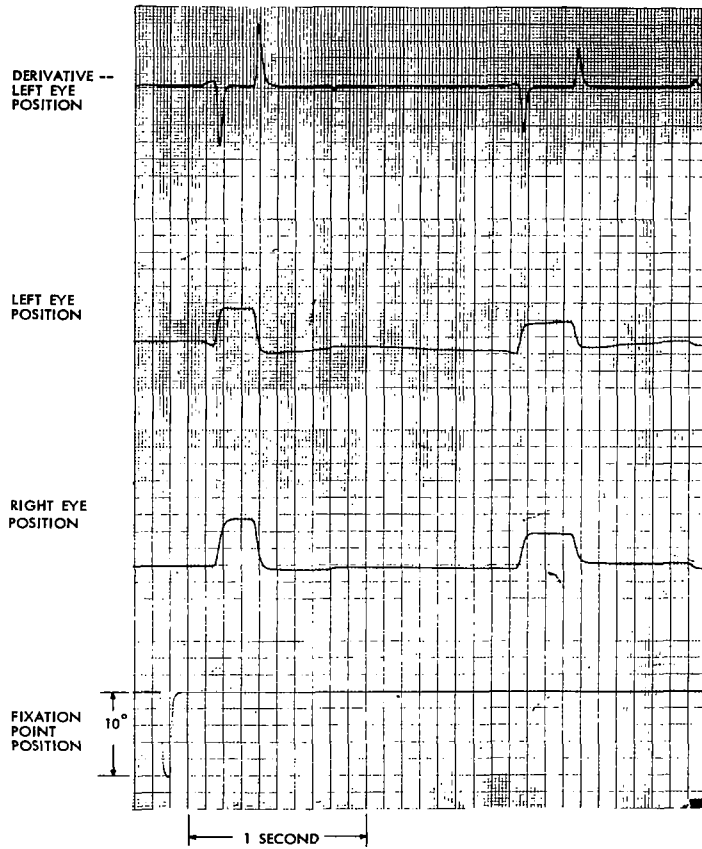
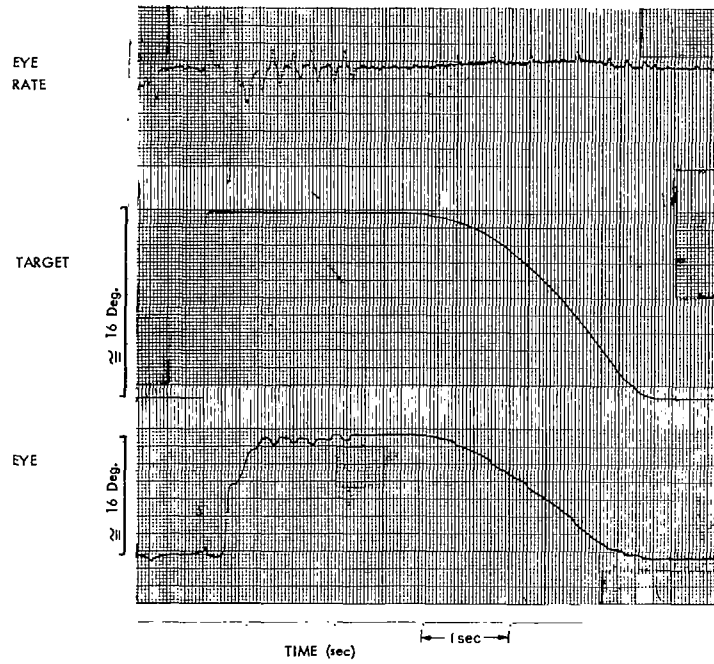


Figure 2.5 Response of eye movement system to a parabolic input.



stationary. There is a series of small saccadic corrections about target position which occur approximately 0.2 second apart during this preliminary phase of the experiment. It can be noted in the top trace, the eye-rate or eye-derivative trace, that the velocity of the eye is varying from positive to negative during this series of small saccades. Now the target starts its parabolic course and it is seen that the responses of the eye are a series of constant velocity segments separated by short corrective saccadic jumps. The constant velocity segments are the best that the eye movement system can do for an unpredictable signal since it has only position and velocity-correcting loops and no acceleration-correcting loop. If it had an acceleration-correcting loop it could put in a constant acceleration term and then the corrections in velocity would be random about this constant acceleration response. However, the fact that all the position and velocity corrections are in the same direction, that is, the eye is always lagging the target and the velocities are always getting greater, is evidence that there is no acceleration control loop in the eye movement system. By looking at the eye derivative trace, one can see that all the velocity segments are going in the same direction during the parabolic target movement, that is, they are all going upward in this particular top trace.

In Figure 2.6 is shown some film recordings of persons reading textual material. In both illustrations, the same course of events is shown. The first two strips of film show normal reading and here the saccadic nature of the eye movements in reading is very apparent. The right hand long strip of film in the illustrations of the combined figure 2.6 is designed to show the effect of "speed-reading" training upon eye movements. Here it is shown that the saccadic movements even though they appear, are very small in amplitude and the eyes remain relatively fixed in horizontal position, only moving from right to left at the end of a page (in the very right hand film trace) to go from the left hand to the right hand pages of the open book. Although this illustration is in this present context used mainly to illustrate the saccadic nature of normal reading movements, it serves to also show the importance of eye tracking movements to the normal functioning performance of a human being (and especially in a difficult or stressful task such as control of a space vehicle).

Figure 2.7 is a block diagram of the sampled data model for eye tracking movements. It includes the target angle, the error, or difference between eye angle and target angle, a sampler for the intermittency operator, two correction loops --one the saccadic position correction and the other the pursuit velocity correction. These two corrections then sum to command the muscle and eyeball dynamics to produce eye angle. Several non-linearities such as dead zones, limiters, and pursuit saturations are also indicated although for many purposes these can be omitted in predicting responses of the model with sufficient generality to be useful. As well, the muscle and eyeball dynamics can be omitted for certain predictions.

For the present argument the most important features of this model are the sampling operator or the intermittency operator. Further evidence will shortly be given concerning another control system, the pupil control system, which does not have such a sampler, so that the reader can evaluate for

Figure 2.6 Examples of discrete movements occurring with normal reading.

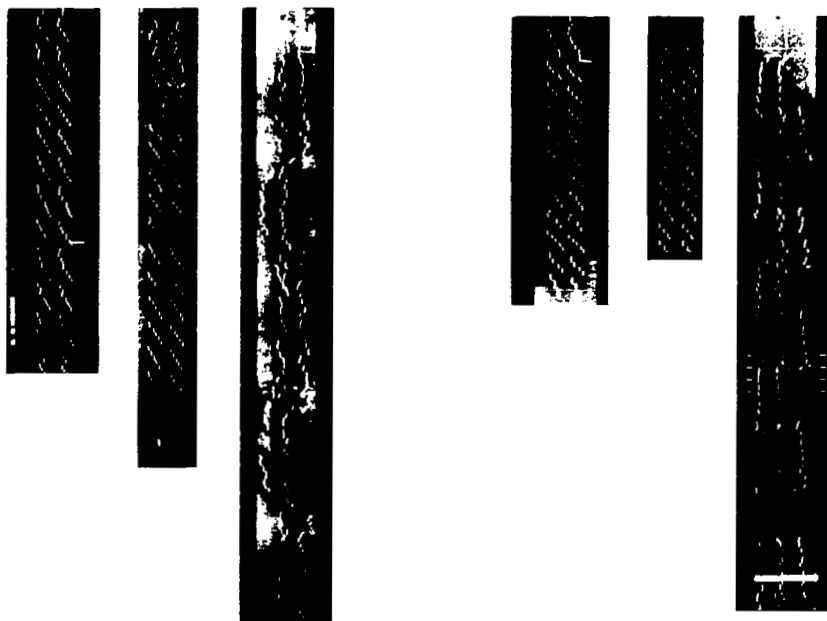
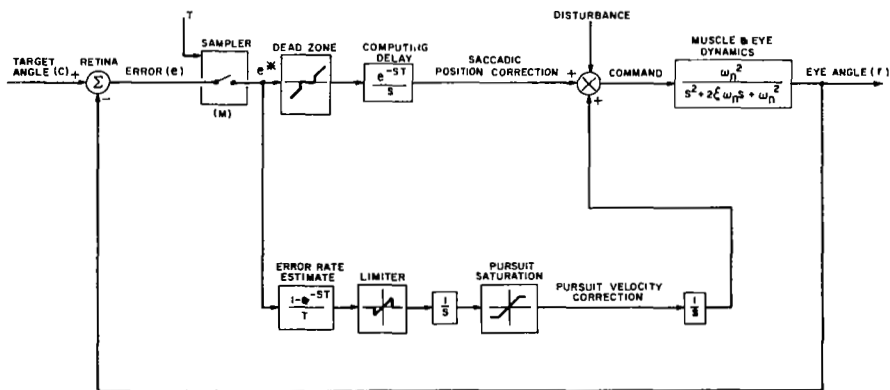


Figure 2.7 Sampled data model of the eye movement system (20)



himself the importance of the data indicating the sampling properties of the eye-tracking movement system.

A second point of importance, and this will be the main point of this section of the report, is that the sampling operator in this model need not be in any one particular topological position. For purposes of convenience in illustration it has been placed near the sensory end of the system. It could as well be placed in the motor pathway or in any of the intervening control pathways. When we try to penetrate beneath this "black box" description of the control system for eye-tracking movements and to understand the nature of the neurological and neurophysiological operations and operators that exist in the brain to perform these various functions, we will see that experimental evidence exists which helps us to determine where indeed the sampling operator or intermittency operator exists in the brain.

### The Pupillary Control System

The pupillary control system is a continuous system. By this we mean that it does not have a refractory period such as illustrated in the eye movement tracking system. Clear evidence of this can be seen in Fig. 2.8 which shows a series of average responses to light pulses of varying widths. As the width of the light pulse gets very small the pulse approaches an impulse. We see that the pupil has a similar 0.2 to 0.3 second time delay as the eye-tracking movement system does. However, the pupil responds to the end of the impulse as soon as the end of the impulse has occurred. It does not have to wait an additional refractory period for this part of the response to occur. The dynamics of the pupillary system are in the main constrained by the triple lag elements in the neuro-muscular and muscular elements of the pupillary system.

A block diagram of the pupil system is shown in Fig. 2.9. Here we see the continuous path from retinal flux through the log and retinal adaptation operators to optic nerve impulses, a transport delay through the neuro-muscular and muscular elements which then yield the pupillary area. This pupillary area is then multiplied by external intensity due to the geometry of the pupillary aperture to yield retinal flux. Because of the slow dynamics of the pupillary musculature it is difficult to see the operation of the neural elements clearly in these experiments. However, the pupillary system has the following characteristics which are different than that of the eye-tracking system. 1) There is no refractory period in following successive stimuli (the 0.2 sec delay is not a refractory period). 2) Under open loop conditions the pupil drifts continuously rather than in steps. 3) With constant target acceleration the pupillary response is a continuous movement. 4) The frequency response of the pupillary system has no marked peak in gain and thus no feature consistent with a possible sampled data operator. And 5) although the pupil does not have any predictive ability it is clear that any sequence of stimuli have their resultant effect on the pupillary system one delay time later.

