A short title for the binding is:

A PREDICTIVE COMPONENT IN VISUAL TRACKING

AN ANALYSIS OF A PREDICTIVE COMPONENT IN THE HUMAN VISUAL TRACKING SYSTEM

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

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April, 1964.

ACKNOWLEDGMENTS

I wish to thank Dr. Geoffrey Melvill Jones, Head of the Aviation Medical Research Unit, whose supervision made this thesis possible. Dr. Melvill Jones introduced me to the idea of applying systems analysis to the study of physiological mechanisms and suggested the eye movement control system as a suitable mechanism for study. His suggestions and advice were of great value throughout the course of this work, particularly during the writing of the thesis.

I also wish to acknowledge the assistance of a number of other people. Dr. John Milsum, Department of Electrical Engineering, McGill University, patiently assisted me in the understanding of some of the aspects of control engineering, and generously permitted me to use the analog computer in his laboratory.

Mr. E. R. R. Funke and the staff of the Analysis Section of the Division of Mechanical Engineering, National Research Council, Ottawa, assisted in the development of the stimulus generation and analysis techniques and permitted me to use the facilities of their laboratory where the analysis of my data was carried out.

Dr. George Fergeson, Department of Psychology, McGill University, suggested the statistical tests used in analyzing the significance of the results.

Mr. George Mandl valiantly maintained in good repair the electronic equipment used, and Mr. Fritz Lewertoff constructed most of the mechanical equipment used.

Mrs. P. Taylor, Neurology Section, Massachusetts Institute of Technology, made many constructive suggestions while typing the manuscript.

This work was supported by D. R. B. Grant No. 9310-92.

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I. INTRODUCTION

In man, maximum visual acuity is obtained when the image of the visual target falls on that part of the retina known as the fovea. This condition results when a subject "looks at" a stationary target with his eyes still, and the subject is then said to be fixating the target.

The maintenance of visual fixation is relatively easy when both the target and the head are stationary in space. But with the introduction of target and head movement the problem of fixation becomes much more difficult and the requirement can only be met by close integration of several different physiological mechanisms. These are first the elaborate processes jointly referred to as body postural control, second the various patterns of neck reflexes controlling movement of the head on the shoulders, and thirdly vestibular and optokinetic reflexes controlling the angle of the eye in the head.

It would be difficult, and indeed unrealistic, to attempt to investigate simultaneously all of the processes concerned with maintenance of fixation, and the present study has therefore been confined to what will be referred to hereafter as the visual tracking system; that system which is responsible for following of a moving target with the head still.

One of the essential features of this system is that it is to a considerable extent reflexive in nature. That is, given a moving target in the visual field and a "desire" to look at that target, the eyes will be driven by the visual tracking system with the aim of maintaining fixation. In addition, a uniform visual field in motion will produce eye movements tending to follow the field; again, this response is largely automatic and cannot be completely voluntarily suppressed. Also, a target suddenly appearing in the periphery of the visual field will cause the eyes to move so as to fixate this target.

The visual tracking system may therefore be looked upon, in an engineering sense, as a form of servo-control system, and there are advantages to be gained from approaching the physiological processes involved from this point of view. Perhaps the most important advantage is the capability of identifying the parameters most pertinent to the dynamic behavior of the system under study. And having identified these parameters the techniques, both experimental and analytical, of the systems engineer provide concise mathematical methods of describing the behavior of the system. Moreover, control theory can often provide a conceptual framework within which to formulate testable hypotheses about the functioning of the organism.

Of course, it must always be borne in mind that, since the properties of living material are far more complex and less understood than the properties of inert material, the methodology of the engineer is not self-sufficient in a physiological investigation. In the present study the aim has been to make use of the advantages outlined above to promote functional understanding of the physiological processes involved in the visual tracking system. The extent to which this has been achieved will be reviewed later in the Discussion.

This kind of approach to the study of physiological mechanisms is not without precedent. Already many systems have been investigated along these lines, examples being the pupil system (Stark, 1959; Clynes, 1961), motor co-ordination (Stark etal, 1961), the cardiovascular system (Warner, 1958; Clynes, 1960), and the respiratory system (Horgan & Lange, 1962). The visual tracking system has proven to be a particularly fruitful area for the application of control theory, and a number of significant studies have been carried out (Melvill Jones & Drazin, 1960; Fender & Nye, 1961; Young, 1962; Dallos & Jones, 1963). Jury and Pavlidis (1963 have compiled an extensive bibliography of recent work in the area of control system studies of biological systems, and Grodins (1963 and Milsum (in press) have written textbooks dealing with this subject.

II. THE PHYSIOLOGY AND ANATOMY OF THE VISUAL TRACKING SYSTEM

Since our ultimate goal is the understanding of a physiological mechanism it will prove valuable to review the known anatomy and physiology of the visual tracking system.

1. The Visual System

Only the neural events directly contributing to visual perception will be considered here. Thus, such topics as the vegetative physiology of the eye, physiological optics, accommodation, and the pupil reflex will be ignored. Further, since color vision, binocular perception, and perception of form are not required for visual tracking these too will be ignored.

The visual system essentially begins at the retina, continues back towards the central nervous system (of which it is a direct outgrowth) via the optic nerve and tract to the lateral geniculate body, and then continues to the visual cortex. The neurophysiological events occurring along this path, namely transduction of the photic stimulus by the visual pigments, interaction of signals within the retina, possible integration at the geniculate level, and the final projection to the visual cortex where "seeing" occurs, will be described in an attempt to place in perspective the role played by the visual system in visual tracking.

a. The retina

For light to interact with matter, as it obviously does in vision, it must first be absorbed. The human retina contains two substances whose function is the absorption of light and the transduction of the light energy into a neural signal. These substances are known as the visual, or photoreceptor, pigments, and they represent the first step along the visual pathway.

The first pigment studied was visual purple or rhodopsin. It was isolated in solution by Kuhne in the 1870s, and since then extensive work has been done on the nature of this substance and the photo-chemical reactions it undergoes.

Rhodopsin is a complex molecule made up of two components, a color absorbing group, retinen (a yellow carotenoid), and a supporting protein chain, opsin. When exposed to light rhodopsin undergoes a process known as bleaching; a solution containing rhodopsin can be visibly seen to change color in the light. The bleaching process actually consists of the breakdown of rhodopsin into retinene and opsin. This process, which takes place via a number of important intermediates, is reversible, and in the dark rhodopsin is resynthesized via a series of reactions involving vitamin A. This chemical cycle is complicated by the fact that all the participants must possess the proper stereo-isomeric structure (Wald, 1936; Hubbard & Wald, 1952).

It is worth noting that different species utilize rhodopsins with slightly different light absorbing properties although all are very similar chemically (Dartnall, 1962).

A second visual pigment, iodopsin, was isolated by Wald (1937), from the retinae of chickens, and has been shown to be present in the human retina (Rushton, 1957). Iodopsin is very similar chemically to rhodopsin; the retinene groups are identical, but the opsins are different. The photo-chemical reactions of iodopsin are completely analogous to the reactions of rhodopsin (Wald, Brown & Smith, 1955).

The manner in which the photochemical reactions of the visual pigments initiate a nervous impulse is still not really understood. Wald and Brown (1952) have shown that the bleaching of rhodopsin liberates sulfhydryl groups on the opsin molecule. These are highly reactive groups, and it was further observed that under the proper conditions electrical variations in the rhodopsin containing solution were obtained. More refined experiments (Radding & Wald, 1956) demonstrated a definite pH change in solutions containing rhodopsin exposed to light. This is the result of the release of acid binding groups on the opsin molecule, some of which may be sulfhydryl groups. It is possible that such physico-chemical changes occurring in the receptors may cause a movement of ions leading to nervous excitation.

It is not surprising that the properties of vision parallel the properties of the visual pigments. This is most evident in the close agreement between the absorption spectra of the pigments, their ability to absorb light of different wavelengths, and the spectral sensitivity of vision, the ability to perceive light of different wavelengths.

The absorption spectra of rhodopsin and iodopsin are similar in shape, but not identical; the iodopsin curve is shifted towards the red end of the spectrum, its maximum being at 560 mμ while the maximum for rhodopsin is at 500 mμ (Wald, Brown, Smith, 1955).

If the spectral sensitivities of vision, both photopic and scotopic, are examined it is found that there is a close correlation between these and the absorption spectra of the corresponding pigments.

Crescitelli and Dartnall (1953) have shown a close correspondence between scotopic vision and the absorption spectra of rhodopsin in man, and Rushton (1957) has demonstrated a similar relationship between photopic vision and iodopsin. Thus, the Purkinje shift, the displacement of the scotopic and photopic curves, has its origin in the different absorption spectra of the visual pigments.

The phenomena of light and dark adaptation have also been linked to the visual pigments. Campbell and Rushton (1955) and Rushton (1957), using a technique for the observation of the density of the visual pigments in the living human eye, have shown a close agreement between the time course of the changing densities of the pigments and the course of adaptation.

These facts leave little doubt that the visual pigments that have been extracted from retinae and studied chemically are indeed the first stage in the visual process.

The photoreceptive processes play a vital role in vision, and much remains to be learned about the mechanisms involved in these processes. However, in spite of our relative ignorance in this area, it does not appear likely that any higher-order processing of visual information occurs at this stage. Transduction of light can only play a "passive" role in the visual tracking system.

The visual pigments are found in the receptor cells of the retina; the rods contain rhodopsin and the cones contain iodopsin. Structurally the receptors consist of two parts, an inner and an outer segment. The outer segment contains the visual pigment and is made up of sacs composed of double membranes with the plane of the sacs being at right angles to the direction of incident light (Sjostrand, 1953).

There is evidence that the molecules of pigment are not distributed at random in the sacs, but that the long axis of the chromophore group is at right angles to the incoming light. Such an arrangement greatly increases the light absorbing capability of the visual pigments (Denton, 1954).

The inner segment of the receptor contains many closely packed mitochondria and thus appears to be concerned with the metabolism of the cell. The two segments are connected by a cilium (deRobertis & Lasansky, 1958).

The retina essentially consists of three cell layers and two intermediate layers of synapses. The most posterior layer contains the receptor cells, the rods and cones. These make synaptic connection with the bipolar cells which in turn synapse with the ganglion cells. The axons of the ganglion cells run across the retina and leave the eye as the optic nerve. Thus, light must traverse the entire thickness of the retina before reaching the receptor cell layer (Polyak, 1941).

The distribution of rods and cones in the retina is not uniform in the higher primates and in man. A small central area, approximately 1° in diameter in man, is completely free of rods; this area is known as the fovea. From the fovea to the periphery the number of cones decreases and the number of rods increases.

The relation between the number of receptors and the number of bipolar cells and ganglion cells is important for the understanding of the manner in which the visual system processes information. Vilter (1949) found that in the human fovea each cone diverges to three bipolar cells but to only two ganglion cells. The relationship between the bipolar cells and the ganglion cells was not determined. As the number of rods increases peripherally the system becomes a convergent one so that 100 rods synapse with 17 bipolar cells. Convergence to the ganglion cells is also great, which is not surprising when it is borne in mind that there are 125 million rods in the retina but only about 1 million optic nerve fibers (Polyak, 1957).

The interaction between retinal elements is increased by the presence of horizontal cells linking receptors and amacrine cells linking the bipolar cells (Polyak, 1957).

The existence of centrifugal fibers in the retina, fibers whose cell bodies lie outside the retina, is an interesting and controversial question. In addition, it is an important question because of the important role played by feedback in many control systems. A functional system of centrifugal fibers from the central nervous system to the retina could provide a form of control over the peripheral processes of vision similar to the feedback system recently demonstrated in the auditory system (Rasmussen, 1946; Fex, 1962).

Anatomical evidence for the existence of centrifugal fibers is divided. Cajal first reported the presence of fibers in the plexiform layer of the retina with no apparent connections in the retina. Such fibers have also been seen by Polyak (1941).

von Monakow (1889) saw degeneration in the superior colliculi following ennucleation of the eye, although this may have been an example of trans-synaptic degeneration. After cutting the optic nerve, Elinson (1896) saw Wallerian degeneration in both the peripheral and central stumps of the nerve.

More recently, Wolter and Liss (1956) examined the optic nerves of two subjects many years after ennucleation and saw surviving nerve fibers. Maturana (1958) sectioned the optic nerves of toads and found some undegenerated fibers on the central side. These studies all point to the presence of centrifugal fibers in the retina.

There is also some physiological evidence for the presence of centrifugal fibers. Muller-Limmroth (1954) has demonstrated that illumination of one guinea pig eye produces an electrical response in the other eye that is dependent on the lateral geniculate bodies being intact. Granit (1955) has shown that electrical stimulation of the tegmental portion of the reticular formation potentiates or inhibits the responses of retinal ganglion cells to light, and this phenomenon was shown to be distinct from the effects of antidromic stimulation. Stimulation of the optic nerve was shown by Dodt (1956) to produce an electrical response in the contralateral retina that was also distinct from the effect of antidromic stimulation.

However, there is much evidence against the presence of such fibers. Bodian (1937) and Hess (1958) could find no undegenerated fibers after ennucleation. And a comparison of the number of ganglion cells and the number of optic nerve fibers reveals a correspondence so close that "no room" is left for centrifugal fibers (Arey & Gore, 1942; Bishop, 1953).

It is perhaps significant that the physiological effects suggesting the presence of a centrifugal system appear to be "trivial" in that their role in vision is probably minimal. In addition, there seems to be little "need" for a centrifugal system; the unsolved problems in visual physiology do not appear to require a feedback system for solution (Brindley, 1960).

There is thus conflicting evidence on the presence of a centrifugal system in the retina. Certainly much more work, anatomical and physiological, needs to be done before the presence and functional importance of efferent fibers to the retina can be stated with assurance.

One of the classical techniques for the study of retinal physiology is electroretinography (see Granit, 1947). An electrode placed on the cornea detects a slowly changing potential when the retina is illuminated; the representation of this response constitutes the electroretinogram (ERG). In the typical ERG waves can be seen corresponding to both the onset and cessation of activity. The source of these recorded potentials is not completely clear, but correlations between the ERG and both the initiation of action potentials in the optic nerve as well as inhibitory processes have been found (Granit, 1933; Granit & Riddell, 1934). A comparison of the ERG and micro-electrode recordings of single cell activity in the retina has led Brown and Wiesel (1959) to suggest that at least one component of the ERG arises from the pigment epithelium cells; the responses of bipolar and ganglion cells have a time course that makes them unlikely candidates for the origin of the much slower ERG.

The ERG of the human eye has been studied and is apparently not very different from that obtained from animals (Riggs, 1958).

Retinal phenomena can be studied more directly by observing the electrical activity in the optic nerve, since it is the axons of the retinal ganglion cells that make up this nerve. This was first done by Adrian and Matthews (1927a, 1927b, 1928). They recorded from the entire nerve with surface electrodes and observed a burst of activity upon illumination of the retina, the "on" response, a steady discharge while illumination continued, and an increased burst following termination of illumination, the "off" response. They also observed that the retina was organized into receptive fields, areas of the retina that when stimulated give rise to a response.

Hartline (1938) was able to dissect the optic nerve down to a single functional unit, and was thus able to examine the responses of a single ganglion cell. His results are similar to those of Adrian and Matthews, but he found units that respond only to turning the light on, units that respond to turning the light off, and units that respond to both on and off, but are silent during continued illumination. In addition, he showed that the receptive fields seen by Adrian and Matthews represent those areas of the retina that give rise to responses in a single optic nerve fiber.

Further work by Hartline (1940a, 1940b) revealed some of the properties of these receptive fields. The center of the field is maximally sensitive, and illumination of the periphery must be much more intense than illumination of the center to produce a response. However, the fields are homogeneous in that illumination of any equal areas the same distance from the center of the field produces the same response. With a given light intensity sensitivity is a function of the area of the field illuminated as long as stimulation does not extend outside the boundary of the field; in that case, a decreased response is seen. It was also found that receptive fields in the periphery of the retina tend to be larger than fields in the center of the retina; this is physiological evidence of the convergence of receptors to ganglion cells in the periphery.

Barlow (1953a, 1953b), using micro-electrodes to record directly from the ganglion cells of an opened frog's eye, confirmed and extended the results of Hartline. He found that the receptive fields, stimulation of which leads to activity, were surrounded by an area in which stimulation has an inhibitory effect on activity in the receptive field.

Kuffler (1953) carried out similar studies on the retina of the cat and found a slightly different organization of the receptive fields. If, for example, the center of a field has an "on" response the periphery of the field will have an "off" response and some intermediate zone will have both an "on" and an "off" response. If both "on" and "off" areas are stimulated simultaneously little activity is produced, the "off" response in effect inhibiting the "on" response.

Much remains to be learned about the anatomical structure and physiological function of the retina. Two of the most important unsolved problems are the question of the existence of a centrifugal feedback system and the question of the interaction between retinal elements. However, as the transducer of the visual system the retina plays a vital role in vision, and the complete understanding of this process requires a more complete understanding of retinal events than is now available. Thus, the retina represents an area of study meriting serious efforts in the future.

b. The optic nerve and tract

The optic nerve is made up of the axons of the retinal ganglion cells. These fibers proceed back to the optic chiasm where a partial decussation occurs. Fibers from the nasal half of each retina cross and continue back towards the lateral geniculate body. Each optic tract is therefore made up of fibers from the ipsilateral temporal retina and the contralateral nasal retina. The effect of this is to project the right half of the visual field onto the left half of the brain and the left half of the field onto the right half of the brain.

c. The lateral geniculate body

The majority of fibers in the optic tract enter the lateral geniculate body (LGB). In the monkey and in man the lateral geniculate consists of six laminae, and the entering fibers are distributed to these layers on the basis of their origin; optic fibers from the contralateral eye synapse in layers 1, 4, and 6 while those fibers from the ipsilateral eye synapse with cells in layers 2, 3, and 5 (Glees & LeGros Clark, 1941). Thus, in man there appears to be no interaction of activity from the two retinae at the level of the lateral geniculate body.

In the cat there are only three laminae, two of which receive fibers from the contralateral eye, the remaining lamina receiving fibers from the ipsilateral eye. There is, however, evidence that intralaminar areas receive fibers from both eyes, thus providing for some interaction of the two retinae (Silva, 1956; Hayhow, 1958).

The retina projects onto the lateral geniculate body in a point to point fashion. That is, receptive fields in the retina project onto specific locations in the lateral geniculate (Penman, 1934; Bishop etal, 1962). Further, Hubel and Wiesel (1961) have shown that in the cat the geniculate receptive fields have properties that are essentially identical with retinal receptive fields. However, the fact that the retina is two dimensional while the lateral geniculate is three dimensional means that the projection of retinal points is to a column of cells in the lateral geniculate (Bishop etal, 1962).

The lateral geniculate may play more than just a passive role as a relay station along the visual pathway. Bishop etal (1953) observed a form of repetitive firing in lateral geniculate cells from optic nerve stimulation that led them to suggest that the lateral geniculate acts as an integrating center. Widen and Ajmone-Marsan (1961) report that corticofugal fibers from the occipital cortex influence the activity of lateral geniculate cells. A form of lateral inhibition in which collaterals from strongly excited cells inhibit the activity of less excited cells, thus "sharpening" the image, has been suggested by Vastola (1960) to be present in the lateral geniculate. And Hubel and Wiesel (1961) have demonstrated suppression of activity of receptive fields by activity of peripheral fields. All these studies point to the lateral geniculate body having a definite integrative role in the visual system.

d. The visual cortex

Neurons from the cells of the lateral geniculate body (the third along the visual pathway) project via the optic radiations to the occipital cortex where they arborize in the granular layer. By mapping the blind spots in the visual field caused by gun-shot wounds, Holmes (1945) was able to show that the retina projects onto the visual cortex in a point-to-point fashion. One half of the retina projects onto one striate area with the macular projection area posterior and the peripheral areas anterior. The size of the macular projection area is quite out of proportion with the size of retinal area it represents, but the predominant role of the macula in vision accounts for this disparity. This map of the visual cortex was confirmed by Spaulding (1952a, 1952b) in an extensive study of the visual projection systems.

This point-to-point projection can also be mapped electrophysiologically. Talbot and Marshall (1941) mapped the projection in an anesthetized monkey by finding the position of a light in the visual field that gave a maximum evoked response from a point on the cortex. Later work (Hubel, 1958; Hubel & Wiesel, 1962) has shown that the functional characteristics of this mapping in the cat are rather complex; cortical receptive fields respond in characteristic patterns to complex stimuli such as spatially oriented bars of light. Here too, columns of cells were shown to represent one point in the visual field.

Projection from the lateral geniculate to the cortex has also been studied by recording the evoked potentials arising from direct electrical stimulation of the lateral geniculate (Chang, 1952), and Crescitelli and Gardner (1961) have demonstrated the projection of retinal activity, as evidenced by the electroretinogram,to the visual cortex.

The cortical projections of the visual fields represent only a small part of the role played by the cortex in vision. Numerous complex interacting processes apparently mediate between the arrival of activity at the cortex and the subjective perception of visual targets. These processes are just beginning to be understood, and efforts by anatomists, neurophysiologists, and psychologists will undoubtedly eventually elucidate the mechanism of perception. But, it does not appear that information at this level is necessary for an understanding of the visual processes involved in visual tracking.

e. The superior colliculus

In lower mammals the superior colliculus plays a definite role in vision; complete decerebration leaves these animals with a considerable portion of their visual processes intact.

Although early neuro-anatomists were unable to demonstrate a pathway from the retina to the superior colliculus, Barris etal (1935) and O'Leary (1940) have shown that fibers to the lateral geniculate give off collaterals that penetrate the stratum opticum of the superior colliculus in the cat.

