CONTROL MECHANISMS
IN THE HUMAN
BINOCULAR OCULOMOTOR SYSTEM

Thesis by

Gaetan Joseph St-Cyr

In Partial Fulfillment of the Requirements
For the Degree of
Doctor of Philosophy

California Institute of Technology
Pasadena, California
1969
(Submitted December 6, 1968)

ACKNOWLEDGMENTS

This work has been undertaken during my course of graduate studies in Electrical Engineering at the California Institute of Technology, while I participated in an interdisciplinary program in vision research administered under the joint supervision of the Division of Engineering and Applied Science and the Division of Biology.

I would like to express my appreciation for the advice and assistance that I have received from many people during this investigation.

First, I would like to thank Professor Derek H. Fender, my advisor, for his patient guidance and encouragement throughout the course of this research.

David S. Gilbert (DSG) and Stephen A. Muscanto (SAM) faithfully served as subjects and provided invaluable technical assistance during my experiments.

Dr. Patrick W. Nye critically reviewed this manuscript and afforded many helpful comments.

Grant H. Snellen was responsible for transmitting most of my data to digital tape for subsequent processing.

Mrs. Roberta I. Duffy greatly assisted in the preparation of this manuscript.

My colleagues, Robert Kavanagh, Cary Lu, and William Hill patiently listened to the presentation of the material in this thesis.

I am grateful to Hughes Aircraft Company and to the National Institutes of Health for their financial support.

ABSTRACT

A study of human eye movements was made in order to elucidate the nature of the control mechanism in the binocular oculomotor system.

We first examined spontaneous eye movements during monocular and binocular fixation in order to determine the corrective roles of flicks and drifts. It was found that both types of motion correct fixational errors, although flicks are somewhat more active in this respect. Vergence error is a stimulus for correction by drifts but not by flicks, while binocular vertical discrepancy of the visual axes does not trigger corrective movements.

Second, we investigated the non-linearities of the oculomotor system by examining the eye movement responses to point targets moving in two dimensions in a subjectively unpredictable manner. Such motions consisted of band-limited Gaussian random motion and also of the sum of several non-integrally related sinusoids. We found that there is no direct relationship between the phase and the gain of the oculomotor system. Delay of eye movements relative to target motion is determined by the necessity of generating a minimum afferent (input) signal at the retina in order to trigger corrective eye movements. The amplitude of the response is a function of the biological constraints of the efferent (output) portion of the system: for target motions of narrow bandwidth, the system responds preferentially to the highest frequency; for large bandwidth motions, the system distributes the available energy equally over all frequencies.

Third, the power spectra of spontaneous eye movements were compared with the spectra of tracking eye movements for Gaussian random target motions of varying bandwidths. It was found that there is essentially no difference among the various curves. The oculomotor system tracks a target, not by increasing the mean rate of impulses along the motoneurons of the extra-ocular muscles, but rather by coordinating those spontaneous impulses which propagate along the motoneurons during stationary fixation. Thus, the system operates at full output at all times.

Fourth, we examined the relative magnitude and phase of motions of the left and the right visual axes during monocular and binocular viewing. We found that the two visual axes move vertically in perfect synchronization at all frequencies for any viewing condition. This is not true for horizontal motions: the amount of vergence noise is highest for stationary fixation and diminishes for tracking tasks as the bandwidth of the target motion increases. Furthermore, movements of the occluded eye are larger than those of the seeing eye in monocular viewing. This effect is more pronounced for horizontal motions, for stationary fixation, and for lower frequencies.

Finally, we have related our findings to previously known facts about the pertinent nerve pathways in order to postulate a model for the neurological binocular control of the visual axes.

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I. INTRODUCTION

1. Purpose of This Work

It is very tempting to draw analogies between biological control systems and man-made servomechanisms. Broadly speaking, both function by measuring the difference between the actual state of the system and that state it is desired to achieve, and by processing this error in such a way as to reduce it to zero in some optimal fashion. When the engineer designs a servosystem, optimality is usually quite well defined by the nature of the problem and by the materials available. On the other hand, it is impossible to determine exactly what is optimum for a biological system. The difficulty lies in the fact that the precise nature of the desired biological state eludes us.

A case in point is the oculomotor control system in the human. It is easy to state the problem in general terms: the eyeball must be rotated so that the image of the desired object falls on the fovea in such a way that clarity of vision is maximized. However, clarity of vision is a function of the co-ordinated activity of aggregates of nerve cells in the retina and the cerebral cortex. Since we have no intimate knowledge of the neural process which mediates vision, we cannot *a priori* predict the optimum way in which the retinal image should be brought on-target. For example, should it be confined to a very small area of the fovea; should it be centered in the fastest possible manner; or is it more important to keep the image stationary on the retina? In an attempt to answer these questions as well as to evaluate the performance of a human operator in a visual tracking task, several investigators have studied spontaneous eye movements and the response of the human oculomotor system to moving targets. Cornsweet (3) examined the horizontal component of spontaneous flicks and drifts made during monocular fixation of a stationary target; and Krauskopf, et al. (7) extended the study to binocular fixation. They concluded that drifts are "noise" -- the result of instabilities in the oculomotor system -- while flicks correct the resulting fixational error. However, Nachmias (9) considered both the vertical and horizontal components of spontaneous eye movements (monocular fixation) and found that flicks correct fixational errors along certain directions, but that drifts subserve the corrective role along other directions.

In the work that follows, we shall examine the flow of control in the binocular oculomotor system by studying the vertical and the horizontal components of motions of both visual axes under monocular and binocular viewing conditions. We will first perform a statistical analysis of the spontaneous involuntary eye movements (flicks and drifts) that occur when fixating a stationary target. We will show that, contrary to what had been previously believed, drifts are not noise but instead correct monocular fixational errors almost as efficiently as flicks. It will moreover be shown that there exists a binocular mechanism which measures the horizontal retinal disparity -- that is, errors of vergence -- and acts to correct such discrepancies by means of symmetric smooth movements, the so-called drifts. In contrast, we will see that there is no comparable mechanism for vertical retinal disparities.

A number of investigators have studied the oculomotor system by means of standard techniques commonly used in the analysis of man-made systems. The subject was instructed to track a target moving in a well defined manner; from the eye movement responses, a block diagram was then derived. The oculomotor system was then described in terms of Laplace transfer functions, integrators, differentiators, summers, limiters, and in short, all those elements which have proven to be so useful in the description of man-made servomechanisms.

Fender and Nye (6) derived a feedback model of the oculomotor system by studying the response to targets moving sinusoidally; they concluded that the system behaved as a low-pass network with frequency cut-off at about 2.5 - 3 cps. However, the phase lag proved to be less than that to be expected from a minimum phase network. These results suggested that there might exist a predictive mechanism which enabled the subject to anticipate target motion. Young (13) undertook similar experiments using targets whose motions consisted of the sum of several non-integrally related sinusoids; such motions appeared to be subjectively unpredictable. Dallos and Jones (4) also studied the response of the oculomotor system to band-limited Gaussian random motion. To summarize and compare these results: the phase lag of the system at a given frequency was lowest for single-sinusoidal motions and highest for Gaussian random motion; lags for sum-of-sinusoids motion fell between these two extremes. Somewhat later, Michael and Jones (8) examined the lag of the oculomotor system for motion consisting of single sinusoids on which had been superimposed Gaussian noise of various bandwidths; they concluded that the phase lag was proportional to the bandwidth of the superimposed

Gaussian noise. They interpreted these results to mean that the ability of the oculomotor system to anticipate target motion depended on the degree of predictability of that motion.

Modelling of the oculomotor system is further hampered by the fact that there are two basic types of eye movements: flicks or saccades are rapid "step-function" changes in the position of the visual axis, while the rest of the waveform (the smooth component) contains a continuum of frequencies from DC up to about 2.5 cps (33 db down at that frequency). Young (13) has attempted to deal with this problem by constructing a sampled-data model, while Beeler (1) has derived a purely stochastic model describing the saccadic system only. The latest model of the oculomotor system, postulated by Young, et al. (15), consists of an open-loop continuous branch for smooth eye movements and of a sampled-data system for saccadic movements; the sampling period is assumed to vary in a random manner.

With the exception of Beeler (1), who has studied the two-dimensional motions of the visual axis, the above authors have examined horizontal eye movements only, and moreover there have as yet been no comparable studies of the binocular system. An even more important limitation of these models is that, except for Beeler's purely stochastic description of the saccades, all these schemes assume at least piece-wise linearity of the oculomotor system.

In this work, we will perform a study of the non-linearities of the oculomotor system by examining the eye movement responses to point targets moving in two dimensions in a subjectively unpredictable manner. Such motions will consist of Gaussian noise and also of the sum of several non-integrally related sinusoids; we will study the power spectra of the tracking eye movements as the frequencies of these components are varied throughout the bandwidth of the oculomotor system. Others (14) have previously considered this problem, but have been careful to avoid any detailed discussion of non-linear responses. Gain and phase curves have been presented as average results with no reference to the spectral content of the target motion.

We shall not attempt to derive quasi-linear models consisting of blocks with appropriate Laplace transforms. We feel that the latest model postulated by Young, et al. (15) represents the limits of usefulness of such an approach. The non-linearities inherent in the human oculomotor systems are of such a nature that it is not profitable to attempt to account for them by means of simple devices such as limiters or dead zones. Moreover, such black boxes do not in general lead to an understanding of the underlying biological mechanism. In fact, the use of Laplace transforms dictates a definite relationship between the gain of the system and the minimum phase lag. Any discrepancies between that phase and the actual measured value has been accounted for by previous authors by means of predictors whose efficiency is a function of target complexity. We shall find that the concepts of phase and gain are not particularly fruitful in explaining the underlying biological phenomena. Instead of phase, we will consider average delay time with respect to target motion; instead of gain, we will examine the power spectra of eye movements. We will assume no relationship between the power spectra of eye movements and the average delay time. There is after all no a priori reason why the oculomotor system should process retinal information in the same manner as artificial passive elements such as resistors or capacitors.

We shall then find that delay time in the oculomotor system is not the result of inefficient predictors or target-motion analyzers, but is instead determined by the very basic biological fact that a minimum afferent signal must be generated by the retina in order to initiate corrective eye movements. Moreover, by comparing the power spectra of spontaneous eye movements with those of tracking motions, we will infer that the oculomotor system tracks a moving target, not by increasing the mean rate of impulses along the motoneurons of the extraocular muscles, but rather by co-ordinating those spontaneous impulses which propagate down the motoneurons during stationary fixation.

In short, we will use the concepts of systems analysis, not to derive yet another abstract model of the oculomotor system, but rather to arrive at an understanding of the underlying neurological networks that control and coordinate the motions of the two visual axes.

2. Basic Neurophysiology of the Oculomotor System

This section presents a very brief description of the extraocular muscles and of the principal nerve pathways of the oculomotor system. Only that portion pertinent to this work will be covered; thus, we will not deal with the vestibular system, since all experiments have been done with the subject's head firmly held stationary.

Light from the external world is focussed onto the retina where it is absorbed and transduced into chemical energy by the photoreceptors, the rods and cones. Excitation from these receptors is conducted to a dendrite of a bipolar cell, which in turn transmits the signal to the ganglion cells whose axons compose the optic nerve. In general, many bipolar cells terminate on one ganglion cell and vice versa. There are about 125 million photoreceptors altogether, but only about 1.25 million optic nerve fibers; there is thus an average reduction of 100:1 (10). In addition to bipolar and ganglion cells, the retina also contains amacrine and horizontal cells whose main function seems to be to provide interconnections between photoreceptors and bipolar cells respectively. Although the ratio of photoreceptors to ganglion cells is about 100:1, most of this reduction appears to take place in the periphery of the retina. According to Polyak (11), there exists a "central bouquet of cones" of about 15 min arc diameter where the average mapping is 1:1. Davson (5) defines an "outer fovea" of about 80 min arc diameter in which the receptors are virtually all cones and are comparatively densely packed. In the periphery, most of the receptors are rods; these respond to much lower levels of light than cones, and the peak of sensitivity is at shorter wavelengths (.51 microns cf. .57 microns). The fovea is the retinal region of maximum sensitivity, and consequently, one looks at an object by rotating the orb (eyeball) until the desired portion of the retinal image falls on the fovea. It is located about 5^o nasally and 1.5^o below the optic axis of the eye.

Figure 1.1 shows a schematic of the basic afferent (input) visual information flow. Axons from the ganglion cells proceed from the

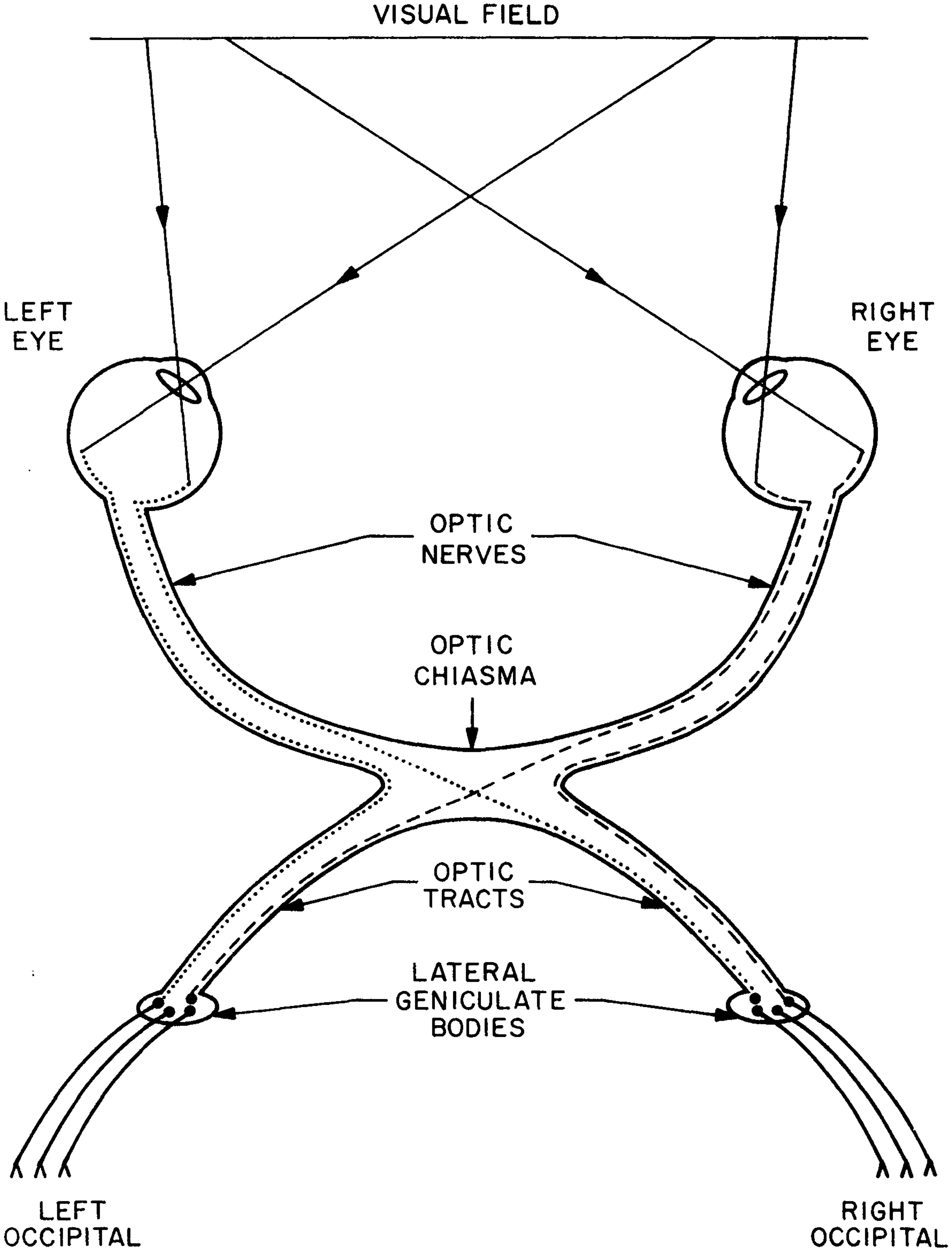
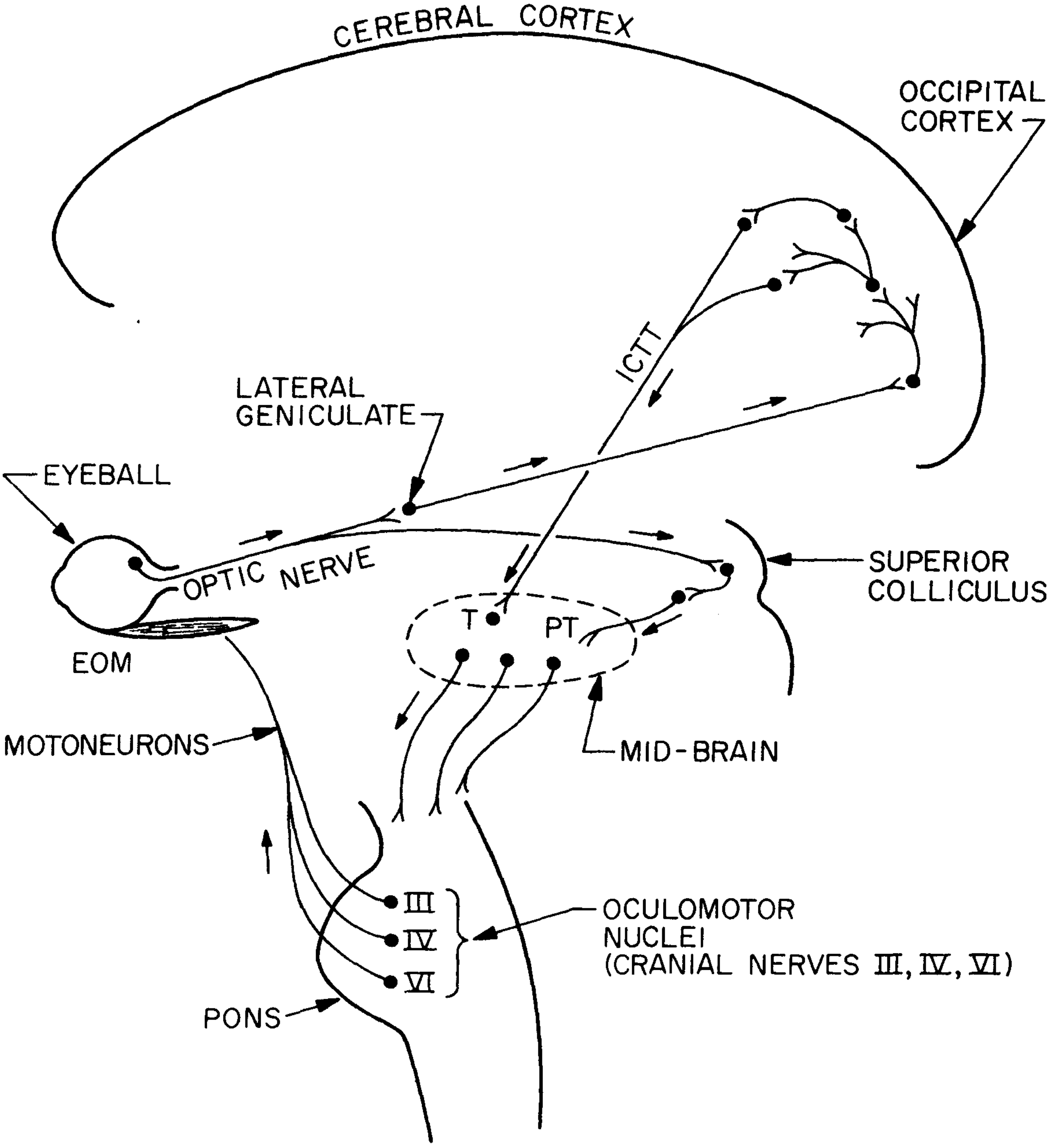


Figure 1.1: Afferent information flow in the oculomotor system

retinae through the optic chiasma and synapse (terminate on other neurons) at the lateral geniculate bodies. At that point, spatial remapping may take place (12) before signals are relayed to the occipital cortex. It may be noted that axons from the nasal part of the retina (receiving information from the temporal visual fields) decussate (cross over) to the other side at the optic chiasma, while axons from the temporal receptors stay on the same side. Thus, inputs from the right visual field are relayed to the left hemisphere, and vice versa. Although there are no direct connections between the left and the right lateral geniculate bodies, both receive inputs from the two eyes. After the visual signals have reached the cerebral cortex, information can cross over between the two hemispheres via the commisures.

Figure 1.2 shows the afferent (input) and efferent (output) nerve network for one side of the oculomotor system; the entire scheme is duplicated for the other side. Afferent visual information from the retina is sent to the lateral geniculate body via the optic nerve (IInd cranial nerve), after which the signals are relayed to the occipital cortex. Efferent signals from the cortex are then sent down to the tegmentum via the internal corticotectal tract where they are then relayed to the oculomotor nuclei (IIIrd, IVth, and VIth cranial nerves) in the brain stem. The optic nerve (IInd) also sends processes to the superior colliculus which then relays the signals to the pretectal nuclei just behind the tegmentum in the midbrain. This particular loop consists of visual information that is supposedly not processed by the cerebral cortex. This scheme suggests that such "short-



EOM = EXTRAOCULAR MUSCLES
T = TEGMENTUM
PT = PRETECTAL NUCLEI
ICTT = INTERNAL CORTICOTECTAL TRACT

Figure 1.2: Basic nerve pathways of the oculomotor system

circuit" information may mix with that from the cortical levels before efferent messages are finally relayed to the oculomotor nuclei. In Chapter XI (Conclusions), we shall discuss the role of this inner loop in the correction of fixational errors.

Figure 1.3 shows a diagram of the eyeball and the extraocular muscles that rotate the orb; this figure has been redrawn from Cogan (2). There are three pairs of extraocular muscles in the human as well as in all other vertebrate classes. All muscles except the inferior oblique originate at the Annulus of Zinn, a cartelaginous structure which surrounds the optic nerve. The inferior oblique originates from the nasal wall of the orbit. The medial (not shown) and lateral recti serve to rotate the eyeball in the horizontal direction; the superior and inferior recti tend to rotate the orb in the vertical plane, although for large motions, this movement includes a horizontal and torsional component as well. The inferior and superior obliques' main action is torsional. In the primary position, the medial and lateral recti are the only pair whose action is purely horizontal; the other four muscles must act in conjunction in order to produce a large vertical movement. For the small eye movements considered in this work, however, vertical rotations are produced solely by the superior and inferior recti, while horizontal motions are the results of contractions by only the medial and lateral recti. We are pleased to refer the reader to Beeler (1), pp. 15 - 22 and pp. 231 - 232 for a detailed analysis of the interactions of the extraocular muscles for large eye movements.

The superior oblique is innervated by the trochlear (IVth

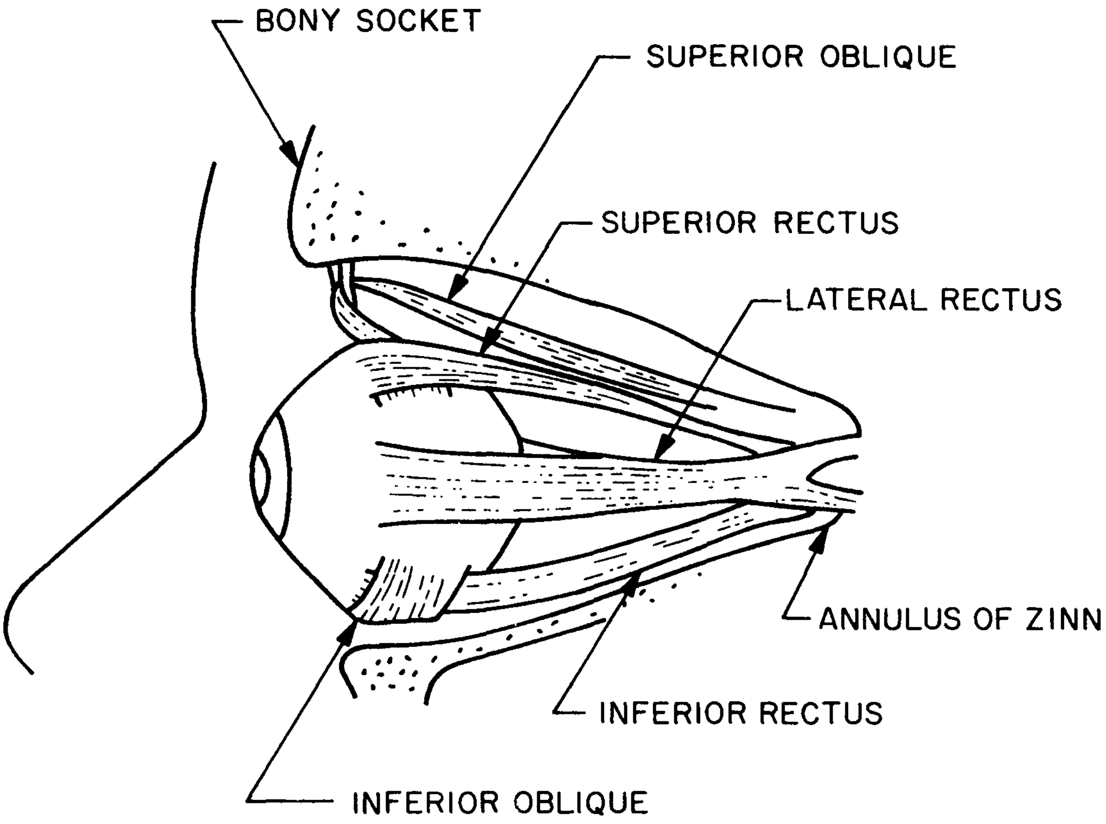


Figure 1.3: The extraocular muscles
(Redrawn from Cogan (2))

cranial nerve), the lateral rectus is controlled by the abducens (VIth), and the other four receive discharges from the oculomotor nerve (IIIrd). Nerves III and VI are homolateral (same side) in their actions, but the IVth (trochlear: to the superior oblique) innervates the contralateral side. There is no evidence (17) for any oculomotor nuclei in the brain stem whose action is bilateral or convergent.

REFERENCES FOR CHAPTER I

1. Beeler, G. W., "Stochastic Processes in the Human Eye Movement Control System," Ph. D. Dissertation, California Institute of Technology (1965).

2. Cogan, D. G., Neurology of the Ocular Muscles, Charles C. Thomas, Springfield, Ill. (1956).

3. Cornsweet, T., "Determination of the Stimuli for Involuntary Drifts and Saccadic Eye Movements," J. Opt. Soc. Amer. 46 (1956), pp. 987-993.

4. Dallos, P. J. and Jones, R. W., "Learning Behavior of the Eye Fixation Control System," IEEE Trans. on Automatic Control, AC-8 (July 1963), pp. 218-227.

5. Davson, M., The Eye, Vol. III: Muscular Mechanisms, Academic Press, New York (1962).

6. Fender, D. H. and Nye, P. W., "An Investigation of the Mechanisms of Eye Movement Control," Kybernetik 1 (July 1961), pp. 81-88.

7. Krauskopf, J., Cornsweet, T., and Riggs, L., "Analysis of Eye Movements during Monocular and Binocular Fixation," J. Opt. Soc. Amer. 50 (1960), pp. 572-578.

8. Michael, J. A. and Jones, G. M., "Dependence of Visual Tracking Capability upon Stimulus Predictability," Vision Research 6 (1966), pp. 707-716.

9. Nachmias, J., "Two-dimensional Motion of the Retinal Image during Monocular Fixation," J. Opt. Soc. Amer. 49 (1959), pp. 901-908.

10. Netter, F. M., The CIBA Collection of Medical Illustrations, Vol. I: Nervous System, New York (1964).

11. Polyak, S. L., The Retina, University of Chicago Press, Chicago, Ill. (1941).

12. Richards, W., "Spatial Remapping in the Primate Visual System," Kybernetik 4 (1968), pp. 146-156.

13. Young, L. R., "A Sampled Data Model for Eye Tracking Movements," D. Sc. Dissertation, Massachusetts Institute of Technology (1962).

14. Stark, L., Vossius, G., and Young, L. R., "Predictive Control of Eye Tracking Movements," IRE Trans. on Human Factors in Electronics, HFE-3 (Sept. 1962), pp. 52-57.

15. Young, L. R., Van Houtte, N., and Forster, J. D., "A Hybrid Model for Eye Tracking Movements," Proc. of Annual Conference on Engineering in Medicine and Biology, Vol. 10 (1968), p. 25.7.

16. Young, L. R. and Stark, L., "Variable Feedback Experiments Testing a Sampled Data Model for Eye Tracking Movements," IEEE Trans. on Human Factors in Electronics, HFE-4 (Sept. 1963), pp. 38-51.

17. Warwick, R., "The So-Called Nucleus of Convergence," Brain 78 (1955), pp. 92-114.

II. EXPERIMENTAL APPARATUS AND DATA PROCESSING

This chapter describes the experimental apparatus and data processing which are common to all experiments in this thesis. Details which are pertinent to a particular case, such as stimulus presentation, will be discussed in the appropriate chapter. Figure 2. 1 outlines the basic information flow. The solid arrows represent the transmission of eye movement measurements, while the dotted arrows indicate the control of experimental conditions. The subject's eye movements are measured, and the four channels of information -- left vertical, left horizontal, right vertical, and right horizontal -- are recorded by both analog and digital methods. Analog recording is accomplished by the use of a CEC (Model PR-3300) AM/FM 7-channel tape recorder. Four of the channels are used to record eye movements, a fifth carries the voice, and the remaining two contain prerecorded signals which are used to drive the target vertically and horizontally during tracking experiments. Digital recording is also done directly during the experiment whenever possible. However, in some cases of computer failure, digital transmission must be postponed and is subsequently carried out by playing back the appropriate analog signal from the CEC tape recorder. Voltages proportional to eye movements are processed by the BSDT , which incorporates a multiplexer and an analog-to-digital converter. Channels of information are sampled one at a time, and the appropriate quantities are stored sequentially into a buffer of the IBM-7040, which then writes the results on digital tape for further processing by the main computer (IBM-7094). In addition, the Biological Systems Data Terminal

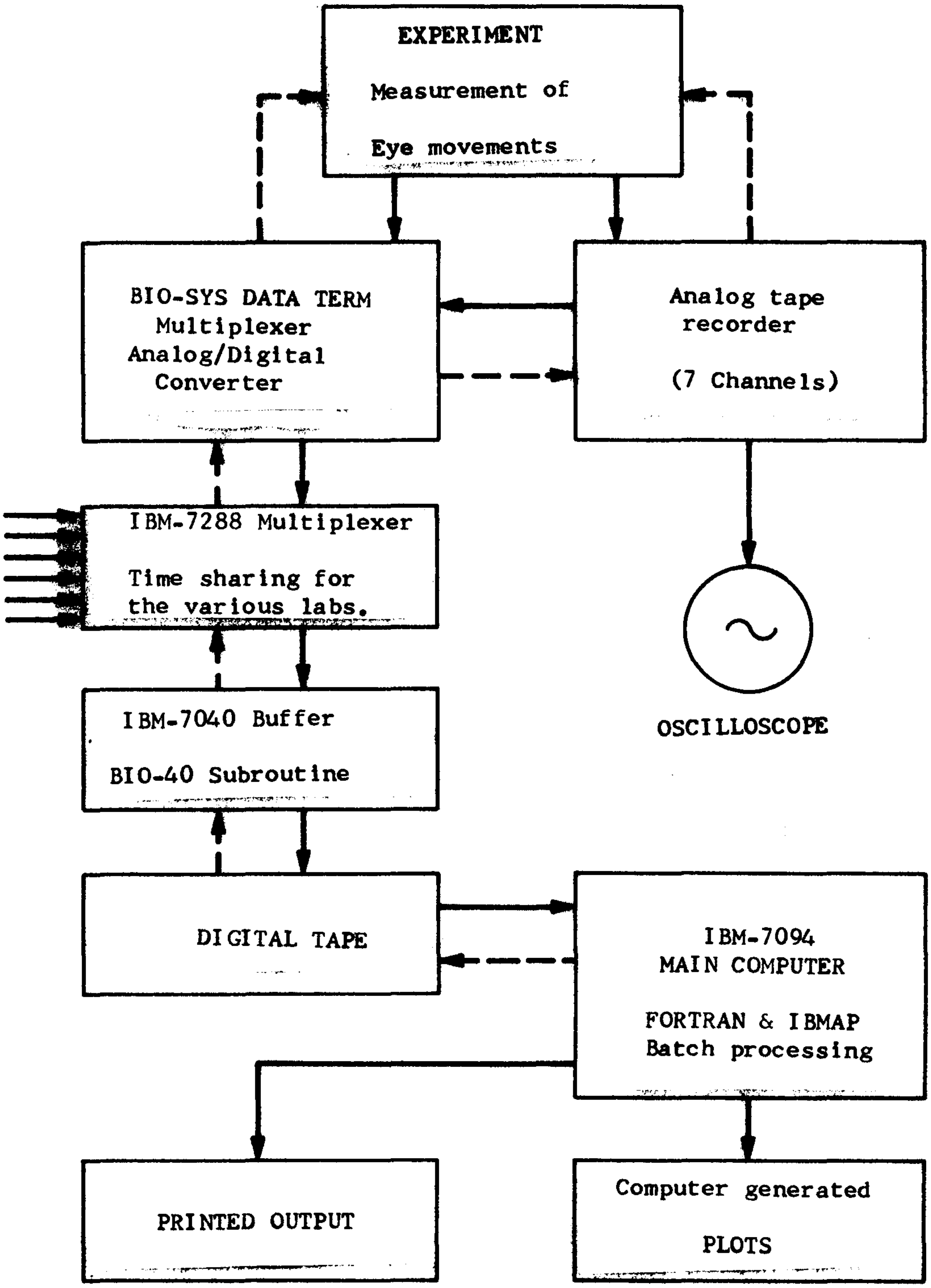


Figure 2.1: Flow chart for processing of experimental data

(BSDT) sends appropriately timed signals to control various circuits in the experimental apparatus. The data transmission chain can also be reversed for the preparation of stimuli functions: a certain waveform is computed on the IBM-7094, stored on digital tape, sent to the IBM-7040, converted to an analog signal by the digital-to-analog converter in the BSDT, and finally recorded on the CEC tape recorder. This is subsequently used to drive the target which is to be tracked.

1. The Subjects

Three human male subjects were used: all were graduate students in the inter-disciplinary field of Biological Systems Analysis. The first, GSC, is the author of this thesis and served in all experiments. The second, DSG, was used in the case of binocular fixation (Chapter IV). SAM served as subject for the remainder of the experiments. All were experienced subjects and were free of extra-ocular muscular imbalances.

2. Measurement of Eye Movements

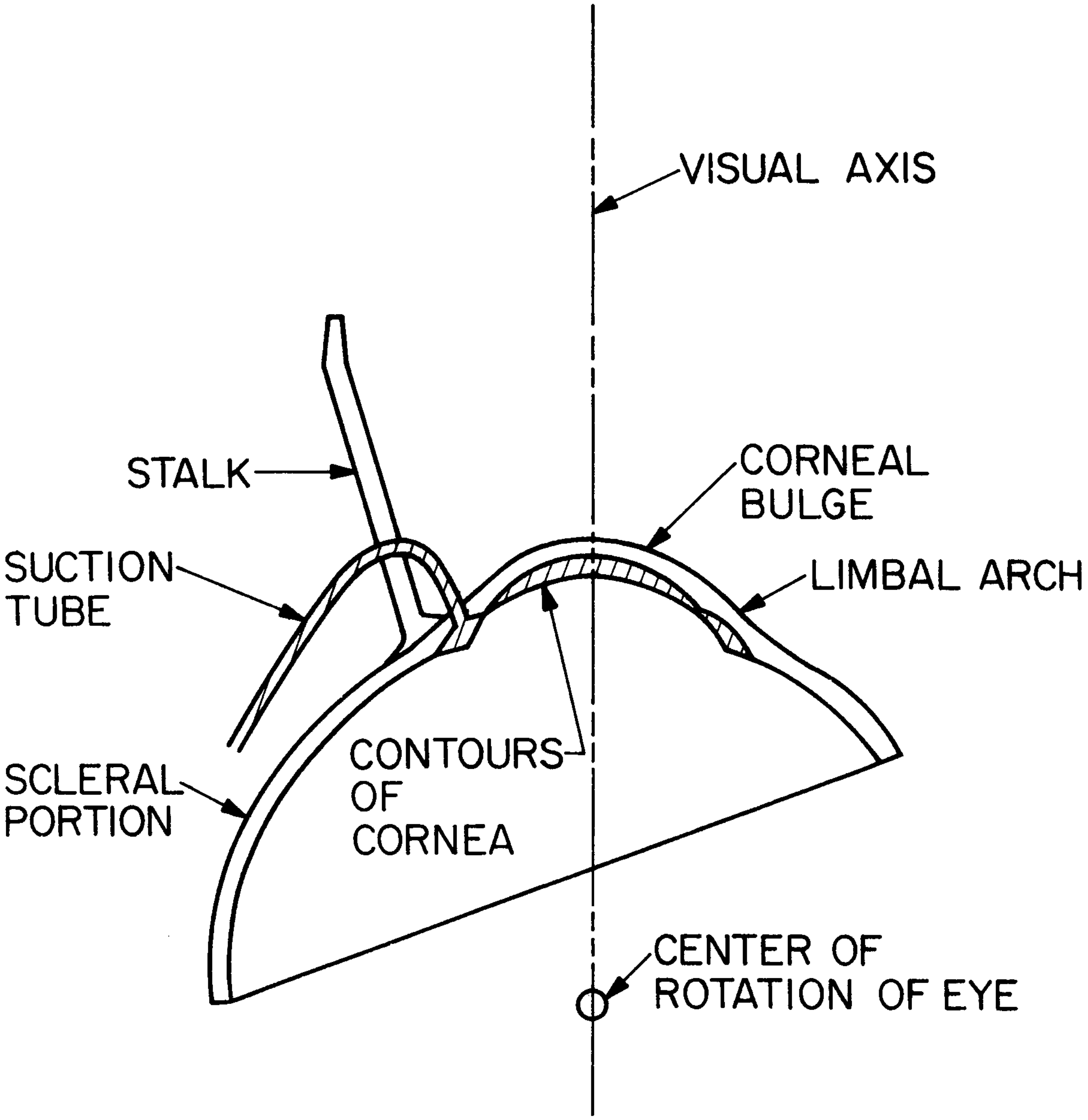
The study of interactions between the two visual axes for small fixation and tracking eye movements requires the simultaneous measurement of the vertical and horizontal motions of both eyes with an accuracy of a few minutes of arc. Moreover, the data must be collected at a rate sufficient to determine the flick trajectories: about 100 samples/sec. Finally, a large quantity of data points must be accumulated for statistical validity. Ideally, the method of measurement should not interfere with the normal eye movements; it would be preferable if no contact were made with the eye. Such techniques have been tried in the past.

In 1961, Byford (1) measured the vertical and horizontal components of eye motion by direct photography and claimed to have achieved a sensitivity of 30 sec arc. Moreover, he succeeded in taking 100 frames/sec. Unfortunately, the mechanical difficulties involved were staggering, and such a high rate could be sustained for only about 5 seconds. Thus, although this method can meet our requirements of speed or volume, it cannot satisfy both of them simultaneously. Other techniques have involved the reflection of light from the eye. Lord and Wright (3) used the surface of the cornea as a spherical reflector, and in this manner measured both vertical and horizontal components. However, this method is much more sensitive to minute lateral displacements of the head than to rotations of the eyeball. Stark, <u>et al.</u> (7) took advantage of the different reflective properties of the iris and sclera to measure horizontal eye motions, but because of unavoidable interference from the eyelids, it was impossible to measure the vertical components. This method appears to be applicable to large rotations of the eyeball, since they claimed linearity within $\pm 15^{\circ}$, but the accuracy was only about $1/4^{\circ}$. Rashbass and Westheimer (6) improved this technique by using a flying spot scan and quoted 6 min arc accuracy. However, any measurement based on the different reflective properties of the iris and sclera is highly vulnerable to variations in the wetness of the eye, and in any case, is suitable only for horizontal eye motions. Recently, Honeywell, Inc. (5) developed an instrument which measures both the vertical and the horizontal components of eye movements by sweeping an infra-red beam of light along the contour of the pupil; however, the resolution is only 2°.

Clearly, none of the above methods met all our requirements of accuracy, speed, volume, and vertical/horizontal measurement capability. Thus, we were forced to resort to the use of a tightly-fitting contact lens.

2.1 The contact lens. Contact lenses should be designed so as to be comfortable and so as to follow the movements of the eye without slippage. Yarbus (8) constructed a contact lens which resembled a beer bottle cap and which was attached to the eye by suction. Slippage was of course minimal, but we hate to contemplate the possibility of corneal damage. Ditchburn and Ginsborg (2) used a double curvature contact lens without suction: adhesion was achieved strictly by a tight fit. In our experiments, we used tightly-fitting triple curvature contact lenses, individually made for each subject by taking full scleral molds of their eyes. These were worked to correct the subject's errors of refraction.

Figure 2.2 shows the cross-section of such a lens. The scleral part is designed to fit snugly on the sclera. The corneal portion bulges out from the cornea so as to avoid contact and the possibility of corneal abrasions. The limbal arch is specifically designed to avoid contact with the limbus, which contains most of the pain receptors. A 2 percent sodium bicarbonate solution is used as a buffer during insertion. Excess fluid is then sucked out through a thin polyethelene tube (Intra-medic, ID .015" × OD .043") attached to the lens in the region of the limbal arch. The other end of the tube is attached to a water manometer which is used to apply suction between the lens and



<u>Figure 2.2</u>: Contact lens worn by the subject for the measurement of eye movements (Cross section).

the eye in order to limit slippage.

To measure lens slippage, rectangular grids of very accurately spaced grooves were machined on the inner surface of the lens; these were filled with black wax to enhance visibility. The lines were 0.0025" apart. These grids were located roughly on the scleral part of the lens and extended from the corneal portion to the temporal edge as shown in Figure 2.3. The smallest divisions of the grid subtended 6 min arc. Lens slippage was measured by observing (through a 24X Wild M-5 stereomicroscope) the movement of the scleral blood vessels against the grid. With no suction, relative motion of the lens with respect to the eyeball occurred: increasing the suction gradually reduced lens slippage, but increased the time required for the lens to return to its original position after a blink. As a compromise, we chose -23 cm water pressure; this allowed the lens to return to its original position 5 seconds after a blink, and no slippage was detected while the subject fixated a stationary point.

When the subject made voluntary saccades in any direction from the center, the lens came to rest at a position somewhat short of the corresponding eyeball rotation. This steady-state error increased with the size of the saccade; with a 4° movement, this error was 9 min arc. All experiments discussed in this thesis consisted of fixation or tracking tasks in which the visual axis did not deviate more than 0.5° and 1.5° respectively from the mean center position. Consequently, the error in the measured angular position of each visual axis was probably less than 1 min arc for stationary fixation and less than 3 min arc for tracking tasks. Moreover, suction

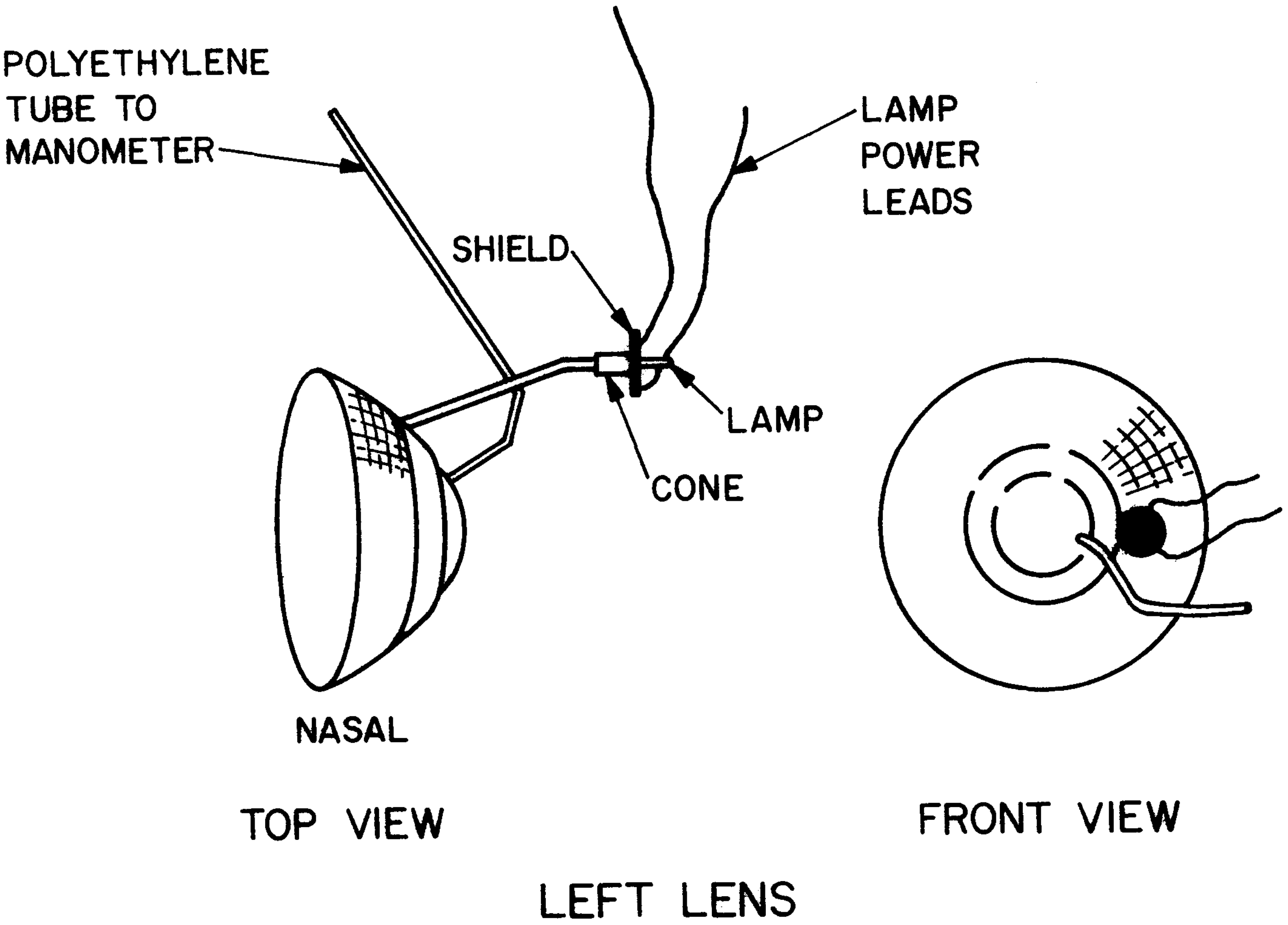


Figure 2.3: Contact lens worn by the subject for the measurement of eye movements (Perspective).

greatly flattened the blood vessels of both the conjunctiva and the sclera, indicating that they were pressed together by the partial vacuum. Under those circumstances, the contact lens was much more likely to follow the motions of the eyeball than would have been the case had the conjunctiva been separated from the sclera by a layer of fluid. The above results were about the same for all three subjects.

2.2 Photomultiplier tube assembly. A small medical lamp (Rimmer Bros. #C11) was epoxied to a cone joint and a black circular paper shield. The assembly was then slid onto the end of the stalk protruding from the contact lens as shown in Figure 2.3. The function of the shield was to prevent the lamp from shining directly into the subject's eyes. Very fine wire (Belden 44 AEG) was connected to the lamp in order to provide power from a 3-volt dry cell battery. The use of a battery was dictated by the need to avoid superposition of AC ripple on the eye movement records. The wires and the polyethelene tube were taped to the subject's head during the experiment in such a manner as to minimize inferference with the free movements of the eye.

The subject's head was positioned so that the lamp at the end of the stalk was located directly over the rectangular guides leading to the photomultiplier tubes as shown in Figure 2.4. The head was held firmly in place by means of a head-rest and a bite-bar. These were molded to the individual subject's features by means of plaster-of-Paris and dental cement, respectively. The rectangular tubes were 7 × 12 × 120 mm and lined with non-reflecting black paper; at 60 mm from the photocathodes (95 mm from the lamp), there was a

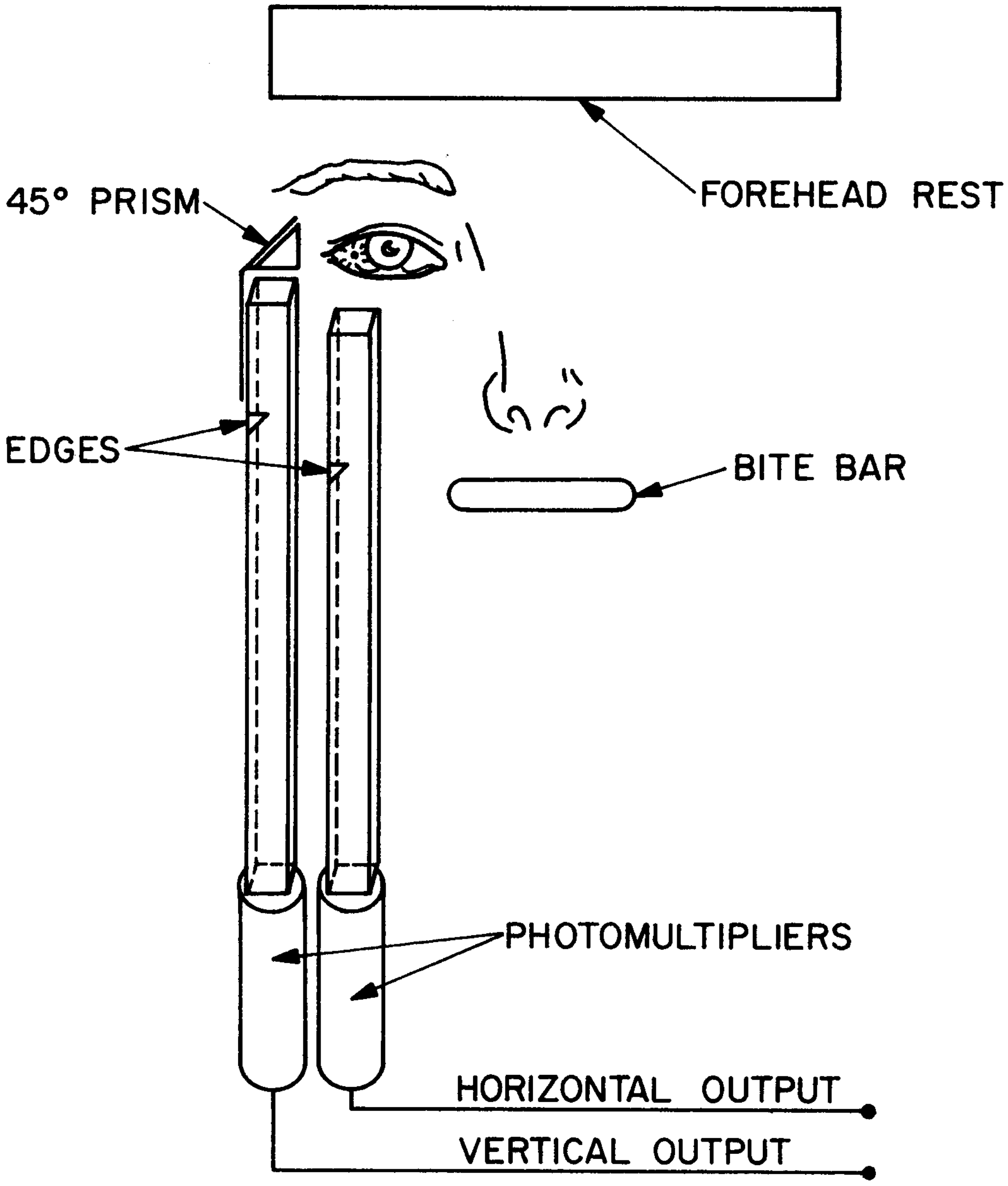


Figure 2.4: Photomultiplier tube assembly for the measurement of eye movements. The pin-light attached to the contact lens casts the shadow of the edge onto the face of the photomultiplier tube; the output of the PMT's is thus proportional to rotation of the eyeball.

fixed edge which occluded about half the opening. The medical lamp at the end of the stalk cast the edge's shadow on the photo-sensitive surface of the PMT. As the eye rotated, the length of the shadow varied, and therefore so did the amount of current emitted by the photomultiplier tube. This current was then transformed to a proportional voltage by battery-powered transistor amplifiers.

The photomultiplier tubes were RCA #7767 powered by Kepko #ABC 150M DC power supplies: two PMT's were powered in parallel by one power supply unit. The usual operating level was 1200 volts DC with a maximum of 1 mv rms ripple, 0.05 percent variation with changes in load, and less than 0.05 percent drift in eight hours.

2.3 Phototube positioning and calibration steps. At the beginning of each experimental session, the phototubes were adjusted so that, when the subject fixated a stationary target straight ahead, the shadow cast by the edge in the rectangular guides covered exactly half the area of the photo-sensitive surface of the PMT. This was accomplished by moving the PMT to one extreme position until a maximum voltage output was passed: the gains of the appropriate DC amplifiers were adjusted so as to set this maximum to a standard value (8 volts). The PMT assembly was then moved back until the output voltage became half the maximum. This process was repeated for each of the four channels.

At the beginning and at the end of each 2-minute experimental run, a calibration step was superimposed on the eye movement record as follows. A solenoid was used to pull an opaque vane a short predetermined distance across the face of each photomultiplier tube.

The vane was restricted to move between two rigid stops. After about a second, the solenoid was de-energized and the vane allowed to spring back to its original position. Since motion of the vane is equivalent to a known value of eyeball rotation, subsequent measurement of the calibration step on the eye movement record enabled us to convert the recorded voltages to angular rotation of the visual axis. The values of the calibration step varied from channel to channel, but the average was about 30 min arc, and the rise time less than 50 ms. Thus, superimposed eye movements had little effect on the calibration step.

2.4 Optical system for stimulus presentation. For the tracking experiments, the optical system described here was not used. Instead, an oscilloscope was placed directly in front of the subject: this will be described in Chapter VI. For the fixation of various stationary targets (Chapter IV), the optical system shown in Figure 2.5 was used to present the various patterns to the subject. The entire diagram is symmetrically duplicated for the right eye. The light source is a GE 18-amp T10 bulb with a horizontal ribbon filament; its intensity can be controlled by means of a neutral density filter represented here as an optical wedge. The lens L1 collimates the source beam so that the transparency T is illuminated by parallel light. The lens L2 focusses the resulting beam on a fixed mirror M2, from which it is then routed into the eye by the remaining lenses L3 through L7. The light source aperture A is imaged into the plane of the eye pupil, a condition known as Maxwellian view. Thus, the complete beam illuminates the retina. Were the light source to be focussed elsewhere,

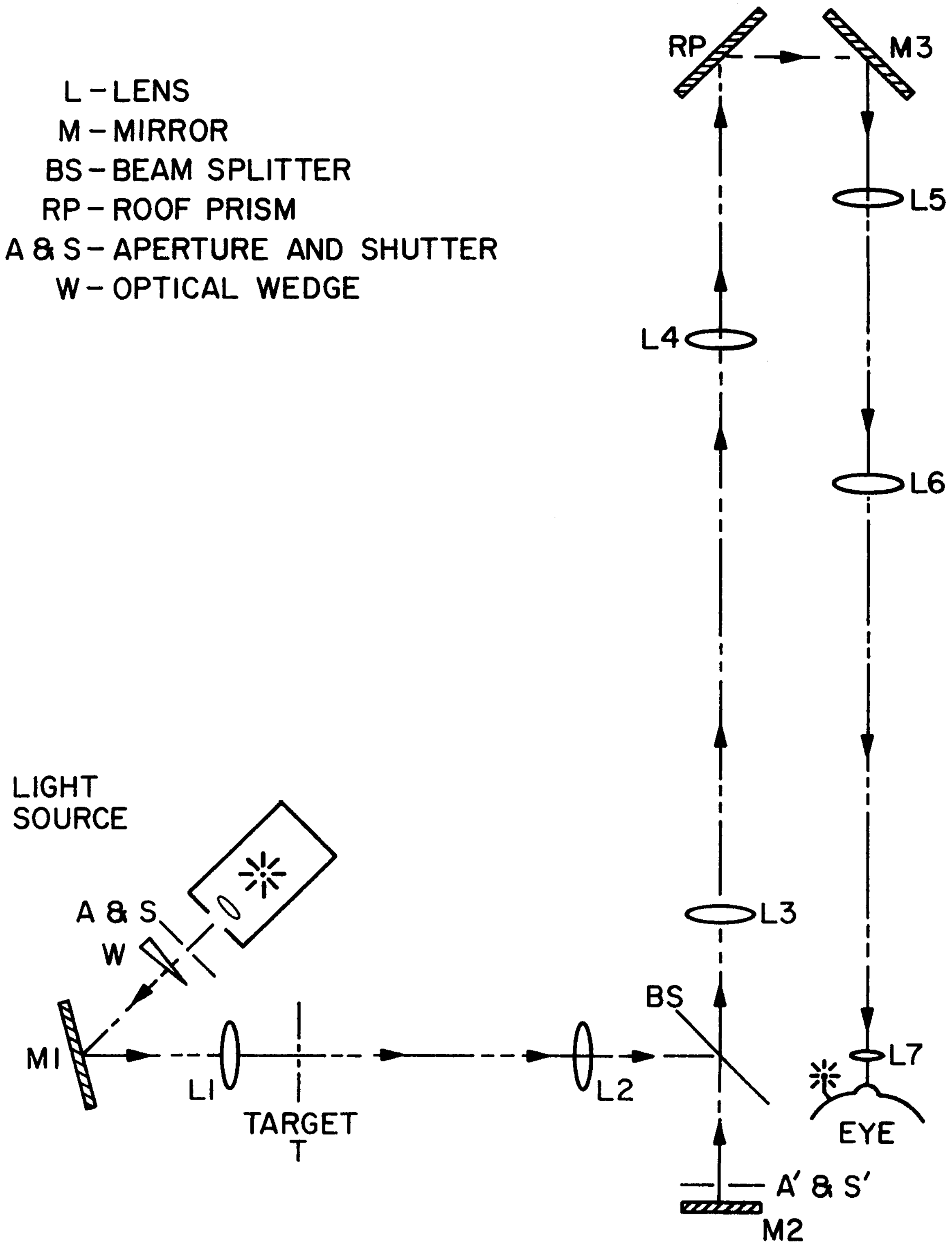


Figure 2.5: Optical system for the presentation of the stimuli during stationary fixation experiments.

part of the beam would be lost, resulting in dimmer illumination. The target is optically at infinity, since it is illuminated by parallel rays from the source which is in turn focussed on the pupil. The exit pupil of the apparatus is about 2 mm diameter so that the eye pupil encloses the complete image for all eye movements measured in this work. The lenses L5, L6, and L7 are part of a telescope with a 7° field of view.

The various 35 mm transparencies are mounted at location T and can be adjusted by the subject only in a plane perpendicular to the light beam. Thus, the magnification of the system is pre-set, but the patterns can be moved laterally in order to superimpose the images seen by the left and the right eyes. Details of this procedure will be discussed in Chapter IV.

2. 5 Calibration and linearity check of the apparatus. In section 2. 3, we mentioned that the movement of the vane across the face of the phototube was equivalent to a known value of eyeball rotation. This quantity was determined as follows. A dummy eyeball was constructed from a one-inch diameter steel sphere; two micrometers could rotate this sphere about vertical or horizontal axes, with an accuracy of 1 min arc per division. One of the small medical lamps described in section 2. 2 was attached to a shaft protruding from the sphere at 3. 5 cm from the center of rotation, just as it was on the stalk of the contact lens. This assembly was then mounted so that the lamp was positioned directly over the photomultipliers, just as it would be during an actual experiment. The gains of the DC amplifiers were adjusted as described in the first paragraph of section 2. 3. The

opaque vanes were drawn across the face of the PMT's by the solenoids, and the resultant voltage change was noted. Then the vanes were allowed to return to their original positions, and the artificial eyeball was rotated by means of the micrometer screw until the same voltage change was achieved. This then yielded the value of the calibration step in min arc for that particular channel.

The same set-up was also used to check the linearity range of the PMT's and the associated electronics. The artificial eyeball was set at various values of rotation and the corresponding voltage output noted. Figure 2.6 shows that the eye movement measuring system was linear in both the vertical and the horizontal directions within $\pm 2^{\circ}$. In all cases discussed in this thesis, all eye movements were confined to a 1.5° radius from mean center position.

3. Analog Recording

The four channels of eye movements were recorded on a CEC (PR-3300) 7-track tape recorded at 1 7/8 inches per second. All channels of information except for the voice track were recorded by means of FM modulation, which resulted in a flat response to 300 cps. The sensitivity was adjusted so the maximum input for linear response was ±1.4 volts. On playback, a small 25 cps, 10 mv rms noise from the tape drive had to be filtered out. This was accomplished by a simple RC network. Off-line digital transmission (from this tape recorder) sometimes had to be made because of computer failure during the experiment. Fortunately, this happened only during those stationary fixation experiments discussed in Chapter IV. For subsequent experiments involving spectral analysis, all digital transmissions were suc-

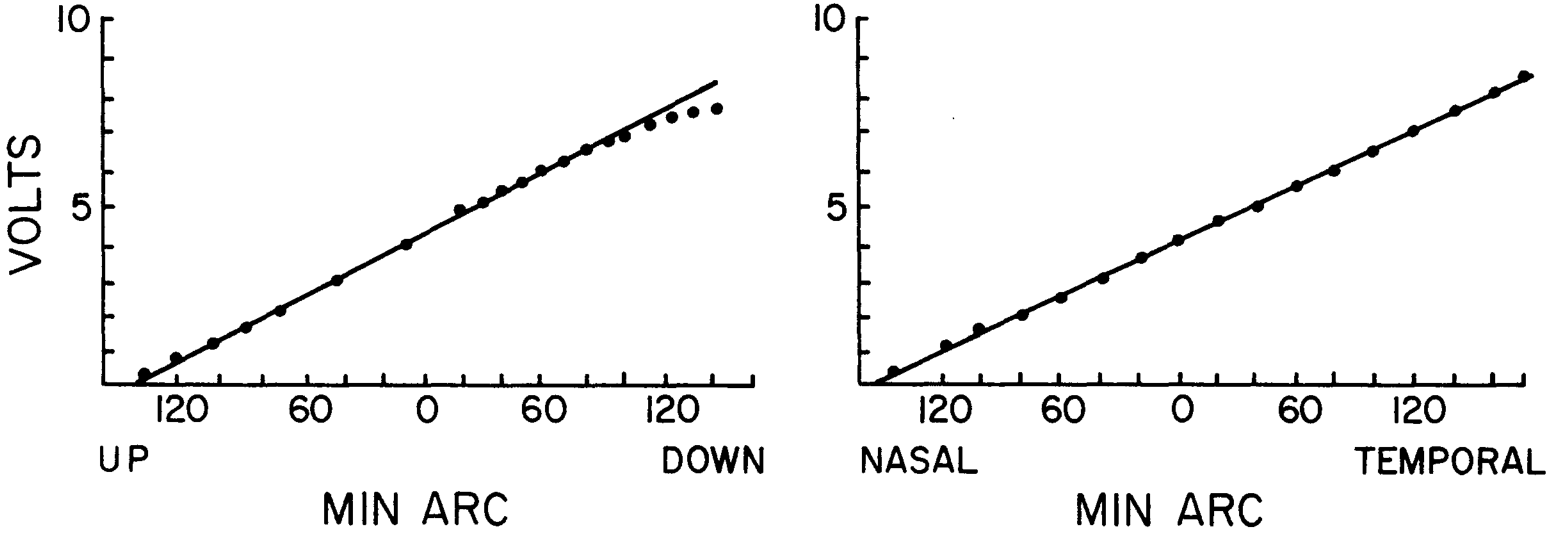


Figure 2.6: Linearity check: Amplified output of the photomultiplier tubes (volts) vs. rotation of the artificial eyeball (min arc).

cessfully made on-line.

The analog tape records were displayed on oscilloscopes and were primarily used to check that the recorded eye movements were free of artifacts, to indicate which method of analysis to use, and finally to insure that results obtained from digital computation were compatible with the analog records.

4. Digital Recording

The computer complex used to gather data from biological experiments has been described in detail by McCann and Fender (4), so that only a compact summary will be given here. The basic system consists of an IBM-7094 which performs all computations, and an IBM-7040 which acts as an input-output dispatcher for the main computer, the 7094. In addition, the 7040 accepts the transmission of data for storage on digital tape from several laboratories simultaneously. All of these functions are performed on a time-shared basis.

From our laboratory, up to six channels of analog information can be sent to the BSDT, a plugboard-programmed, no-memory computer and analog-to-digital converter. The analog signals from the various channels are sampled one at a time, converted to digital form, and then stored sequentially into a buffer of the 7040. A collection subroutine called BIO-40 has been permanently stored on disc and is used to control the storage of information into buffers and the writing on digital tape as the buffers become filled. Between the BSDT and the 7040, the IBM-7288 multiplexes incoming data from various laboratories on campus on a time-sharing basis.

In addition to controlling the rate of information flow to the

7040, the BSDT can also be used to send appropriately timed signals to our laboratory for the control of experimental stimuli. Thus, the calibration steps at the beginning and end of each two-minute run are automatically executed by a signal from the BSDT, which energizes the proper solenoids. For a moving stimulus, the plugboard has been programmed so that the target is held stationary during the calibration steps. This will be taken up in greater detail in Chapter VI. After the BSDT has been appropriately programmed, the experimenter needs only to push one button to set the whole experimental sequence in motion. This facility is quite important, since the sessions are limited to a maximum of one hour in order to avoid damage to the subject's cornea, and since 15 - 30 minutes must be taken from that one-hour limit for the initial set-up.