Figure 2.8 Average response of pupil to light pulses of decreasing width. (12)

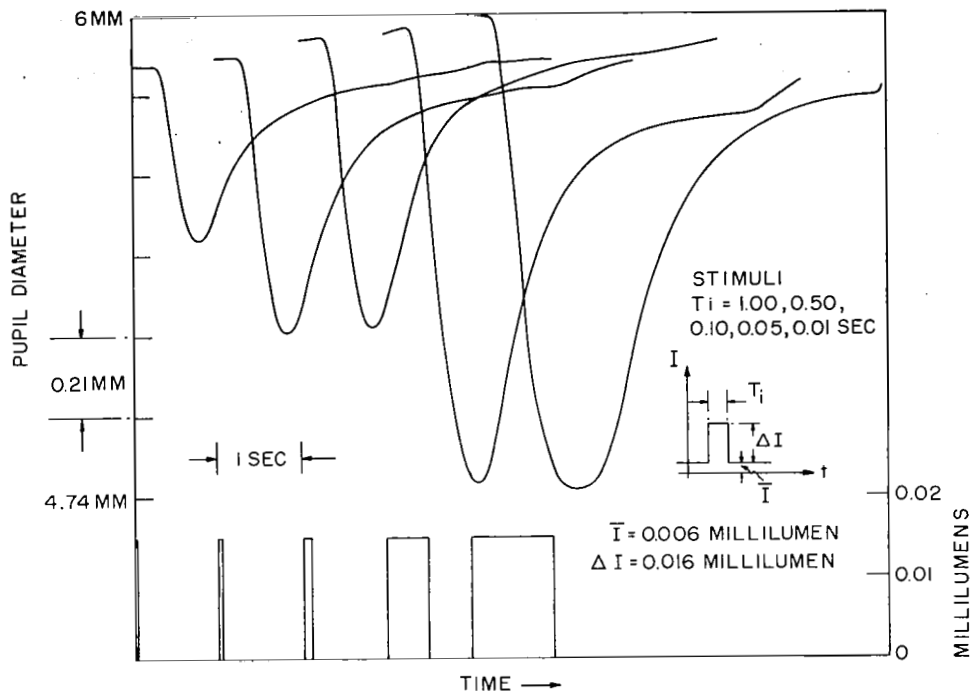
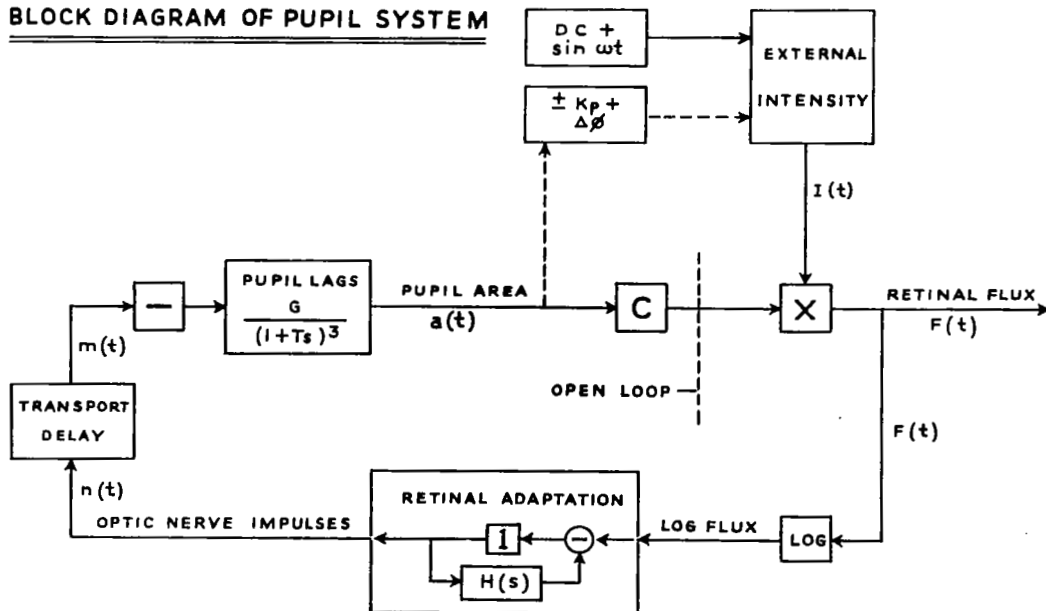


Figure 2.9 Block diagram of pupil system. (13)

**BLOCK DIAGRAM OF PUPIL SYSTEM**



## Summary

We have attempted to bring together the evidence for intermittency or sampling in the eye movement system and to make this evidence more apparent by contrasting it with the continuous pupillary control system. Although this servoanalytic description of the eye-tracking system definitely requires a sampled data or intermittency operator it makes no specification as to the locus of this intermittency operator. The location of the intermittency operator is a problem for the physiologist interested in dissecting into the "black box".

### POSSIBLE LOCATION OF THE INTERMITTENCY OPERATOR AT EITHER THE SENSORY OR THE MOTOR END

#### The Sensory End

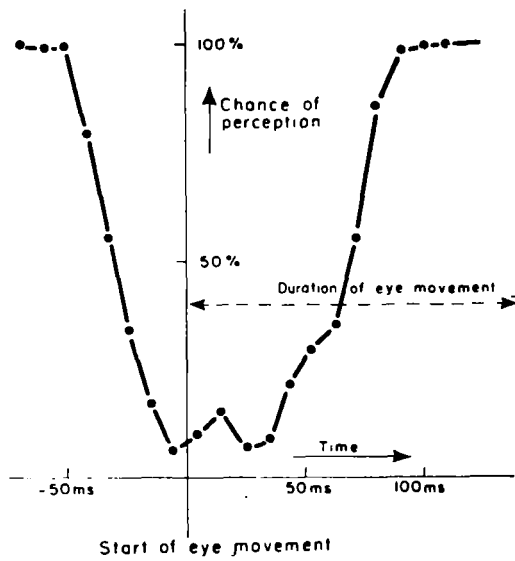
There has now accumulated a good deal of evidence indicating that the visual threshold is considerably elevated for a period of time during an eye movement. Ditchburn in 1959 (3), Lettvin in 1960 (8), Volkman (18) Latour (7) and Davis (2) in 1962, all have demonstrated this phenomenon. The clearest published results are those of Latour and are illustrated in Fig. 2.10. This shows that the chance of perception of a flash of light is reduced to less than 10% during an eye movement. If visual perception is "blanked out" at intermittent periods related to eye movements then this might very well be the sampling mechanism or intermittency operator for which we are searching. It would have the effect of suppressing the visual image or the intake of visual information during a fast movement of the eye when the retinal image is moving rapidly with respect to the retinal elements. In this way a good deal of blur and loss of contrast would be eliminated. With visual threshold again lowered at the end of this blanking the visual system could take another sighting or reading on the target and transmit this information to the eye muscle command system.

Of great interest is Latour's further finding that the suppression of visual sensitivity occurred even before an eye movement started. This clearly proves that it is not the relative velocity of the target to the retina that plays a role in this raising of visual threshold, even though it had been shown by other authors that visual thresholds are a function of the target velocity.

Although, as we have seen above, it is possible from this external evidence that the intermittency operator is located at the sensory end of the control system and further that we have seen that it might have certain teleologically satisfying functions, we must merely let the argument rest here and conclude by saying, a possible locus for the intermittency operator is at the sensory end.



Figure 2.10 Suppression of visual sensitivity with a saccadic eye movement. (7)



## The Motor End

The control system for hand movement has been studied from a servoanalytical point of view by a number of authors (1,5,11,14,15). This system is an especially interesting one from the servoanalytic point of view since so much of the intimate neurophysiology has been studied by such authors as Granit (4), and Matthews and Rushworth (9). The postural servomechanism that subserves this system can be approached by the techniques of the neurophysiologist and an interesting review of this material is available in Granit's book (4). One of the difficulties in studying the hand system is that the inertia of the motor portion of the system and of the load are quite well matched to the neurological elements of the control system, and therefore, the CNS dynamical behavior is not as clear cut as in the eye movement control system. However, by carefully designing experiments to eliminate some of these "inertial confusion factors" it has been possible to show the sampled data nature of the hand control system (10). Figure 2.11, a block diagram of the control system for hand movement, indicates the pull-pull nature of the control system, the double integration between force and position, and the two important postural feedback control loops for the agonist and antagonist muscles via the spindle afferent nerve which dominate the performance of the hand control system. In the eye movement control system, although proprioceptors exist in the eye muscles, they probably play no role in the eye movement itself, but rather might have an effect on coordinating head movement with eye movement.

It has been shown that there is an essential competition for the alpha motor neuron or final common pathway by two main elements for the control of hand movements; the postural feedback system and the voluntary control system. Figure 2.12 (10) shows an engineering block diagram representation of the control system for hand movement. First the system has been simplified to a unilateral representation. Secondly the two feedback paths, visual feedback and the proprioceptor feedback path, are shown. At the point where the proprioceptor feedback path feeds back into the feed forward portion of the loop the switching or sampling mechanism is placed. This indicates that the postural feedback system is turned off for brief periods of time during which time voluntary-control-signals exercise dominance over the final common pathway. Then at the end of a voluntary movement the postural feedback control system is again permitted to control the limb.

Although it is not possible at this time to describe more fully this very interesting control system, it serves an essential point in this argument. This is to illustrate a sampling operator occurring at the motor end of a biological control system. This system was especially favorable for neurophysiological studies by means of dissection of animal preparations. Unfortunately the eye movement system is not as accessible and no similar evidence is available at present. We thus end this discussion by merely stating that a possibility for the locus of the intermittency operator for the eye-tracking movement system might be at the final common pathway itself.



Figure 2.11 Block diagram of the control system for hand movement. (10)

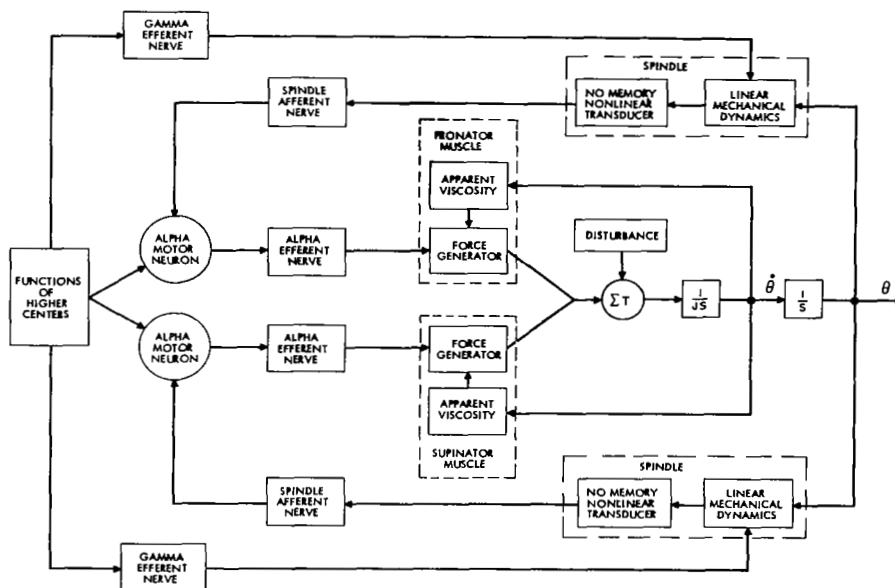
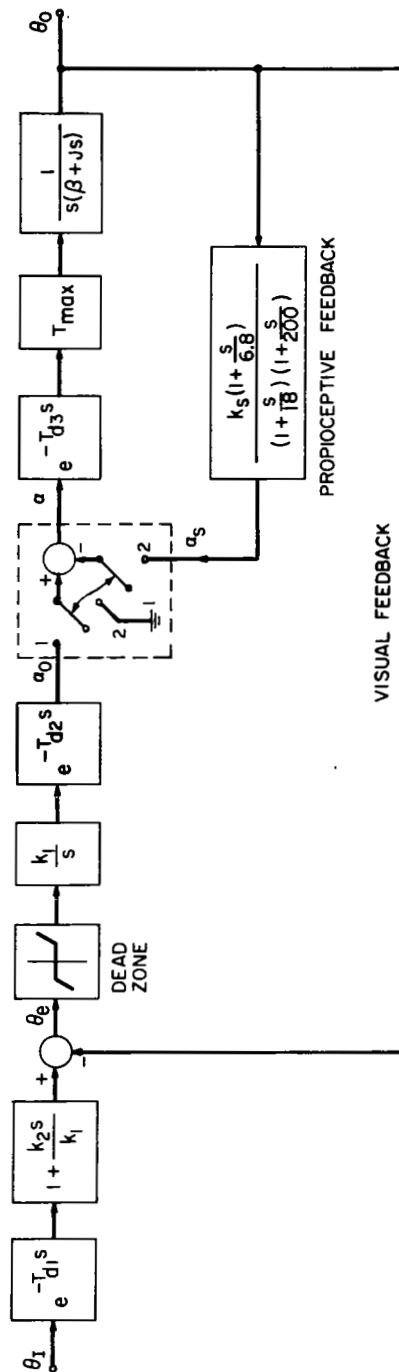


Figure 2.12 Block diagram for hand movement showing sampling occurring at the motor end. (10)



## Neuroanatomy

The complex neuro-anatomical pathways and nuclei involved in the control of eye movements have been studied for many years, each generation of anatomists asking questions that physiological discoveries have made pertinent. As yet, little anatomical evidence relating to servoanalytic problems has appeared. Figure 2.13 is a diagram presenting the chief components of the medial longitudinal fasciculus, an essential tract linking together the nuclei of the eye muscles in the brain stem. Especially prominent are various vestibular nuclei present in the angle of the brain stem. These vestibular nuclei make many complex connections with the motor nuclei of the ocular muscles. In another section a review is attempted of the available neuroanatomical evidence concerning the control system for eye movements. Here, we must only summarize by stating that clear cut entities, the extraocular muscle nuclei, exist and are the final common pathways for the motor command signals to the eye muscles. There are some accessory extraocular muscle nuclei as well as some accessory vestibular nuclei which probably play an essential role in integrating the command signals for eye-tracking movements. In lower animals the superior colliculi play an important role in visual integration and there is some clinical evidence that the superior colliculi play an important role in primates in the control function for eye muscles. Various higher centers such as the occipital cortex and the "eye field" portion of the frontal lobe cortex as well as the lateral geniculate bodies exist closer toward the sensory end. The retina itself is the most peripheral portion of the sensory pathway and is actually part of the central nervous system itself.