Bishop and O'Leary (1942) recorded visually evoked responses from the superior colliculus, and Apter (1945) was able to map the retinal projection onto the superior colliculus of cats. Hamdi and Whitteridge (1953) have obtained similar maps for the rabbit and the goat.

In man the superior colliculus plays a much less important role than it does in the lower animals since no visual function is present if only the superior colliculus is spared. But, as will be shown later, the superior colliculus may be an important site for the interaction of vision and eye movements.

2. The Oculo-motor System

a. The extraocular muscles

Movements of the eyes in the head are produced by the extraocular muscles. There are six such muscles attached to each globe: four recti, superior, inferior, medial or internal and lateral or external, and two obliques, superior and inferior. The inferior oblique has its origin in the floor of the anterior part of the orbit, the other muscles arise from the apex of the orbit. All six muscles insert into the scleral coat of the globe approximately at its equator. (Wolff, 1948).

The action of the individual muscles and the manner in which they interact to produce the complete range of possible eye movements is somewhat complex. However, horizontal eye movements of the kind of interest here are produced by the reciprocal activity of only two of the muscles, the medial and lateral recti (Wolff, 1948).

Histologically the extraocular muscles are highly specialized. The muscle fibers are extremely small, in the cat some being no more than 9-11μ in diameter (Brown & Harvey, 1941); in man the size of the fibers ranges from 10-50μ in diameter (Cooper & Daniel, 1949). The range of the diameter of fibers is also great, the largest fibers being 2-3 times as thick as the smallest fibers (Woolard, 1931). However, medium size fibers are the most numerous and make up the body of the muscle; the thin fibers are most prevalent in the periphery of the muscle (Cooper & Fillenz, 1955). There is some evidence that each muscle fiber runs the entire length of the muscle (Lockhart & Brandt, 1938), although a later study (Voss, 1957) could not confirm this.

Some unique physiological properties accompany the specialized histology of the extraocular muscles. The most striking property of these muscles is their speed of contraction; the time for a single twitch is approximately 7-8 msec (Cooper & Eccles, 1930; Brown &

Harvey, 1941). This is to be compared with the twitch time for the soleus, 104 msec, or of the gastrocnemius, 39 msec (Cooper & Eccles, 1930). The refractory period is also short, around 0.5 msec (Brown & Harvey, 1941). The short twitch time and refractory period results in a very high fusion frequency, 350/sec (Cooper & Eccles, 1930). There is also a very low twitch tension to tetanus tension ratio. The combined action of these factors gives the extraocular muscles the ability to produce finely graded contractions (Davson, 1963).

The natural rate of motor unit discharge in the extraocular muscles is also very high. Reid (1949) found rates as high as 170/sec in cats, and Marg etal (1962) showed rates of 100/sec for tonic activity and up to 350/sec for phasic activity in human extraocular muscles.

The response of the extraocular muscles to drugs is also unique. Although skeletal muscles respond to an injection of acetylcholine with a contracture, the extraocular muscles undergo a slow, tonic contraction (Duke-Elder & Duke-Elder, 1930). This unusual property has been confirmed by Brown and Harvey (1941) who also recorded the oscillatory action potentials produced by this tetanic contraction. They also demonstrated a "spontaneous" twitching produced by eserine which was accompanied by repetitive discharge. The extraocular muscles are also more sensitive to curare than are the skeletal muscles.

The precision with which eye movements can be controlled is due, to a considerable extent, to the unusual properties of the extraocular muscles. In fact, it will be seen later that the response limitations of the oculomotor system arise from the control elements of the system and not from the motor elements.

b. The innervation of the extraocular muscles

The extraocular muscles receive their motor innervation from the III, IV, and VI cranial nerves. The superior oblique is innervated by the IV (trochlear) nerve, the lateral rectus by the VI (abducens) nerve, and the other muscles are innervated by the III (oculomotor) nerve (Wolff, 1948).

These nerves are large in comparison with the size of the muscles they innervate, and in consequence the motor units of the extraocular muscles are quite small, a single nerve fiber innervating perhaps six muscle fibers (Bors, 1925; Torre, 1953).

A variety of motor endings have been described in the extraocular muscles. Hines (1931) reported three kinds of motor endings, motor end-plates, naked endings, and "accessory" endings. Wolter (1954, 1955) has reported similar results. He saw standard end-plates, thin unmedullated endings with loops in or outside the end-plate, and another form of thin ending that spreads out over the muscle fiber. Further, Wolter (1954) showed that the thin muscle fibers are innervated by the thin endings. He has hypothesized that the thin endings are part of the autonomic system, those accompanying the motor endings being parasympathetic, and the other thin endings, arising from the perivascular plexus not the cranial nerves, being sympathetic.

Alpern and Wolter (1956) have proposed that the fine unmedulated fibers are motor fibers for a slow vergence movement system, while the thick medulated fibers are part of a rapid version system. This suggestion is supported by the fact that the two kinds of movement are quite distinct and are often dissociated in pathological states.

There is also a variety of sensory endings in the extraocular muscles. Hines (1931) and Woollard (1931) describe a particularly distinctive ending referred to as terminaisons en grappe. Wolter (1955) describes five varieties of endings he felt were sensory. Perhaps most important are the muscle spindles first definitively described by Cooper and Daniels (1949) and confirmed by Sunderland (1949) and Merrillees etal (1950). The role played by these sensory endings will be more fully discussed in a later section.

These afferent fibers reach the central nervous system via the cranial nerves, thus giving these nerves a sensory as well as a motor function. However, some of these fibers leave the orbit in the V nerve; Kiss (1935) found branches running from the III, IV, and VI nerves to the V nerve in many animals.

Donaldson (1960) analyzed the diameters of nerve fibers in the cranial nerves and found a bimodal distribution with peaks at 11-17μ and at 4-6μ. The first peak is composed of motor fibers while the second peak is made up of fibers that are part of the sensory system, either from the fine, unmedulated fibers seen by Wolter (1954) or from efferents to the muscle spindles.

c. The cranial nerve nuclei

The cranial nerve nuclei innervating the extraocular muscles lie in the brainstem. Nucleus VI is the most caudal and lies in the tegmental portion of the pons. It innervates the ipsilateral lateral rectus.

Nucleus IV lies in the periaqueductal grey matter deep to the upper portion of the inferior colliculus. The nerve fibers leaving the nucleus cross almost completely, and the IV (trochlear) nerve thus innervates the contralateral superior oblique muscle.

Immediately rostral to the IV nucleus is the III nerve nucleus. It lies in the grey substance below the superior colliculus and extends for 6-10 mm to the floor of the third ventricle. The medial longitudinal fasciculus lies on its ventral aspect (Davson, 1963).

The anatomical relations just described are well established. However, there is much disagreement about the arrangement of the cell groups in the III nucleus innervating the different muscles; no definitive statement is possible as yet (Alpern, 1962).

A variety of techniques have been applied to this problem. Brouwer (1918) arrived at an arrangement on the basis of clinical observations. Electrical stimulation with stereotactically placed electrodes has been used by Szentagothai (1942), Bender and Weinstein (1943), and Danis (1948). Warwick (1953) studied retrograde degeneration after section of the III nerve.

Szentagothai and Danis obtained similar cephalocaudal arrangements of cell groups. Bender and Weinstein in addition saw a dorsoventral arrangement of groups. All three saw relatively sharply definited groups. Warwick reports both a cephalocaudal and a dorsoventral arrangement of cell groups, but he found that these areas were rather diffuse. No two investigations have obtained the same results as to the specific locations for cell innervating particular muscles.

Horizontal conjugate movements of the two eyes require the simultaneous activity of the medial and lateral recti. This coordinated activity is provided by the parabducens nucleus, a group of cells lying adjacent to the abducens nucleus (innervates the lateral rectus). This nucleus sends fibers to the nucleus of the medial rectus on the opposite side via the medial longitudinal fasciculus; stimulation of these fibers produces deviations of the eyes towards the side of stimulation (Crosby, 1953).

The cranial nerve nuclei provide the origin of the final common pathway for the control of eye movements. The motor cells of these nuclei have properties very similar to the properties of the spinal motoneurons (Sasaki, 1963). But the control of eye movements, both reflex and voluntary, depends on the activity of higher nervous centers. As is the case of many areas of neurophysiology the higher one goes in the central nervous system the less definite is our knowledge of the pertinent anatomy and physiology. We will, nevertheless, attempt to sketch some of the details of the systems controlling eye movements.

d. Other brainstem control centers

The vestibular system is an important one for the control of eye movements. Fixation, or direction of gaze, can be maintained while the head is in motion by reflex movements of the eyes; the stimulus for this activity is excitation of the vestibular system. Szentagothai (1950) demonstrated a definite relationship between a particular semicircular canal and activity of two of the extraocular muscles. Crosby (1953) has found connections between the lateral vestibular nucleus and the abducens and parabducens nuclei via the medial longitudinal fasciculus. This appears to be at least a portion of the pathway involved in vestibular control of eye movements.

The superior colliculus plays a definite role in the control of eye movements, particularly in lower animals in which this structure still has an important role in vision. Apter (1946) found that after application of strychnine to the surface of the colliculus flashes of light on the retina produced eye movements directed to particular points. In this manner Apter was able to map the distribution of movements and found a close correspondence to the mapping of the visual field on the colliculus. Burgi (1957) has shown that electrical stimulation in the superior colliculus produces head movements that are proceeded by conjugate deviations of the eyes.

Of additional interest are the findings of Cooper, Daniel, and Whitteridge (1953a, 1953b, 1953c). They found that afferent activity from the muscle spindles of the extraocular muscles can be recorded from the superior colliculus, suggesting that this may be a site of interaction between vision and the oculomotor system.

e. Cortical control centers

Cortical control of eye movements apparently arises from two areas, an occipital motor field and a frontal motor field. The occipital field is related to the projection of the visual field onto the cortex and is thought to be involved in reflex eye movements such as following movements. Fibers from the occipital field project to the midbrain cranial nerve nuclei and to the superior colliculus. Much of the work of elucidating this system has been carried out by Crosby and her coworkers (see Crosby etal, 1959) and has been confirmed by Wagman etal (1958).

The frontal eye fields are thought to be concerned with voluntary eye movements. Fibers from this motor field project through the internal capsule to the midbrain, to both ipsi- and contralateral sides. There are also projections to the occipital motor fields, and frontal stimulation is said to override occipital stimulation (Henderson & Crosby, 1952). The presence of frontal eye fields in man has been demonstrated by stimulation of these areas during surgery (Penfield & Boldrey, 1937; Lemmen etal, 1959).

f. Extraocular proprioception

As was the case in the question of the existence of centrifugal fibers in the retina, the question of the presence of proprioception in the extraocular muscles has been a controversial one. The importance of proprioception, particularly from the muscle spindle, in the regulation and coordination of general skeletal muscular activity has been recognized since the work of Sherrington (1906) at the turn of the century. Considering the accuracy with which voluntary eye movements can be made, and the precision with which the various reflex compensatory movements are carried out, the question of the role of proprioception in the oculomotor system immediately arises.

Two schools of thought have arisen around the question of how the position of the eyes is known. One theory had its origin with Helmholtz (1867), who proposed that our knowledge of eye position depends solely on our "knowledge" of the motor outflow responsible for the eye movement. This has come to be known as the "outflow" theory. Working before the discovery of the muscle spindle and its role in muscle regulation, Helmholtz designed a series of simple experiments to show that "muscular sensation" provides no information about eye position. For example, he demonstrated that passive movement of the eyes causes an apparent movement of the environment, an effect not seen during active movement. He also showed that efforts to move the eyes with paralyzed muscles also produces apparent movement, although there is, of course, no possibility of proprioception from these muscles.

Sherrington was the chief proponent of the second theory. He strongly supported the idea that knowledge of eye position is derived from the proprioceptive information arising in the active muscles. This theory is now known as the "inflow" theory. However, acceptance of this theory was hampered by the failure of observers to find muscle spindles in the extraocular muscles. In spite of this, Sherrington was able to demonstrate some phenomena pointing to a definite contribution from extraocular proprioception to interpretation of the moving visual world. For example, fixation on three vertically positioned points with the eyes in the primary position produces an after-image which, when the eyes are moved out of the primary position, does not appear vertical (Sherrington, 1918). Thus, the perceived effects of retinal stimulation can be altered by changing the position of the eyes.

The lack of histological evidence for the existence of extraocular muscle spindles was, of course, the perplexing problem. Sherrington (1894, 1897) made a number of attempts to find these structures, but without success. Batten (1897) also reported failure in this search. Later work by Sherrington led to the observation of structures which could only be identified as "receptive spindle (muscle spindles) of peculiarly simple form" (Tozer & Sherrington, 1910). After this work it was assumed for many years that no proprioceptive organs existed in the extraocular muscles.

However, there was some contrary evidence which was, unfortunately, almost completely ignored. Buzzard (1908) made a definite report of spindles in human extraocular muscles; they were reported to be similar to skeletal muscle spindles, but with thinner capsules and intrafusal fibers comparable in size to the extrafusal fibers surrounding them. This feature may in fact account for the difficulty in detecting them.

Spindles were also reported in the lateral rectus of sheep (Cilimbaris, 1910), where over 200 were counted.

Because of the unfortunate neglect of contrary findings the weight of histological evidence seemed firmly on the side of the "out-flow" theory, and many experiments were performed confirming the lack of proprioceptive influence on the control of eye movements. No stretch reflex could be elicited in the extraocular muscles (McCouch & Adler, 1932). It was also shown that nystagmus was uneffected by procedures designed to reveal a proprioceptive component (McCouch & Adler, 1932; McIntyre, 1939). Adler (1945) further showed that past-pointing in patients with lateral rectus paresis was dependent on the position of the retinal image and not on proprioception.

Irvine and Ludvigh (1936) carried out a particularly complete series of experiments designed to reveal extraocular proprioception. They concluded that the lack of histological evidence, the lack of vibration sense, a myotactic reflex, or position sense all justify the claim that proprioception plays no role in the activity of the extraocular muscles.

The certainty of this claim is now open to doubt, however. In 1946 Daniel described a form of spiral nerve ending in the eye muscles of man that are probably affected by activity of the muscle; these, however, are not muscle spindles. Prompted by this, Cooper and Daniel (1949) made an extensive histological search of human extraocular muscles and succeeded in finding as many as 47 spindles in one muscle (an inferior rectus). These spindles were found in only certain regions of the muscle, and they differ somewhat in appearance from skeletal muscle spindles (their description agrees closely with that of Buzzard), being found primarily in the peripheral zone of small fibers near the proximal end of the muscle (Cooper, Daniel & Whitteridge, 1955). The pertinent facts regarding the histology of the muscle spindles have been confirmed by Sunderland (1949) and Merrillees etal (1950).

Spindles have also been observed in the extraocular muscles of the goat and sheep (Cilimbaris, 1910; Cooper, Daniel & Whitteridge, 1951), but not in the cat and monkey (Cooper & Daniels, 1949; Cooper &Fillenz, 1955).

Electrophysiological evidence of the presence of muscle spindles in extraocular muscles is also accumulating. Recording from the branch of the oculomotor nerve going to the inferior oblique muscle in the sheep and goat Cooper, Daniel and Whitteridge (1951) were able to observe afferent impulses from single units. The response of these units to stretch applied to the muscle is similar to the response seen by Matthews (1933) from the muscle spindles of skeletal muscles. Cooper and Fillenz (1955) saw similar responses from intraorbital branches of the III nerves in cats and monkeys despite the lack of histological evidence for the presence of spindles in these animals; physiological investigation has thus provided information unavailable histologically. In addition, they saw responses similar to Matthew's B type response, probably originating in the tendon organs.

The path of these impulses into the central nervous system is still somewhat of a mystery. No afferent discharges have been seen in the intracranial portions of the III nerve (Whitteridge, 1960), but there is evidence that branches of the V nerve supply the extraocular muscles. Thus Whitteridge (1955) has succeeded in recording afferent discharges in such branches in the goat and sheep. It would thus seem that the V nerve may be the chief pathway of proprioceptive inflow to the central nervous system, at least in the goat and sheep.

The destination of afferent discharges in the central nervous system has proved difficult to determine. In a series of papers Cooper, Daniel, and Whitteridge (1953a, 1953b, 1953c) have described the brainstem responses in goats to stretching the eye muscles. Short latency responses nearly identical in pattern with the responses seen in the III nerve were recorded in the V nerve complex of the brainstem, particularly in the mesencephalic nucleus of V (1953a). Longer latency responses, probably from higher order neurons, were found in various sites such as the central tegmental tract, the medial longitudinal fasciculus, the superior cerebellar peduncle, and the superior colliculus (1953b). In the last paper of this series (1953c) they demonstrated a juxtaposition of collicular responses to retinal stimulation and proprioceptive responses, and they point out the possible significance of this in oculomotor reflexes.

Fillenz (1955) has obtained a similar picture from recording in the brainstem of cats, although the frequency of finding units is very much reduced.

The role played by the efferent system in the regulation of the muscle spindle in skeletal muscles has been elucidated by Eldred, Granit, and Merton (1953), and the presence of a similar system has been demonstrated in the oculomotor system (Cooper & Daniels, 1957; Whitteridge, 1958, 1959). Donaldson (1960) analyzed the distribution of fiber sizes in the III, IV, and VI nerves and found a significant group of small fibers (3-7μ) that he identified with efferent fibers.

To summarize thus far, muscle spindles have been histologically observed in the extraocular muscles of man, goats, and sheep. Single unit afferent responses, clearly identifiable as arising from spindles, have been seen in the goat, sheep, cat, and monkey. Proprioceptive responses have been seen in the brainstem of the goat and cat, and the presence of the efferent system has been demonstrated.

However, attempts to discover the role played by this proprioceptive system in oculomotor activity have remained as inconclusive as ever. Ludvigh (1952a) carried out an experiment in which subjects were asked to tell which direction they had moved their eyes in response to peripheral retinal stimulation. He found that ocular movements of greater than 6° were needed to obtain 75% accuracy. He went on to conclude that "the muscle spindles in the extraocular muscles give little, if any, acceptable information concerning the position of the eyes".

Brindley and Merton (1960) have carried out a series of experiments involving passive movements of the eyes, and they concluded that no evidence for the action of proprioception could be seen.

Hyde and Davis (1960) could find no influence of proprioception on electrically induced eye movements (stimulation of brainstem sites).

However, there have been experiments supporting the possibility that proprioception plays a role in the control of eye movements. Merton (1961) studied the accuracy of directing the eyes and hand in the dark, and found the two to be comparable; since control of the limbs is undoubtedly exerted via the spindle system this at least suggests a comparable role for proprioception in the extraocular muscles.

A novel experiment carried out by Gurevich (1959) also supports this view. He produced a conditioned change of fixation, and found that upon receipt of the conditioned stimulus, a sound, the eyes could be accurately directed to the new fixation point even in the dark.

Crawford (1960) asked subjects to line up their head with visual fixation points under conditions where the only clues were proprioceptive ones from the eye muscles, and he found mean errors of only $0.5^{\circ} - 1.9^{\circ}$.

The problem of extraocular proprioception is thus still unsolved. There is no doubt that a proprioceptive system is present and that it responses in a manner completely analogous to the spindle system in skeletal muscle. However, the role, if any, played by these responses is still undetermined.

It does not appear likely that proprioception plays an important role in conscious control of eye movements, but a number of alternative roles remain. It is possible that a stretch reflex mechanism exists that is only evident under dynamic rather than static conditions. Such a mechanism could play a role in the control of rapid saccadic eye movements. A second possibility is that the information arising from the extraocular proprioceptive system is utilized to control the movement of the head on the neck, thus contributing to the stabilization of the visual image. Ludvigh (1952b) has proposed still a third alternative. He has suggested that the system provides a form of parametric feedback enabling the oculomotor system to compensate for changes in its own parameters.

This problem, like that of the existence of a centrifugal system in the retina, requires attention because of the crucial role played by feedback in any control system.

3. Properties of Horizontal Eye Movements

Dodge was perhaps the first to carry out an objective study of the kinds of eye movements possible and the properties of such movements (Dodge, 1903). He recorded eye movements by photographing the movement of a collimated beam of light reflected from the cornea. He classified five types of movements, but we will be concerned with only two of them, the saccadic movement and the smooth pursuit movement.

a. Saccadic movements

A saccadic movement is a rapid eye movement in response to a retinal image located off of the fovea; its function is thus the establishment and maintenance of fixation. Such movements can be voluntary changes of fixation such as occur constantly during "seeing", or there may be reflex movements to fixate an object suddenly appearing in the periphery.

The latency of the saccadic movement, the time between the displacement of the fixation point and the initiation of eye movement, has been measured by many investigators, and values of 200 msec (Travis, 1936), 120-180 msec (Westheimer, 1954a), 150-250 msec (Rashbass, 1961), and 200 msec (Young, 1962) have been reported. Two hundred milliseconds can thus be taken as an approximate mean value for the latency.

The velocity of these eye movements is very high, and is proportional to the angular size of the movement (Dodge, 1903; Travis, 1936; Brockhurst & Lion, 1951; Hyde, 1959); velocities as high as 830°/sec have been seen for 90° deflections (Hyde, 1959). The velocity profile of such saccadic movements shows a high initial acceleration and a rapid deceleration at the end (Westheimer, 1954a; Hyde, 1959).

Sudden changes of fixation rarely place the eye perfectly on target, and smaller corrective saccades are needed to accomplish this (Westheimer, 1954a); the frequency of such corrective saccades increases with the size of the initial saccade (Hyde, 1959). These saccades can only occur after the same latency seen for the larger movements.