5. Subsequent Digital Analysis

After the digital tape has been prepared, IBMAP or FORTRAN programs are written in order to analyze the results. The program depends, of course, on the particular type of analysis we desire to perform; however, the following sequence is common to all operations. A subroutine called KERFUS has been stored on disc in order to "unpack" the data which have been previously stored on tape in the format of 3 numbers to one computer "word." The raw data are then converted to angular measurements in units of min arc in this fashion. The calibration steps at the beginning and end of each record are found and measured by a subroutine specifically written for this purpose. Since the corresponding angular rotations are known (section 2.5), we can then convert all data to min arc. Since the calibration values at the beginning and end of each record differ slightly in general, linear interpolation is used to compute the conversion factor. The mean value is subtracted from all records to remove the arbitrary DC level, and the results are then written on a second tape in BCD format. In addition, the time records of eye movements (and stimuli when appropriate) are plotted automatically by the CALCOMP plotter, and this is examined and checked against the corresponding records on analog tape. In this manner, we guard against the multitude of errors which can occur in such a complex system.

In addition to simple records of eye movements, we also plot processed results, such as flick trajectories and power spectra, directly from the computer. In fact, the bulk of the diagrams presented in this thesis were drawn in this fashion. The work required to write the necessary programs is staggering, but we feel that it is amply justified by the results. First, we can present a much larger variety of data than would otherwise be possible. Second, after initial verification of the subroutines, the results which are shown are free of human error. Third, honesty is guaranteed by the fact that no anomalous points can be left out of the picture.

REFERENCES FOR CHAPTER II

1. Byford, G. H. and Stuart, H. F., "An Apparatus for the Measurement of Small Eye Movements," J. Physiol. 159 (1961).

2. Ditchburn, R. and Ginsborg, B., "Involuntary Eye Movements During Fixation," J. Physiol. 119 (1953), pp. 1-17.

3. Lord, M. and Wright, W., "Eye Movements during Monocular Fixation," Nature 162 (1948), pp. 25-26.

4. McCann, G. D. and Fender, D. H., "Computer Data Processing and Systems Analysis Applied to Research on Visual Perception," Neural Theory and Modeling, edited by Richard F. Reiss, Stanford University Press (1964), pp. 232-252.

5. Merchant, J., "The Oculometer," NASA Report CR-805 (July 1967).

6. Rashbass, C. and Westheimer, G., "Disjunctive Eye Movements," J. Physiol. 159 (1961), pp. 339-360.

7. Stark, L., Vossius, G., and Young, L.R., "Predictive Control of Eye Tracking Movements," IRE Trans. on Human Factors in Engineering, HFE-3 (1962), pp. 52-57.

8. Yarbus, A., "Motion of the Eye on Interchanging Fixation Points at Rest in Space," Biofizika 2 (1957), pp. 698-702.

III. INTRODUCTION: FIXATION PATTERNS OF THE EYE WHEN VIEWING STATIONARY TARGETS

The literature now contains a number of papers describing the nature of the spontaneous eye motions which occur during fixation of stationary targets. At this juncture, no purpose is served by a historical review of research on eye movements from the days of Helmholtz (9) or even Dodge and Cline (7) since the earlier publications dealt with monocular fixation and were mainly descriptive (11, 17, 1, 18). Binocular eye movements were first treated by Ditchburn and Ginsborg (6) who measured the vertical and horizontal components of eye movements during binocular fixation; however, only two of these four quantities could be measured at any one time. This section presents a review of modern work pertinent to this thesis.

In previous publications, it has become customary to divide eye movements into three categories, viz.: flicks, drifts, and tremor. "Flicks" are involuntary changes in the angular position of the visual axis of at least 1 min arc occurring during less than 40 milliseconds (Figure 3.1); similar movements resulting from a voluntary change of fixation are called "saccades." The eye movement between two flicks is commonly called a "drift," on which is superimposed a relatively high frequency, low amplitude "tremor." These movements have recently been categorized by Ditchburn and Foley-Fisher (5).

It is generally agreed that tremor serves no useful oculomotor function, but results from the incomplete fusion of the microcontractions of the extraocular muscles. Fender (8) has measured the frequency spectrum of tremor by using special optical techniques which

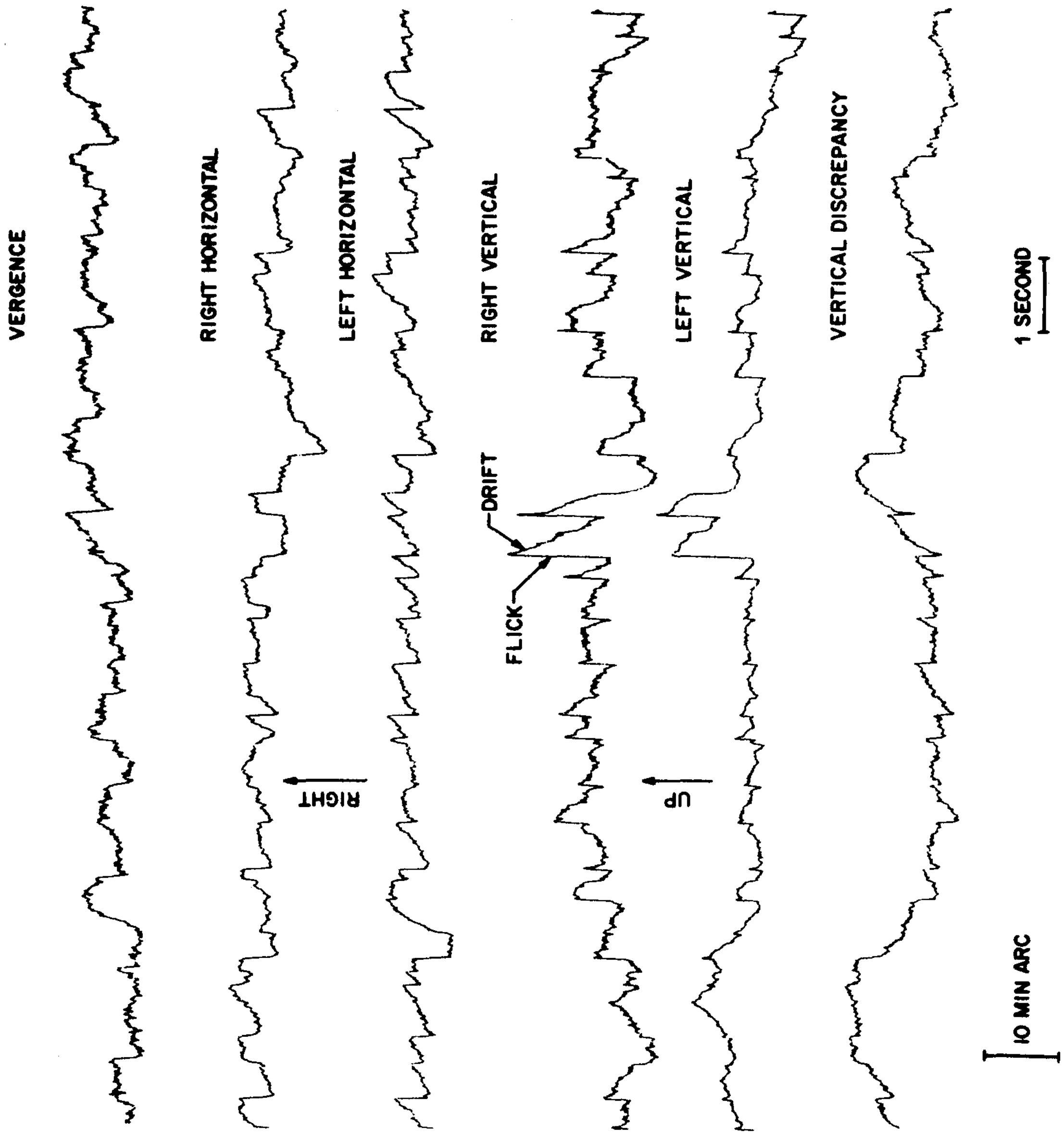


Figure 3.1: Time record of spontaneous eye movements during fixation of stationary targets.

eliminated flicks and drifts from the measurement. The amplitude of tremor was found to be 30 sec arc at 1 cps, and to decrease to 4 sec arc at 10 cps. Such quantities are below the resolving power of our recording apparatus, and we shall not consider tremor in this thesis.

In order to ascribe purpose to the spontaneous eye movements of fixation, Ditchburn and Ginsborg (6) suggested that flicks were responsible for confining the image of the fixated point within a foveal area of 20 min arc diameter. The choice of words used to describe the categories of eye movements reflects their assumption that drifts are merely noise in contrast to the flicks which seem so definite and purposeful.

Data obtained from tracking experiments have reinforced the hypothesis that smooth eye movements are noise when the target is stationary. Westheimer (21) and Vossius (20) have found that the direction and magnitude of flicks are such as to correct for position errors in tracking tasks. Westheimer (22) reported that smooth movement of a target gave rise to smooth pursuit eye movements, and Rashbass (14) showed that the velocity of the smooth pursuit movement matched that of the target. Saccades and smooth motions were found to be independently elicited by target displacement and velocity, respectively. Thus, in tracking tasks, there appears to be a separate control mechanism for saccades, triggered by target displacement, and another system for smooth eye movements, stimulated by target velocity. Recent experiments (24) have suggested that spontaneous flicks occurring during fixation and voluntary tracking saccades are produced by the same mechanism, and hence that spontaneous flicks subserve the same functions as their voluntary counterparts, i.e., correct image displacement. Then, since a target at rest has no velocity, we are led to believe that (at least in the monocular case) any drifts occurring during the fixation of a stationary target are simply the result of instabilities in the oculomotor system, and that the resulting errors are subsequently corrected by flicks.

Cornsweet (4) attacked this problem in detail: the eye movements of two subjects were studied when monocularly fixating a stationary vertical line; only horizontal eye movements were recorded. As evidence that drifts are noise, he advanced the following points: the drift rate was the same under normal and stabilized vision, as well as in the absence of a target; the drift rate was not a function of the displacement of the visual axis from the mean position; and drifts on the average moved the visual axis away from the center of fixation. On the other hand, flick direction and magnitude were such as to decrease the fixational error, especially at large values of the error, and there were about half as many flicks in stabilized vision as in normal vision. It was thus concluded that drifts were noise -- perhaps instabilities in the oculomotor system -- and that flicks were on the average corrective.

Nachmias (12) extended the Cornsweet experiment by measuring the vertical as well as the horizontal component of eye motions as the subject fixated stationary cross hairs. The eye movements were decomposed into the sum of motions along eight retinal meridia to ascertain the extent of the motion in any direction. It was found that flicks correct for fixational errors along certain meridia, but in those directions where compensation by flicks is poor, correction by drifts becomes appreciable. Moreover, in a subsequent experiment (13), the drift rate was found to increase when the fixation mark was extinguished or brought closer to the subject. Thus, to describe drifts as merely noise during monocular fixation is no longer adequate. Further, measurements made on spontaneous flicks by Beeler (2) and Boyce (3) have shown that at most 30 percent of these played a corrective rôle other than by chance.

In view of the wide disparity between results obtained by various authors, it behooves us to re-examine the whole problem of the relative role of flicks and drifts in the maintenance of monocular fixation on a stationary target. All of the authors mentioned above have argued their case by citing various corrective criteria. First, we will define very precisely just what is meant by the word "correction." We will measure a large number of flicks and drifts and we will perform statistical tests to determine whether there exists any significant relationship between the corrective action brought about by eye movements and the fixational errors at the beginning of those motions. We will study the problem for the horizontal direction only, then for the vertical, and finally for both together.

When the case for monocular fixation has been clarified, we will extend our investigations to binocular fixation, where we will consider the mechanisms which correct the disparity between the two visual axes (either in horizontal vergence or in vertical discrepancy) in addition to that amount of correction brought about by two parallel monocular mechanisms.

Yarbus (23) has shown that when the point of fixation is changed from a far point off the primary position to a nearer one in the primary position, the eyes perform a continuous smooth convergence movement interrupted by a conjugate saccade. Riggs and Niehl (19) also showed that if the fixation target is brought closer along the line of sight of one eye so that only the other eye need move, there will nevertheless be smooth convergent movements in both eyes followed by a conjugate saccade to correct the side-to-side error. Rashbass and Westheimer (15, 16) have demonstrated the independence of the conjugate and the vergence mechanisms during tracking tasks. In their experiment, both types of movements occurred with no observable interaction, and the velocity of the convergent movement was proportional to the retinal image disparity. Thus, the study of the binocular stationary fixation mechanism must take into consideration the two independent control systems for conjugate and for vergence motions.

Krauskopf, Cornsweet, and Riggs (10) examined vergence correction during fixation on a stationary vertical line. They dismissed drifts as noise, and therefore concentrated on correction of vergence by flicks. Flicks always occur in both eyes simultaneously and are of approximately the same direction and magnitude. However, if the nasalward movement of one visual axis is greater than the simultaneous temporalward movement of the other, the result is an increase in the convergence of the visual axes. Such a pair of flicks will be noted as "convergent" in spite of the fact that flicks are seldom convergent in the sense that they move in opposite horizontal directions. Krauskopf, et al. (10) found that the percentage of such "convergent" flicks increased with increasing vergence error of the visual axes, but that neither the magnitude of the resulting vergence correction nor the probability of the occurrence of flicks were functions of the vergence error. If the vergence correction is not a function of the vergence error, it is difficult to understand how the motion can be identified as corrective, and their conclusion that vergence error is not a stimulus for corrective flicks but that the vergence mechanism during fixation consists of two parallel monocular flick mechanisms, appears to be confused. Moreover, in view of the fact that the vergence mechanism operates by means of smooth movements, their dismissal of drifts as noise is most unfortunate.

In the next chapter, we will investigate the mechanisms of eye movement control during binocular stationary fixation. We will pay particular attention to the relative actions of flicks and drifts, and we will strictly differentiate those mechanisms which correct binocular discrepancies between the two visual axes from those which correct monocular fixational errors. We will, moreover, deal with the variations of eye movement parameters which might be expected between one subject and another, for we believe that the pattern of eye motions is characteristic of an individual and that any attempt at model-making must be tempered by the wide inter-subject differences which occur in this work. The conformation of the fixation target also has a profound influence on the involuntary eye movements in some cases: we will describe the effect of a limited number of fixation target structures -- point, vertical line, and horizontal line.

REFERENCES FOR CHAPTER III

1. Barlow, H. B., "Eye movements during fixation," J. Physiol., Lond. 116 (1952), pp. 290-306.

2. Beeler, G. W., "Stochastic Processes in the Human Eye Movement Control System," Doctoral Dissertation, California Institute of Technology (1965).

3. Boyce, P., "Monocular fixation in human eye movements," Proc. Roy. Soc. B167 (1967), pp. 293-315.

4. Cornsweet, T., "Determination of the Stimuli for Involuntary Drifts and Saccadic Eye Movements," J. Opt. Soc. Amer. 46 (1956), pp. 987-993.

5. Ditchburn, R. and Foley-Fisher, J., "Assembled data in eye movements," Optica Acta 14 (1967), pp. 113-118.

6. Ditchburn, R. and Ginsborg, B., "Involuntary eye movements during fixation," J. Physiol., Lond. 119 (1953), pp. 1-17.

7. Dodge, R. and Cline, T. S., "The Angle Velocity of Eye Movements," Psychol. Rev. 8 (1901), p. 145.

8. Fender, D. H., "The Function of Eye Movements in the Visual Process," Ph. D. Dissertation, University of Reading (1956).

9. Helmholtz, H. von, Treatise on Physiological Optics, Vol. II, translated from the Third German Edition, edited by J. P. C. Southall. The Optical Society of America, George Banta Publishing Co., Menasha, Wisconsin (1924).

10. Krauskopf, J., Cornsweet, T., and Riggs, L., "Analysis of Eye Movements during Monocular and Binocular Fixation," J. Opt. Soc. Amer. 50 (1960), pp. 572-578.

11. Lord, M. and Wright, W., "Eye movements during monocular fixation," Nature, Lond. 162 (1948), pp. 25-26.

12. Nachmias, J., "Two-dimensional Motion of the Retinal Image During Monocular Fixation," J. Opt. Soc. Amer. 49 (1959), pp. 901-908.

13. Nachmias, J., "Determiners of the Drift of the Eye During Monocular Fixation," J. Opt. Soc. Amer. 51 (1961), pp. 761-766.

14. Rashbass, C. "The relationship between saccadic and smooth tracking eye movements," J. Physiol., Lond. 159 (1961), pp. 326-338.

15. Rashbass, C. and Westheimer, G., "Disjunctive eye movements," J. Physiol., Lond. 159 (1961), pp. 339-360.

16. Rashbass, C. and Westheimer, G., "Independence of conjugate and disjunctive eye movements," J. Physiol., Lond. 159 (1961), pp. 361-364.

17. Ratliff, F. and Riggs, L., "Involuntary Motions of the Eye During Monocular Fixation," J. Exp. Psychol. 40 (1950), pp. 687-701.

18. Riggs, L., Armington, J., and Ratliff, F., "Motions of the Retinal Image During Fixation," J. Opt. Soc. Amer. 44 (1954), pp. 315-321.

19. Riggs, L. and Niehl, E., "Eye Movements Recorded During Convergence and Divergence," J. Opt. Soc. Amer. 50 (1960), pp. 913-920.

20. Vossius, G., "Das System der Augenbewegung," Z. Biol. 112 (1960), pp. 27-57.

21. Westheimer, G., "Mechanism of Saccadic Eye Movements," Am. Med. Assoc. Archs. Ophthal. 52 (1954), p. 710.

22. Westheimer, G., "Eye Movement Responses to a Horizontally Moving Visual Stimulus," Am. Med. Assoc. Archs. Ophthal. 52 (1954), p. 932.

23. Yarbus, A., "Motion of the eye on interchanging fixation points at rest in space," Biofizika 2 (1957), pp. 698-702.

24. Zuber, B. and Stark, L., "Microsaccades and the velocity-amplitude relationship for saccadic eye movements," Science 150 (1965), pp. 1459-1460.

IV. INTERPLAY OF FLICKS AND DRIFTS IN BINOCULAR FIXATION

A. Stimulus

Two parallel optical systems were used to present identical stimuli to the left and to the right eye simultaneously, as described in Chapter II (section 2.4). Each target consisted of a 35 mm transparency placed in the focal plane of the collimator, as shown in Figure 2.5.

Three stimuli were used: a vertical line, a horizontal line, and a small illuminated circular aperture. The lines were black bars 3 min arc wide and 7° long on a bright background; the background gradually graded into a dark field at the ends of the line so that no fixation cues could be obtained along the length of the lines. The circular aperture was 2 min arc in diameter. The background luminance of the bars and the luminance of the aperture were 24 cd/m^2. Prior to each run, the left and right sources were turned off and on alternately at about 1 sec intervals. Unless both targets were in the proper position to be fused, the image seen by the subject appeared to move as one light was turned off and the other one was turned on. The subject adjusted the target positions until no apparent target motion could be detected. The appropriate light sources were then turned on and the recording began. The subject was instructed to view the target as steadily as possible, but in such a manner as to keep the target visible at all times.

The eye movements were recorded on analog and digital tape, as described in sections 3 and 4 of Chapter II. The sampling rate was

125 samples per channel per second.

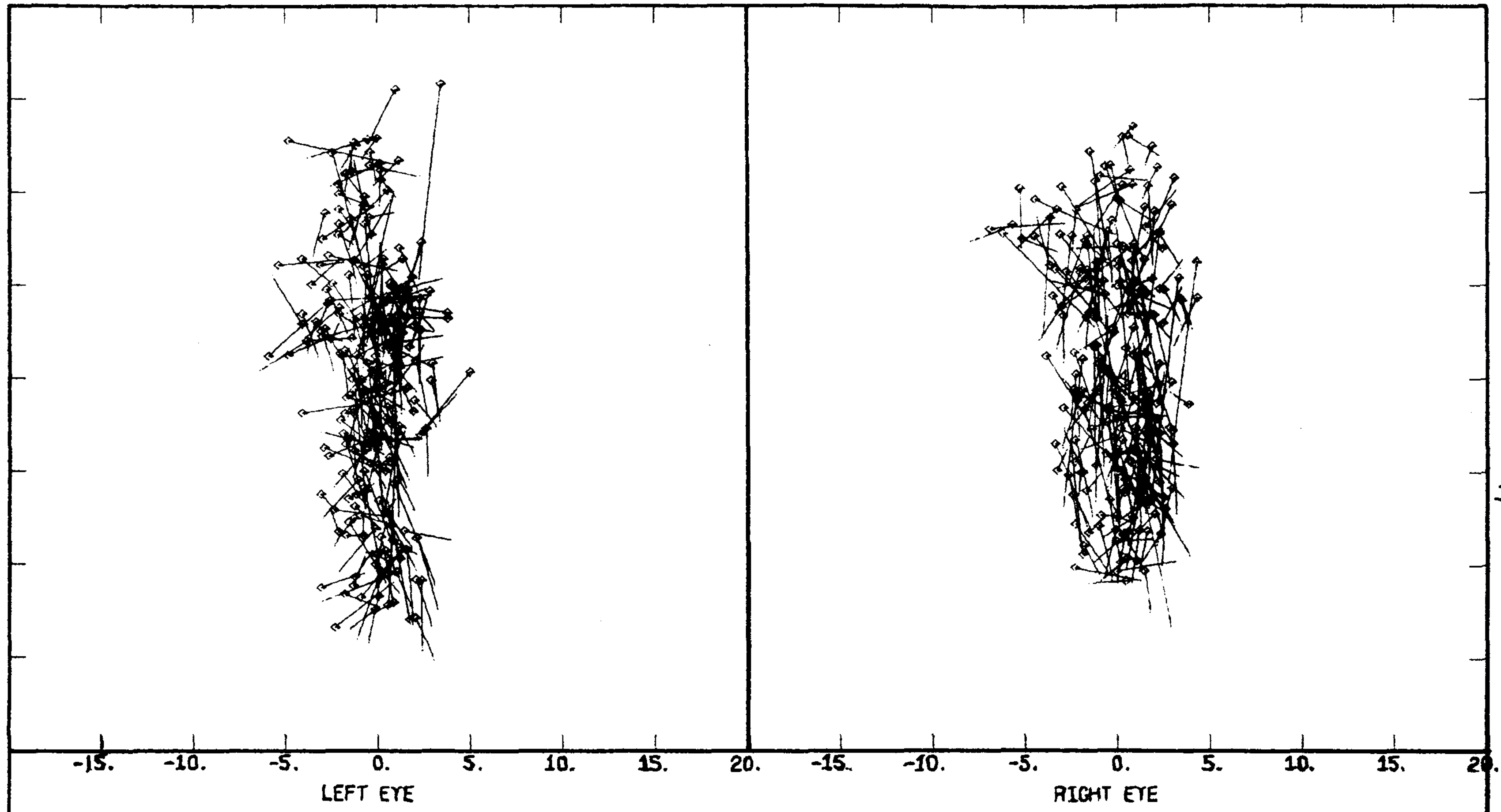
A FORTRAN computer program was used to search all 4 channels, one at a time, for the occurrence of flicks. These were defined as changes of at least 1.0 min arc occurring within 40 ms. For each suspected flick, the time of occurrence and the angular position of the visual axes before and after the flick were computed. The list was then checked by eye against the time record of the eye movements to insure that only genuine flicks were recorded. Blinks, rapid drifts, and random noise were detected sometimes as flicks: after these spurious events had been discarded, the analysis was begun.

B. Results

1. General Characteristics of Eye Movements During Fixation

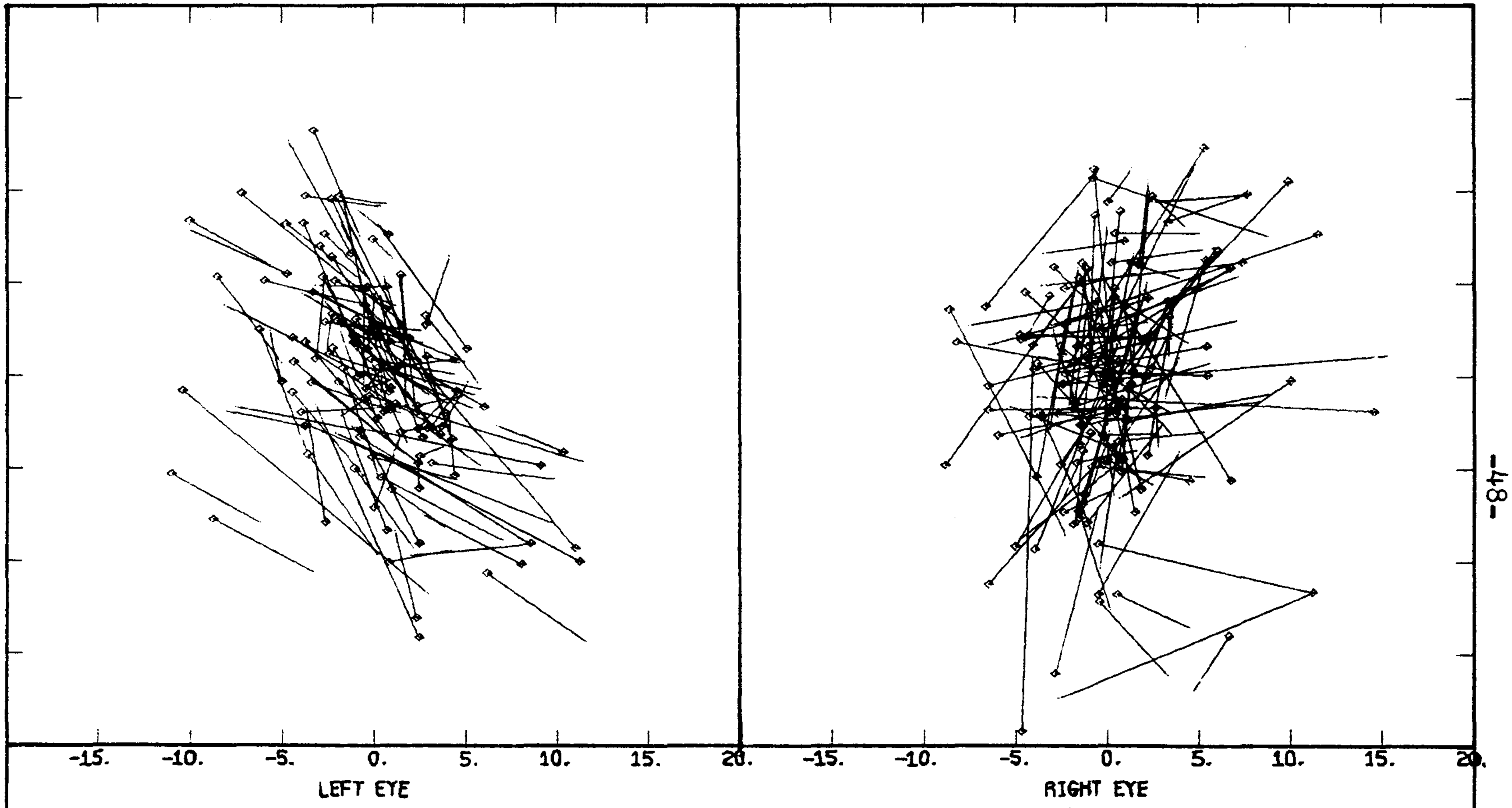
There are many problems involved in the adequate pictorial presentation of two-dimensional eye movements for two eyes simultaneously. "Pin-diagrams" are perhaps the most graphic for an overall view. An array of these diagrams for two subjects viewing three different types of target in binocular conditions is illustrated in Figure 4. 1. Each straight line in the diagram illustrates the path swept by the visual axis during one flick; the blob indicates the end-point. The flicks are illustrated in their correct translation positions, but the temporal sequence of events is lost in this display, so that no drift information can be obtained from these diagrams.

We wish to treat these displays in more detail under a number of headings, viz.: the flick motion, the drifting motion, and the overall fixation pattern. Incidentally, we will examine the influence of the



<u>Figure 4.1(a)</u>: Flick trajectories (Binocular fixation)
Vertical line target
Subject GSC

(Scale in min arc)



<u>Figure 4.1(b)</u>: Flick trajectories (Binocular fixation)
Vertical line target
Subject DSG

(Scale in min arc)

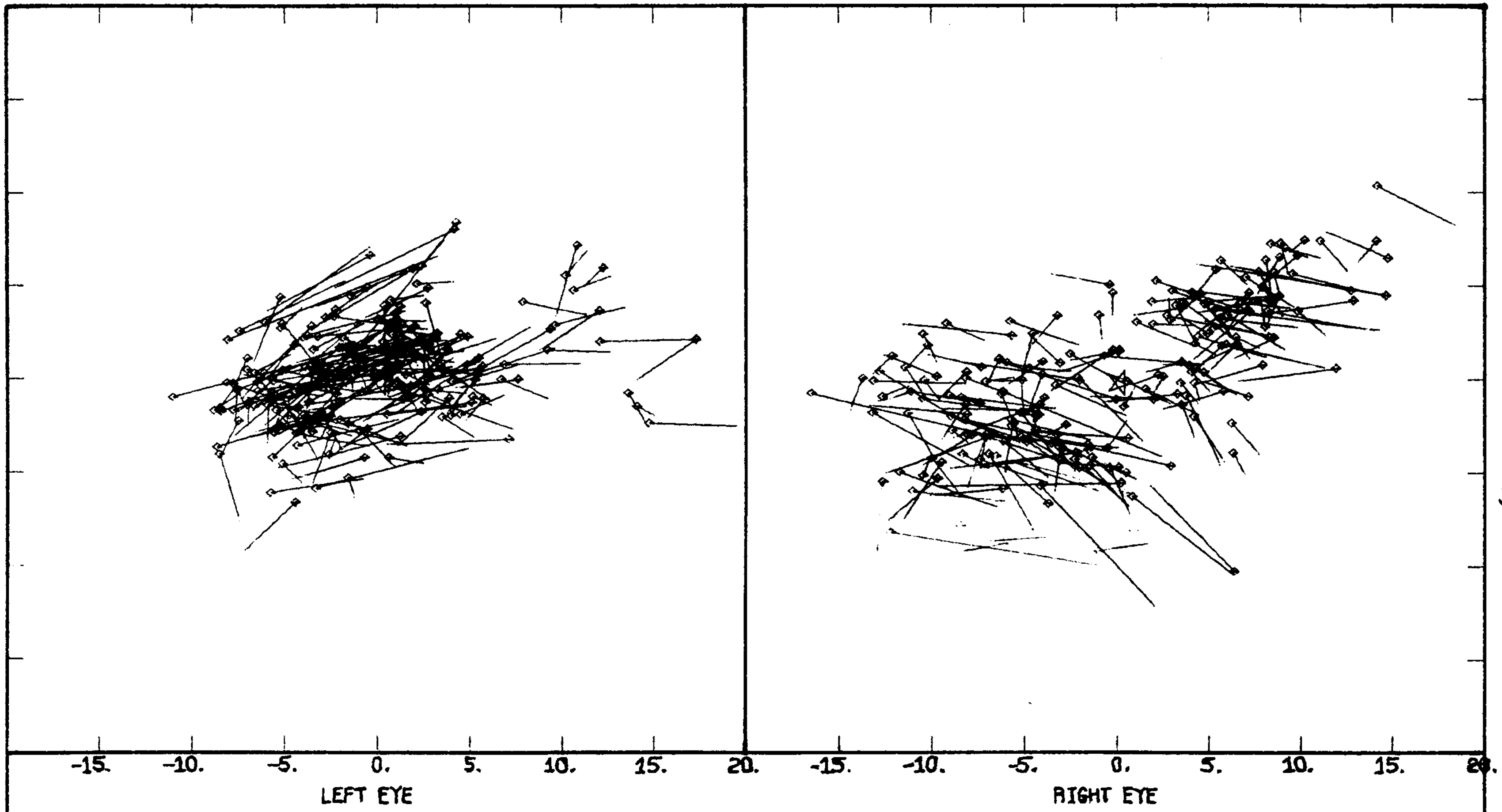
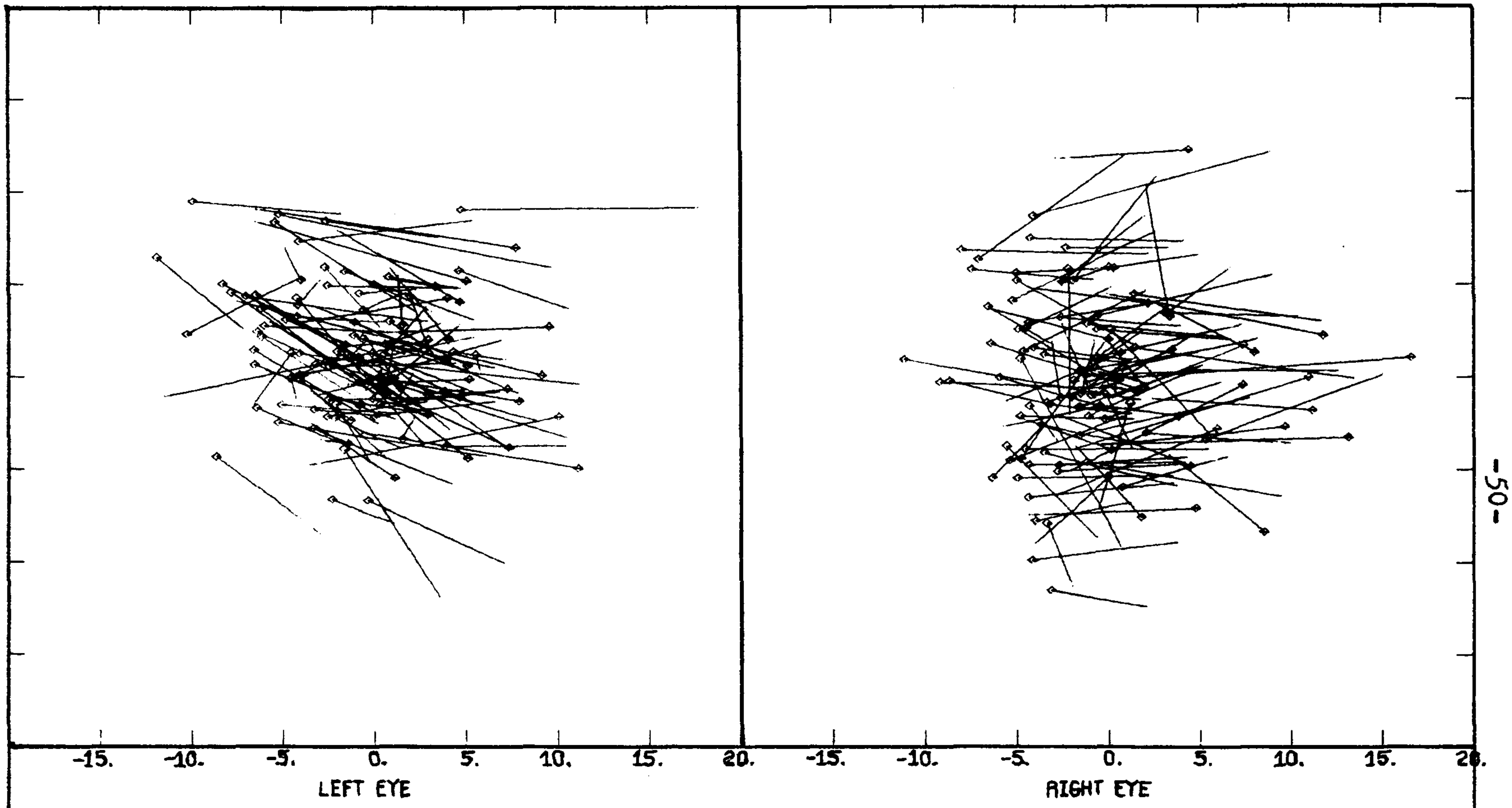


Figure 4.1(c): Flick trajectories (Binocular fixation)
Horizontal line target
Subject GSC

(Scale in min arc)



<u>Figure 4.1(d)</u>: Flick trajectories (Binocular fixation)
Horizontal line target
Subject DSG

(Scale in min arc)

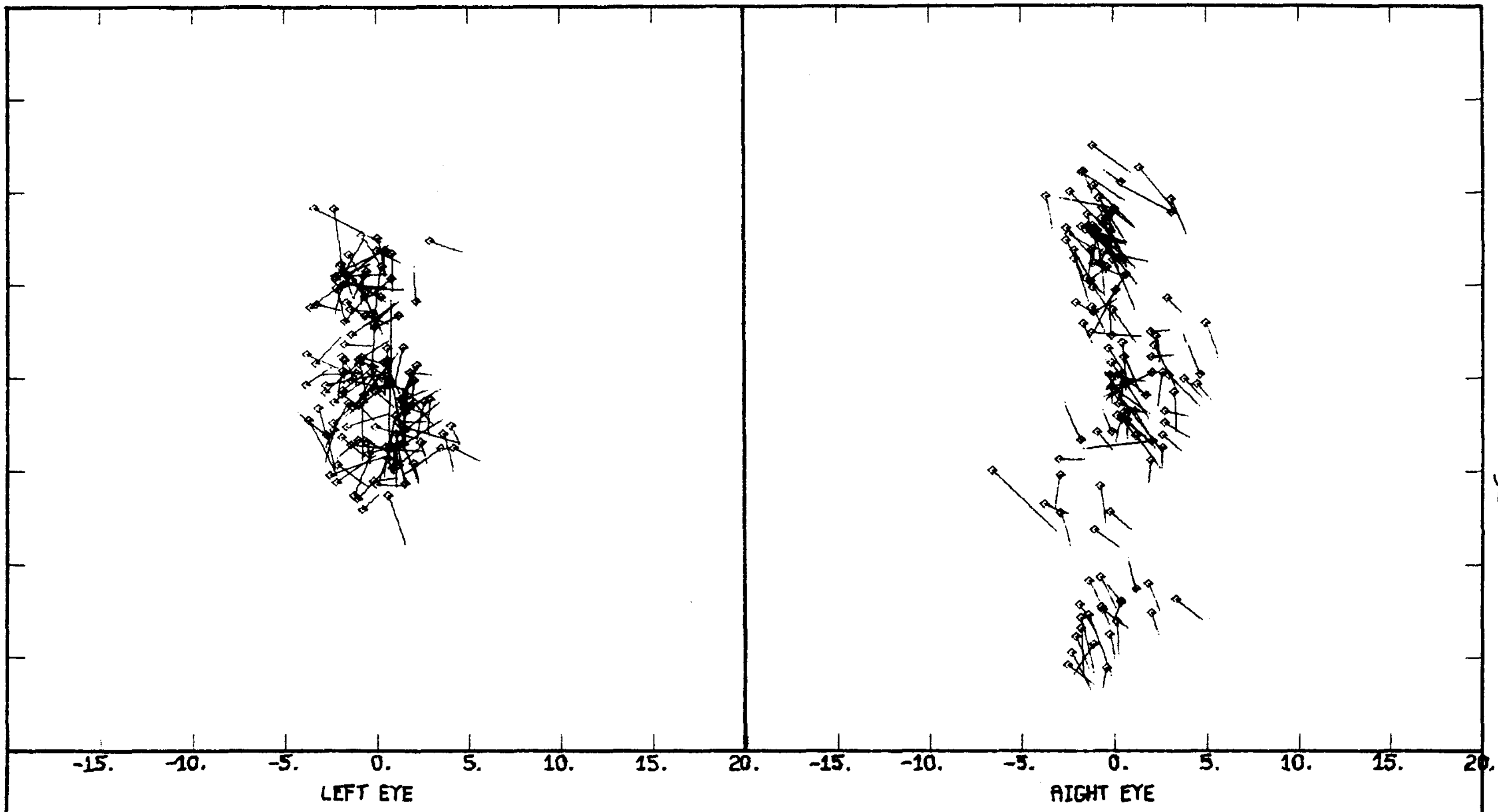


Figure 4.1(e): Flick trajectories (Binocular fixation)
Point target
Subject GSC

(Scale in min arc)

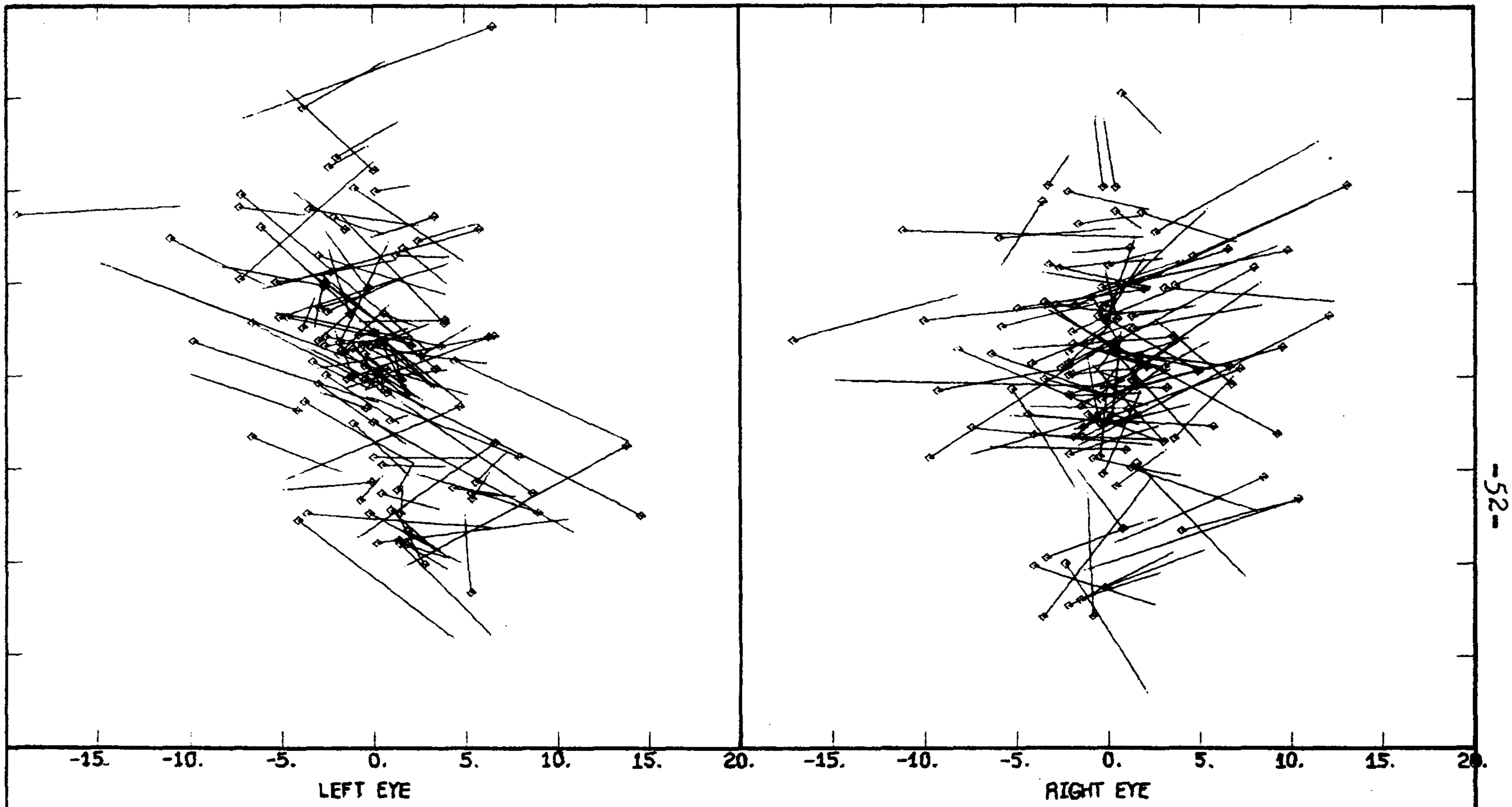


Figure 4.1(f): Flick trajectories (Binocular fixation)
Point target
Subject DSG

(Scale in min arc)

target structure on the fixation pattern, inter-subject differences, and the correlation between the motions of the visual axes.

1.1 An examination of the flicks.

1.1.1 Binocular fixation. The directions of the flicks for the two eyes are shown in Figure 4.2. The direction of the flick for the right eye is plotted against that for the left. Broadly speaking, the points lie close to the line of unit slope, so apparently the directions of the flicks are fairly well correlated between the two eyes.

Table 4-1 presents mean values and standard deviations of certain differences between the left and right flick vectors; the actual difference in direction (degrees), the retinal disparity resulting from pairs of flicks (min arc), and the ratio of the magnitudes of flick pairs.

For both subjects, the values of the magnitude ratios are closer to unity for the line targets than for the point target. The surprisingly large value of the mean difference in flick directions for both subjects arises mainly from the smallest flicks, as indicated by the symbols in Figure 4.2.

It is obvious from Figures 4.1 and 4.2 that the flick directions depend both on the subject and on the target. For subject GSC, the nature of the target has a marked influence: a vertical line target gives rise to flicks which are directed mainly upward; a horizontal line target generates flicks to the left and to the right; a point target results in flicks upward and to the left. Subject DSG has quite a different response pattern. Whatever the target, he flicks mainly to the left, with a smaller number of flicks to the right; a vertical line tar-

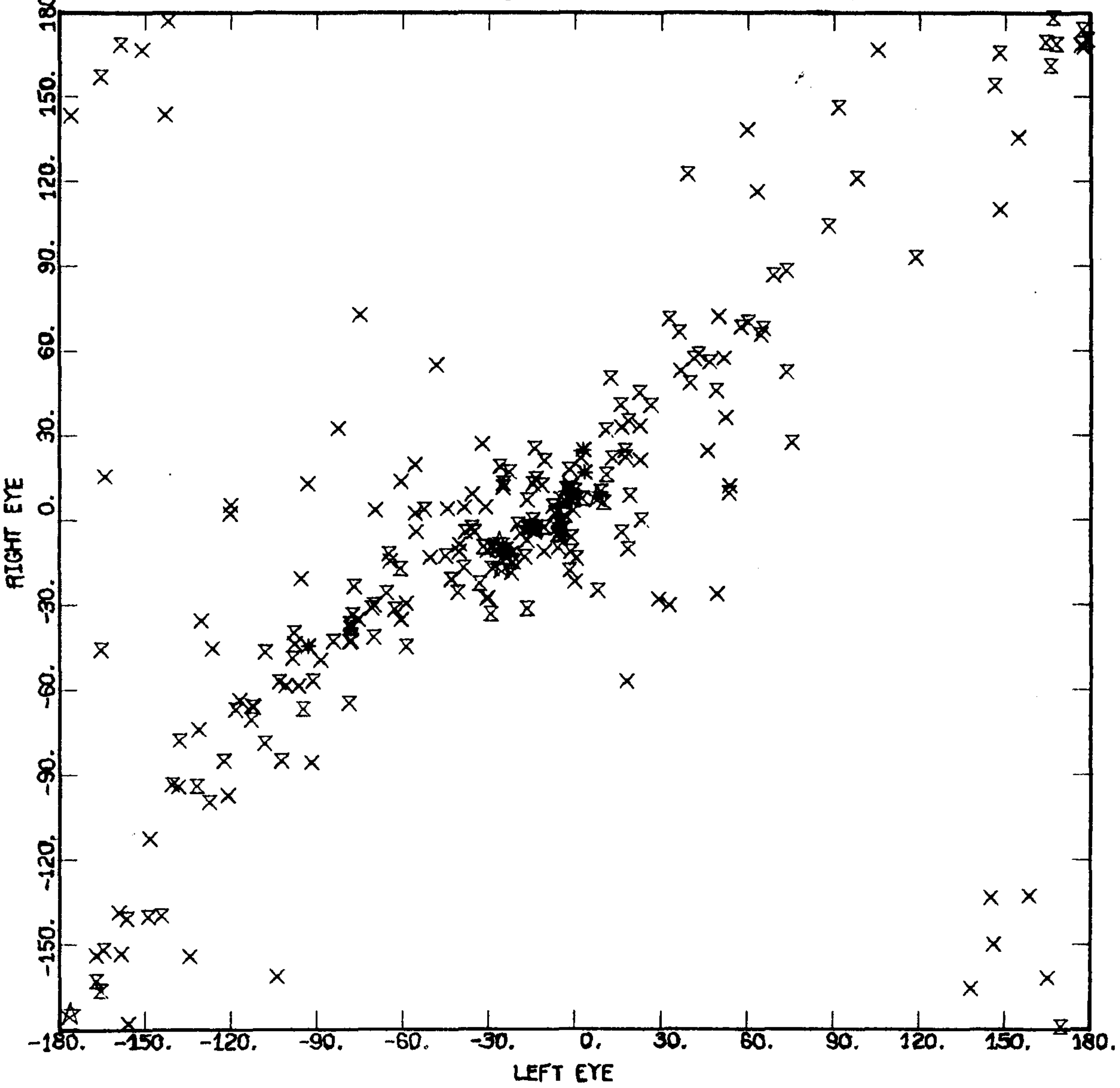
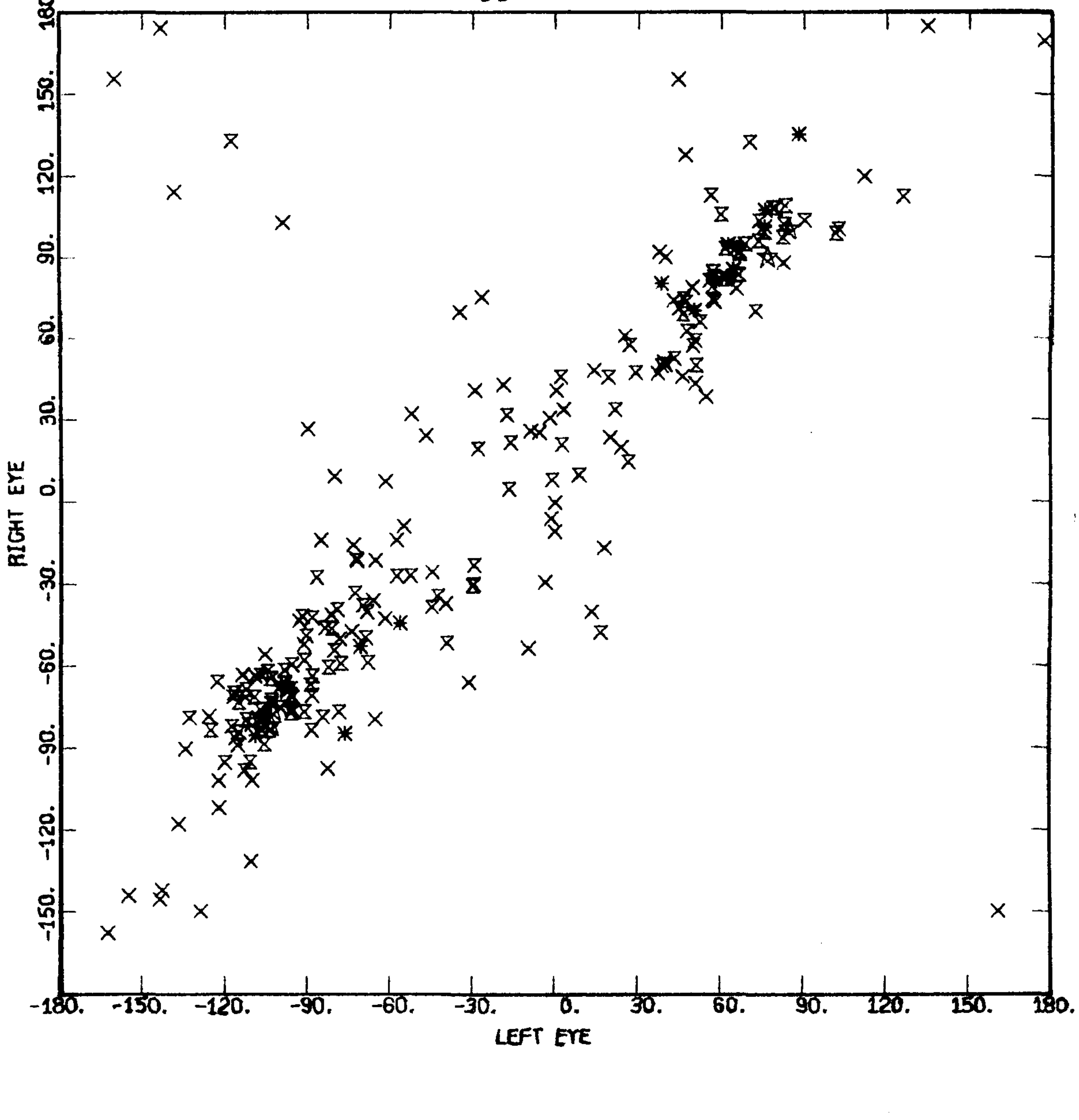


Figure 4.2(a): Flick direction histogram (degrees)
Binocular fixation
Vertical line target
Subject GSC

0° = up
90° = right
-90° = left
±180° = down

Symbol indicates flick size:

X = less than 3 min arc
X̄ = 3 - 6 min arc
⧖ = 6 - 9 min arc
* = 9 -12 min arc
✱ = more than 12 min arc



<u>Figure 4.2(b)</u>: Flick direction histogram (degrees)
Binocular fixation
Horizontal line target
Subject GSC

(Legend on Fig. 4.2(a))

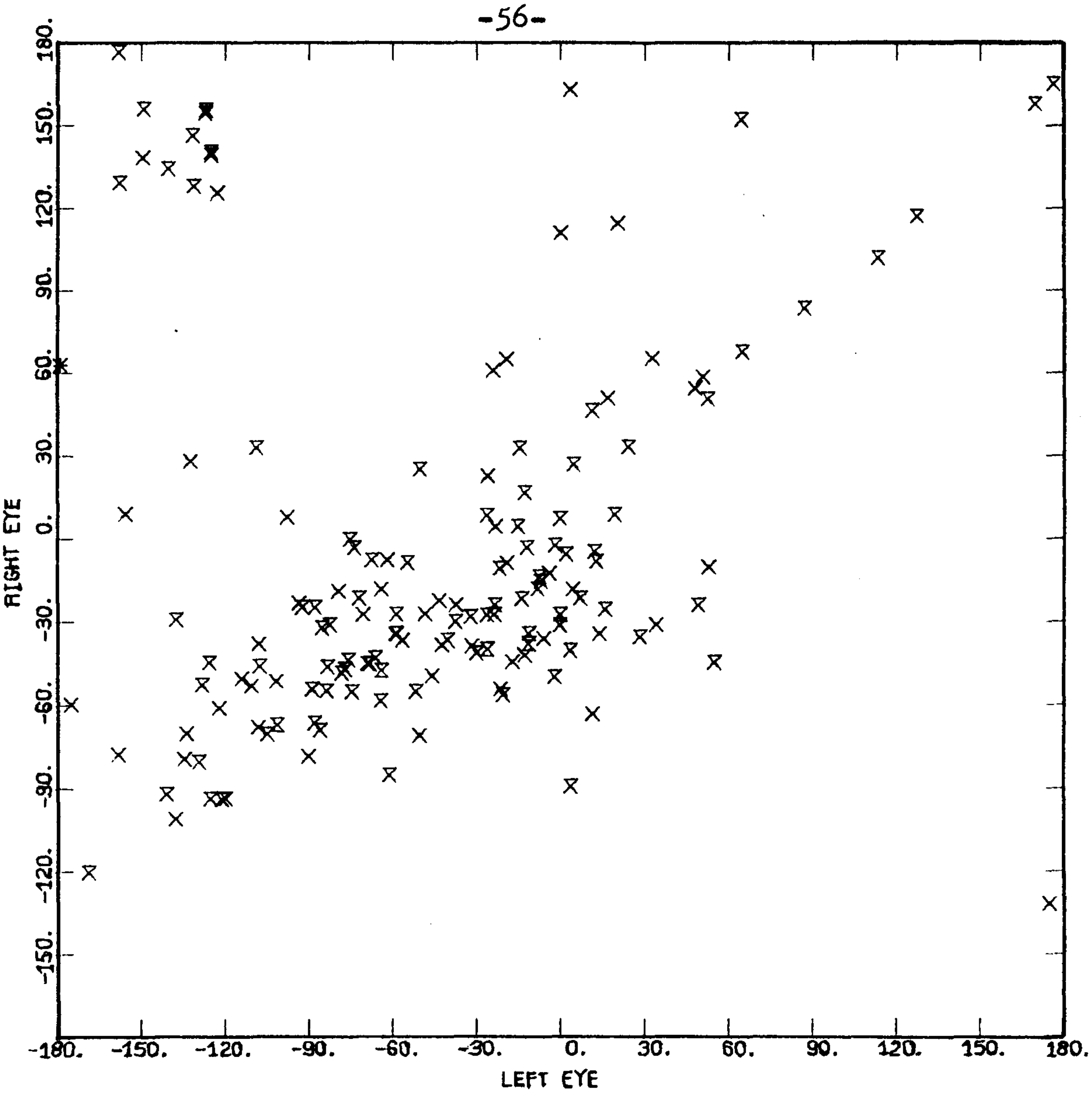


Figure 4.2(c): Flick direction histogram (degrees)
Binocular fixation
Point target
Subject GSC

(Legend on Fig. 4.2(a))

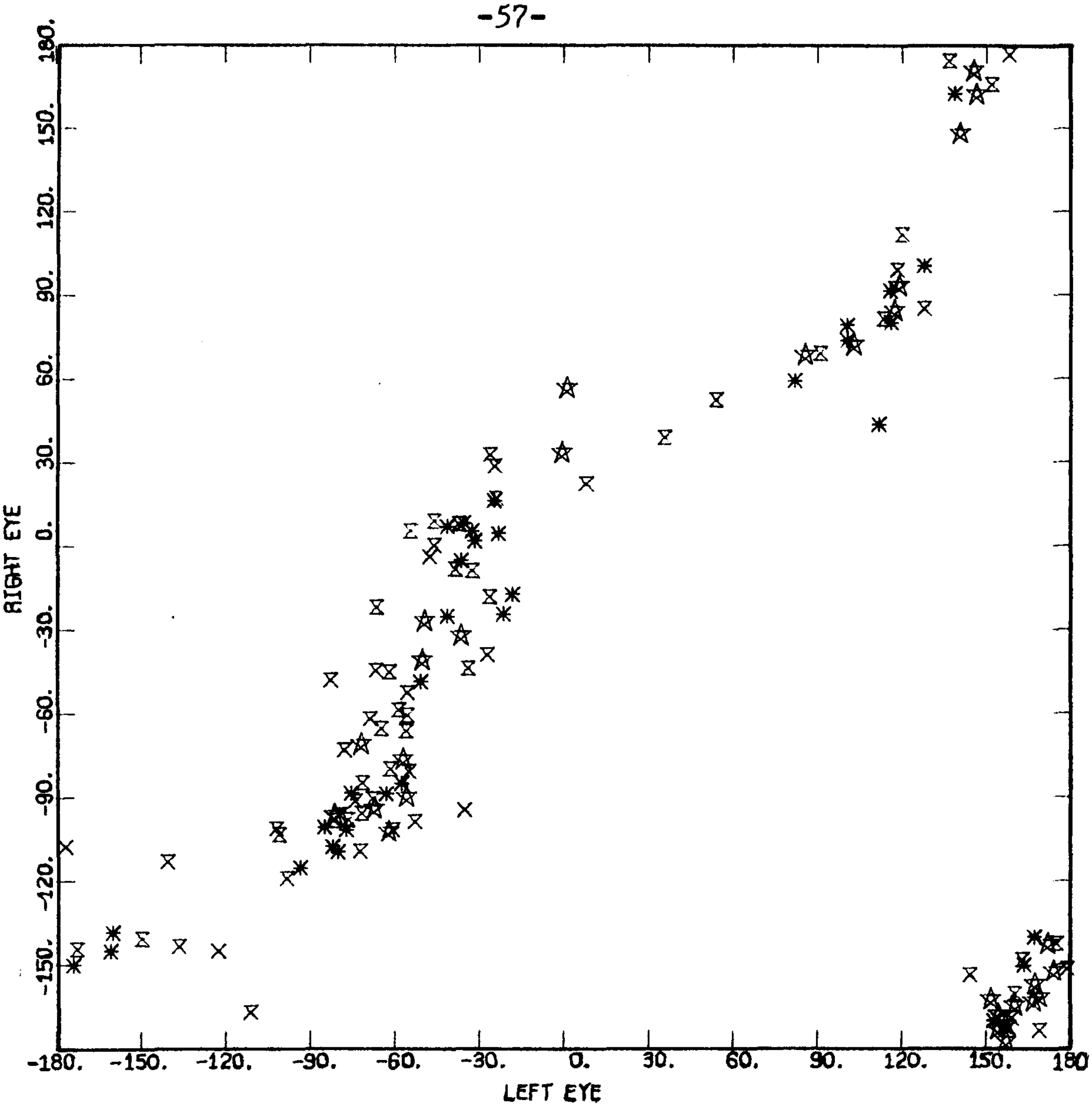


Figure 4.2(d): Flick direction histogram (degrees)
Binocular fixation
Vertical line target
Subject DSG

(Legend on Fig. 4.2 (a))

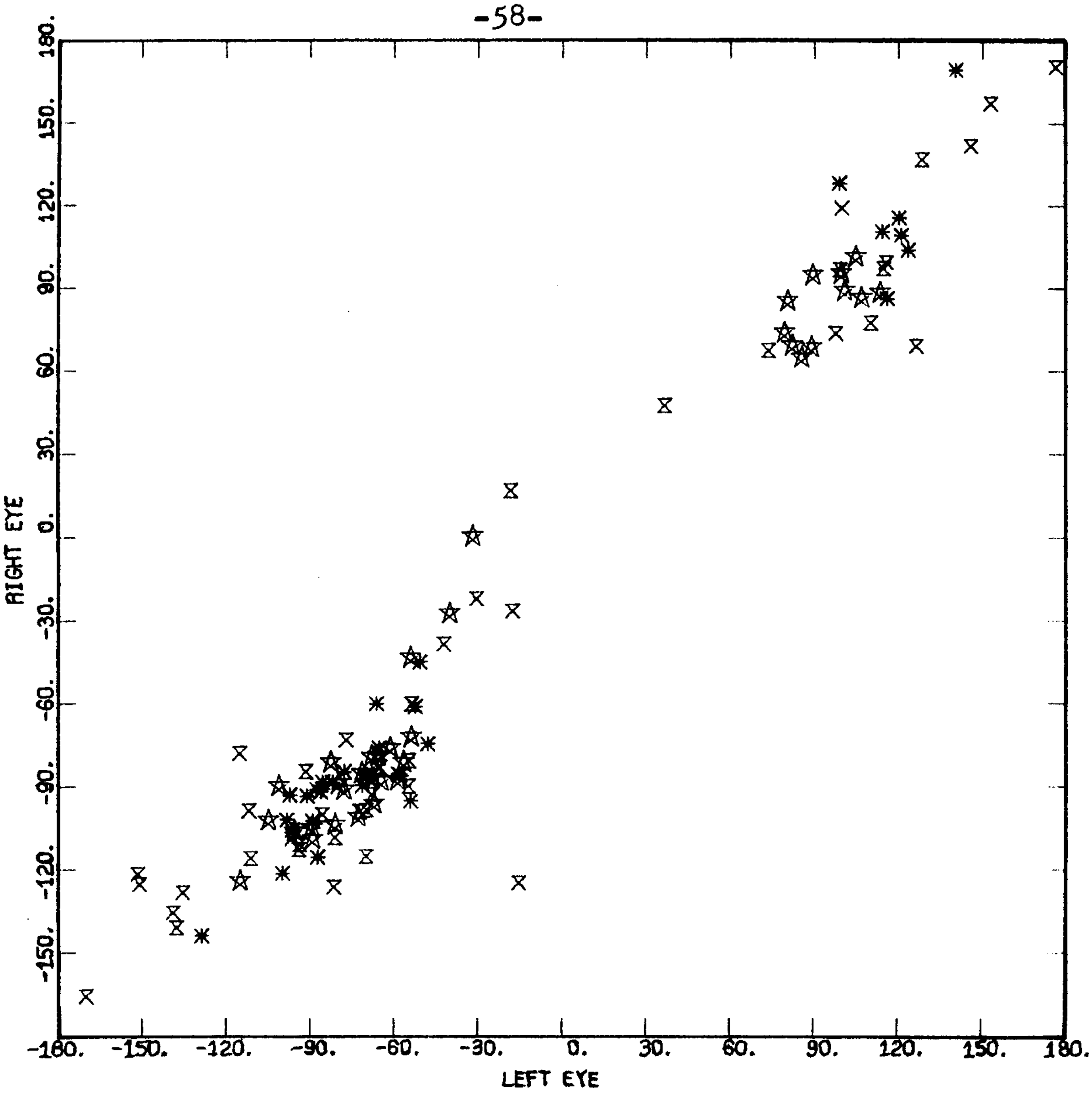


Figure 4.2(e): Flick direction histogram (degrees)
Binocular fixation
Horizontal line target
Subject DSG

(Legend on Fig. 4.2(a))

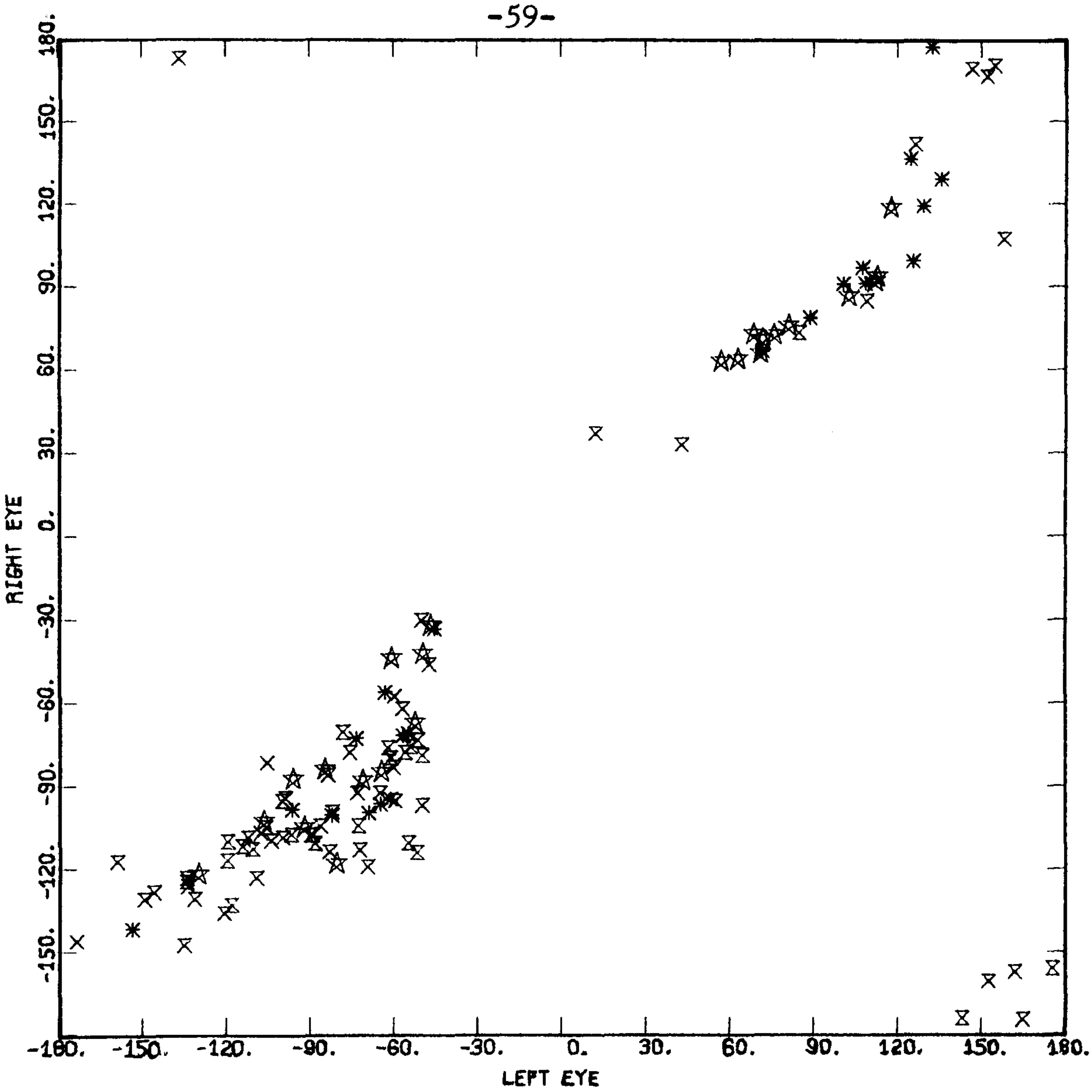


Figure 4.2(f): Flick direction histogram (degrees)
Binocular fixation
Point target
Subject DSG

(Legend on Fig. 4.2(a))

TABLE 4-1. Differences Between the Flicks of the Left and Right Eyes

(A) BINOCULAR FIXATION

Target		GSC					DSG				
		Difference in direction (degrees)		Retinal disparity caused by flicks (min arc)		Ratio of magnitudes (right/left)	Difference in direction (degrees)		Retinal disparity caused by flicks (min arc)		Ratio of magnitudes (right/left)
L	R	Mean	σ	Mean	σ		Mean	σ	Mean	σ	
|	|	30.5°	27.5°	1.53	0.97	1.308	27.1°	15.9°	4.11	2.49	0.940
—	—	31.0°	23.2°	1.77	1.12	1.035	16.9°	14.3°	2.89	1.47	0.933
•	•	43.6°	35.0°	1.48	1.06	0.555	17.3°	13.8°	2.60	1.45	0.818

(B) DICHOPTIC FIXATION

L	R	Mean	σ	Mean	σ		Mean	σ	Mean	σ	
|		34.4°	31.8°	2.02	1.14	1.428	27.3°	20.2°	5.05	3.43	1.248
	|	31.5°	25.5°	1.60	0.83	1.111	25.3°	20.8°	3.83	1.96	0.949
—		35.8°	28.5°	1.93	1.08	1.142	16.9°	10.4°	3.14	1.69	0.982
	—	34.0°	27.4°	1.71	0.90	0.989	18.8°	17.1°	3.87	2.48	0.882
•		40.2°	32.3°	1.54	0.94	1.782	18.7°	18.1°	3.21	1.92	0.987
	•	36.4°	33.0°	1.30	0.80	0.776	16.6°	13.5°	2.60	1.31	0.907

get generates a few up-and-down flicks in addition. However, the structure of the target has little influence on the mean value of the retinal disparity shown in Table 4-1A except perhaps in the case of subject DSG, when the orientation of the vertical line target conflicts with his preferred direction of flicking to the left.