## Summary

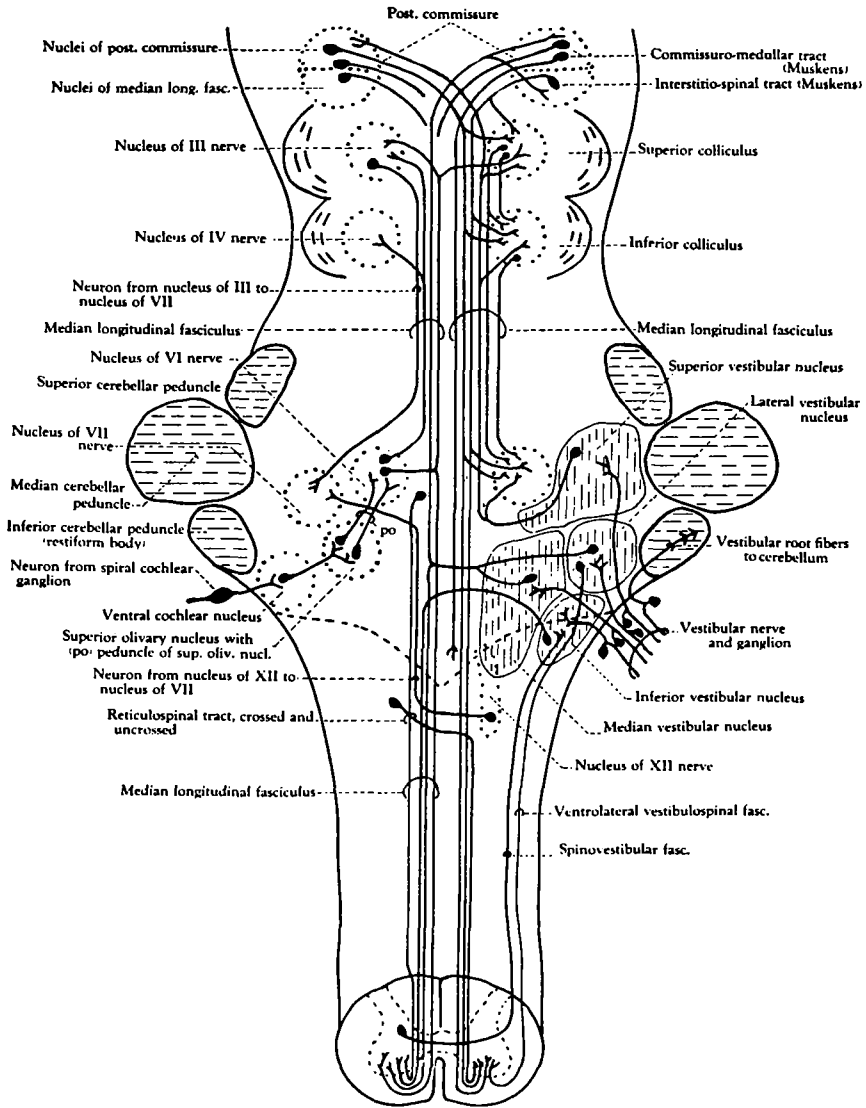
This second section of this chapter has attempted to assemble evidence for the location of the intermittency operation. This evidence has been shown to be reasonable but not complete. A further portion of this section has attempted to describe briefly some of the neuroanatomical regions for the control of eye movements wherein the intermittency operator might be located.

## MULTI-INPUT ANALYSIS METHOD

### Simplified Block Diagram of the Eye Movement System

The multi-input analysis method is one especially adapted to biological systems wherein often one motor control element serves as the effector organ for a number of sensory input elements. The eyeball musculature is an excellent example of this. The eyeballs respond by voluntarily

Figure 2.13 A diagram presenting the chief components of the medial longitudinal fasciculus. (6)



tracking visual targets, by converging and diverging upon targets moving closer and further away, by making reflex movements in response to vestibular stimuli, by making compensating reflex movements to rotations of the head, and by several other types of movements. Biological control systems are often difficult to dissect into and to take apart in order to study their isolated elements. We, therefore, must often use more subtle input-output "black box" techniques (such as the multi-input analysis method) in order to substitute for actual dissection. This technique is to study responses to different types of sensory inputs which enter the control system at different regions and thus effectively isolate and define intermediate elements.

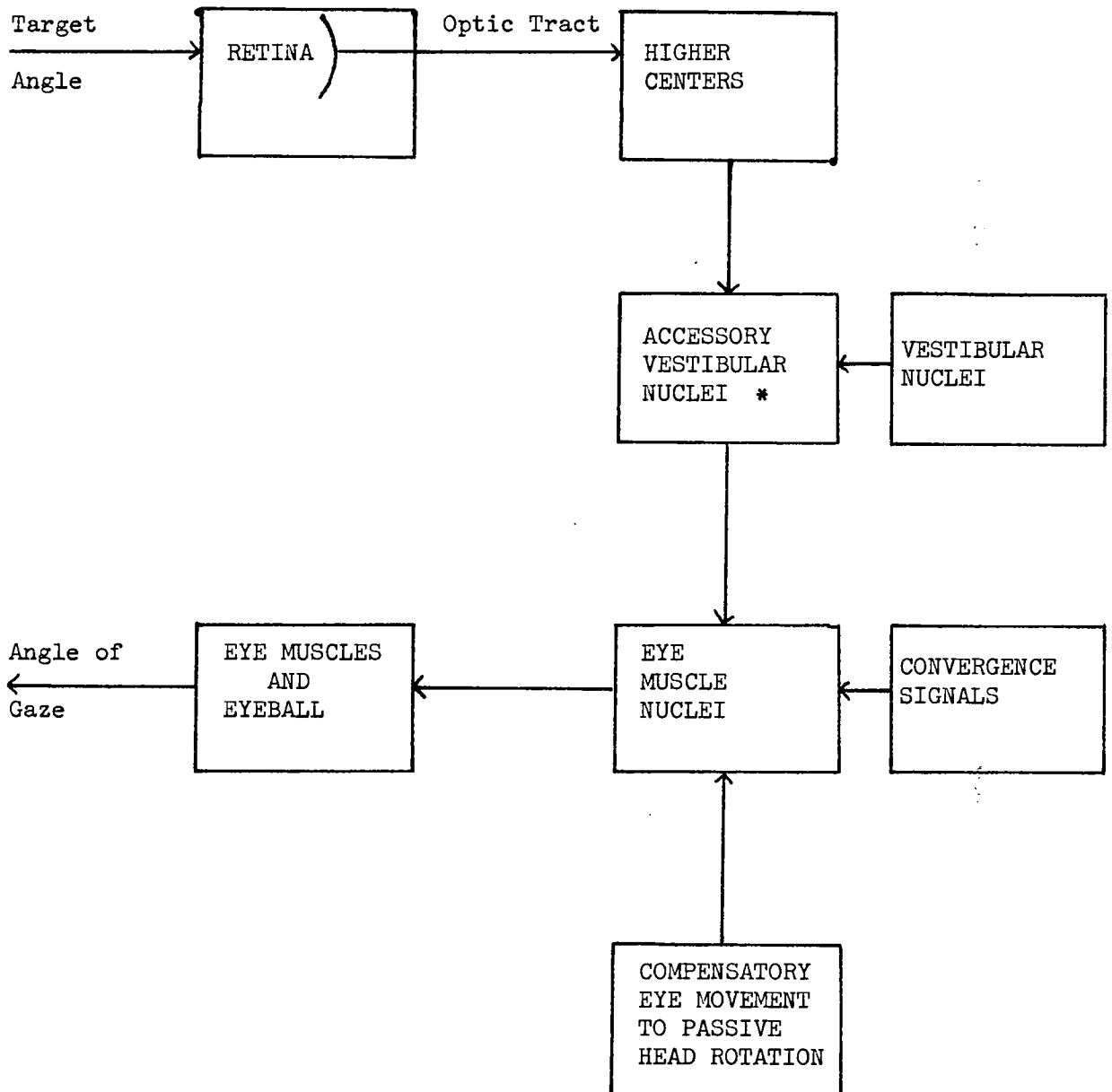
Figure 2.14 is a simplified block diagram of the eye movement control system. First is shown the target angle impinging on the first block or the retina. Information is carried by the optic tract to the higher centers, which includes the lateral geniculate bodies, the visual and frontal motor cortex and the collicular areas. The next block is labeled accessory vestibular nuclei and may also include such accessory nuclei as the accessory abducens nucleus. Then as we descend further toward the motor system we come to the eye muscle nuclei or the final common pathway. This leads, by means of the motor nerves, to the eye muscles and the eyeball which finally determine the angle of gaze. A visual target impinges on the retina at the very beginning of the system. A vestibular stimulus goes via the vestibular nuclei into the accessory vestibular nuclei and then to the eye muscle nuclei. Other pathways, leading more directly to the eye muscle nuclei, are the convergence signals and also the signals driving compensatory reflex eye movements in response to passive head rotation.

With this simplified diagram to help us organize behavioral evidence we will attempt to show that the starred block, called accessory vestibular nuclei, is the location of the intermittency operator or the sampling element of the sampled data system. Briefly the evidence is as follows. That all inputs which pass through this accessory vestibular nuclei show evidence of intermittency. All inputs which enter below this nucleus do not show such evidence of intermittency but are rather continuous control systems. Therefore, it is suggested that the locus of the intermittency operator is here.

### Behavioral Evidence.

Eye-tracking movements. We have already rather fully reviewed the evidence that the eye-tracking movements are the responses of a sampled data control system. This is true for both the position and velocity control elements and we have shown that there is no acceleration or higher derivative feedbacks. This is true, of course, only for unpredictable movements because as has been shown by Stark, Young and Vossius (16), the control system for eye tracking movements has an excellent prediction operator which serves to mask the basic intermittent operation of the system in response to unpredictable inputs.

Figure 2.14 Block Diagram for Motor Control.





Optokinetic nystagmus movements. Optokinetic nystagmus movements are an example of a visual input different from a voluntarily tracked target. Here the subject is directed to gaze ahead and to ignore the scene upon which he gazes. This scene is a constrained series of stripes traveling across a television screen at a rate and a direction determined by the experimenter. The slow phase of the optokinetic nystagmus represents a "sticking" of the retina on the striped target. The fast phase represents, most probably, an attempt by the fixation or the position-correction system to keep the eye approximately in the direction of forward gaze. Figure 2.15 shows a number of experiments on optokinetic nystagmus of this type. The insets in the upper right hand corner of the figure show ordinary optokinetic nystagmus going in either direction. The inset in the upper left hand corner shows a period of slow decline of optokinetic nystagmus and then again an increase in velocity of the slow phase. Why this alternation in slow phase velocity occurred is not known. The main traces show eye rate and eye position as a function of time when the target consists of two sets of stripes moving in opposite directions on the same television screen. Here we see there is an alternation between movement in one direction and movement in the other direction with periods of very slow moving slow phase in between. The essential point to be noted is that there is an intermittency in this optokinetic nystagmus in that the fast phases do not come closer together than 0.2 seconds apart. This is evidence that even in this reflex eye movement the intermittency operator is active. Thus we would expect to look for the intermittency operator in some portion of the eye movement control system common to both the voluntary and reflex response to image input.