That the stimulus for a saccadic movement is the location of the retinal image was nicely shown by Cornsweet (1956). He photographed eye movements using a tight fitting contact lens with which stabilized images could be provided. He showed that the probability of occurrence, the direction and the magnitude of these movements depend on the position of the image on the retina. Thus, images off the fovea cause movements tending to place the fovea under the image.

However, there is a displacement threshold below which saccades do not occur. Rashbass (1961), using a sensitive photoelectric measuring technique, reported that retinal image movements of 0.25-0.50° cause no corrective saccade, and Young (1962) has confirmed this.

The manner in which saccadic movements are produced has been fairly well determined. Westheimer (1954a) states, ".....a saccadic movement is iniated as a single, unitary step by means of simultaneous changes in innervation of the various muscles..........", this change producing a change in the tension exerted on the eyeball by the extraocular muscles. The eye then moves in an unguided, ballistic fashion to a new position. Westheimer (1954a, 1958) has derived a differential equation to describe the saccadic response of the eye.

Hyde (1959) has offered some evidence that Westheimer's theory does not hold for large saccades. She examined the responses to saccades of 90°, and found that the deceleration phase began after only one third of the distance had been covered, i. e. before the primary position had been passed. However, it follows from Westheimer's theory that the forces opposing the movement will be minimal in this position, giving a maximum velocity. It is possible that the extremely high velocities produced in a saccade of this size produces a stretch reflex in the extraocular muscles, thus introducing a new term into Westheimer's equation. Or, with these high velocities muscle viscosity may become a significant factor.

Recordings of the electromyographic activity of the extraocular muscles during saccadic movements have confirmed the qualitative details of Westheimer's theory. The general picture seen is of increased activity in the agonist muscle and complete inhibition of activity in the antagonist; no activity occurs in the antagonist to bring the movement to an end (Bjork & Kugelberg, 1953b; Bjork, 1955; Miller, 1958; Tamler, Marg & Jampolsky, 1959b). The burst of increased activity seen in the agonist has a duration proportional to the duration of the eye movement (Miller, 1958).

Bjork (1954) has made the interesting observation that a saccadic movement made by a subject with an abducens palsy produces a normal pattern of activity in the muscle normally antagonistic to the paretic muscle, even though the movement of the paretic eye is not normal.

b. Smooth pursuit movements

The major properties of smooth pursuit movements were first described by Dodge (1903). These movements occur in response to a moving visual target, and there is a latency between the commencement of target motion and the initiation of eye movement. Within certain limits the velocity of eye movements varies with the target velocity. When the eye lags behind the target corrective saccades occur to bring the eye back on target. Dodge also reported that smooth pursuit movements can "habituate" in that they may continue after target motion has ceased.

Later studies have confirmed these observations and provided additional information. The stimulus for smooth movements is the "movement of the target across the retina or the illusion of movement....." (Westheimer, 1954b). Rashbass (1959) goes even further, saying that pursuit movements aim at "a stationary image on the retina irrespective of error in the position of fixation".

Further, it is commonly felt that in the absence of a vestibular stimulus, smooth pursuit movements can only occur when a moving visual stimulus is present. However, Westheimer and Conover (1954) have reported on two subjects who were able to move their eyes smoothly between two fixation points in a manner closely resembling the published records of stimulus driven smooth pursuit movements.

Although eye movement velocities of up to 830^{o}/sec (Hyde, 1959) are possible, smooth pursuit movements are limited to much lower values. Westheimer (1954b) reports that target velocities of 25^{o}-30^{o}/sec can be closely matched by eye movement velocities, but Rashbass (1961) found velocity matching only up to 10^{o}/sec.

The latency for the initiation of a tracking movement is about the same as the latency for a saccadic movement, around 180 msec (Westheimer, 1954b). A similar value, 150 msec, was obtained by Rashbass (1959), who in addition has found that the latencies for the two kinds of movements can vary independently.

Positional errors arising from a failure of the smooth pursuit system to match the target velocity are corrected by saccades (Westheimer, 1954b; Rashbass, 1959), but the error must be greater than 0.1° (Rashbass, 1959). These saccades can only occur with the normal latency of 150-200 msec.

Another interesting property of smooth pursuit movements is the absence of smooth changes in velocity (accelerations) under normal conditions; velocities change in discrete steps with a normal latency, 150 msec, proceeding each change. If, however, the stimulus is a sinusoidally moving target, "anticipation" and "prediction" are possible, and the subject can "learn" to produce smooth velocity changes (Westheimer, 1954b).

In fact, the smooth pursuit system was found by Westheimer (1954b) to function differently with sinusoidal stimuli than with random stimuli. In the latter case, no "learning", i.e. improvement in performance, could be seen even after 20 repeated "cycles" of the stimulus. These responses also showed no smooth changes in velocity. But with a sinusoidal stimuli "learning" occurred and anticipation of the stimulus permitted smooth velocity changes.

Using barbiturates, Rashbass (1959, 1961) has succeeded in showing that saccadic and smooth pursuit movements are probably subserved by different systems. Under pentothal subjects were unable to produce smooth pursuit movements when tracking a moving target. Instead, a series of saccadic movements were used to follow the target.

Smooth pursuit movements have also been studied electromyographically. Bjork and Kugelberg (1953b), Breinin and Moldaver (1955), and Tamler, Marg, and Jampolsky (1959b) have all demonstrated the reciprocal activity of the medial and lateral recti that produce horizontal following movements; activity in the agonist increases at a rate determined by the velocity of the eye movement and activity in the antagonist undergoes a concommitant decrease.

Bjork (1955) has examined the electromyogram in optokinetic nystagmus, a form of eye movement in which slow pursuit movements alternate with rapid saccades. Under these conditions the myographic activity characteristic of both kinds of eye movements could be seen. During the slow pursuit phase activity in the agonist slowly increased while activity in the antagonist decreased, while during the saccade a sudden increase in activity was seen in the agonist and complete inhibition was observed in the antagonist.

4. System Studies of Eye Movement Control

Westheimer (1954a, 1958) was the first to attempt to describe eye movements mathematically. From his studies of the properties of the saccadic eye movement Westheimer was able to derive a differential equation relating the forces acting on the eye ball, the torque provided by the extraocular muscles, friction of the eye ball in the orbit, inertia, and the elastic resistance of the antagonist muscle to stretch. Examination of this equation reveals that the eye ball itself is capable of very rapid responses (its frequency response is essentially flat to 30-40 c/s), much more rapid than are ever seen in naturally occurring eye movements. Thus, in any study of the oculomotor control system it can be assumed that the response characteristics of the system are limited by the control elements, not by the motor system itself.

The first systems analysis of the visual tracking system was undertaken by Fender and Nye (1961), and their experiments are illustrative of the kinds of experimental techniques employed.

A sinusoidally moving target was presented to a subject instructed to fixate the target and follow it with his eyes as it moved. The eye movements of the subject were monitored and could be compared with the target movements. Such an apparatus permits the determination of the normal frequency response of the system. That is, the change in response with a change in frequency can be determined. This relationship can be specified by measuring the gain, the ratio of eye movement amplitude to target amplitude, and the phase shift, the time relationship between the input signal and the output response, of the system at different input frequencies. From plots of this data and the mathematical transfer function that can be obtained some of the properties of the system can be determined, providing the system is linear under the conditions studied.

However, additional information can be obtained by studying the system responses under conditions where the information flow in the system has been altered (varying the feedback pathways), and Fender and Nye also studied the system under such conditions. Of course, this can not be done directly using human subjects since surgical intervention would be required. However, it can be effectively accomplished by altering the relationship between eye movements and the position of the retinal image. For example, under normal conditions moving the eyes through a certain angular displacement results in a given movement of the image on the retina. If, however, the eye position is used to drive the target it can be arranged that there will never be a retinal error (image off the fovea). Or, the apparatus can be arranged so that a given eye movement causes the retinal image to move by twice the normal amount. Determining the frequency response characteristics under these conditions reveals properties of the system not seen under normal conditions.

The results and conclusions obtained by Fender and Nye (1961) are of some interest. Accurate tracking of target movements was possible at frequencies up to 1.2 c/s. At higher frequencies the subjects tend to track the target with saccadic movements and even at low frequencies corrective saccades were seen.

The two subjects tested showed quantitatively different frequency response curves, although the shapes of the curves were similar.

The use of different amplitudes of input revealed that the system is a non-linear one. Further, the measured phase lag of the system was less than the phase lag calculated from the Bode equations, making the system a non-minimum phase network; the phase shift of the system does not asymptotically approach 180° as the frequency increases, but increases past this value.

It is of interest that the block diagram of the eye movement control system developed from these results contains a feedback loop identified with extraocular proprioception.

Similar but more sophisticated studies of the visual tracking system have been carried out by Stark, Vossius, and Young (1962) and Dallos and Jones (1963). One significant difference in these two studies is that both groups utilized other forms of inputs in addition to sinusoidal signals. In fact, one of the most significant findings of both studies resulted from this.

In addition to using periodic inputs such as sinusoids or square waves, both groups used stimuli referred to as "unpredictable". Stark etal (1962) utilized an input consisting of a mixture of sinusoids the appearance of which was such that the subjects could not predict its future behavior on the basis of its present or past behavior; thus the term "unpredictable". Dallos and Jones (1963) utilized Gaussian random noise, a form of signal also impossible to predict.

However, it should be pointed out that the terms "predictable" and "unpredictable" may carry with them certain connotations that are probably not valid in the present context. There is no evidence that the component in the visual tracking system that responds to periodic stimuli does so by any conscious analysis of the input signal; in fact, no special conscious effort on the part of the subject is required for this component to function. The use of these terms is only justified by the fact that they are descriptive of the mode of response of the system; the system responds as if the input were literally being predicted. Therefore, it should be understood that these terms will be used in the present work only in their descriptive sense; nothing is being implied about the nature of the components in the system giving rise to these responses.

The significant finding was that the visual tracking system responded quite differently to predictable and unpredictable stimuli. This was revealed by two phenomena. When subjects were presented with regular square waves, changes in eye position regularly occurred before the target movement. This type of response seems to be correlated with stimulus repetition rate, maximum prediction occurring with stimuli of frequencies of 0.4 to 1.0 c/s. And with unpredictable stimuli both groups obtained frequency responses markedly different from the frequency response to single sinusoid inputs.

Other interesting properties of the visual tracking system revealed by systems analysis are the separateness of the saccadic and the smooth pursuit systems (confirming the results of Rashbass, 1961, obtained with drug studies), (Young, 1962) and the sampled data operation of the tracking system when responding to unpredictable inputs (Young & Stark, 1963).

III. STATEMENT OF PROBLEM

The results obtained by Stark etal (1962) and Dallos and Jones (1963) raise two interesting questions. The first has to do with the relationship between the dynamic response of the visual tracking system and the predictability of the input stimulus.

It should be obvious that predictability of a stimulus is not an either-or condition. A continuum of stimuli exists ranging from the completely predictable sinusoid to the completely unpredicable wide-band random noise signal; at intermediate points along this continuum the stimuli possess a certain periodicity that permits prediction with varying certainty.

The question to be answered, then, is, does the predictor operate in a continuous fashion along this continuum? That is, does its response vary in some continuous way with the predictability of the input stimulus? Or, is the predictor a flip-flop device, operating in a predictive mode with a narrow range of periodic inputs, but functioning in a non-predictive mode (or perhaps being switched out of the circuit) when the input becomes less than completely predictable?

This question can be answered by presenting a series of stimuli of graded predictability to subjects whose responses to these stimuli can then be determined. If the predictor operates in a continuous fashion a series of response curves will be obtained which range from the curve obtained for a predictable sinusoid to the curve obtained for a completely unpredictable noise signal. If however, the predictor operates in an either-or mode all of the response curves will cluster about either the predictable or the unpredictable curve.

However, some new technique for generating suitable unpredictable stimuli is needed for such an experiment. Addition of sinusoids, the technique used by Stark and his co-workers, does produce a stimulus that can not be predicted by the subject, but such a stimulus is not suited for the experiment outlined above. The appearance of these stimuli, and thus their predictability, depends on three parameters, the ratio between the frequencies of the components, the relative amplitudes of the components, and their phase relations. There is thus no signle parameter whose variation will uniquely produce stimuli of graded predictability. And, with no *a priori* knowledge of the effect of varying any of the parameters on predictability, it would be impossible to decide which of the three parameters in the system should be varied to "best" produce the desired stimuli. A large number of experiments would then be required to look at the responses to all possible unpredictable stimuli that could be produced by variation of the three parameters.

The relatively wide-band Gaussian noise (half-power point of 1.25 c/s) used by Dallos and Jones (1963) is in itself not a suitable stimulus, although it does point to the possible use of random noise in formulating the desired stimulus. For the present investigation, therefore, it was necessary to devise a new technique for stimulus generation. In practice, as will be described in the Methods section, random signals of varying bandwidth were employed, in which predictability could be continuously varied in terms of a single parameter, namely bandwidth of the noise.

The second question has to do with the role of learning in the visual tracking system. Both Westheimer (1954b) and

Dallos and Jones (1963) report that learning occurs with periodic inputs. Westheimer observed that during the first 12 cycles of a sinusoidal input the subject's responses became progressively smoother and the phase lag progressively reduced, often to zero. Dallos and Jones, however, found that the first cycle of a sinusoidal input incorporated as much learning as the fourth cycle, but that with square wave inputs a decrease in the latency of eye movements was found.

Westheimer (1954b) also studied learning with cam-generated random stimuli and found that even after 20 "cycles" of the stimulus no improvement in performance was evident.

If the predictor improves system performance by learning the stimulus pattern it would be expected that repeated exposure to the same stimulus would result in progressively improved performance. Westheimer's failure to see any learning with unpredictable stimuli may be due to the degree of unpredictability of his stimuli, suggesting that learning might be seen if a set of stimuli of graded predictability are used.

To test whether any learning occurs with repeated exposure to the same stimulus, and if such learning might be dependent on the predictability of the stimulus used, subjects can be presented a series of trials using stimuli of various degrees of predictability, and their performance on successive trials compared.

The experimental program actually undertaken in this investigation thus falls under four main headings:

1. development of the technique for generating and presenting stimuli of graded predictability,
2. development of a method for measuring the subject's responses to these stimuli,
3. experiments designed to determine the relationship between the dynamic response of the visual tracking system and the predictability of the target movement,
4. experiments designed to examine the role of learning in the visual tracking system.

IV. METHODS

1. Apparatus

a. Stimulus generation

The production of completely predictable stimuli requires only an oscillator capable of generating low frequency sinusoidal signals of variable amplitude.

Stimuli of graded predictability are by no means as easy to produce. A technique is required that will produce this gradation with the variation of a single parameter; in this way a continuum of predictability can be established. For this reason the addition of sinusoids (Young, 1962), although easily achieved, is unsuitable; the stimuli produced are a function of three parameters.

Two alternate approaches suggest themselves. One is the addition of wide-band noise to a sinusoid of the desired test frequency (Fig. 1a). In this case continuous gradation of predictability can be achieved by varying the amplitude of the noise, thereby varying the signal to noise ratio. Then, the smaller the signal to noise ratio the less predictable the stimulus.

However, this approach has the disadvantage that the effect of the frequency content of the noise used (its bandwidth) remains unknown. Moreover, the subject is now presented with the problem of signal detection in addition to the required tracking task.

A second approach was therefore adopted, based on the use of narrow but variable bandwidths of noise centered about the desired test frequency (Fig. 1b). In this case gradation of predictability can be produced by varying the bandwidth of the noise; at a given center

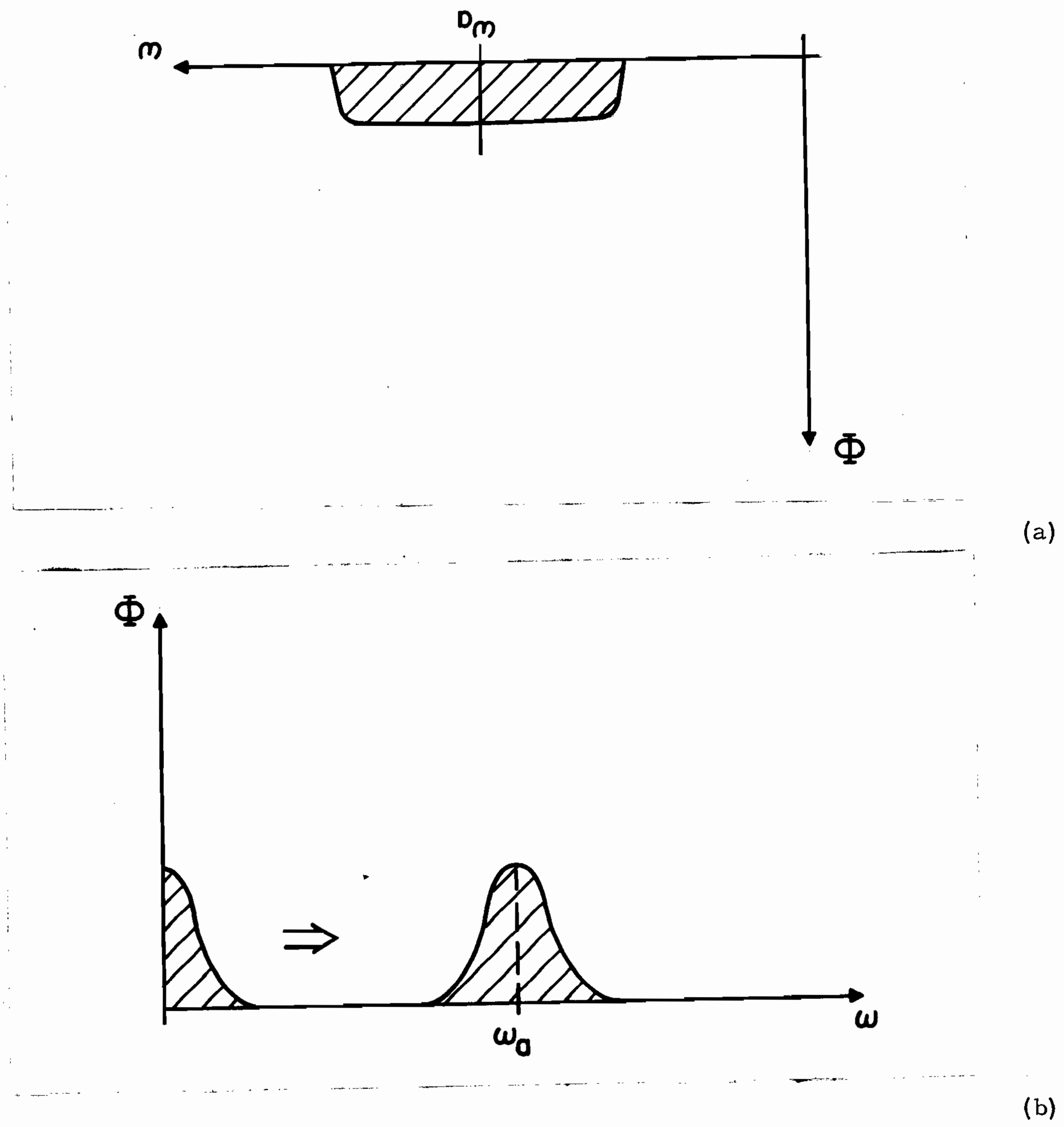


FIGURE 1

The spectral power distribution of possible unpredictable stimuli is shown above. Power (Φ) is plotted along the Y-axis and frequency (ω) along the X-axis. (a) A sinusoid of the desired test frequency (ω_a) and a fixed power or amplitude can be masked with wide band noise of variable amplitude. The greater the amplitude of the noise, the smaller the signal to noise ratio, the less predictable will be the stimulus. (b) Random noise of a narrow and variable bandwidth centered about the desired test frequency (ω_a) is a more suitable form of stimulus; the wider the bandwidth of the noise the less predictable the stimulus.

frequency the narrower the bandwidth the more predictable the stimulus. It is, however, possible that with changes in center frequency the predictability will depend on the bandwidth to center frequency ratio.

Such stimuli were produced in the following manner. A Pace low frequency Gaussian noise generator with a power spectral density constant to approximately 35 c/s was used as a noise source. Low band pass filtering of this signal produced narrow bands of noise, the width of the bands being determined by the parameters of the filter. Bandwidths of 0.05, 0.10, 0.20, 0.50, and 1.00 c/s were produced in this way.

To position these bands of noise about the desired test frequency a process known as suppressed carrier modulation was used. This essentially consists of multiplying the signal to be modulated, in this case the narrow bands of noise, by a sinusoid of the desired frequency. An oscillator providing both the sine and cosine function was used to produce the sine- and cosine-modulated signals (both are needed for the analysis of the subject's responses) at frequencies of 0.3, 0.7, 1.0, and 1.5 c/s (a more complete description of the stimulus generating technique can be found in Appendix I). The 24 signals (6 bandwidths at 4 frequencies) were recorded on a Philips 400 stereo tape recorder for later use.

b. Stimulus presentation

To present these stimuli to the subject the sine-modulated signal was fed, after suitable amplification, onto the horizontal plates of a Tektronix 502 oscilloscope having a short persistence screen. Thus, the signal caused the oscilloscope spot to oscillate along a horizontal line. The face of the oscilloscope was magnified and back-projected with an F/2.9 lens onto a frosted glass screen, providing the moving visual target to be tracked by the subject.

To provide subject eye movements of a known magnitude the target spot was moved through a known angular displacement by applying a fixed voltage to the oscilloscope.

c. Eye movement recording

DuBois Reymond was the first to discover the resting potential of the eye; using surface electrodes placed on an excised eye he observed that the cornea was positive and the fundus negative. During the period when string galvanometers were in wide use this potential was often observed but little or no interest in its nature or possible use was evidenced.