1.1.2 Dichoptic viewing. If only one eye sees the target while the other views a dark, blank field, the fixational pattern changes somewhat, as can be seen from the pin-diagrams (Figures 4-3 and 4-4); but measurement shows that the flick directions do not change. Table 4-1B shows that the mean difference in direction between left and right flicks does not change much. The retinal disparity on the average gets marginally larger, although the significance of the change is not high. If we regard the ratios obtained when both eyes see the target as representing the normal bias between the eye motions for each subject, then we find that in dichoptic viewing the motion of the eye which does not see the target increases in 9 cases out of 12.

1.2 Examination of the drifting motions.

1.2.1 Binocular fixation. In this chapter, a drift is treated as the vector displacement of the visual axis from the end of one flick to the onset of the next.

Table 4-2 lists parameters for these drift vectors similar to those parameters given for flick vectors in Table 4-1. Comparing these values with the results for flicks, it is evident that the angles between the drift directions are much larger. In most cases, the mean value for retinal disparity is also larger for drifts than for

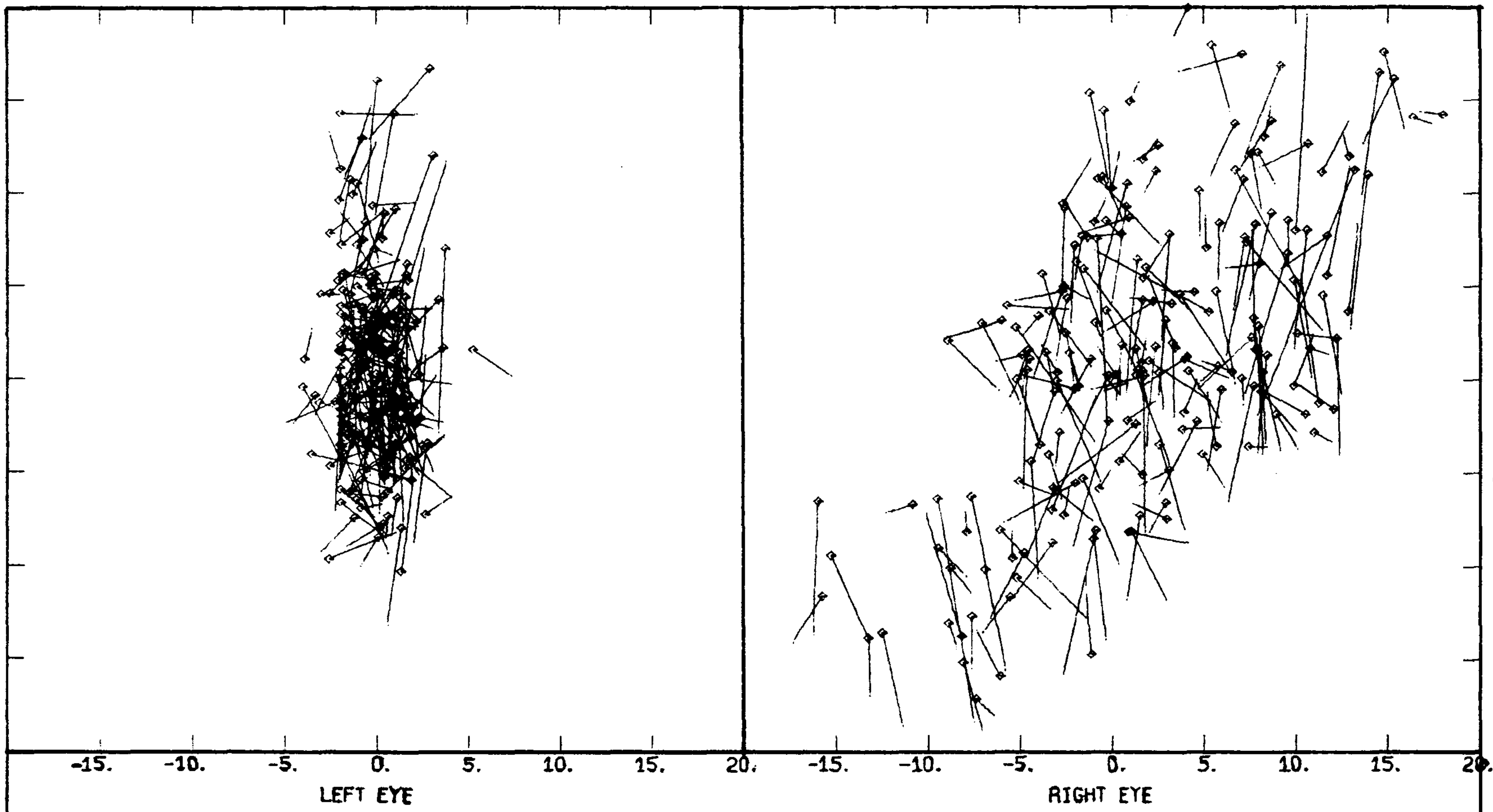


Figure 4.3(a): Flick trajectories (Monocular fixation: LEFT EYE)
Vertical line target
Subject GSC

(Scale in min arc)

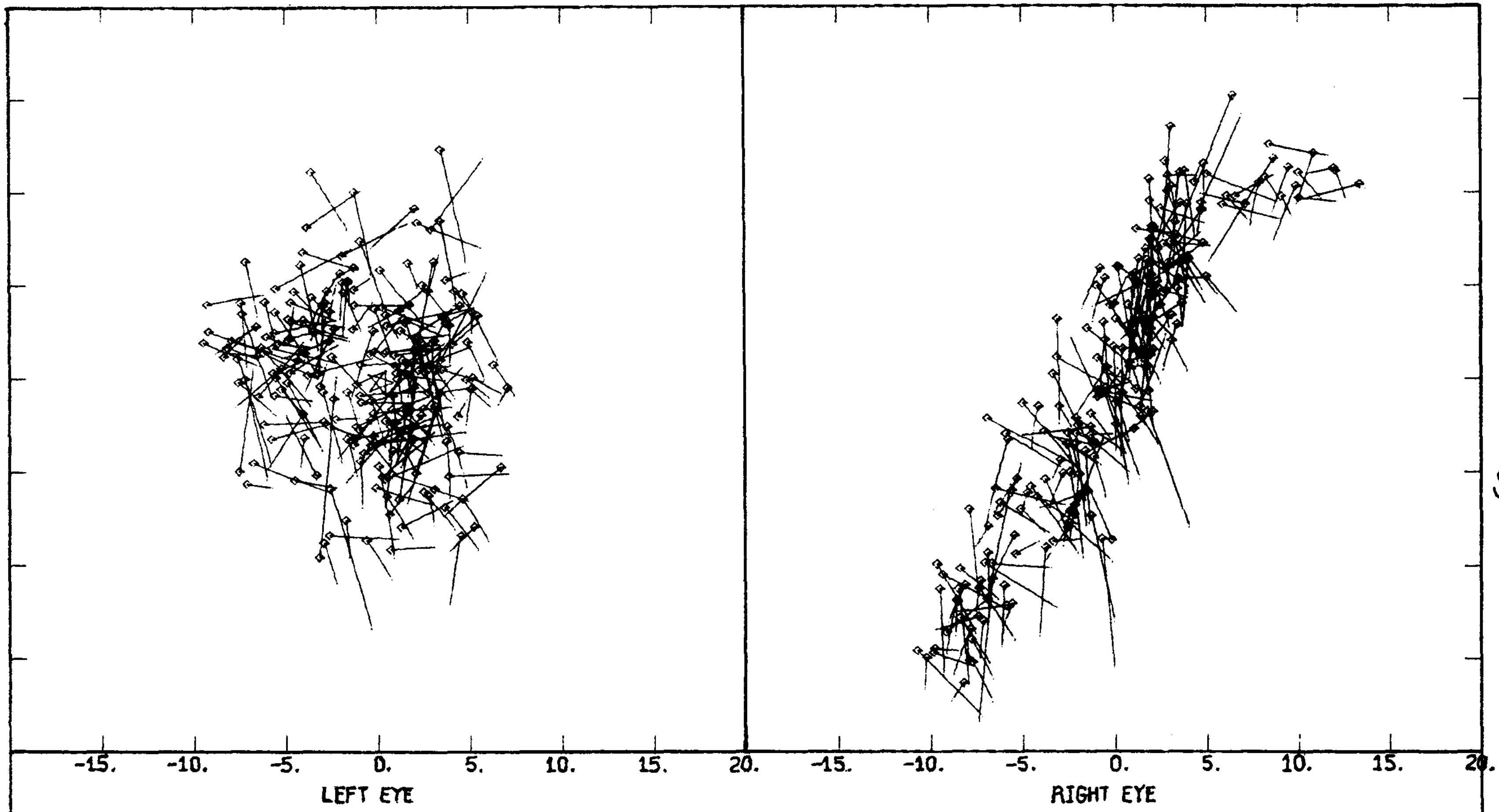


Figure 4.3(b): Flick trajectories (Monocular fixation: RIGHT EYE)
Vertical line target
Subject GSC

(Scale in min arc)

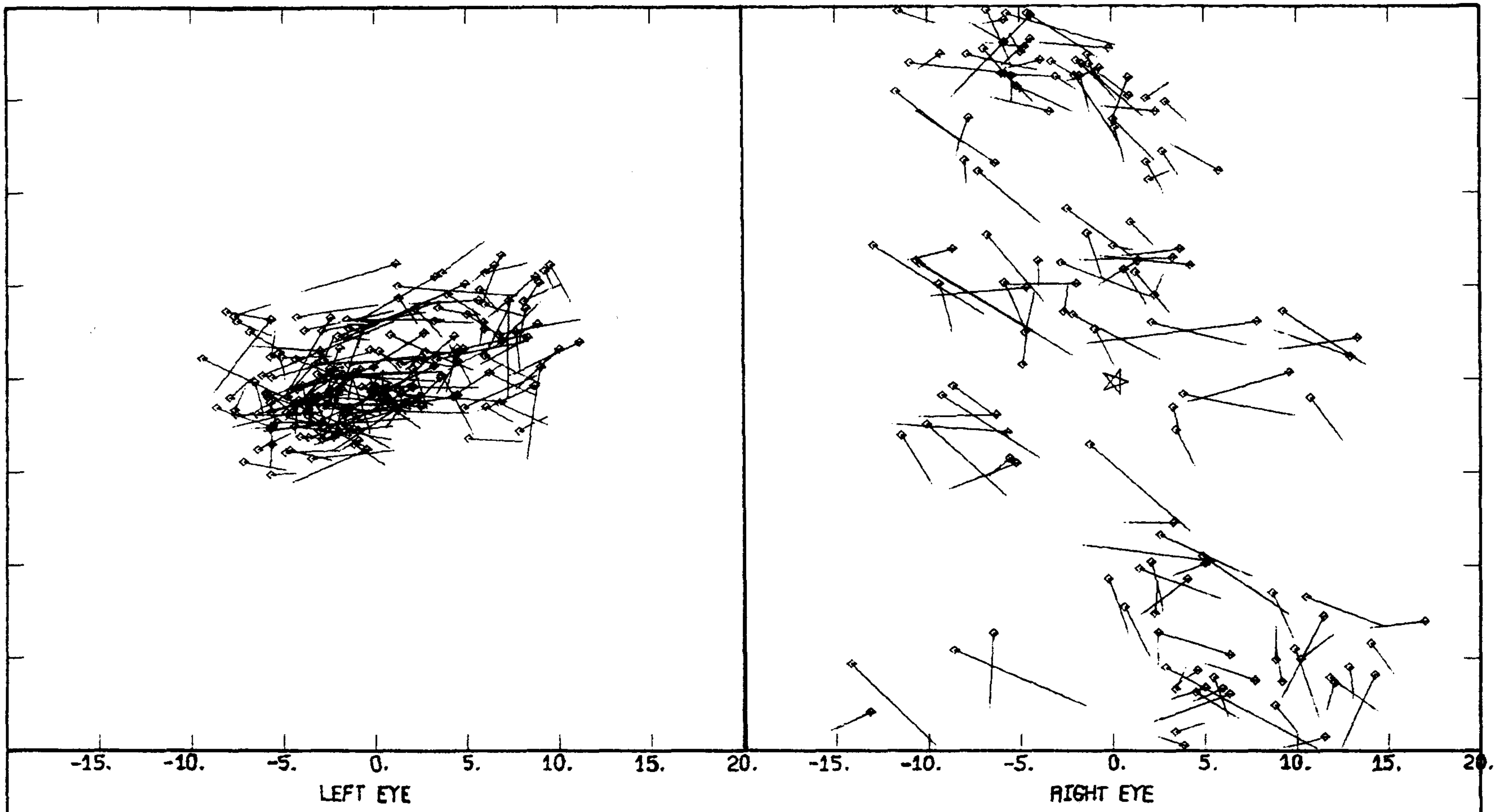


Figure 4.3(c): Flick trajectories (Monocular fixation: LEFT EYE)
Horizontal line target
Subject GSC

(Scale in min arc)

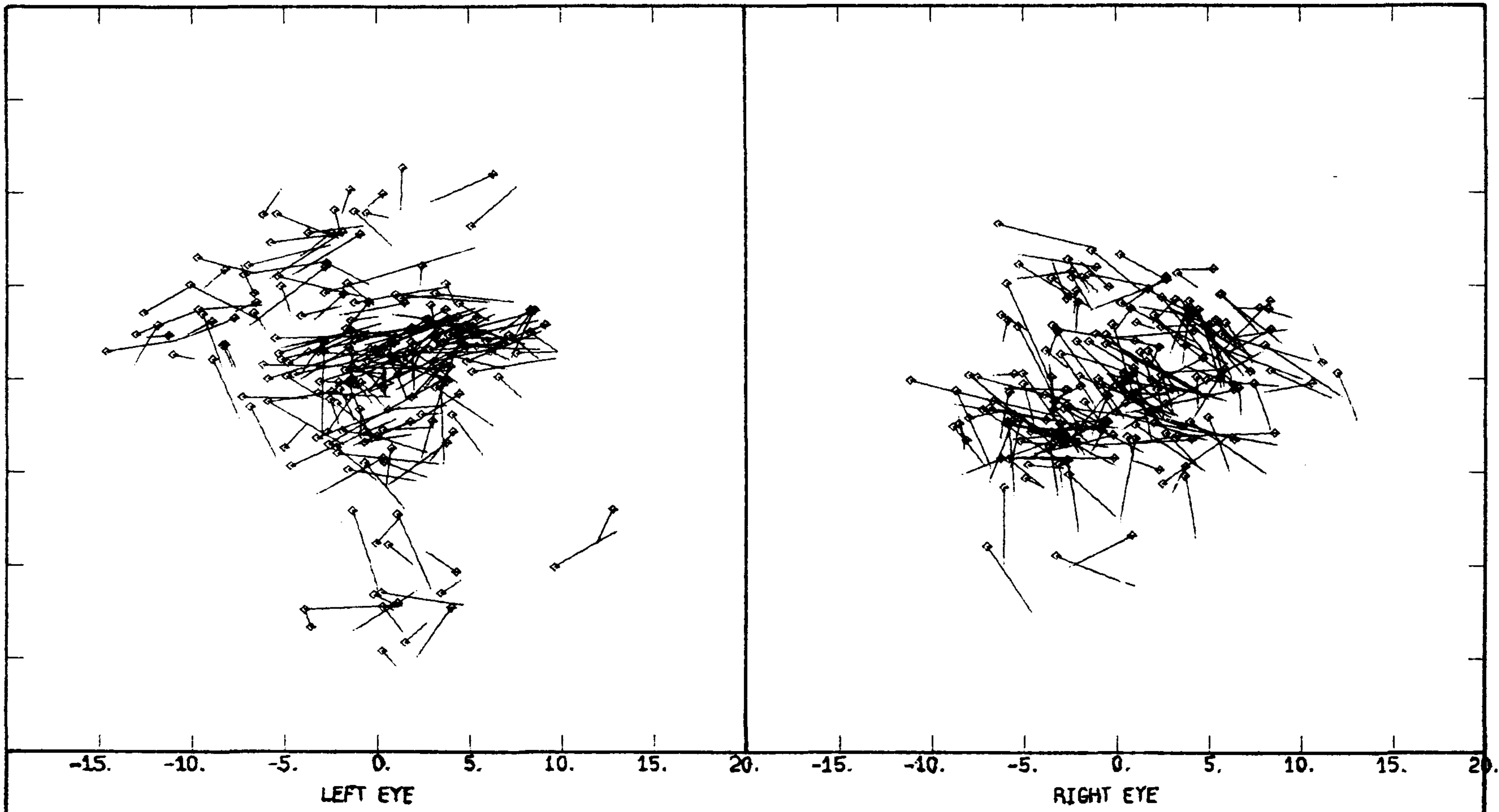


Figure 4.3(d): Flick trajectories (Monocular fixation: RIGHT EYE)
Horizontal line target
Subject GSC

(Scale in min arc)

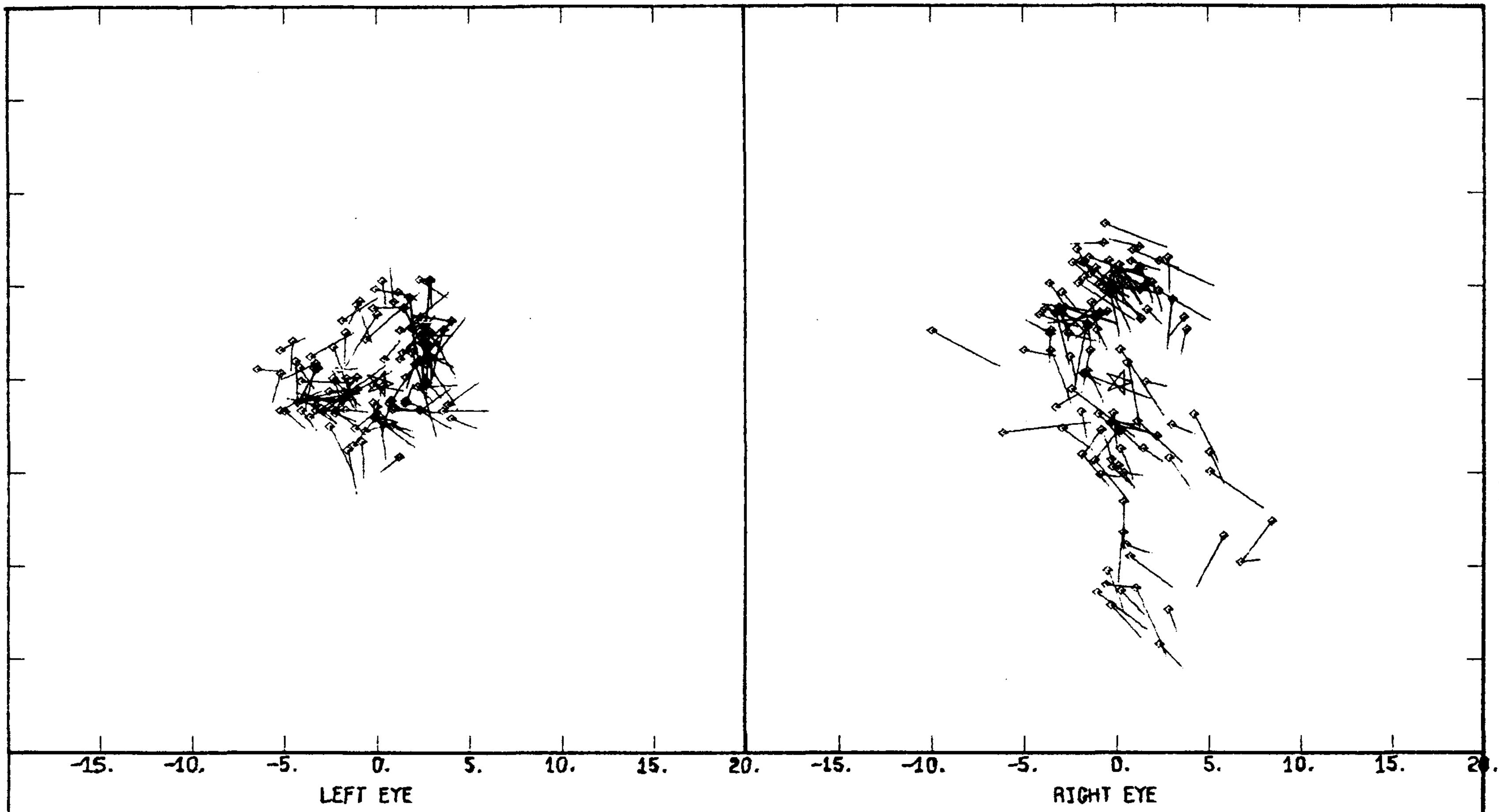


Figure 4.3(e): Flick trajectories (Monocular fixation: LEFT EYE)
Point target
Subject GSC

(Scale in min arc)

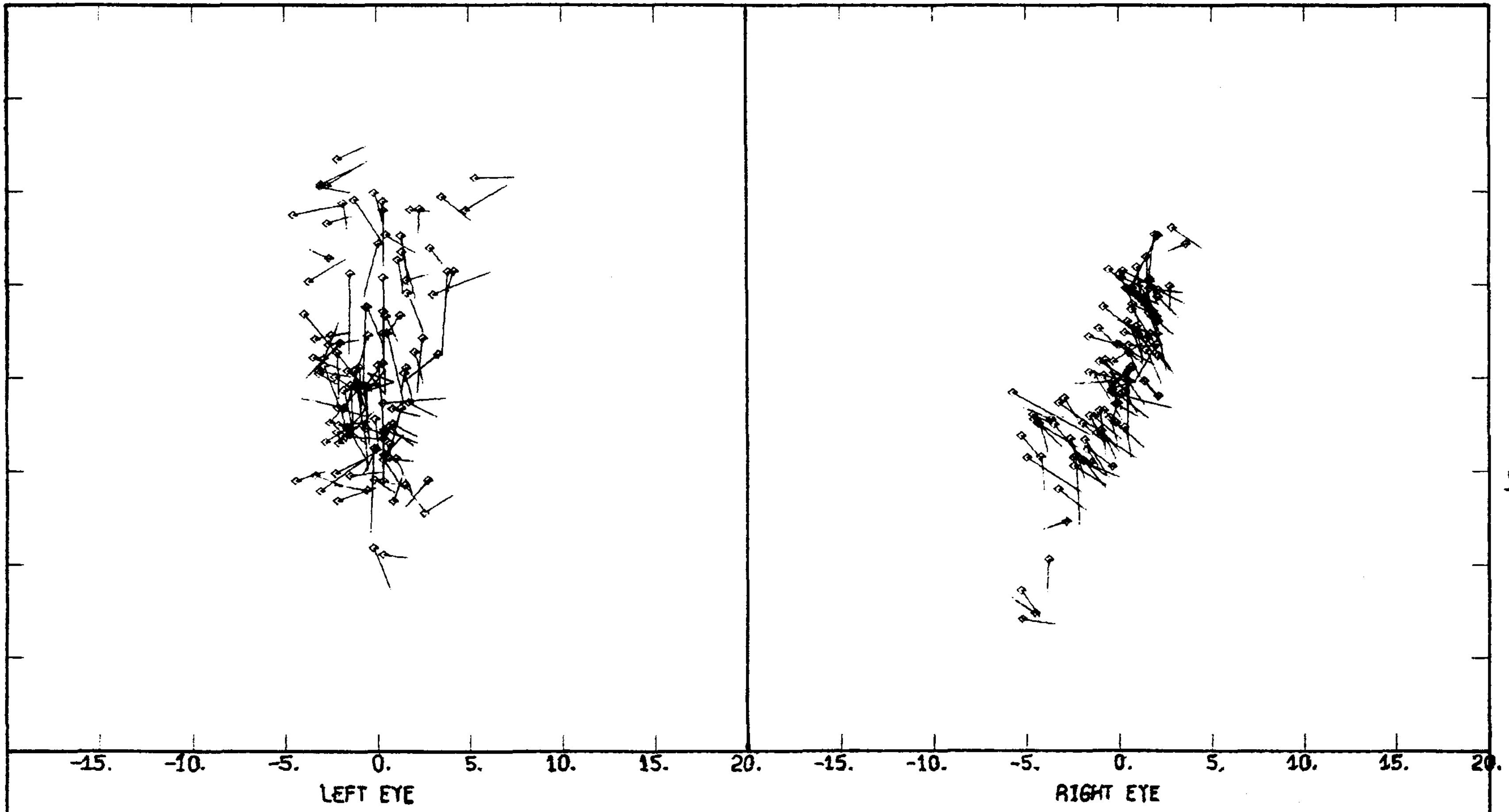
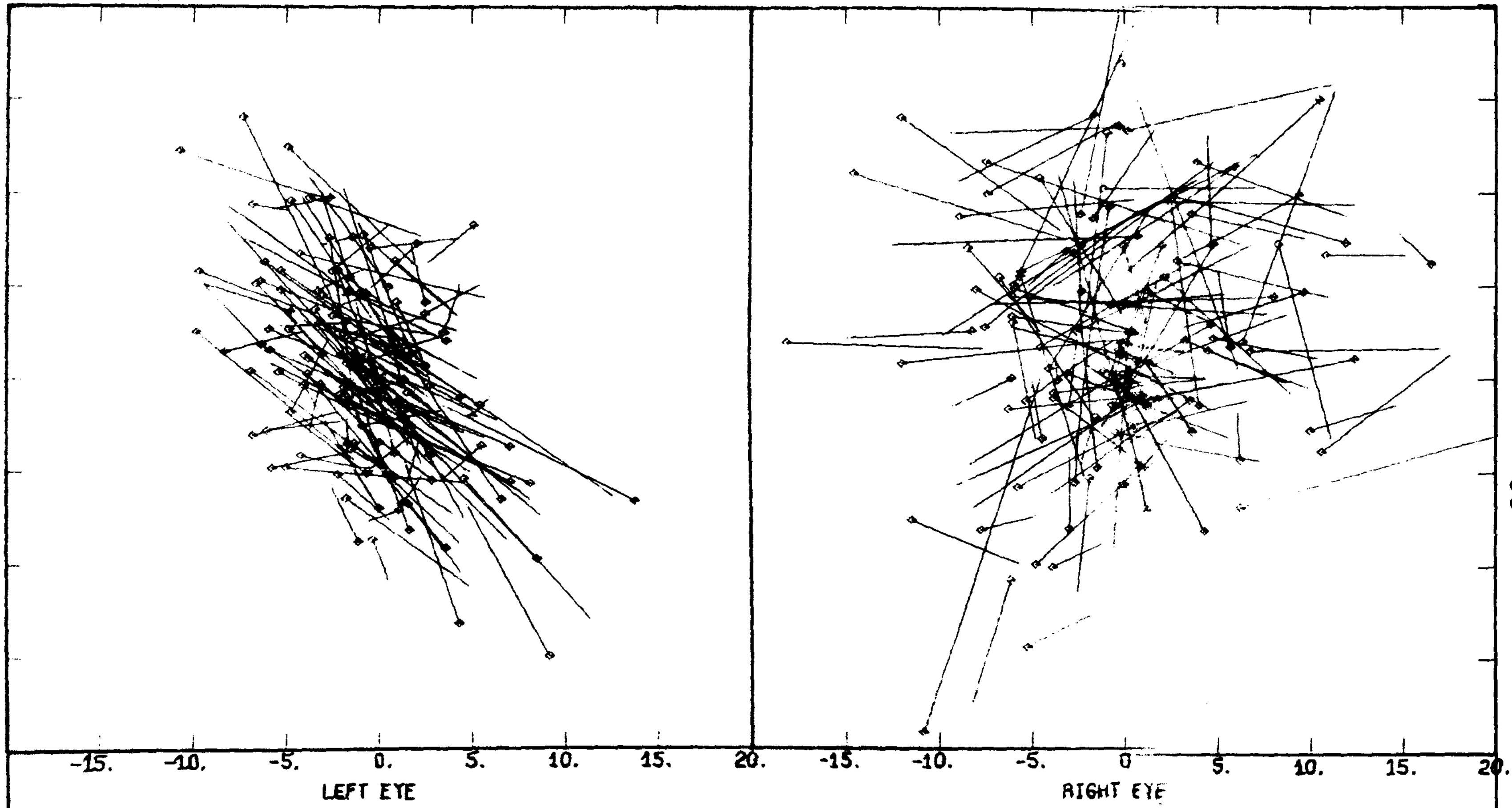


Figure 4.3(f): Flick trajectories (Monocular fixation: RIGHT EYE)
Point target
Subject GSC

(Scale in min arc)



<u>Figure 4.4(a)</u>: Flick trajectories (Monocular fixation: LEFT EYE)
Vertical line target
Subject DSG

(Scale in min arc)

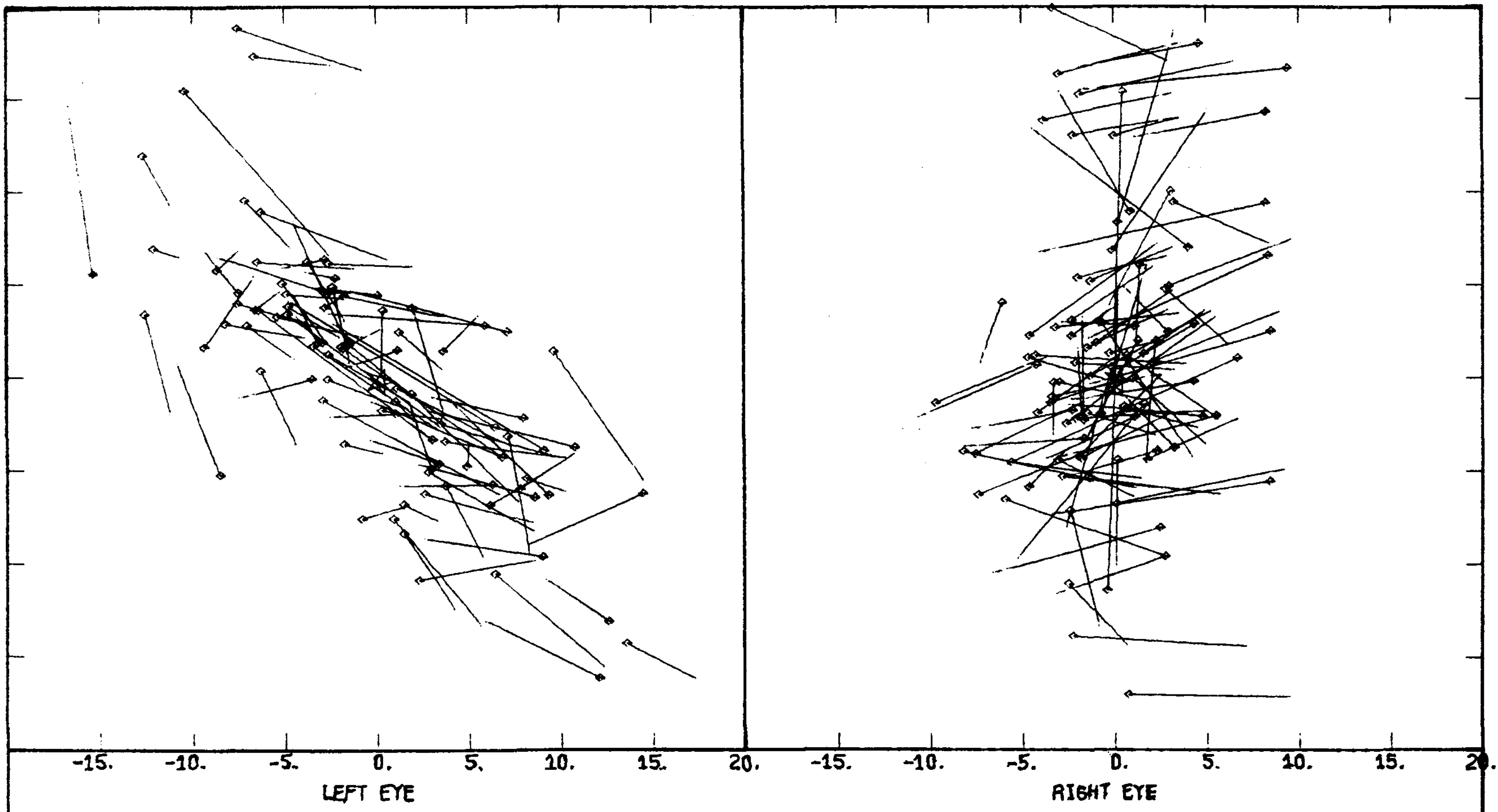


Figure 4.4(b): Flick trajectories (Monocular fixation: RIGHT EYE)
Vertical line target
Subject DSG

(Scale in min arc)

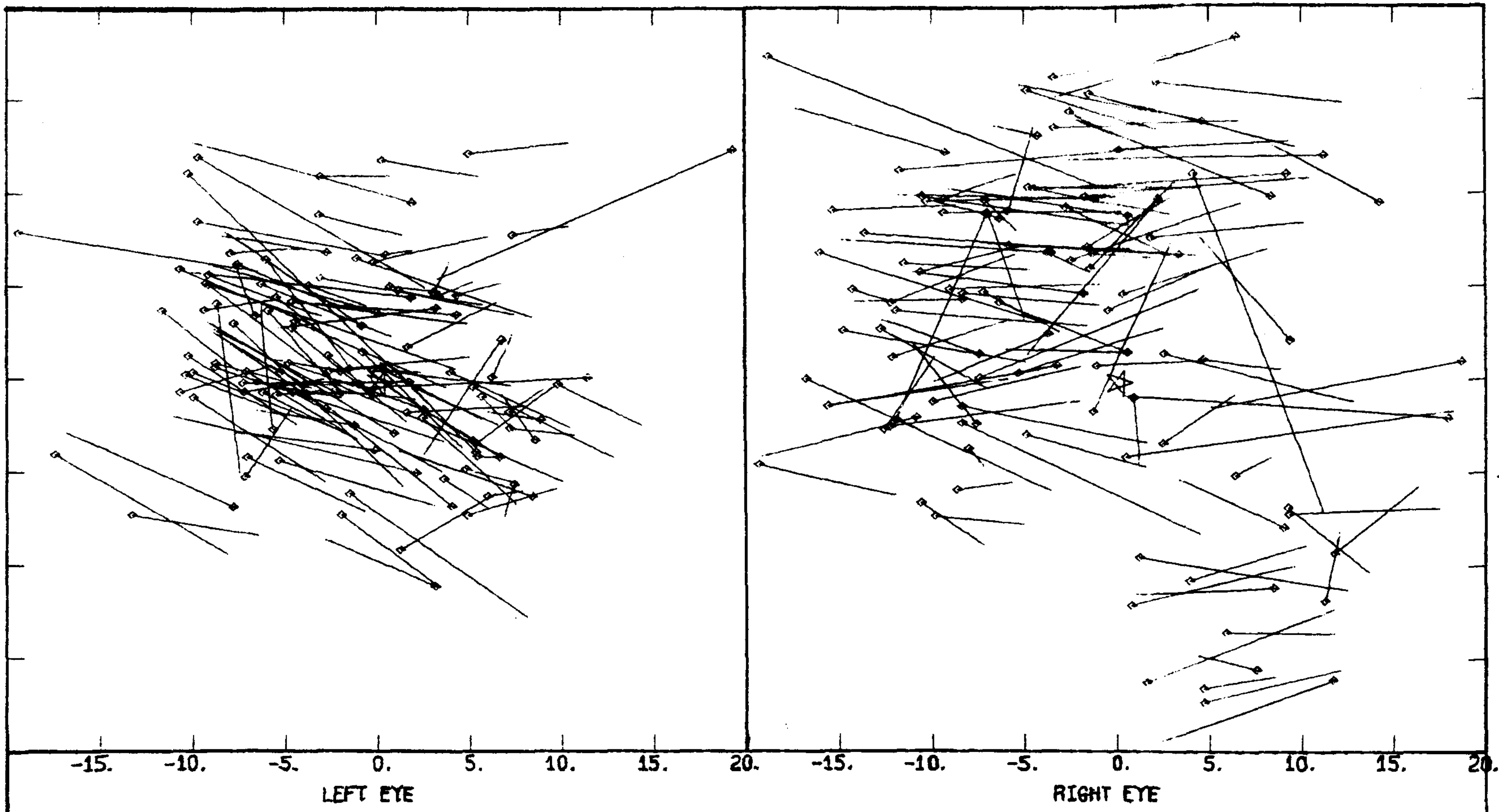


Figure 4.4(c): Flick trajectories (Monocular fixation: LEFT EYE)
Horizontal line target
Subject DSG

(Scale in min arc)

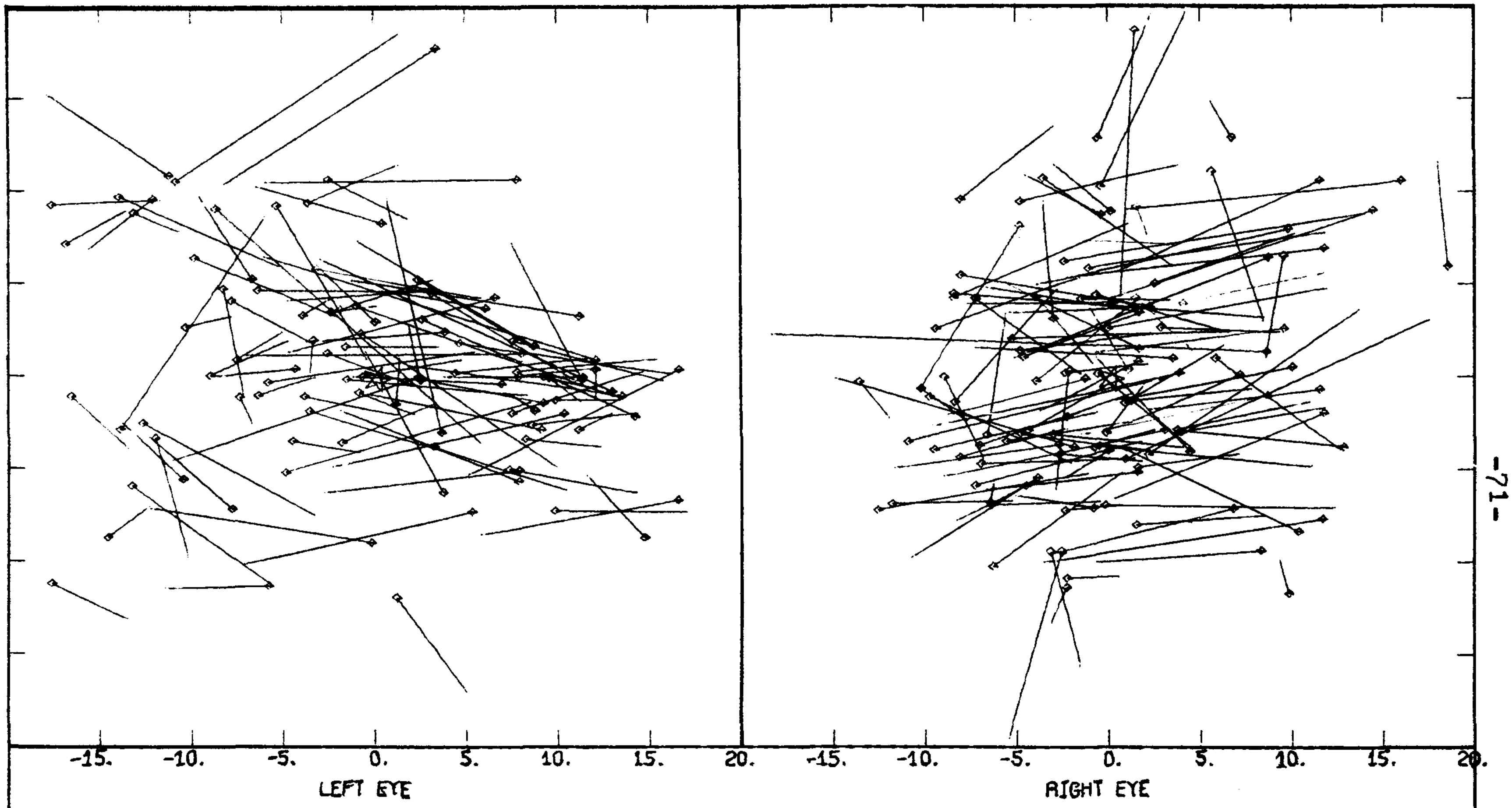


Figure 4.4(d): Flick trajectories (Monocular fixation: RIGHT EYE)
Horizontal line target
Subject DSG

(Scale in min arc)

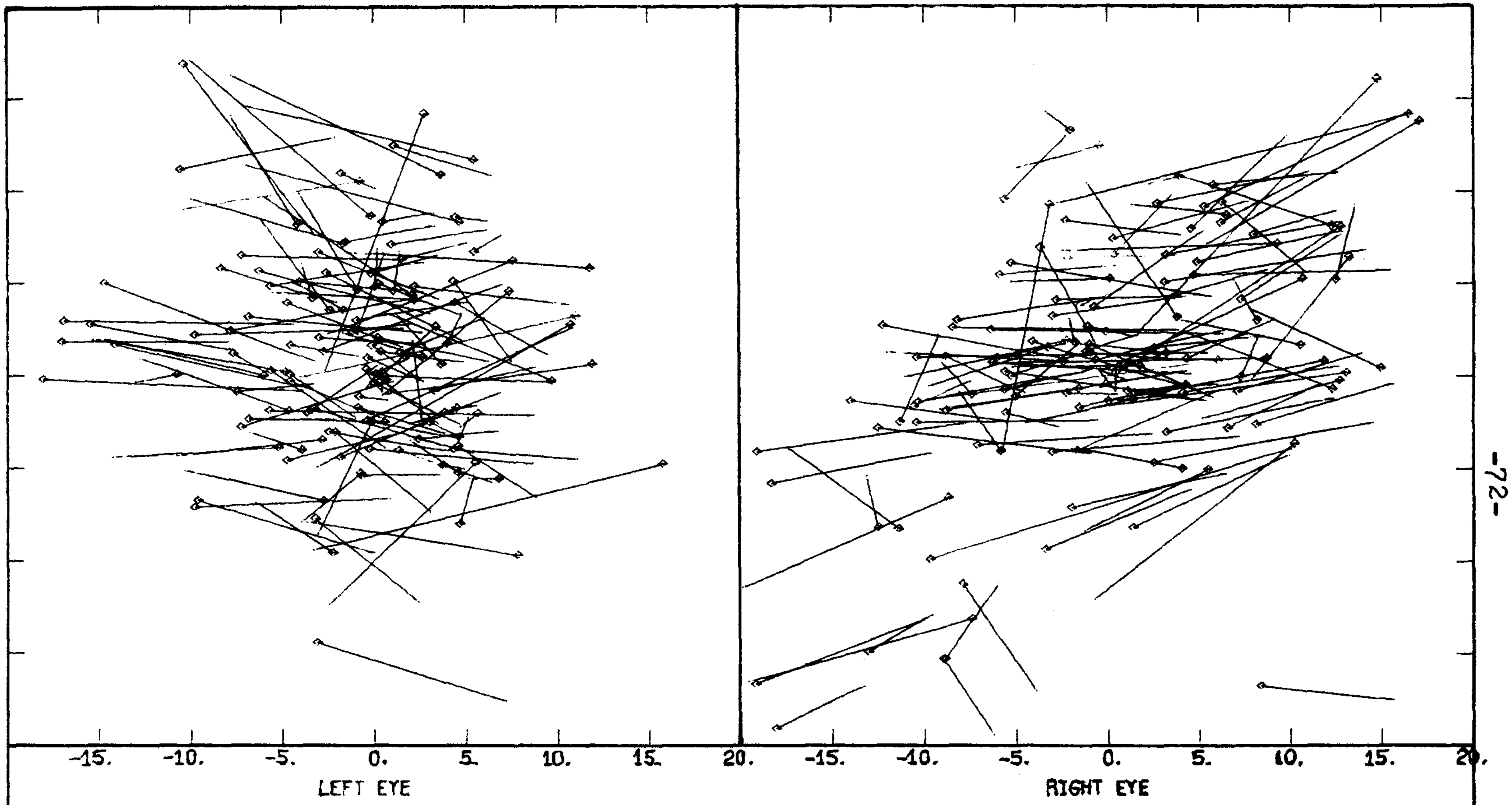


Figure 4.4(e): Flick trajectories (Monocular fixation: LEFT EYE)
Point target
Subject DSG

(Scale in min arc)

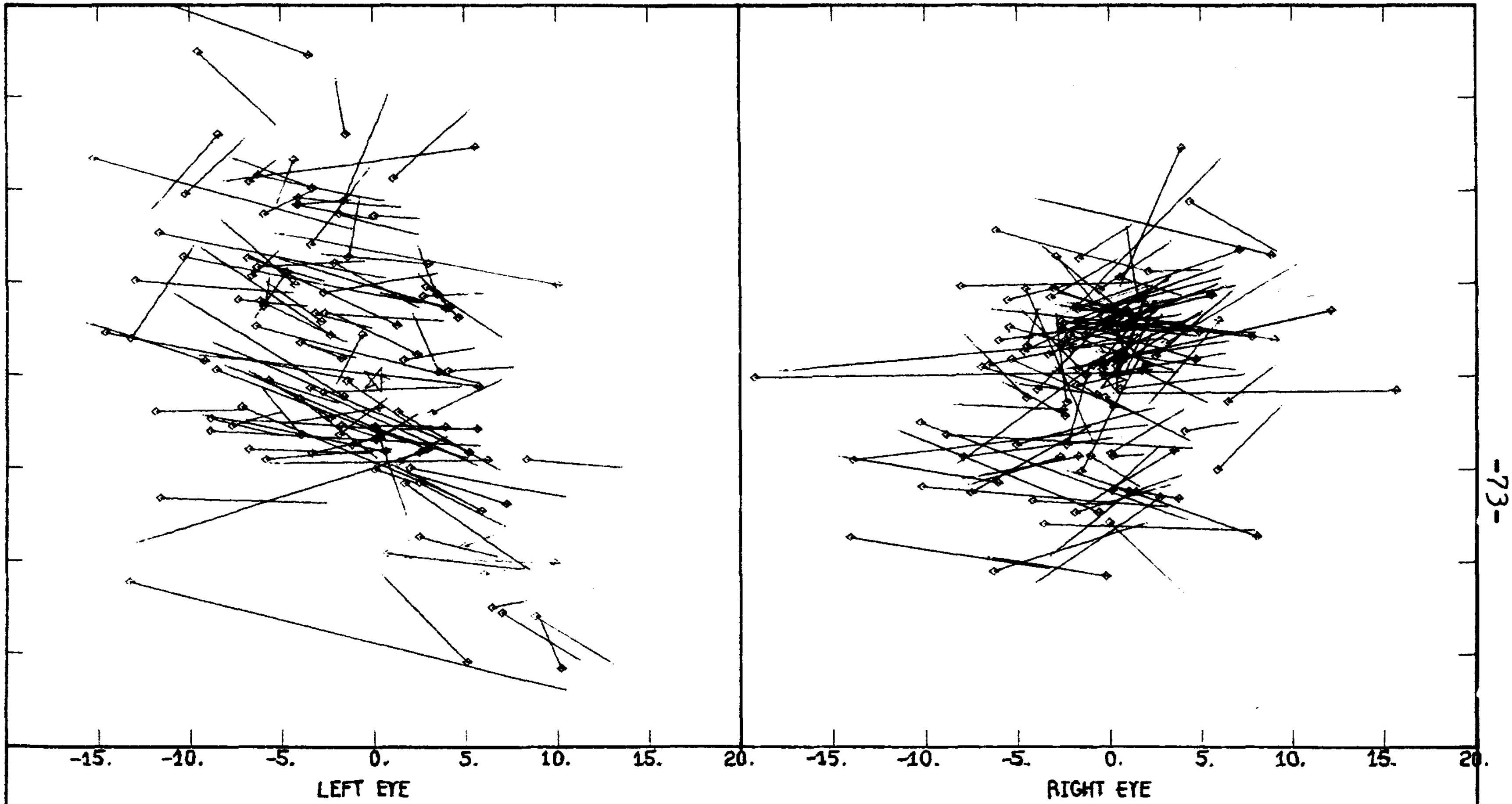


Figure 4.4(f): Flick trajectories (Monocular fixation: RIGHT EYE)
Point target
Subject DSG

(Scale in min arc)

TABLE 4-2. Differences Between the Drifts of the Left and Right Eyes

(A) BINOCULAR FIXATION

		GSC					DSG				
Target		Difference in direction (degrees)		Retinal disparity caused by drifts (min arc)		Ratio of magnitudes (right/left)	Difference in direction (degrees)		Retinal disparity caused by drifts (min arc)		Ratio of magnitudes (right/left)
L	R	Mean	σ	Mean	σ		Mean	σ	Mean	σ	
|	|	53.2°	45.0°	1.85	1.63	1.429	58.4°	44.6°	3.24	2.39	1.065
—	—	64.8°	49.8°	1.78	1.27	1.391	50.9°	42.1°	3.69	2.98	1.178
•	•	72.4°	47.9°	2.16	1.50	0.598	50.4°	40.8°	3.26	2.78	1.372

(B) DICHOPTIC FIXATION

L	R	Mean	σ	Mean	σ		Mean	σ	Mean	σ	
|		64.6°	48.7°	2.43	1.72	2.290	61.5°	49.1°	4.43	4.14	2.140
	|	57.1°	41.2°	2.00	1.33	1.529	66.3°	47.6°	4.76	3.23	1.175
—		61.5°	45.0°	2.49	1.83	2.540	47.7°	42.8°	4.29	3.77	1.760
	—	57.4°	43.2°	2.18	1.54	1.368	64.1°	49.3°	4.57	4.28	0.778
•		63.3°	49.6°	2.25	2.16	3.440	47.4°	41.2°	4.08	3.86	1.032
	•	58.0°	47.7°	1.70	1.10	0.780	59.5°	40.5°	3.85	2.95	0.862

flicks, although the significance of the change is not high. The changes in position of the visual axes during drifts are thus less well correlated than the changes produced by the flicks.

Drift direction depends on both subject and target. For a vertical line target, the visual axes of subject GSC tend to flick upward and drift downward; a horizontal line generates flicks to the left and to the right, while the drifts occur in all directions except upward. For a point target the flicks are mainly upward and to the left, while the drifts occur in all directions. Subject DSG again displays his individuality; for all targets, his visual axes flick upward and to the left, but drift upward, downward, and to the right. Through all of this, for both subjects and for all targets, there is an element of compensation: the major direction of motion of the flicks is generally matched by oppositely directed drifts. In this respect, they can be regarded as nullifying each other.

1.2.2 Dichoptic viewing. When one eye is occluded, the mean angle between the drift directions does not change much (Table 4-2B), but the ratio of the right to the left visual axis drift magnitudes changes in a systematic way; in this case, the motion of the eye which does not see the target increases in 8 conditions out of 12. The retinal disparity produced by a pair of drifts also increases.

1.3 Overall effect of flicks and drifts on the wander of the visual axes.

The effects which have been described in the preceding paragraphs represent marginal changes in the mean values of certain eye-movement parameters when changing from binocular to dichoptic viewing. The accumulative results of these changes over prolonged

(2 min.) viewing periods are well illustrated by contrasting the pin-diagrams shown in Figures 4.3 and 4.4 with those of Figure 4.1. Consider the eye movements of GSC in dichoptic viewing of a vertical line target. For the eye which sees the target, the visual axis is confined to a region 5 min arc wide and 30 min arc long, almost parallel to the stimulus. The pattern traced by the visual axis of the occluded eye has little correspondence with the target structure. This effect is particularly pronounced when the right eye is occluded. For a horizontal line stimulus in dichoptic presentation, the results are similar though not as obvious, mainly because of a vertical spread of the fixation pattern. The point target gives rise to a fixation pattern which is very similar to that obtained for the vertical line; once again, there is a larger spread in the vertical direction. It appears that the right eye of subject GSC is dominant in the sense that innervation elicited from an error signal in the right fovea controls both eyes more equally than if the error signal is derived from the left. The second subject (GSG) has much larger fixational areas, but the differences between the seeing and occluded eyes are similar to those for subject GSC.

2. Quantitative Measure of the Spread of the Fixation Pattern; Correction of Fixational Errors

So far, we have given a colloquial description of the eye movements of two subjects in a number of fixational tasks. Our purpose was to illustrate the wide variation and individuality which might be encountered in this work. We now wish to quantify the effect of flicks and drifts on the overall fixation pattern of the visual axis. Consider first the position of the visual axis at the beginning of each flick (which coincides with the end of the preceding drift). This pattern of points can be approximated by a bivariate normal probability distribution, which can then be illustrated by a set of concentric elliptical contours of the same orientation; there is an equal probability of a flick originating at any point along a given contour. The ellipse whose semi-axes are equal to 1.5 standard deviations should contain 75 percent of the starting points of all the flicks; choice of any other value of equiprobability will merely expand or contract the ellipse symmetrically.

We can repeat this analysis for the pattern of points representing the positions of the visual axis at the end of each flick (which coincides with the start of the following drift). These two ellipses thus represent the conditions before and after a flick, or equally well, after and before a drift. The influence of target structure of the fixation pattern is clearly shown in the diagrams of Figure 4.5. In dichoptic viewing, the ellipse corresponding to the seeing eye conforms more closely to the target structure than does the ellipse for the occluded eye. The overall effect of this phenomenon can be seen in these diagrams.

If a particular type of eye movement is corrective on the average, the "after" ellipse should be smaller and narrower than the "before" ellipse, and should in general conform more closely to the fixation mark. However, Figure 4.5 shows that, for each case, the two ellipses are essentially the same. Thus, on the average, neither the flicks nor the drifts play the major corrective role. The part played by these motions will be analyzed in the following sections.

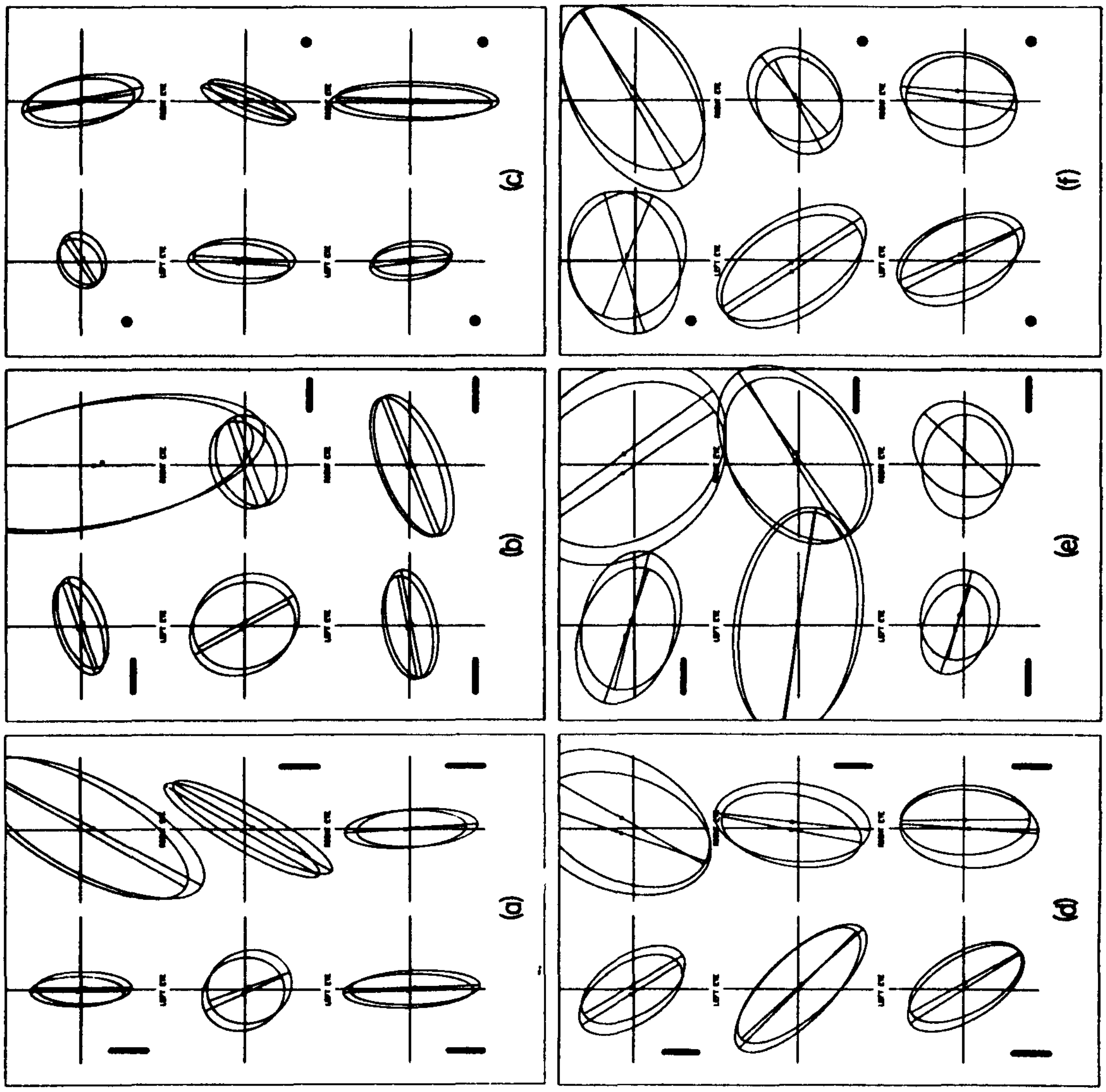


Figure 4.5: Equiprobability ellipses representing the position of the visual axes before and after flicks. For each distribution, 75% of the points should fall within the ellipse. Reference axes are 22.5 min arc.
(a) thru (c): Subject GSC (d) thru (f): Subject DSG

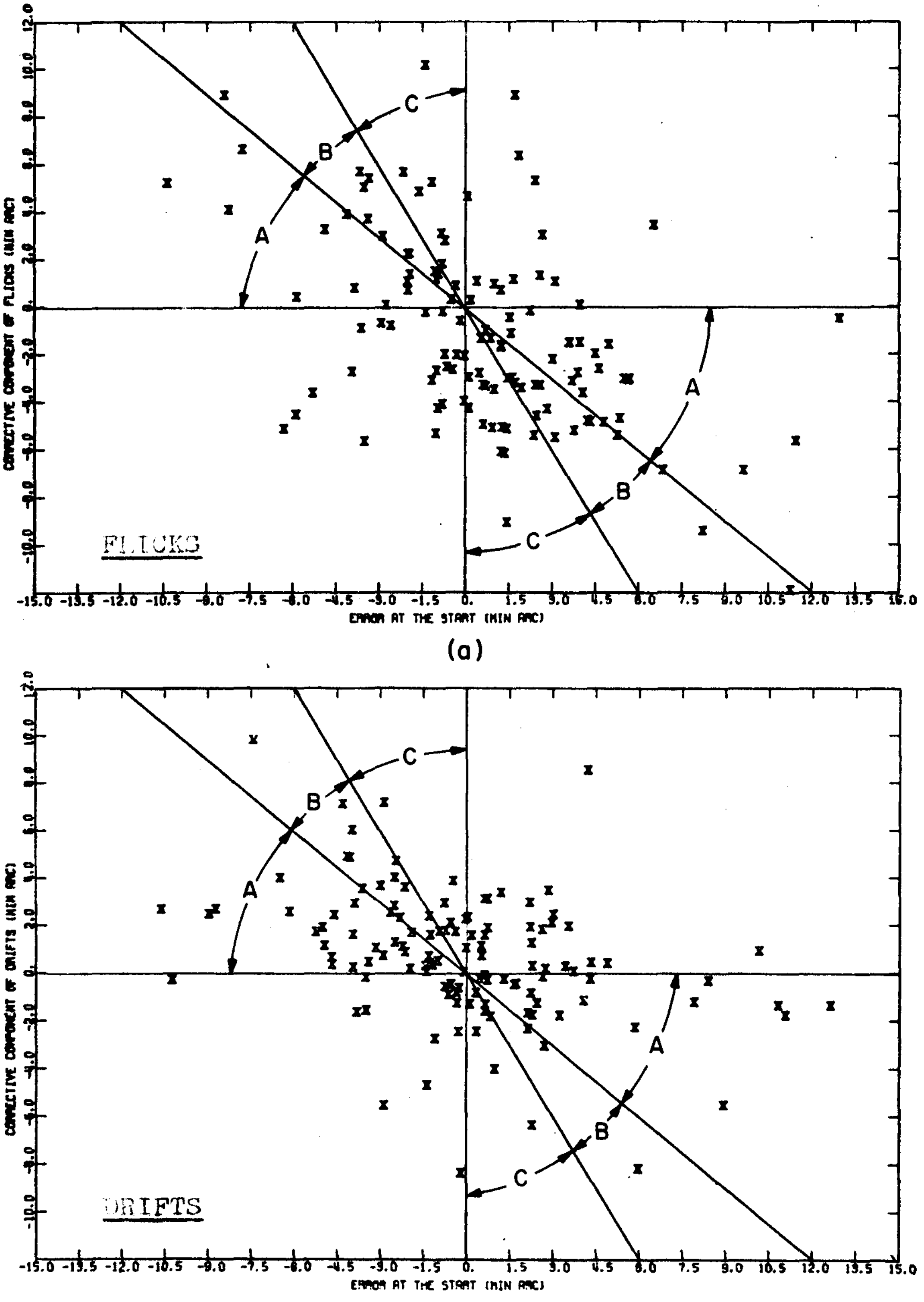
3. Ipsilateral Corrective Action of Flicks and Drifts

A normal human uses two eyes for most visual tasks. It is possible, therefore, that studies of monocular fixation mechanisms do not reflect the true operating conditions of the eye-movement control system. The remainder of this chapter is a study of the ipsilateral and contralateral corrective action of eye movements under binocular viewing conditions, but the results will not be presented until section 4. 4, for there is no way in which a direct comparison can be made between such a study and the work of those authors who have examined the monocular mechanism only. The analysis of this section is intended to form a link between previous work on monocular mechanisms and the present study of binocular mechanisms. To do this, we will compare the measures of ipsilateral corrective actions of eye movements under monocular viewing conditions with those obtained under binocular viewing conditions.