Vestibular nystagmus. Vestibular nystagmus can be caused by stimulating the vestibular system either by rotating the subject in which case one produces primary vestibular nystagmus, or by stopping the subject after he has been rotated in which case one produces a post-rotatory vestibular nystagmus. Other methods of stimulating the vestibular organs or semi-circular canals are by means of hot or cold caloric stimuli or by means of DC electrical currents. It has been shown that the semi-circular canals respond to acceleration either indirectly by accelerating the head as in normal vestibular stimuli or in rotatory or post-rotatory vestibular nystagmus, or directly by producing forced acceleration of the fluid in the semi-circular canals by means of the caloric stimuli. The Galvanic or electrical stimulation situation presumably stimulates the sensory cells or the nerve endings directly. Figure 2.16 taken from an article by Wendt (19), illustrates the slow and fast phase of vestibular nystagmus. Of interest in this diagram is first, the lack of an initial delay time or response time, and second, the intermittency in the vestibular nystagmus which seems to occur at approximately 0.2 second intervals. The lack of delay time probably has to do with the input of vestibular nystagmus circumventing the higher centers and going directly through the vestibular nuclei and the accessory vestibular nuclei to the eye motor nuclei, eye motor nerve fibers and thence to the eye muscles. It has been shown above that the dynamics of eye muscles and eyeball are not limiting in the response of the eye or only very slightly so and thus one might expect that if the main delays are in the higher centers that vestibular nystagmus might not show these delays. Most importantly, however, is the fact that the intermittency appears to be very similar to that seen in the

Figure 2.15 Optokinetic nystagmus. (Work in progress at M.I.T. on optokinetic nystagmus)

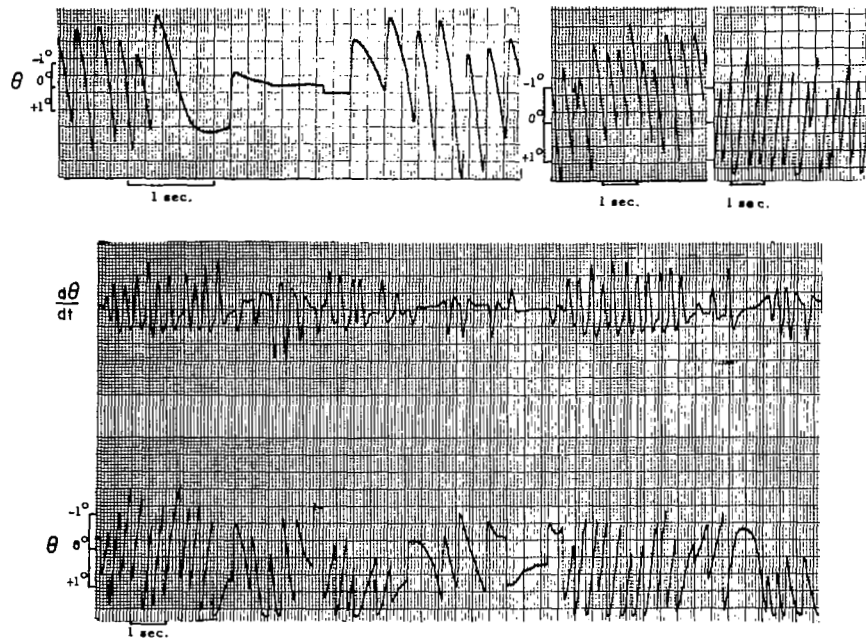
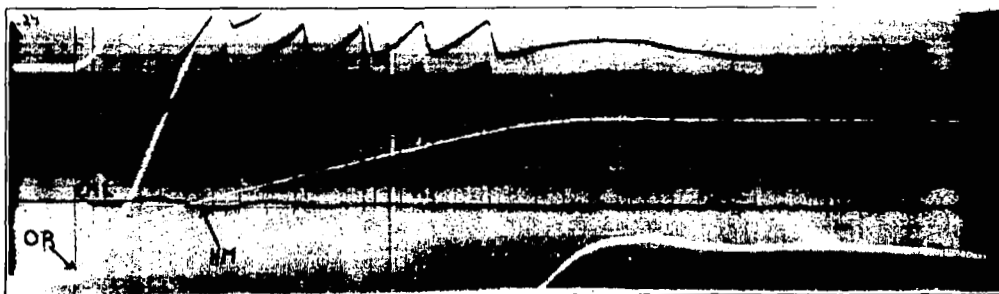


Figure 2.16 Vestibular nystagmus. (19)



tracking movements and in the optokinetic nystagmus. This suggests that the intermittency operator might be present in some common part of the pathway. The only common parts of the pathway now remaining for both the visual inputs and vestibular inputs are the accessory vestibular nuclei, the eye muscle nuclei and the eye muscle and eyeball.

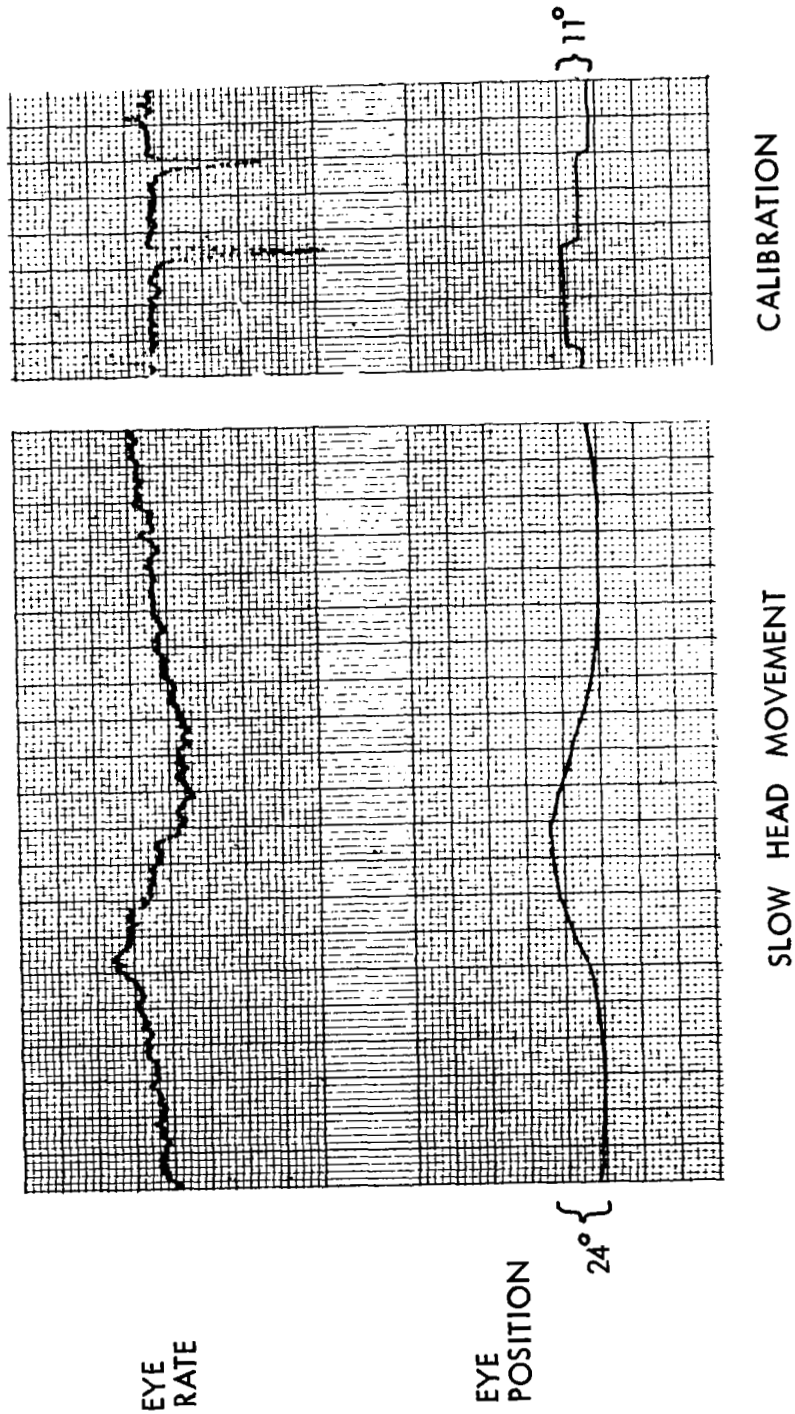
Convergence eye movements. Convergence eye movements were reviewed in the previous chapter and it was shown that this is a clear cut continuous system. The convergence eye movements must at least utilize the eye motor nuclei and eye muscles and eyeball. Thus we have definite evidence that the intermittency operator does not exist in the eye motor nuclei or in the eye muscles and eyeball itself.

Compensatory eye movements. Compensatory eye movements occur to passive rotation of the head. These are very primitive reflexes and can be shown in humans easily only in pathological cases. For example, if a subject has suffered severe brain disease and is unable to voluntarily follow a moving target he may still be able to maintain fixation of his eyes in a particular direction and further maintain this fixation by means of compensatory movements acting against disturbances produced by passive rotation of his head. This is a well-known phenomenon in clinical neurology although no evidence with recordings seems to exist in the published literature of this phenomenon. It might be possible also to demonstrate this phenomenon in subjects whose vestibular system is saturated by means of ongoing stimuli and responses, by superimposing compensatory eye movements as described here upon this active vestibular response. It might also be possible by means of drugs to eliminate the intermittency operator. There is evidence that barbiturates, although they do not affect the intermittency operator, seem to prevent the pursuit phase of eye tracking movements and the slow phase of optokinetic nystagmus. It might be that some drug would act to knock out the intermittency operator and still permit the compensatory eye movements to occur. Figure 2.17 shows a response of a normal subject making compensating eye movements to passive rotation of the head. It can be seen that no intermittency effects appear in this experiment. Again as in the case of the convergence signals the compensatory signals must pass through the eye motor nuclei, the eye muscles and eyeball. Thus the intermittency operator should be located above the eye motor nuclei.

#### Location of the Intermittency Operator by means of the Multi-Input Analysis Technique

We now see that by means of at least five different inputs to the eye muscle system we have been able to suggest a location for the intermittency operator at about the level of the accessory vestibular nuclei. Later reports will indicate neuroanatomical evidence which is consistent with this point of view. However, we can now tentatively

Figure 2.17 Compensatory Eye Movement in Response to Passive Head Turning.



eliminate both the sensory end and the motor end in this system as candidates for the locus of the intermittency operator. It will be remembered that there was no direct evidence concerning the eye muscles and the location of the intermittency operator at the motor end. This was merely an argument by analogy with the control system for hand movement.

Evidence for the presence of the intermittency operator at the sensory end was, however, quite interesting, although also indirect, and it may pay us to review this evidence at the level of the accessory vestibular nuclei. However, we will postpone these speculations until the last section of this report.

### Summary

In this section we have attempted to illustrate the usefulness of multi-input analysis by reviewing the behavioral evidence in the light of a simplified block diagram for the eye movement control system. We have been able tentatively to locate the intermittency operator at the level of the accessory vestibular nuclei and we have been able apparently to exclude all regions closer to the sensory or motor end of this system.

## SUGGESTIONS FOR FUTURE EXPERIMENTS

### Motor Experiments

It is suggested from the review of the behavioral experiments in the preceding section that evidence exists in the literature to locate the intermittency operator at the level of the accessory vestibular nuclei. However, much of this evidence was obtained with varying degrees of accuracy of recording instrumentation and in different laboratories without the intention of comparing results or having the results come out in similar form for easy and valid comparison. The first experiment that should be done in conjunction with the above hypothesis for the locus of the intermittency operator is to repeat all of these motor experiments on the same set of subjects under the same conditions and to show eye tracking movements, optokinetic nystagmus, vestibular nystagmus, convergence movements, compensatory eye movements, all done at the same time under similar conditions for comparative purposes. Although one can roughly outline and sketch, as we have done in the preceding section, what the results of these experiments will be, it is not clear that in detail the results can be predicted from evidence now available in the literature.

## Visual Suppression Experiments

We have seen in the second section of this report how the visual suppression experiments were shown to correlate with eye movements. We now know that they are probably not the source of the intermittency operation; however, they are clearly linked with the intermittency operator. In Figure 2.18 which is a more complex block diagram of the control system for eye movements, there is a dashed line leading from the accessory vestibular nuclei to the higher centers. This is postulated to be a feedback path for visual suppression from the locus of the intermittency operator to the higher centers. Thus, we are reversing the relationship initially suggested. That is, instead of the visual suppression being the mechanism for producing intermittency, we now are looking at the intermittency as a primary operator and searching for pathways by which it may control the visual suppression mechanism.

A series of experiments should be performed whereby the various movements, such as vestibular nystagmus and optokinetic nystagmus (although optokinetic nystagmus is of less importance) are shown to produce or not to produce the visual suppression phenomenon that occurs in correlation with the voluntary saccadic movements. Of primary importance would be the demonstration that vestibular saccades do produce visual suppression. This is an important and crucial experiment and we understand that the Systems Biology Laboratory at M.I.T. is undertaking these experiments.

Although a centrifugal pathway from higher centers to retina is sketched in, it is not believed that such a pathway exists in humans or at least there is as yet no clear-cut evidence that such a pathway exists. An experiment of interest would be to compare the electroretinogram, ERG, and the evoked potential from the visual cortex,  $E_VP$ , with visual sensitivity as a function of the temporal relationship of visual stimulus and saccadic eye movement. If  $E_VP$  and visual sensitivity showed corresponding suppression during a saccade then this would be a nice objective correlate of the visual suppression. Next, one could look at the ERG. If this showed the suppression during a saccade it would be important evidence for centrifugal fibers from the eye movement control centers back to the retina.