However, the existence of such a potential offers a convenient method for measuring the movement of the eyes. Electrodes placed at the outer canthi of the eyes will detect a varying potential as the eyes rotate in the horizontal plane; the electrode nearer the cornea will become positive and the one nearer the fundus will become negative (see Fig. 2). Measurement of the voltage between the two electrodes thus provides a means of recording horizontal eye movements. This technique is known as electro-oculography (EOG).

Schott (1922) was apparently the first investigator to use electro-oculography for recording eye movements. He used saline filled clay cups for electrodes and a string galvanometer to record the varying potentials produced by rotationally induced nystagmus. However, his theory as to the origin of the potential being recorded was thoroughly inadequate.

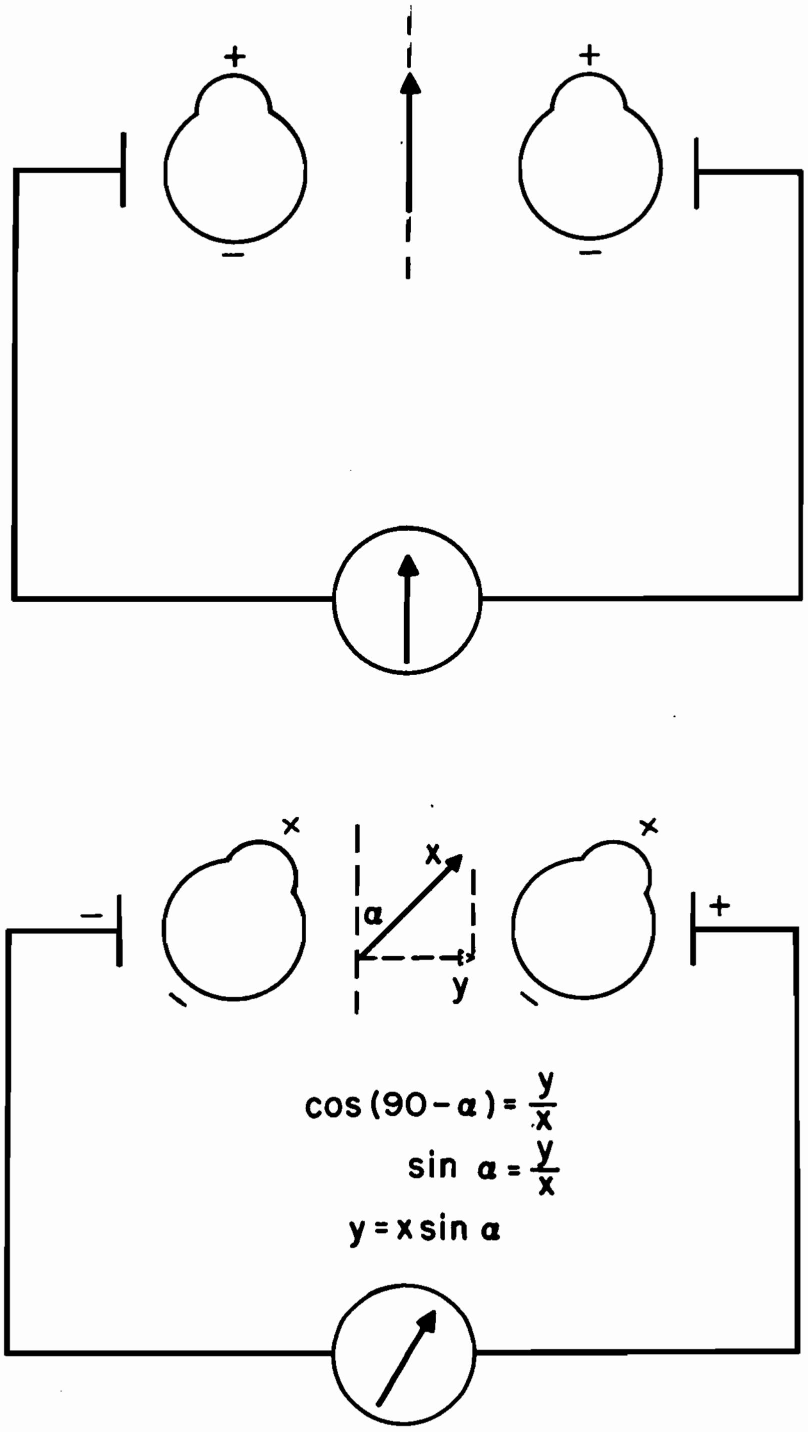


FIGURE 2

Electro-oculography provides a means of measuring eye position by utilizing the electrical dipole property of the eye; with the eyes deviated from center, electrodes detect a component of the resting potential proportional to the sine of the angle of deviation.

Although, following the work of Schott, EOG came into wide use, Mowrer etal (1936) were the first to show that the potential being recorded arose directly from the eye, and was neither the product of activity of the extraocular muscles nor a direct physical effect of the movement of the eyes. They established that the retina was the site of origin of the potential, and that the eye was acting as an electrical dipole rotating in the skull.

The exact site of origin in the retina of the resting potential has still not been definitively established. Ottoson and Svaetichin (1952) found a D. C. component in the electroretinogram at a distance of 200-225μ from the anterior surface of the retina, the location of the external limiting membrane. By actually inserting their micro-electrode into the receptor layer they were able to identify the receptor cells as the source of this potential. Brindley (1956b) found a potential of 10 to 30 mV across the "R membrane", tentatively identified as the external limiting membrane.

However, Brown and Wiesel (1958) claim that Bruch's membrane is the site of the resting potential, although Ottoson and Svaetichin (1952) found no potential drop on moving their electrode through this membrane.

Brindley (1956a) has also reported a resting potential across the lens, due to the difference of ionic concentration between its interior and the vitreous and aqueous humours, that may contribute to the total resting potential measured across the eye.

Whatever the origin of the resting potential it has been demonstrated that it is generated by the eye itself, and that it can be used to record the movement of the eye.

Quantitative measurements, however, require a knowledge of the relation between the position of the eye in the skull and the size of the observed potential. Referring to Figure 2 we can see that, with electrodes placed at the outer canthi of the eyes, horizontal deflections of the eye produce a potential proportional to the sine of the angle through which the eyes have rotated. Fenn and Hursh (1937) and Leksell (1939) had subjects fixate on points a known angular distance apart, and were able to demonstrate that the potential is indeed proportional to the sine of the angle.

If, however, angular deflections of less than 30° are to be measured, a simpler relation can be used. In this range the sine of the angle is very nearly equal to the angle itself (in radians). This then gives a nearly linear relation between angular deflection and potential. Careful measurements by Leksell (1939), Law and DeValois (1957), and Shackel (1960) have established that such a relationship can be obtained in practice.

One property of the resting potential that makes possible its use for the measurement of eye movements is its stability. Miles (1939) ran a series of calibration trials on two successive days and found a correlation coefficient of +0.81 between the values of the potentials seen on the two days. In trials carried out eight weeks apart a corresponding correlation coefficient of +0.91 has been reported (Davis & Shackel, 1960), and over a ten month period correlations of + 0.83 have been seen (Shackel & Davis, 1960).

Furthermore, there is apparently no correlation between sex and the behavior of the potential (Miles, 1939), and only a slight correlation with age, older subjects having a slightly smaller and perhaps less stable potential (Miles, 1939; Shackel & Davis, 1960).

On the other hand, electro-oculography does have a number of definite limitations. "Noisy" baselines limit the sensitivity of eye movement recording to $\pm 0.5^{\circ}$ (Shackel, 1959b). In addition, the electrodes used invariably pick up other biological potentials such as the EEG, the EMG of facial musculature, and the EMG activity of a blink. These artifacts can make the use of EOG unreliable (Byford, 1961; Byford, 1963). Unexplained artifacts seen on recording vertical eye movements can also lead to false interpretation of the records (Ford, 1959), although this phenomena is of no concern here.

Of perhaps a more serious nature are the factors that lead to variation in the recorded potential during a single trial. The most important of these is changes in the light- or dark-adapted state of the subject's eyes. Sudden changes in illumination produce transient changes in the resting potential lasting 60 to 80 seconds, and slower fluctuations lasting up to thirty minutes (Kris, 1958; Arden & Kelsey, 1962). Psychological effects, perhaps acting through the psychogalvanic skin reaction, can also produce changes in the potential, particularly after the apprehension generated by the experimental situation is gone (Miles, 1939). There are also unexplained daily fluctuations in the resting potential (Davis & Shackel, 1960).

These difficulties can be overcome with the use of two procedures. One is the employment of a calibration procedure following every experimental run. The second is the use of averaging techniques to obtain results from a single trial and the use of many subjects to average out individual differences.

Having weighed the relevant factors it was decided that electro-oculography could be employed in the experiments to be carried out. This decision was based on the relative simplicity of the technique and the belief that sufficient accuracy and reliability could be obtained with care. The results seem to justify this belief. h. p.

The electro-oculographic system employed consisted essentially of non-polarizing surface electrodes to detect the resting potential, a DC amplifier to increase the signal level, and tape recording equipment to provide a permanent record of the data (Fig. 3).

The electrodes used were small, soft rubber suction cups with a chlorided silver pin extending into the cup (Shackel, 1958). The cups were filled with a saline (0.9%)-agar conducting jelly, and the electrodes were placed on the temples as close to the outer canthi of the eyes as possible. An indifferent (ground) electrode was placed on the forehead. Increased electrode stability and a relatively noise free baseline were obtained by carefully scrubbing the skin with acetone-soaked cotton. This is not as satisfactory as the technique of "skin drilling" described by Shackel (1959a), but experience showed that in the relatively short time needed for an experiment this procedure was adequate.

Of course, this did not eliminate the artifacts that can be picked up by the system. However, the two most common artifacts, the EMG of the jaw muscles and the response from a blink, were reduced by relaxation of the jaws and suppression of blinking during an experimental run. Furthermore, such artifacts are easily detected, and thus could be ignored during data analysis. Figure 4 contains samples of

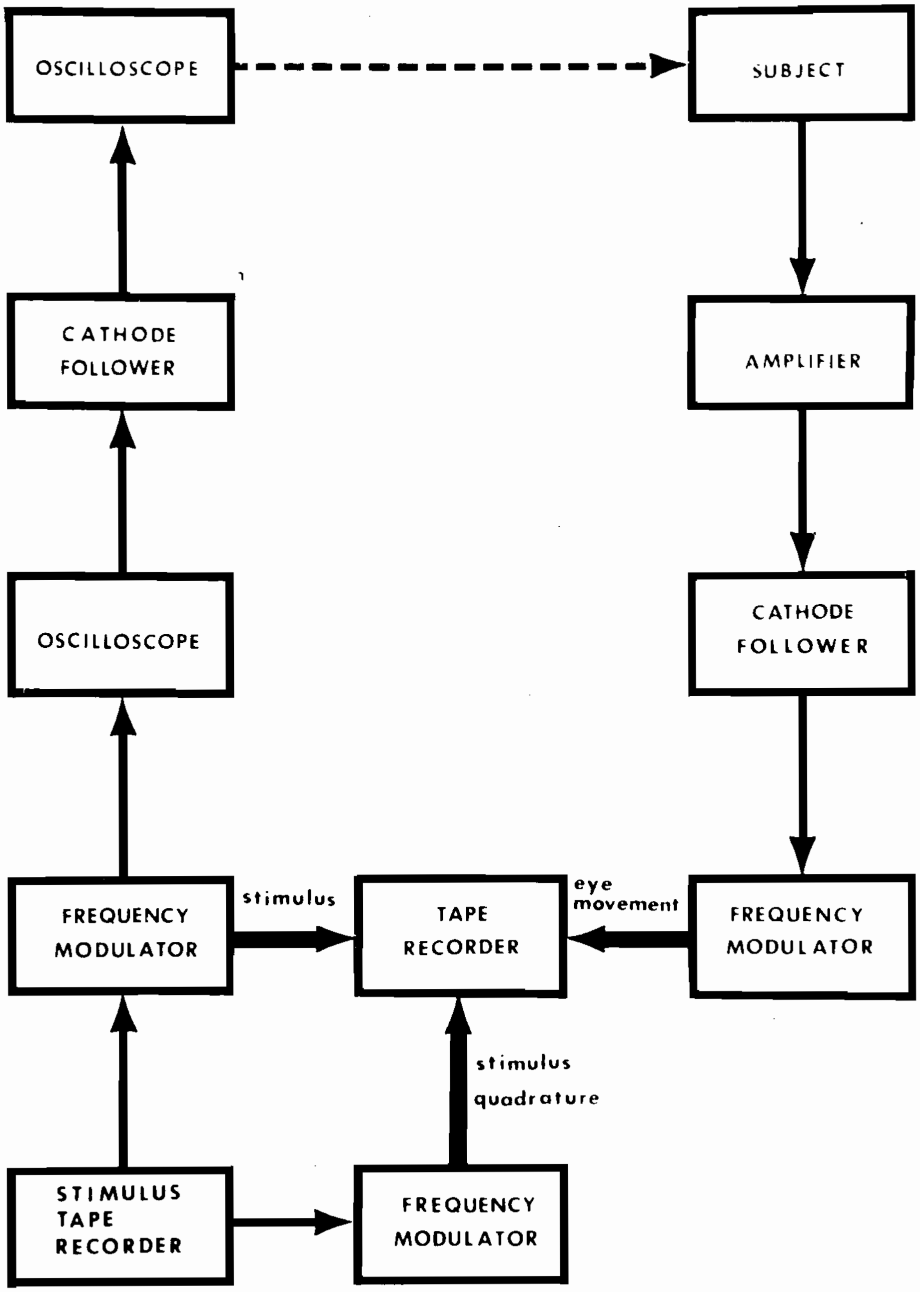


FIGURE 3

A stimulus tape is played back through a tape recorder and after amplification the stimulus signal is displayed on the target oscilloscope. The stimulus, and its quadrature, are simultaneously recorded on a second tape recorder. The eye movement responses of the subject are detected electro-oculographically, amplified, and then recorded on the third channel of the second recorder.

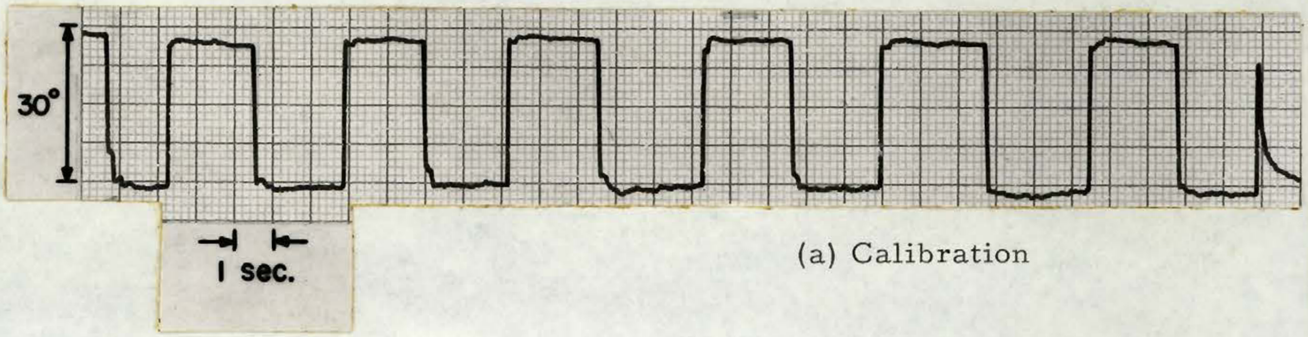
typical records, demonstrating the relatively noise-free baseline, the stability of recording, and some of the artifacts obtained with the system employed.

The potential picked up by the electrodes was passed through a simple input circuit (Fig. 5) which served two purposes. It acted as a filter to remove some of the 60 c/s noise picked up by the system, and it protected the subject from the possibility of a malfunction in the amplifier causing a high voltage to appear across the electrodes.

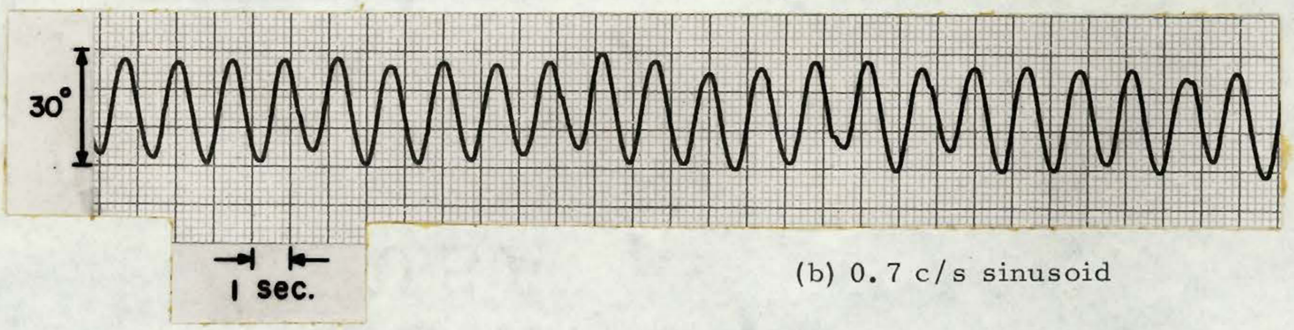
The signal was then displayed on a Tektronix 502 oscilloscope. At a gain of 200 μV/cm, DC coupled, and with a differential input a standard calibration eye movement of 30° (15° either side of the center position of the eyes) produced a deflection of about 2 cm.

The voltage appearing on the vertical plates of the oscilloscope was fed to a cathode follower (also DC coupled) from which an output of 7.5 V was obtained for every centimeter deflection of the oscilloscope trace.

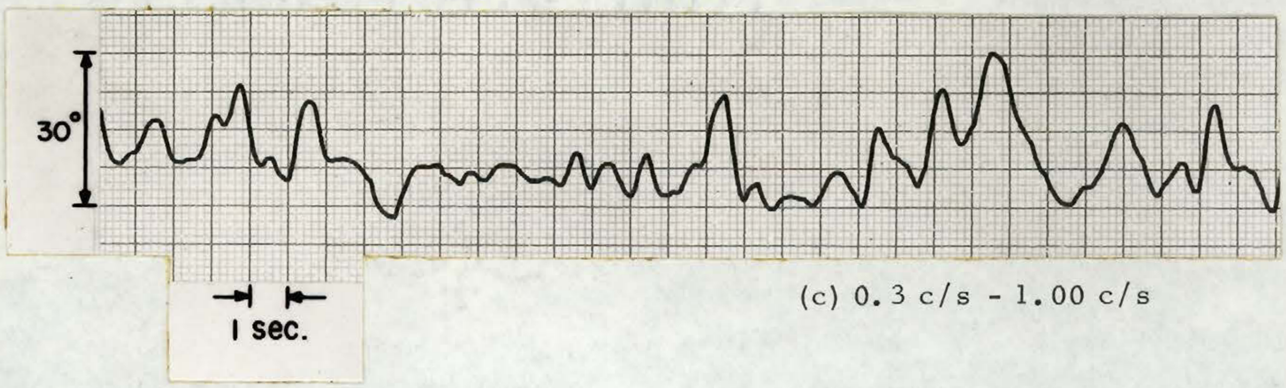
Because signals of less than 100 c/s can not normally be faithfully recorded directly onto magnetic tape a frequency modulating system was required. The particular system utilized operates in the following manner. A free-running multivibrator produces a square wave carrier pulse train at a certain frequency. The impressed signal voltage varies the frequency of this carrier, and the train of pulses produced is recorded on the tape recorder. Both a commercial Philips stereo recorder and a custom-built 4-track tape deck were used. To play back the recorded data the frequency modulated signal is passed back through a demodulating circuit where the pulses are



(a) Calibration



(b) 0.7 c/s sinusoid



(c) 0.3 c/s - 1.00 c/s

FIGURE 4

Samples of eye movement responses to different stimuli, obtained electro-oculographically, are presented above. The stable, relatively noise-free baseline of the calibration record should be noted. The sharp spike at the end of this record (a) is a blink response.

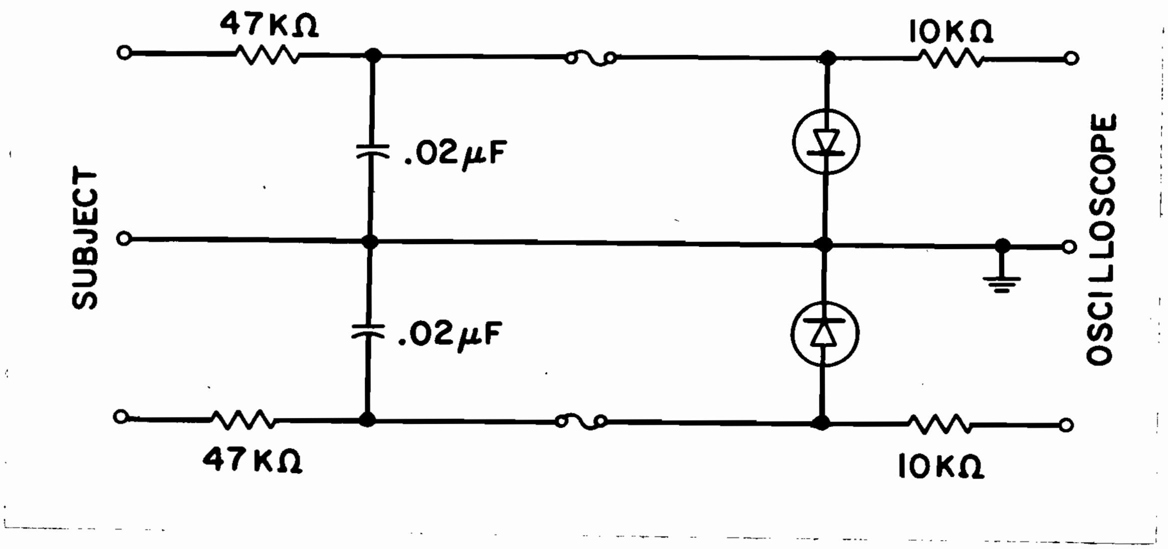


FIGURE 5

The subject was protected from the possibility of a high voltage from the amplifier appearing on the electrodes by a fused input circuit that also acted as a filter to remove any 60 c/s noise picked up by the electrodes.

essentially integrated, reproducing the original signal wave form.