3. 1 Fixational error correction by flicks and drifts.

We define the corrective component of an eye motion to be that component which moves the visual axis towards the fixation mark. If the target is a straight line, then the error is taken to be the deviation of the direction of gaze normal to the length of the line; similarly, the corrective eye motion is the component of movement along the same direction. We choose a sign convention so that if the initial motion is in the correct direction to reduce the error, the error and initial motion will have opposite signs. For point targets, distances are measured radially from the point.

Figures 4. 6a and 4. 6b show the corrective component of flicks



(a)

(b)

Figure 4.6: Corrective component of eye movements vs. fixational error at the beginning

and drifts, respectively. All points in the upper left and lower right quadrants of the diagrams represent eye motions which initially move the direction of the gaze towards the fixation mark. However, even though a movement starts out in the corrective direction, its net effect may not be corrective, for the direction of gaze may overshoot the fixation mark and leave the visual axis farther from the target than before. The "corrective" regions of Figures 4.6a and 4.6b have each been divided into three areas by lines through the origin of slopes -1 and -2. Those points between the horizontal axis and the line of slope -1 (sectors A) represent motions which start out in the correct direction and fall short of the target. The points between the lines of slopes -1 and -2 (sectors B) indicate movements in the correct direction which overshoot the target but still end up with a net correction. Finally, the points between the line of slope -2 and the vertical axis (sectors C) illustrate motions which start in the correct direction, overshoot and move too far, giving rise to a larger error than existed at the beginning of the movement.

We can thus derive two parameters to describe the corrective actions of eye movements; (a) the probability of an eye movement starting in the correction direction, and (b) the probability of the same movement having a net corrective effect. These values are given in Table 4-3. Rather more than $\frac{1}{2}$ of the eye motions start in the corrective direction; the figure for flicks is slightly higher than that for drifts. The probability that there is net correction, however, is only very slightly greater than $\frac{1}{2}$. The visual axis, therefore, is not constrained exactly to the fixation point, but the fact that eye movements

TABLE 4-3. Fraction of Eye Movements Which Are Corrective

(A) SUBJECT GSC

Target		Recording Eye	Flicks		Drifts		
L Eye	R Eye		Start in corrective direction	Produce net correction	Start in corrective direction	Produce net correction	Number of eye movements
|		L	0.739	0.542	0.616	0.502	238
	|	R	0.584	0.554	0.513	0.487	233
|	|	L	0.690	0.537	0.639	0.527	242
|	|	R	0.628	0.533	0.589	0.494	242
—		L	0.667	0.565	0.519	0.456	207
	—	R	0.665	0.585	0.540	0.422	212
—	—	L	0.704	0.587	0.586	0.468	223
—	—	R	0.574	0.529	0.523	0.464	223
•		L	0.679	0.555	0.566	0.449	137
	•	R	0.623	0.500	0.591	0.482	138
•	•	L	0.649	0.519	0.582	0.458	154
•	•	R	0.558	0.494	0.529	0.471	154

TABLE 4-3. Fraction of Eye Movements Which are Corrective

(continued)

(B) SUBJECT DSG

Target		Recording Eye	Flicks		Drifts		
L Eye	R Eye		Start in corrective direction	Produce net correction	Start in corrective direction	Produce net correction	Number of eye movements
|		L	0.734	0.523	0.646	0.504	128
	|	R	0.862	0.553	0.570	0.473	94
|	|	L	0.734	0.508	0.661	0.543	128
|	|	R	0.773	0.484	0.638	0.504	128
—		L	0.630	0.543	0.675	0.508	127
	—	R	0.565	0.532	0.561	0.480	124
—	—	L	0.636	0.527	0.624	0.431	110
—	—	R	0.673	0.545	0.596	0.450	110
•		L	0.843	0.582	0.729	0.579	134
	•	R	0.872	0.607	0.621	0.448	117
•	•	L	0.832	0.628	0.554	0.429	113
•	•	R	0.841	0.469	0.598	0.491	113

start in the right direction with a probability above chance serves to keep the fixation pattern centered on target even though the fixation pattern may not be bounded. This condition will be satisfied only if the corrective action of eye movements is an increasingly negative function of fixational error (the negative value results from the sign convention).

It is evident that the second definition of correction, (b) above, is a more complete description of the correction of fixation errors than the first; therefore, in the remainder of this chapter we will define corrective action as the absolute value of the angular distance of the visual axis from the fixation mark after an eye movement minus the corresponding value before the movement. Thus, a positive quantity indicates a disruptive eye motion. If a particular type of eye movement -- a flick or a drift -- is under retinal control, there should be some negative correlation between the corrective action and the fixational error, although the slope of the regression line should be significant: Table 4-4 lists these values.

The slope of the regression line can be regarded as a measure of the average fractional correction of the error brought about by flicks or drifts. A zero value implies no correction, and -1 means perfect correction. We see that the slopes are all negative and highly significant. For subject GSC, flicks reduce the fixational error on the average by about 1/3, while drifts produce a reduction of only 1/4. Subject DSG uses flicks to reduce fixational errors by about 2/3; drifts are less effective, reducing the error on the average by only 2/5. Nevertheless, both flicks and drifts have qualitatively similar corrective actions. There are a number of inter-subject and target vari-

TABLE 4-4. Ipsilateral Correction of the Fixational Error as a Function of the Error at the Beginning of the Eye Movements

(A) SUBJECT GSC

Target		Recording Eye	Flicks			Drifts		
L Eye	R Eye		Slope of regression line	Standard deviation of slope	Correlation coefficient	Slope of regression line	Standard deviation of slope	Correlation coefficient
|		L	-0.703	0.050	-0.672	-0.414	0.068	-0.366
	|	R	-0.098	0.032	-0.199	-0.082	0.022	-0.238
|	|	L	-0.662	0.060	-0.578	-0.350	0.050	-0.415
|	|	R	-0.578	0.059	-0.533	-0.333	0.047	-0.414
—		L	-0.274	0.055	-0.326	-0.288	0.042	-0.434
	—	R	-0.373	0.045	-0.497	-0.358	0.062	-0.368
—	—	L	-0.422	0.053	-0.474	-0.249	0.047	-0.335
—	—	R	-0.247	0.038	-0.399	-0.196	0.045	-0.280
•		L	-0.547	0.069	-0.564	-0.458	0.082	-0.436
	•	R	-0.060	0.034	-0.150	-0.144	0.040	-0.294
•	•	L	-0.246	0.058	-0.326	-0.416	0.062	-0.477
•	•	R	-0.087	0.025	-0.271	-0.040	0.032	-0.099

TABLE 4-4. Ipsilateral Correction of the Fixational Error as a Function of the Error at the Beginning of the Eye Movements (continued)

(B) SUBJECT DSG

Target		Recording Eye	Flicks			Drifts		
L Eye	R Eye		Slope of regression line	Standard deviation of slope	Correlation coefficient	Slope of regression line	Standard deviation of slope	Correlation coefficient
│		L	-0.945	0.095	-0.663	-0.424	0.066	-0.501
	│	R	-1.177	0.099	-0.777	-0.462	0.089	-0.480
│	│	L	-0.844	0.096	-0.618	-0.294	0.056	-0.424
│	│	R	-1.165	0.096	-0.734	-0.313	0.056	-0.447
—		L	-0.377	0.072	-0.423	-0.392	0.069	-0.454
	—	R	-0.326	0.053	-0.485	-0.163	0.068	-0.214
—	—	L	-0.478	0.071	-0.545	-0.451	0.093	-0.424
—	—	R	-0.428	0.058	-0.576	-0.433	0.102	-0.381
●		L	-0.810	0.104	-0.561	-0.543	0.060	-0.618
	●	R	-0.919	0.113	-0.605	-0.528	0.062	-0.625
●	●	L	-0.480	0.084	-0.475	-0.348	0.068	-0.438
●	●	R	-0.604	0.085	-0.561	-0.358	0.076	-0.409

ations; for example, subject GSC on the average corrects fixational errors best when the stimulis is a vertical line; this applies to both flicks and drifts. Correction is worst with a point target. Subject DSG also does best with a vertical line stimulus, but poorest with the horizontal line: it will be remembered that his preferred direction of eye motion is from side to side. Subject GSC also has a poor fixational response when viewing either a vertical line or a point with the right eye only. This is also the case for a point target in binocular vision.

4. Corrective Action of Eye Movement as a Function of Left Eye and Right Eye Fixational Errors

In section 3.1 we examined the magnitude of the corrective action of eye movements as a function of the fixational error in the ipsilateral eye; calculation of the regression of the movement on the fixational error gives a direct measure of the average fractional correction. However, in binocular fixation, motion in one eye may be influenced by error signals from the contralateral eye. Therefore, we have computed the regression planes which describe the dependence of the correction on the fixational errors of the left and right eyes. Thus, we may plot the fixational errors of the left and right visual axes along X and Y, respectively, and the correction of one eye movement along Z. Then the slopes of the regression plane in the X and Y directions are measures of the relative corrective action that can be ascribed to the fixational error of each eye. Negative slopes indicate corrective movements, and positive slopes signify disruptive motions. Table 4-5 lists the slopes of the regression

TABLE 4-5. Slopes of the Regression Planes Between the Correction in One Eye and the Fixational Errors of Both Eyes

(A) SUBJECT GSC

Target	Eye in which the correction is measured	Flicks				Drifts			
L Eye R Eye		Left Eye Error		Right Eye Error		Left Eye Error		Right Eye Error	
		Slope	σ	Slope	σ	Slope	σ	Slope	σ
│ │	L	-0.673	0.066	+0.026	0.063	-0.415	0.055	+0.133	0.052
	R	+0.059	0.068	-0.601	0.065	+0.040	0.057	-0.350	0.053
— —	L	-0.428	0.053	+0.052	0.038	-0.244	0.048	-0.022	0.035
	R	+0.040	0.054	-0.249	0.038	-0.064	0.062	-0.189	0.046
• •	L	-0.396	0.053	+0.170	0.022	-0.427	0.079	+0.008	0.035
	R	+0.161	0.063	-0.111	0.026	+0.162	0.090	-0.084	0.040

(B) SUBJECT DSG

Target	Eye in which the correction is measured	Flicks Left Eye Error Slope	σ	Flicks Right Eye Error Slope	σ	Drifts Left Eye Error Slope	σ	Drifts Right Eye Error Slope	σ
│ │	L	-0.704	0.110	-0.312	0.126	-0.348	0.065	-0.121	0.073
	R	+0.063	0.098	-1.202	0.113	+0.165	0.056	-0.407	0.063
— —	L	-0.467	0.071	-0.070	0.058	-0.451	0.093	-0.095	0.083
	R	+0.042	0.072	-0.432	0.059	-0.003	0.115	-0.433	0.102
• •	L	-0.466	0.087	-0.061	0.088	-0.351	0.078	+0.006	0.083
	R	+0.190	0.084	-0.647	0.085	-0.038	0.082	-0.339	0.087

planes as well as the standard deviations of the slopes.

4.1 Ipsilateral control of flicks and drifts. The slopes of the regression planes for control of eye motion by the fixation error of the ipsilateral eye are negative and significantly different from zero in all cases; thus, there is ipsilateral control of fixation mediated both by flicks and drifts. This is merely a restatement of conclusions reached in the previous section, 3.

4.2 Contralateral control of drifts. In this case, the three stimuli have very different effects on the eye movements. For the horizontal targets, the slopes of the regression planes for both subjects are all negative but are not significantly different from zero; thus, the errors of fixation in the vertical direction exert no significant control of the drifts of the contralateral eye.

Vertical line stimuli give rise to positive slopes for both eyes of both subjects. Three out of the four values are significantly greater than zero. Thus, for example, if the right visual axis is to the right of the vertical line, a corrective drift to the left may be triggered in that eye, as suggested in the above section; but the left eye drifts to the right, apparently in the wrong direction. However, the net effect is a convergence movement. This suggests that drift motions play a significant role in the correction of vergence error: this will be examined in detail in the next section.

Finally, the point target gives mainly positive slopes for the regression planes, but the values are not significantly different from zero. Thus, the point target must be regarded as only a very weak stimulus for contralateral control.

4.3 Contralateral control of flicks. The effects of the three stimuli can be summarized as follows. Horizontal line targets have no effect on the contralateral control of flicks; this is the same as the conclusion we reached for drifts. Vertical line targets give rise to slopes for the regression planes which are not significantly different from zero in three cases, and significantly less than zero in one case. This is different from the conclusion we reached for drifts; contralateral control of flicks plays no part in the correction of vergence errors. For a point target, in three cases out of four, the slopes of the regression planes are significantly positive; this indicates that contralateral control is mainly disruptive. However, errors are measured radially from the point; thus, no conclusions regarding vergence errors or vertical discrepancy can be drawn from these values.

5. Vergence and Vertical Discrepancy

In the above sections we have investigated the control of monocular corrective movements by fixational errors in either the ipsilateral or contralateral eye. The corrective effect, while present in most cases, was found to be far from complete. We would now like to ask whether there exists a mechanism which, in addition to correcting monocular fixation errors in each eye, also acts so as to reduce the retinal disparity, that is, vergence errors or vertical discrepancies, above that amount of correction to be expected from two independent monocular mechanisms.

We have computed the regression of retinal disparity correction produced by an eye movement on the retinal disparity at the beginning of that movement. These values are shown in Table 4-6.

5.1 Control of vergence. For both subjects and for both vergence stimuli (vertical lines and points), the slopes of the regression lines are significantly different from zero at the $p = 0.95$ level and are all negative, indicating that flicks and drifts have some corrective action on vergence error. The degree of correction by flicks appears to be better than that produced by drifts for subject DSG, while for subject GSC the drifts are significantly better.

However, these corrections could very well be brought about by two parallel monocular mechanisms. In order to determine how much of this correction is due to retinal disparity, we must compare the regression values with the corresponding ones for ipsilateral corrections (Table 4-5). For flicks, the correction for vergence on the average is the same as the ipsilateral monocular values for the two eyes for subject DSG and less for subject GSC; thus, there is no binocular mechanism for the correction of vergence errors by flicks. For drifts, on the other hand, both subjects have a vergence correction which is better than the higher of the corresponding monocular values. Thus, binocular vergence correction is mediated solely by drifts.

5.2 Control of vertical discrepancies. The same analysis can be applied to the vertical discrepancy between the two visual axes. All regression values are significantly less than zero, but in contrast to vergence, the correction for vertical discrepancy is less than or equal to the lower of the two corresponding ipsilateral monocular corrections for both flicks and drifts. Therefore, we conclude that

TABLE 4-6. Slope of the Regression Line Between Binocular Corrective Eye Movements and Discrepancy of the Visual Axes

Subject	Target		Vergence				Vertical Discrepancy			
	L Eye	R Eye	Flicks		Drifts		Flicks		Drifts	
			Slope	σ	Slope	σ	Slope	σ	Slope	σ
GSC	│	│	-0.324	0.048	-0.625	0.059	-	-	-	-
	—	—	-	-	-	-	-0.169	0.035	-0.104	0.032
	●	●	-0.374	0.070	-0.563	0.068	-0.033	0.012	-0.009	0.021
DSG	│	│	-0.818	0.105	-0.439	0.055	-	-	-	-
	—	—	-	-	-	-	-0.249	0.058	-0.495	0.088
	●	●	-0.606	0.078	-0.465	0.092	-0.025	0.029	-0.159	0.048

vertical discrepancy is not a binocular stimulus for vertical correction.

C. Discussion

The two subjects whose eye movements we have chosen to present in this chapter represent extremes in what we presume is a continuum of fixational behavior. Subject DSG has his own characteristic eye movements which, for all practical purposes, are independent of the target configurations we have used. On the other hand, the eye movements for subject GSC are strongly dependent on the target configuration, and for him it is not meaningful to quote a norm for fixational movements unless the target is also specified. This behavior may be responsible for many of the apparent discrepancies which exist between the recent quantitative studies of eye movements by various authors (3, 5, 6, 4, 2); points, lines, crosses, and annuli have all been used as fixation marks. However, even though eye movements may be influenced by the target, we find that the mean values for the differences between the movements of the left and right eyes (direction, magnitude, and retinal disparity) are not strongly influenced by various target configurations.

The overall fixation pattern is determined not only by the direction and magnitudes of the individual eye movements, but also by the temporal sequence in which they occur; for both subjects and for almost all targets, the vertical spread of the fixation pattern is larger than the horizontal spread. This fact can also account for disparity of results between different authors who measure only one component of eye movements.

It was pointed out in Chapter III that the drifting motions of the visual axes are generally categorized as instabilities of the oculomotor system, while the flicks are thought to correct errors of fixation. This was the case stated by Cornsweet (3); however, Nachmias (5), by measuring the vertical as well as the horizontal component of monocular eye motions, found that flicks correct for fixational errors in certain directions, but that drifts play the major corrective role along other meridia. Furthermore, Beeler (1) and Boyce (2) have shown that at most 30 percent of spontaneous flicks play a corrective role other than by chance.

This apparent array of contradictions between various authors may have arisen for a number of reasons, some of which we have made earlier. First, there is a lack of agreement on the definition of "correction." Cornsweet defines it as that component of motion perpendicular to the fixated vertical line target; Nachmias analyzes the eye movement vector into the sum of motions along 8 directions from the center of cross-hairs; and Beeler counts the percentage of flicks which bring the visual axis closer to the fixation point. As we have pointed out, a considerable number of eye movements which start out in the correct direction overshoot the fixation mark to such an extent that they are actually disruptive. We feel that the most meaningful way to measure correction is to plot the correction (fixational error after the eye movement minus the value before the motion) versus the amount of fixational error at the start, and to calculate the slope of the regression line between these two quantities. The standard deviation of the slope is then a measure of the statistical reliability of the correction factor. We find that although flicks are generally more corrective than drifts, nevertheless, drifts do correct for fixational error to a significant degree.

Other sources of disagreement can arise from inter-subject and target differences. One of our subjects has eye movements which correct fixational errors by a significantly higher amount than the other subject. The target configuration can also influence the corrective factor. Thus, while both of our subjects correct fixation error somewhat better when the target is a vertical line, one does poorly when viewing a point and the other while viewing a horizontal line. Even the behavior of the two eyes of the same subject can be significantly different; for subject GSC, the left eye generally corrects fixational errors much better than the right eye (under monocular conditions) when the target is a vertical line or a point. For a horizontal line, both eyes do about equally well. This behavior holds for both flicks and drifts.

There can also be a substantial change in the corrective factor of one eye when the other eye is allowed to see the target as well. Thus, for subject GSC, when the viewing condition is changed from monocular to binocular, there is a significant increase in the corrective factor of the right eye if the target is a vertical line, but a significant decrease if the target is a horizontal line. This is true for both flicks and drifts. For subject DSG, if the target is a point, changing from monocular to binocular viewing conditions worsens the corrective factor for both eyes for flicks and for drifts.

The contralateral control of eye movements in binocular viewing conditions is at best a very weak function, except perhaps in the case of drifts when viewing a vertical line. In this case, the operation of a vergence correction mechanism might be confused with contralateral control. This conclusion, however, appears to conflict with the paragraph above, in which it was pointed out that the ipsilateral correction may change in marked fashion, depending on whether the other eye does or does not see the target, thus pointing to contralateral control in some cases. However, these two cases may not be comparable, and we believe that the correct interpretation is that the absence of fixational error (as in the occluded eye) is not equivalent to zero fixational error and represents a different control mechanism whose characteristics have still to be studied.

Finally, we have to argue the case for mechanisms which correct the disparity between the two visual axes (either in horizontal vergence or in vertical discrepancy) versus two monocular fixation mechanisms. It has been shown (8, 9) that during tracking tasks, conjugate and disjunctive eye movements are organized independently and can occur simultaneously. Rashbass and Westheimer (7) have conclusively demonstrated the independence of the conjugate and the vergence mechanisms. Krauskopf, et al. (4) recorded the horizontal movement of both eyes under the condition of binocular stationary point fixation. They dismissed drifts as noise, focussed attention on the flicks, and found that conjugate flicks corrected vergence errors. These authors hypothesized that the corrective action for vergence is a byproduct of the two monocular flick mechanisms; they suggested that corrective fixational flicks would be triggered by the eye which had the larger fixation error, while the other one followed suit with a smaller flick, thus correcting vergence automatically.

However, we have seen that the determination of the corrective effect of retinal disparity is a subtle problem; by measuring the regression between the retinal disparity correction and the retinal disparity, we might have concluded from our results that both vergence error and vertical discrepancy control corrective flick and drift movements. However, this conflicts with the fact that contralateral correction is not significant except for horizontal drifts. This point is resolved when we compare the measure of retinal disparity correction with that of ipsilateral correction. We then find that those corrections apparently brought about by retinal disparity can be accounted for by two independent monocular mechanisms; the notable exception is vergence errors which control corrective vergent drifts above the amount of correction to be expected from two monocular mechanisms. Thus, we agree with the conclusions of Krauskopf, et al. regarding vergence correction by flicks, but not with their conclusion that drifts are merely noise. On the contrary, we find that drifts are significantly corrective for vergence errors during fixation of a stationary target. In contrast, vertical disparity between the two visual axes does not trigger corrective eye movements of either type.

REFERENCES FOR CHAPTER IV

1. Beeler, G. W., "Stochastic Processes in the Human Eye Movement Control System," Doctoral Disseration, California Institute of Technology (1965).

2. Boyce, P., "Monocular fixation in human eye movements," Proc. Roy. Soc. B167 (1967), pp. 293-315.

3. Cornsweet, T., "Determination of the Stimuli for Involuntary Drifts and Saccadic Eye Movements," J. Opt. Soc. Amer. 46 (1956), pp. 987-993.

4. Krauskopf, J., Cornsweet, T., and Riggs, L., "Analysis of Eye Movements During Monocular and Binocular Fixation," J. Opt. Soc. Amer. 50 (1960), pp. 572-578.

5. Nachmias, J., "Two-dimensional Motion of the Retinal Image During Monocular Fixation," J. Opt. Soc. Amer. 49 (1959), pp. 901-908.

6. Nachmias, J., "Determiners of the Drift of the Eye During Monocular Fixation," J. Opt. Soc. Amer. 51 (1961), pp. 761-766.

7. Rashbass, C. and Westheimer, G., "Independence of conjugate and disjunctive eye movements," J. Physiol., Lond. 159 (1961), pp. 361-364.

8. Westheimer, G. and Mitchell, A., "Eye Movement Responses to Convergence," Archs. Ophthal., N. Y. 55 (1956), pp. 848-856.

9. Yarbus, A., "Motion of the eye on interchanging fixation points at rest in space," Biofizika 2 (1957), pp. 698-702.

V. INTRODUCTION TO EYE MOVEMENTS MADE WHEN TRACKING A MOVING TARGET

Having established the relative roles of smooth and rapid eye movements in maintaining fixation on stationary targets, we will now examine the manner in which the eye movement control system keeps the image of a moving point centered on the fovea. It is now generally accepted that there are two distinct tracking systems: the saccadic and the smooth movement system. It has been thought that saccades correct for position errors, while the smooth system is sensitive to target velocity. However, the situation is not that clear-cut. As has been shown in Chapter IV, drifts serve to correct fixational errors when the target is stationary. Moreover, we shall present evidence to show that both smooth movements and saccades are used to track a target which moves in a step-wise fashion, and that saccadic responses are functions of target velocity as well as position.

Rashbass (4) demonstrated that smooth eye movements are elicited by target velocity rather than position. A point target was displaced to the right in a stepwise manner, but was then immediately moved to the left at constant velocity. The subject responded by making a smooth eye movement to the left, in spite of the fact that the target was actually to the right at that time. Fender (2) also did this step-ramp experiment, but under open-loop conditions (where, by means of optical feedback systems, the retinal image motion is made to be independent of eye movements). The subject attempted to fixate the target by making a series of useless saccades in one direction and equally fruitless smooth pursuit movements in the other. However, there were also smooth eye motions in the same direction as the saccades, indicating that position errors trigger both types of corrective eye movements.

Robinson (5) measured the velocity of smooth eye movements made in response to a target moving at constant speed. At 5 deg/sec, eye movement velocity overshot that of the target; at 10 and 15 deg/sec, the overshoot had disappeared, and at 20 deg/sec, the speed of the tracking eye motions fell short of the target's. Thus, from this evidence, it appears as if the smooth movement system attempts to bring the image of the target to the fovea by moving the visual axis faster than the target; however, saturation occurs at about 15 deg/sec and the visual axis must of necessity fall behind. This position error is corrected by one or more saccades. In fact, in all of these experiments, the smooth eye movements were interrupted by saccades.

In the same paper, Robinson (5) demonstrated that the saccadic and the smooth systems have different characteristics of instability. Under normal viewing conditions, if the visual axis sweeps through an angle ϕ, the retinal image moves the same distance ϕ, but in the opposite direction. This is referred to as a feedback value of minus one. If a voltage proportional to eye movements is used to control the target motion, it is then possible to adjust the gains of the amplifiers so that the retinal image travels through a distance ϕ', which is different from the angle ϕ swept by the visual axis. Thus, if $\phi' = K\phi$, then K is defined as the amount of feedback: $K = -1$ for normal vision, and $K = 0$ for stabilized vision (image stationary on the retina). If K is made more negative, then eventually the oculomotor system becomes unstable and the visual axis oscillates about the target direction; this condition is called a limit cycle. Robinson determined the values of K required to produce this phenomenon. Furthermore, by differentiating, clipping, and integrating the eye movement signal, the saccades could be removed from the feedback path. He found that K had to be increased to -5 in order to sustain the limit cycle when saccades were present, but that this value had to be further increased to -8 when the saccades were removed. Moreover, with only smooth eye movements in the feedback path, the oscillations were more rapid: 3.3 cps cf. 2 - 2.5 cps. Further evidence for the neurological independence of the two tracking systems is the fact that there are different reaction times for the two types of movements: about 250 ms for saccades and about 125 ms for smooth movements. Moreover, Rashbass (4) managed to completely suppress smooth tracking movements by the administration of pentothal; the constant velocity target was then tracked solely by saccades.

In spite of the fact that the saccadic and the smooth movement systems are neurologically independent, it is an oversimplification to ascribe position correction to the first and velocity matching to the second. Thus, in Rashbass' step-ramp experiment mentioned above, the occurrence and latency of a corrective saccade depended on the relative magnitude of the step-displacement and of the ramp velocity. As pointed out by Robinson (5), it appears as if both position and velocity signals are measured by the saccadic system. Moreover, we have done a short experiment to confirm Fender's (2) results which seemed to indicate that smooth pursuit movements are sometimes made in addition to saccades when tracking targets which move in a step-wise fashion. Figure 5-1 shows binocular vertical eye movements made in response to a point target which steps at 45° down and to the left. Note the smooth movements between the successive saccades.

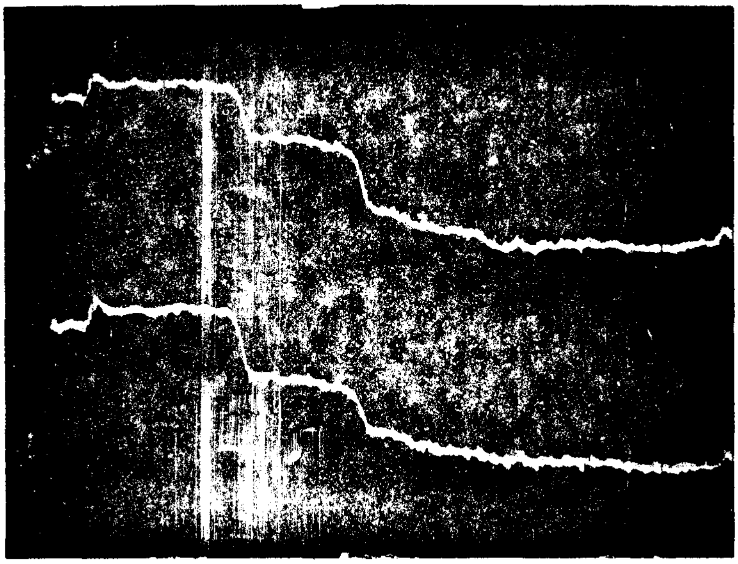


Figure 5-1. Vertical eye movements made when tracking a point target which steps down and to the left. Target motion is $\frac{1}{2}$ degree. Target motion has been used to trigger the sweep.
Subject: GSC (Binocular viewing)
Vertical division = 10 min arc
Horizontal division = 100 ms

Thus, while the saccadic and smooth movement systems appear to be distinct efferent mechanisms, their functional dichotomy is not well defined. If the target motion consists only of steps and ramps, then it may be more efficient to respond to steps by means of saccades and to ramps by means of smooth eye movements. However, even for this extreme case, the functional division is not that clear-cut. For more complicated target motions -- such as Gaussian random motion -- the relative roles of saccades and smooth movements remain to be clarified. While this is a most interesting problem, it is really beyond the scope of this work: we are primarily interested in the correlation between movements of the left and right visual axes under binocular and dichoptic viewing conditions. The above discussion has been presented to provide the reader with the background knowledge necessary to properly evaluate the results of the work that follows. Consequently, we shall examine the overall response of the oculomotor system without differentiating that part of the response brought about by saccades and that part produced by the smooth movements. Moreover, if the target moves slowly, a practiced subject can respond with a very small number of saccades. Thus, when Fender and Nye (3) presented a sinusoidally moving target to an observer, the subject's tracking eye movements were relatively free of saccades for frequencies below 2.5 - 3 cps if the amplitude was limited to 3^{o} or less.

This leads one to attempt to analyze the human oculomotor system by means of a straightforward engineering approach. In general, if the point target is moved sinusoidally, the tracking eye movements consist mainly of a sine wave at the same frequency, but with a smaller amplitude and some phase lag. These two functions of frequency completely describe the normal (closed-loop) tracking system if we assume linearity. Moreover, by stabilizing the image on the retina, the feedback loop can be opened, and the overall transfer function can be separated into a forward and a feedback transfer function. A priori, we would expect the feedback function to be unity, since the most reasonable measure of position error is simply the distance of the retinal image from the center of the fovea, and this distance, in turn, is directly proportional to rotation of the visual axis. Fender and Nye (3) did this open-loop experiment, and indeed obtained a feedback value of 0.92.

Thus, given the assumption of linearity, it is tempting to use sinusoidal stimuli because, from an analysis of the response, the system is completely described. However, before making too hasty a beginning, it behooves us to examine the validity of our assumption more closely. Figures 5-2 and 5-3 show the Bode plots (gain in decibels and phase lag in degrees) derived by various authors for the monocular horizontal tracking system under normal (closed-loop) conditions. In Figure 5-2, the two dotted curves represent the gain of the system for one subject when the amplitude of the target motion is 1.1° and 3.4°, respectively; these two curves were derived by Fender and Nye (3). One type of non-linearity is immediately apparent: the gain is lower for larger target motions. This implies saturation of response, in contrast to the dead-space theory where it is proposed that there is a position-insensitive region in the center of the fovea. However, the discrepancy between these two curves is not extreme, and they both have roughly the same shape. In addition, since we will restrict our investigations to the study of response to target displacements on the order of 1.5°, we can simply choose one value for the amplitude of

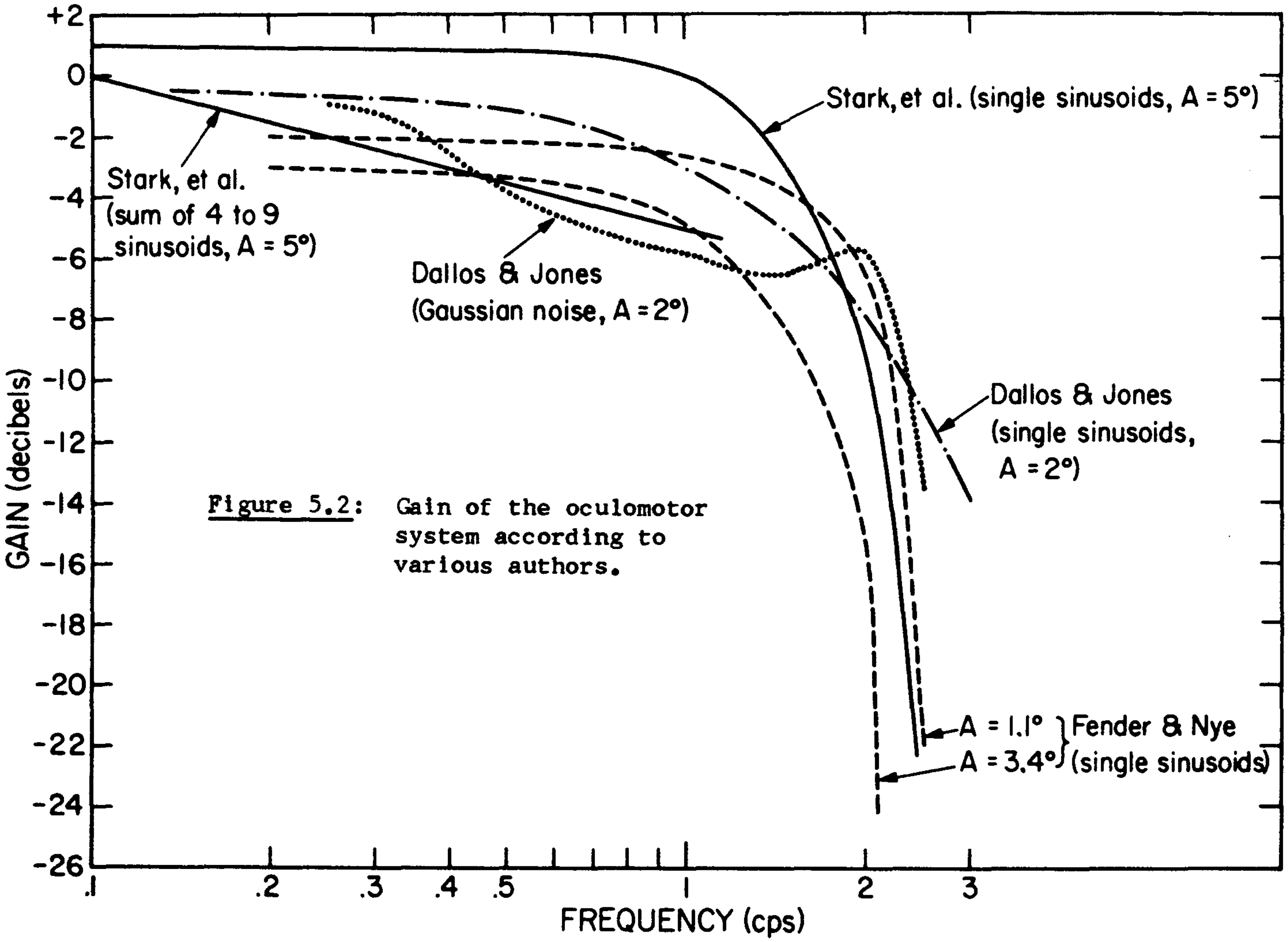


Figure 5.2: Gain of the oculomotor system according to various authors.

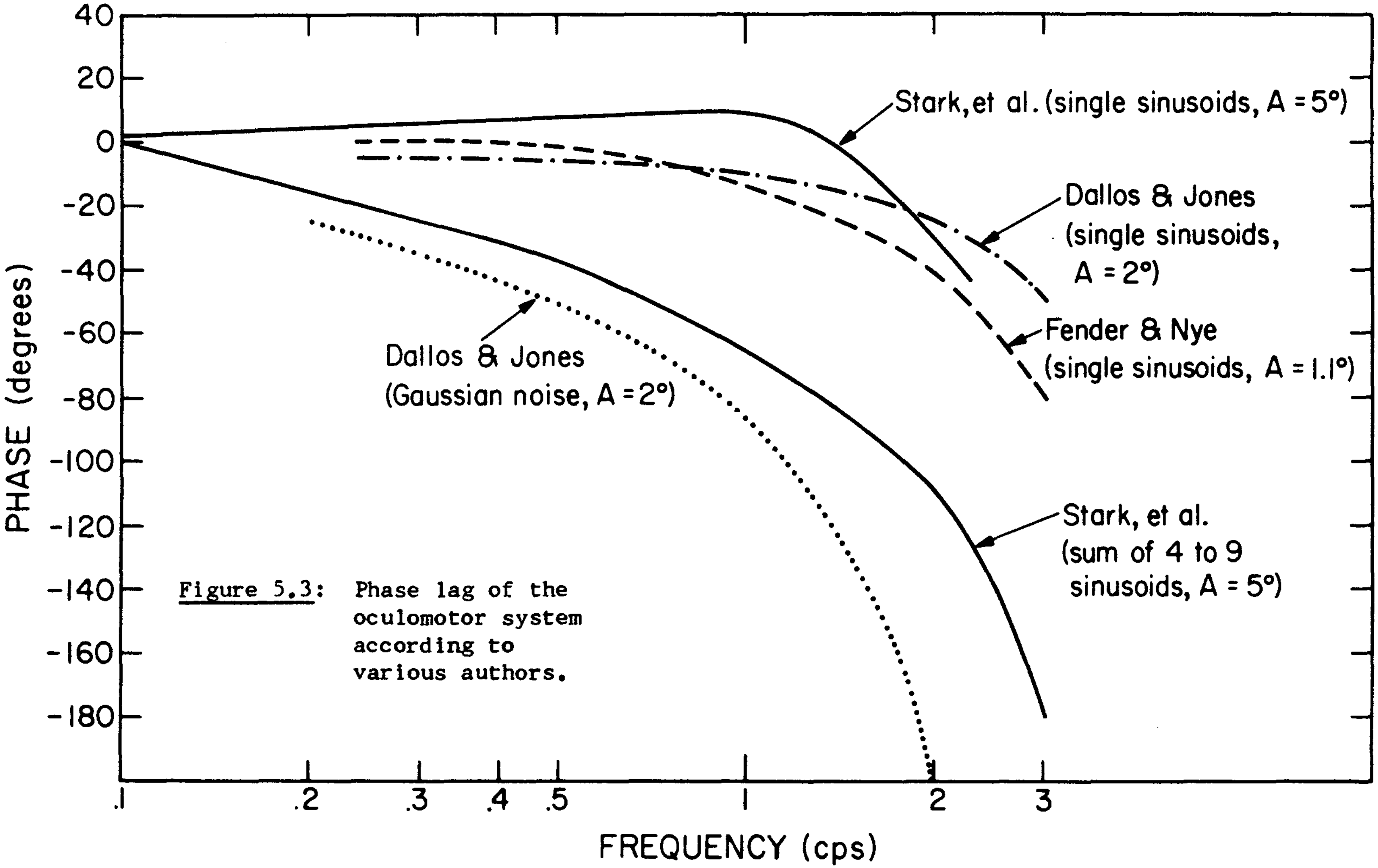


Figure 5.3: Phase lag of the oculomotor system according to various authors.

our sinusoids and proceed with the analysis, keeping in mind that we should expect slightly different curves for different values of stimulus amplitude. We should moreover expect slightly different curves for different subjects. The upper solid curve and the dot-dash curve of Figure 5-2 represent the gains of the eye movement tracking systems for two other subjects at two other amplitudes of target motion; the first one was derived by Stark, et al. (6), and the second one by Dallos and Jones (1). As expected, they differ from the Fender and Nye curves, but the overall shapes are not dissimilar. Going over to Figure 5-3, we can examine the corresponding phases. Fender and Nye (3) and Dallos and Jones (1) agree fairly well: phase lag increases from zero at low frequencies to a maximum of 80° at 3 cps, the upper limit for a valid sinusoidal response. Stark, et al. (6) show an interesting deviation from the other two: there is actually a phase lead of up to 10° at 1 cps before the expected phase lags at higher frequencies. Moreover, for all three investigators, the measured phase lag is much less than one would expect for a minimum phase network. The reason for this discrepancy appears to be quite obvious and was noted by the investigators: sinusoidal target motion is quite regular and relatively easy to predict. However, we are now faced with the difficulty of having to account for the neural activity by means of which the subject manages to predict target position. The authors thus resorted to the obvious device of including another black box in the system, labeled appropriately enough "predictor." This function is found by determining the open-loop transfer function for predictive and for non-predictive tracking by a method described below and then by dividing the first by the second. Dallos and Jones (1) found that this predictor consisted of a high-gain, low-pass network plus a pure phase advance which increased linearly with frequency. We will return to this point later.

We can form mathematically well-defined motion which appears to be unpredictable to the observer by summing three or more non-integrally related sinusoids or by computing band-limited Gaussian noise. Stark, et al. (6) have used the first device, and Dallos and Jones (1) the second. The curves on Figures 5-2 and 5-3 are solid and dotted, respectively. As the authors expected, phase lags are much greater for "unpredictable" target motion than for pure harmonic motions. However, the lag is also greater for the subject who is tracking Gaussian noise than for the other one who followed the sum of sinusoids. Is this merely due to subject differences, or is it caused by increased complexity of the motion? Subjectively, one cannot detect any difference between a "sum of sinusoids" motion and a "Gaussian noise" movement. To the subject, both appear to be purely random motion. However, Gaussian noise is inherently more complex than a simple "sum of sinusoids" motion in that it contains a continuum of frequencies and can only be described statistically. Is the difference in phase lag due to the fact that target motion is "unpredictable" or that it is "complex?" Can we really distinguish between the two? Are there in fact neural networks that analyze and/or predict target motion?

In the work that follows, we shall examine the response of the oculomotor system to target motions that are subjectively unpredictable: i.e., Gaussian random motion and "sum of sinusoids" motion.

We shall thus avoid the difficulty of conscious prediction. We will show that the different lags of the oculomotor system response to various target motions can be explained without reference to predictors or analyzers. We will first consider the question of system linearity. Is the system linear enough so that the response to four or more simultaneously presented sinusoids is the same as the sum of the responses to each one presented separately? Is it linear enough so that we can choose any combination of sinusoids? Will Gaussian noise yield the same frequency dependence as a finite sum of sinusoids? Results from previous authors, shown in Figures 5-2 and 5-3, are very ambiguous on this matter. Stark, et al. (6) state that they used the "sum of from 4 to 9 non-integrally related sinusoids." This particular phrase seems to imply that it makes no difference how many sinusoids were chosen or whether they were chosen to lie within some narrow frequency band or whether they were more or less evenly dispersed over the whole frequency range. In addition, no information is given on the amplitude of the individual sinusoids. Finally, it should be noted that all the above curves have been drawn through a cloud of points or through "averages" of points measured at different times. The standard deviation at any one frequency is usually quite large, and one has considerable freedom in drawing the curve.

Thus, examination of the linearity -- more precisely, the superposability of sinusoids -- of the eye-movement tracking system has been sadly neglected. Before we can apply systems analysis to the study of the nerve network of the oculomotor system, we must first examine the limitations of our techniques.

We will demonstrate that there is no direct relationship between the lag and the amplitude of the response of the oculomotor system. We will show that the lag of the response must be such that a minimum afferent signal is generated by the retina in order to trigger corrective movements. On the other hand, the amplitude of the corrective eye movements does not depend on the target motion, but is instead determined by the fact that the efferent portion of the oculomotor system operates at "full output" for both stationary fixation and for small target movements.

REFERENCES FOR CHAPTER V

1. Dallos, P. and Jones, R. W., "Learning Behavior of the Eye Fixation Control System," IEEE Trans. on Automatic Control, AC-8 (July 1963), pp. 218-227.

2. Fender, D. H., "The Eye Movement Control System: Evolution of a Model," Neural Theory and Modeling (Proc. Ojai Symposium), edited by R. F. Reiss, Stanford University Press, (1962).

3. Fender, D. H. and Nye, P. W., "An Investigation of the Mechanisms of Eye Movement Control," Kybernetik 1 (July 1961), pp. 81-88.

4. Rashbass, C., "The Relationship between Saccadic and Smooth Tracking Eye Movements," J. Physiol. 159 (1961), pp. 326-338.

5. Robinson, D. A., "The Mechanics of Human Smooth Pursuit Eye Movement," J. Physiol. 180 (1965), pp. 569-591.

6. Stark, L., Vossius, G., and Young, L. R., "Predictive Control of Eye Tracking Movements," I. R. E. Trans. on Human Factors in Engineering, HFE-3 (Sept. 1962), pp. 52-57.

VI. PREPARATION OF EXPERIMENT AND DATA REDUCTION FOR TRACKING EXPERIMENTS

The tracking experiments in the remainder of this thesis utilized the experimental apparatus and preliminary data processing discussed in Chapter II. In addition, we must now describe the computation of the target trajectory, the stimulus presentation, and the subsequent spectral analysis. The desired target motion was first computed on the IBM-7094 and written on computer tape in digital form; this was then transformed to an analog signal which was recorded on a CEC FM tape recorder. During the experiment, the pre-recorded waveforms drove the spot on an oscilloscope which was located directly in front of the subject and which replaced the optical system described in Chapter II, section 2. 4. During the experiment, the resulting eye movement information as well as the stimulus waveforms were transmitted to the Biological Systems Data Terminal (BSDT) and written on digital tape as described in Chapter II, section 4. At the same time, the eye movement signals were recorded on the CEC machine on different channels from the pre-recorded stimulus waveforms.

1. Computation of the Stimulus Trajectory

Two types of trajectories were used: the sum of several sine waves and band-limited Gaussian random motion. The first was quite straightforward to compute; the several sinusoids were equal in amplitude and initially in phase. The frequencies were chosen so that they were not low-integrally related, that is, so that none could be derived by sums or differences of the others. In order to distinguish responses to vertical target motion from those to horizontal motion, those sets of frequencies used for the vertical component were different from those used for the horizontal. We discarded the first 15 - 20 seconds of the record in order to obtain random initial phase.

Computing band-limited Gaussian motion was more difficult. Franklin (4) has derived a method for computing random numbers with a Gaussian distribution; 20, 000 of these have been calculated and stored on disc at the Caltech computing center. The results of several tests have guaranteed the randomness of these samples. Thus, if we take this list, construct a function of time, and carry out a spectral analysis, we find that there is equal power at all frequencies. However, if this waveform were viewed on an oscilloscope, the high frequency motions, being beyond the response capability of the human eye, would appear as a noisy blur. It was therefore necessary to process this function through appropriate low-pass filters.

A computer program was written to filter the raw Gaussian waveform digitally. A three-stage low-pass filter was used with corner frequencies at 2 cps, 3 cps, and 4 cps. Each stage was of the form

$$|G(f)|^2 = \frac{1}{1 + (f/f_o)^2} , \qquad (1)$$

f_o being the corner frequency. In addition, during digital-to-analog transmission, the higher frequencies were further attenuated by passing the signal through successive RC networks before analog recording.

2. Digital-to-Analog Transmission of the Stimulus Waveforms

In Chapter II, we mentioned that the normal analog-to-digital information flow could be reversed. The path is shown by the dashed arrows in Figure 2-1. After computing the waveform (200 points/sec) as described in section 1 above, the numbers were packed 3 per computer "word" and written on digital tape. This format is precisely the same as that used for recording eye movements. The digital tape was read and the information stored into buffers of the IBM-7040, which then sent it to the BSDT where the numbers were converted to voltages. This analog signal was directly recorded on the CEC tape recorder for the sinusoidal waveforms and for one record of the Gaussian process. Two more recordings were made for the Gaussian waveform; each was first passed through RC networks in order to further attenuate the higher frequencies. This was in addition to digital filtering. Thus, three Gaussian random processes were recorded: the first was filtered only by digital methods as described in section 2 above; in the second, the higher frequencies were further attenuated by means of an electrical RC network; and for the third waveform, an additional RC stage was used. Thus, the three recordings differed only in the high-frequency cut-off: Figure 7. 10 shows the power spectra. When a subject viewed the oscilloscope spot which was driven by these Gaussian waveforms, he reported that the target appeared to move faster as the bandwidth of the driving signal increased. Thus, these three Gaussian stimuli are labeled low-, medium-, and high-bandwidth Gaussian noise, respectively.

As stated in section 1 above, different sets of frequencies were used for the vertical and the horizontal sinusoidal stimuli. However, the same Gaussian waveform was used to drive the spot both vertically and horizontally. When recording the stimulus signals, a 15-second delay was therefore introduced between the two channels in order to avoid correlation between the two directions.

3. Experimental Procedure

A Hewlett Packard 122A oscilloscope with a short persistence trace (P2 phosphor) was placed directly in front of the subject at a distance of 2.63 meters. The optical system described in Chapter II, section 2.4, was removed, and the subject viewed the simulus directly. The dot subtended 2 min arc and the face of the oscilloscope 3°. The dot was driven in both the vertical and the horizontal directions by the two pre-recorded waveforms; the amplitude was adjusted so that the target never wandered off the face of the scope.

Signals from the BSDT controlled the stimulus presentation as well as the calibration steps for the eye measuring apparatus. The tape recorder was started, but a switch prevented the pre-recorded signals from moving the spot on the oscilloscope. After a delay of about 10 seconds, the operator pushed the "arm" button; this initiated the experimental sequence of events which then proceeded automatically. During the first three seconds, the BSDT sent appropriate signals to energize the solenoids which produced the calibration step as described in section 2.3, Chapter II. The switch between the tape recorder and the oscilloscope was then closed automatically and the spot was thus driven by the pre-recorded signals. The subject followed it as well as he could. After 116 seconds, the switch was again opened and the calibration sequence repeated. Thus, the oscilloscope spot was stationary during the calibration steps. Out of the 116 second record, only the central 78.8 seconds were used. The reason for choosing this particular record length will be discussed in section 4 below.

The four channels of eye movements and the two channels of stimulus information were directly transmitted to the BSDT for storage on digital tape as described in Chapter II, section 2.4. The sampling rate was 52 per second per channel. This unusual number was dictated by BSDT's multiplexing restrictions. This particular sampling rate determines a folding (Nyquist) frequency of 26 cps. Appropriate RC networks with 26 cps corner frequencies were therefore placed at the input of the transmission lines to the BSDT in order to avoid aliasing difficulties.

At the same time, the tracking eye movements were recorded on the analog tape recorder. The recording amplifiers had been removed from those two channels containing the stimulus information. Because of the finite distance between the recording and the playback heads, the analog records contain a constant delay between stimulus and response. However, this delay does not occur in the digital record, since all six channels were transmitted simultaneously. As mentioned in section 5, Chapter II, the analog record is used to check the digital data.

4. Spectral Analysis

After preliminary data processing (Chapter II, section 5), the digital records were analyzed in order to determine the power spectra and cross-power spectra. The Cooley-Tukey algorithm (2, 3) was used to compute the Fourier Transforms of the individual functions of time; this method is much faster than the straightforward calculations. A subroutine using this algorithm has been written and is available on disc at the Caltech computing center; it is an adaptation from the System/360 Scientific Subroutine Package (#360A-CM-03X). A fundamental restriction of this algorithm is that the data must be used only in quantities exactly equal to a power of 2. We therefore used 4096 samples per channel from our records (2^{12}); since the sampling rate was 52/sec , this is equivalent to 78.8 seconds.

If X(f) is the Fourier Transform of the time function x(t) and Y(f) that of y(t), then the cross-power spectrum of x(t) and y(t) is:

$$P(f) = \frac{1}{T} X(f)Y^*(f) \ , \tag{2}$$

where the asterisk signifies the complex conjugate, and T is the length of the time record (78.8 seconds in this case). The sampling interval Δt (1/52 sec) determines the Nyquist frequency:

$$f_n = \frac{1}{2\Delta t} = 26 \text{ cps} \ , \tag{3}$$

and the length of the record T dictates the spectral resolution δf which is equal to twice the frequency bin width Δf :

$$\delta f = 2\Delta f = 1/T = 0.0127 \text{ cps} \tag{4}$$

for T = 78.8 seconds. The Nyquist frequency is 26 cps, which is more than enough to cover the bandwidth of the oculomotor system, which is about 3 cps. However, the next lower available sampling rate would have been too slow. The spectral resolution is 0.0127 cps, which is really about 10 times finer than needed, so that we might have used a shorter time record with proportional savings in computing expenses. However, the problem is not that simple. There is a statistical error, e, associated with every calculation of power spectra, P(f); it is defined as:

$$e = \frac{\text{rms } \Delta P(f)}{\text{avg } P(f)} \quad . \tag{5}$$

It may be shown (1, 5) that, for Gaussian signals,

$$e^2 T \delta f \approx 1 , \tag{6}$$

which means that the expected error is on the order of unity if the original record is used directly (from Eq. (4)). This situation can be improved by dividing the time record into M segments and averaging the M power spectra. The spectral resolution then becomes wider:

$$\delta f = M/T , \tag{7}$$

but the expected error is decreased (from Eq. (6)):

$$e^2 \approx 1/M . \tag{8}$$

Thus, there is a trade-off between spectral resolution and statistical error.

We define the cross-correlation function R(τ) to be the Fourier Transform of the power spectrum P(f) in Eq. (2). It may be shown that this segmental averaging of power spectra is statistically equivalent to multiplying the original cross-correlation function R(τ) by the "window" function:

$$\begin{aligned} g(\tau) &= \frac{T - M|\tau|}{T - |\tau|} \qquad \text{for} \qquad |\tau| \le T/M \; ; \\ &= 0 \qquad\qquad\qquad \text{otherwise,} \end{aligned} \tag{9}$$

and then by transforming the results once again into the frequency domain. A number of variations of segmental averaging then becomes possible by the proper selection of the window g(τ). In this work, however, we chose the simplest smoothing function available (Eq. (9)), since we had no evidence to indicate that any other would have been preferable.

Consequently, the cross-power spectra in this thesis have been computed as follows. The appropriate functions of time $x(t)$ and $y(t)$ were first processed by subtracting the DC and the linear trend components. This was accomplished by fitting a straight line $w(t)$ to each function by minimizing the root-mean-square error; $w(t)$ was then subtracted from the appropriate function $x(t)$ or $y(t)$. The processed functions $x(t)$ and $y(t)$ were then transformed to $X(f)$ and $Y(f)$ by the Fast-Fourier Transform subroutine, which used the Cooley-Tukey algorithm. The raw power spectrum $P(f)$ was then computed from Eq. (2), and this was transformed back to the time domain to yield the raw cross-correlation function $R(\tau)$. This was then multiplied by the triangular window function

$$\begin{aligned} g(\tau) &= 1 - |\tau| / \tau_m \quad \text{for} \quad |\tau| \leq \tau_m = T/M \\ &= 0 \qquad \text{otherwise,} \end{aligned} \tag{10}$$

where the maximum τ_m was chosen at 4.82 sec. Equation (10) is a very close approximation to Eq. (9) for T much greater than τ, which was true in this case: 78.8 sec cf. 4.8 sec. The smooth correlation function

$$R'(\tau) = g(\tau)R(\tau) \tag{11}$$

was then Fourier transformed once more into the frequency domain to yield the smooth power spectrum $P'(f)$, which is the function quoted in the following chapters.

As a result of this statistical averaging, the spectral resolution δf was smeared

$$\delta f = M/T = 1/\tau_m = 0.203 \text{ cps} , \tag{12}$$

so that the separation between points in the computed power spectra was increased to

$$\Delta f = \tfrac{1}{2}\delta f = 0.1015 \text{ cps} . \tag{13}$$

Comparing Eq. (12) to Eq. (4) shows that the spectral resolution has been decreased by a factor of 20, but as a result the statistical error has been reduced from unity to a maximum of about 3 db. Typical power spectra of the oculomotor system are usually down about 33 db at 3 cps.

Thus, the power spectra presented in the following chapters have data points every 0.1015 cps; we could have shown 20 times as many, but these would have been most unreliable from a statistical point of view. Straight lines have been drawn between the points to facilitate the identification of a given curve. Moreover, a few of the points have been represented by a symbol to distinguish the various curves on the same graph.

5. Electrical Noise

In some of the experiments, a 1 cps signal was spuriously introduced into the eye movement records. Ironically, the source was found to be a flip-flop circuit which controlled a flashing warning light which had been placed outside the laboratory door in order to prevent intrusions during experimental runs. The polarity of this signal was such that it could have been mistaken for vergent eye movements or for conjugate vertical motions. However, none of the frequencies present in the stimuli were equal to 1 cps; we therefore decided not to discard the experimental results, since the artifact was so obvious and did not affect any of the valid results.

Hence, any sharp peaks at 1 cps in the power spectra of the following chapters must be interpreted as artifacts; these will be pointed out in each appropriate figure. Specifically, this spurious noise is present in the low-bandwidth Gaussian noise experiments, and not in the medium- or high-bandwidth Gaussian motions.

Moreover, for subject SAM, the right vertical eye movement channel was accidentally removed from the record for the medium- and high-bandwidth Gaussian target motions.

REFERENCES FOR CHAPTER VI

1. Blackman, R. B. and Tukey, J. W., The Measurement of Power Spectra, Dover, New York (1958).

2. Cochran, W. T., "What is the Fast Fourier Transform?", Proc. of IEEE 55 (October 1967).

3. Cooley, J. W. and Tukey, J. W., "An Algorithm for the Machine Calculation of Complex Fourier Series," Math. of Computation 19 (April 1965), pp. 297-301.

4. Franklin, J., "Numerical Simulation of Stationary and Non-Stationary Gaussian Random Processes," SIAM Review 1 (January 1965), pp. 68-80.

5. Richards, P. I., "Computing Reliable Power Spectra," IEEE Spectrum 4 (January 1967), pp. 83-90.

VII. NON-LINEARITIES OF THE OCULOMOTOR SYSTEM

1. Response to "Sum of Sinusoids" Target Motion

1.1 Description of the stimulus. In this section we will examine the tracking eye movements when the subject attempts to fixate binocularly on a point whose motion is the sum of several sinusoids. Sixteen frequencies were chosen between 0.1 cps and 3.0 cps for the vertical component of the stimulus, and sixteen other frequencies for the horizontal. These were picked so as to be approximately equidistant on a logarithmic scale and so as to have no low-integral relationship among themselves. For the first set of experiments, the 32 frequencies were divided into 4 bands of 8 frequencies each (4 per channel) as listed in Table 7-1:

TABLE 7-1

Frequencies of the Stimulus Waveform (cps)

	Vertical				Horizontal			
Band 1:	0.112	0.137	0.170	0.212	0.123	0.154	0.190	0.235
Band 2:	0.260	0.323	0.400	0.495	0.280	0.360	0.445	0.550
Band 3:	0.61	0.76	0.94	1.16	0.68	0.84	1.03	1.28
Band 4:	1.43	1.76	2.20	2.72	1.60	1.97	2.45	3.00

Only one frequency band was used during one experimental session, and only one session was done in one day. Thus, four days were required to complete this set.

The second set of experiments was accomplished in one session and consisted of two bands containing 7 and 13 sinusoids per channel, respectively. The first band contained every other frequency listed in Table 7-1 beginning with the lowest one, and the other band contained every frequency; these are listed in Table 7-2. In each case, the highest three frequencies were not used. In all experiments, total target motion was restricted to 1.5° radius.