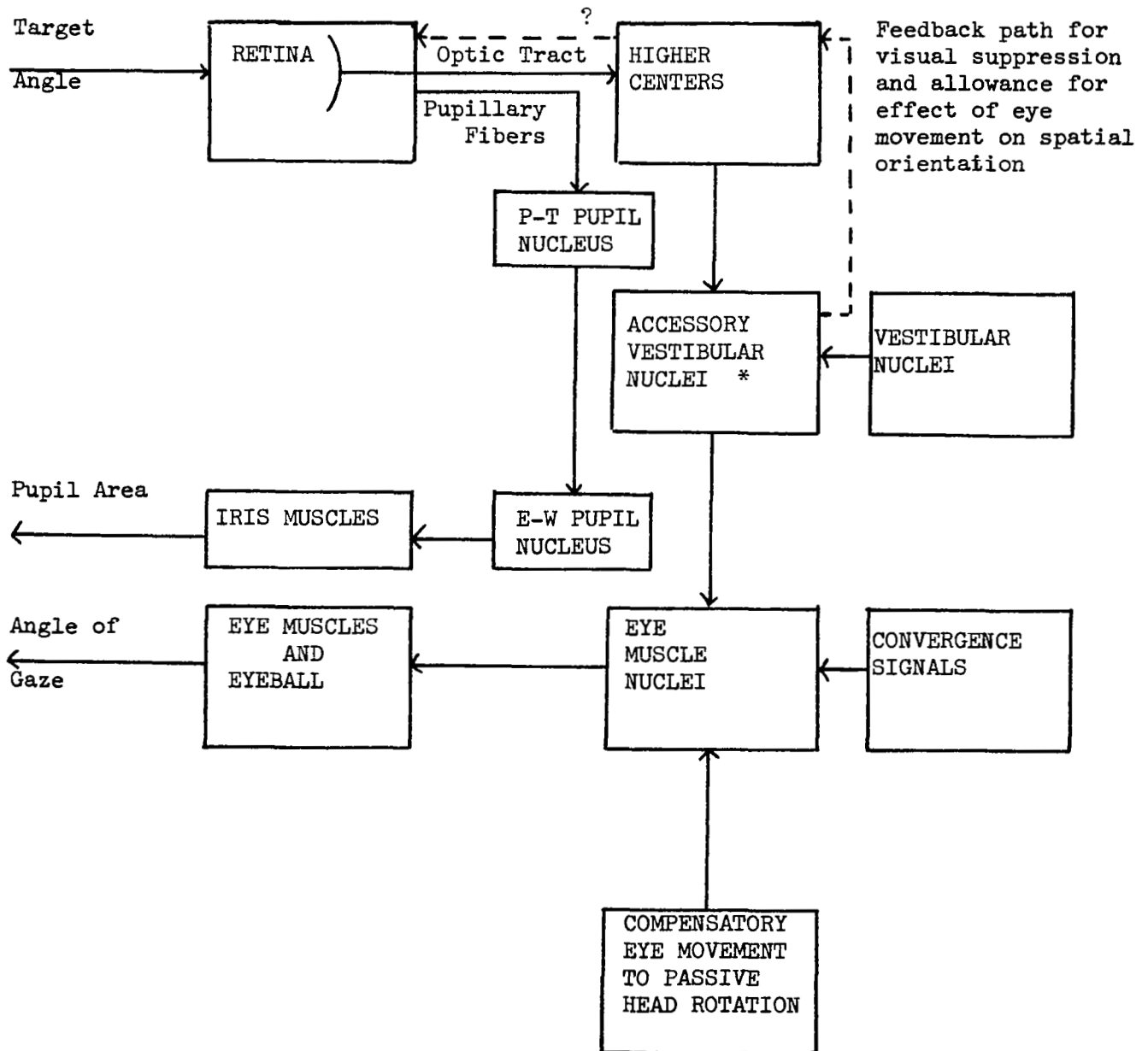
The lack of present evidence for such centrifugal fiber feedback is most astonishing since one would expect in any present day engineering system a great deal of feedback would exist to a complex peripheral computing center receiving sensory information. Perhaps some new principle of control systems whereby such feedback would be disadvantageous from a higher level point of view should be explored.

It would also be of interest to show that convergence and compensatory movements do not produce visual suppression since they do not activate the intermittency operator.

The well-known phenomenon that the saccadic movement of an eye has no effect on the person's spatial orientation since the predicted change in position of the retina has already been allowed for in terms of the general spatial orientation of the individual, may have a bearing in this connection.

Figure 2.18

Block Diagram for Motor Control and for Feedback Pathways for Visual Suppression and Allowance for Effect of Eye Movement on Spatial Orientation.





Might not the same feedback path from intermittency operator to visual suppression at the higher centers also be the pathway whereby the pre-computed eye movement is allowed for in terms of spatial orientation. Since the eye muscles operate with large forces on a fixed small load most pre-computations of expected eyeball position would be accurate and there is no need for proprioceptor feedback to check this as in the case of the hand where varying loads are always present. Thus between samples the eye movement system is essentially operating open-loop and this is, teleologically speaking, a wise thing to do. It may lead to some confusion if there is a paralysis of a muscle in that the expected movement of the eye does not occur and the pre-computation causes the spatial orientation system to make an error and to visualize the world as moving when neither the eye nor the world moved.

There have been clinical reports of patients without vestibular function, due to streptomycin toxicity, who report "dancing movements" of the world. Evidently without vestibular compensation the neck proprioceptors have to perform compensatory eye movements. Since these are continuous movements no intermittency operator with its associated visual suppression and spatial-precomputation operators acts. Thus, these reflex compensatory eye movements without spatial-precomputation may produce "dancing movements" of the world. It would be interesting to see if accommodative-convergence-eye-movements activate the spatial-precomputation operator.

### Pupillary Experiments

Also shown in Figure 2.18 are the pupillary pathways: the pupillary fibers of the optic fibers of the optic tract lead to the pre-tectal nucleus, then to the Edinger-Westphal nucleus in the third nerve nucleus complex, and thence to the iris muscles to control pupil area. The higher centers and accessory vestibular centers do not seem to be directly involved in the pupillary pathways. We thus would expect and, indeed, find no intermittency operator, as shown in the first section where the pupil was shown to be a continuous system. We further expect no visual suppression mechanism and we thus expect to see no elevation of threshold in terms of pupillary sensitivity. This is an experiment that could be done with equipment present in the Systems Biology Laboratory of M.I.T. In fact, its execution is presently being planned. Here a voluntary saccadic eye movement will occur, a flash of light will produce a pupillary response which will be measured when the eye is in its final position in the pupillometer at the end of the saccadic movement. Parallel graphs of elevation of visual threshold and non-elevation of retinal threshold as is measured by pupillary sensitivity will be plotted. This is the expected result, but this again is a crucial and important experiment.

### Summary

DeMorgan in his "Budget of Paradoxes" has stated that the wrong hypothesis rightly worked is more fruitful than chaos. We hope that our analysis of the

location of the intermittency operator using the block diagram above and the multi-input, servoanalytic, and neurophysiological techniques discussed in this report will enable a number of experiments to be performed and their results interpreted. If the hypothesis and theories are incorrect they will be able to be quickly and cleanly eliminated. If they still stand after the suggested experiments have been performed then it will be a tribute to the application of engineering analysis to a complex biological system.

#### BIBLIOGRAPHY

1. Bekey, G.A. (1962) An investigation of sampled data models of the human operator in a control system. Tech. Doc. Rep. No. ASD-TDR-62-36, Wright Patterson Air Force Base.
2. Davis, Jon (1962) Unpublished experiments. Neurology Section, Massachusetts Institute of Technology.
3. Ditchburn, R.W. (1959) Physical methods applied to the study of visual perception. Bull. Inst. Phys. 10:121-125.
4. Granit, Ragnar (1955) Receptors and Sensory Perception. Yale University Press.
5. Hammond, P.H., P.A. Merton, and G.G. Sutton (1956) Nervous gradation of muscular contraction. Brit. Med. Bull., 12:214-218.
6. Kappers, C.U.A., G.C. Huber and E.C. Crosby. (1960) Comparative anatomy of the nervous system of vertebrates, including man. Hafner Publishing Co., N.Y., Vol. II, p. 1079.
7. Latour, P.L. (1962) Visual threshold during eye movements. Vision Res., Vol. 2, pp. 261-262.
8. Lettvin, J.Y. (1960) Human Vision. QPR No. 58, Res. Lab. Electronics, Massachusetts Institute of Technology, 254-258.
9. Matthews, P.B.C. and G. Rushworth (1958) The discharge from muscle spindles as an indicator of  $\gamma$  efferent paralysis by procaine. J. Physiol. 140:421-426.
10. Navas, F. (1963) Sampling or quantization in the human tracking system. M.S. Thesis, Dept. of Electrical Engineering, Massachusetts Institute of Technology.
11. Navas, F. and L. Stark (1963) Experiments on discrete control of hand movement. QPR No. 69, Research Laboratory of Electronics, Massachusetts Institute of Technology.

12. Sandburg, A.A. and L. Stark (1963) Model of pupil reflex to light  
QPR No. 68, Research Laboratory of Electronics, Massachusetts  
Institute of Technology, 237-240.
13. Stark, L. (1959) Stability, oscillation and noise in the human pupil  
servomechanism. Proc. Inst. Radio Engineers, Vol. 47:1925-1939.
14. Stark, L., M. Iida and P.A. Willis (1961) Dynamic characteristics of  
the motor coordination system in man. Biophysical J. 1:270-300.
15. Stark, L., Y. Okabe and P.A. Willis (1962) Sampled data properties of  
the human motor coordination system. QPR No. 67, Massachusetts  
Institute of Technology, pp. 220-223.
16. Stark, L., L. Young and G. Vossius. (1962) Predictive eye movement  
control. Inst. of Radio Engineer's Trans. on Human Factors in  
Electronics, Vol. HFE-3, pp. 52-57.
17. Stevens, S.S., ed. Handbook of Experimental Psychology, "Vestibular  
Functions". Wiley Co., N.Y., 1951.
18. Volkman, F.C. (1962) Vision during voluntary saccadic eye movements.  
J. Opt. Soc. Am., 52:571-578.
19. Wendt, G.R. (1936) The form of vestibular eye movement response in man.  
Psychol. Monogr., 47:311-328.
20. Young, L. and L. Stark (1963) A discrete model for eye-tracking  
movements. IEEE, Trans. on Military Electronics, Vol. MIL-7,  
pp. 113-116.

## CHAPTER III

### CONTROL OF EYE MOVEMENTS: NEUROANATOMICAL CONSIDERATIONS

#### INTRODUCTION

Although there is an extensive literature on the anatomy of the control of eye movements in all animal species including primates and man, the data has been gathered by many different techniques during the last one hundred years. Much of the data is in conflict depending upon the particular technique used, the animal species used, as well as the approach of the experimenter. Perhaps it would be best to begin this discussion with a survey of the techniques available for the study of the anatomy of the central nervous system. The particular assets and liabilities of each technique will be discussed.

#### Anatomical Techniques

Histologic stains. The central nervous system comprising the brain and the spinal chord, consists of groups of nerve cells, the neurons, which are organized into nuclei. The extensions of these neurons, the axons, can be as short as 0.050 mm or as long as several centimeters. The axons end on other neurons, the connection being via a synapse. In addition, there is an extensive network of other cellular elements, the glial cells, which are thought to have some secondary effect on nervous activity by affecting the metabolism of the neurons. However, at the present time, nerve impulses appear to pass from one neuron along its axon across a synaptic cleft to the next neuron. The vast majority of axons are covered with a fatty sheath of myelin, which acts as an insulating material for the axon. One can selectively stain the Nissl granules in the cell bodies of the neurons by using cresyl violet, and the myelin sheath by using an appropriate hematoxylin stain (Weigart or Loyez stain). In this manner, the various nuclei can be defined on the basis of their cresyl violet staining, and the fiber tracts of the axons ensheathed in myelin can be delineated. However, since there are many millions of cells and nerve fibers in the central nervous system, it is impossible to determine how one cell is connected with another using this technique exclusively. Consequently, additional experimental maneuvers are necessary.

Neuron and axon degeneration. If a small surgical lesion is made in a particular nerve pathway of the central nervous system, the axon and its myelin covering distal to this lesion, will degenerate. This is

called Wallerian degeneration. On the other hand, the proximal portion of the nerve fiber with its cell body of origin may or may not degenerate. Very often there will be changes seen in the cell body of the neuron, noted with cresyl violet stains. This change consists of a difference in the pattern of the Nissl granules of the cell body and is referred to as chromatolysis. If these changes are particularly severe, the cell body may actually degenerate and disappear. This process is called retrograde degeneration. Wallerian degeneration can be detected by staining the degenerating myelin sheath using the Marchi stain and one can trace the course of the axon. This had been the most popular technique until approximately ten years ago. Although it did give an accurate picture of the course of the axon by its myelin degeneration, it was quite difficult to determine where any particular axon ended. More recently this has been accomplished by the use of the Nauta stain. With this stain, the degenerating axon and its endings stain, and these endings can be seen to terminate on a particular neuron. It would be desirable for the fiber tracts previously described by the Marchi method to be reinvestigated using the Nauta technique. This is not possible from the practical point of view. In selective cases, however, the picture determined by the Nauta stain has been much clearer than that determined previously by the Marchi technique. When retrograde degeneration results in a loss of cell bodies in a nucleus, it can be determined by the loss of staining with cresyl violet.

Transneuronal degeneration. In some tract systems such as the optic nerve, Wallerian degeneration proceeds distally from the eye and does not stop at the next cell connection but proceeds across the synapse and results in atrophy of the next neuron. This atrophy which proceeds across the synapse is called transneuronal degeneration. Using this technique, the projection of the retina on the lateral geniculate nucleus one synapse removed from the optic nerve, has been mapped (1).