Figure 3 is a block diagram of the recording system used for the electro-oculographic recording of eye movements.

In order to determine the accuracy with which eye movements could be measured with the EOG technique described above a calibration test was performed. A cine-photographic technique for directly recording eye movements, developed by Melvill Jones (1963), was simultaneously utilized together with the EOG technique while a subject performed a series of known eye movements.

The photographic technique makes use of a helmet on which is mounted a camera and a periscope. Pictures can then be taken of the moving eye using the pupil as the chief land mark. By projecting the film one frame at a time and tracking the pupil with a semi-automatic analyzer a record of the changing eye position can be obtained. This technique is accurate to $\pm 0.5^\circ$ and the photographically obtained records of the calibration run were then used as a standard.

Both a static and a dynamic calibration were obtained. In the first, the subject was asked to fixate on points a known angular distance apart. In the dynamic calibration the subject was asked to track a spot moving sinusoidally at a frequency of 0.3 c/s, well within the range of highly accurate visual tracking (Young, 1962; Dallos & Jones, 1963).

A comparison of the two records (Table 1 and Fig. 6) revealed that the electro-oculographic technique employed was accurate to $\pm 0.5^\circ$ and is thus of sufficient accuracy for this investigation.

STATIC TEST

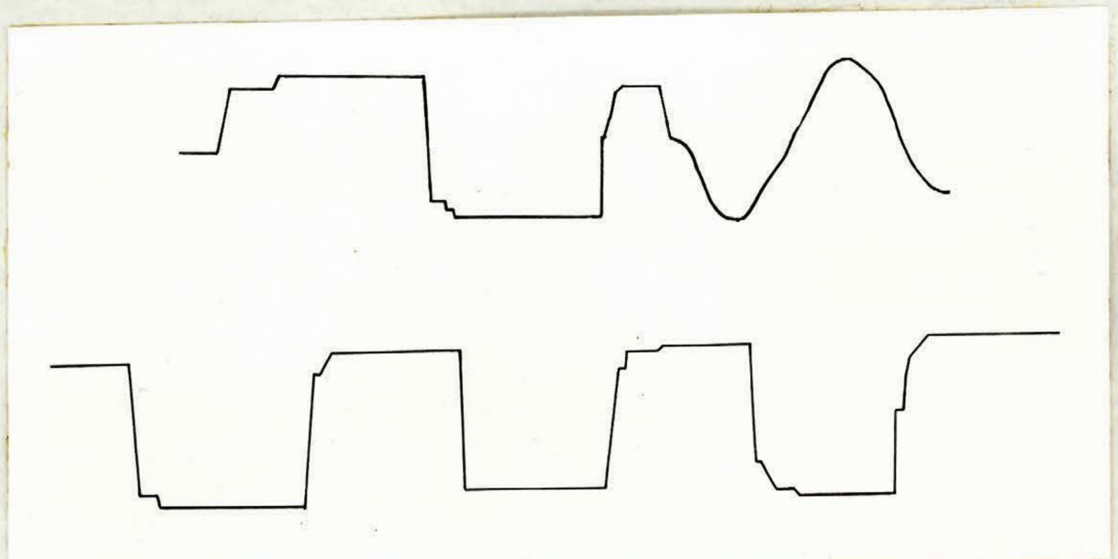
EOG	Photo. (Degrees)	Diff.
6.1	6.4	-0.3
10.2	10.8	-0.6
12.2	12.0	+0.2
14.2	14.4	-0.2
19.4	19.2	+0.2

DYNAMIC TEST (0.3 c/s)

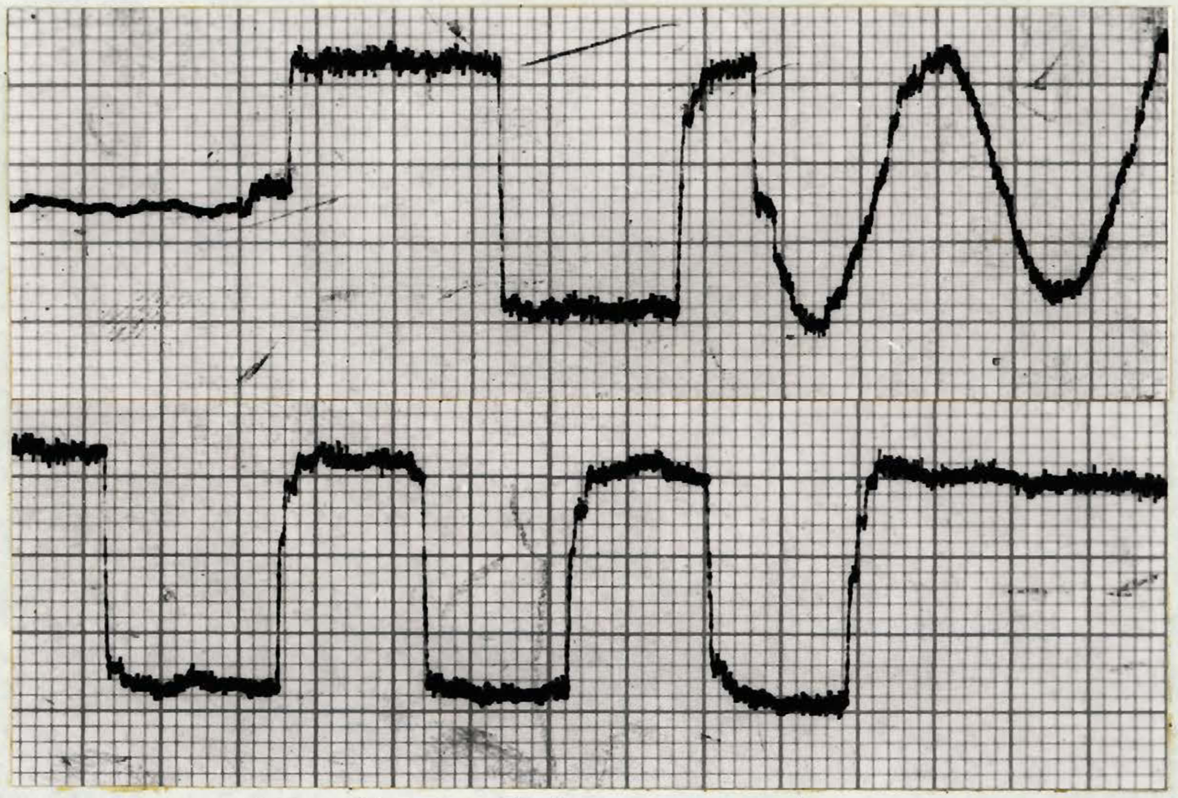
EOG	Photo. (Degrees)	Diff.
32.0	32.2	-0.2
34.0	32.5	+1.5
30.0	31.0	-1.0
32.0	31.6	+0.4

TABLE 1

The subject's eye movements were recorded both electro-oculographically and photographically. Thirty degree peak-to-peak movements served as calibration runs. In the static tests the fixation target was moved to various positions and the subject instructed to maintain fixation. In the dynamic test the subject was asked to track a sinusoidally moving target (0.3 c/s). Both sets of records were analyzed and the angular deflections of the eyes during the two tests were measured. The figures obtained can be compared above. The photographic method was taken as a standard and the differences calculated by subtraction. The average error of the EOG technique does not exceed $\pm 0.5^{\circ}$.



(a) From photographic measurement of eye movement.



(b) Electro-oculographic record of eye movement.

FIGURE 6

Electro-oculographic records of eye movements can be compared with results of the photographic recording of the same movement. Because of the nature of the photographic technique the time scale of the record seen above (a) is arbitrary. It can be seen that the EOG recordings faithfully represent the eye movement.

2. Experimental Procedures

The subject was seated on a stool in front of the projection screen upon which the stimulus appeared. A bite-board made of dental impression material was mounted so that when gripped by the subject the head was held in the proper position. A ball and socket joint made it possible to alter the orientation of the bite-board, and it was possible to position each subject with his eyes level with the stimulus, and parallel to and a known fixed distance from the screen.

The experiments were carried out in an electrically shielded room to reduce electrical interference. Ambient lighting was maintained at a constant, reduced level throughout any one experiment, and little variation in this level was encountered during the series of experiments. The noise level of the laboratory was reduced, but no attempt was made to maintain silence.

The 24 stimuli used, six bandwidths of noise centered about four frequencies, were presented during a single experimental session lasting approximately two and a half hours. The stimuli were presented in a random order, no two subjects receiving the same sequence. It was, of course, impossible to utilize all possible sequences in the limited number of experiments performed.

Each stimulus was presented for approximately three minutes and was followed by a 15-30 sec calibration procedure. After each run the subject was allowed to release the bite-board and relax while the experimenter prepared for the next stimulus; this generally took one to two minutes. The subject was allowed a longer rest period if desired (following the spot has a soporific, almost hypnotic, effect on some subjects), and a long rest period was always given after presentation of half the stimuli.

Eight of the ten subjects used were either staff members of the laboratory or medical students, and they were thus relatively accustomed to being experimental subjects. The remaining subjects were non-medical undergraduates at McGill University.

The experimental procedures were explained to all the subjects, the apparatus demonstrated where necessary, and every effort was made to reduce any nervousness or apprehension that might be present. The subjects were only informed of the task required of them, i.e., maintaining fixation on the moving spot of light. No information about the nature or purpose of the experiment was offered, and nothing was said about the expected results. Furthermore, the subjects were not informed of the level of their performance during the experiment. The goal was the maintenance of the subjects in a relaxed but motivated state so as to obtain the best performance possible.

The learning experiments were carried out in an essentially similar fashion. Three stimuli covering a range of difficulties were selected, 0.1 c/s bandwidth centered at 0.3 c/s, 0.2 c/s centered about 0.7 c/s, and 0.5 c/s centered about 1.0 c/s. Each stimulus was presented either three or four times in succession (three experiments) or the sequence of stimuli was repeated three times (one experment). Care was taken to begin recording just before the beginning of each run so that the first few seconds of each response were recorded.

The four subjects used here had all previously taken part in the first experiment, and thus they were thoroughly familiar with the experiments. For these experiments the subjects were carefully briefed as to the nature of the problem being studied. They were shown pen recordings of the stimuli and any pertinent features of the stimuli were pointed out. After each trial the subjects were informed of the "goodness" of their response and suggestions for improving their performance were offered. Thus, every effort was made to enable the subjects to improve their performance.

3. Analysis of Data

The frequency response of a system is specified by the gain and phase shift of the system at different input signal frequencies. Thus, the response of the human visual tracking system to stimuli of graded predictability can be completely characterized by the frequency response of the system to the six sets of stimuli used.

The ideal method of analyzing low frequency, complex signals so as to obtain the desired frequency response measurements is the conversion of the analog voltages into digital form and the processing of the data on a high-speed digital computer. Lacking the necessary facilities a purely analog method of analysis was developed.

Given the stimulus, its quadrature (the stimulus phase shifted 90°, in this case the cosine-modulated stimulus), and the system response, the phase shift can be obtained by cross correlating the response with the stimulus and with the quadrature. The appropriate cross correlation coefficients can be obtained from measurements of the RMS (root mean square) values of these three signals and certain of their combinations. The mathematical derivations of the techniques used here can be found in Appendix II.

This technique, although in theory capable of providing gain measurements, could only conveniently be used to provide phase measurements. However, this is not a serious limitation in the studies to be undertaken. The questions being asked here are essentially qualitative in nature, and any measure of system performance, either phase or gain, will provide the desired information about predictor response to stimuli of varying predictability. Only if a complete analytic study of the system was to be carried out would it be essential that both phase and gain measurements be available.

Further, there is evidence that the visual tracking system functions so as to minimize the phase shift between target position and eye position (Melvill Jones & Drazin, 1961). Two observations led to this conclusion. First, assuming the system to be of the second order, the experimentally determined phase shift is less than the theoretically expected phase shift. Second, errors in reading a moving scale seem to correlate most closely with the increasing phase shift, not with the steadily decreasing gain. This may be due to the fact that maintenance of the proper phase relationship, whatever the gain, results in a nearly stationary retinal image at the extremes of the target traverse. Thus phase is more important than gain in the maintenance of visual acuity. For these reasons phase measurements probably represent the most suitable single measure of visual tracking system response.

The actual processing of data by the technique described is made difficult by the low frequency of the signals to be handled; RMS measurements of higher frequency signals can be made easily with commercially available instruments, but this could not be done with the signals to be processed here.

To overcome this problem the following procedure was adopted. A short segment of data was transcribed at low tape speed onto an Ampex tape-loop recorder. When played back at a greatly increased tape speed the frequency range of the signals recorded on the tape loop was increased from approximately 0-3 c/s to approximately 2-90 c/s. This is within the range of available instruments.

The complete data processing system is seen in Figure 7. The loop recorder was played back through a Pace analog computer and the necessary addition of signals was carried out on two operational amplifiers. The five signals now present, the stimulus, the quadrature, the response, the stimulus plus the response, and the quadrature plus the response, were then applied to potentiometers that were adjusted so as to give full-scale deflections of a Bruel & Kjaer RMS meter (the meter is most accurate when deflected full-scale). The RMS value of the signals is thus proportional to the "pot" settings which were automatically typed out by the computer.

The cross correlation coefficients with zero time delay are then defined by:

$$\rho_{rs}(o) = \frac{E\left[(r + s)^2\right] - E\left[(r)^2\right] - E\left[(s)^2\right]}{2\sqrt{E\left[(r)^2\right]}\ \sqrt{E\left[(s)^2\right]}}$$

$$\rho_{rq}(o) = \frac{E\left[(r+q)^2\right] - E\left[(r)^2\right] - E\left[(q)^2\right]}{2\sqrt{E\left[(r)^2\right]}\sqrt{E\left[(q)^2\right]}} ,$$

(see Appendix II) where $E\left[(r^2)\right]$ is the mean square value of r (= the Expected value of r^2). The phase shift, ψ, is then given by

$$\psi = \arctan\left[\rho_{rq}(o) / \rho_{rs}(o)\right] .$$

In the cases where pure sinusoids were used similar techniques were employed. However, the quadrature components of these stimuli were not recorded, and a method of generating them had to be employed. Simple integration of a sinusoid will, of course, provide the 90° phase shift needed, but there are practical reasons why this may be difficult or impossible to do. Chief among these is the fact that any DC voltage component present in the signal to be integrated will be continuously added and will eventually "block" the integrator. The use of approximate integration (1/Ts + 1), in which the DC component is fed-back to cancel itself, eliminates this problem. However, this process does not yield a true quadrature component, but an appropriate mathematical correction can be applied to the phase measurements to account for this (Funke, 1963).

An IBM 1401 computer was used to calculate the correlation coefficients from the RMS values and to calculate the phase shift from these coefficients.

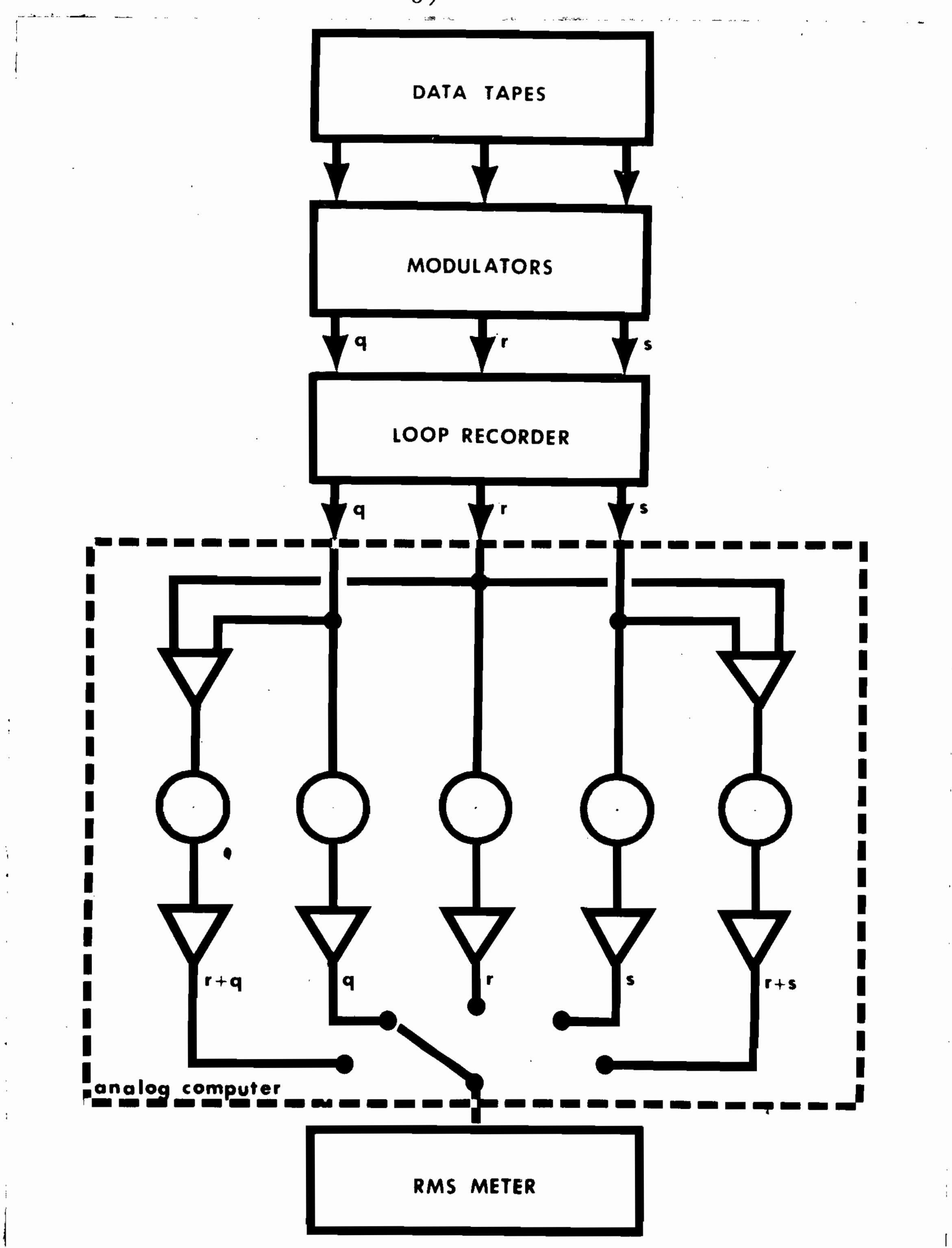


FIGURE 7

The correlation coefficients needed to give phase information were obtained from RMS measurements of the recorded signals. These were re-recorded on a loop recorder, played back at increased speed, and then appropriately added on an analog computer using operational amplifiers (   ). Adjustment of the potentiometers (   ) permitted full-scale meter deflections, the amplitude of the signals then being proportional to the potentiometer setting.

V. RESULTS

1. Stimuli

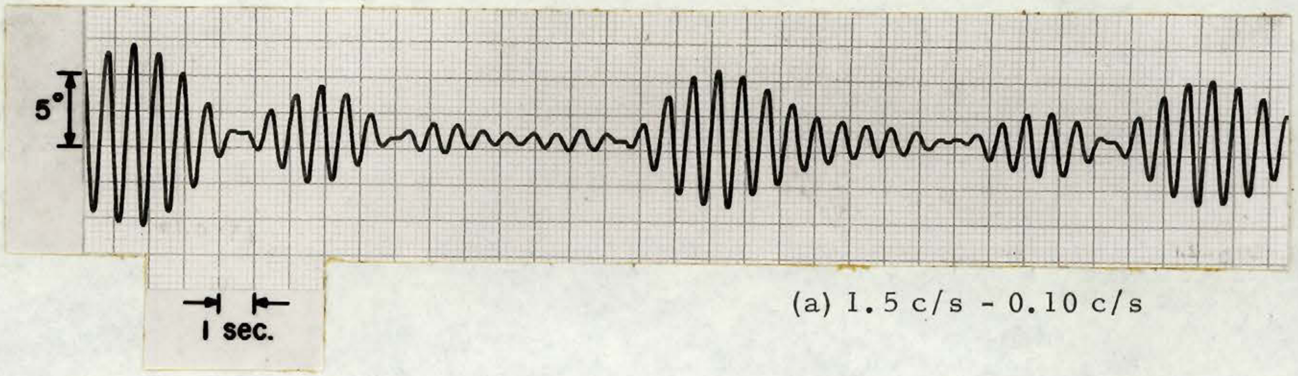
Figure 8 contains a representative sample of the stimuli produced by the technique outlined in the previous section. The gradation of predictability is clearly evident; the stimuli vary in appearance from an amplitude modulated sinusoid (Fig. 8a) that is highly predictable to a signal that seems to be completely random and thus unpredictable (Fig. 8c).

Because of the possible amplitude dependence of the response, in producing these stimuli an effort was made to maintain the RMS values of the signals constant. RMS measurements of the stimuli during analysis yielded the values seen in Table 2. The average RMS value of the stimuli, excluding the single sinusoids, is $6.29^\circ \pm 1.0^\circ$ (mean ± twice the standard error of the mean). This apread is sufficiently small and randomly distributed to be acceptable.