TABLE 7-2

Frequencies of the Stimulus Waveform (cps)

Vertical				Horizontal			
7-Frequencies Band:							
0.112	0.170	0.260	0.400	0.123	0.190	0.280	0.445
0.610	0.940	1.43		0.68	1.03	1.60	
13-Frequencies Band:							
0.112	0.137	0.170	0.212	0.123	0.154	0.190	0.235
0.260	0.323	0.400	0.495	0.280	0.360	0.445	0.550
0.610	0.760	0.940	1.16	0.680	0.840	1.03	1.28
1.43				1.60			

1.2 <u>Power spectra of tracking eye movements.</u> All subjects reported that the resulting target motion appeared to be completely unpredictable and was a joy to behold. Figure 7.1 shows a 15 sec record of such a trajectory, together with the corresponding tracking eye movements. The Fourier transforms of the target motion and eye movements were computed as described in Chapter VI. Since the sampling frequency was 52 samples per second, the bandwidth ranges from DC to 26 cps and is divided into 2048 bins on a linear scale. Figures 7.2 and 7.3 show these power spectra for subjects GSC and SAM, respectively, when the stimuli consisted of the 4-frequencies bands listed in Table 7-1. Power (min arc sq) is plotted on a linear scale and frequency (cps) on a logarithmic scale. On each plot, one scale is used for the vertical channels and a different one for the hori-

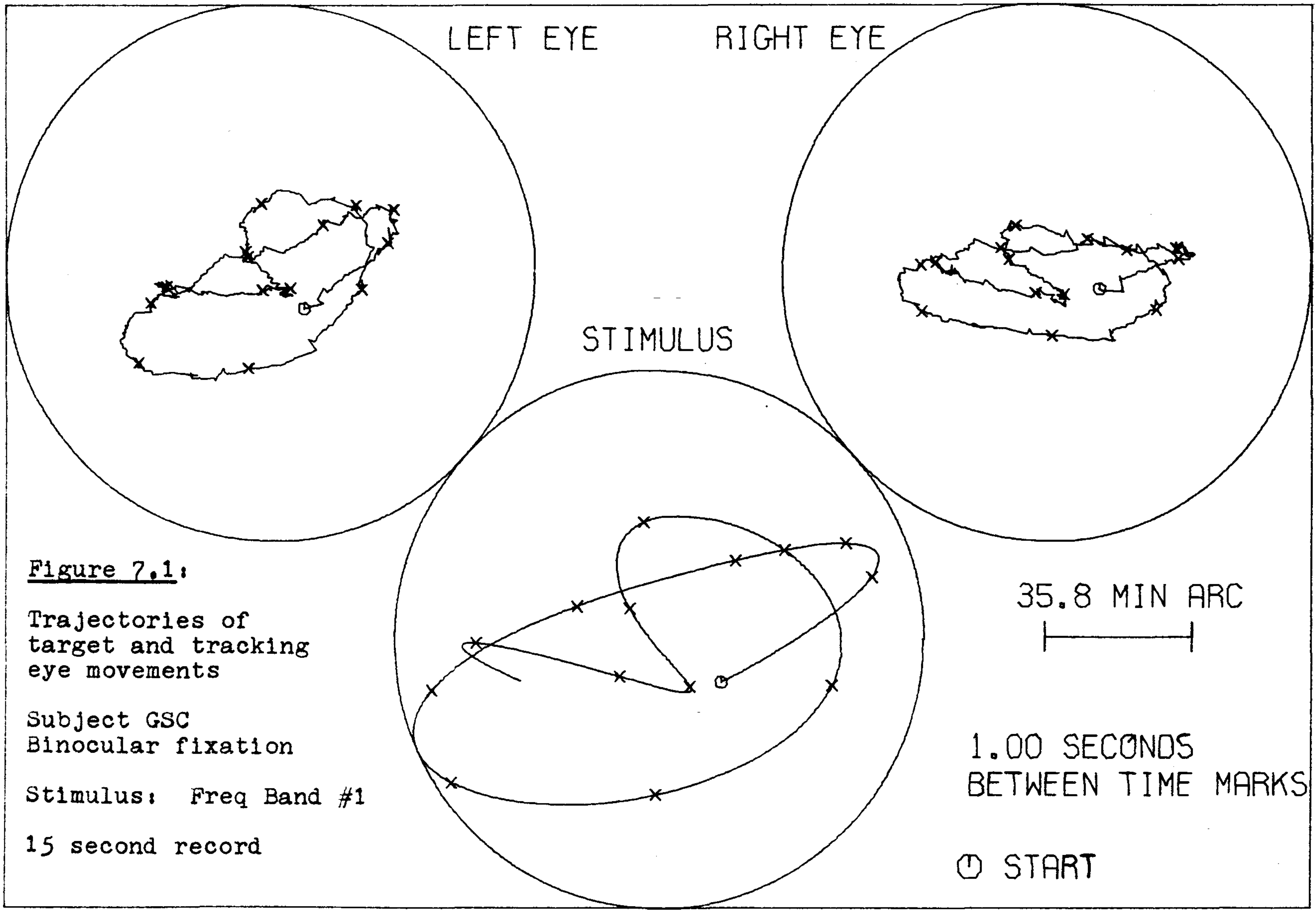


Figure 7.1:

Trajectories of target and tracking eye movements

Subject GSC
Binocular fixation

Stimulus: Freq Band #1

15 second record

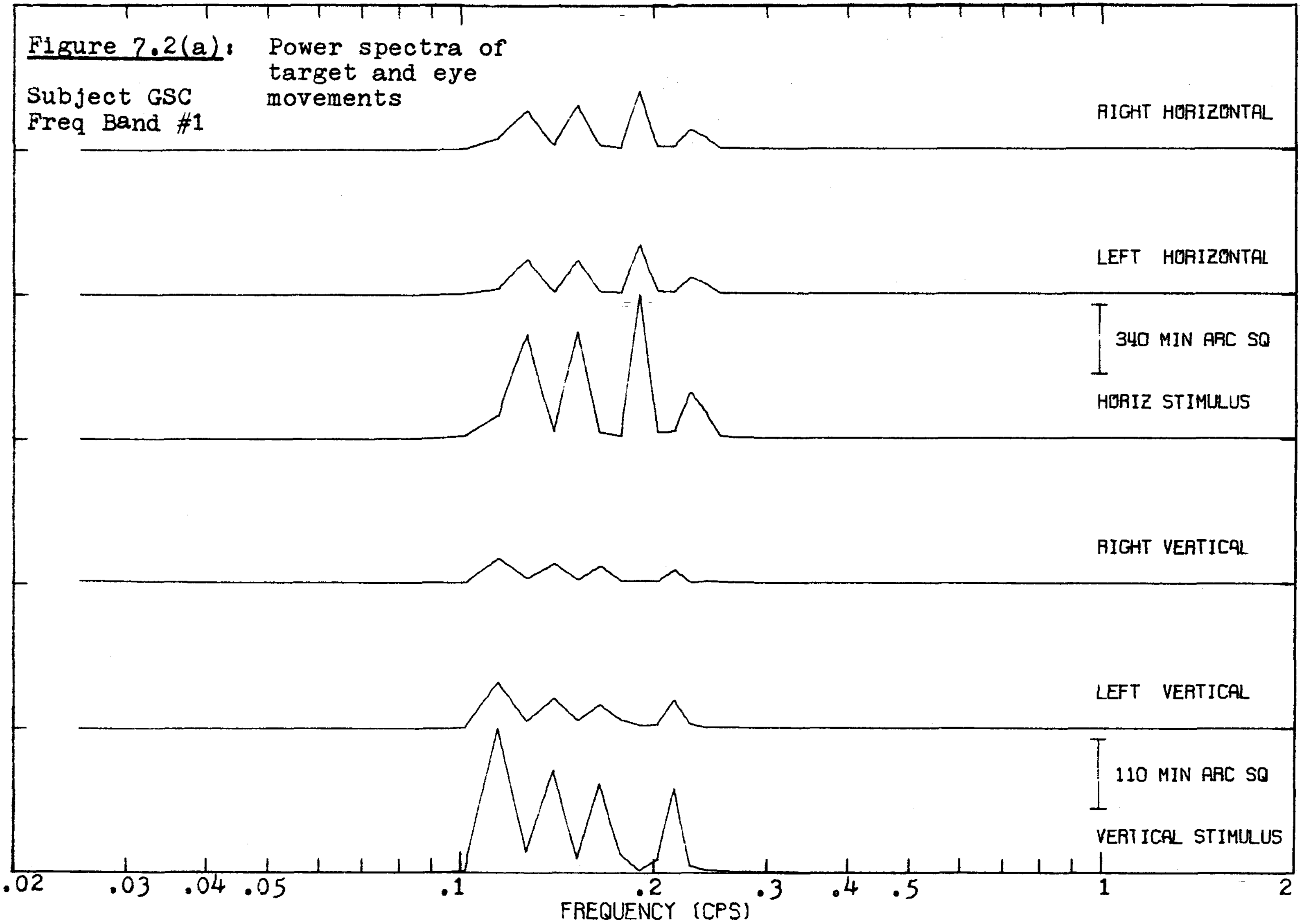
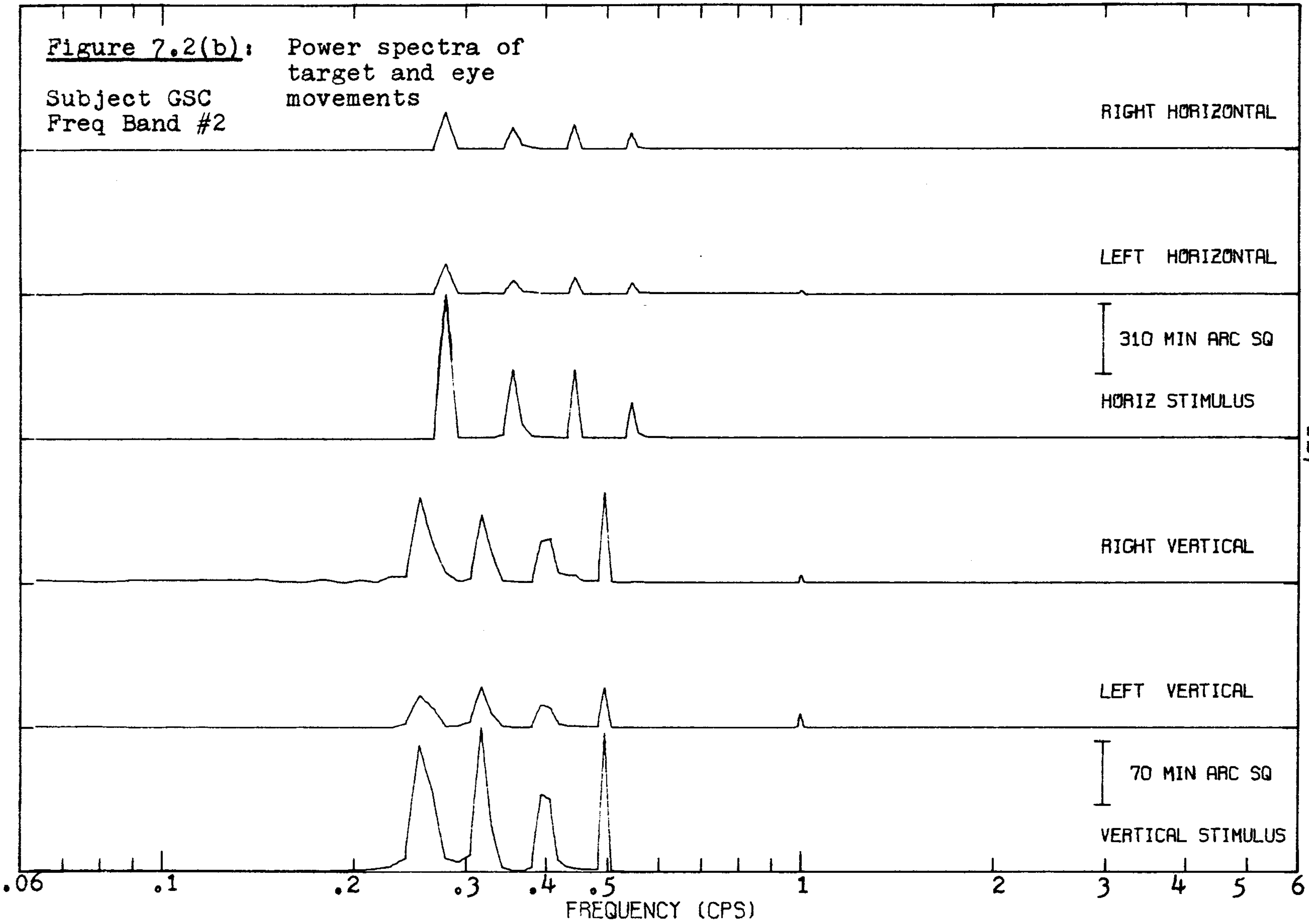


Figure 7.2(a): Power spectra of target and eye movements

Subject GSC
Freq Band #1

Figure 7.2(b): Power spectra of target and eye movements

Subject GSC
Freq Band #2



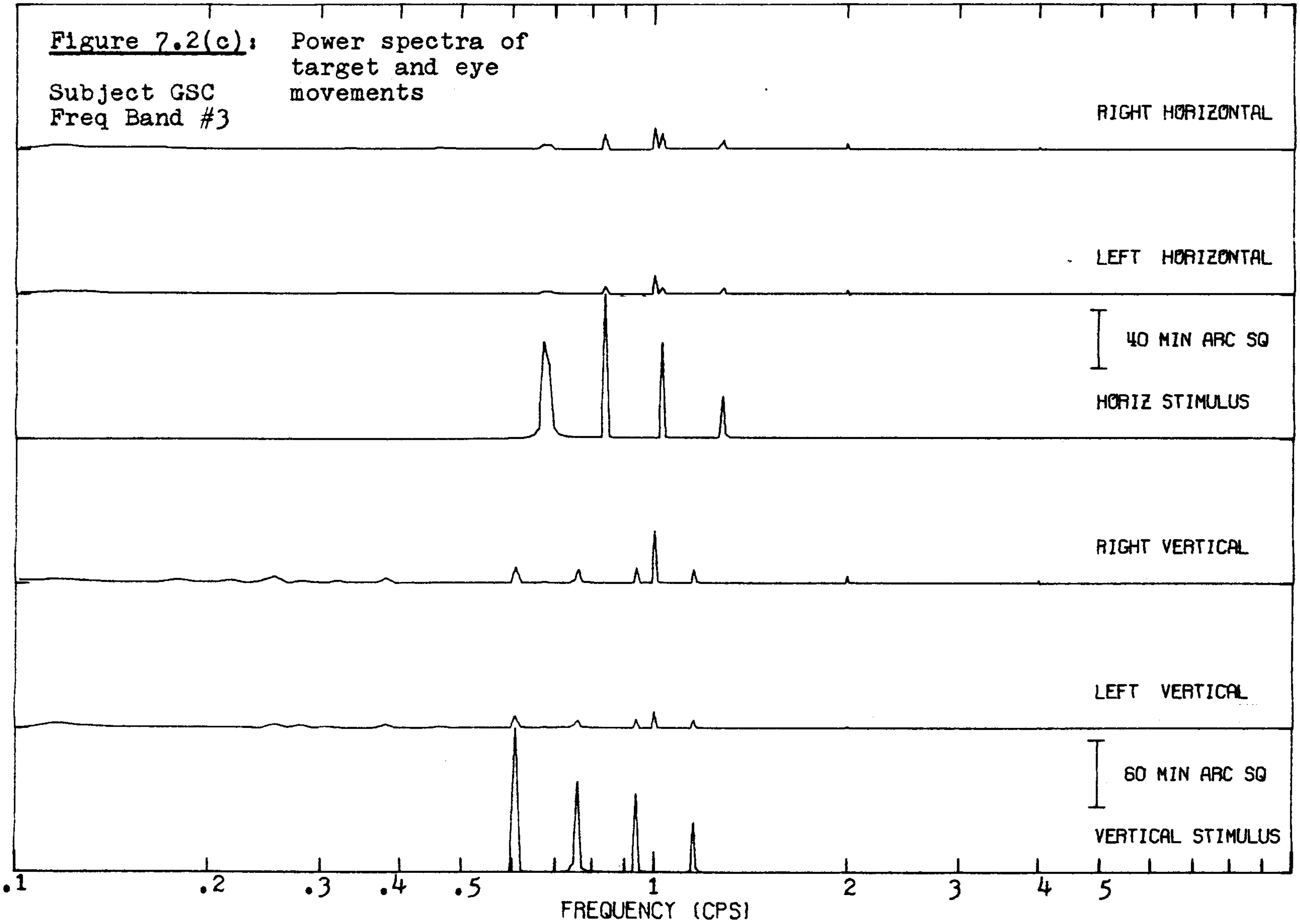


Figure 7.2(c): Power spectra of target and eye movements

Subject GSC
Freq Band #3

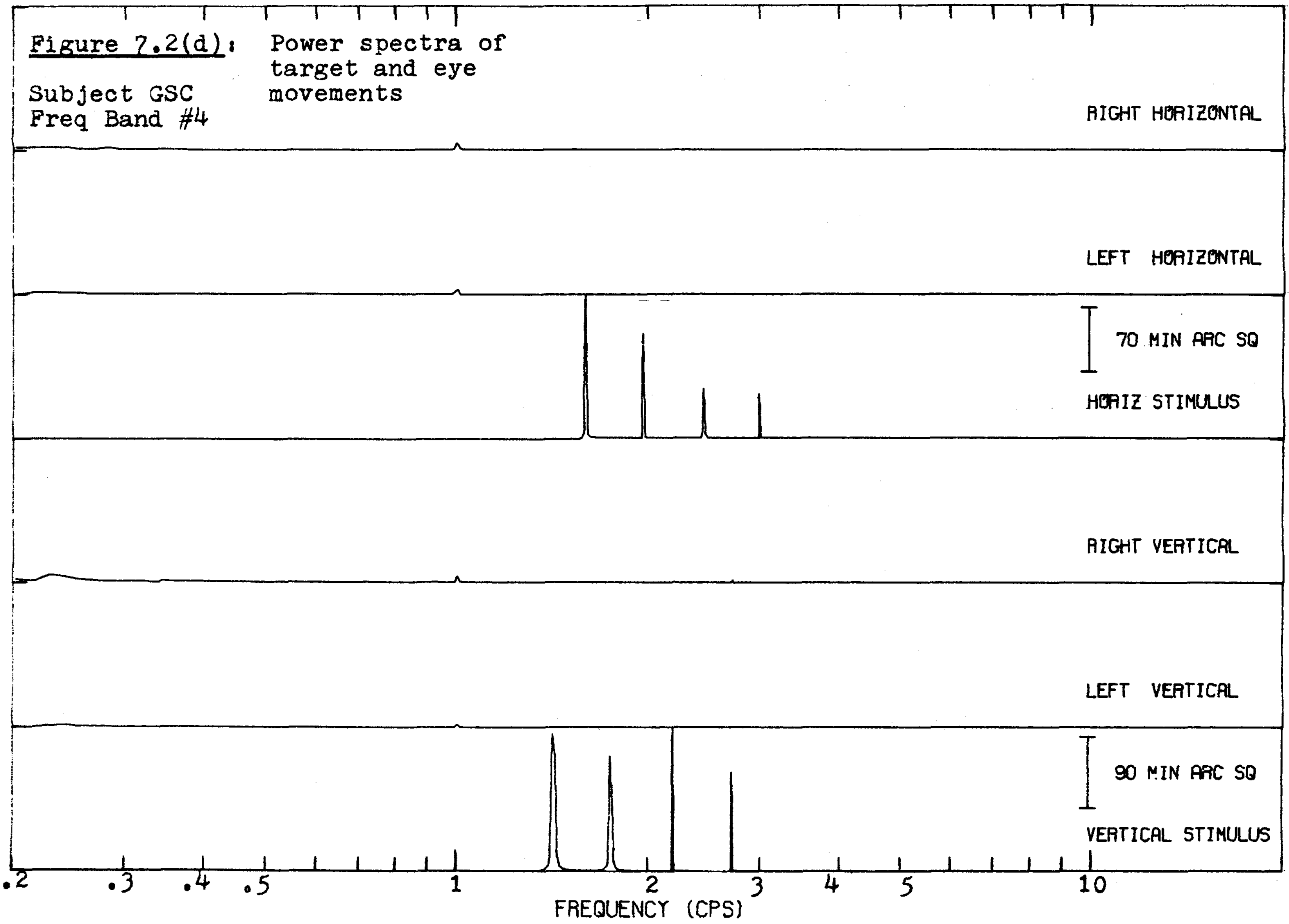


Figure 7.2(d): Power spectra of target and eye movements

Subject GSC
Freq Band #4

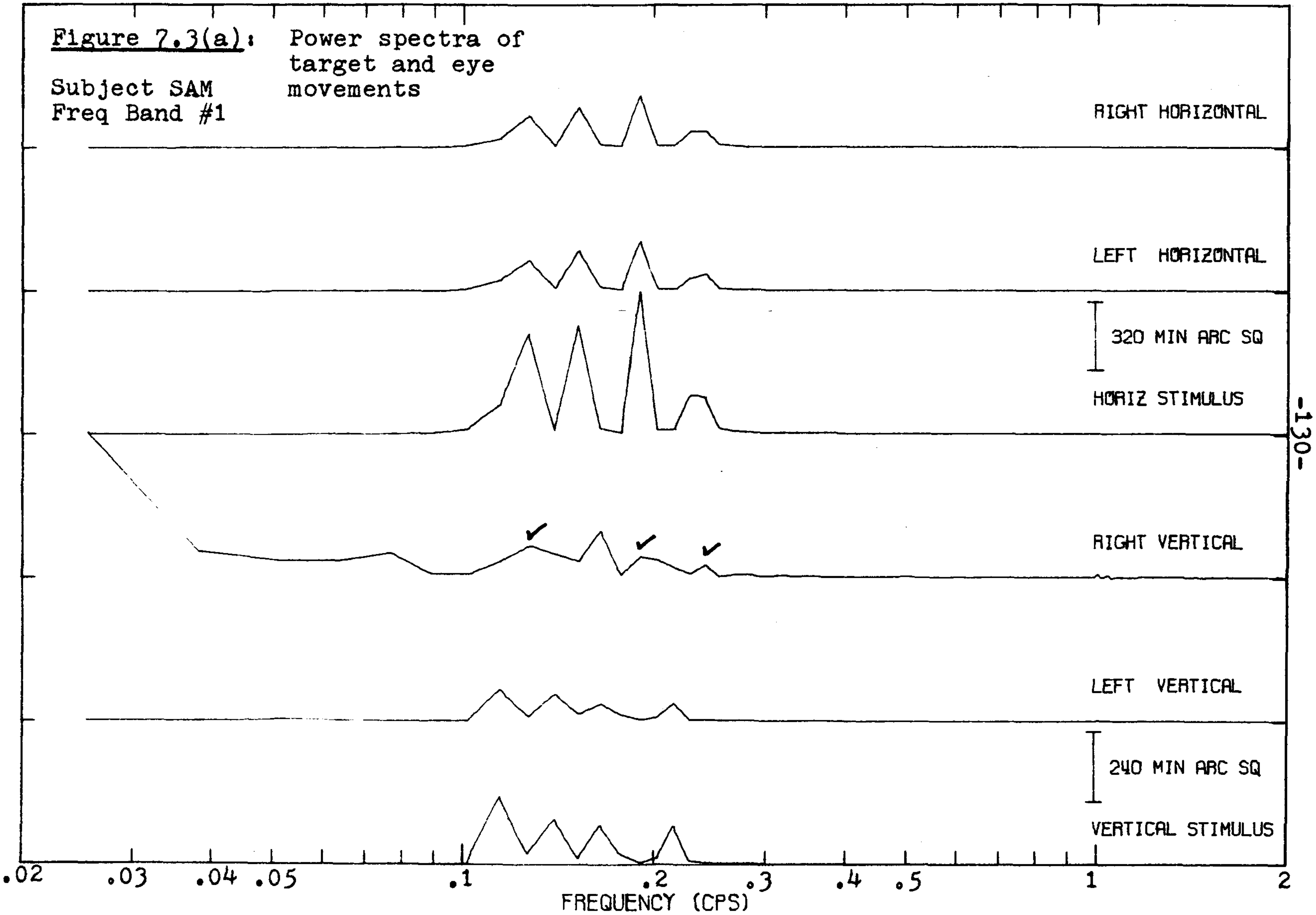


Figure 7.3(a): Power spectra of target and eye movements

Subject SAM
Freq Band #1

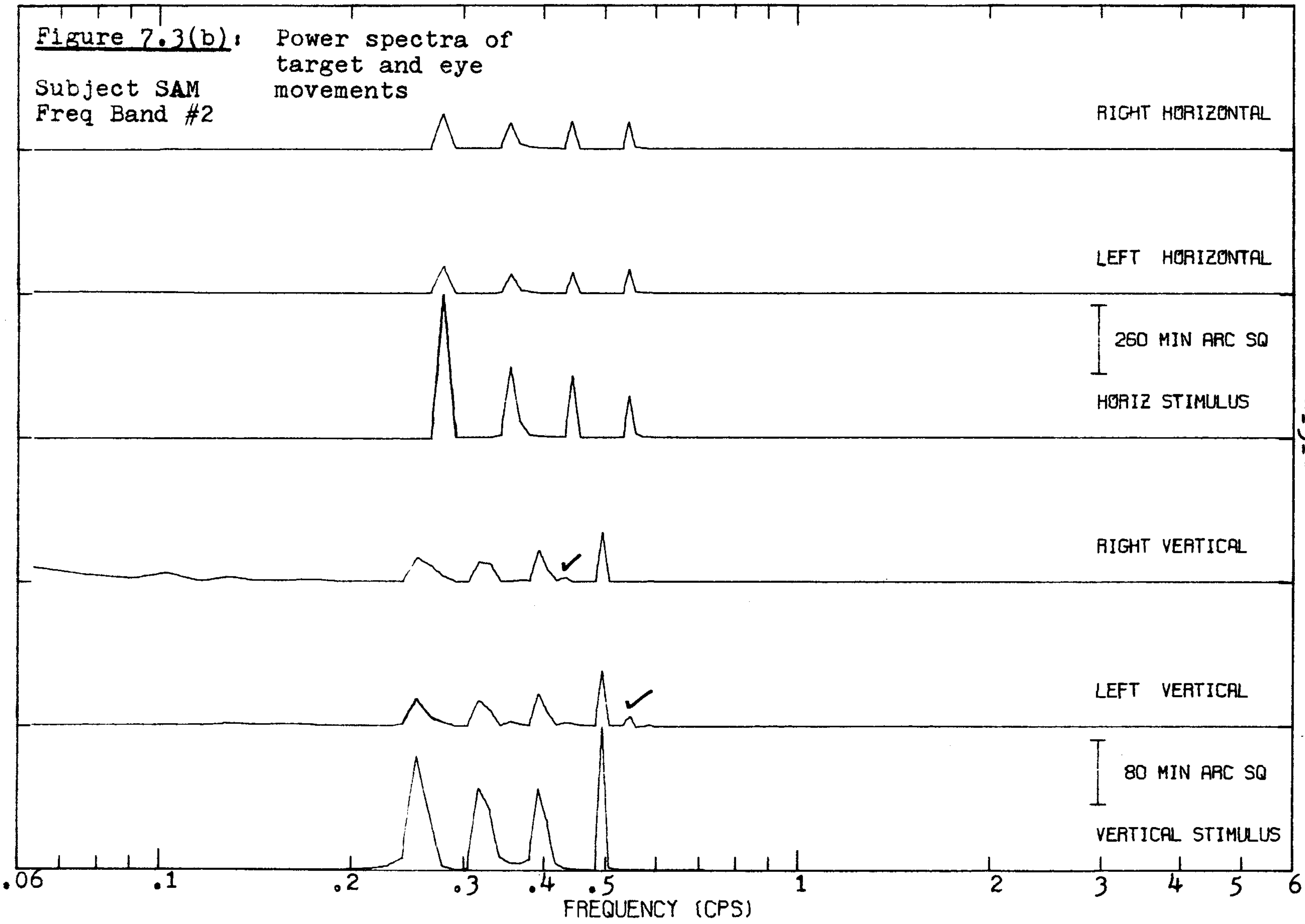


Figure 7.3(b): Power spectra of target and eye movements

Subject SAM
Freq Band #2

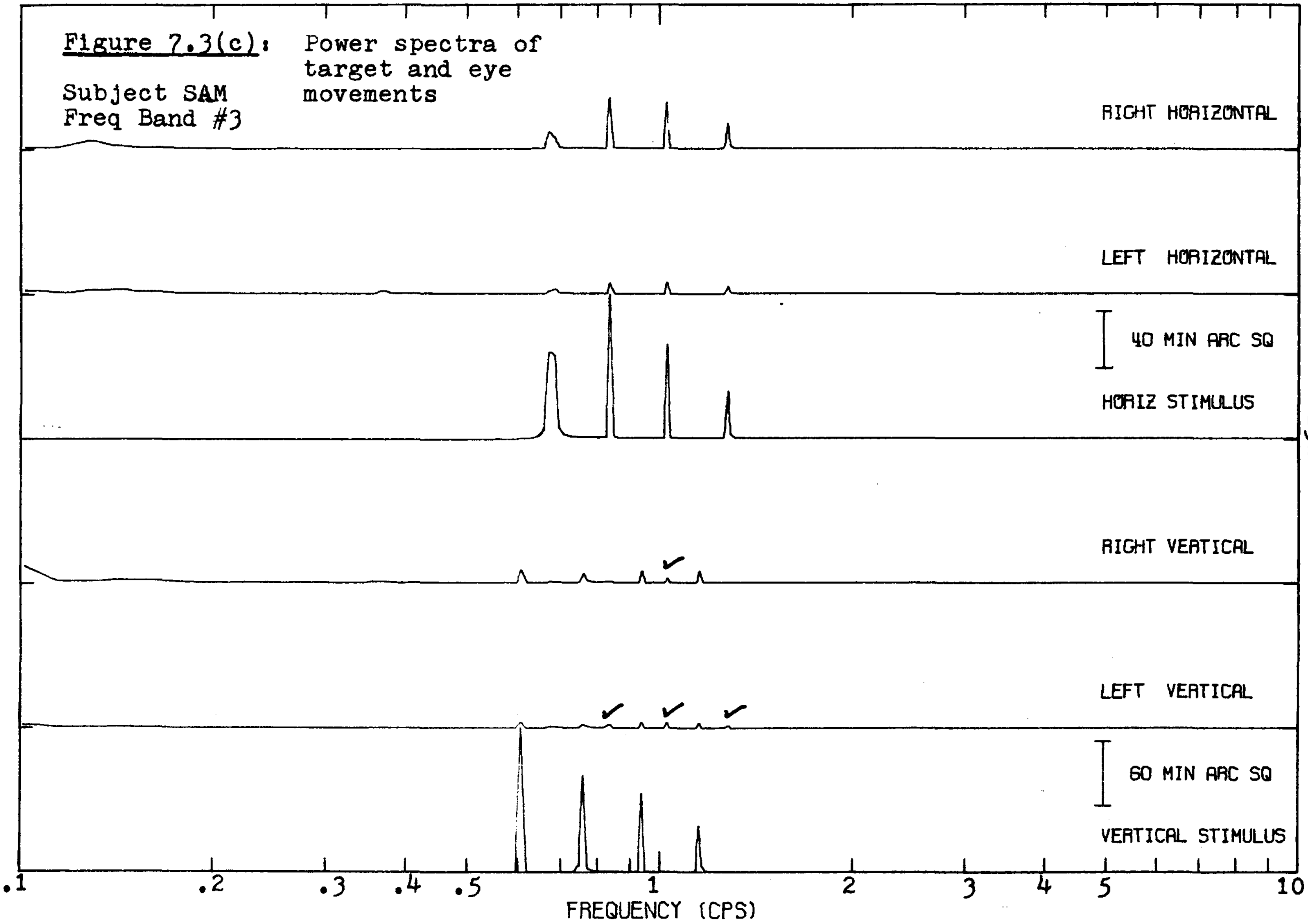


Figure 7.3(c): Power spectra of target and eye movements

Subject SAM
Freq Band #3

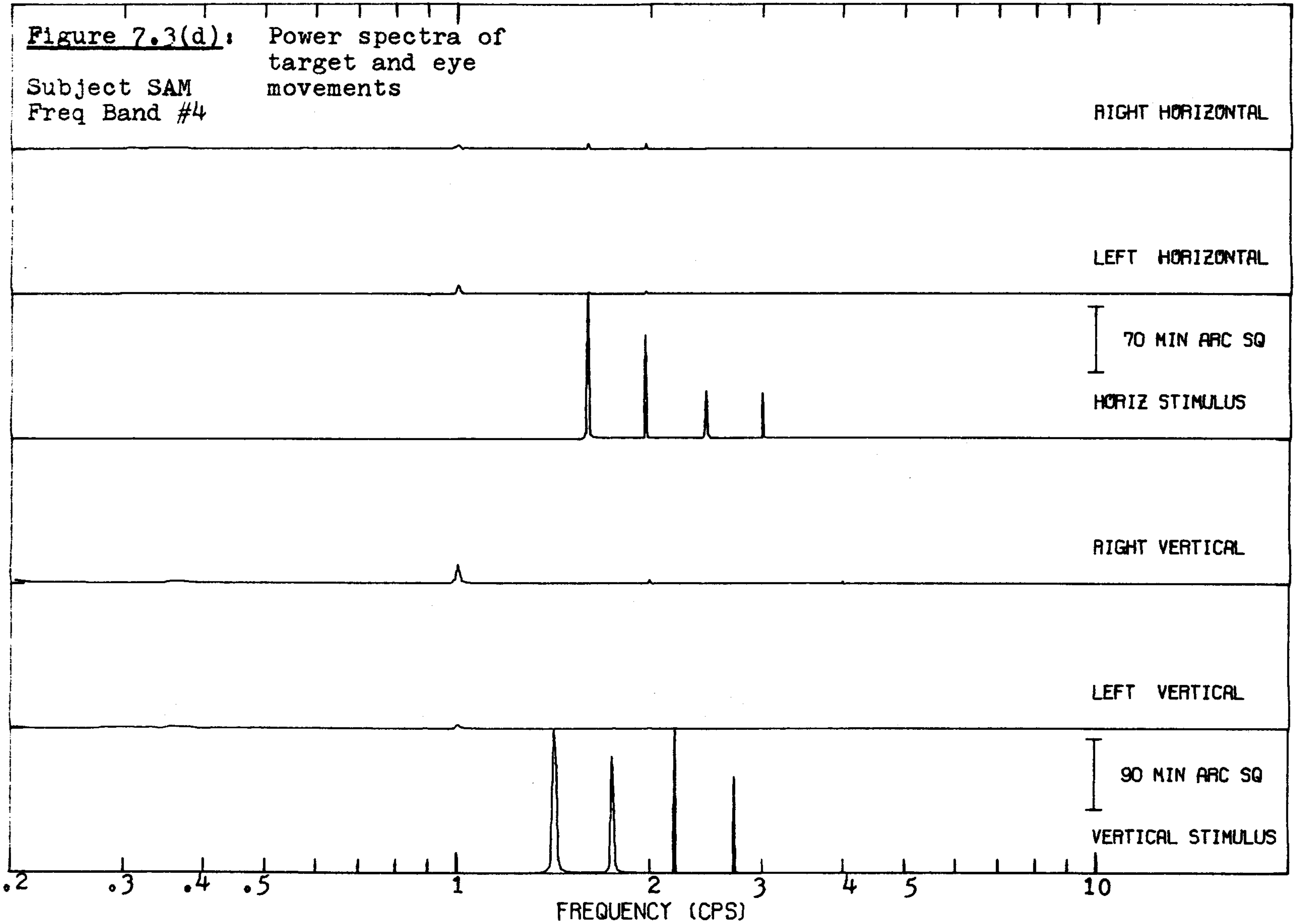


Figure 7.3(d): Power spectra of target and eye movements

Subject SAM
Freq Band #4

zontal channels. The peaks appear to be broader at the lower frequencies simply because the frequency range is computed linearly and plotted logarithmically. Note that those peaks which occur at 1 cps and its harmonics result from electrical noise in the system and do not represent eye movements. This has been discussed in Chapter VI.

Despite the apparent randomness of the target motion, both subjects nevertheless managed to follow the spot closely enough so that, in general, the resulting eye movements consist only of those frequencies present in the stimulus. In addition, for subject GSC, vertical and horizontal eye movements contain only those frequency components present in the vertical and the horizontal stimuli, respectively. There is no cross-talk between vertical and horizontal channels. For subject SAM, however, there is some cross-talk from the horizontal to the vertical, but not vice-versa. That is, the vertical eye movements contain some frequencies present only in the horizontal component of the stimulus. These occur in all four bands and may occur in either or both eyes; they are indicated by checkmarks in Figure 7. 3. Now, the eye movements made in these experiments are small enough so that there should be no cross-talk between vertical and horizontal motions as a result of the geometry of muscular action. It is true that for large eye movements the superior and inferior recti, which mediate vertical motions of the visual axis, may cause the visual axis to move horizontally as well. However, the medial and lateral recti, which mediate horizontal motion, act in such a way as to produce no vertical motion from the primary position even for large eye movements. Hence, if there is cross-talk, we would expect it to be exhibited as horizontal motion resulting from a vertical stimulus, but not vice-versa. Note, however, that precisely the opposite holds true for subject SAM. Thus, this anomaly cannot be explained by the geometry of muscular action. The cross-talk must occur at or before the nuclei of the extra-ocular motoneurons.

For subject GSC there are essentially no frequencies in the eye movements which are not present in the stimuli. Figure 7.2c shows that in Band 3, there is some power below 0.5 cps, but these small peaks occur at frequencies which are random, not differences of stimulus frequencies. For SAM this is also true, with one exception. In Band 1, the power spectrum of the right vertical eye movement record contains two substantial peaks at frequencies which happen to be differences of two stimulus frequencies; these, however, occur in only one eye. With this one exception out of 16 cases, there are no frequencies present which are sums or differences of input frequencies or of their harmonics. Thus, one important class of non-linearities can be dispensed with.

Figures 7.4 and 7.5 show the power spectra of the tracking eye movements when the stimulus spectrum has been increased to 7 and 13 frequencies per channel. As the number of component sinusoids increases, the eye movement response becomes more erratic. Several input frequencies are absent in the response, and there are several spurious frequencies present in the eye movement record which are not present in the stimuli. This represents the inability of the neural networks to mediate efferent signals in such a way as to enable the visual axis to track the target linearly. The results of the next

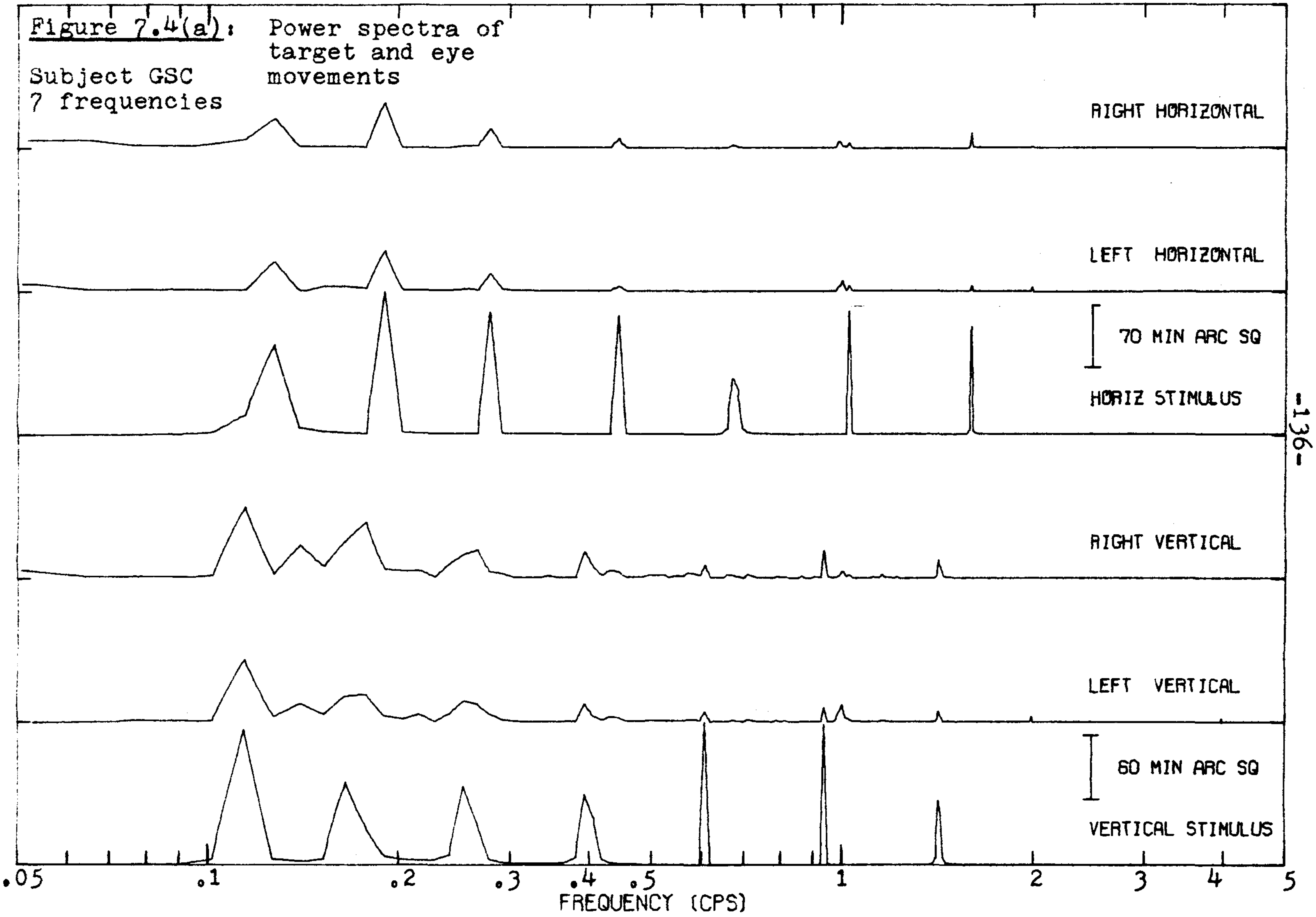


Figure 7.4(a): Power spectra of target and eye movements

Subject GSC
7 frequencies

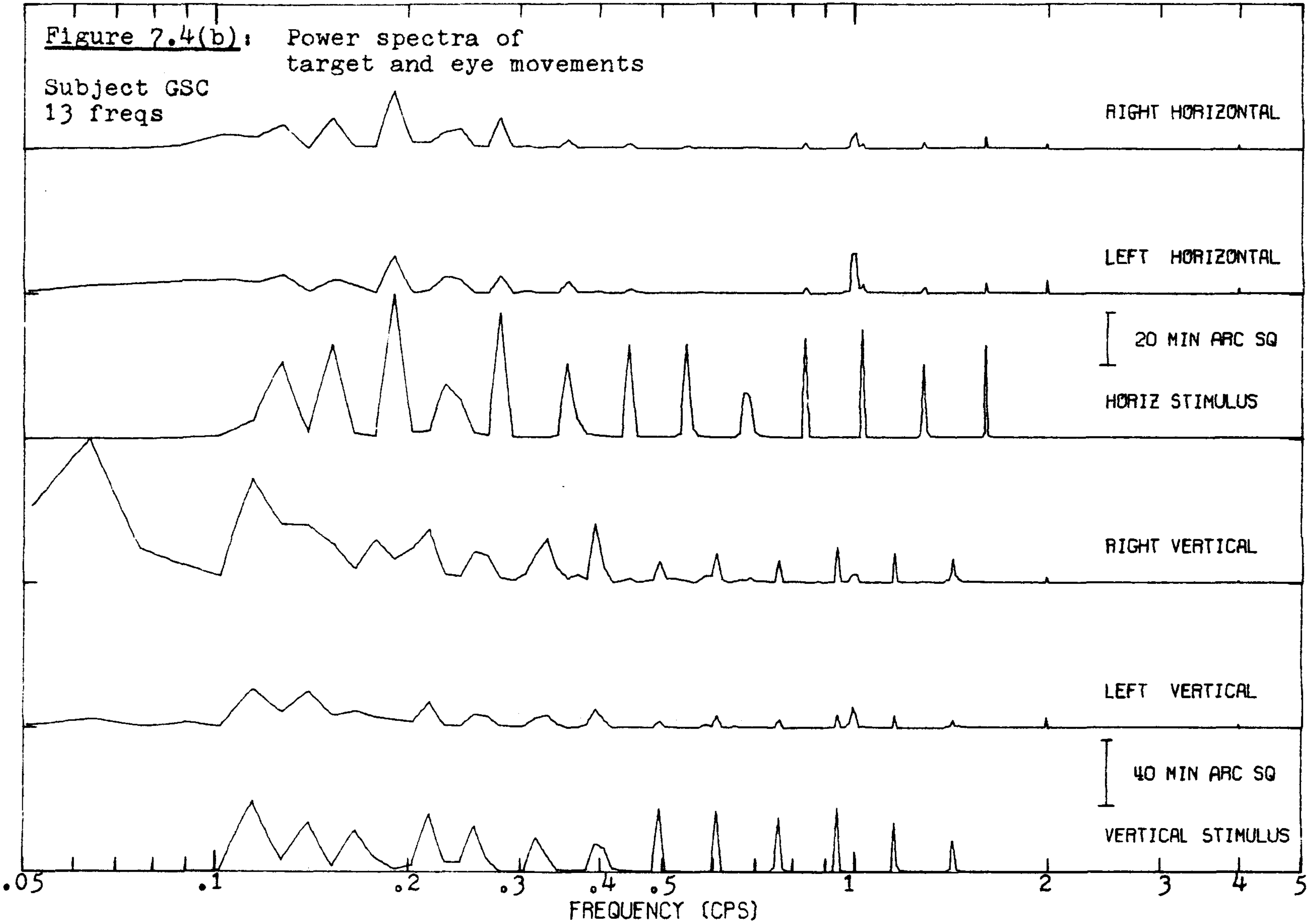


Figure 7.4(b): Power spectra of target and eye movements

Subject GSC
13 freqs

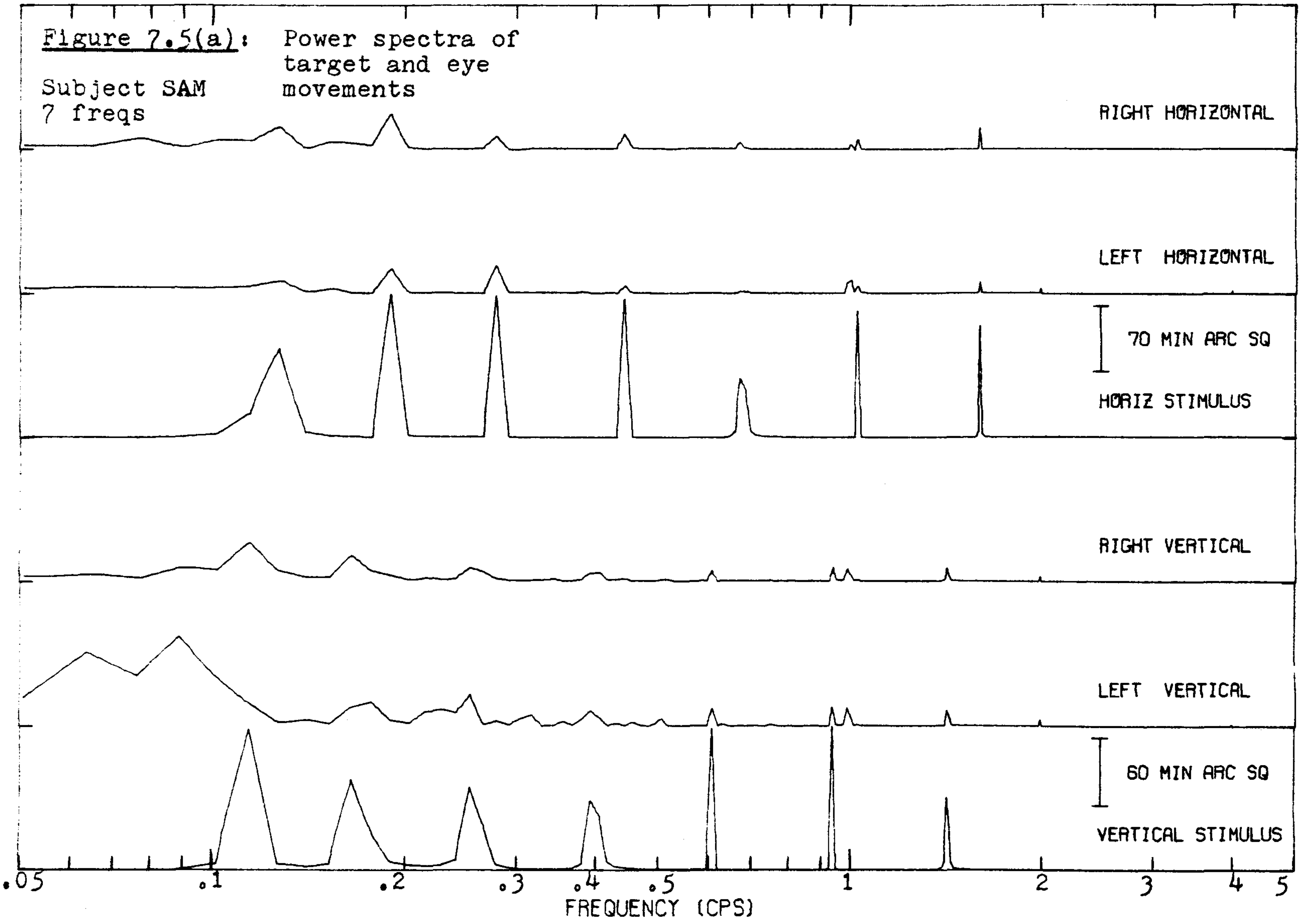


Figure 7.5(a): Power spectra of target and eye movements

Subject SAM
7 freqs

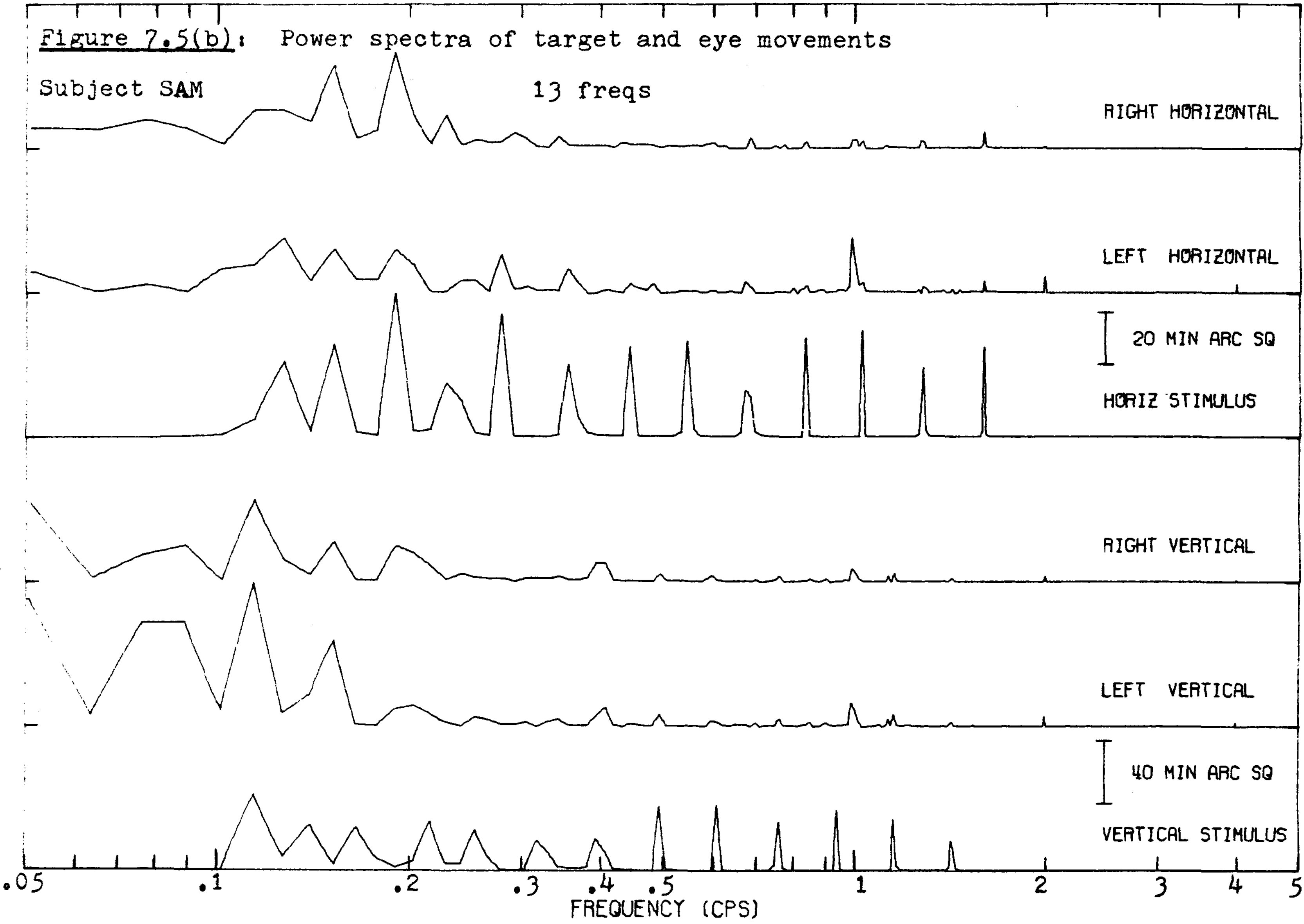


Figure 7.5(b): Power spectra of target and eye movements

Subject SAM 13 freqs

section will suggest a possible explanation for this uneven response.

1.3 Gain as a function of frequency. We will first examine the gain of the eye movements relative to target motion at the stimulus frequencies for the four 4-frequencies bands described above. The target was viewed binocularly and the eye movements of both eyes were recorded. For this purpose, however, examination of one eye is sufficient, since the responses of the two eyes are similar. Figures 7.6a through 7.6d show the gain in decibels as a function of frequency for the vertical and the horizontal movements of the left eye for both subjects. It will be noted that only straight lines have been drawn between successive data points within a given band. No attempt has been made to draw smooth curves through all data points, since we wish to examine the responses to specific combinations of sinusoids. Consequently, the graphs may be a bit harder to understand, but the effort is well worth while. The results are qualitatively the same for both subjects and for both vertical and horizontal eye movements. As expected, the average gain for a band decreases as the average frequency of the band increases. However, within a given band, the gain as a function of frequency behaves in a very unexpected way: in general, the gain increases with increasing frequency. This increase is by no means monotonic, but if one attempts to fit a straight line through the four data points of a given band, in general, the slope is positive. Table 7-3A lists the values of these slopes as well as their standard deviations. The absolute value of the slope is not in itself particularly enlightening, but together with its standard deviation, it indicates whether the line points up or down or whether

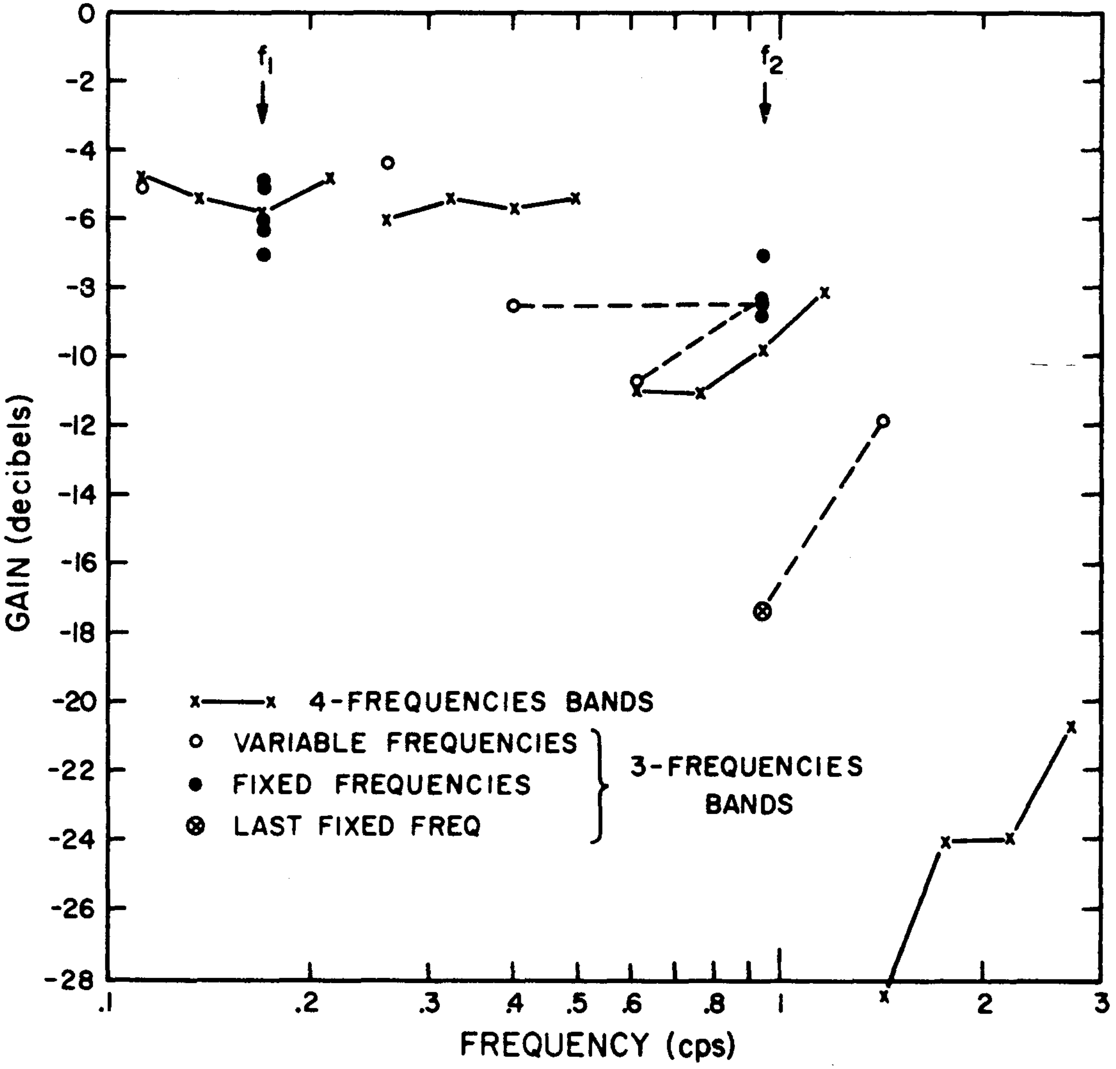


Figure 7.6(a): Gain of the oculomotor system
Subject GSC
Left vertical eye movements
Binocular fixation

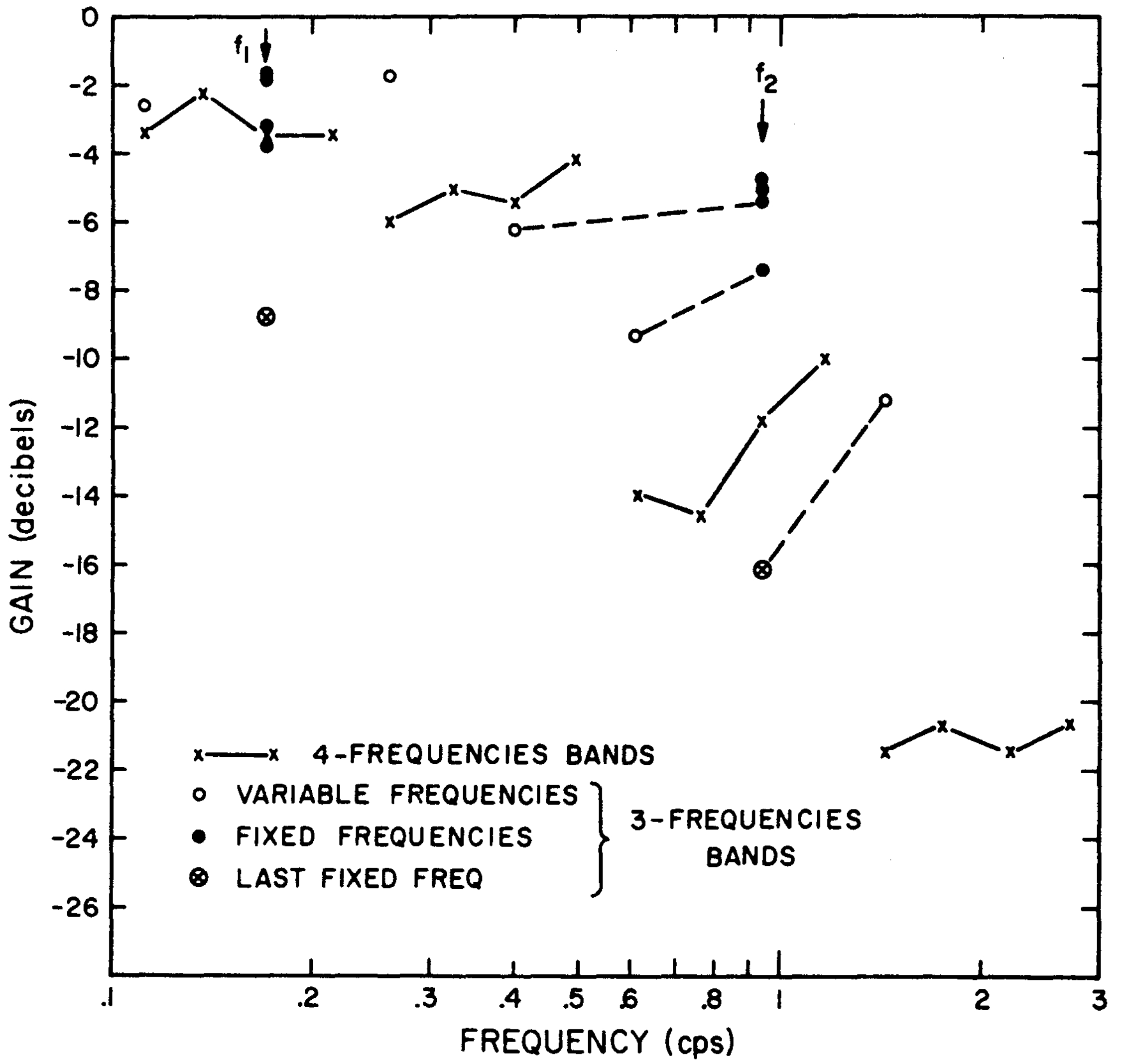


Figure 7.6(b): Gain of the oculomotor system
Subject SAM
Left vertical eye movements
Binocular fixation

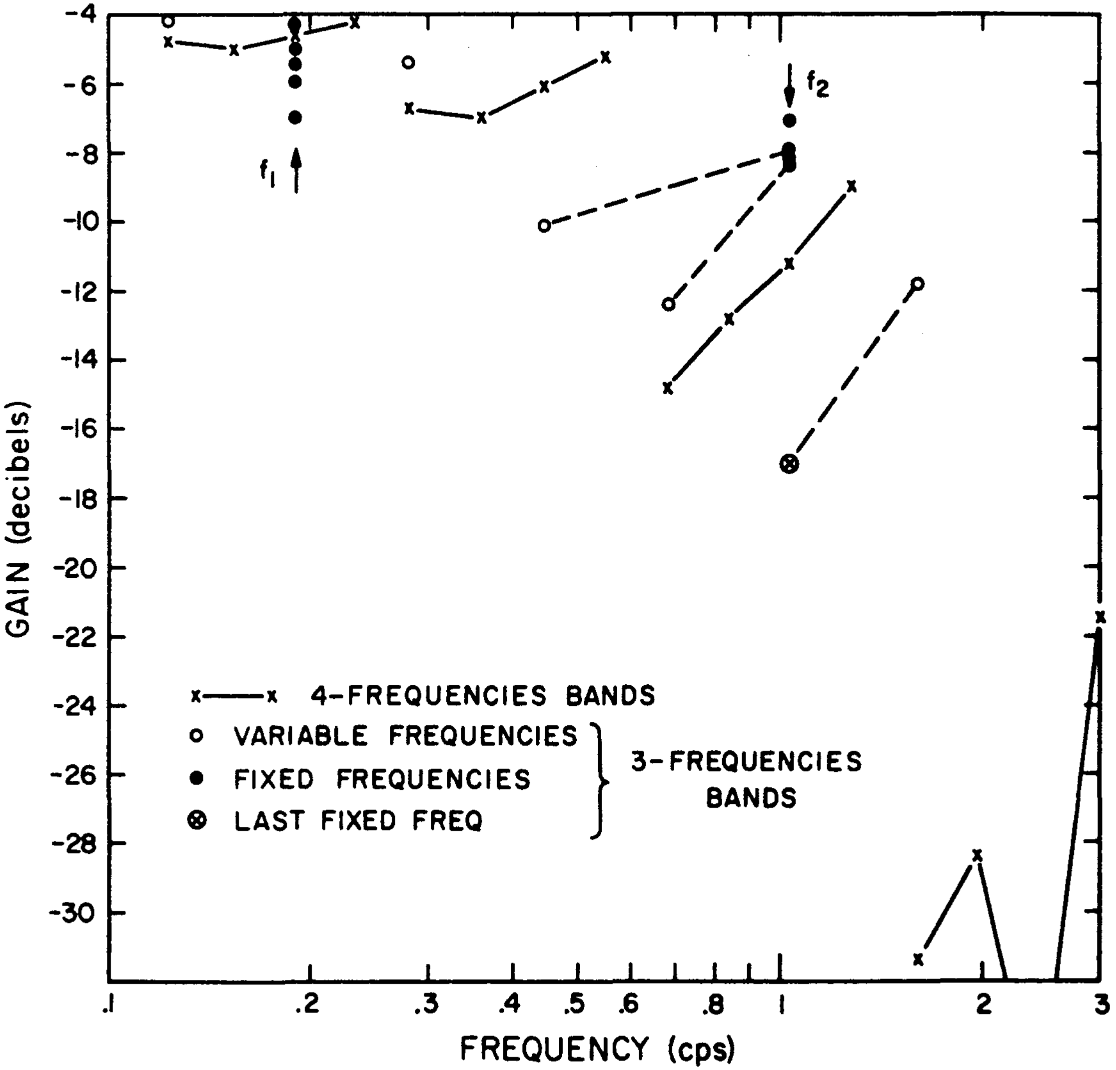


Figure 7.6(c): Gain of the oculomotor system
Left horizontal eye movements
Subject GSC
Binocular fixation

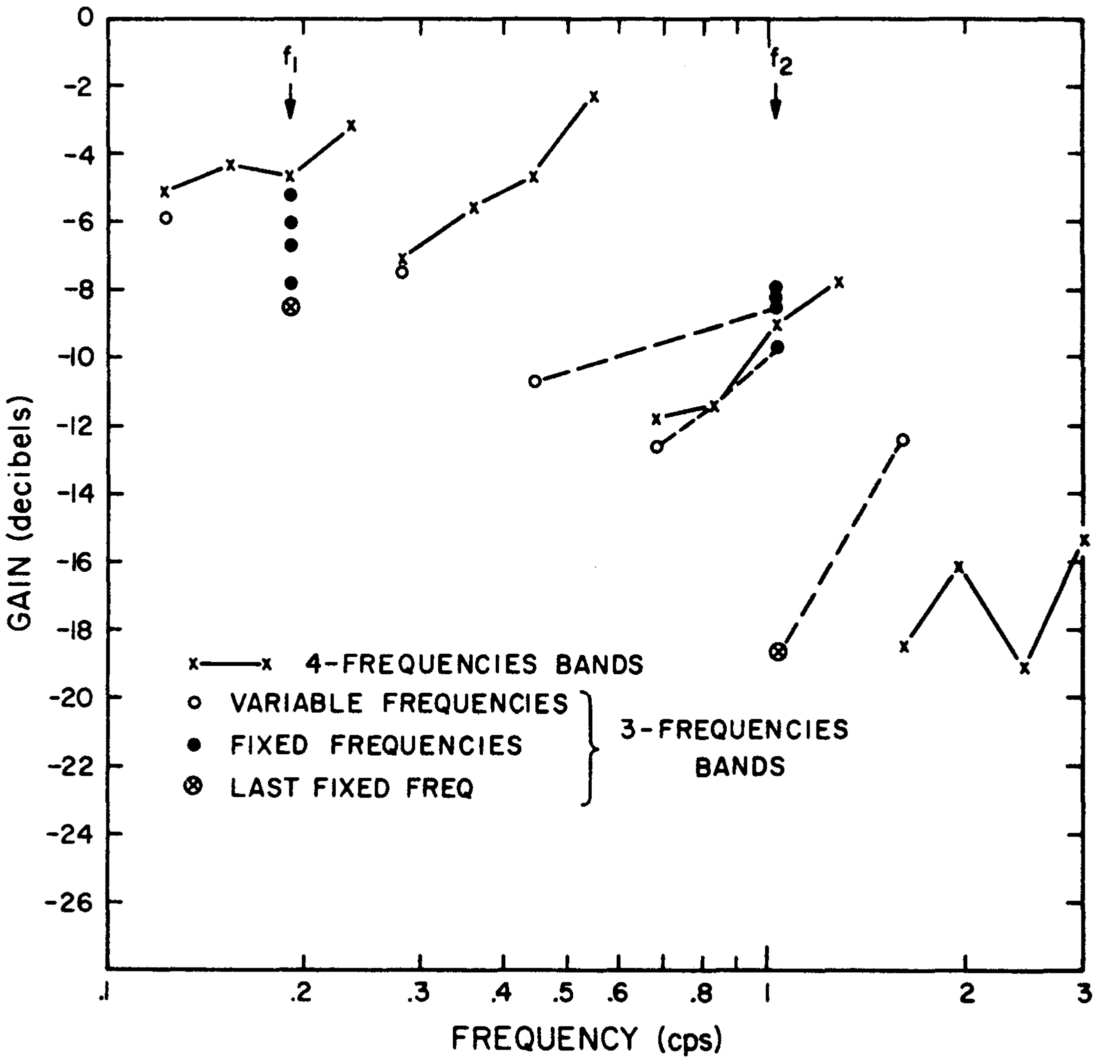


Figure 7.6(d): Gain of the oculomotor system
Subject SAM
Left horizontal eye movements
Binocular fixation

TABLE 7-3

Slope of the Regression Line Between Sizes of Eye Movements and Log Frequency for the 4-Frequencies Band

(A) Gain (db)

Subject	Band	Left Vertical		Left Horizontal	
		Slope	σ	Slope	σ
GSC	1	-0.04	2.75	+2.33	1.14
	2	+1.61	1.15	+5.74	2.14
	3	+10.71	3.23	+20.53	2.56
	4	+25.03	6.20	+23.33	34.03
SAM	1	-1.80	3.35	+5.78	2.34
	2	+5.58	2.60	+15.99	2.24
	3	+15.63	5.58	+15.32	2.77
	4	+1.89	1.98	+6.60	9.86

(B) Absolute Value (min. arc)

GSC	1	-6.48	4.03	-16.87	18.06
	2	-0.33	5.68	-13.57	5.97
	3	-1.74	1.36	+1.75	2.28
	4	+1.82	0.17	+0.63	1.16
SAM	1	-10.46	2.70	-7.85	14.56
	2	+6.08	8.99	-0.96	3.96
	3	-0.23	1.26	+1.18	2.27
	4	+0.44	0.90	-1.89	1.69

the slope is not significantly different from zero. In 11 out of 16 cases, the slope of the line is significantly positive, and in the other 5, the slope is not significantly different from zero. In no case is it substantially negative. However, from Figures 7. 2 and 7. 3, it may be observed that in many cases the magnitudes of the four sinusoids in the stimulus are not equal within a band: quite often there is a monotonic decrease with frequency. This results from the various filters which have been placed in the data transmission line to cut off the high-frequency noise (see Chapter VI). There is a possibility, then, that the eye movements themselves are fairly constant within a band and that the apparent increase in gain with frequency is simply the result of decreasing stimulus intensity.