All the above techniques can be applied to the experimental animal quite successfully. These techniques can often be applied to clinical cases coming to autopsy, as mentioned below in the section on clinico-pathological correlations.

### Physiological Techniques

Ablation. In experimental animals, a lesion of a nucleus or a nerve tract has been produced surgically or by placement of microelectrodes in the brain. Following such lesions in which the tissue is destroyed, one can observe the change in behavior of the experimental animal, along with the pattern of eye movements. The observation of behavior can be done immediately following the acute production of the lesions or at some later time in the chronic animal.

Electrical stimulation. Instead of removal of brain tissue, nuclei or tracts of the central nervous system can be stimulated electrically. During or following such stimulation, the behavior and eye movements of the animal may be observed immediately or sometime following the positioning of chronically implanted microelectrodes into the brain. If the stimulation is confined to a very small area of the brain, presumably certain neurons and nervous pathways will be brought into activity; these pathways would be correlated with the particular behavior observed.

Physiological stimulation. It is generally assumed that electrical stimulation as outlined in the above section is quite artificial. The behavior resulting from such stimulation may have no bearing on the behavior of the ambient animal. Consequently more physiological stimuli are used such as flashes of light to test the visual system.

Stimulation of a nucleus, tract or particular sensory system while recording electrical activity elsewhere in the brain. This technique has gained much importance recently. If one wishes to follow the course of the response to a stimulus, for example, that to a flash of light along the sensory pathways in the brain, it is possible to place recording electrodes in the appropriate sites and record the electrical activity secondary to the light stimulus. In this manner one could trace the course of the nervous impulse set off by the light flash. This technique can often be combined with ablation experiments.

Split-brain preparation. A more recent development of neurophysiological technique has made use of the fact that the brain consists of two cerebral hemispheres with similar if not identical properties, at least in sub-human species. The hemispheres are interconnected with each other via a series of fiber tracts, the largest being the corpus callosum. If the connections are severed surgically, one can isolate activity in one cerebral hemisphere from activity in the other. If all optic nerve fibers which cross in the optic chiasm are surgically cut, all information seen by the right eye will enter the right cerebral hemisphere. All information seen with the left eye will only enter the left cerebral hemisphere. Consequently an animal can learn one task using the right eye with the left eye covered and another using the left eye with the right eye covered. Ablation experiments in one cerebral hemisphere or the other will allow a comparison between the normal hemisphere with the hemisphere containing the particular lesion. Such experiments are more reliable as to the repeatability of the data.

In general only those experiments having the site of lesion verified anatomically will be discussed in this paper. Most desirable is an anatomical-physiological correlation. If one stimulates a nucleus, it must be required that a lesion be made in this nucleus which can be determined anatomically at the conclusion of the experiment. Correspondingly if a nerve fiber tract is seen to degenerate following an ablation, one should be able to record the absence of nervous activity along this tract using electrophysiological techniques.

## Clinico-pathological Correlations

Many of the experiments noted above occur spontaneously in man through the occurrence of disease of the central nervous system. There are defects produced in nuclei or nerve tracts by tumors or other lesions as well as pathological stimulation of nuclei and nerve tracts as in cases of epilepsy. On the basis of clinical experience with such cases, certain correlations have been made relating the clinical symptoms and the site of the particular lesion. Such empirical correlation is the basis upon which the practice of neurology and neurosurgery rests. There has not been, however, as frequent pathological verification of the actual site of lesion as one might wish. Consequently neither the extent of the actual lesion nor the presence of other lesions in addition to those considered clinically can always be determined. Nevertheless, in some selective studies, there has been excellent pathological verification of clinical disease. From such data, valuable contributions have been made to the anatomy and function of the central nervous system. Such contributions are few.

### PURPOSE OF THIS REPORT

#### Material Used

Two sources of experimental material with some exceptions, will form the basis of this report. Material based upon primate anatomy and physiology of the central nervous system will be used provided there is agreement between the physiological and anatomical data. In addition, clinical data from human material will be used provided there is good pathological confirmation. Due to wide species variations, information from the cat, rabbit and other mammals will not be considered in this discussion.

#### Specific Objectives

There are two objectives in this report. The first is to define those neural pathways for the control of eye movements for which there is no major disagreement concerning the experimental data. Secondly, the possibilities for localizing the intermittency operator will be discussed.

## THE VISUAL SYSTEM

### Sensory Input - Visual

Retina. The retina is part of the central rather than the peripheral nervous system, being an outgrowth of the primary neural tube. The layers of the retina are differentiated from the neuroectoderm. There are three distinct cell layers with interconnections as follows (2): a- The layer of rods and cones represent the percipient elements and contain the photopigments which react to light falling on the retina and presumably initiate the electrical impulse. The rods and cones respond only to changes in the amount of light and to the color (wavelength) of the light. The cell bodies of the rods and cones constitute the first or outermost layer of cells and are connected with the second layer of cells called bipolar cells. b- The bipolar cells receive input from either small numbers of cones in the fovea (the area of highest light sensitivity and visual acuity in the retina), or from large numbers of rods and/or cones in other areas of the retina. They in turn relay the electrical impulse to the third layer of cells, the ganglion cells. The ganglion cells make up the most internal layer of cells of the retina, being close to the vitreous cavity. It may be noted that light entering the eye anteriorly passes through the ganglion cell layer, the bipolar cell layer, the layer of cell bodies of the rods and cones, to reach the photopigments in the outer segment of the rods and cones. This inverted retina is characteristic of all vertebrates. The ganglion cell receives input from a relatively large number of rods and/or cones. Its axon extends from the retina to the lateral geniculate nucleus in the thalamus of the brain. In the first portion of this course, the axon of the ganglion cell is referred to as the optic nerve. At the chiasma, those ganglion cells nasal to the fovea have axons which cross to the opposite side of the brain. Those ganglion cells which are temporal to the fovea, remain uncrossed. After the chiasma the axon is referred to as the optic tract until it reaches the lateral geniculate nucleus. Electrical recording has not been possible from either the cell bodies of the rods and cones or the bipolar cells. The first data available are recordings from the ganglion cell. It appears that the ganglion cell can be excited or inhibited in its electrical activity by light falling on a discrete area in the visual field of the experimental animal. This area in the visual field subtends a specific number of degrees of visual arc and involves a number of rods and/or cones. That portion of the visual field which, when stimulated by a spot of light, will cause the ganglion cell to be excited or inhibited is called the receptive field of the ganglion cell. The receptive field is divided into two concentric areas with either a central area causing excitation of the ganglion cell and the peripheral doughnut shape area causing inhibition, or vice versa. (For further discussion of the organization of receptor field, consult reference 3.) In primates and man, it appears that all the optic nerve fibers are myelinated. There do not seem to be any efferent nerves, i.e. nerve fibers coming from the cortex to the retina. However, it must be stated that optic nerve from primates



or man has not been examined with the electron microscope to determine whether very thin non-medullated nerve fibers do exist.

The lateral geniculate nucleus. In primates and man, all optic nerve fibers subserving vision appear to synapse with a neuron of the lateral geniculate nucleus. There does not seem to be any other afferent input to the lateral geniculate nucleus. Neither are there any afferent fibers from higher visual centers. The projection of the retina in the lateral geniculate nucleus has been determined for monkey and man on the basis of transneuronal atrophy studies. There is a definite retinotopic representation of the retina on the lateral geniculate nucleus with the fovea being represented at the caudal pole of the nucleus, and the peripheral portions of the retina represented as one moves rostrally in the nucleus. The exact connection between optic nerve fiber and geniculate neurons has not yet been examined. Although there are about one million optic nerve fibers and one million geniculate neurons, one cannot state that each optic nerve fiber ends on only one geniculate neuron. However, there is good evidence to indicate that small retinal lesions of one eye will produce a transneuronal atrophy in three of the six lamina of each lateral geniculate nucleus. Each nucleus consists of six laminae, numbered 1 through 6 from ventral to dorsal surface. Laminae 1, 4 and 6 of each nucleus receive optic nerve fibers from the nasal retina of the contralateral eye while laminae 2, 3 and 5 receive fibers from the ipsilateral temporal retina. Again, receptive fields of the geniculate neurons can be mapped (4).

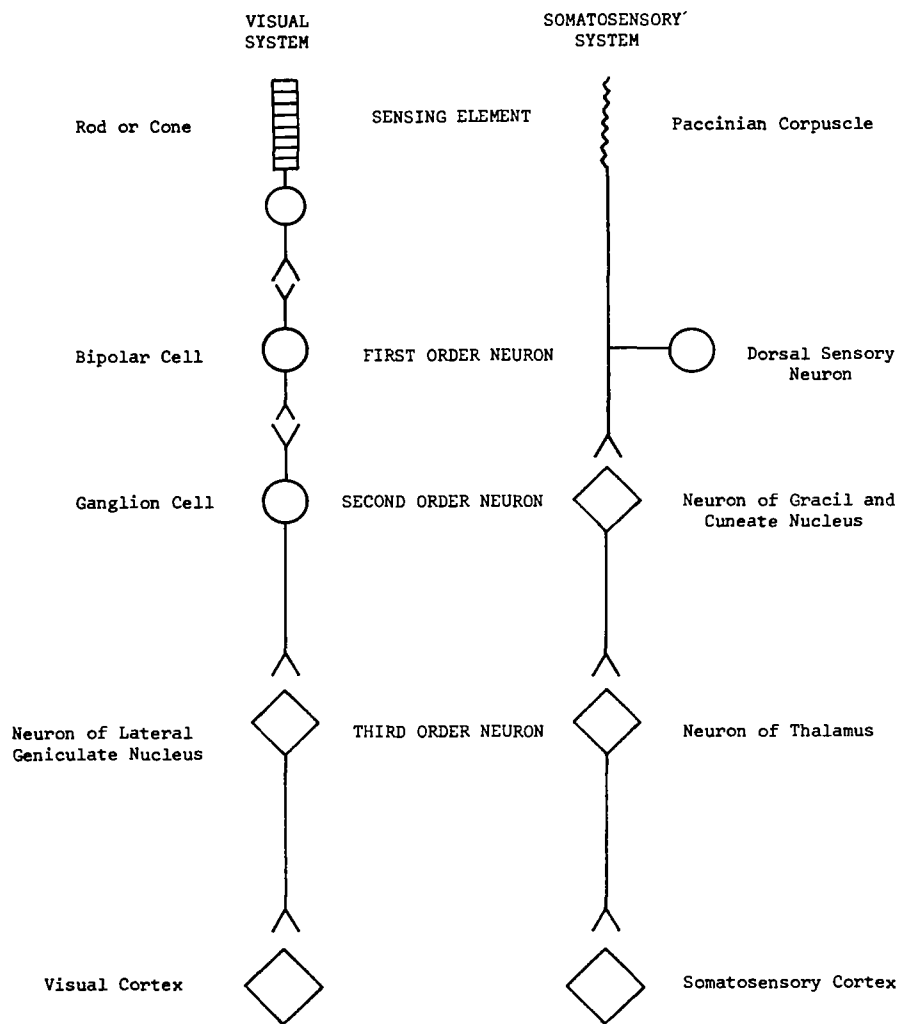
Visual cortex - area 17. The neurons of the lateral geniculate nucleus send their axons to area 17 of the visual cortex. Apparently all axons from the geniculate nucleus enter the visual cortex. From area 17, there are additional fibers which can be traced to adjacent areas 18 and from there, to area 19 of the visual cortex. These are considered association areas. From this point onward, no definite evidence for the course of fibers in the visual system is available. The visual cortex has a functional architecture and its neurons have receptive fields which are much more selective in terms of the type of stimulus necessary to evoke a reaction. (For further information see reference 5.)

In summary, it would be of interest to compare the arrangement of the afferent portion of the visual system with the afferent portion of the somato-sensory system which subserves touch. Figure 3.1 diagrammatically illustrates an older concept of some comparable way stations from the sensory input to the representation in the cortex.

### Sensory Input - Pupil

When light falls upon the retina, not only is there a visual (sensory) impression, but an additional (motor) system is stimulated, the pupillary

Figure 3.1 A comparison between the visual system and somatosensory system.