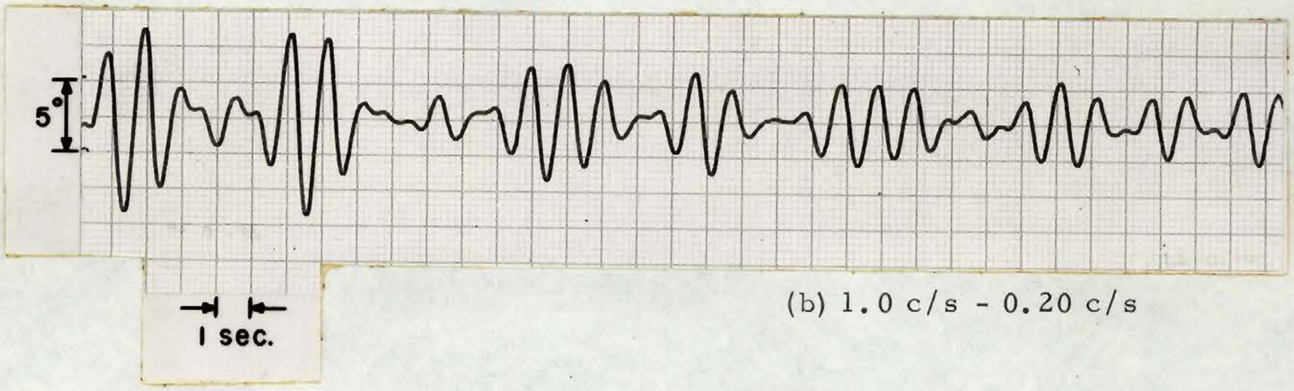
Unfortunately, the single sinusoids used to provide the predictable stimuli were appreciably larger than these unpredictable stimuli; the average RMS value for the sinusoids alone is $10.8^\circ \pm 0.4^\circ$ (the relative smallness of the variability here reflects the greater ease in controlling the output of the oscillator used to provide the sinusoids).

2. Evaluation of the Analytic Techniques

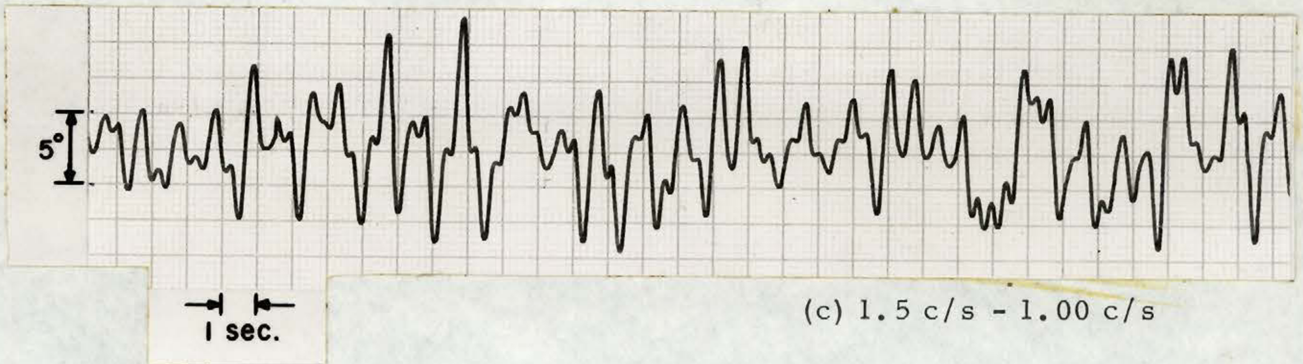
To test the accuracy of the technique for obtaining phase measurements with the stimuli used, a known second-order system was "patched" on an analog computer and samples of the stimuli were used to determine the response of this system. The expected theoretical



(a) 1.5 c/s - 0.10 c/s



(b) 1.0 c/s - 0.20 c/s



(c) 1.5 c/s - 1.00 c/s

FIGURE 8

A graded series of unpredictable stimuli are presented above. Each stimulus is specified by its center frequency and its bandwidth. The increasing unpredictability with increasing bandwidth is quite evident.

	FREQUENCY (C/S)			
BANDWIDTH (C/S)	0.3	0.7	1.0	1.5
0.00	11.14	11.35	11.12	9.65
0.05	5.47	6.94	12.98	4.97
0.10	6.42	6.56	3.80	9.33
0.20	6.39	3.55	5.41	3.39
0.50	5.97	6.45	4.78	5.93
1.00	8.54	7.98	6.38	4.51

(degrees)

Mean of sinusoids = 10.82 ± 0.24
Mean of "unpredictable" stimuli = 6.29 ± 1.00

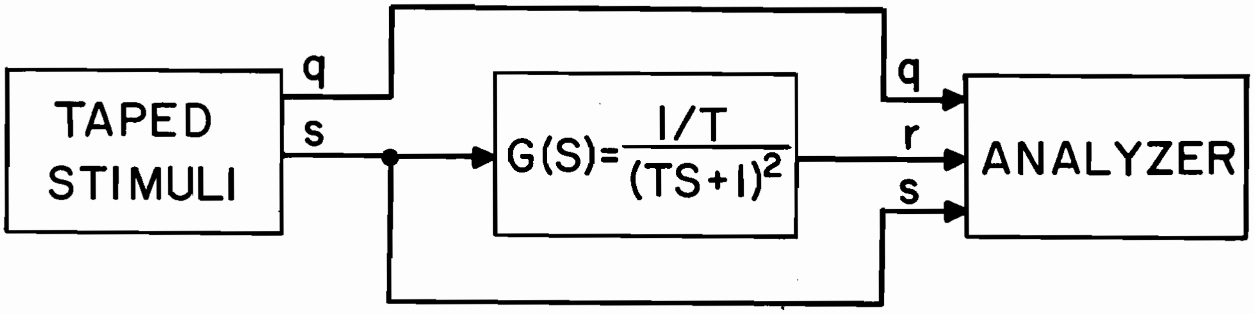
TABLE 2

The RMS values of the stimuli were determined during the data analysis procedure and converted into degrees. The values obtained for the sinusoids correspond to peak-to-peak deflections of approximately 30°, representing full scale deflections. If eye movements of greater angular deflection than this are used the linear relationship between angle of deflection and EOG potential detected is no longer valid.

response was then calculated from the transfer function of the system and compared with the experimentally determined response. These figures can be seen in Table 3. The experimentally determined values are consistently low, and the error is approximately 13%.

The computer used was only accurate to ± 5%, but this will contribute errors in both directions. Therefore, the systematic error seen must arise elsewhere. The most probable source of this error is the analytic technique itself. Implicit in the method is the assumption that the response of the system to the center frequency of the stimulus can be obtained by linearly averaging the the response over the entire bandwidth presented. This, however, is not valid since a logarithmetic weighting should be given to each contribution to the average. Thus, it can be shown that the results obtained with this technique will be consistently too low, and the wider the bandwidth the greater the error. An examination of Table 3 shows that this is actually the case.

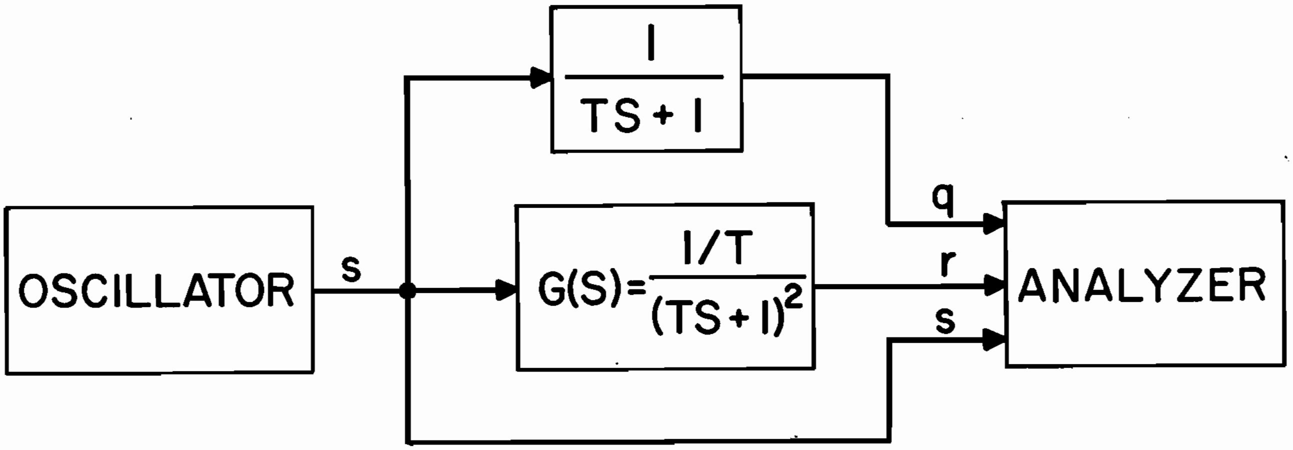
A test of the phase measuring technique using approximate integration was also performed. Again, a second-order system was "patched" on the computer and its response obtained using sinusoidal stimuli and an approximate integrator to provide the quadrature of the stimuli. A comparison of the experimentally determined responses and the calculated responses shows a close agreement, deviations averaging less than 6%. It should be noted that in this case the direction of the error is not consistent, indicating that this error probably arises mainly in the computer. These figures can be seen in Table 4.



FREQ-BNDW (C/S)		PHASE(EXP) (DEG)	PHASE(CAL) (DEG)
0.3	0.05	-51.33	-61.98
0.7	0.05	-96.62	-108.93
1.0	0.05	-110.40	-126.87
2.0	0.05	-134.72	-151.93
0.3	0.20	-41.68	-53.13
0.7	0.20	-92.00	-108.93
1.0	0.20	-109.85	-126.87
2.0	0.20	-132.53	-151.93
0.3	0.50	-30.96	-77.40
0.7	0.50	-115.90	-108.93
1.0	0.50	-100.50	-126.87
2.0	0.50	-129.57	-151.93

TABLE 3

As a test of the phase measuring technique the response of a known second-order system was experimentally determined and compared with the phase shift calculated from the transfer function of the system.



FREQ (C/S)	PHASE(EXP) (DEG)	PHASE(CAL) (DEG)
0.1	-27.80	-22.60
0.3	-64.00	-61.98
0.5	-88.40	-90.00
1.0	-123.50	-126.87
2.0	-154.80	-151.93

TABLE 4

The technique of using approximate integration to provide the quadrature component of the stimulus was also tested. Here again a system with a known transfer function was utilized and the measured response compared with the calculated response.

3. Variation of Response with Predictability

The average phase shift of the ten subjects can be seen in Figure 9, with phase shift plotted against the center frequency of each stimulus (note that frequency is plotted on a logarithmetic scale, a standard practice in systems analysis). The six curves represent the responses to the six degrees of predictability employed.

At the low frequency employed, 0.3 c/s, all six points cluster together, and there is apparently no variation of response with predictability. The two intermediate frequencies, 0.7 and 1.0 c/s, both show a progressive increase of phase shift as predictability decreases. At the highest frequency, 1.5 c/s, there appears to be no regular increase of phase shift with increasing unpredictability.

The relationship between phase shift and predictability can better be seen in Figure 10 where phase shift is plotted as a function of the bandwidth of the stimulus. Here it can be clearly seen that even at 1.5 c/s there is a regular increase of phase shift as predictability decreases if the first two "paradoxical" points are ignored (see Discussion).

The 24 mean phase shifts along with twice their standard error have been tabulated and these values can be seen in Table 5. The variability at each point is fairly large, and overlaps between adjacent points occur. This means that it is possible that the ordered sequence of phase shifts obtained is a chance occurrence. Thus it is necessary to test the statistical significance of the results.

The Friedman two-way analysis of variance by ranks (Siegel, 1956) was used to test whether the means at any one frequency

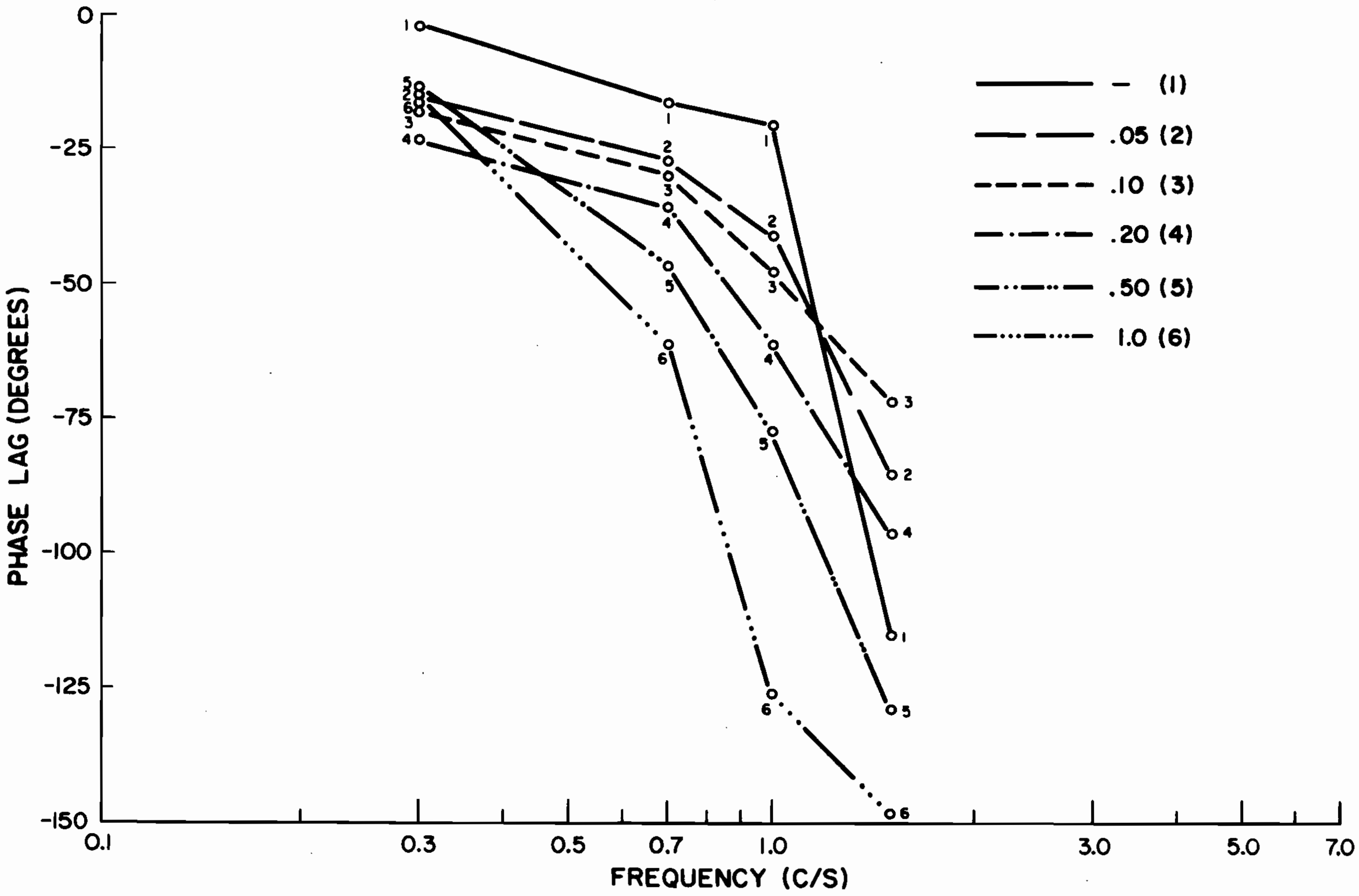


FIGURE 9

The mean phase shift of 10 subjects is plotted as a function of frequency for each of the 24 stimuli used. The standard error of the mean at each point can be seen in Table 5. The progressive increase of phase shift with increasing unpredictability can be clearly seen at 0.7 and 1.0 c/s.

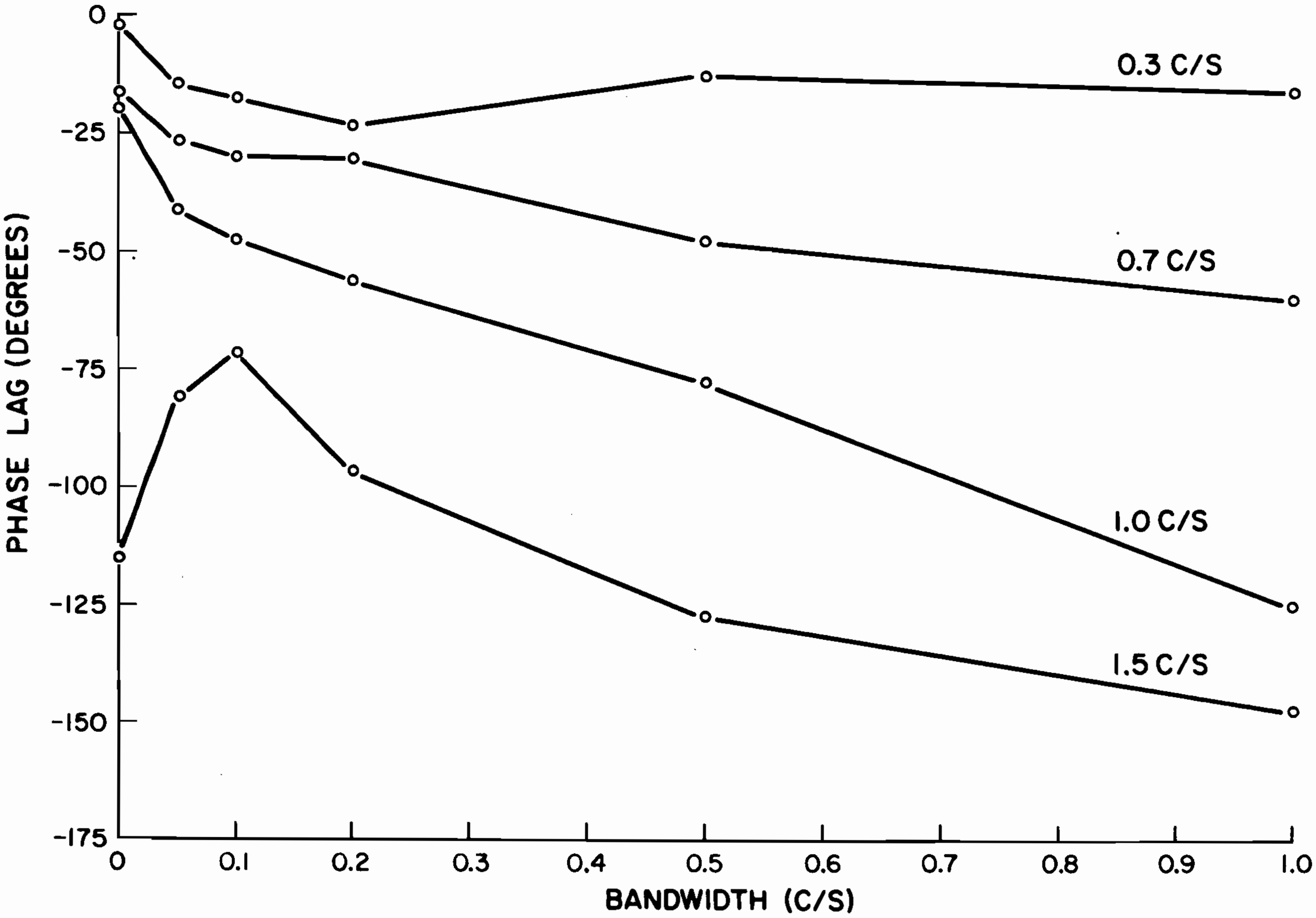


FIGURE 10

The data from Figure 9 has been re-plotted to make more evident the increase in phase shift with increasing unpredictability. This can now be seen even at 1.5 c/s if the two initial "paradoxical" points are ignored.

	FREQUENCY (C/S)			
BANDWIDTH (C/S)	0.3	0.7	1.0	1.5
0.00	-1.6 ± 9.0	-16.8 ± 15.0	-20.6 ± 22.4	-114.4 ± 32.8
0.05	-15.3 ± 6.0	-26.9 ± 15.0	-41.4 ± 8.8	- 85.7 ± 24.8
0.10	-17.4 ± 12.0	-29.2 ± 10.2	-47.0 ± 6.0	-71.7 ± 28.4
0.20	-23.6 ± 7.6	-30.7 ± 14.2	-61.4 ± 21.8	-96.2 ± 25.8
0.50	-13.8 ± 5.6	-47.2 ± 5.6	-77.4 ± 22.0	-128.3 ± 27.0
1.00	-16.4 ± 4.6	-60.4 ± 27.2	-126.0 ± 31.2	-148.5 ± 22.8

(degrees)

TABLE 5

The mean phase shift and twice the standard error of the mean, in degrees, is given for the 24 stimuli presented to the subjects. The values given can be seen plotted in Figure 9.

were actually drawn from separate populations, and a non-parametric analysis of trends (Fergeson, 1963) was used to examine the significance of the order of the points at any frequency.

At 0.3 c/s there is, of course, no significant difference between the phase shifts seen with different stimuli.

However, at 0.7 and 1.0 c/s both the differences between the means and the order of the means is significant at the 0.001 confidence level.

At 1.5 c/s, if the two "paradoxical" points are ignored, the differences of the means are significant at the 0.01 level and the order of the points is significant at the 0.001 level.

There is thus no doubt that the predictor operates in a continuous fashion dependent on the predictability of the input to the system; the family of curves expected to result from such a mode of operation has in fact been obtained.

It is interesting to note that the average variability of the means is a function of frequency, the higher the frequency the greater the variability. Figure 11 is a plot of the average standard error of the mean at each of the four frequencies and the linear relationship can be seen from the closeness of fit of the points to the calculated regression line.