We can plot the absolute value of eye movement (rather than gain) as a function of frequency and fit a straight line through the four points of a band as before. The resulting slopes and their standard deviations are listed in Table 7-3B,together with the earlier values. Eleven values out of sixteen are not significantly different from zero; four are significantly negative; and only one is substantially positive. If there is a real preference for the higher frequencies within a band, both the gain and absolute value of the eye movement should go up with frequency. This happens in one case out of sixteen. In the other cases, where the gain increases with frequency, the absolute value of the eye movement is essentially constant, and in fact actually decreases in one case.

Thus, it is not clear from these results whether the preference for higher frequencies within a narrow band is a real effect or whether it results merely from an uneven stimulus spectrum. In order to resolve this problem, the following experiment was performed. Two frequencies, f_1 and f_2, were fixed at the low and at the high end of the scale; these are indicated by arrows in Figure 7.6. The third test frequency, f_o, was consecutively set at five different values; the first one was lower than f_1 ; the last one was higher than f_2 ; and the other three were between f_1 and f_2. The three frequencies, f_o, f_1, and f_2, define the horizontal target motion for one experiment: at the same time, three other frequencies define the vertical motion. All three sinusoids were of equal amplitude. The gains at the test frequency f_o are indicated by circles in Figure 7.6; the gains at the fixed frequencies f_1 and f_2 are indicated by dots, except that the last point -- when f_o is at its highest value -- is indicated by a cross within a circle. At f_1, most of the dots fall very near the values previously obtained in the four 4-frequencies bands experiment (slightly below for horizontal motion). At f_2, most of the dots are above the previous values. However, as the test frequency f_o takes its highest value, there is a sudden and dramatic decrease in the gains at f_2 (cross within a circle), and in addition, subject SAM exhibits a drop at f_1 as well. Dotted lines have been drawn between corresponding points at f_o and f_2 for the last three cases. All three lines slope upward, and the value of the slope increases as the test frequency increases.

The situation is now clear: if a subject attempts to follow a target whose motion may be described as a sum of two components which are close in frequency, he responds preferentially to the higher one at the expense of the lower one, in spite of the fact that normally the response goes down with increasing frequency (single sinusoidal response). This preference is more pronounced as the frequencies in the target motion increase, and in fact, may become so extreme that power is robbed from much lower frequencies (f_1) to meet this requirement. This type of non-linearity is undesirable from a systems analyst's point of view, but one can appreciate its survival value.

Figure 7. 7 shows the gain as a function of frequency when the stimulus motion is composed of 7 and 13 sinusoids, respectively. In general, the two curves agree with each other and with the previous values obtained for the 4-frequencies bands insofar as it is possible to draw comparisons. The 13-frequencies curve is quite erratic, especially for subject SAM. On the other hand, the 7-frequencies curve is much more well-behaved. For subject SAM there is a slight peak at 0. 3 cps, a broad minimum at about 0. 7 cps, and another sharper peak at about 1. 5 cps, after which there is a sharp final plunge. This is true for both vertical and horizontal motion. Subject GSC exhibits similar behavior, although the lower peak is absent. It should be noted that the sharp peak at 1. 5 cps is in good agreement with the Gaussian noise curve derived by Dallos and Jones (1); see the dotted curve in Figure 5. 2, Chapter V. Young and Stark (6) have also found this peak for a finite sum of sinusoids. This peak has been explained by the fact that saccades begin to predominate at that particular frequency. At higher frequencies, saccades also occur, but they are no longer at the same frequency as the input, hence the sharp drop. On the other hand, we have seen that the oculomotor system responds

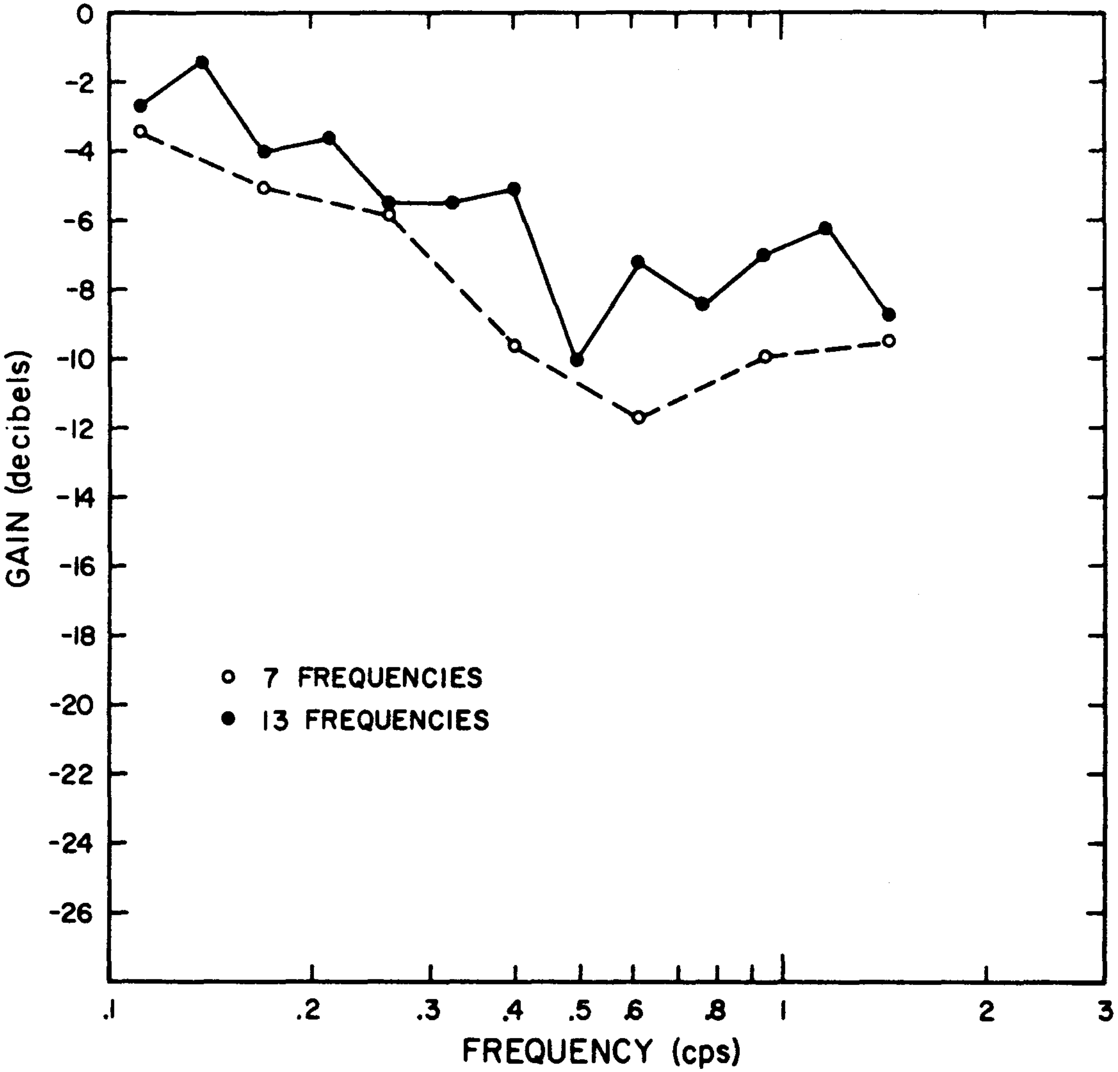
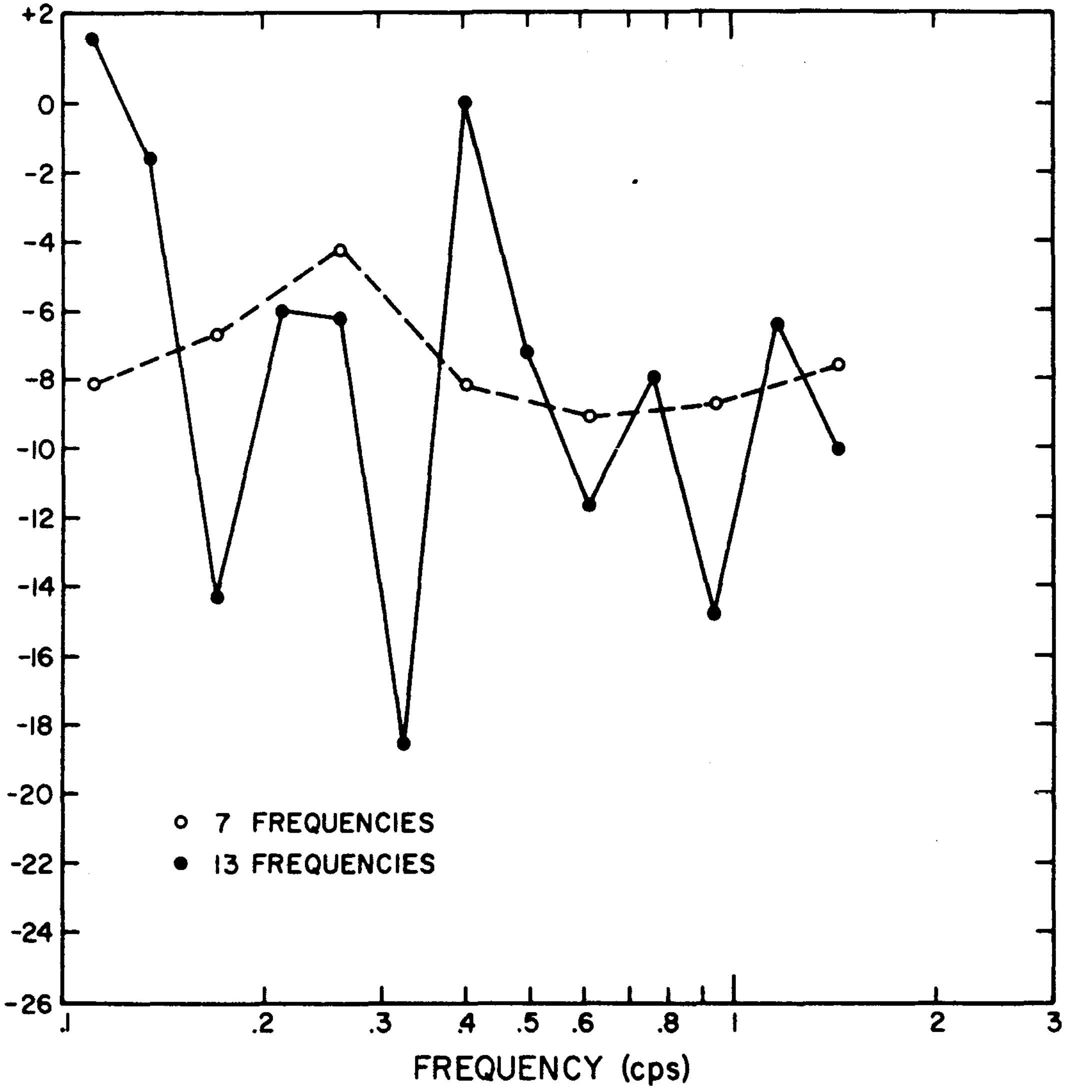
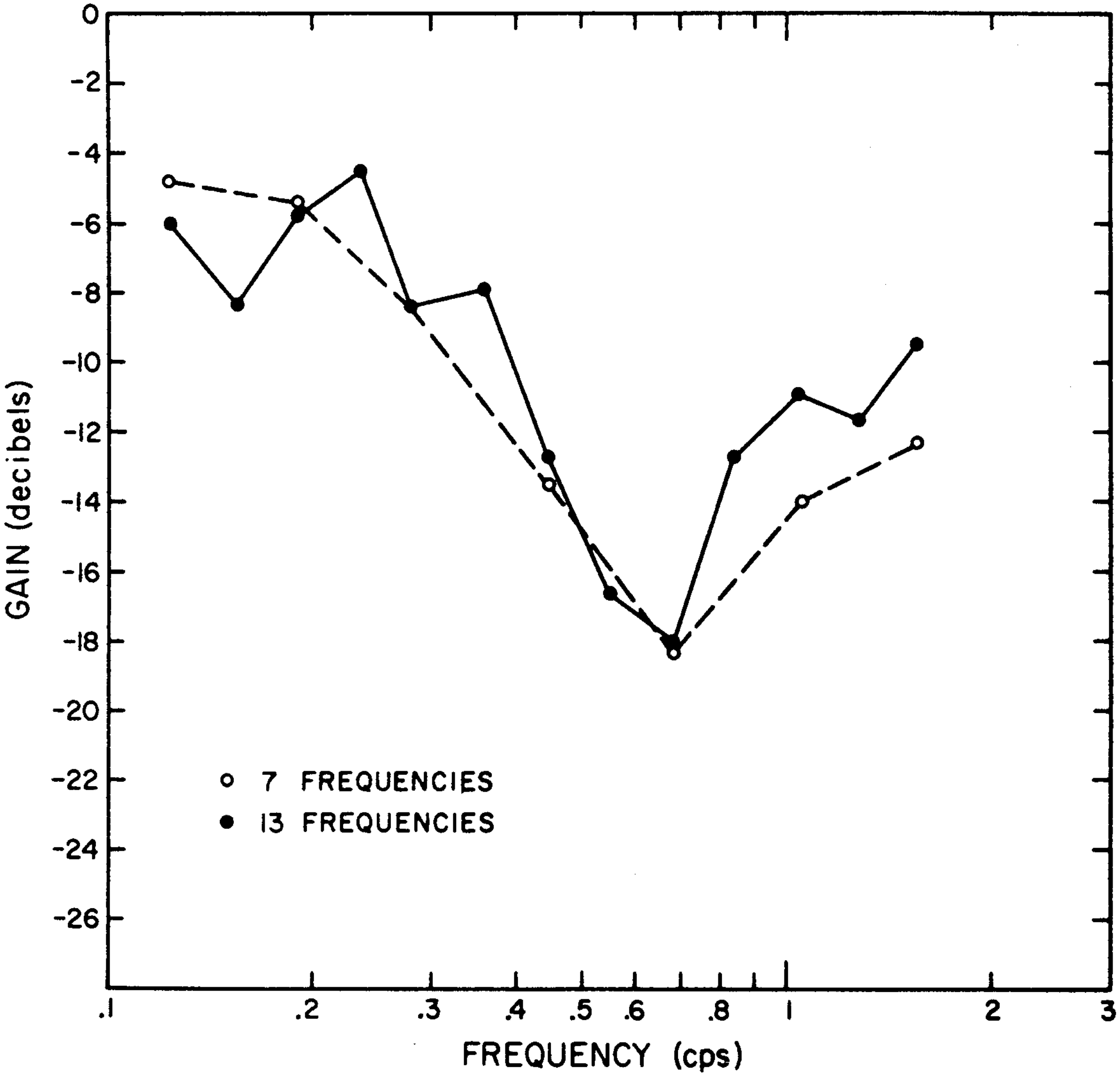


Figure 7.7(a): Gain of the oculomotor system
Subject GSC
Left vertical eye movements
Binocular fixation

Figure 7.7(b): Gain of the oculomotor system
Subject SAM
Left vertical eye movements
Binocular fixation





<u>Figure 7.7(c)</u>: Gain of the oculomotor system
Subject GSC
Left horizontal eye movements
Bonocular fixation

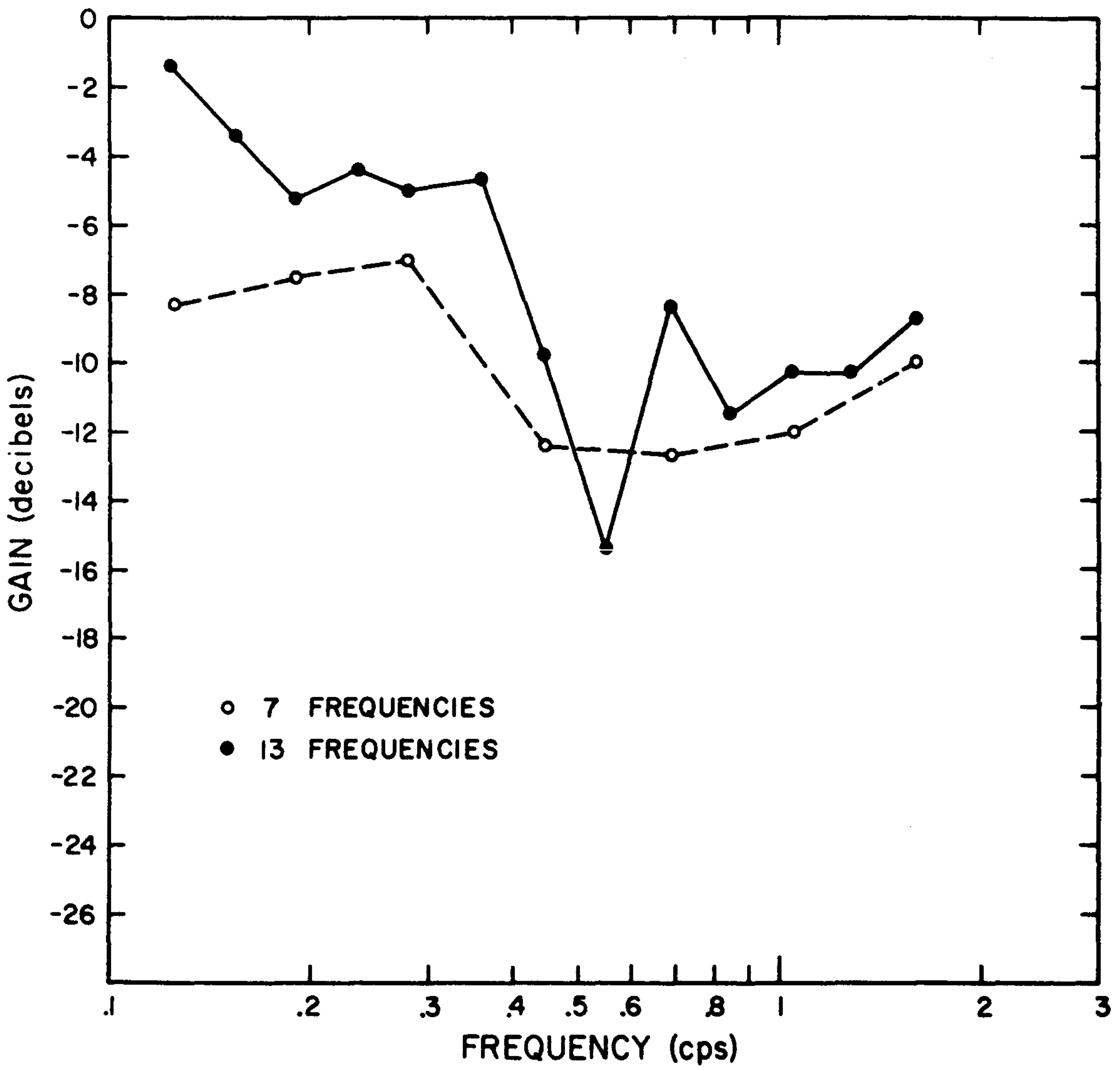


Figure 7.7(d): Gain of the oculomotor system
Subject SAM
Left horizontal eye movements
Binocular fixation

preferentially to the higher of the frequencies when the motion of the stimulus is composed of rather closely spaced sinusoids. It is quite possible that this preferential response accounts for the anomaly at 1.5 cps and for the erratic response to the 7-frequencies and 13-frequencies stimuli.

1.4 Phase as a function of frequency. We now investigate the phase of tracking eye movements with respect to the target motion. Figure 7.8 shows phase as a function of frequency for the 4-frequencies bands experiments and for the 7- and 13-frequencies bands. For the 4-frequencies bands, the phase behavior is much more well-behaved than the gain characteristic. With few exceptions, the increasing phase lag from 0° to 180° is almost monotonic, both between successive bands and within bands. In fact, the lines could have been continued between the adjacent bands without serious discontinuities. Considering the fact that these four bands were measured on four different days and that the gain characteristic is so anomalous, this well-behaved phase behavior is particularly striking. It is interesting to compare the gain function with the phase. Within a band, the first rises with frequency and the second decreases.

The customary approach to a problem of this sort is to derive a transfer function as the ratio of two polynomials which best fit the gain curve. This transfer function then dictates the phase characteristics, and the difference between this theoretical phase and the actual measured values is attributed to a constant delay. This delay time is interpreted as the time required for target information to be relayed through the optic nerve to the cerebral cortex, and for the efferent

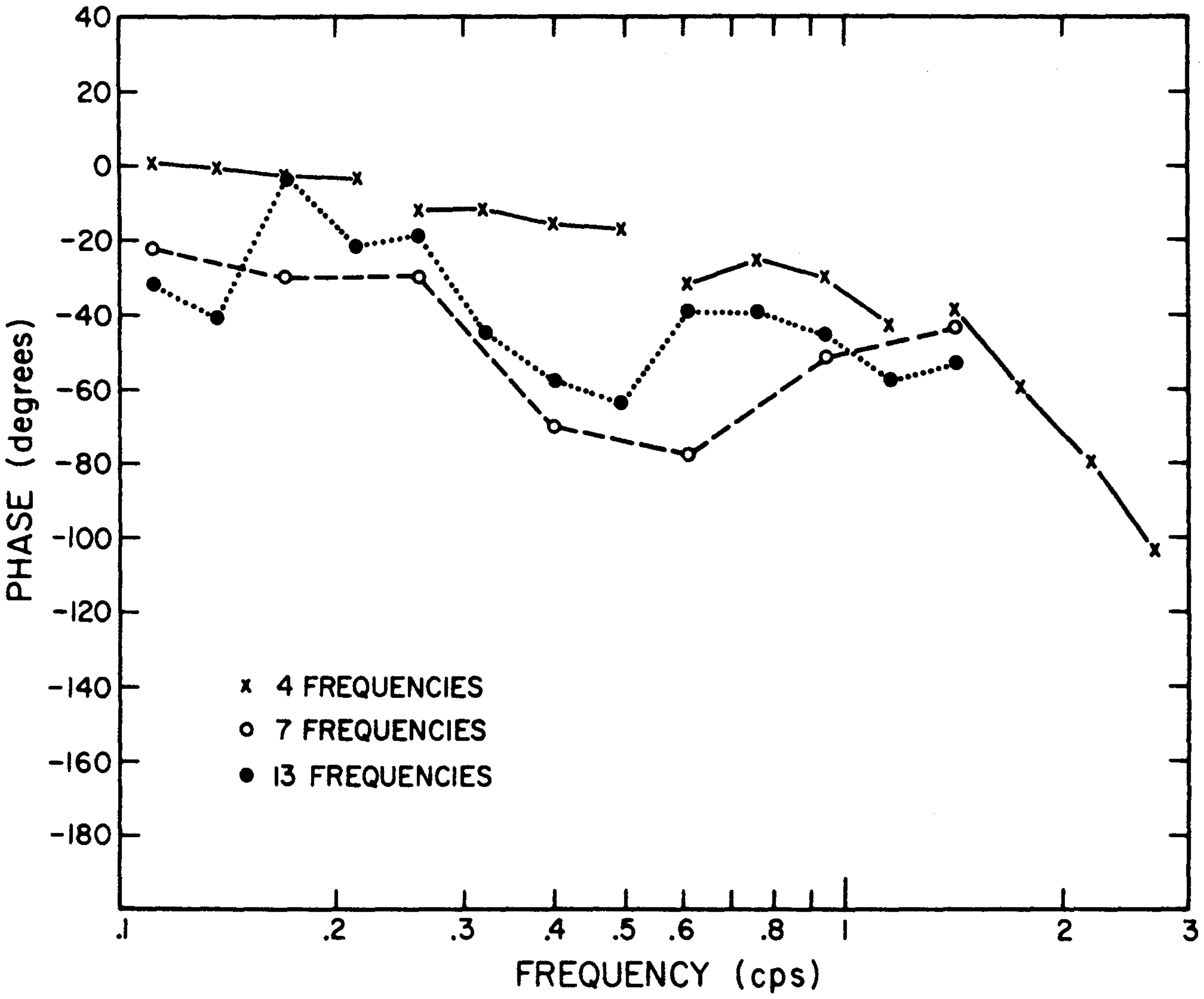


Figure 7.8(a): Phase lag of the oculomotor system
Subject GSC
Left vertical eye movements
Binocular viewing

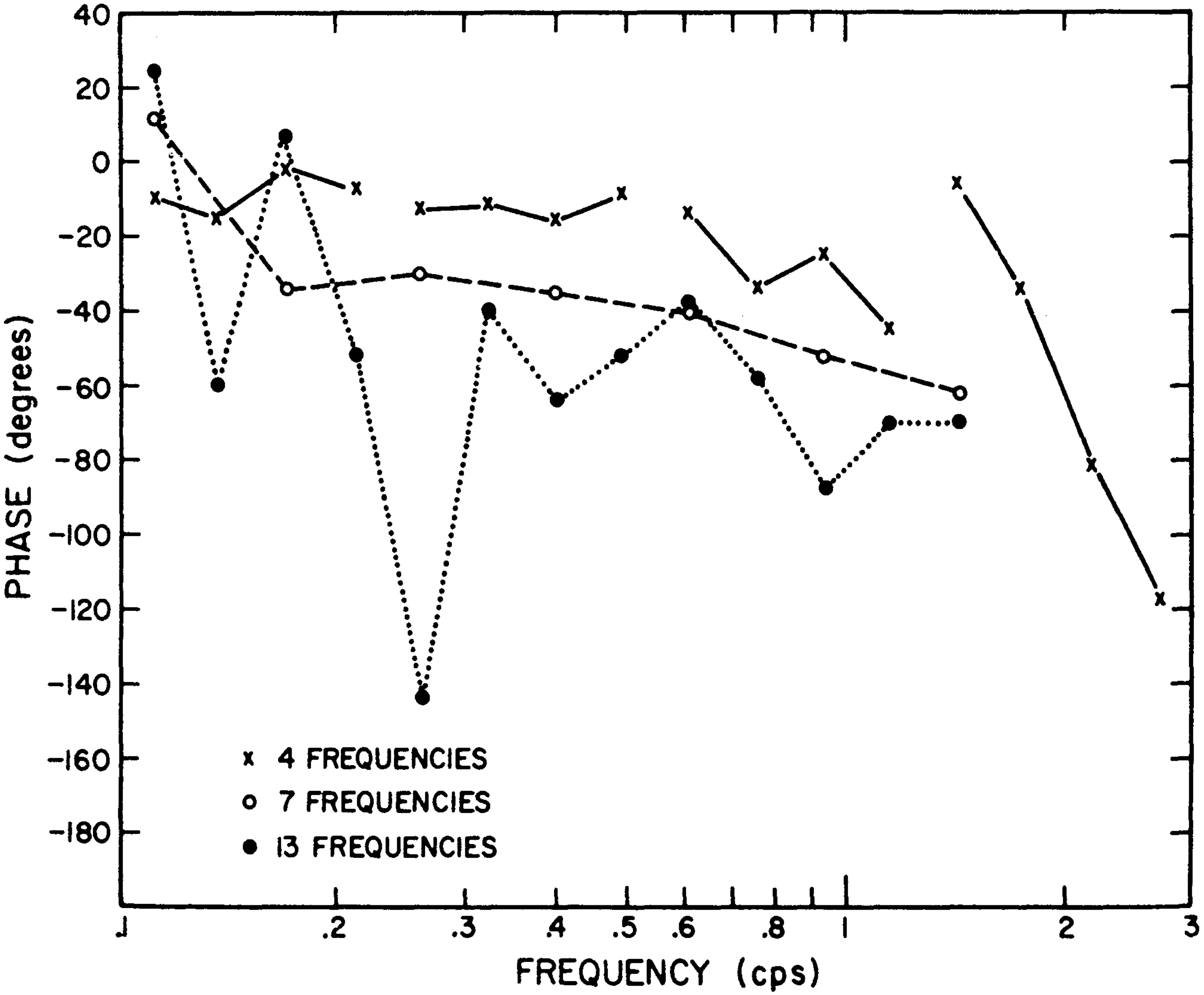


Figure 7.8(b): Phase lag of the oculomotor system
Subject SAM
Left vertical eye movements
Binocular viewing

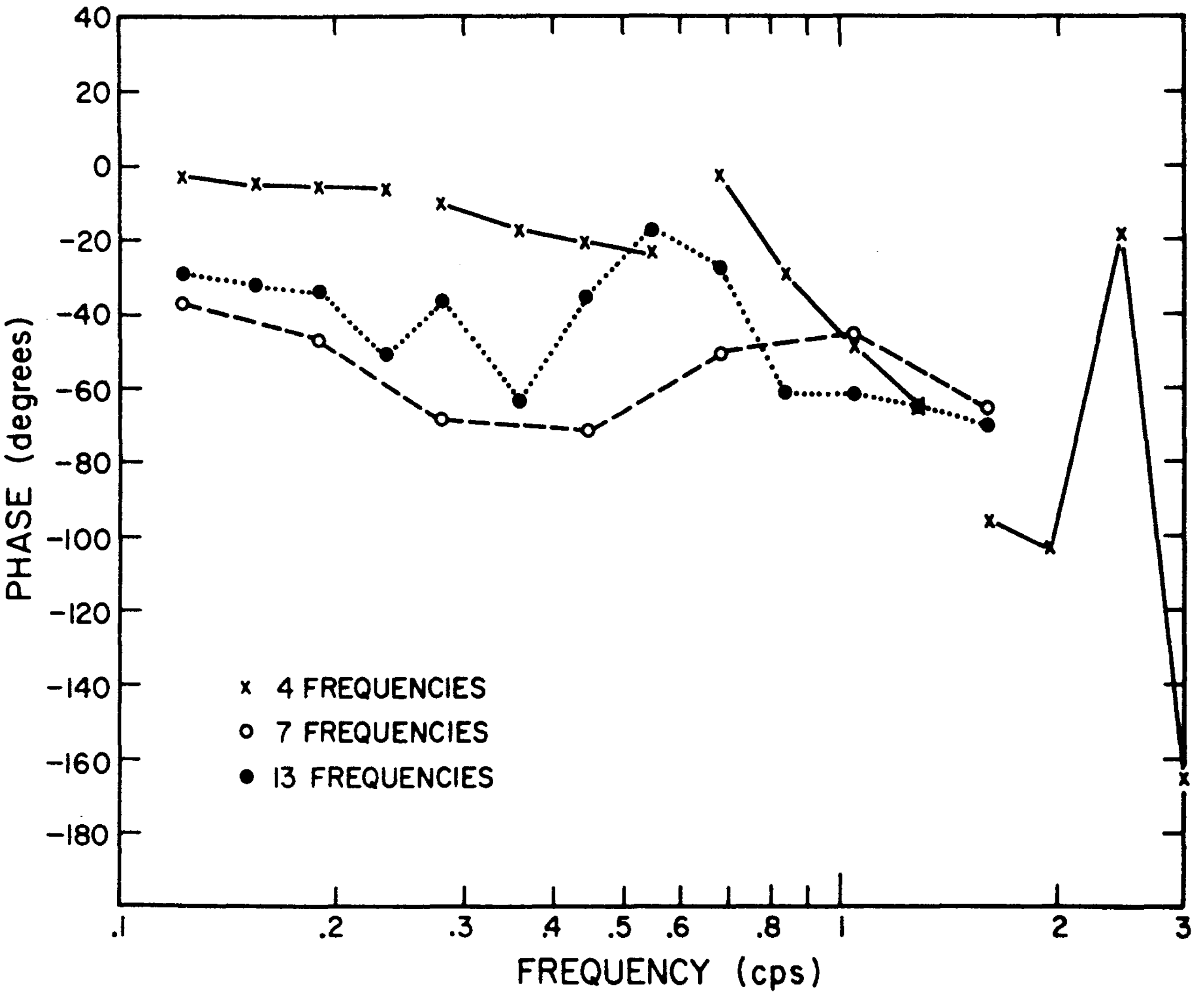


Figure 7.8(c): Phase lag of the oculomotor system
Subject GSC
Left horizontal eye movements
Binocular viewing

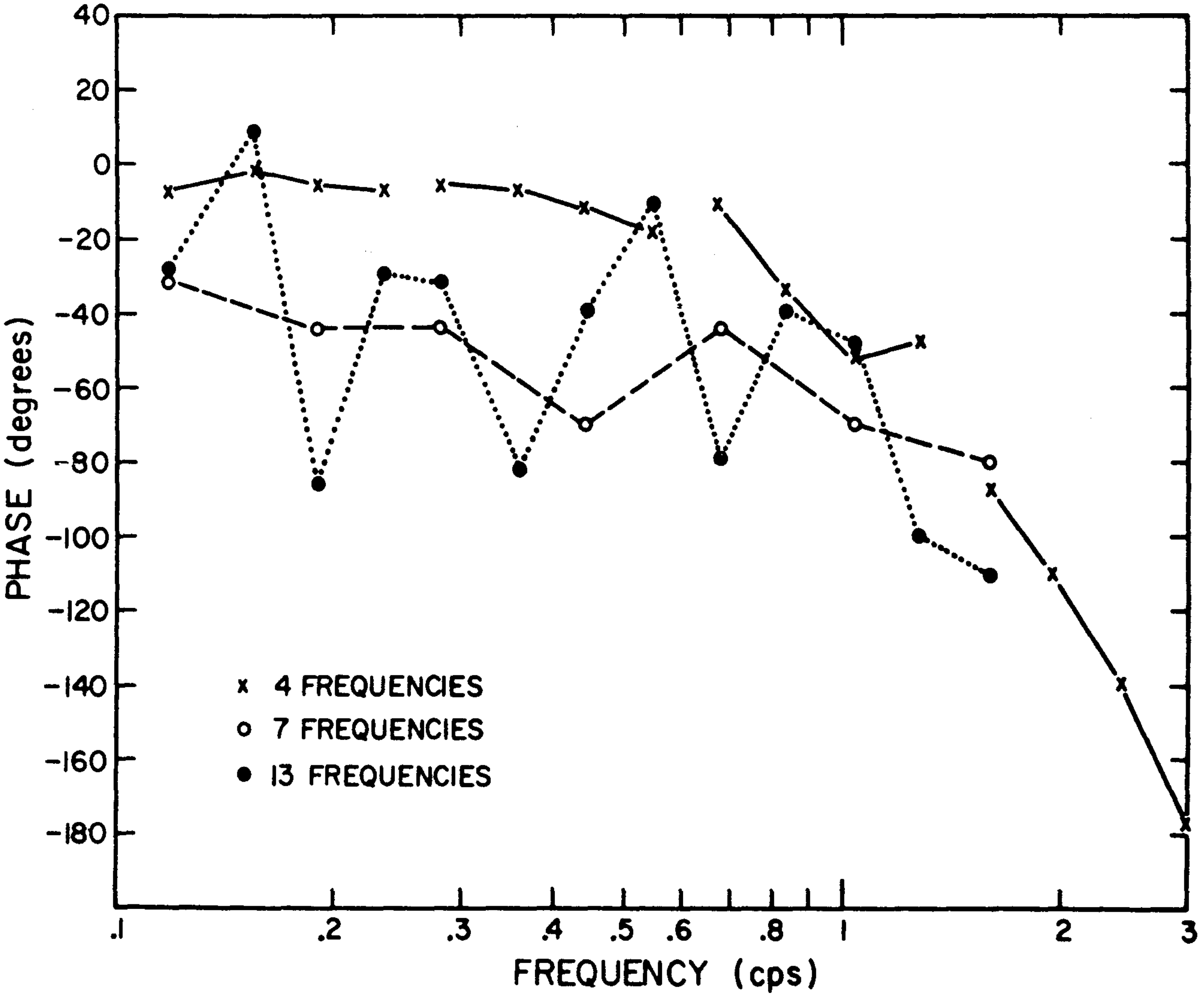


Figure 7.8(d): Phase lag of the oculomotor system
Subject SAM
Left horizontal eye movements
Binocular viewing

signals to be propagated through the midbrain to the extra-ocular muscles. However, in this case, one would have to be most imaginative to derive a transfer function which adequately describes the gain behavior of the oculomotor system for the four 4-frequencies bands. If one did succeed in deriving such a function, then the phase discrepancies could not be accounted for by means of a constant delay. Of course, one way out of this difficulty is simply to ignore these "irregularities" and simply fit an average gain curve through all points at once. This is probably what has been done by the various authors who have dealt with this problem, for none of them describe experimental results in detail, but merely state an average value and a standard deviation at certain frequencies. However, one tends to look at such linear models with the utmost suspicion, for they gloss over the most interesting characteristics of the oculomotor system.

If we examine the phase lags for the 7- and the 13-frequencies experiments (Figure 7. 8), further non-linearities become apparent. The phase curve is much more erratic than the one for the 4-frequencies experiment, and in general, there is more phase lag at a given frequency. In the last chapter, it was pointed out that the phase lag was greater for a subject who tracked a target with Gaussian noise motion than for another who tracked a target whose motion consisted of a finite sum of sinusoids (Figure 5. 3, Chapter V). At that time, we asked whether this was due to differences between the two subjects or whether it was caused by an increased complexity of the motion. Now, our experiments show that, for a given subject, increasing the spectral content of target motion, and hence of the required tracking eye movements, increases the phase lag. Since the subject can detect no difference between the two motions -- they appear equally "unpredictable" to him -- it is tempting to attribute the increased phase lag to the increased computation time required in order to mediate the proper signal pattern. We shall see later that this is not the case.

However, it now appears as if "delay time" in the oculomotor system is a function of the target motion. In order to understand the relationship between this phase lag (or delay time) and the characteristics of the target motion, we must study the tracking eye movements made in pursuit of a target whose motion is band-limited Gaussian noise.

2. Response to Gaussian Random Target Motion

2.1 Description of the stimulus.

The most general way to analyze a non-linear system is to use Gaussian white noise as input. However, in this case, "white noise" means target motion with a flat power spectrum up to about 30 cps, one order of magnitude above the system bandwidth. Unfortunately, such a target is visible only as a diffuse blur and is untrackable. In practice, the tracking of a moving point target can be accomplished only if the high-frequency cutoff of the power spectrum for the target motion is roughly the same as that for the oculomotor system itself. For example, if the stimulus has a substantial component above 3 cps, it is perceived as a blur and the subject simply gives up all attempts at tracking.

Gaussian white noise waveforms were suitably filtered (see Chapter VI) and then used to drive the spot both vertically and horizontally on the oscilloscope. Figure 7. 9 shows such a motion together with the tracking eye movements. Comparison with Figure 7. 1 shows that the overall speed is much higher (note the time marks) and that the eye movements tend to lag the stimulus to a greater degree. Note that Figure 7. 9 shows a 5-second record while Figure 7. 1 shows a 20-second trace. While the "sum of four sinusoids" motion appears smoother than the "Gaussian noise" motion when the traces are compared, nevertheless to the subject who is tracking the moving spot, the motions are indistinguishable.

Three waveforms were used; they differed only in the high-frequency cutoff. Figure 7. 10 shows the power spectra of these three stimuli: they have been labeled low-, medium-, and high-bandwidth noise, respectively. Target motion was constrained to a radius of 1. 5° from the center position as in the previous experiments.

For reference, it will be noted that Dallos and Jones (1) describe their Gaussian noise stimulus as having a half-power point at 1. 25 cps. This would correspond roughly to our medium-bandwidth waveform.

2. 2 Phase of eye movements relative to the target. Figure 7. 11 shows the phase of horizontal tracking eye movements with respect to the target for the three waveforms. Generally, the phase lag starts from zero and increases almost monotonically with frequency until about 2 cps. Above that frequency, the magnitude of the eye movements is about 30 db down, so that phase information is not likely to be very reliable. We will consider only that part of the curve before the wild oscillations from -180° to $+180^\circ$. It will be

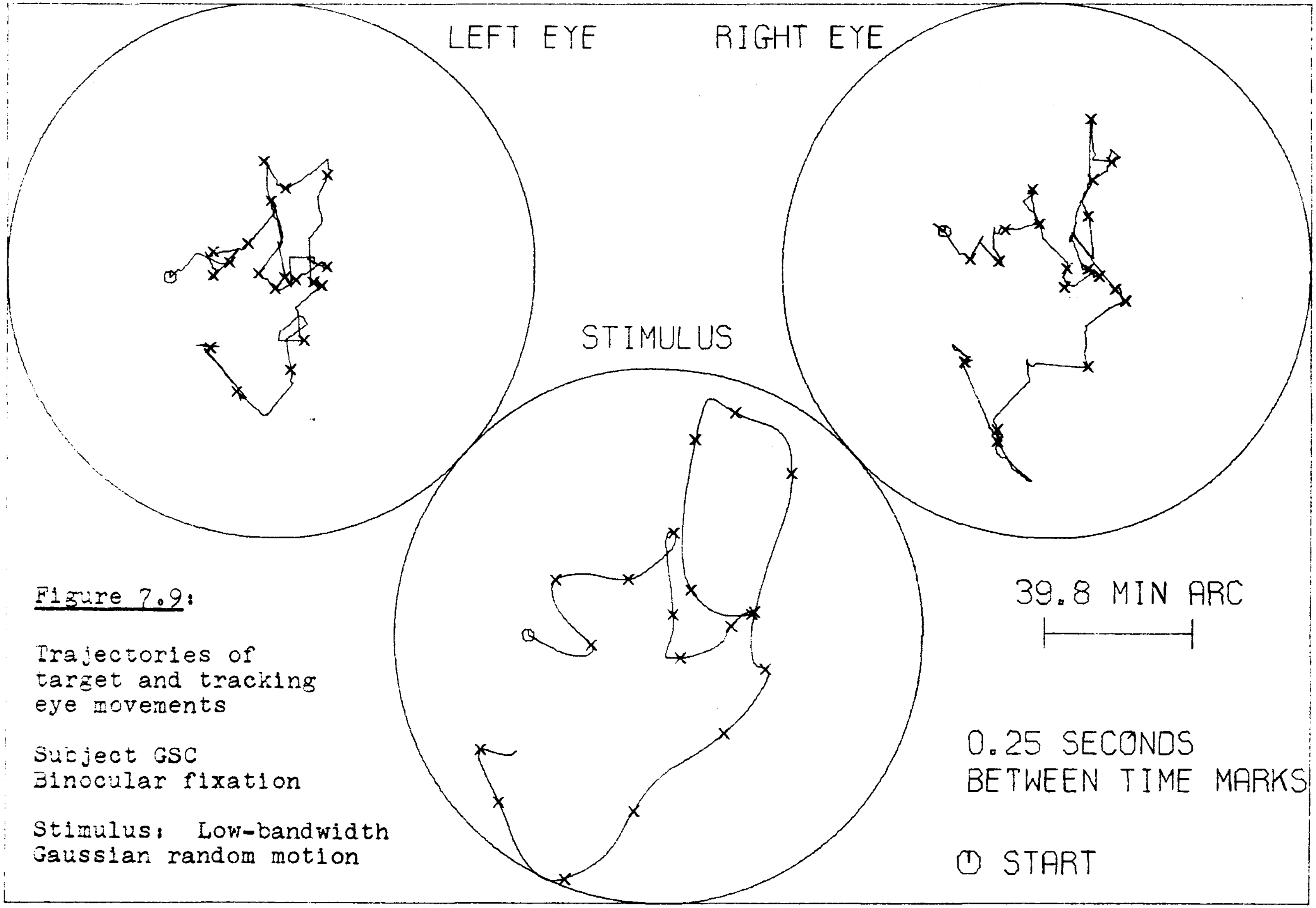


Figure 7.9:

Trajectories of
target and tracking
eye movements

Subject GSC
Binocular fixation

Stimulus: Low-bandwidth
Gaussian random motion

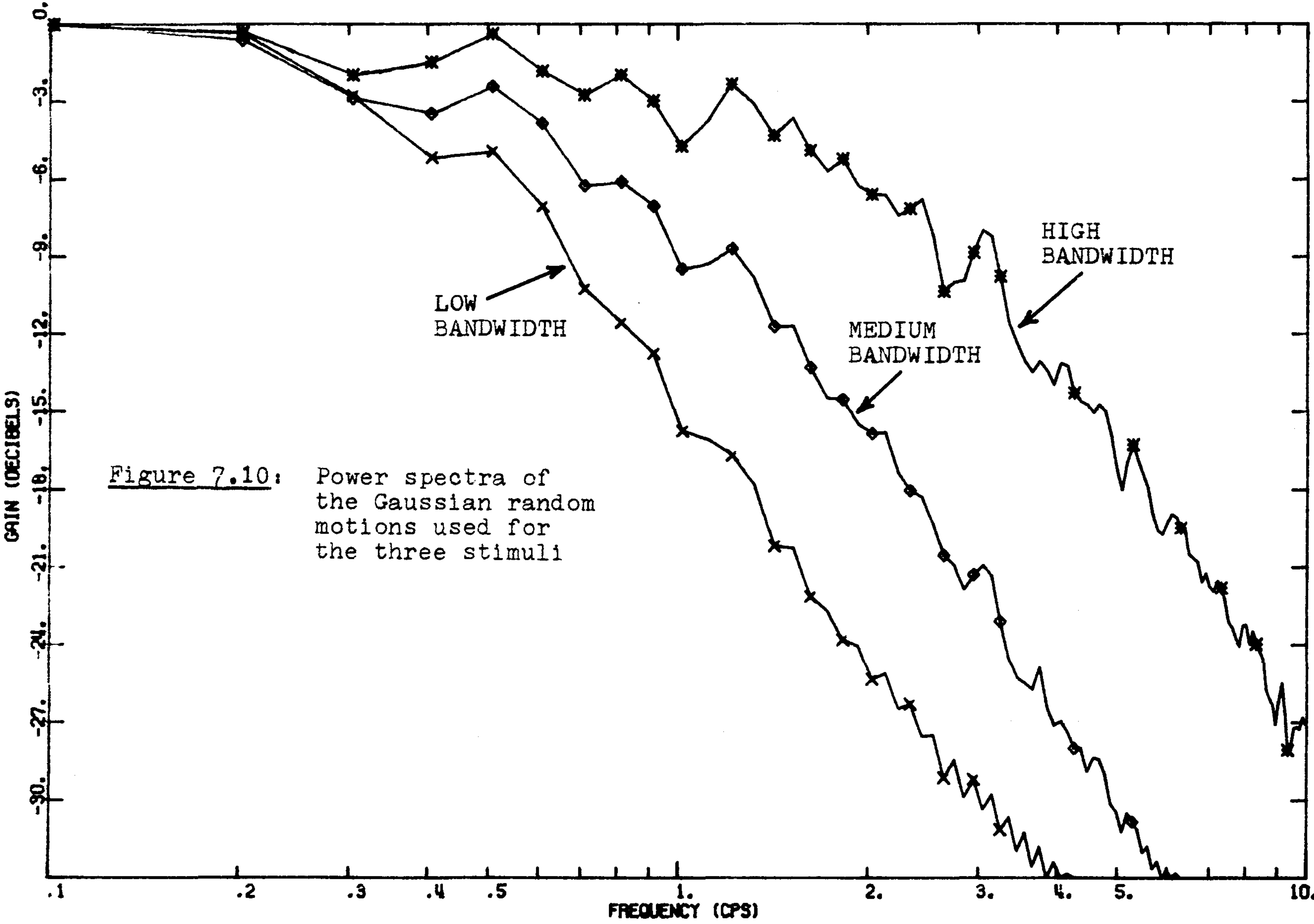


Figure 7.10: Power spectra of the Gaussian random motions used for the three stimuli

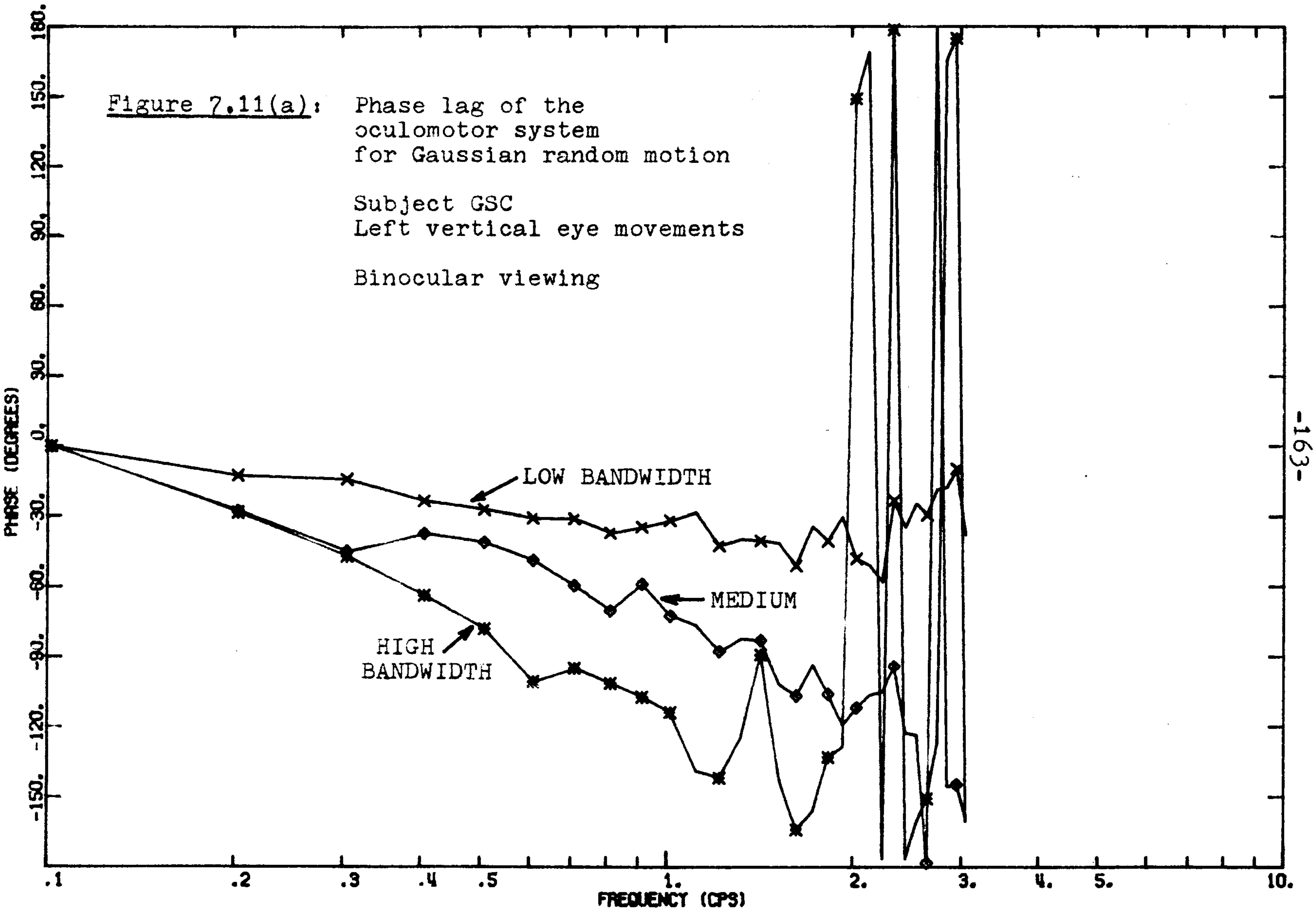


Figure 7.11(a): Phase lag of the oculomotor system for Gaussian random motion

Subject GSC
Left vertical eye movements

Binocular viewing

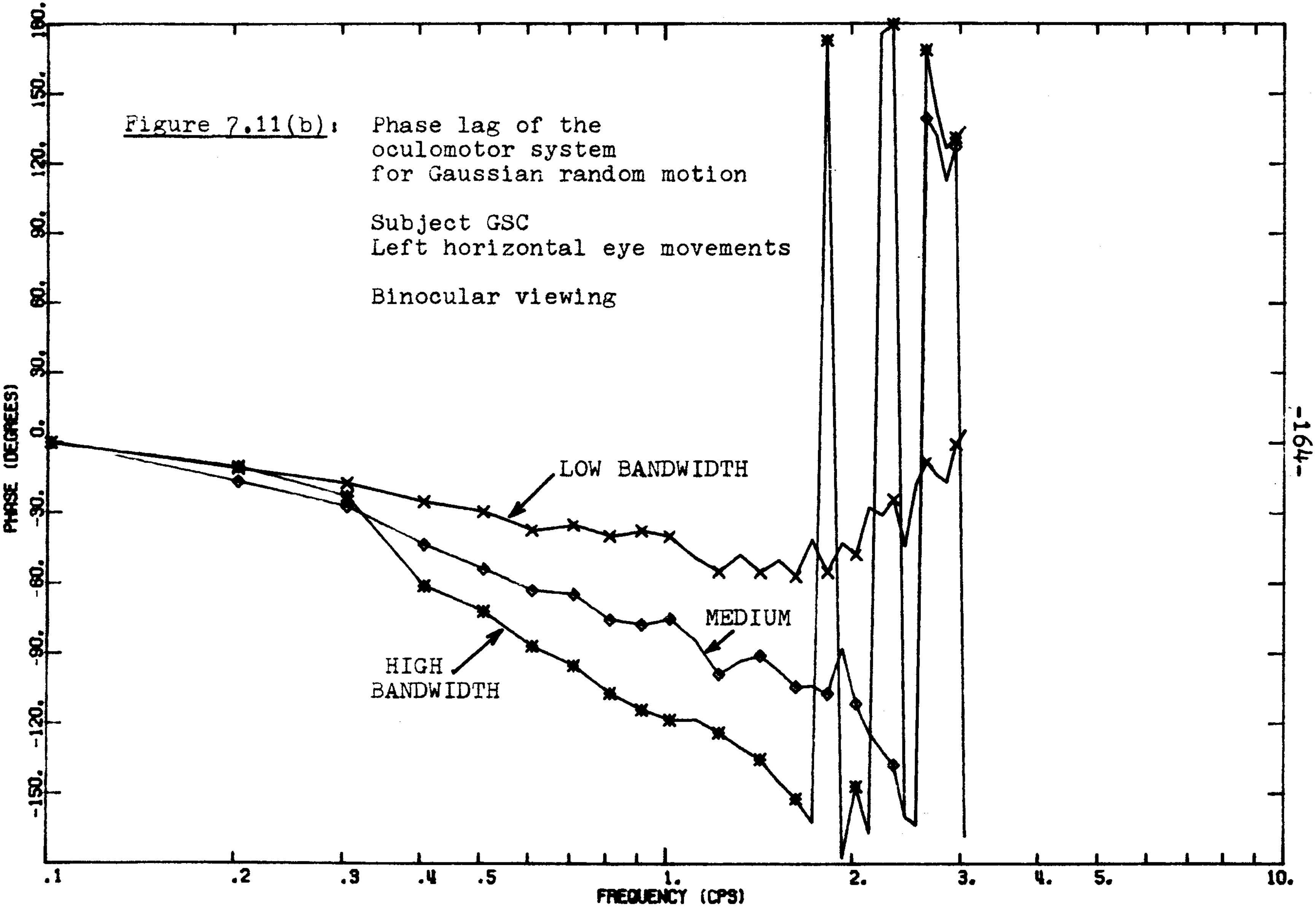


Figure 7.11(b): Phase lag of the oculomotor system for Gaussian random motion

Subject GSC
Left horizontal eye movements

Binocular viewing

noted that, for any given frequency, the phase lag increases as the bandwidth of the Gaussian noise stimulus increases (low, medium, and high). This is particularly noticeable for subject GSC. It is interesting to compare this behavior with the corresponding increase in phase lag as the number of frequencies is increased in the "sum of sinusoids" stimulus (Figure 7. 8). In section 1. 4, we suggested that the increase in phase lag could be due to the increase in spectral content of the stimulus, i. e., more sinusoids. However, it is now apparent that this is not a satisfactory explanation. First, all three Gaussian waveforms contain all frequencies from DC to about 3 cps; they differ only in the high-frequency cutoff (corner frequencies). Second, comparison with Figure 7. 8 shows that the phase lag for the low-bandwidth Gaussian stimulus is somewhat less than that for any of the "sum of sinusoids" motions, but that the phase lag for medium- and high-bandwidth Gaussian motion is greater. Thus, it appears as if phase lag is a function of the bandwidth of the target motion spectrum. Strangely enough, increasing the number of sinusoids from 4 to 7 or 13 causes the phase curve to become more erratic, but if the number of frequencies is increased until the spectrum is continuous, the resulting phase curve becomes quite smooth and well-behaved. One possible explanation is that the 7- and 13-frequencies stimuli were transmitted so that all frequency components were approximately equal in magnitude. In contrast, the Gaussian noise gradually tapers off at the higher frequencies.

3. Discussion

We have seen that the oculomotor tracking system is highly non-linear. If the number of frequencies in the target motion is small enough, in general the tracking eye movements are composed of a sum of those sinusoids present in the stimulus. However, as the number of frequencies increases, or as the bandwidth of the spectrum of target motion gets wider, the phase lag at a given frequency increases. Any discrepancy between the phase lag expected by the authors and the measured values has, in the past, been attributed to the action of a predictor. Michael and Jones (4) measured the phase lag of tracking eye movements when target motion consisted of a single sine wave on which had been superimposed Gaussian noise of varying bandwidth. At a given frequency, as the noise bandwidth increased, the phase lag likewise became larger. This was interpreted as progressive failure of the predictor as the target motion became more "unpredictable." However, in our experiments with target motion consisting of nothing but Gaussian noise, we have found that phase lag became larger as the total bandwidth of the target spectrum increased. Clearly, it does not seem reasonable to describe "low-bandwidth Gaussian noise" motion as more predictable than "high-bandwidth" motion. It appears then that phase lag at a given frequency is more dependent on the overall bandwidth of target motion than on "predictability" of that motion. We shall return to this point later.

In essence, the existence of a predictor is a direct consequence of describing the tracking oculomotor system by linear transfer functions. To see how this happens, let us examine the work of Dallos and Jones (1). Target motion consisted of band-limited Gaussian noise with a half-power cutoff at 1.25 cps. The authors plotted the gain and phase of the tracking eye movements as functions of frequency. (Only horizontal eye motions and monocular viewing were considered.) From the gain curve, appropriate corner frequencies were chosen, and the closed-loop transfer function could then be written directly:

$$G(j\omega) = \frac{44\,(5 + j\omega)}{(2.2 + j\omega)(-\omega^2 + 12j\omega + 100)} \,. \tag{1}$$

However, this function $G(j\omega)$ dictates phase lags $\phi'(j\omega)$ which are smaller than the experimentally determined values $\phi(j\omega)$. The difference is then attributed to a constant delay T of about 70 ms ; this is not an unreasonable value for the transit time it would take nerve impulses to travel from the retina to the lateral geniculate, to the cerebral cortex, then to the oculomotor nuclei, and finally to the extraocular muscles. As we shall see below, the net transit times for the subjects used in this thesis are very close to this value. A constant delay T simply adds the term

$$e^{-j\omega T} \tag{2}$$

to $G(j\omega)$ of Eq. (4), and this does not affect the gain characteristics. Assuming unity feedback, the open-loop transfer function $g(j\omega)$ can be obtained directly from the closed-loop function $G(j\omega)$:

$$g(j\omega) = \frac{G(j\omega)}{1 - G(j\omega)} \,. \tag{3}$$

This procedure was then repeated for pure sine wave stimuli, and the resulting open-loop transfer function $g'(j\omega)$ was computed. Since $g(j\omega)$ and $g'(j\omega)$ are different, it is necessary to postulate a predictor $P(j\omega)$ which can be "switched in" series with the forward loop whenever it is decided that the target is predictable. Then

$$P(j\omega) = \frac{g'(j\omega)}{g(j\omega)} \quad . \tag{4}$$

This is derived graphically: the gain of the predictor is first computed, and this function in turn dictates the phase characteristics. This phase function does not agree with the experimental values, and this difference is finally attributed to pure prediction. The "predictor" consists of a low-pass minimum phase network whose gain is larger than unity at all frequencies within its bandwidth, and of a pure "phase-advance" which increases linearly with frequency. However, for a constant delay T, phase ϕ is linearly related to frequency f:

$$\phi = 360 f T \quad , \tag{5}$$

and the "phase-advance" can be translated as a constant "negative delay" of about 214 ms, as measured from the authors' curve. It is extremely difficult to visualize such a cortical predictor which manages to anticipate target motion by 214 ms regardless of the frequency. However, the nature of the predictor is a direct consequence of the description of the oculomotor system by means of linear transfer functions.

Since we have found that the system is highly non-linear, we shall abandon all attempts to describe it by means of linear transfer functions. Consequently, we rid ourselves of the gain-phase restrictions imposed by functions such as $G(j\omega)$ of Eq. (1). In fact, the very concept of phase is misleading, since it really has obvious meaning only for linear systems. We will then translate all phase values to constant delay times by means of Eq. (5). Figure 7.12 shows the phase curve experimentally determined for single sine waves by Dal-

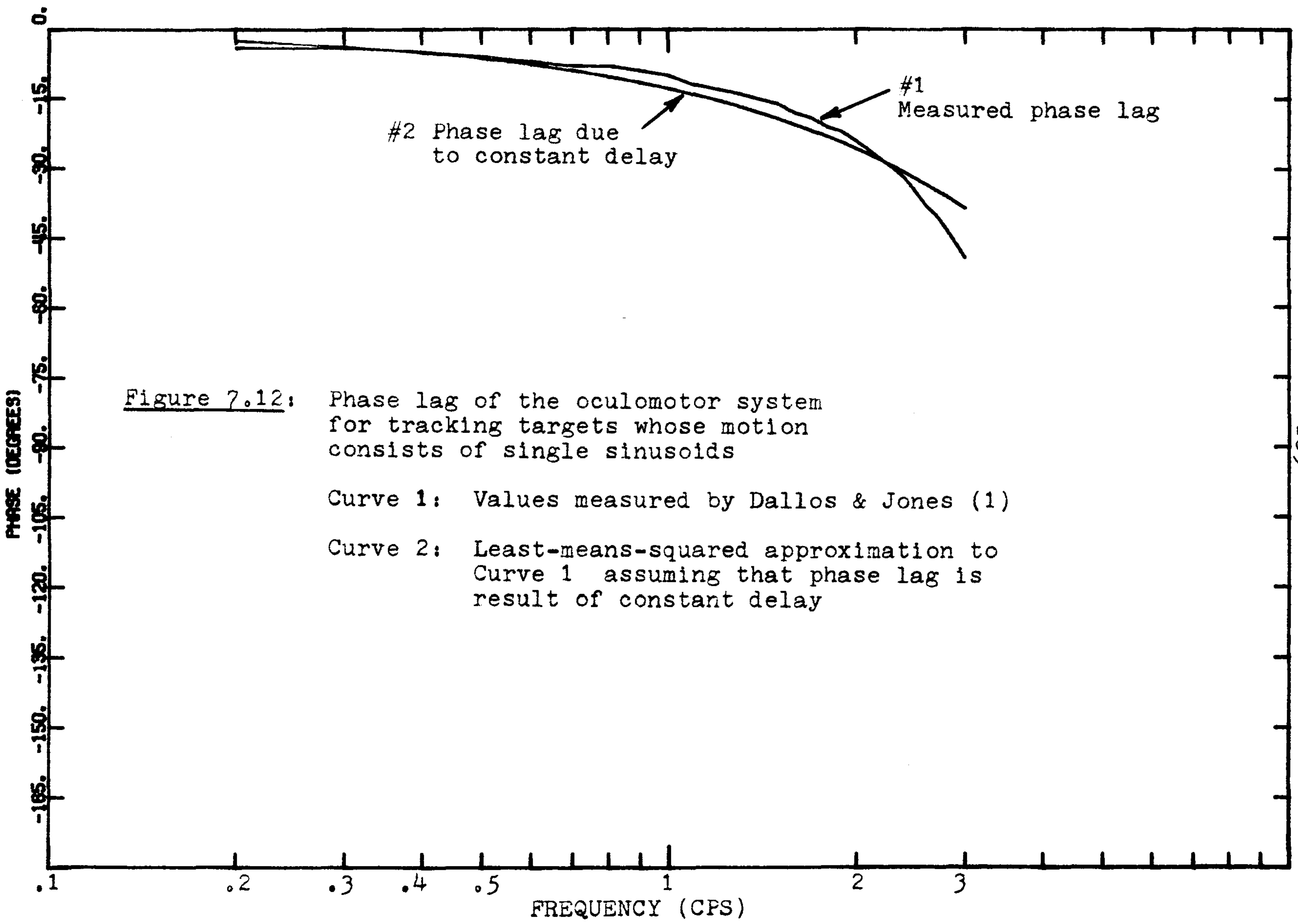


Figure 7.12: Phase lag of the oculomotor system for tracking targets whose motion consists of single sinusoids

Curve 1: Values measured by Dallos & Jones (1)

Curve 2: Least-means-squared approximation to Curve 1 assuming that phase lag is result of constant delay los and Jones (1). On the same graph, the second curve describes the phase one would get if the system contained only pure delay T as described by Eq. (5). The value of T was computed so that the mean square difference between the two curves is a minimum. Figure 7.13 shows the same two curves for the unpredictable Gaussian noise stimulus, also from Dallos and Jones (1). The two delay times were found to be 36 ms and 246 ms for the single sine wave and for the Gaussian noise stimulus, respectively. The difference in delay is 210 ms, which is quite close to the 214 ms "predictive time" derived from Dallos and Jones for their predictor! Thus, after tedious mathematical detail and graph fitting, they have derived a "predictor" with most unusual gain characteristics (much larger than unity) and whose predictive qualities consist mainly in anticipating target movement by 214 ms. A much simpler interpretation is simply that there is no predictor nor phase-lag, but merely some delay time T which is the sum of the minimum time T_o required for nerve impulses to travel the required distance plus some computing time T_c determined by the bandwidth of the target motion.