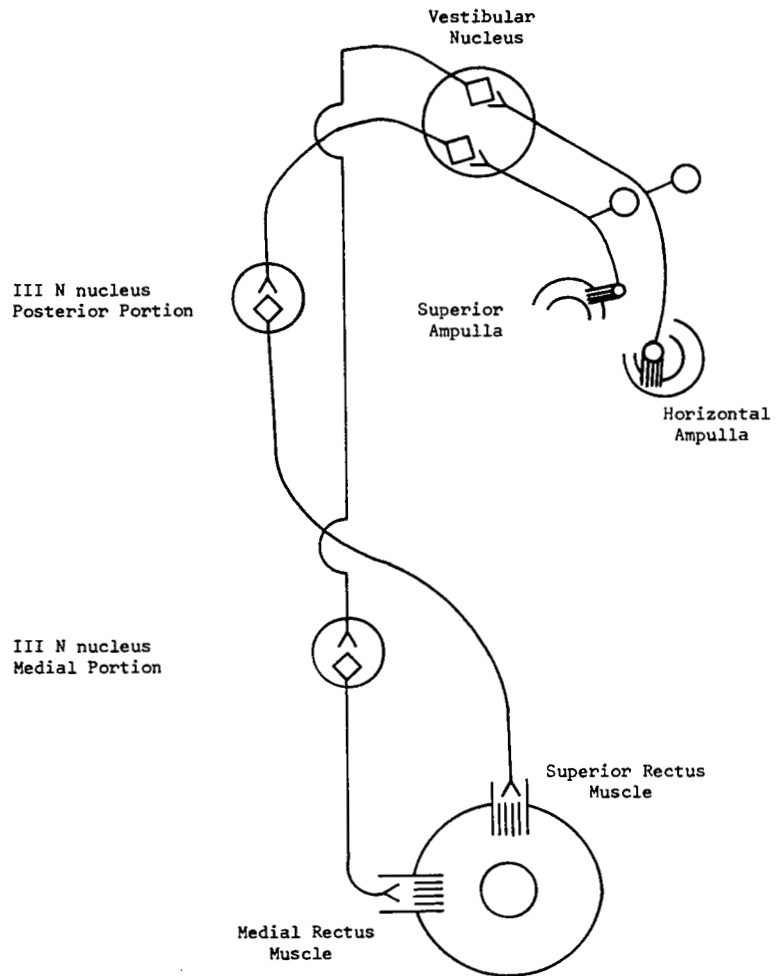


system. This system controls the size of the pupil which regulates the total luminous flux entering the eye. It is not known whether the optic nerve fibers subserving pupillary changes are identical with those subserving visual function. In either case, the rods and cones, bipolar cells, and ganglion cells are all present in the afferent portion of the pupillary control system. The pupillary afferent fibers, either separate fibers or collaterals of the visual fibers, leave the optic tract just before the visual fibers enter the lateral geniculate nucleus. The pupillary afferent tract swings medially and ends on the pretectal nucleus. This nucleus is located close to the superior colliculus. In the monkey, some of the pupillary fibers from the periphery of the retina end in the superior colliculus but for all practical purposes, the pupillary afferent projection which is most dense from the macula, ends in the pretectal nucleus (6).

### Sensory Input - Vestibular System

There is some anatomical information from studies in monkeys on the connections between the labyrinth and the extraocular muscles (7, 8). The sensory receptor cells of the labyrinth and its cell body (primary vestibular neuron) synapse with the secondary neuron in the vestibular nuclei, of which there are four - namely the medial (triangular nucleus), the superior (Bechterew), the lateral (Deiter), and the inferior nucleus (spinal nucleus of Roller). In man there are no important accessory vestibular nuclei although some cells are scattered along the inferior nucleus and are considered of importance in some mammals. Stimulation of the cristae in the labyrinth by endolymph currents artificially evoked in individual semicircular canals has indicated that the posterior ampulla is connected with the ipsilateral superior oblique and contralateral anterior rectus muscles, the superior ampulla with the ipsilateral superior rectus and contralateral inferior oblique muscles, and the horizontal ampulla with the ipsilateral medial and contralateral lateral rectus muscles (Figure 3.2). These connections may occur via the medial longitudinal fasciculus. However there is some suggestion that these connections may proceed by pathways other than this fiber bundle. As noted in Figure 3.2, lesions in the vestibular nucleus result in degeneration of terminal synaptic endings of the axon from the vestibular nucleus in the posterior third and medial portion of the third nerve nucleus. This is determined using the Nauta method. In addition there are other pathways, first described by Lorente de No (9), which traverse the reticular formation and are unaffected by transection of the medial longitudinal fasciculus. Just as there are two sensory inputs to the vestibular nuclei, there are two types of nerve endings on the neurons in the oculomotor nucleus. The large type A synaptic terminals are thought to belong to the secondary vestibular neurons coming directly from the vestibular nuclei, while the finer type B synaptic terminals appear to come from those fibers traversing the reticular formation. In addition, there may be an indirect pathway from the vestibular nucleus via the medial longitudinal fasciculus and the interstitial nucleus of Cajal. Some fibers of the vestibular nerve do not enter the vestibular nuclei, but bypass the nuclei and go directly to the cerebellum, to the region of the solitary

Figure 3.2 Illustrative pathways from ampullae of semicircular canals to oculomotor nucleus.



tract and its nucleus, to the dorsal motor nucleus of the vagus, and to the dorsal lateral region of the medullary reticular formation (Fig. 3.3). No primary vestibular fibers enter the medial longitudinal fasciculus. In addition, there is a large afferent inflow, which is thought to be of an inhibitory type, into the vestibular nuclei from the cerebellum. It is of interest that the reticular formation provides an internuncial "relay" not only for the conduction of vestibuloocular impulses but also impulses from auditory and somatic sensory structures.

#### Sensory Input - Optokinetic Nystagmus

The normal optokinetic nystagmus cycle is a very complex process. Since fixation is necessary for optokinetic nystagmus, some if not all of the afferent visual tracts must be intact.

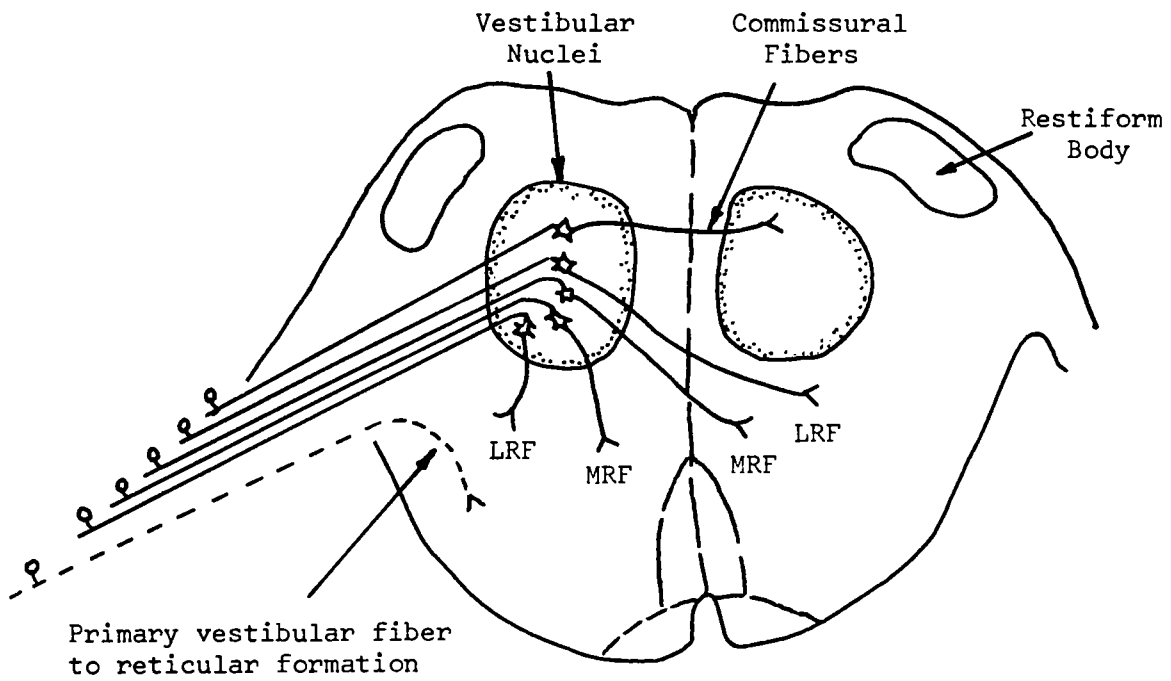
#### Sensory Input - Convergence

Convergence occurs when the optic axes of the two eyes are aligned on some relatively near point. Contraction of both medial rectus muscles brings about this movement. However, the movement upon convergence differs somewhat from adduction of either eye. Not only is the adductive amplitude less for convergence than for conjugate movements, but convergence induces an associated intortion whereas conjugate movements cause an extortion of the adducting eye. In addition, convergence usually occurs in conjunction with accommodation and pupillary constriction ("the near point triad"). However, these components are mutually independent to the extent that if for any reason, one component is prevented from acting, the others act independently. Since convergence depends upon aligning the optic axes of the two eyes on some relatively near point, the afferent limb is apparently identical to that for vision.

#### Sensory Input - Compensatory Eye Movements

Compensatory eye movements can best be demonstrated in the normal subject by tilting the head to one shoulder. During this maneuver, there is a partially compensatory rolling of the eyes which does not occur if the labyrinth is first destroyed. There is no voluntary control of this compensating eye movement. The effect of the labyrinthine stimuli on maintaining the position of the eyes can also be demonstrated in man under certain pathological conditions in which volitional and fixational reflexes are abolished. Under these conditions, the eyes turn downward when the head is rotated backward and upward when it is rotated forward, an action which has been likened to that of a mechanical doll's eye (10). The sensory input for this is from the labyrinth to

Figure 3.3 Bulbar cross-section at level of VIII N .  
 Note abundant vestibulo-reticular connections.  
 MRF - medial reticular formation  
 LRF - lateral reticular formation



the vestibular nerve. Whether the sensory pathway is identical with that of the slow component of vestibular nystagmus is not known.

### Sensory Input - Proprioception

It is now generally accepted that the extraocular muscles have a well-developed proprioceptive stretch reflex system including muscle spindles with large sized afferent nerves running in the third, fourth and sixth cranial nerves to the brain stem (11, 12). The afferent fibers leave the oculomotor nerves and enter the ophthalmic branch of the fifth cranial nerve, ending in the region of the mesencephalic nucleus of the fifth cranial nerve. The sensory input has not been traced past this point. It may be worthwhile to state at this point that the arguments concerning lack of position sense on the part of the eye have no bearing on the presence of a proprioceptive stretch reflex system in eye muscles. Position sense is mediated through joint receptors and is represented in the cerebrum. Proprioceptive impulses are represented only as high as the thalamus and do not reach the cerebrum. They are not appreciated consciously. The eye has no joint receptors, and there is no conscious position sense (for review of this problem, see ref. 13).

### MOTOR OUTPUT FOR EYE MOVEMENTS

Although there is abundant clinical information unverified by pathological verification, the oculomotor pathways will be interpreted in this report only from anatomical and physiological experiments in monkeys and the occasional clinical case with pathological verification. Electrical stimulation over approximately 34% of the convexity of the cerebral hemispheres results in the occurrence of eye and head movements. Approximately 38% of the cerebral hemispheres as shown by stimulation are related to movements of hand, arm and shoulder. The frontal and occipital eye fields do not appear to be as well delineated as previously considered (14). On the contrary, eye movements appear to be diffusely represented in the cerebral hemispheres. The rationale for this widespread representation may be related to the fact that eye movements represent an integral part of some sensory functions such as visual or auditory functions, in that they provide a more efficient sensory input by directing the eyes and head to the appropriate location. Eye movements often are directed towards that portion of the extremity which is stimulated and appear to play a role in other behavioral functions such as arousal to sensory reaction and orientation reaction.

The outflow of fibers from the cerebral hemispheres to brain stem appears to remain quite separate on the way to the oculomotor nuclei. This is demonstrated as follows: if a small lesion is made in the pontine

reticular formation, there is an ipsilateral paresis of gaze. On stimulating the contralateral arcuate cortex, the threshold for eye and head movements is greatly increased. However, the threshold stimulation in the contralateral occipital cortex nearby is increased to a smaller extent. This would suggest that the separation of pathways from the two cerebral areas to the brain stem are maintained quite caudally on their way to the final common pathway (14). From the effects of stimulation and production of lesions, there is a large portion of the brain that appears to be involved in the production of eye movements. Besides the wide representation in the cortex and subcortex, the oculomotor pathway can be found to pass the regions medial to the internal capsule such as the fields of Forel, the zona inserta, and the median thalamus. The pathways then converge at the level of the pretectum and become concentrated in the tegmentum of the brain stem. In general, the oculomotor pathway is situated medially to the internal capsule except in its most rostral portion where fibers from the frontal lobes are located. In the pretectum the pathway is better defined in the paramedian zones which are first located laterally then ventrally to the medial longitudinal fasciculus. At the level of the third to fourth nerve nuclei, the pathway appears to decussate. After the decussation, which in all probability is incomplete, the pathway can be traced down to the level of the paramedian reticular formation on the pontine tegmentum. The descending pathway is situated on both sides of the tegmentum, ventral to the median longitudinal fasciculus. Although the oculomotor pathway does not run through the vestibular nuclei, there is no doubt that a substantial contribution from the vestibular nuclei is made to the principal oculomotor pathways (15). Although the medial longitudinal fasciculus is involved in movement of the eyes, it has no effect on conjugate eye movements. A lesion in the medial longitudinal fasciculus only effects adduction of the ipsilateral eye.