4. Learning Capabilities of the System

The results of the four learning experiments can be seen in Table 6. No evidence of improved performance over repeated trials can be seen. In three of the experiments the intrasubject variability is of the same order of magnitude as the intersubject

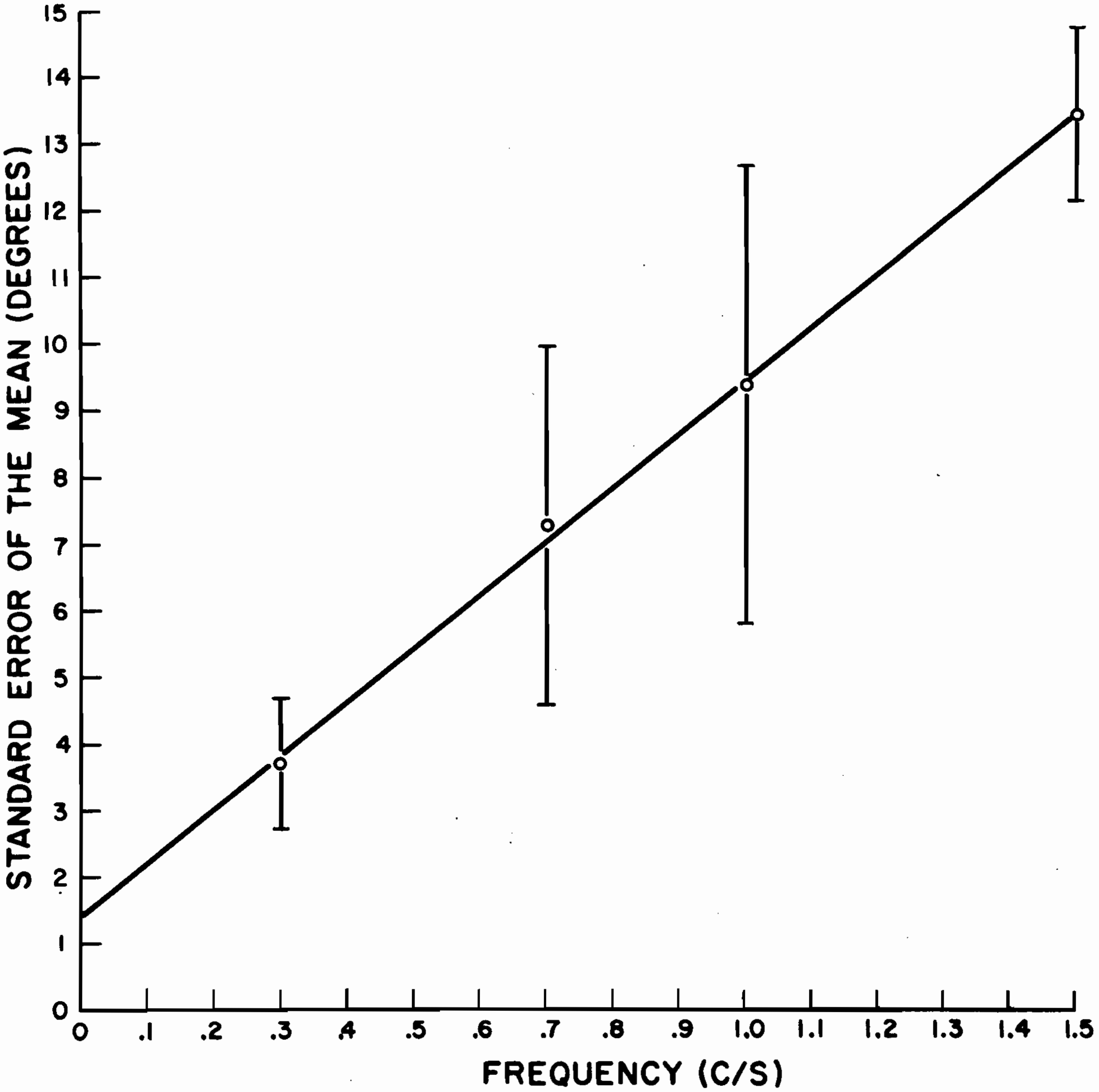


FIGURE 11

The average standard error of the mean (of the six mean phase shifts at any one frequency) is plotted as a function of frequency; the brackets indicate ± twice the standard error of these means. It can be seen that intersubject variability of response is a definite function of frequency. This is probably due to the heterogeneous response patterns being sampled at the high frequencies.

SUBJECT	TRIAL	FREQ (C/S)	BNDW	PHASE SHIFT (DEGREES)
P.P.	1	0.3	0.10	-35.00
	1	0.7	0.20	-11.44
	1	1.0	0.50	-66.41
	2	0.3	0.10	-27.69
	2	0.7	0.20	-92.35
	2	1.0	0.50	-33.16
	3	0.3	0.10	-27.96
	3	0.7	0.20	-32.59
	3	1.0	0.50	-93.89
L.C.	1	0.3	0.10	-11.37
	2	0.3	0.10	+ 9.71
	3	0.3	0.10	-11.45
	1	0.7	0.20	-17.53
	2	0.7	0.20	-32.96
	3	0.7	0.20	-35.36
	1	1.0	0.50	-64.15
	2	1.0	0.50	-46.05
	3	1.0	0.50	-83.72
J.W.	1	0.3	0.10	+2.09
	2	0.3	0.10	+0.47
	3	0.3	0.10	+6.59
	4	0.3	0.10	-10.01
	1	0.7	0.20	-43.85
	2	0.7	0.20	-39.55
	3	0.7	0.20	-34.76
	4	0.7	0.20	-32.60
	1	1.0	0.50	-60.28
	2	1.0	0.50	-51.04
	3	1.0	0.50	-56.18
	4	1.0	0.50	-46.17
W.B.	1	0.3	0.10	-3.55
	2	0.3	0.10	-3.26
	3	0.3	0.10	-11.60
	4	0.3	0.10	-10.86
	1	0.7	0.20	-47.64
	2	0.7	0.20	-49.11
	3	0.7	0.20	-42.50
	4	0.7	0.20	-47.00
	1	1.0	0.50	-58.68
	2	1.0	0.50	-59.65
	3	1.0	0.50	-63.41
	4	1.0	0.50	-60.30

TABLE 6

The phase shifts of four subjects to a series of stimuli of graded predictability reveal no evidence of learning with repeated exposure to the same stimulus; no progressive decrease in phase shift is to be seen with repeated exposure. The values seen here agree closely with those seen in Table 5.

variability seen in the predictability-response experiments, and the average response to any stimulus agrees closely with the results seen in Figure 9. In Table 7 the responses obtained here can be compared with the responses from the first experiment. It is evident that lack of learning is not due to abnormal responses in this set of experiments.

Subjective evaluation of the initial segments of each trial revealed no noticeable reduction of transient response time with repeated testing.

There thus seems to be no evidence for any ability of the visual tracking system to learn a nonperiodic stimulus, regardless of its degree of predictability.

STIMULUS (C/S)	SUBJECT	MEAN PHASE SHIFT (ALL TRIALS)	MEAN PHASE SHIFT (ALL SUBJECTS)	MEAN PHASE SHIFT (FROM TABLE 5)
0.3 0.10	P.P.	-30.21	-10.54	-17.4 ± 12.0
	L.C.	-4.37		
	J.W.	-0.28		
	W.B.	-7.32		
0.7 0.20	P.P.	-45.46	-39.51	-30.7 ± 14.2
	L.C.	-28.61		
	J.W.	-37.69		
	W.B.	-46.56		
1.0 0.50	P.P.	-64.48	-60.84	-77.4 ± 22.0
	L.C.	-64.97		
	J.W.	-53.43		
	W.B.	-60.51		

TABLE 7

The responses obtained in the learning experiments (in degrees phase shift) can be compared with the responses obtained in the first experiment. It is evident that lack of learning is not due to abnormal responses here; the means for the three stimuli used fall within the range of values obtained in the first set of experiments.

VI. DISCUSSION

The resemblance between physiological control systems and the engineer's concept of a servo-control system was pointed out in the Introduction. Following this lead, the present study has attempted to apply some of the methodology of servo-system analysis to an investigation of the human visual tracking system. Such an approach can contribute to the realization of three goals. First, it can assist in the identification of parameters relevant to the dynamic behavior of the system. Second, means are provided for the analysis and quantification of the system's dynamic behavior. Finally, systems analysis presents a fruitful source of ideas for hypothesis formulation about the functional nature of the system under study. It is convenient, therefore, to discuss the results obtained with these points of view.

The important stimulus parameters for the visual tracking system are the amplitude, frequency, and predictability of the input, and the response parameters of interest are the amplitude-ratio (gain) and phase shift of the response. In the present investigation variations in stimulus amplitude have been minimized, and the study has been confined to the investigation of the effect of frequency and predictability of target movement (the stimulus) on the response of the system. Technical limitations of the response measuring technique made it impractical to obtain gain measurements, and phase measurements had to be taken as a measure of the system's response.

The results, summarized in Figures 9 and 10, clearly indicate that the functional effectiveness of the response, defined in terms of phase shift, is systematically dependent on the predictability of the stimulus; the more predictable the target movement the better the response (the smaller the phase shift). This dependence is seen as an increasing phase shift as the bandwidth of the random noise describing the stimulus increases. This is particularly obvious at the two middle frequencies studied, 0.7 and 1.0 c/s, where the observed trends are statistically significant.

At the lowest frequency studied, 0.3 c/s, the response appears to be independent of bandwidth, probably because of the great ease, and therefore accuracy, of visual tracking at this and lower frequencies.

The behavior of the system at the highest frequency employed, 1.5 c/s, is, however, not immediately clear. Here a decrease in phase shift is initially seen as the bandwidth increases, the minimum phase lag occurring at a bandwidth of 0.1 c/s. As the bandwidth of the stimuli increases past this point an increase in phase shift is finally seen that is statistically significant. A possible explanation for this phenomenon is that the narrow bandwidth signals contain appreciable portions of low amplitude excursions, and these portions are considerably easier to track than are the high amplitude portions (the question of amplitude dependence of the system will be discussed below). Subjectively such signals have the appearance of amplitude modulated sinusoids and thus seem to be easy to follow.

On further examination of the results of the first experiment it emerged that a definite relationship between frequency and intersubject variability of response is evident. The higher the frequency the greater the standard error of the mean at that frequency. This relationship can be seen in Figure 11. A possible explanation of this is that the location of the break-frequency (the point where the system response begins to fall off steeply) varies among subjects. Then at high frequencies the averaged response will show a large spread due to the heterogeneous response patterns being sampled.

At this point two limitations of the experimental program should be noted. First, as already mentioned, technical problems made it feasible to obtain only phase information, although to completely characterize the system response both phase and gain information is required. Second, responses at only four frequencies were examined, and although these extend over the significant range, they do not provide complete coverage.

When comparing the results obtained here with those obtained by other workers, attention must be confined, of course, to the two extremes of stimulus predictability, since stimuli of graded predictability have not previously been used in studying the responses of the visual tracking system. Moreover, even with this restriction in mind, direct comparison is difficult, since no two sets of experiments have been carried out under the same conditions. Perhaps the most important source of variation here is the choice of angular amplitude of target movement subtended at the eye; since the response is undoubtedly amplitude dependent, this variability will lead to variations in the quantitative measure of system response. Furthermore, the methods of stimulus generation have differed widely, and no previous work has been done with unpredictable stimuli of the type utilized here.

However, despite these difficulties there is good qualitative agreement between the shapes of the extreme curves obtained here and the corresponding curves obtained by Stark etal (1962) and Dallos and Jones (1963). Quantitative comparison of the actual phase shift obtained at any given frequency shows considerable variation as illustrated in Figure 12. The responses to a completely unpredictable stimulus agree fairly closely, but the present results tend to show a greater phase shift at the higher frequencies. This discrepancy is even more marked for the predictable responses; not only are greater phase lags seen but the response falls off much faster with increasing frequency.

The main contribution to these relatively wide discrepancies probably arises from a dependence of the response on the amplitude of the stimulus. At any frequency, the angular velocity of target motion increases directly with amplitude. However, the maximum angular velocity at which accurate following is possible is quite low; Rashbass (1959) found error-free tracking possible only up to 10°/sec, and Westheimer (1954b) reported 25-30°/sec as the limit.

For a target moving sinusoidally, the angular position, θ, is given by:

$$\theta = A \sin\omega t$$

where A = angular amplitude

ω = frequency of sinusoid (radians/sec)

t = time.

Then, the angular velocity, $\dot{\theta}$, can be obtained by differentiating with

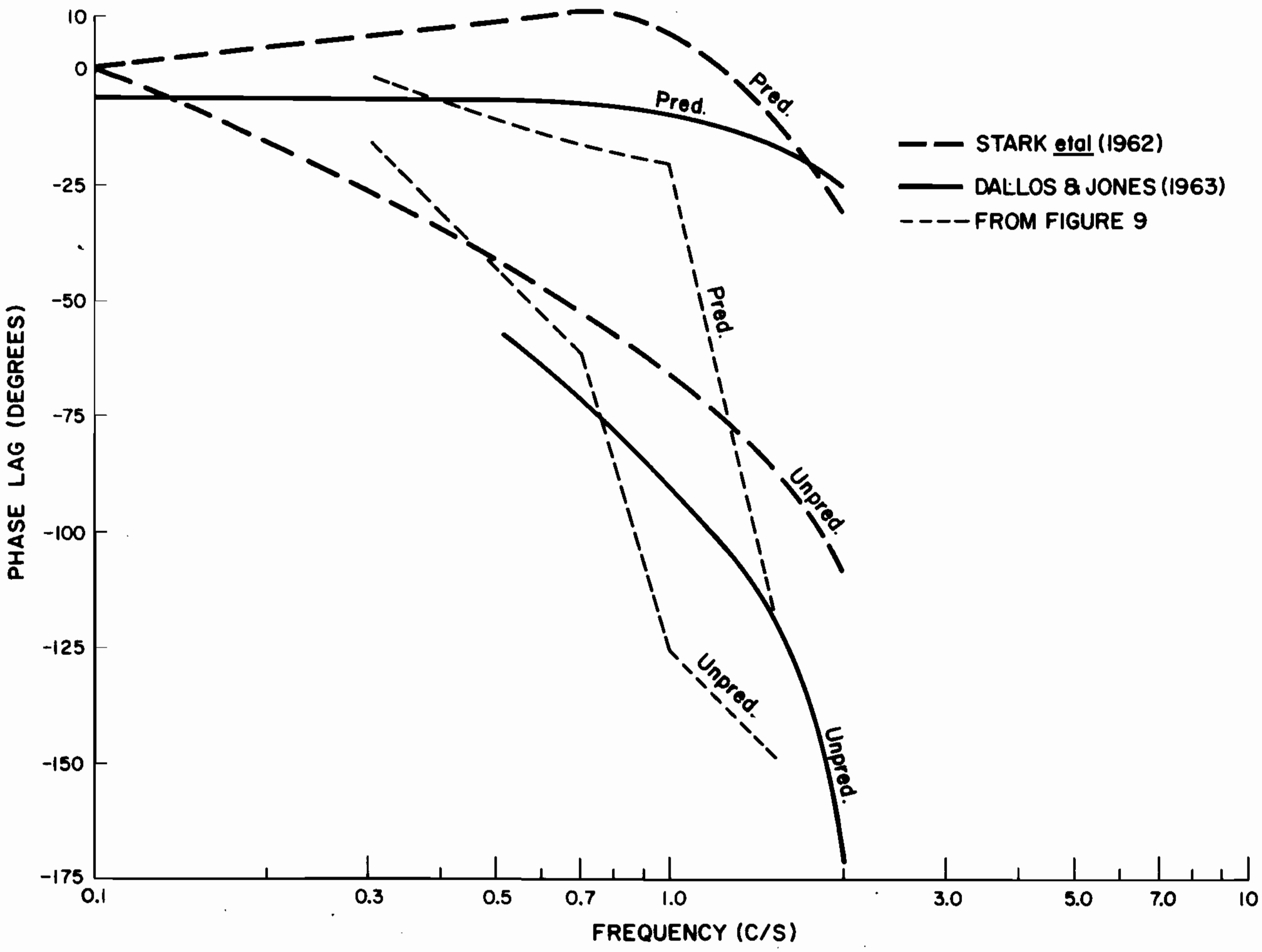


FIGURE 12

The phase responses obtained by Stark etal (1962) and Dallos and Jones (1963) can be compared with the results obtained in the present study. Qualitatively, the agreement in the shape of the curves is relatively close. The major quantitative disagreement lies in the increased phase shift and rate of fall-off of response seen with predictable, high frequency stimuli.

respect to time giving:

$$\dot{\theta} = A\omega \cos\omega t.$$

The maximum value of $\dot{\theta}$ will occur when $\cos\omega t = 1$ and hence:

$$\dot{\theta}_{max} = A\omega$$

$$= A2\pi f$$

where f = cycles/sec.

In the present experiments $A = 15^{\circ}$ and hence $\dot{\theta}_{max} = 94^{\circ}/\text{sec}$, whereas in the experiments of Stark etal (1962) $A = 5^{\circ}$ and $\dot{\theta}_{max} = 31^{\circ}/\text{sec}$. Thus at any given frequency a better response, i.e. smaller phase shift, would be expected with the stimulus of smaller amplitude, thus explaining the relatively large phase shifts seen here when compared to the results of Stark etal (1962) and Dallos and Jones (1963).

In summary, it seems reasonable to conclude from the results presented in Figures 9 and 10 that the main findings of these experiments is a systematic dependence of the capability of following a moving visual target upon the predictability of that movement. The functional interpretation of this general conclusion will be discussed later.

Before proceeding further, however, the second problem studied must be discussed. The question was asked whether the learning capabilities of the visual tracking system are dependent on the predictability of the input. Westheimer (1954b) showed that although learning occurred with periodic inputs, no learning occurred with random appearing stimuli. However, in the present investigation an attempt was made to determine if stimuli of graded predictability could elicit learning.

The results are unequivocal. Repeated exposure to stimuli of three different degrees of predictability produced no significant improvement of response on successive trials. In fact, the question can be asked whether the responses to periodic inputs seen by Westheimer (1954b) and Dallos and Jones (1963) can properly be referred to as learning. It seems more likely that they simply observed the transient response of the system to periodic stimuli; to call this learning would mean that the transient response seen in all dynamic systems should also be referred to as learning. As used in its accepted psychological sense, the term learning is probably inappropriate here.

Turning now to the functional role of the improvement in response as predictability increases, presumably the important effect of reduced phase shift is to maintain relatively good visual acuity at frequencies where the amplitude of eye movement has fallen below the amplitude of target movement, i.e. where the amplitude ratio has fallen. So long as the phase shift is negligible a stationary retinal image must occur at the velocity nodes of movement. Melvill Jones and Drazin (1961) showed that with sinusoidal target motion, high visual acuity was maintained until the amplitude ratio (eye movement/ target movement) had fallen to 0.5, and it was presumed that this was due to the surprisingly smaller phase shift that occurred. It seems that what might be called the predictor acts in some measure to compensate for the relatively low frequency cut-off exhibited by the system operating in the unpredictable mode.

In real life this capability must be a valuable one since, as shown by Begbie etal (1963), the human body possesses a considerable degree of mechanical tuning so that the complex body movements arising from running or riding in a moving vehicle result in simpler, more periodic and therefore more predictable, movements of the head. It is true that the vestibul-ocular reflex contributes considerably to retinal image stabilization during disturbing head movements. But the visual tracking system must ultimately be used to establish accurate visual fixation, and presumably this is considerably enhanced by the improved response associated with predictable stimuli. No doubt the actual relative movement of target and head encountered normally will exhibit an intermediate degree of predictability rather than either of the extremes.

It might be hoped that if the spectral characteristics of a given target motion are known, it would be possible to make an objective assessment of how well the target would be seen by a human observer from data of the kind presented in these results. This raises the question, in what areas might such information in fact be applied. This question can probably be answered under the three headings of human engineering, personnel selection, and clinical investigation.

Human engineering relates specifically to the matching of man-made machines to the human operator. Certainly one field of concern here is the maintenance of image stabilization, and hence visual acuity, in the face of unfavorable environmental conditions. For example, high speed military aircraft flhing at low altitudes may be subject to violent vibration, and it is important to know how well the pilot can be expected to monitor his instruments and the external environment under these conditions. Similar problems are faced by personnel in armoured vehicles, high speed water craft and even space craft during the critical stages of launch and re-entry. Perhaps more specifically relevant are the many tasks requiring visual monitoring of an indicator, such as occurs in radar control, submarine search, and the presentation of director type information in the aircraft cockpit. The results presented here indicate that in all cases the ability to perform the required task will be dependent, amongst other things, on the predictability of the movement to be followed.

In the light of the wide variability between subjects seen in Table 5, it seems that much could be gained by appropriate selection of personnel for tasks involving visual tracking. It would not be difficult to evolve a routine test employing the methods described here to determine appropriate measures of this aptitude.

Finally, the clinician has found that a study of normal and abnormal eye movements offers valuable diagnostic information, and specific abnormalities may be associated with disturbed visual tracking capabilities. Jung and Kornhuber (1964) regularly include a simple tracking test in their examination of patients with neurologic dificulties. And Shackel etal (1963) have investigated the performance of cerebral palsied children on saccadic and smooth pursuit tasks, and find significantly poorer performance than normal. It may be that responses to more difficult tasks such as tracking of unpredictable stimuli will better serve to reveal neurologic abnormalities.

The question of the nature of the predicting mechanism is of course a speculative one. Although the visual tracking system possesses many reflex-like features it seems unlikely that prediction is a purely reflex process. The dependence of response on stimulus predictability implies a rather sophisticated degree of data processing, and even a complex reflex mechanism seems to be an unlikely candidate for explaining the functioning of this component. Rather, the intervention of some higher central nervous system activity seems called for.