However, "bandwidth" is a vague concept when applied to "information" as seen by the oculomotor system. A more fruitful measure is the rate of information transfer between target motion and the tracking eye movements. If the input and output of a system are Gaussian random processes, the average rate of information transfer can be expressed as:

$$R = \tfrac{1}{2}\int \log_2 \left[\frac{S_x(f)\, S_z(f)}{S_x(f)\, S_z(f) - |S_{xz}(f)|^2} \right] df \qquad \text{bits/sec} \qquad (6)$$

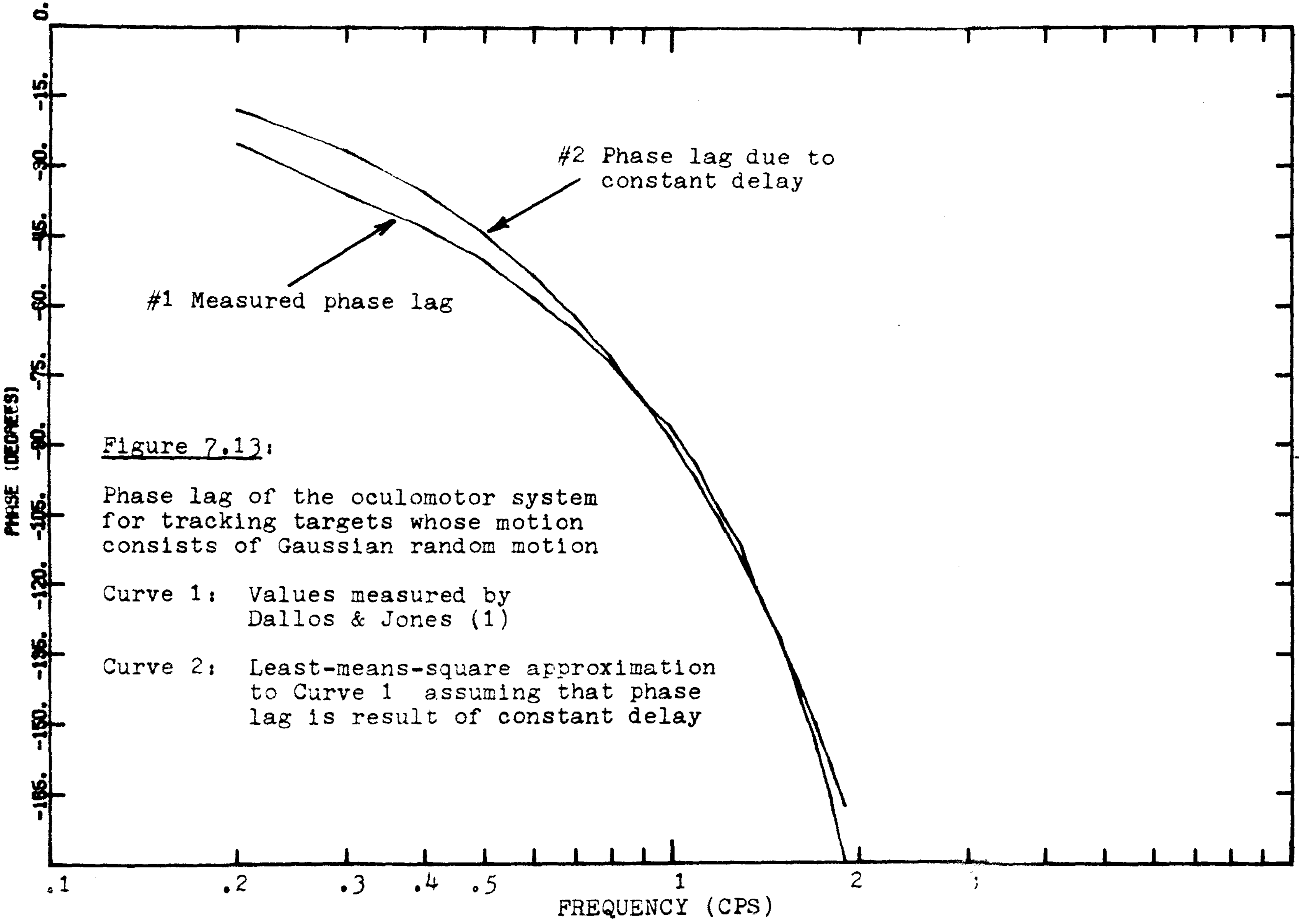


Figure 7.13:

Phase lag of the oculomotor system for tracking targets whose motion consists of Gaussian random motion

Curve 1: Values measured by Dallos & Jones (1)

Curve 2: Least-means-square approximation to Curve 1 assuming that phase lag is result of constant delay where

$S_x(f)$ = power spectrum of the input

$S_z(f)$ = power spectrum of the output

$S_{xz}(f)$ = cross power spectrum between input and output.

The range of integration is the bandwidth of the oculomotor system. In general, it is not possible to describe the rate of information transfer in such a simple and concise manner when the input waveform is not a Gaussian random process. Consequently, we will first consider only the response to Gaussian random motion. In this chapter, we have thus far discussed results pertinent to binocular tracking only. In Chapter X we will examine the differences between monocular and binocular viewing conditions. For the moment, however, we compute the rates of information transfer and the corresponding delay times for both monocular and binocular viewing conditions so as to obtain as many data points as possible.

For a constant signal-to-noise ratio, the maximum rate of information transfer -- that is, the capacity -- of a transmission channel is proportional to its bandwidth. However, the effective bandwidth is a function of the propagation time (2), increasing with increasing delay up to some finite value which is determined by the physical constraints of the particular system. If the oculomotor system operates in an analogous manner, then as the bandwidth of the target motion increases, we would expect the delay time to go up accordingly in order to transmit the added information. That is, delay time and rate of information transfer should be directly proportional.

On the other hand, the oculomotor system may operate by means of a process which samples the position of the retinal image at constant intervals of time, or at intervals which are randomly distributed about some mean value, as proposed by Young (7, 8). In that case, we would expect little variation in the average delay time as the bandwidth of the target motion increases, but the average rate of information transfer should decrease.

A third alternative is that the system may integrate the retinal signals for a finite amount of time and wait until a sufficient "quantum" of information has been gathered before initiating a corrective eye movement. In this situation, the amount of information which has been "averaged out" and therefore lost should be proportional to the delay time. That is, we would expect delay time and rate of information transfer to be inversely related.

Figure 7. 14 shows that the latter case is true: the delay time T is plotted vs. $1/R$, the inverse of the average rate of information transfer, and the relationship can be approximated by a straight line which has been fitted by the least-means-square criterion. That is,

$$T = T_o + T_c = T_o + \frac{H}{R} \quad . \tag{7}$$

Since the integrating (or computing) time T_c restricts the number of information "quanta" that can be sent per unit time, then as R approaches infinity, T_c must approach zero. Of course, none of the data points go as far as the $1/R = 0$ axis, since any physical system can only carry a finite amount of information, but if the straight line approximation is extended to the vertical axis, then the intercept is T_o, the transit time required for the signals to travel from the ret-

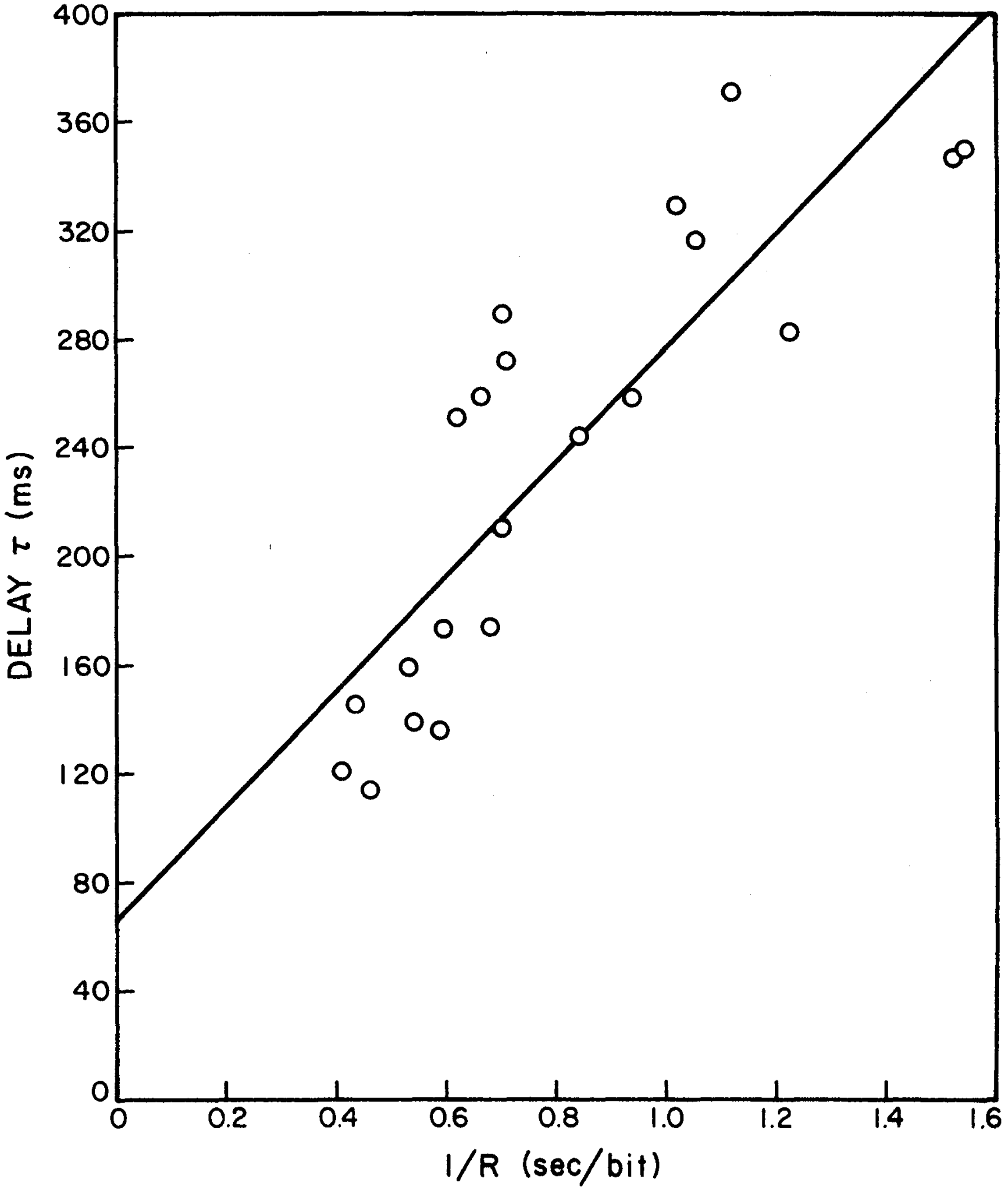


Figure 7.14(a): Average delay of the oculomotor system response to Gaussian random motion vs. the inverse of the rate of information transfer from target to eye motions

Subject GSC

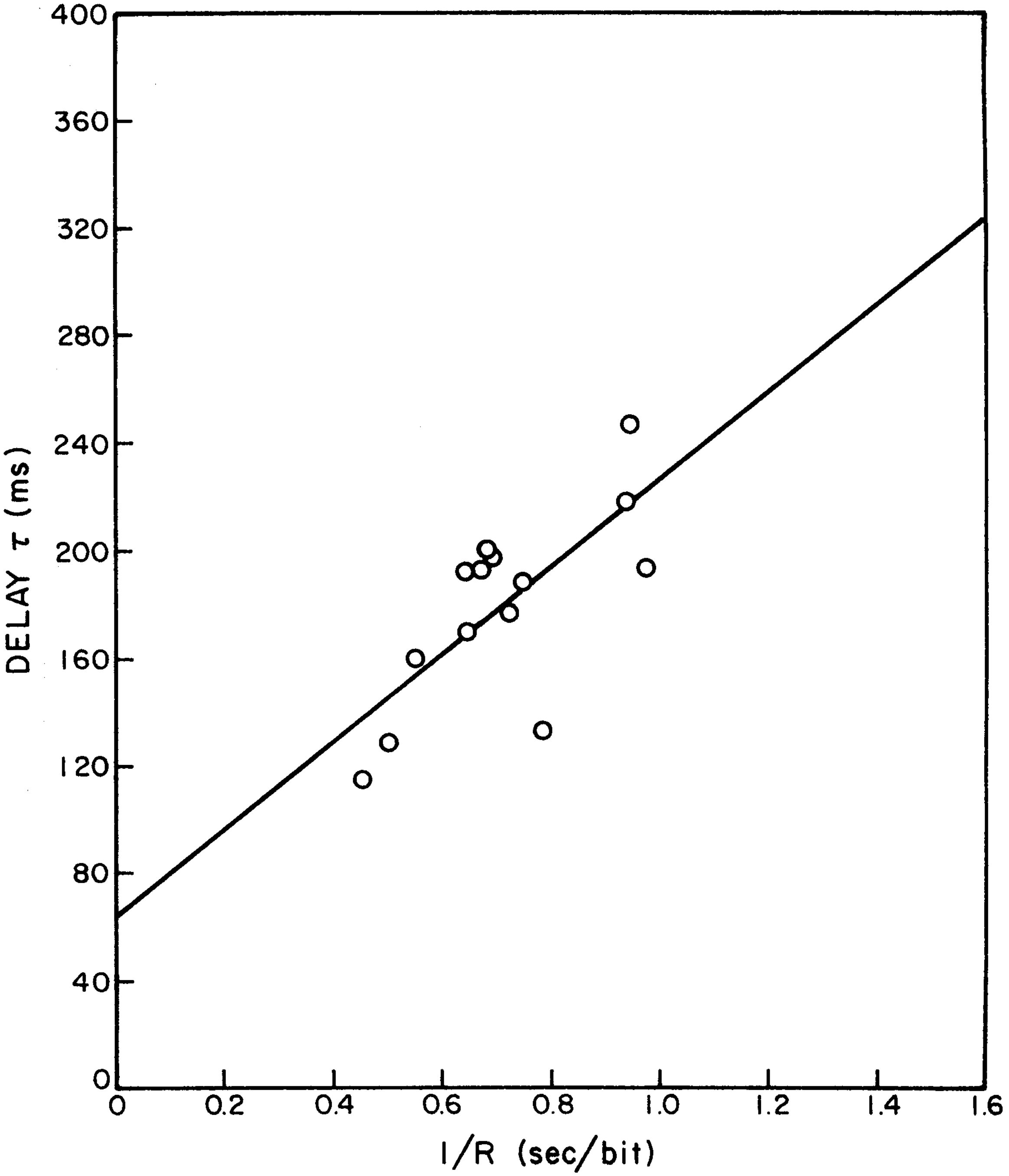


Figure 7.14(b): Average delay of the oculomotor system response to Gaussian random motion vs. the inverse of the rate of information transfer from target to eye motions

Subject SAM

ina to the cerebral cortex and thence to the oculomotor nuclei. Despite the scatter of the data points, the transit time T_o is calculated to be almost exactly the same for the two subjects: 65 ms for GSC and 64 ms for SAM. This is very close to the 70 ms value calculated by Dallos and Jones (1). Since T_c is the computing or integrating time per quantum of information and R is the rate of information transfer in units of bits/sec, the slope H is then the measure of the information content of one quantum. Thus, the smallest amount of information that can initiate a corrective eye movement is 0.211 bits for subject GSC and 0.162 bits for SAM.

What is the physiological nature of this quantum of target position information? Let us consider the mechanism whereby a finite amount of light energy must be absorbed and integrated by the photoreceptors in order to produce, in the optic nerve, the amount of excitation necessary to elicit a corrective eye movement. If the retinal image moves slowly, it may very well spend enough time on one photo-receptor to raise the pre-synaptic potential of the corresponding ganglion cells above the firing threshold. On the other hand, if the retinal image moves more rapidly, less light can be absorbed by each photo-receptor and the image must be allowed to sweep over a larger number before the required number of impulses can be produced. In that case, the computing time T_c would very simply be that time required to permit the retinal image to travel the necessary distance. Let us see if this is feasible.

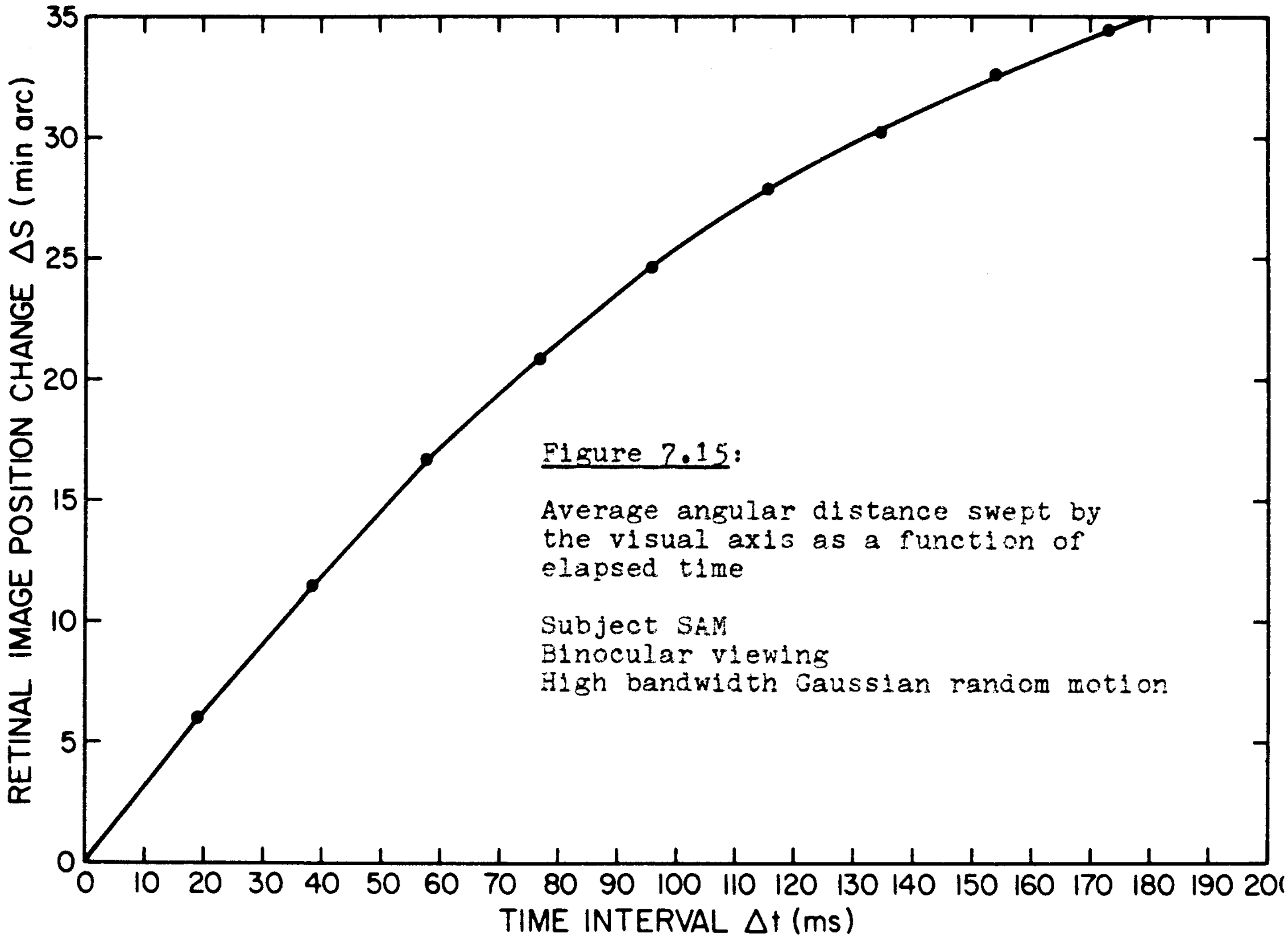
Let s(t) be the path of the retinal image; then the average angular distance swept during the time interval Δt is:

$$\Delta s = \langle |s(t) - s(t+\Delta t)| \rangle_t \quad . \qquad (8)$$

Figure 7. 15 shows Δs as a function of Δt for subject SAM tracking the high-bandwidth target binocularly. The curves for the other cases are quite similar. Assuming that the receptive field of one photoreceptor is about 0. 5 min arc, we can obtain from this curve the value δt, the average amount of time that the retinal image spends on one receptor. Moreover, since we know the delay time T and the transit time T_o and therefore the computing time T_c for all cases, we can compute from the same curve the value δs, the retinal distance swept by the image during the computing time T_c. If our hypothesis is correct, the corresponding values δs and δt should be related this way:

$$(\delta s - \delta s_o)(\delta t - \delta t_o) = C \quad . \qquad (9)$$

In order to obtain the largest possible number of data points, we have computed δs and δt for those cases where the target motion consisted of the sum of several sinusoids as well as those where the motions were Gaussian random processes. Monocular viewing conditions as well as binocular are included. Figure 7. 16 shows the plots of δs vs. δt as well as the "best fit" (3) hyperbola described in Eq. (9). In spite of the fact that the points are somewhat scattered, the derived parameters are remarkably similar for the two subjects. Thus, the minimum amount of time δt_o that must be allowed to any one receptor is 3/4 milliseconds for both subjects. If the retinal image moves faster, the number of receptors which must be excited is greater than the average number of receptors which terminate on



<u>Figure 7.15</u>:

Average angular distance swept by the visual axis as a function of elapsed time

Subject SAM
Binocular viewing
High bandwidth Gaussian random motion

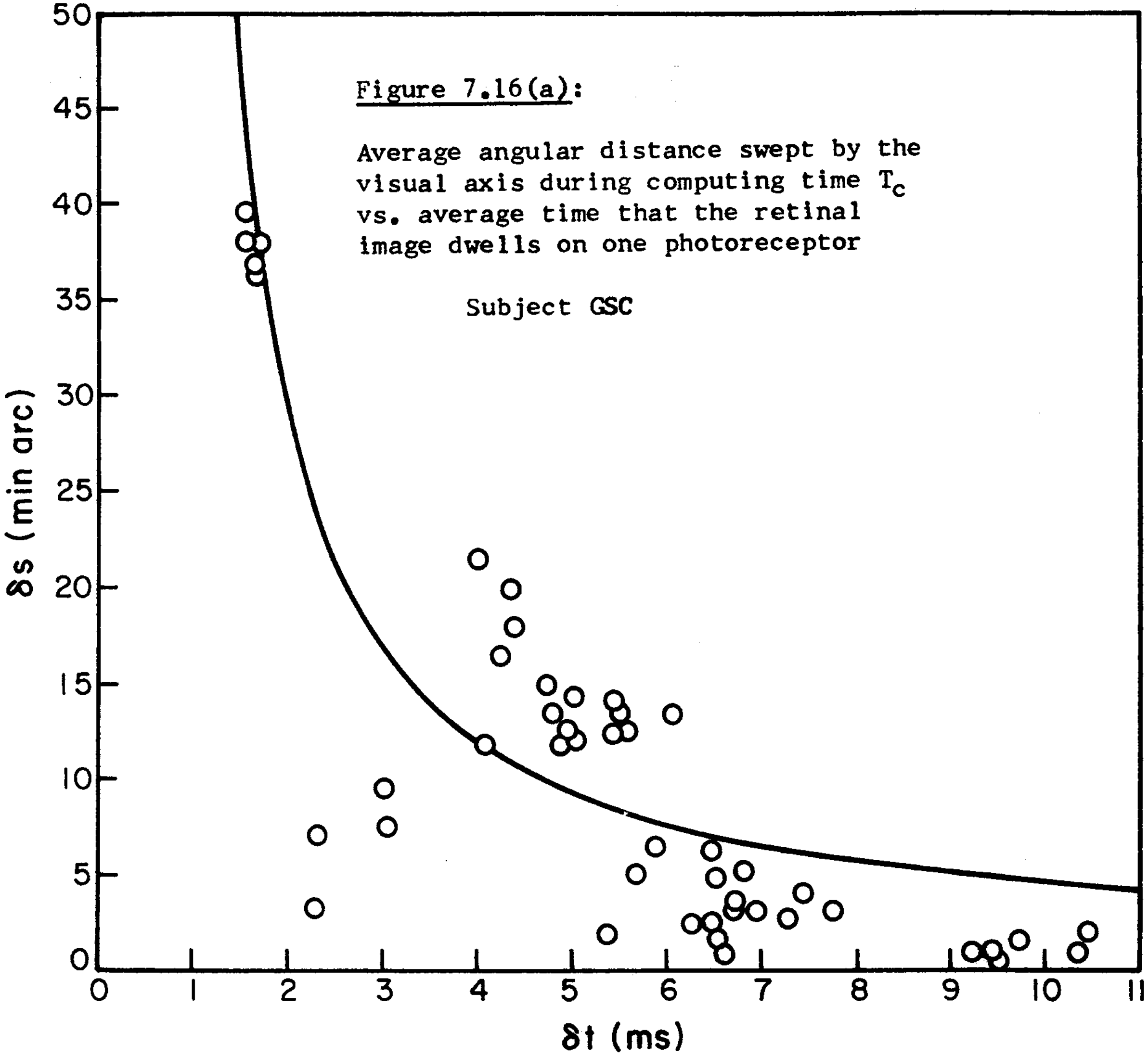


Figure 7.16(a):

Average angular distance swept by the visual axis during computing time T_c vs. average time that the retinal image dwells on one photoreceptor

Subject GSC

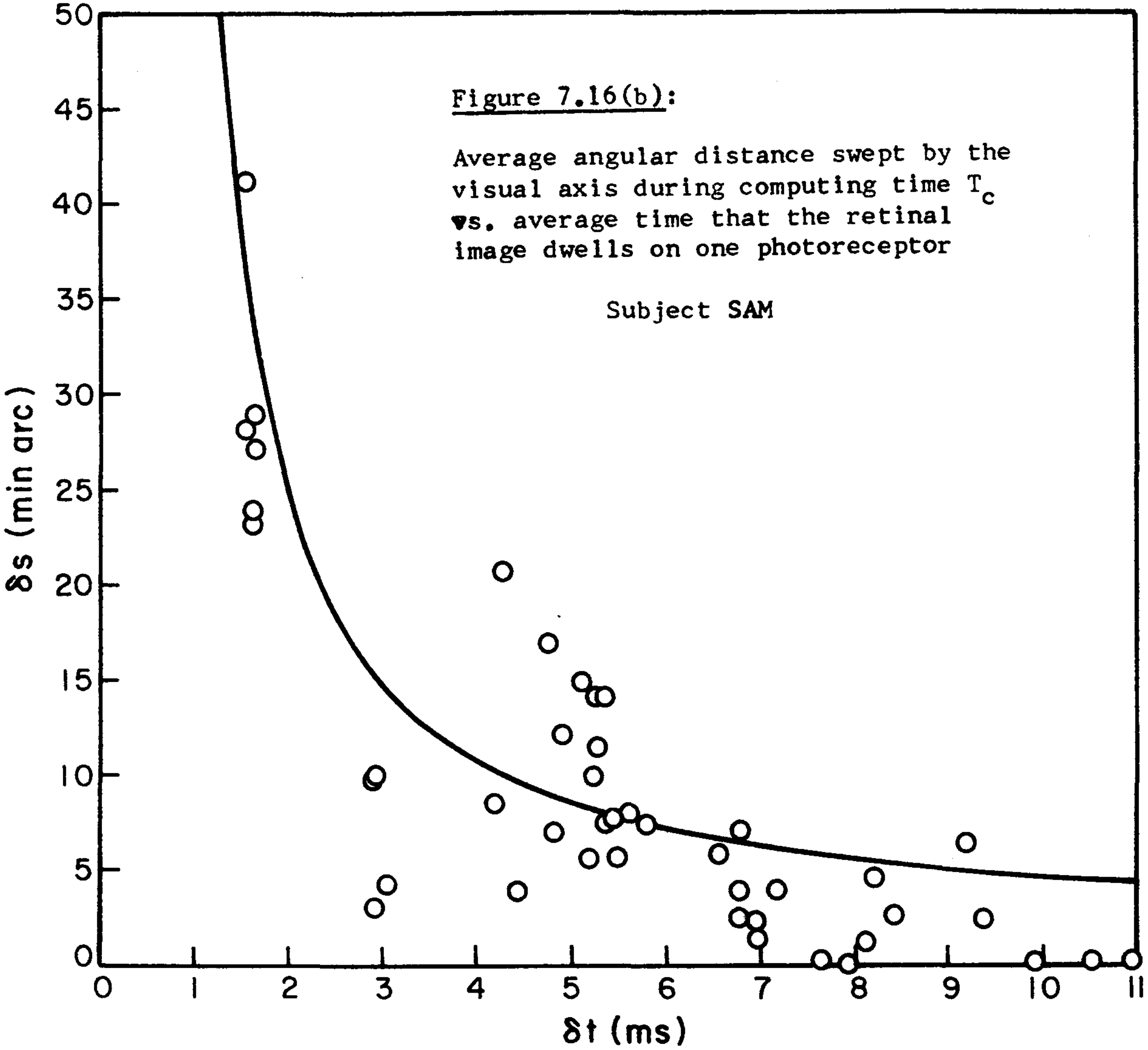


Figure 7.16(b):

Average angular distance swept by the visual axis during computing time T_c vs. average time that the retinal image dwells on one photoreceptor

Subject SAM

the same ganglion cells. Furthermore, for subject GSC, as the dwell time δt becomes very large, the required retinal sweep approaches a minimum value of δs_o of 0.44 min arc, which is quite close to the receptive field of one photo-receptor (about $\frac{1}{2}$ min arc). For subject SAM, the corresponding minimum δs_o is 1.38 min arc, slightly more than 2 photo-receptors.

From this evidence, we conclude that our hypothesis is correct; the computing delay time T_c is simply that time required to allow the retinal image to sweep across enough receptors so that the integrated light energy can cause the corresponding ganglion cells to generate the minimum afferent signal necessary to elicit corrective eye movements. This event can then be considered to be a quantum of target position information. There is no need to postulate complex and unrealistic predictive or analytic computing nerve networks.

It should be noted that our results agree quite nicely with those of Wheeless (5). This investigator studied the monocular phase and gain of the oculomotor system while the subject tracked a target whose motion consisted of the sum of several sinusoids. As the brightness of the target decreased, the phase lag for a given target motion and at a given frequency increased. An increase in phase lag, of course, implies a larger computing time. This is quite consistent with our findings.

It must be recognized that this type of analysis is severely restricted by the fact that the number of data points is extremely small and that there is considerable scatter about the hyperbola (Figure 7.16). The model we have drawn is quite likely an oversimplification and there are undoubtedly other factors which contribute to the information processed by the oculomotor system. We have nevertheless demonstrated that, even with our limited data and simple model, a significant relationship between oculomotor delay time and retinal information can be determined. Such an approach is much more fruitful and yields more insight into the mechanics of the oculomotor system than the abstract concept of phase lag, especially if it must be mathematically related to the gain curves.

In view of the non-linearities we have found in this work, it would seem that attempting to characterize the oculomotor system by means of a linear transfer function is a rather fruitless task. Any such function is bound to be misleading when used to predict system output for an imput other than the specific one used to derive the transfer function. Of course, it is always possible to use Gaussian white noise to determine the non-linear Wiener kernels. However, the expense of computing these increases as N^m, where m is the order of the kernel and N is the number of data points. Moreover, there is no way of knowing when the last significant kernel has been reached. This is not to say that the techniques of systems analysis cannot be successfully applied to the solution of biological problems. However, the limitations of such solutions must be clearly understood.

We will not attempt to derive transfer functions to derive the system for all time. However, we will demonstrate that by the proper selection of experimental stimuli and by the judicious interpretation of the results, one can shed light on biological problems by the techniques of systems analysis.

Thus, in the next chapter, we will examine the power spectra of eye movements made when tracking a target whose trajectory is band-limited Gaussian random motion. We will not attempt to relate power to phase, but we will instead compare these spectra with those of spontaneous eye movements made during fixation of a stationary point. In this way, we will investigate the manner in which the oculomotor system allocates its available energy for various tracking tasks. Furthermore, in Chapter X we will use band-limited Gaussian random motion to study binocular interaction between the two visual axes.

REFERENCES FOR CHAPTER VII

1. Dallos, P. J. and Jones, R. W., "Learning Behavior of the Eye Fixation Control System," IEEE Trans. Automatic Control, AC-8 (July 1963), pp. 218-227.

2. Küpfmüller, K., "Channel Capacity and Propagation Time," Communication Theory, edited by W. Jackson, Butterworths Scientific Publications (1953), pp. 303-309.

3. Marquardt, D. W., "An Algorithm for Least-Squares Estimation of Nonlinear Parameters," J. Soc. Industrial and Applied Math. 11 (June 1963), pp. 431-441.

4. Michael, J. A. and Jones, G. M., "Dependence of Visual Tracking Capability upon Stimulus Predictability," Vision Research 6 (1966), pp. 707-716.

5. Wheeless, L., "The Effects of Intensity on the Eye Movement Control System," Ph. D. Dissertation, University of Rochester, New York (1965).

6. Young, L. R. and Stark, L., "Variable Feedback Experiments Testing a Sampled Data Model for Eye Tracking Movements," IEEE Trans. Human Factors in Electronics, HFE-4 (1963), pp. 38-51.

7. Young, L. R., "A Hybrid Model for Eye Tracking Movements," Proc. Annual Conf. Engr. in Medicine and Biology 10 (1968), p. 25. 7.

8. Young, L. R., Forster, J. D., and Van Houtte, N., "A Revised Stochastic Sampled Data Model for Eye Tracking Movements," Fourth NASA - University Conf. on Manual Control, Ann Arbor, Michigan (March 1968).

VIII. POWER SPECTRA OF SPONTANEOUS AND VOLUNTARY EYE MOVEMENTS

1. Spontaneous Eye Movements

In Chapter IV, we separated the spontaneous eye movements, made during fixation, into flicks and drifts. We found that neither type of eye movement plays the major role in correcting fixational errors of the visual axes. We can thus regard the complete waveform as a sample function of a stationary random process. Since the distribution happens to be Gaussian, the autocorrelation function or its Fourier transform, the power spectrum, completely describes its statistics. We will stay exclusively in the frequency domain as this is more readily interpretable; the computational details have been discussed in Chapter VI.

Figure 8. 1 shows the power spectra of the spontaneous eye movements made during binocular fixation of a stationary point. Four curves are shown: left vertical, left horizontal, right vertical, and right horizontal. In Figure 8. 1b, for subject SAM, the right vertical curve is missing: this channel has not been recorded due to experimental difficulties. For subject GSC, all curves are nearly equal except for the right horizontal which is somewhat lower. For subject SAM, the power spectra differ somewhat at the lower frequencies, but become more nearly equal as the frequency increases.

The most interesting characteristic of these spectra is the attenuation with increasing frequency. This is particularly striking for subject GSC, where all curves fall off at a constant rate of about 26 decibels per decade, starting at 0. 2 cps. For subject SAM, this be-

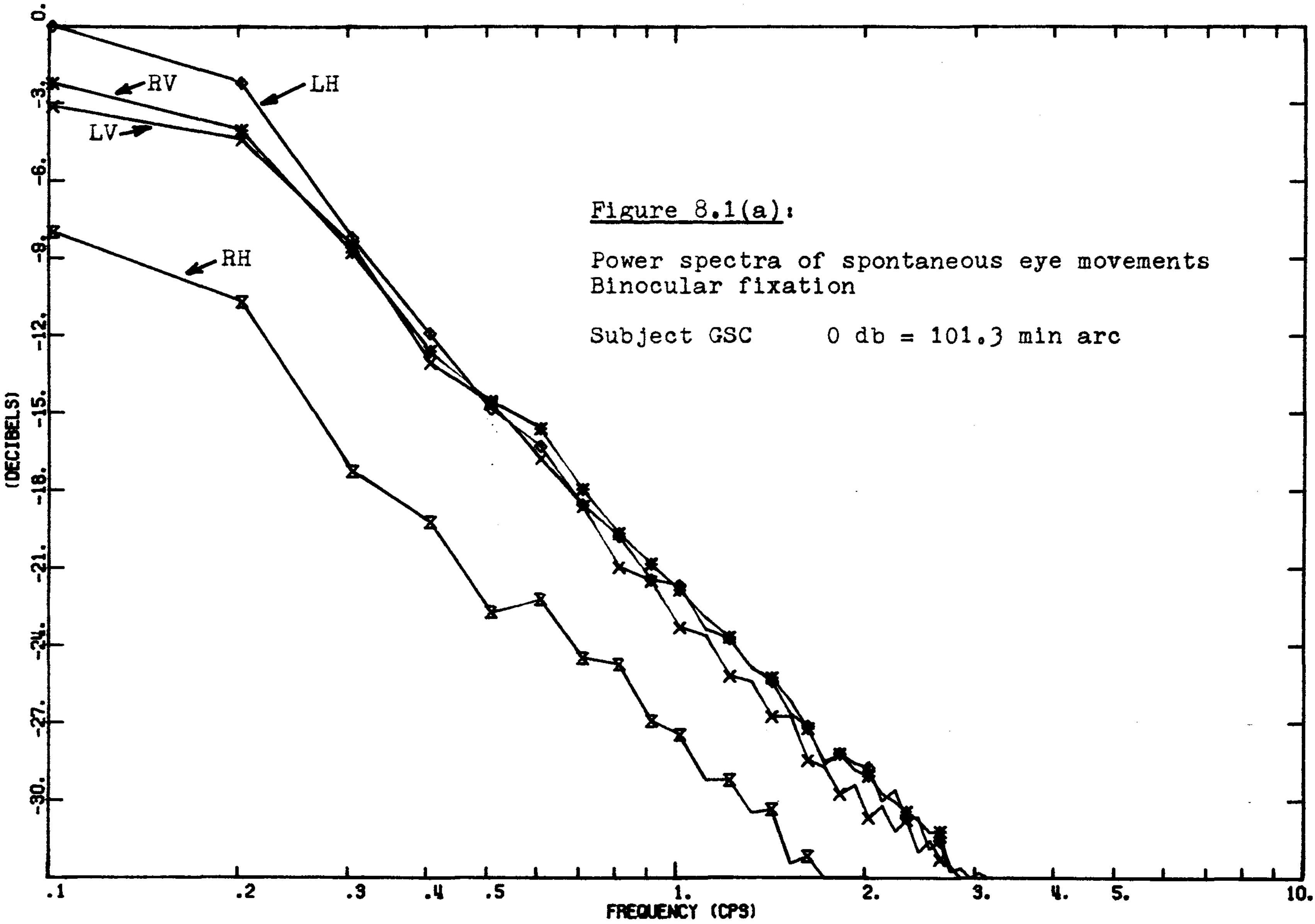


Figure 8.1(a):

Power spectra of spontaneous eye movements
Binocular fixation

Subject GSC 0 db = 101.3 min arc

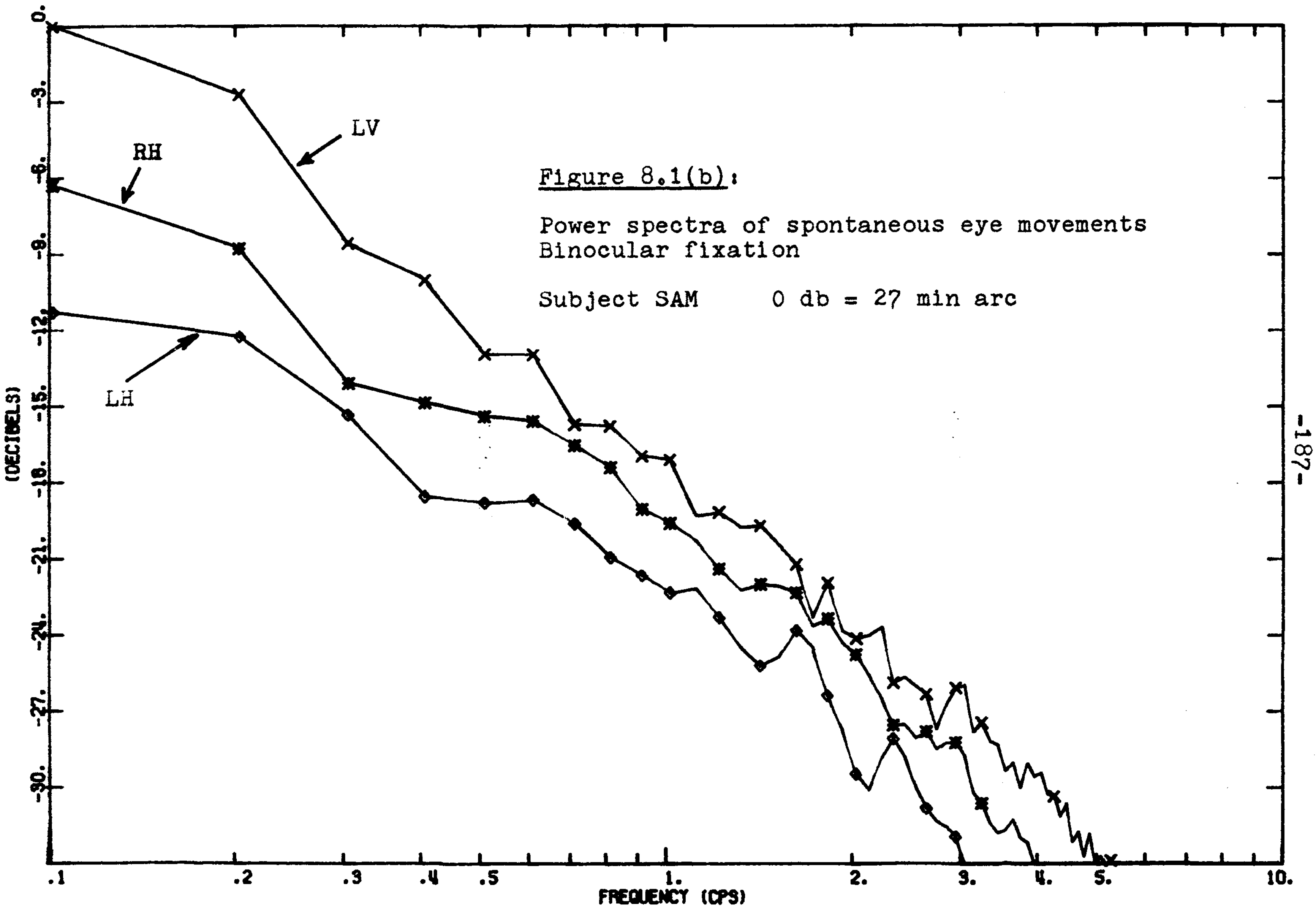


Figure 8.1(b):

Power spectra of spontaneous eye movements
Binocular fixation

Subject SAM 0 db = 27 min arc

havior is not as clear-cut; the constant fall-off does not begin until about 0.75 cps, but at that point, the attenuation rate is also approximately 26 decibels per decade.

It is interesting to speculate on the physiological basis for this behavior. Let us first emphasize that the power spectra we are discussing really means power in the mathematical sense of amplitude squared, not in the physical sense of chemical energy being consumed. Let the rate of chemical reaction in the extra-ocular muscles be dE/dt (the units are of course watts for physical power). Let the eyeball be driven sinusoidally

$$\phi(t) = A \sin 2\pi ft \;; \tag{1}$$

then

$$dE/dt = \text{Torque} \times d\phi/dt \tag{2}$$

$$= (\text{Inertia} \times d^2\phi/dt^2) \times d\phi/dt \;. \tag{3}$$

But from Eq. (1),

$$d\phi/dt \propto Af \tag{4}$$

$$d^2\phi/dt^2 \propto Af^2 \tag{5}$$

so that Eq. (3) can be written

$$dE/dt \propto A^2 f^3 \;. \tag{6}$$

That is, in order to drive the eyeball in a sinusoidal manner at frequency f and with amplitude A, the necessary chemical reactions in the muscles must occur at rates proportional to the square of the amplitude and to the cube of the frequency. Hence, if dE/dt is to remain constant over a frequency band, then the square of the amplitude must be proportional to f^{-3}; in other words, if the chemical reaction rate is to remain the same regardless of the frequency of the motion, then the power spectrum (that is, amplitude squared) must fall off at 30 db/decade. Figure 8.1 shows that the attenuation is about 26 - 28 db/decade, a very good agreement considering that the expected error in the computation of the power spectra is 3 db at the 90 percent confidence level.

Now muscular contracture results from the release of packets of acetylcholine from the end-plate of the motoneuron; this release occurs whenever a pulse propagates down the nerve fiber and reaches the end-plate. Consequently, we can assume that the rate of chemical reaction in the extra-ocular muscles is linearly proportional to the rate of efferent spike discharges in the extra-ocular motoneurons. If we let n(t) be the number of pulses per second propagating down the motoneurons, then its Fourier transform N(f) gives a direct measure of the rate of energy dissipation dE/dt in the extra-ocular muscles as a function of frequency. However, we have found that dE/dt is constant (Eq. (6)) over the bandwidth of the oculomotor system (up to about 3 cps). Hence, this "background noise" of spike discharges during stationary fixation may be regarded as a white Gaussian random process.

2. Voluntary Eye Movements

We now examine the spectra of voluntary eye movements made when tracking a moving target. For a target whose motion is band-limited Gaussian noise, tracking can in practice be accomplished only if the high-frequency cutoff is roughly the same as that of the oculomotor system itself, that is, for the spontaneous eye movements.

For example, if the target has a substantial component above 3 cps, it is perceived as a blur and appears to be everywhere at once; under these circumstances, the subject simply gives up all attempts at tracking. Section 2.1 of Chapter VII and Figure 7.10 describe the power spectra of motion for the three stimuli we have used. They have the same fall-off with frequency and differ only in the corner frequencies, so that the low-bandwidth stimulus differs from the high-bandwidth one only in the relative amount of power at the higher frequencies. Thus, at 2 cps, there is an 8 db difference between the three curves. Target motion was limited to 1.5° and the subject viewed the stimulus binocularly.

Figures 8.2 and 8.3 show the power spectra for tracking motions of the left eye of subjects GSC and SAM, respectively; those for the right eye are similar. The corresponding curves for stationary fixation and for tracking the various moving targets are all shown on one graph for ready comparison. For subject GSC, it is strikingly apparent that the power curves for the various tracking tasks are pretty much the same, and moreover coincide very well with the curve for stationary fixation. For horizontal motion, the curve for stationary fixation is <u>higher</u> below 0.5 cps. For subject SAM, the stationary curve lies below the tracking curves, but the attenuation is roughly the same: 26 db/decade. Moreover, the curve for tracking the low-bandwidth Gaussian stimulus lies above those curves which correspond to the higher bandwidths. Thus, it is quite possible that the change in power spectrum level may be due to the normal run-to-run variations rather than to the target motions.

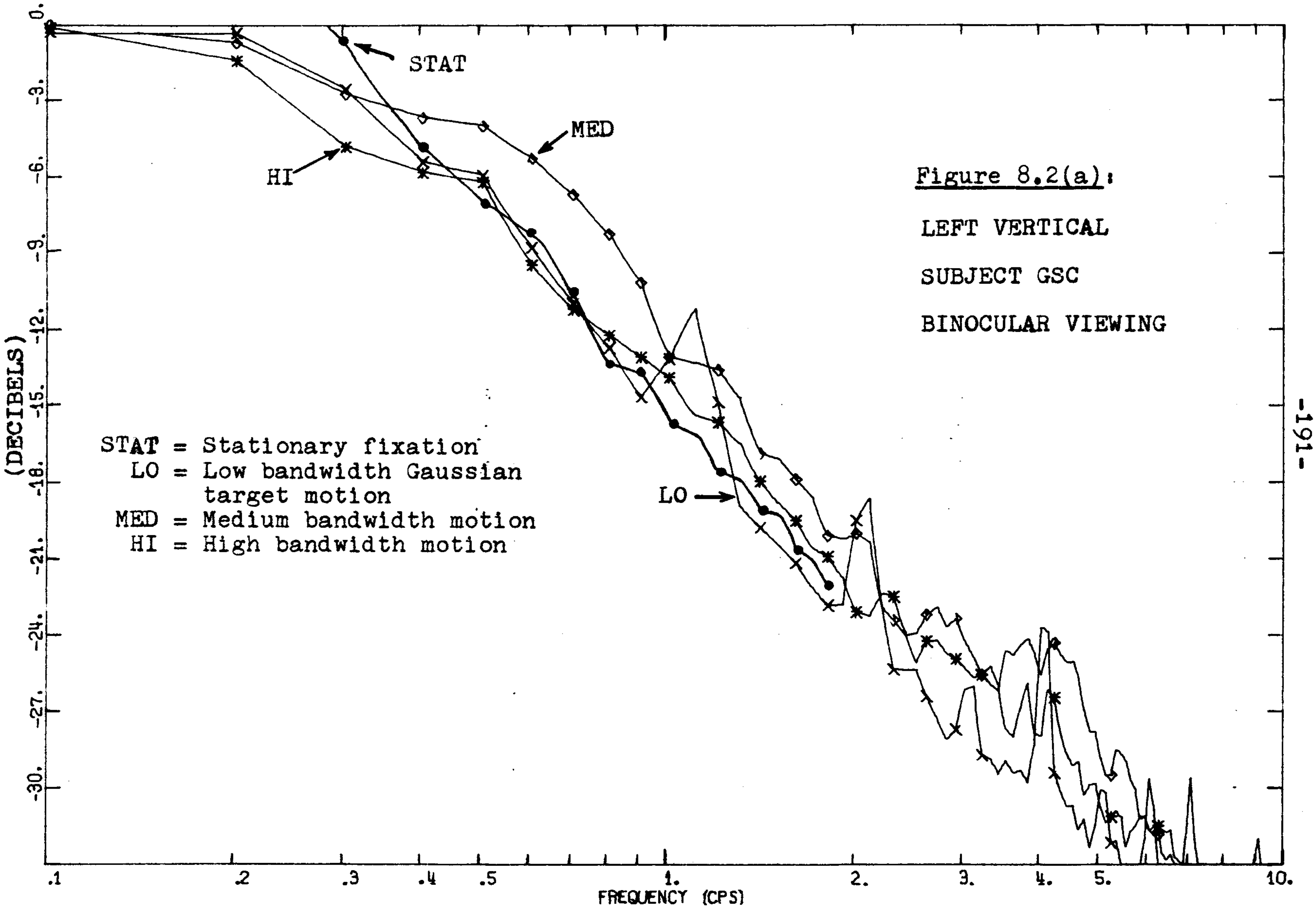


Figure 8.2(a):

LEFT VERTICAL

SUBJECT GSC

BINOCULAR VIEWING

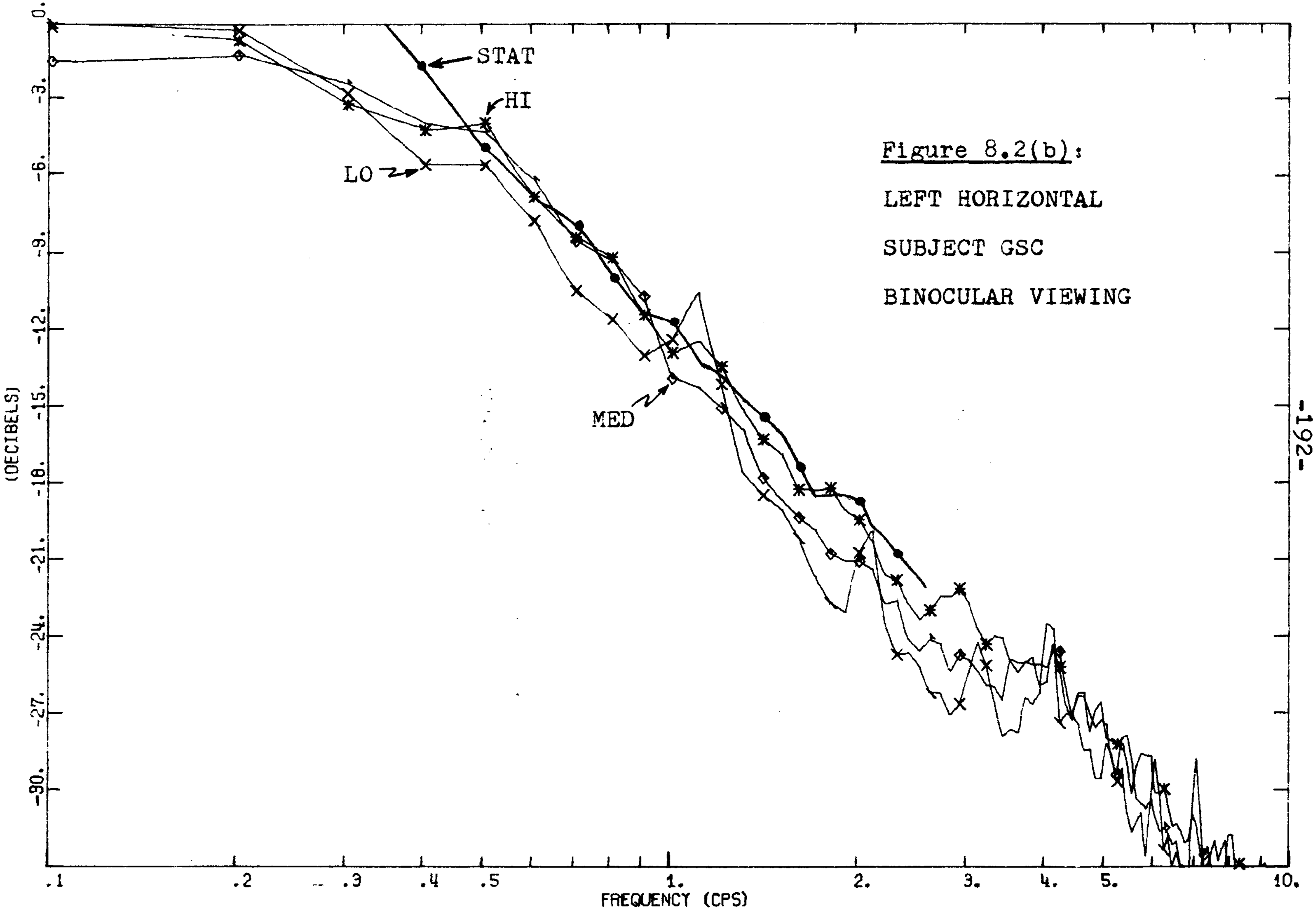


Figure 8.2(b):

LEFT HORIZONTAL

SUBJECT GSC

BINOCULAR VIEWING

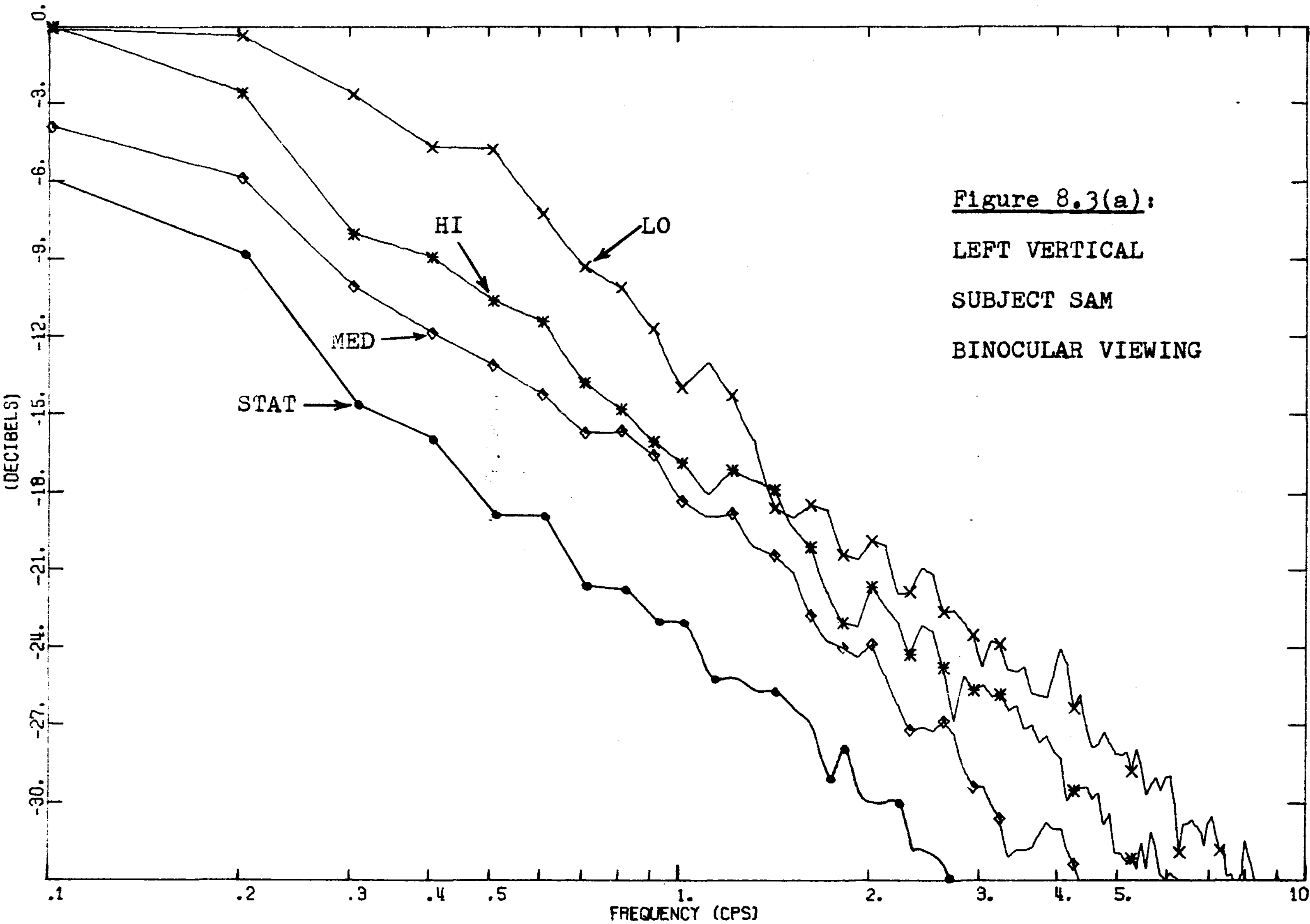


Figure 8.3(a):

LEFT VERTICAL

SUBJECT SAM

BINOCULAR VIEWING

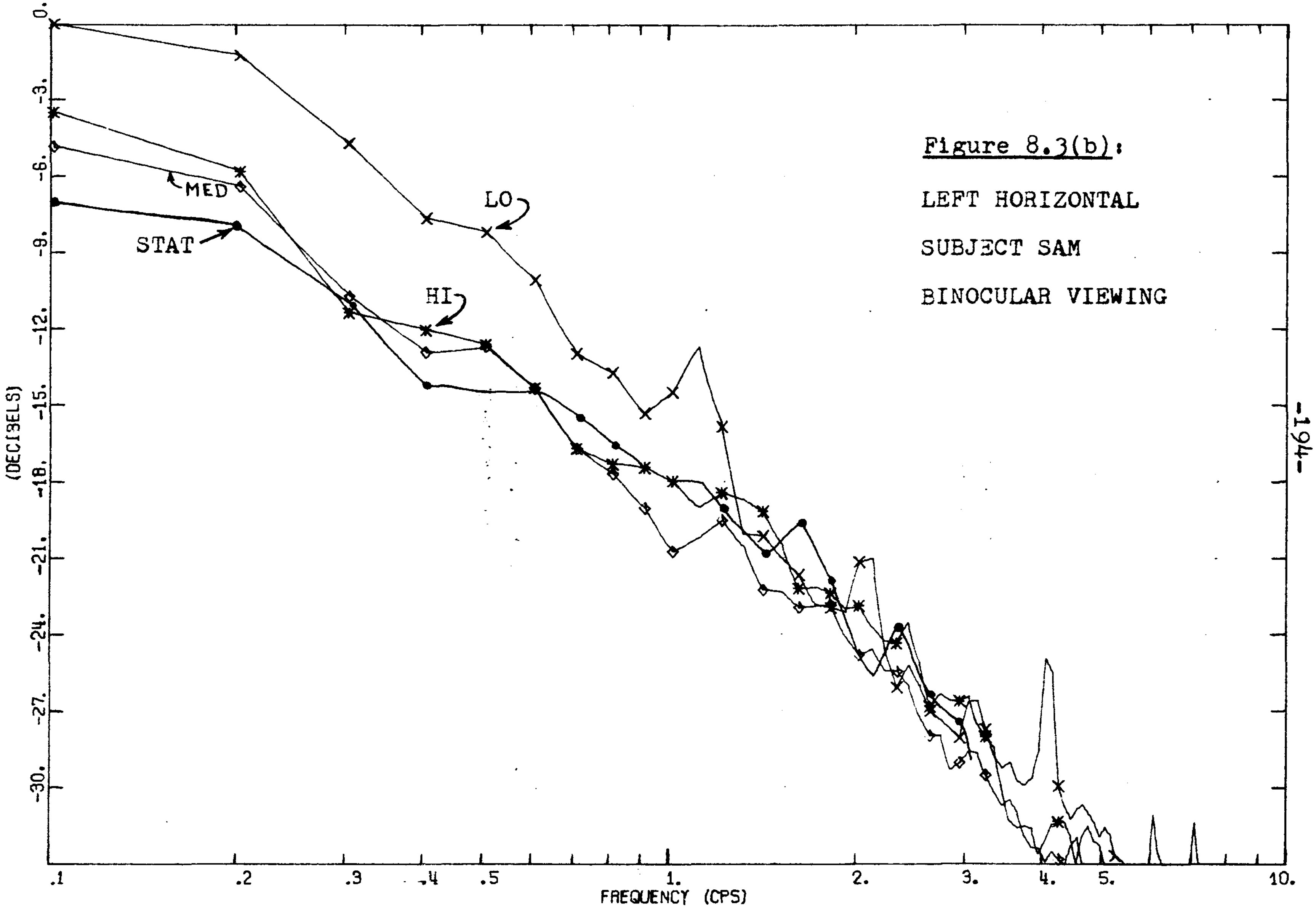


Figure 8.3(b):

LEFT HORIZONTAL

SUBJECT SAM

BINOCULAR VIEWING

In any case, it is quite clear that increasing the power spectrum of the target motion at the higher frequencies does not result in an increase in the spectrum of the tracking eye movements. In fact, for subject GSC, all spectra are virtually identical above 0. 5 cps. It might be tempting to attribute this characteristic to the failure of the tracking mechanism and to state that the eye movements at the higher frequencies (say, over 0. 5 - 1 cps) are merely random noise. If this were true, there would be no correlation between target and eye motions at those frequencies. However, we have seen in Chapter VII that this is not the case. Both subjects track all three Gaussian stimuli up to at least 2 - 2. 5 cps, albeit at increasing phase lag at higher frequencies (see Figures 7. 11). The phase lag is not random, but is a function of the target motion.

Thus, the target entrains the visual axis, but the amplitude of the resulting tracking movements is not significantly larger than that of spontaneous motions at the same frequency. This is added evidence that it is fruitless to attempt to derive a general relationship between phase and amplitude for human eye movements, except in a specific case.

We have seen (Chapter VII) that, if the bandwidth of the target motion is relatively narrow, the oculomotor system responds preferentially to the higher frequencies. On the other hand, when faced with the task of following a target whose motion contains significant power at all frequencies, the oculomotor system attempts to track the target with a constant gain up to some "reasonable frequency" (0. 5 cps for GSC), and thereafter the remaining available energy is distributed evenly over the remaining frequencies.

Thus, it appears as if the efferent portion of the oculomotor system operates at "full output" at all times. During stationary fixation, the spontaneous spike discharges may be described as a Gaussian random process whose spectrum N(f) is white. When it is desired to track a target whose motion has power at all frequencies, the average rate of spike discharges does not increase and N(f) does not change significantly. Instead, the efferent discharges for a pair of muscles are co-ordinated so that the visual axis tracks the moving target.

IX. INTRODUCTION TO BINOCULAR AND DICHOPTIC EYE TRACKING MOVEMENTS

One of the earliest observations (1868) made in the field of neurophysiology of the extra-ocular muscles is known as Hering's Law of equal innervation (5) which states that, for large voluntary saccades., the two visual axes move by precisely the same amount. According to Alpern (1), this principle can be extended to smooth pursuit movements and to vergence. Several experiments have been done to demonstrate that the two visual axes move equally in both conjugate and vergent fashion.

Yarbus (10) instructed his subject to shift his gaze from point A, which was far and to the right, to point B, which was nearer and to the left. The resulting tracking eye movements consisted of a smooth, symmetric vergent motion interrupted by a conjugate saccade of equal magnitude in the two eyes. Alpern (2) inserted a prism in front of the right eye of his subject so that, for that eye, the image appeared to shift to the left by an angle ϕ. Of course, only the right visual axis need move in order to bring the image back to the center of the fovea. Instead, the corrective eye movements consisted of a conjugate saccade to the left by an amount $\phi/2$ followed by a symmetric convergence of $\phi/2$. Variations of this experiment have been repeated by various authors: Riggs and Niehl (8), Westheimer and Mitchell (9), and Alpern and Ellen (3). Basically, the procedure is as follows. Two fixation marks A and B are placed along the line of sight of the right eye, B being closer to the subject. The subject is asked to shift his gaze from A to B. Again, only the left eye need move, but in fact the eye movements again consist of symmetric conjugate saccades and smooth vergent motions.