### Motor Outflow - Visual

It is important to keep in mind that during tracking and saccadic movements, the movement of eyes is being influenced not only by visual stimuli but by other sensory information associated with the visual stimuli, such as spacial and depth perception. Although there is no experimental evidence bearing upon this, it is assumed that the occipital cortex is involved in the movements of eyes induced by visual stimuli while following a moving object and other reflex visual movements. These are referred to as pursuit movements and appear smooth (16). It is of interest that at two to three weeks of age, an infant turns its eyes to affix an object which attracts its attention, but makes no smooth following movements until three to five months of age, suggesting a separation of these functions.



### Motor Outflow - Pupil

Motor fibers from the pretectal nuclei proceed with or without decussation through the posterior commissure to the collection of cells marking the Edinger-Westphal nucleus at the rostral end of the third nerve nucleus complex. The axons leave this nucleus to synapse in the ciliary ganglion. From this ganglion, a small number of fibers connect with the iris. Most of the parasympathetic nerve fibers innervate the ciliary muscle.

### Motor Outflow - Vestibular System

Information on the anatomy of the vestibular system is limited to the material mentioned in the vestibular input section. There is no anatomical evidence to indicate specific pathways for the slow and fast phase of vestibular nystagmus.

### Motor Outflow - Optokinetic Nystagmus

Optokinetic nystagmus appears to be served by a minimum of three neural arcs. The fixation reflex necessitates the integrity of at least part of the visual sensory input. The slow phase or following reflex, is thought to involve the occipital cortex, while the corrective reflex, or fast phase is thought to be related to voluntary gaze and hence would be mediated via the frontal lobe. There is no experimental evidence to support any of these assumptions. The oculomotor outflow probably follows the pathways as previously described. It is interesting to note that although optokinetic nystagmus apparently can exist in the absence of vestibular nystagmus, there is some suggestion that the fast phase of each share the same pathways. Despite frequent literature references, the superior colliculus is not necessary for normal optokinetic nystagmus in monkey, or, presumably in man.

There is evidence that the pathway mediating vestibular nystagmus may in part be different from that mediating optokinetic nystagmus (17). The evidence that optokinetic nystagmus is not mediated through the vestibular nuclei depends upon the pathological observations that degeneration in peripheral vestibular neurons and the vestibular nuclei in the brain stem secondary to severe streptomycin intoxication causes an absence of vestibular nystagmus but permits a normal retention of optokinetic nystagmus. There are other experimental conditions in which optokinetic nystagmus and vestibular nystagmus are not associated. Following removal of the occipital lobes bilaterally in monkeys, the optokinetic nystagmus is abolished. However, vestibular nystagmus in these animals, although not completely normal, is present but in a somewhat lesser frequency and greater amplitude and duration. It is interesting to note that vestibular nystagmus in the normal monkey also shows these alterations when testing is performed in darkness.

### Motor Outflows - Convergence

The oculomotor pathways discussed above probably mediate convergence, the only qualification being that bilateral stimuli appear necessary.

### Motor Outflow - Compensatory Eye Movements

Compensatory eye movements are more clearly seen in rabbit than in primate and man. The "doll's head movements" seen clinically appear to represent the unmasking of compensatory eye movements in the presence of lesions higher than the brain stem. With loss of voluntary gaze upwards or downwards, passive extension or flexion of the head will result in the eyes turning upward and downward involuntarily. The passive movement of the head induces a vestibulogenic deviation of the eyes in the direction opposite to that of intended gaze. These doll's head movements are absent with involvement of the vestibular nuclei. The motor component has not been investigated.

### Motor Output - Proprioception

Experiments in goats have indicated that stimulation of muscle spindles via the gamma efferent nerves increases the sensitivity of the eye muscles to stretch sevenfold (18). Although the role of proprioception in eye muscles seems to be redundant, the visual input being the main source of sensory information concerning eye positions, for reasons previously stated, proprioception is not concerned with position sense in eye muscle or peripheral muscle. It is known that during foveal fixation in the human, there is a continuous micronystagmus. If this micronystagmus is eliminated and the image of regard stabilized upon the retina, the visual detail decreases, rapidly resulting in a loss of contrast in the visual field and a marked decrease in visual acuity after a few seconds. During fixation, the sensitivity of the extraocular muscle to stretch is increased by stimulation of the muscle spindles. This would permit reflex control of the fine movements during fixation rather than providing information about the position of the eyes in the head.

### Summary

Visual tracking, vestibular nystagmus, optokinetic nystagmus, and convergence all appear to be extremely complex systems involving many pathways mediating the eye movements.

Due to species differences, experimental data from subhuman species should be regarded with caution when being applied to man. If alternate white and black stripes are moved in front of many mammals, there is a response to the movement. Even the common house fly will move in a direction determined by the movement of the stripes. This might be considered a primitive optokinetic nystagmus. Caution must be exercised in interpreting the lack of effect of large ablations of occipital cerebral hemisphere on the optokinetic nystagmus in monkeys. There is much clinical evidence to suggest that there would be an effect in the case of the human.

Compensatory eye movements appear to be little-used in man, being phylogenetically an old system. It is possible that these eye movements do not make use of the same pathways shared by visual tracking, optokinetic nystagmus, or vestibular nystagmus. However, there is no evidence on this point.

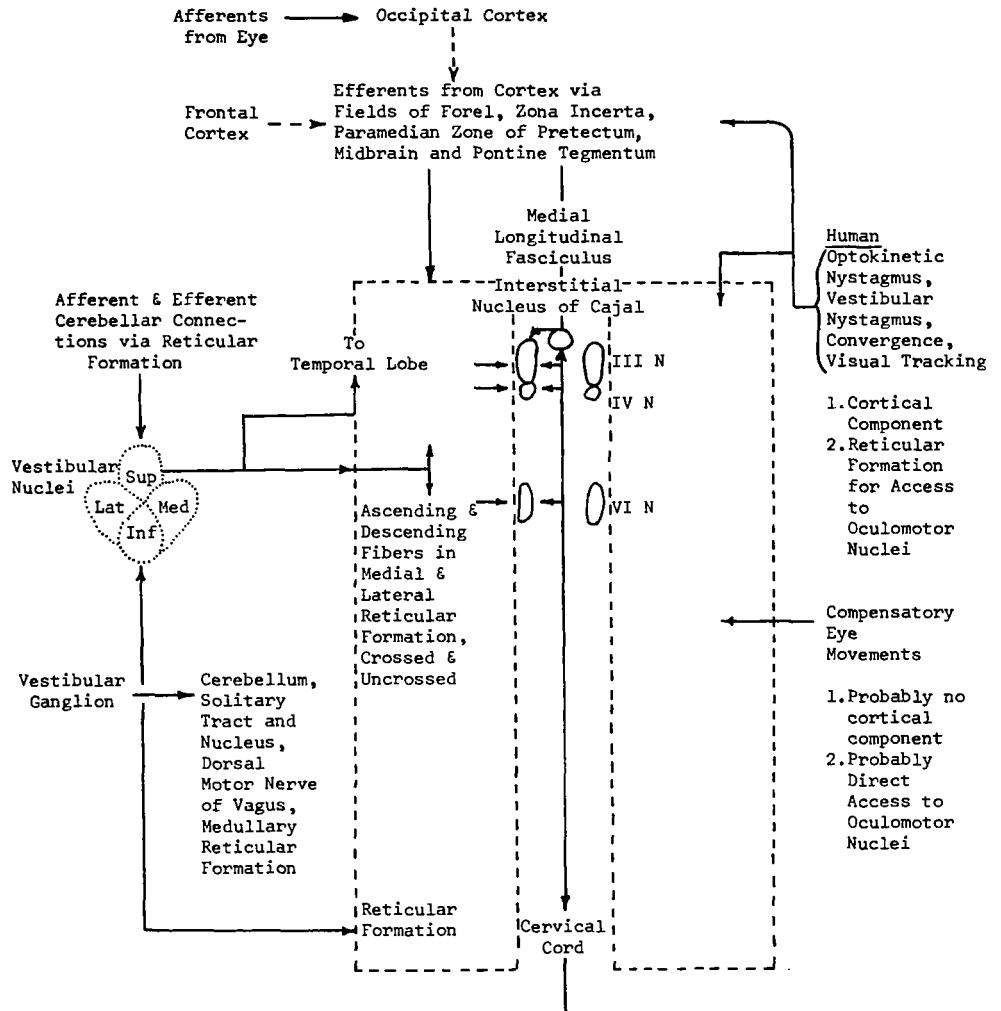
Finally the pupillary system is quite separate from the previous systems discussed in as much as there is a synergy with convergence and accommodation. Proprioception has been discussed to raise once more the question of its functional significance. Figure 3.4 summarizes the information.

#### LOCATION OF THE INTERMITTENCY OPERATOR

The intermittency operator has been described in visual tracking, vestibular nystagmus, and optokinetic nystagmus. There are two levels in which one can contemplate a site of integrative action to justify the presence of an intermittency operator: the cerebral cortex and the brain stem. Although the cortex does not appear essential for vestibular and optokinetic nystagmus in monkey, this is not true for man. However, the cerebral hemispheres may be ruled out on the basis of there being so many separate oculomotor pathways coming from different areas of the cortex. There does not seem to be any convergence of these pathways until they reach the brain stem. Within the brain stem there appear two possibilities: the vestibular nuclei and the reticular formation. The vestibular nuclei appear quite attractive as a site for the intermittency operator. There is no doubt that these nuclei have a very important role in the control of eye movements. However, there are two pieces of information which would suggest that the intermittency operator is located elsewhere. Optokinetic nystagmus which does demonstrate the presence of an intermittency operator does not appear to be mediated through the vestibular nuclei. On the other hand, compensatory eye movements which are thought to be vestibulogenic in nature and presumably are mediated through vestibular nuclei do not demonstrate the presence of an intermittency operator.

It appears that there is a convergence of oculomotor pathways as one reaches the pons especially in the paramedian zone through the pontine tegmentum. The intermittency operator has been described in responses (visual tracking, vestibular nystagmus, and optokinetic nystagmus) which probably use these pathways. One might also assume that convergent eye movements

Figure 3.4 Anatomic scheme for oculomotor pathways influencing eye movement.



would use these same pathways. However there does not appear to be an intermittency operator in the convergence mechanism.

Compensatory eye movements may be considered to be a less complex pathway from the vestibular nuclei directly to oculomotor nuclei, perhaps through the medial longitudinal fasciculus. It would be of interest to explore the convergence mechanisms further and obtain additional data on whether the intermittency operator is in fact absent under all experimental conditions.

The reticular formation has been implicated as an integrative portion of the central nervous system in which auditory, somatosensory, visual and proprioceptive stimuli can come together. Experiments designed to investigate these possibilities would be desirable.

#### BIBLIOGRAPHY

1. Kupfer, C. 1962. Amer. J. Ophthal., 54:597.
2. Polyak, S. 1957. The Vertebrate Visual System. Univ. Chicago Press, Chicago.
3. Wiesel, T.N. 1960. J. Physiol., 153:583.
4. Hubel, D.H. and T.N. Wiesel. 1961. J. Physiol., 155:385.
5. Hubel, D.H. and T.N. Wiesel. 1962. J. Physiol., 160:106.
6. Magoun, H.W., D. Atlas, W.K. Hare and S. Ranson. 1936. Brain, 59:234.
7. Szentagothai, J. 1964. in "The Oculomotor System", ed. Bender, Harper and Row, New York, p. 205.
8. Gernandt, B.E. 1964. in "The Oculomotor System", ed. Bender, Harper and Row, New York, p.224.
9. Lorente de No, R. 1933. Archiv. Neurol. and Psychiat., 30:245.
10. Cogan, D.G. 1956. The Neurology of the Extraocular Muscles. Charles C. Thomas, Illinois.
11. Cooper, S. and P. Daniel. 1949. Brain, 72:1.
12. Whitnall, S.E. 1932. The Anatomy of the Human Orbit and Accessory Organs of Vision. ed. 2, London, Oxford, p.334.
13. Christman, E. and C. Kupfer. 1963. AMA Archiv. Ophthal., 69:184.

14. Wagman, I.H. 1964. in "The Oculomotor System",  
ed. Bender, Harper and Row, New York, p. 18.
15. Bender, M.B. and S.Shanze. 1964. in "The Oculomotor System",  
ed. Bender, Harper and Row, New York, p. 81.
16. Holmes, G. 1938. Brit. Med. J., 2:107.
17. Dix, M.R., C.S. Hallpike and M.S. Harrison. 1949. Brain, 72:241.
18. Whitteridge, D. 1959. in "Handbook of Physiology",  
ed. Field, American Physiological Society, Washington, D.C.