A number of processes may be involved here. A short term memory mechanism of the reverberating activity type (see John, 1962) could presumably play some role here.

A complementary process that might function at a lower level than is usually associated with memory might involve an oscillating neural network driven by a periodic input. Such a mechanism could also explain habituation to periodic vestibular stimulation; the central oscillatory activity could in some manner cancel the sensory input and thus prevent continuous response. Removal of the sensory input would then leave the central oscillatory state active for some period of time, and its unopposed activity might account for the vestibular manifestations observed after cessation of long term rotation (Guedry & Graybiel, 1962). In the visual tracking system this kind of mehcnaism would permit reduction of the phase shift between oculomotor response and target motion below the range of values to be expected from a straight-through system.

VII. SUMMARY

1. In an attempt to determine whether there exists a general relationship between stimulus predictability and visual tracking system responses, a technique for generating tracking stimuli of various degrees of predictability was developed. The stimuli consisted of narrow but variable bandwidths of Gaussian random noise centered about the desired test frequency.

2. An analog technique for determing the phase shift of a system using such unpredictable stimuli was developed and found to be sufficiently accurate for the experiments to be carried out.

3. The stimuli were presented to 10 subjects and their tracking eye movements were recorded electro-oculographically. Also recorded was the stimulus and its quadrature component.

4. The results reveal that the effectiveness of the response, as measured by the phase shift, is systematically dependent on the predictability of the stimulus, as measured by the bandwidth of the random noise. The intersubject variability increased with the center frequency of the stimulus.

5. Repeated exposure to a graded series of stimuli did not result in any improvement of tracking performance. Learning did not occur.

6. Functional interpretation of the results are discussed and possible applications of the methodology employed here are outlined.

7. It is suggested that the mechanism of prediction may be associated with the generation of some form of central oscillatory state in the nervous system.

APPENDIX I.

Stimulus Generation

A fourth-order Butterworth filter (Fig. 13), "patched" on an analog computer, was used to filter the output of a Pace low frequency Gaussian noise generator. Five bandwidths of noise ranging from 0.05 c/s to 1.00 c/s were produced in this manner.

An oscillator producing both the sine and cosine functions was also "patched" on the computer; it is seen in Figure 14.

Suppressed carrier modulation consists of multiplying the signal to be modulated by a second signal, f(t). In the present case narrow-band noise is the signal to be modulated, but for ease of mathematical manipulation consider the signal to be modulated as $A\sin\phi t$. The modulating signal will also be a sinusoid, either $B\sin\omega t$ or $B\cos\omega t$.

Then, the signal produced, $f_o(t)$, is given by:

$$f_o(t) = AB\sin\omega t\sin\phi t.$$

But $\sin\omega t\sin\phi t$ is one term of the expansion for the cosine of the sum or the difference of two angles,

$$\cos(\omega t + \phi t) = \cos\omega t\cos\phi t - \sin\omega t\sin\phi t.$$

$$\cos(\omega t - \phi t) = \cos\omega t\cos\phi t + \sin\omega t\sin\phi t.$$

Therefore,

$$2\ \sin\omega t\sin\ t = \left[\cos(\omega t - \phi t) - \cos(\omega t + \phi t)\right].$$

This then gives:

$$f_o(t) = \frac{AB}{2}\left[\cos(\omega - \phi)t - \cos(\omega + \phi)t\right].$$

The modulated signal produced thus consists of two components, one at a frequency equal to the sum of the input frequencies, the other at a frequency equal to the difference of the input frequencies. This can be seen in Figure 15.

In the case where narrow band noise is being multiplied by a single sinusoid the resulting signal consists of the sums and differences of the frequencies present in the noise and the frequency of the modulating sinusoid. The effect of this is to move the band of noise along the frequency spectrum so that it is now centered about the modulating frequency.

Using five different bandwidths of noise and four modulating frequencies the entire set of stimuli used in these experiments was produced.

APPENDIX II.

Phase Measurements Using Cross Correlation Techniques

Consider a system, G(s), whose phase response is to be determined. With an input to the system, x(t), an output, y(t), will be obtained of the form y(t) = G(s)x(t).

Let x(t) = Asinωt and obtain the quadrature component of x(t), the input phase shifted 90°, by integration (1/s). Figure 16 represents the test situation that results.

Letting "r" represent the response of the system, "s" the input stimulus, and "q" the quadrature of the stimulus, a cross correlation coefficient can be defined by:

$$\rho_{rs}(o) = \frac{1}{t}\int_0^t r\cdot s \, dt.$$

Substituting the values from the test situation described above gives:

$$\rho_{rs}(o) = \frac{1}{\pi/\omega}\int_0^{\pi/\omega} B\sin(\omega t + \phi)\,A\sin\omega t dt$$

$$= \frac{AB\omega}{\pi}\int_0^{\pi/\omega} \sin^2\omega t\cos\phi dt + \frac{AB\omega}{\pi}\int_0^{\pi/\omega} \sin\omega t\cos\omega t\sin\phi dt$$

$$= \frac{AB\omega}{\pi}\cos\phi\left[\frac{t}{2} - \frac{\sin 2\omega t}{4\omega}\right]_0^{\pi/\omega} + \frac{AB\omega}{\pi}\sin\phi\left[\frac{1}{2\omega}\sin^2\omega t\right]_0^{\pi/\omega}$$

$$= \frac{AB\omega}{\pi}\cos\phi\left(\frac{\pi}{2\omega}\right) + 0$$

$$\rho_{rs}(o) = \frac{AB}{2}\cos\phi .$$

Similarly,

$$\rho_{rq}(o) = \frac{1}{t}\int_0^t r\,q\,dt$$

$$= \frac{1}{\pi/\omega}\int_0^{\pi/\omega} B\sin(\omega t + \phi)\,A\cos\omega t\,dt$$

$$= \frac{AB\omega}{\pi}\int_0^{\pi/\omega} \cos^2\omega t\sin\phi\,dt + \frac{AB\omega}{\pi}\int_0^{\pi/\omega} \sin\omega t\cos\omega t\cos\phi\,dt$$

But, it has already been shown that:

$$\int_0^{\pi/\omega} \sin\omega t\cos\omega t\,dt = 0$$

Therefore,

$$\rho_{rq}(o) = \frac{AB\omega}{\pi}\int_0^{\pi/\omega} \cos^2\omega t\sin\phi\,dt$$

$$= \frac{AB\omega}{\pi}\sin\phi\left[\frac{t}{2} + \frac{\sin 2\omega t}{4\omega}\right]_0^{\pi/\omega}$$

$$= \frac{AB\omega}{\pi}\sin\phi\left(\frac{\pi}{2\omega}\right)$$

$$\rho_{rq}(o) = \frac{AB}{2}\sin\phi$$

Dividing the two coefficients gives:

$$\frac{\rho_{rs}(o)}{\rho_{rq}(o)} = \frac{\cos\phi}{\sin\phi}\,.$$

Therefore, the phase shift of the system, ϕ, is given by:

$$\phi = \arctan\left[\rho_{rq}(o) \Big/ \rho_{rs}(o)\right].$$

Correlation Coefficients from RMS Values of Pertinent Signals

Hoel (1954) defines the correlation coefficient of two variables, X and Y, as:

$$r = \frac{\sum xy - n\bar{x}\bar{y}}{\sqrt{\left[\sum x^2 - n\bar{x}^2\right]\left[\sum y^2 - n\bar{y}^2\right]}}.$$

If,

$$\bar{x} = \bar{y} = 0$$

as is the case here, since the output of the noise generator used has a zero average,

$$r = \frac{\sum xy}{\sqrt{\sum x^2}\sqrt{\sum y^2}},$$

Let $E\left[(x^2)\right]$ equal the mean square value of x. Then,

$$E\left[(x^2)\right] = \frac{\sum x^2}{n}$$

$$nE\left[(x^2)\right] = \sum x^2$$

Also,

$$\sum (x+y)^2 - \sum(x^2) - \sum(y^2) = 2\sum xy$$

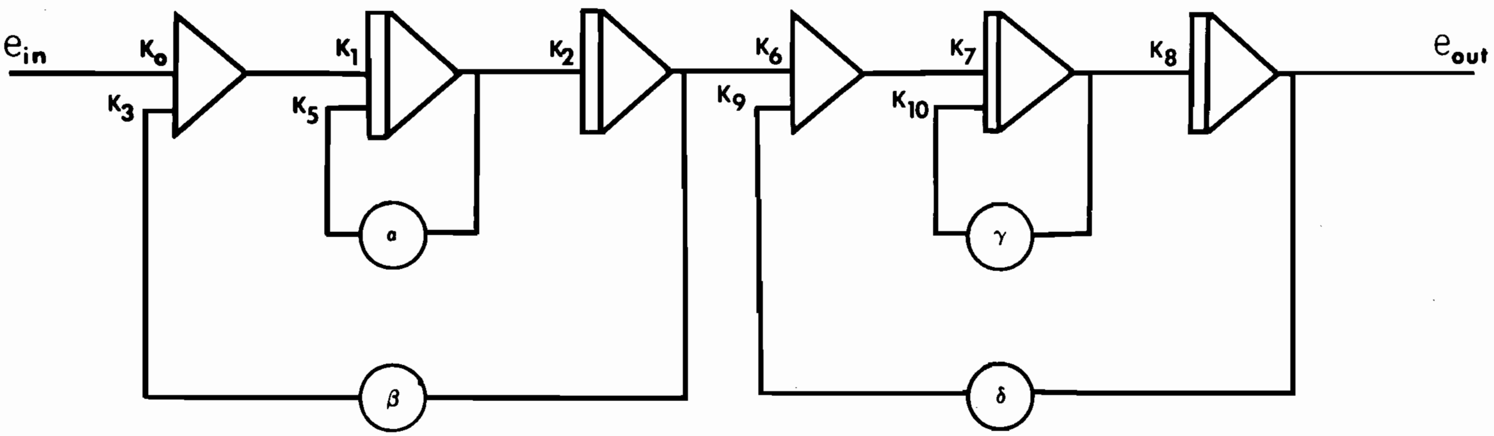
Therefore,

$$r = \frac{\sum(x+y)^2 - \sum(x^2) - \sum(y^2)}{2\sqrt{\sum(x^2)}\sqrt{\sum(y^2)}}$$

$$= \frac{nE\left[(x+y)^2\right] - nE\left[(x^2)\right] - nE\left[(y^2)\right]}{2n\sqrt{E\left[(x^2)\right]}\sqrt{E\left[(y^2)\right]}}$$

This can be rewritten, using the symbols employed on page 67, as:

$$\rho_{rs}(o) = \frac{E\left[(r+s)^2\right] - E\left[(r)^2\right] - E\left[(s)^2\right]}{2\sqrt{E\left[(r)^2\right]}\;E\sqrt{\left[(s)^2\right]}}$$



$$G(s) = 1/(s^2 + 0.765s + 1)(s^2 + 1.848s + 1)$$

FIGURE 13

A fourth-order Butterworth filter was "patched" on an analog computer and used to filter the output of a Gaussian noise generator. Appropriate variations of the parameters of the filter allowed varying bandwidths of noise to be produced.

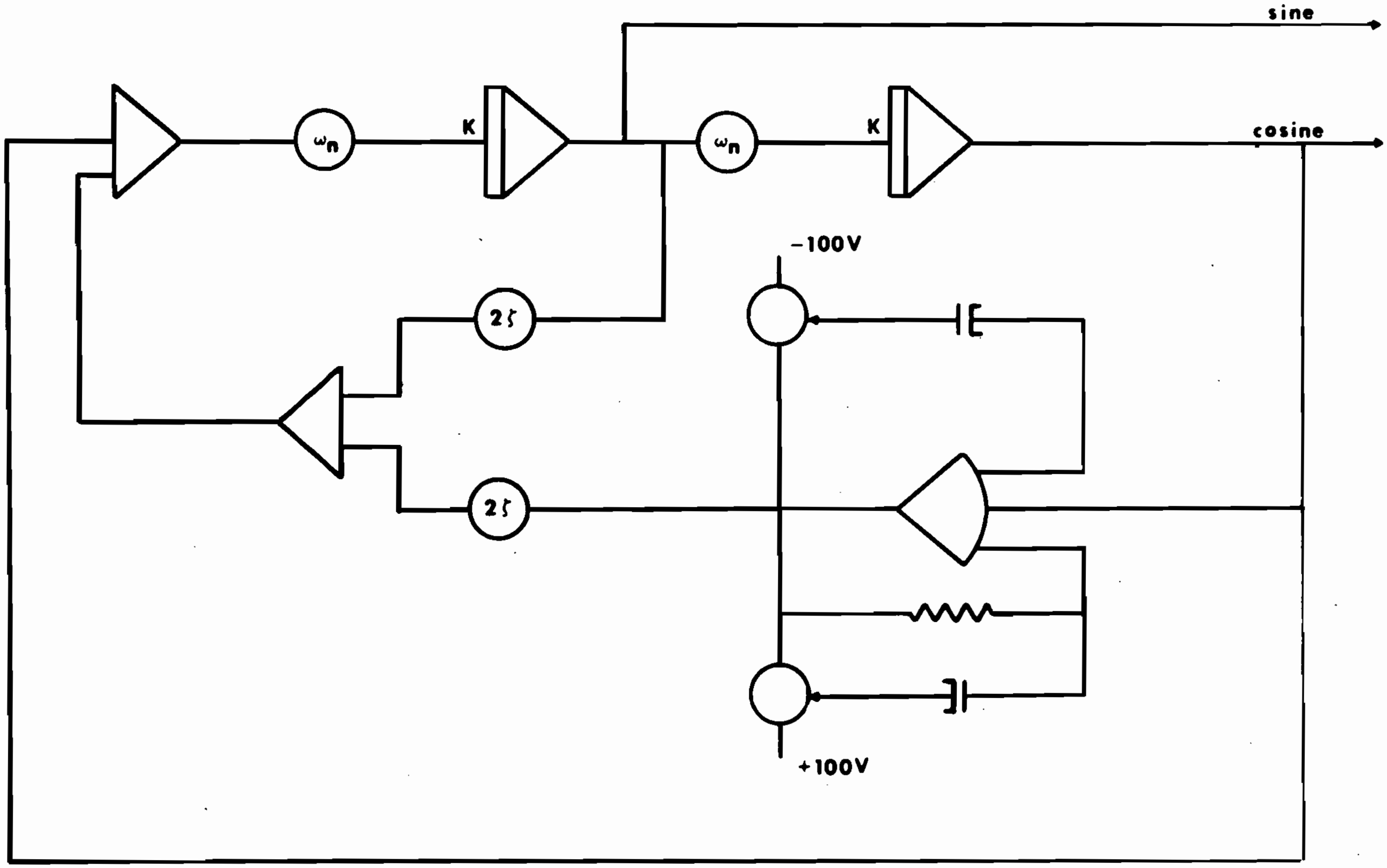


FIGURE 14

The modulating sine and cosine functions were provided by an oscillator "patched" on an analog computer. The amplitude of both functions was held constant at all frequencies.

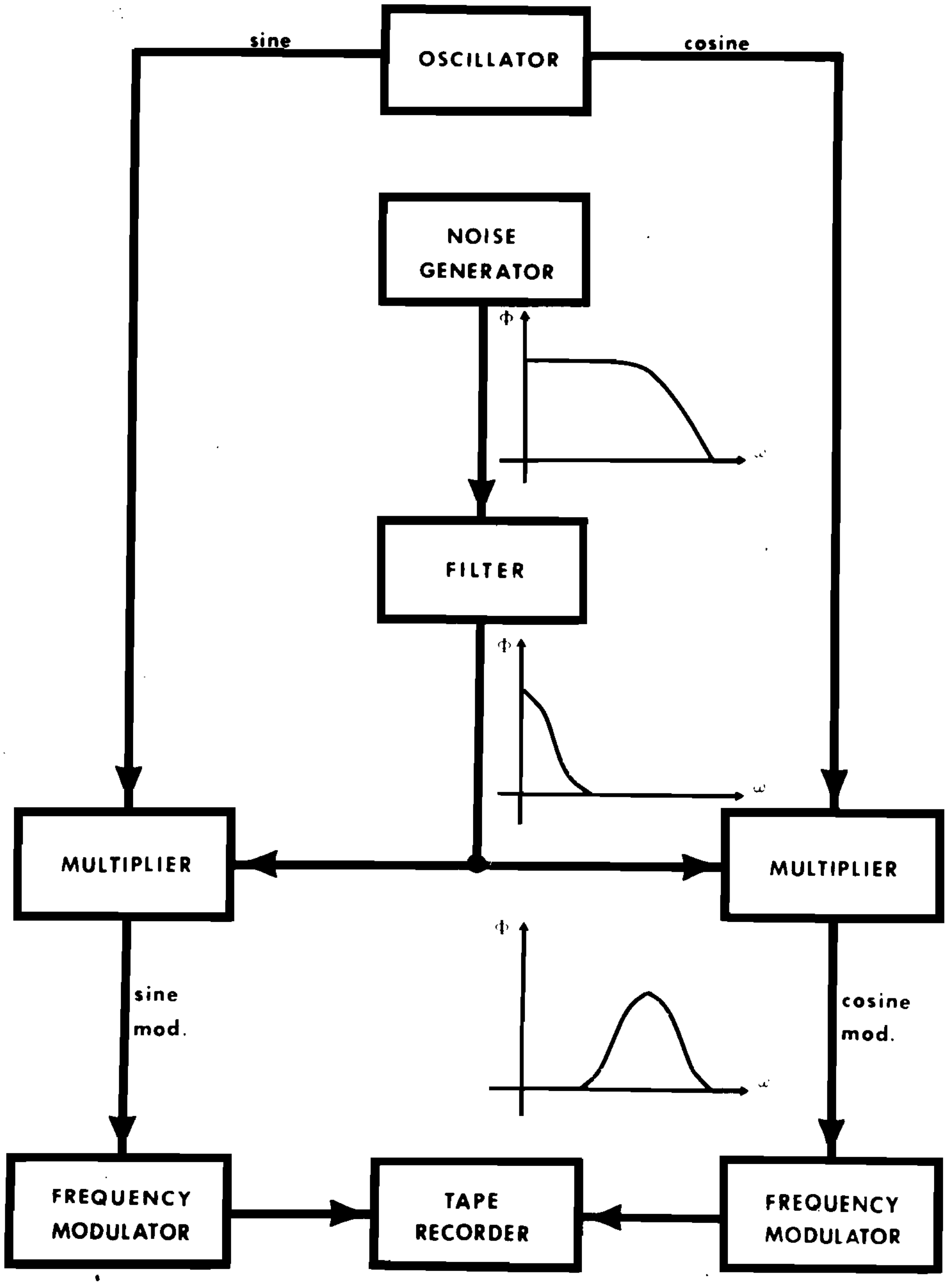


FIGURE 15

Stimuli of graded precitability were produced by suppressed carrier modulation of Gaussian noise signals. A fourth-order filter was used to shape the output of a low-frequency noise generator, and these narrow bands of noise were multiplied by the sine and cosine of the desired center frequency. These signals were then frequency modulated and recorded on tape.

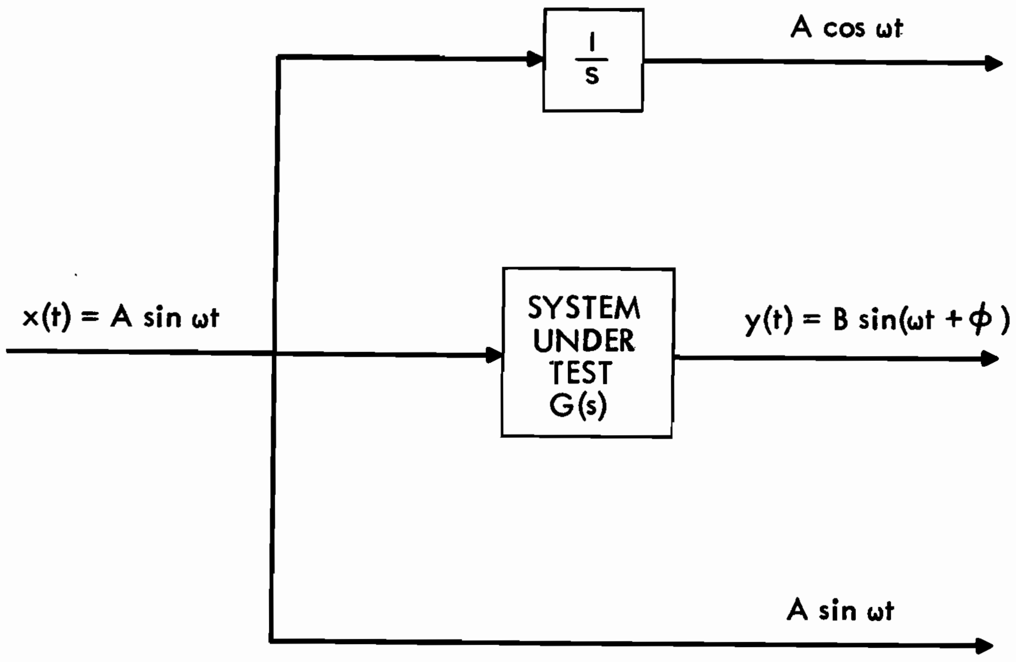


FIGURE 16

In making phase measurements of a system by cross correlation the test situation seen above is required. The system under test receives an input x(t) which results in an output y(t). The input is simultaneously integrated to give the quadrature component of the input. From RMS measurements of the three signals present the correlation coefficients can be determined.

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