All of the above experiments dealt with large eye movements in which the time course of the motions appeared to be obvious. All procedures had one thing in common: the subject was required to change his line of sight rapidly, and he always responded by means of at least one saccade. It is by now common knowledge that saccades always occur simultaneously in the two visual axes and are of roughly the same magnitude. This characteristic of necessity introduces an error of retinal disparity which must then be corrected by the only possible movement: smooth symmetric vergence. Hence, all of the above extensions of Hering's Law are not really extensions, but logical deductions. In fact, it is impossible to generalize this law by measurement of eye movements, because it is always possible to separate the left and right horizontal motions into conjugate and vergent movements equally shared by the two visual axes. This is strictly a mathematical definition which will be discussed at greater length below (Chapter X, section 1).

In this work, we are concerned with small spontaneous and voluntary tracking eye movements within a 1.5° visual area. Investigations of the relative motions of the two visual axes for such small movements has not been extensive. Ratliff and Riggs (7) reported variations in vergence during stationary fixation, but made no extensive quantitative measurements. Ditchburn and Ginsborg (4) examined the time records of spontaneous eye movements and reported that left and right drifts were synchronous in the vertical direction, and that horizontal drifts consisted of equal conjugate motions and symmetric vergences. They apparently did not consider the fact that horizontal motions can always be separated into these two components. Krauskopf, et al. (6) examined only the horizontal flicks of the left and right eyes and neglected the drifts; this paper has been thoroughly discussed in Chapter IV.

We have found that during dichoptic fixation of a stationary point, the fixation pattern of the occluded eye was much more widely scattered than that of the seeing eye. Moreover, the flicks and drifts of one visual axis increased in magnitude when that eye was occluded. Flicks and drifts, however, have been used to characterize eye movements simply because flicks stand out so well during visual examination of the time records. It has been established in Chapter IV that both flicks and drifts correct fixational errors. Hence, all spontaneous eye movements may be regarded as a random process whose distribution happens to be Gaussian. The parameters which describe the Gaussian distributions of spontaneous eye motions have been derived in Chapter IV and have been used to draw the ellipses of Figure 4. 4. However, these numbers provide no information regarding the time course of the random process. For this purpose we must compute the appropriate auto- or cross-correlation functions, or alternatively, their Fourier Transforms; the power spectra. In fact, the representation of the random process by a continuous spectrum of sine waves is, in this case, more readily interpretable than the equivalent description in the time domain. By means of the power spectra, any hidden periodicities can be uncovered. Moreover, it is much easier to describe the relative motion of the two visual axes in the frequency domain: the phase difference at a particular frequency gives a measure of the synchronization, and the frequency itself indicates the speed of the movements at which this measure is valid. Furthermore, using the phase criterion to define conjugate and vergent motions avoids those difficulties resulting from slight errors of calibrations in the measurement of eye movements.

Our previous experiments on stationary fixation have shown that neither flicks nor drifts play the major corrective role for fixational errors of the visual axes, except that the smooth movements serve the additional function of correcting vergence errors. Hence, it appears as if certain eye movements produce fixational errors which are then corrected by other motions. Is it possible to separate corrective from disruptive movements by frequency discrimination? It appears as if there are stochastic noise generators which produce spontaneous flicks and drifts, and error-sensing feedback systems which serve to correct the resulting errors. Is it possible to describe the nature of these noise generators by means of their frequency spectrum? Can we do the same for the correcting systems?

The central purpose of this thesis is to investigate the coordination between movements of the two visual axes. We have seen that if one eye is occluded, its movements increase in size and its fixational pattern gets larger. Nevertheless, the movements of the occluded eye are constrained to follow those of the seeing eye, albeit in some sloppy fashion. What is the precise nature of the link between the two visual axes? How do the left and right corrective mechanisms interact? We propose to answer these questions by studying the cross-power spectra of the movements of the left and right visual axis as the subject fixates a stationary point monocularly and binocularly.

Finally, we must ask how the synchronization of the two visual axes is affected when the eye movements are made voluntarily in response to a moving target rather than spontaneously under stationary fixation. For this purpose, it is important that the motion of the target be such that the resulting eye movements are of a magnitude comparable to that of spontaneous motions. Moreover, we have shown in Chapter VII that responses to various combinations of sums of sinusoids depend considerably on the particular combination used, and that therefore such stimuli are not particularly desirable. Moreover, spontaneous eye movements contain a continuum of frequencies from DC to roughly 3 cps (33 db down at that frequency). Consequently, if we are to compare spontaneous to voluntary movements, it is clear that the motion of the target to be tracked also must contain a comparable continuum of frequencies. We will therefore study the synchronization of the two visual axes as the subject attempts to track a point target whose motion is characterized as a band-limited Gaussian process. By comparing these results with those of stationary fixation, we will elucidate the manner in which the oculomotor system controls the two visual axes so that the two desired retinal images fall on their respective foveas.

REFERENCES FOR CHAPTER IX

1. Alpern, M., "Vergence Movements," The Eye, Vol. III, edited by H. Davson, Academic Press, New York (1962), pp. 91-142.

2. Alpern, M., "The Position of the Eyes during Prism Vergence," A. M. A. Arch. Ophthal. 57 (1957), pp. 345-353.

3. Alpern, M. and Ellen, P., "A Quantitative Analysis of the Horizontal Movements of the Eyes in the Experiment of Johannes Mueller. I: Method and Results," Amer. J. Opthal. 42, No. 4, Pt. 2 (1956), pp. 289-296.

4. Ditchburn, R. W. and Ginsborg, B. L., "Involuntary Eye Movements during Fixation," J. Physiol. 119 (1953), pp. 1-17.

5. Hering, E., Die Lehre von Binocularen Sehen, W. Engelmann, Leipzig (1868), pp. 92-102.

6. Krauskopf, J., Cornsweet, T., and Riggs, L., "Analysis of Eye Movements during Monocular and Binocular Fixation," J. Opt. Soc. Amer. 50 (1960), pp. 572-578.

7. Riggs, L. A. and Ratliff, F., Science 114 (1951), p. 17.

8. Riggs, L. and Niehl, E., "Eye Movements Recorded during Convergence and Divergence," J. Opt. Soc. Amer. 50 (1960), pp. 913-920.

9. Westheimer, G. and Mitchell, A., "Eye Movement Responses to Convergence," Archs. Ophthal. 55 (1956), pp. 848-856.

10. Yarbus, A. L., "Motion of the Eye on Interchanging Fixation Points at Rest in Space," Biofizika 2 (1957), pp. 698-702.

X. RELATIVE MAGNITUDE AND PHASE OF LEFT AND RIGHT EYE MOVEMENTS

1. Method of Analysis

The spontaneous eye movements which occur under conditions of stationary fixation are best described by means of a stationary Gaussian random process. Furthermore, for tracking tasks, the motion of the stimulus was specifically computed to be a band-limited Gaussian random process. Therefore, the most logical way to describe these eye motions is by means of auto-correlation or cross-correlation functions, or equivalently, by their Fourier transforms, which will be subsequently referred to as power spectra or cross-spectra. We will stay exclusively in the frequency domain, as this is more readily interpretable. The computational details have been discussed in Chapter VI.

Power spectra are used to describe the amplitude of one waveform as a function of frequency in units of min arc sq per cps; thus, 6 decibels implies an amplitude change by a factor of 2. Ratios of the amplitudes of two waveforms are computed by dividing their respective power spectra, and phase between two waveforms is obtained by means of the cross-power spectra. It may be noted that in Chapter VII, we mentioned that the concept of phase between stimulus and eye movement was inadequate and that it was better to replace it with a constant delay. At that time, this was desirable because we were trying to describe the input-output characteristics of the oculomotor system by a more intuitive model than the old linear transfer function. Specifically, we were trying to avoid the gain/phase restrictions which are necessarily imposed by such linear functions. We were successful in doing this mainly because the measured phase proved to be a linear function of frequency. In this chapter, we are not trying to derive input-output relationships, but we are merely attempting to describe the relative motions of the two visual axes. In other words, we are dealing only with the efferent portion of the oculomotor system. For this purpose, the concept of phase is valid, since we are making no assumptions of linearity and are not interested in any phase/gain relationships.

Vertical motions of the two visual axes can be described simply by their relative amplitude and phase as functions of frequency. For horizontal motions, however, the situation is not as straightforward. We have seen that horizontal eye movements are the sum of conjugate and vergence motions. Thus, in this case, the relative phase between the horizontal movements of the two visual axes really yields no useful information except in the extreme cases of 0° or 180°. Let X(f) be the power spectrum of horizontal motion for the left eye and Y(f) for the right. Let us postulate each of these to be the sum of a conjugate part C(f) and a vergent part F(f):

$$\begin{aligned} X(f) &= C(f) + V(f) \ , \\ Y(f) &= C(f) - V(f) \ . \end{aligned} \tag{1}$$

Since X, Y, C, and V are complex numbers, these equations can be illustrated as vector additions as shown in Figure 10. 1. Note that there is no _a priori_ justification for setting the conjugate or the vergence spectra equal in the left and right eyes. To be perfectly general, we should express Y(f):

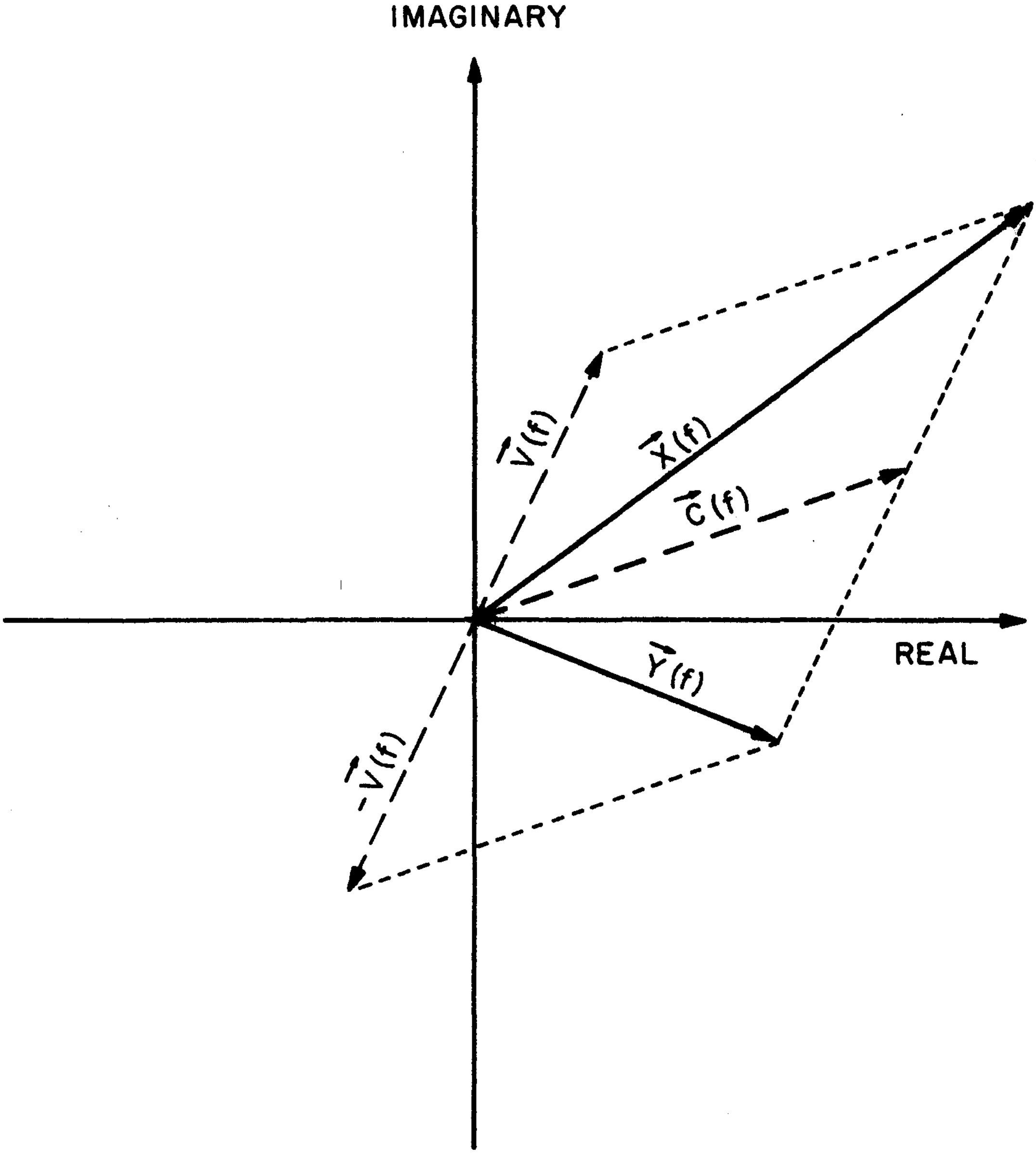


Figure 10.1: Vector representation of the Fourier transforms of horizontal motions of the visual axes.

Decomposition of horizontal eye movements X(f) and Y(f) into conjugate motion C(f) and vergence V(f).

$$Y(f) = a\,C(f) - b\,V(f)\ , \tag{2}$$

where a and b are real functions of frequency as well. Unfortunately, this would require the determination of six unknowns from four measured quantities. Hence, we are forced to define a and b as equal to one. In other words, we can compare the relative motions of the two visual axes either by the ratio of their magnitudes and by their relative phase, or alternatively by a conjugate and a vergent movement equally shared by the two visual axes. This is not to imply that what we compute as "vergence" is necessarily the output of a "vergence control center," although this has to be the only logical interpretation if we assume that the law of equal innervation is true. Therefore, in the following sections we will describe the relative horizontal motions of the left and right visual axes by 4 quantities (measured in decibels): (a) ratio of the absolute values of left and right eye movements $|X(f)|^2 \div |Y(f)|^2$; (b) the conjugate movement $C(f)$; (c) the vergence $V(f)$; and (d) the ratio $V(f)/C(f)$.

2. Vertical Motions of the Left and Right Visual Axes

2.1 Phase difference. Figure 10.2 shows the phase difference (degrees) between left and right vertical eye movements. There are three curves per graph for binocular fixation, for left eye monocular fixation, and for right eye monocular fixation, respectively. For stationary fixation (Figures 10.2a and 10.2e), the phase is essentially zero at most frequencies. There appears to be one exception for subject GSC under mono-left viewing conditions: the motions are 180° out of phase for the one point at 0.1 cps; this anomaly is corrected at 0.3 cps. This behavior probably represents a temporary abnormality

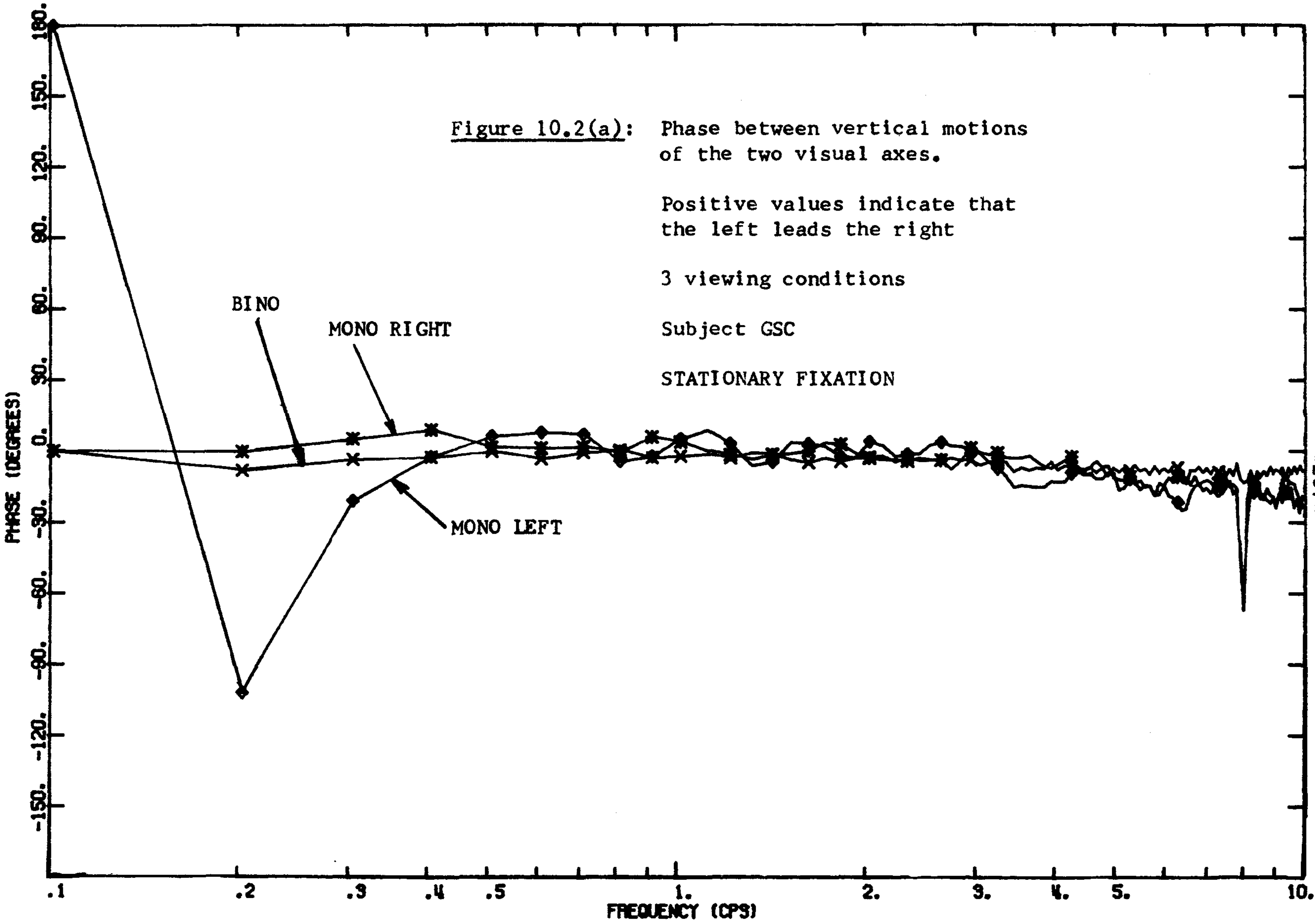


Figure 10.2(a): Phase between vertical motions of the two visual axes.

Positive values indicate that the left leads the right

3 viewing conditions

Subject GSC

STATIONARY FIXATION

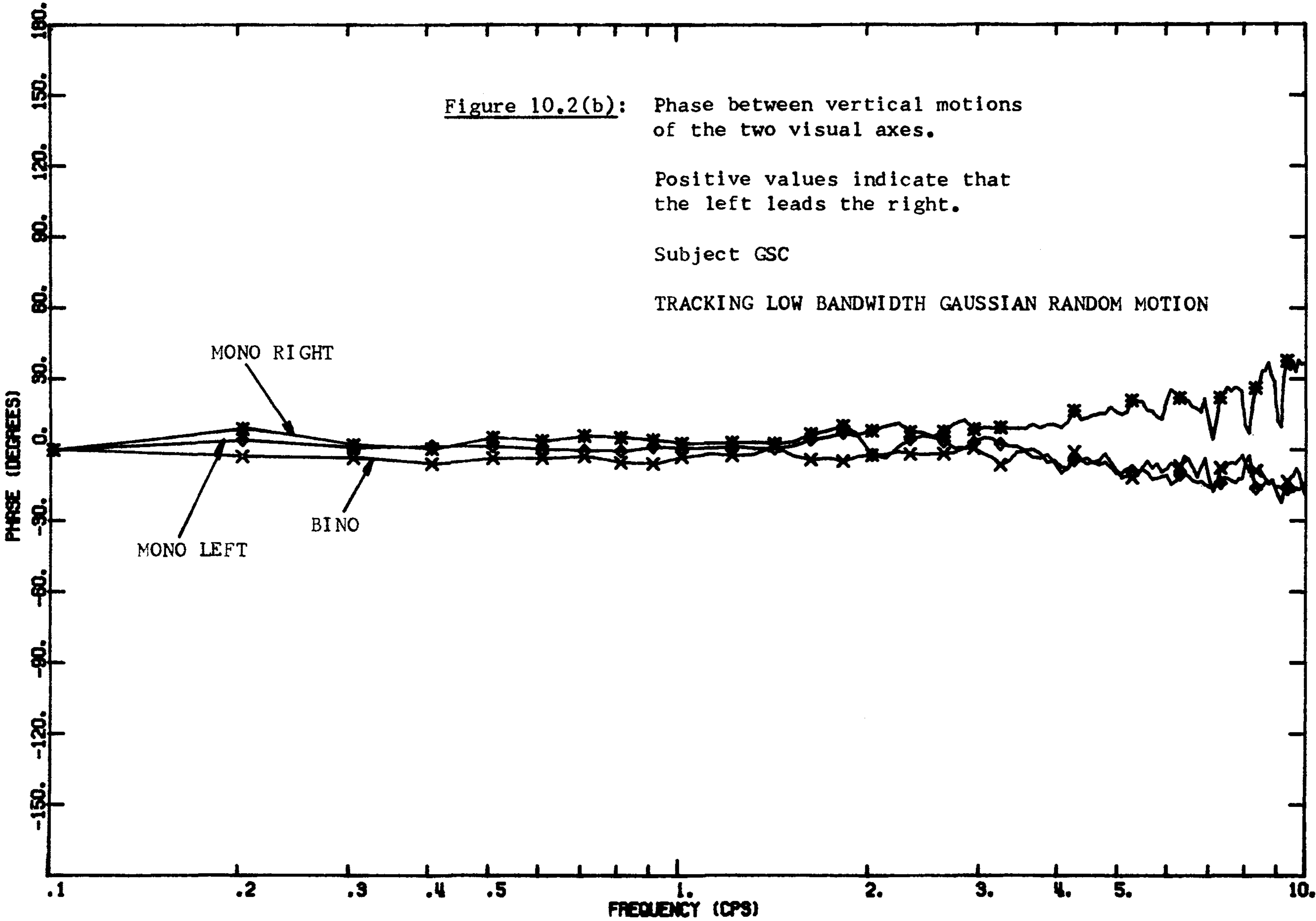


Figure 10.2(b): Phase between vertical motions of the two visual axes.

Positive values indicate that the left leads the right.

Subject GSC

TRACKING LOW BANDWIDTH GAUSSIAN RANDOM MOTION

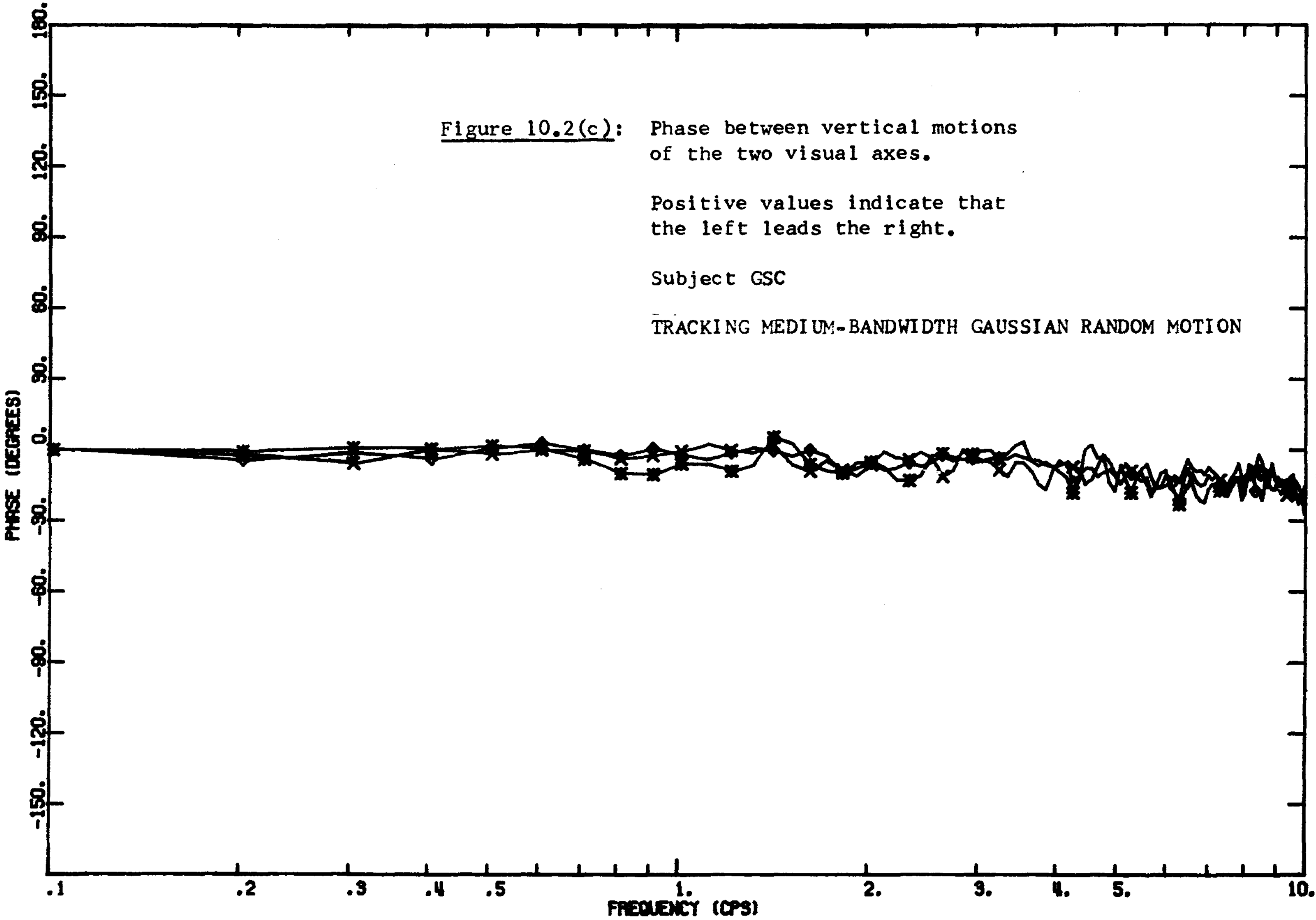


Figure 10.2(c): Phase between vertical motions of the two visual axes.

Positive values indicate that the left leads the right.

Subject GSC

TRACKING MEDIUM-BANDWIDTH GAUSSIAN RANDOM MOTION

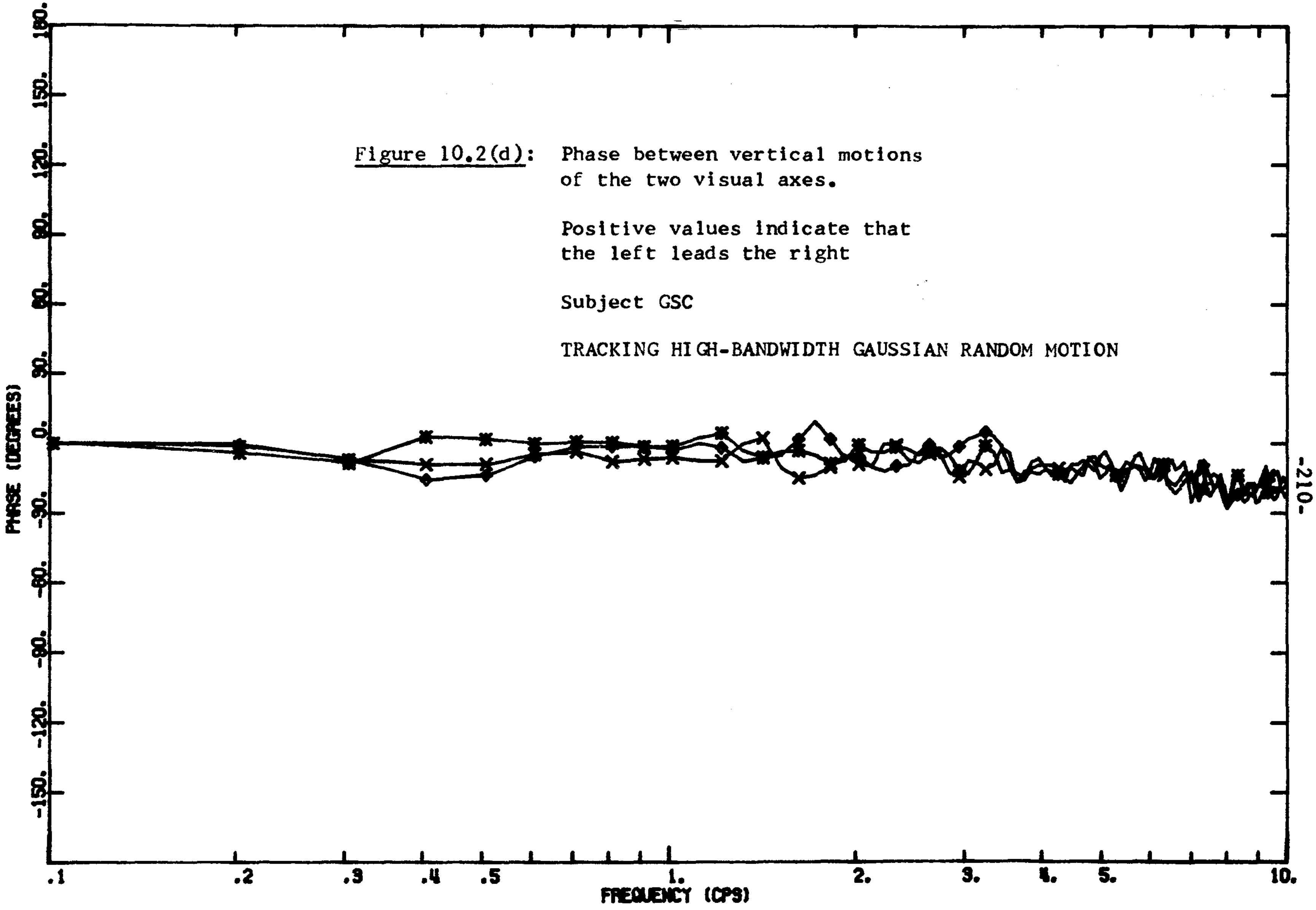


Figure 10.2(d): Phase between vertical motions of the two visual axes.

Positive values indicate that the left leads the right

Subject GSC

TRACKING HIGH-BANDWIDTH GAUSSIAN RANDOM MOTION

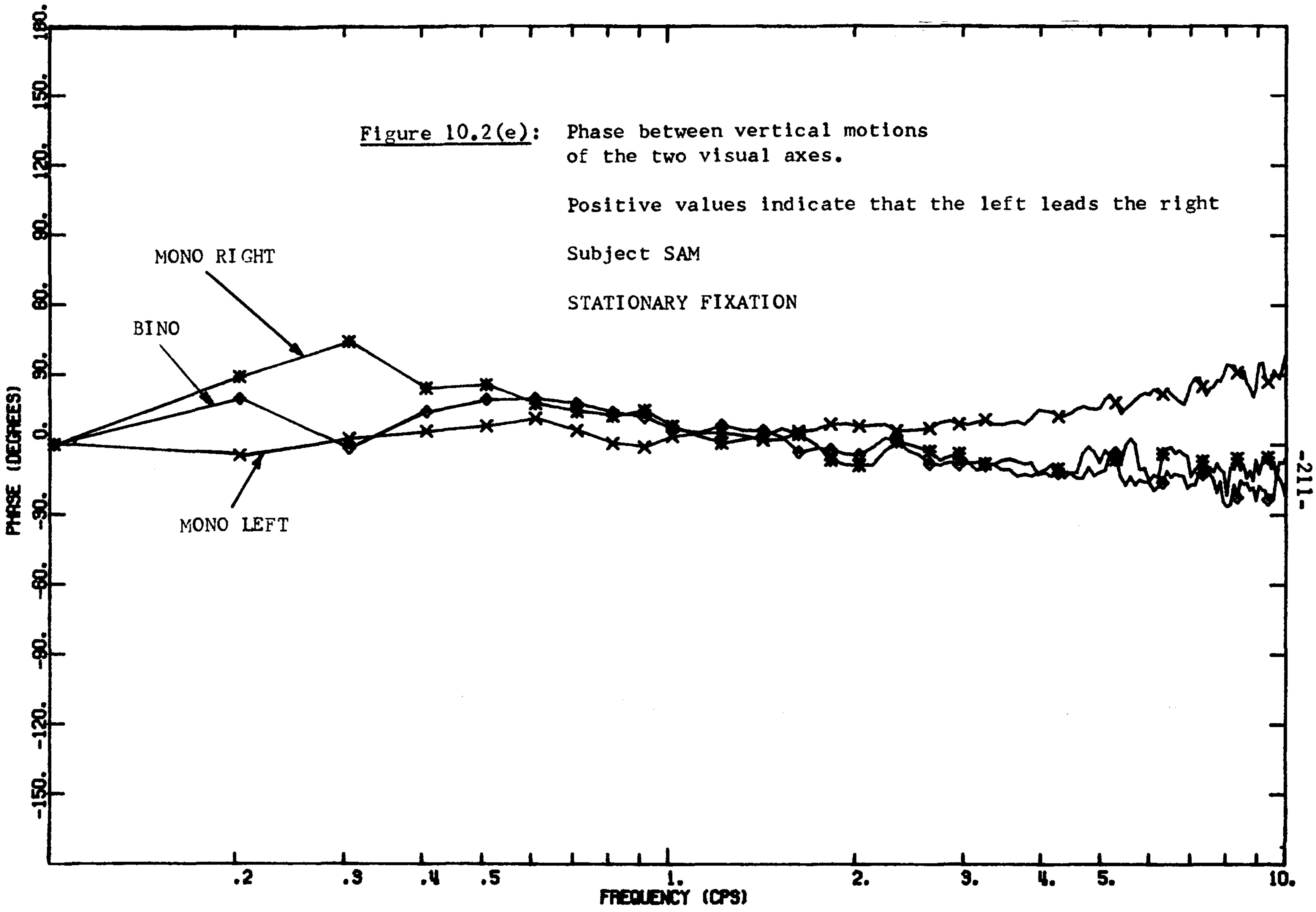
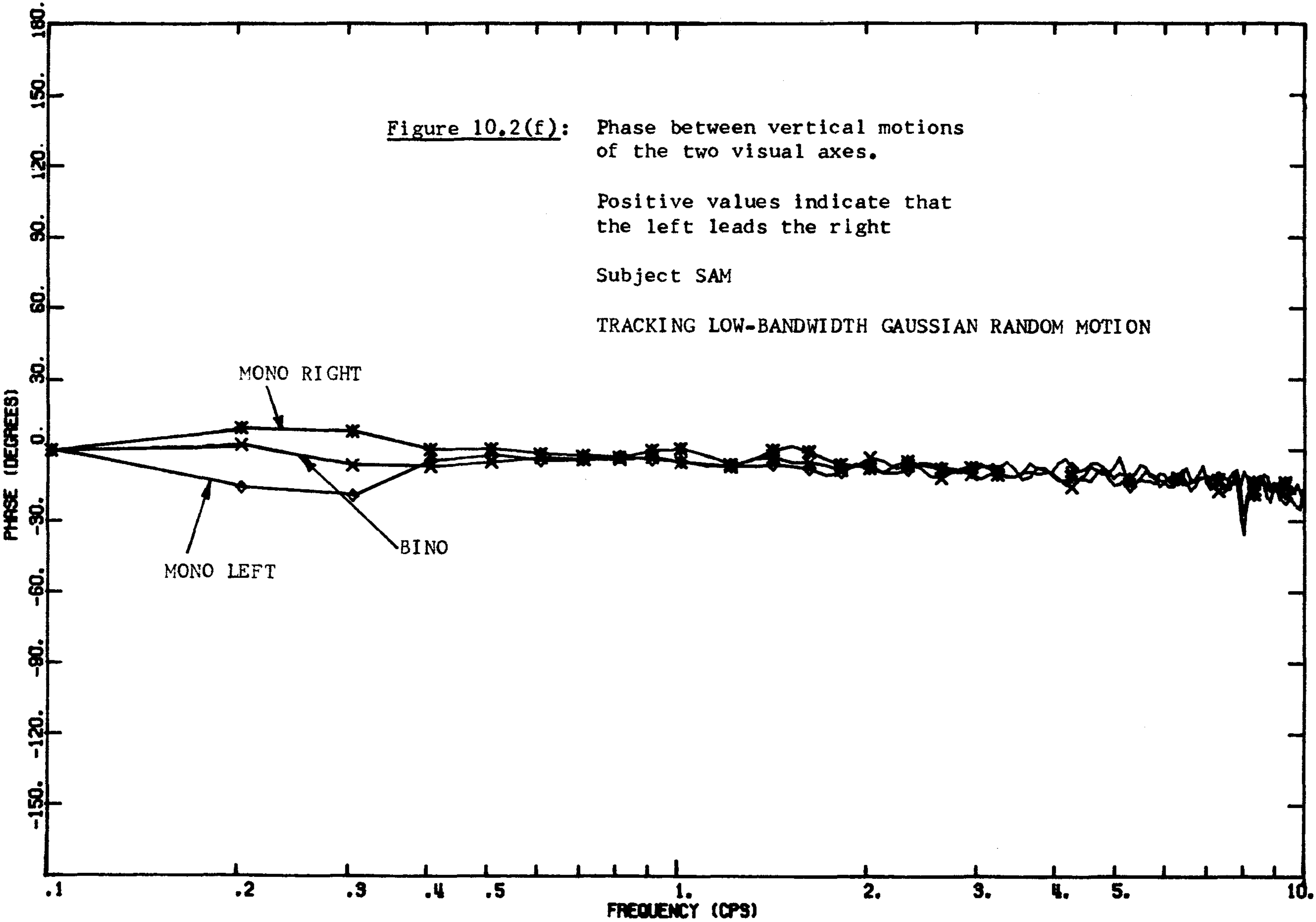


Figure 10.2(e): Phase between vertical motions of the two visual axes.

Positive values indicate that the left leads the right

Subject SAM

STATIONARY FIXATION



<u>Figure 10.2(f)</u>: Phase between vertical motions of the two visual axes.

Positive values indicate that the left leads the right

Subject SAM

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

in view of the fact that the other two curves are quite close to zero at all frequencies. Those small deviations from zero that occur for some low frequencies under stationary fixation all but disappear for tracking tasks. Thus, the two visual axes move vertically in perfect synchrony even for spontaneous movements.

2.2 Amplitude Ratio. Figure 10.3 shows the ratio of amplitude of left vertical movements to that of the right. Positive values indicate that left vertical movements are bigger. As in Figure 10.2, the three curves on each graph represent the three viewing conditions. We have seen in Chapter IV that spontaneous flicks and drifts in one eye tend to increase in magnitude when that eye is occluded. We have here a much more detailed description of the size discrepancy between movements of the left and right visual axes. Figures 10.3a and 10.3d correspond to stationary fixation and to tracking of targets of high-bandwidth Gaussian motion, respectively, for subject GSC. For both cases, the eye movements of the occluded eye in monocular fixation are larger than those of the seeing eye at all frequencies. For binocular fixation, the vertical motions become nearly equal in the two eyes. This size discrepancy is more pronounced at lower frequencies and becomes less at higher frequencies; for high-bandwidth tracking, these ratio differences persist until about 1 cps compared to about 0.5 cps for stationary fixation. Results, of course, are not always this clear-cut: for the low-bandwidth tracking case, contamination from the 1 cps electrical noise is excessive, and for the medium-bandwidth case, both monocular curves are almost equal.

Subject SAM exhibits similar ratio differences: for both sta-

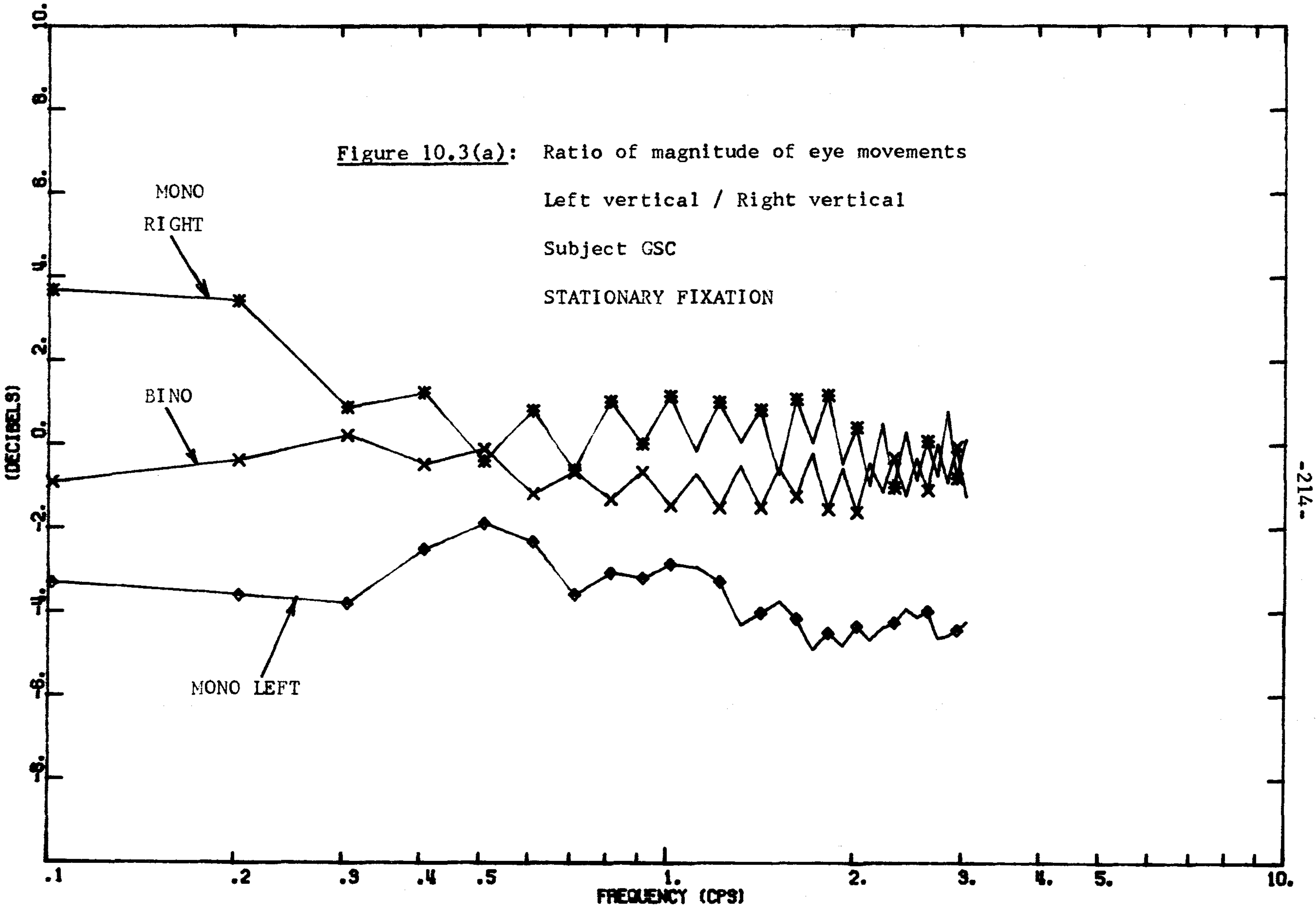


Figure 10.3(a): Ratio of magnitude of eye movements

Left vertical / Right vertical

Subject GSC

STATIONARY FIXATION

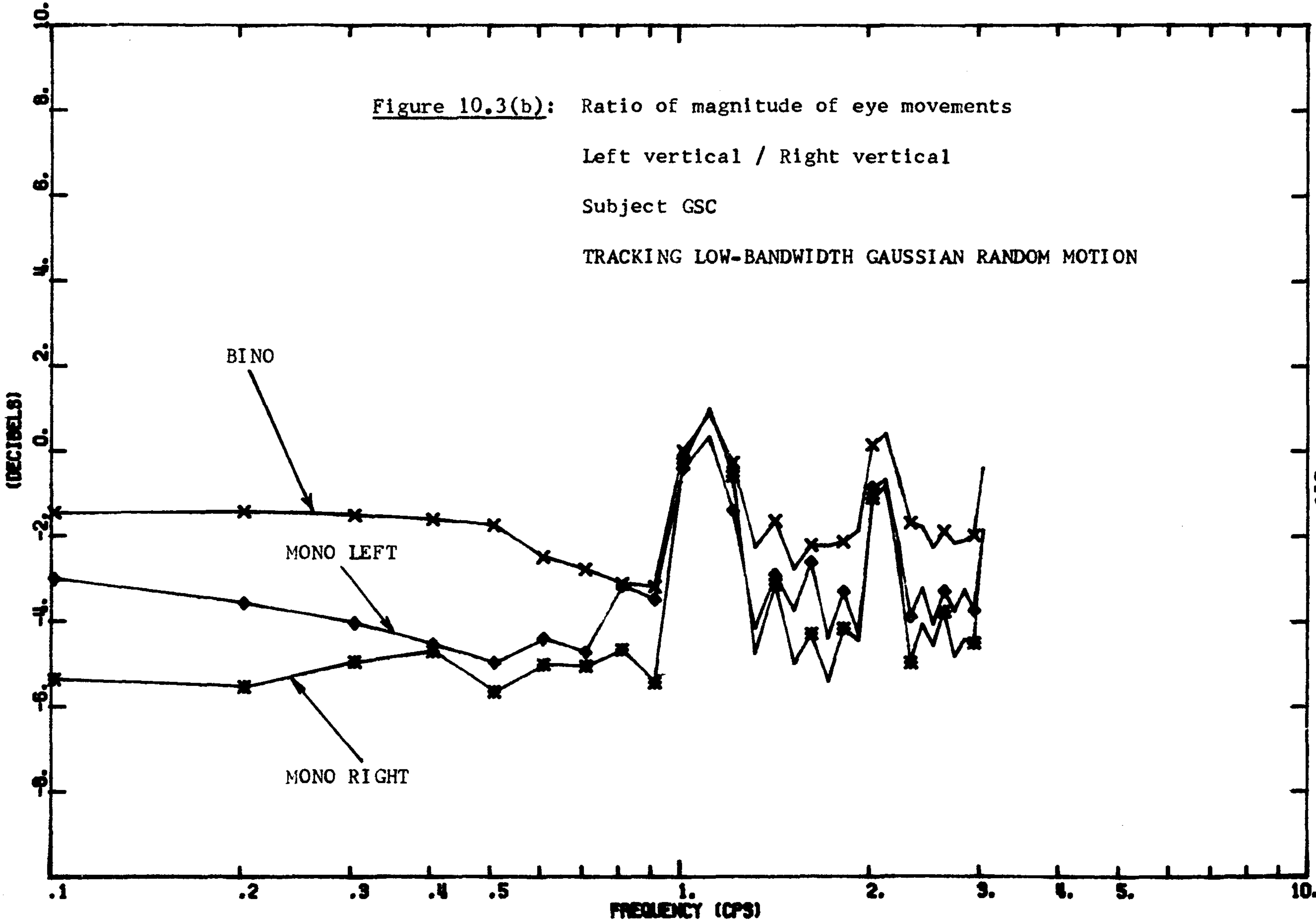


Figure 10.3(b): Ratio of magnitude of eye movements

Left vertical / Right vertical

Subject GSC

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

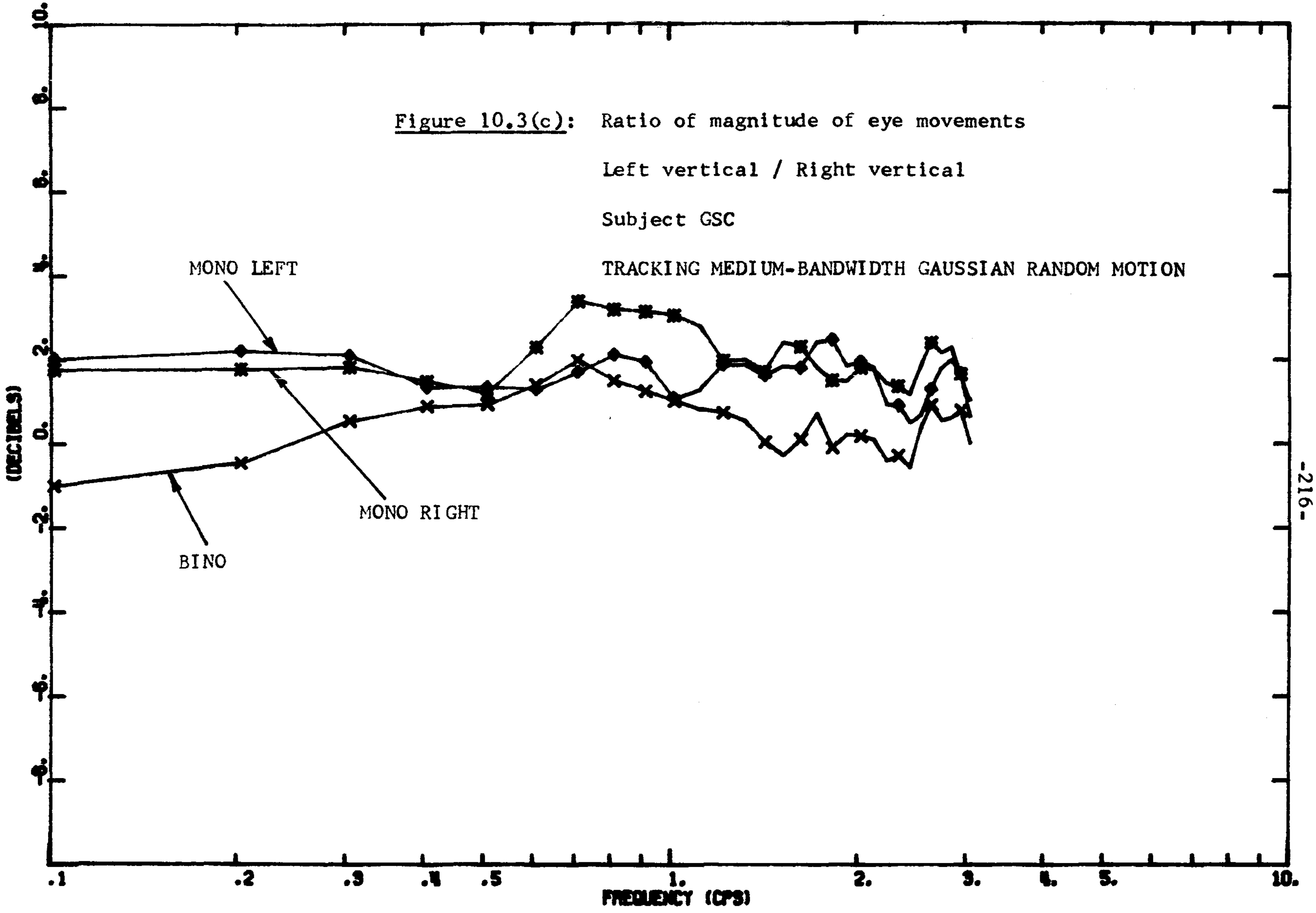


Figure 10.3(c): Ratio of magnitude of eye movements

Left vertical / Right vertical

Subject GSC

TRACKING MEDIUM-BANDWIDTH GAUSSIAN RANDOM MOTION

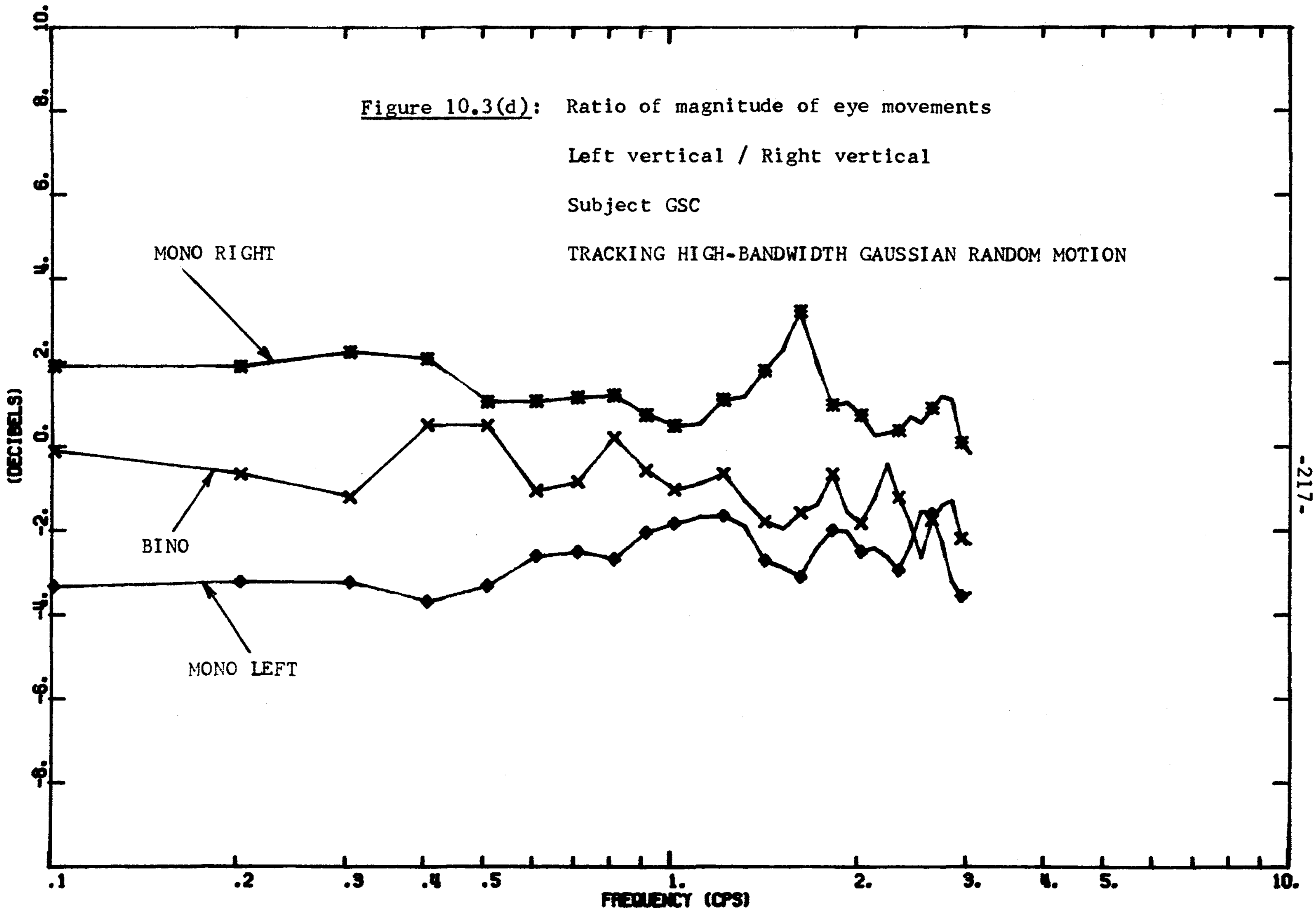


Figure 10.3(d): Ratio of magnitude of eye movements

Left vertical / Right vertical

Subject GSC

TRACKING HIGH-BANDWIDTH GAUSSIAN RANDOM MOTION

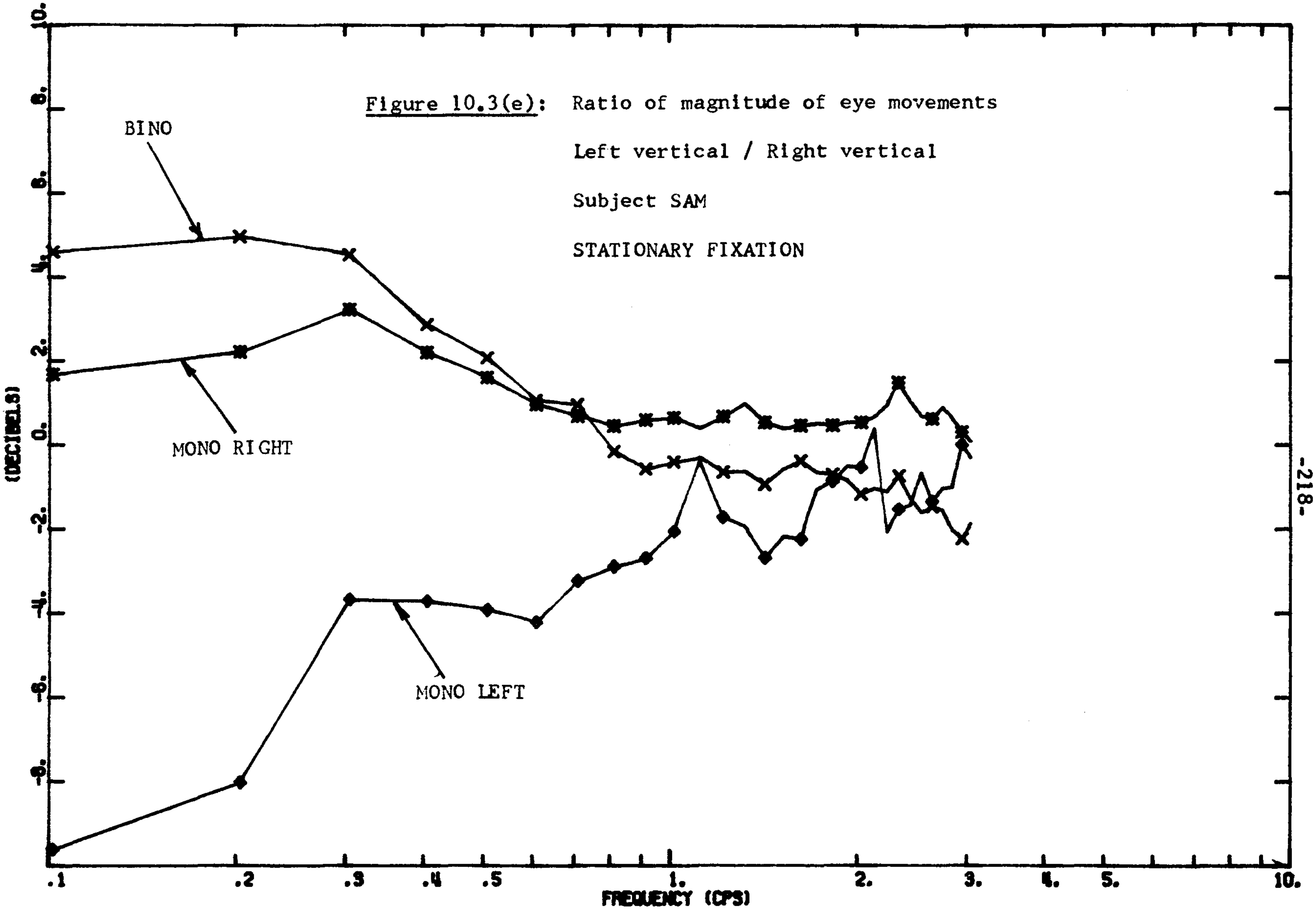


Figure 10.3(e): Ratio of magnitude of eye movements

Left vertical / Right vertical

Subject SAM

STATIONARY FIXATION

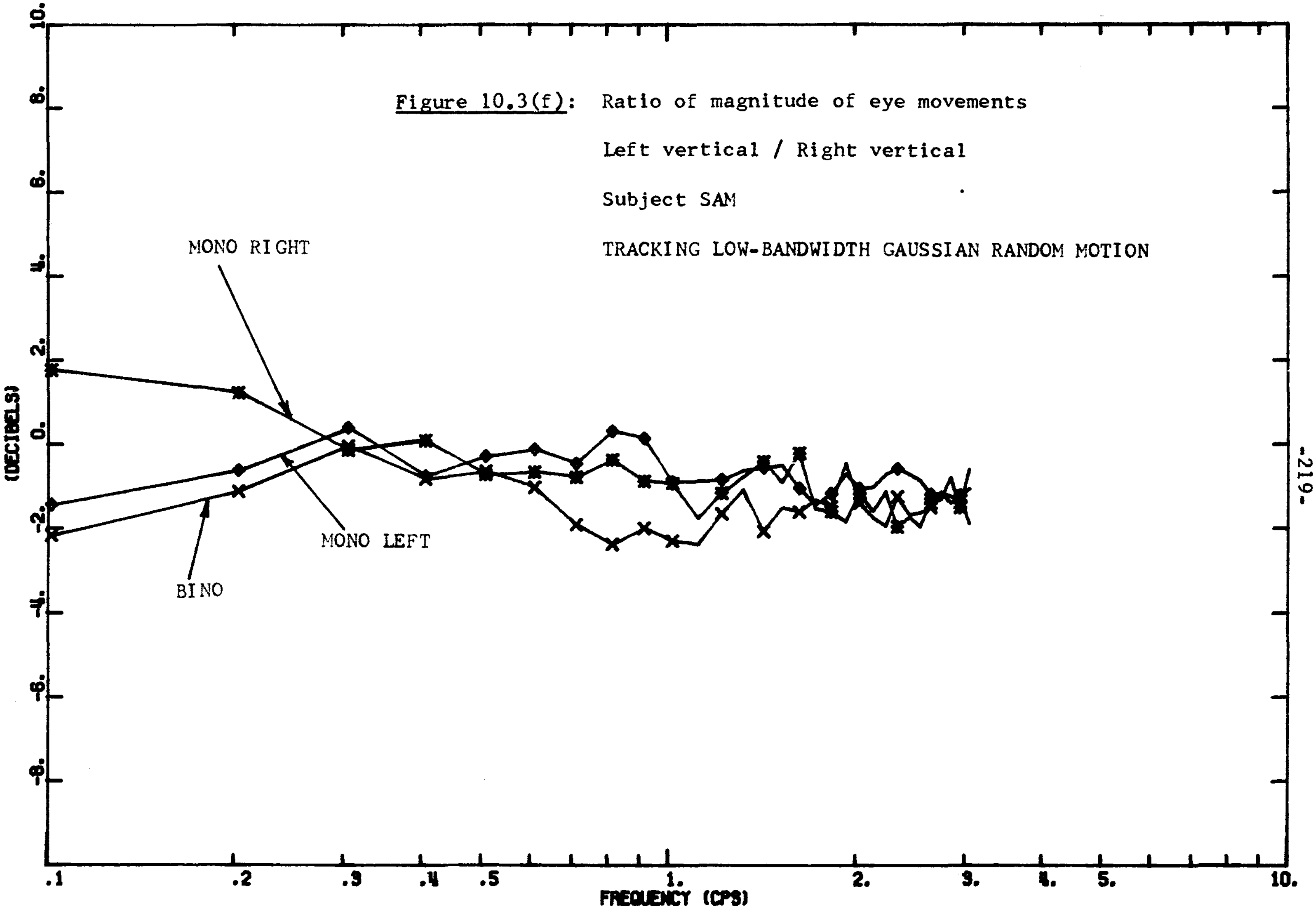


Figure 10.3(f): Ratio of magnitude of eye movements

Left vertical / Right vertical

Subject SAM

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

tionary fixation and low-bandwidth tracking, motions of the occluded eye are smaller during monocular fixation (Figures 10. 3e and 10. 3f). However, in neither case does the binocular curve fall between the two monocular ones. This subject exhibits further asymmetries: for monocular stationary fixation, the left/right ratio is considerably higher when fixation is accomplished with the left eye than when it is done with the right. For tracking motions, however, this asymmetry disappears and in fact, the ratios are considerably reduced and become unity at very low frequencies: 0. 3 cps compared to 1 cps for stationary fixation.

Although these results are not perfectly reproducible from experiment to experiment and subject differences must also be considered, nevertheless, some generalizations can be made from these observations. First, vertical motions in one eye tend to increase relative to those in the other when it is occluded. Second, this ratio is always higher at low frequencies and tends to approach unity as the frequency increases. Third, the ratio discrepancy tends to be more pronounced for stationary fixation than for tracking tasks. Fourth, for binocular fixation, the size ratio may or may not be intermediate between the two monocular values.

In summary, although the two visual axes move vertically in perfect synchrony (zero phase lags), the absolute magnitude of the movement of the occluded eye is generally larger than that of the other. This is particularly well described by Figures 10. 2d and 10. 3d.

3. Horizontal Motions of the Left and Right Visual Axes

3.1 Amplitude ratio of left/right total horizontal movements.

The relative horizontal motions of the two visual axes will first be described in exactly the same manner as the vertical motions in section 2.2, viz.: by dividing the amplitude of horizontal movements of the left eye by that of the right. Figures 10.4a through 10.4d show these ratios as functions of frequency for subject GSC; the three curves on each graph represent the three viewing conditions. Figures 10.5 are the corresponding diagrams for subject SAM.

For monocular fixation, eye movements of the occluded eye are much larger than those of the seeing eye, just as we have found for vertical motions. However, this behavior is much more pronounced for horizontal motions, and is particularly exaggerated in the case of stationary fixation (see Figures 10.4a and 10.5a). Both subjects exhibit ratios of over 10 db at the lower frequencies; this means that the movements of the occluded eye are at least 3 times larger than those of the seeing eye. Moreover, although the ratios decrease towards unity as frequency increases, the values are still significantly different from unity at 2 cps, the upper limit of the oculomotor system bandwidth. For tracking tasks, the ratios decrease substantially and approach equality at much lower frequencies. This is especially well demonstrated for subject SAM: as the average speed of the target increases (i.e., as the bandwidth of the Gaussian random motion stimulus gets larger), the ratios get progressively smaller until finally, for the high-bandwidth stimulus, the differences between the curves are constant at about 2 - 3 db.

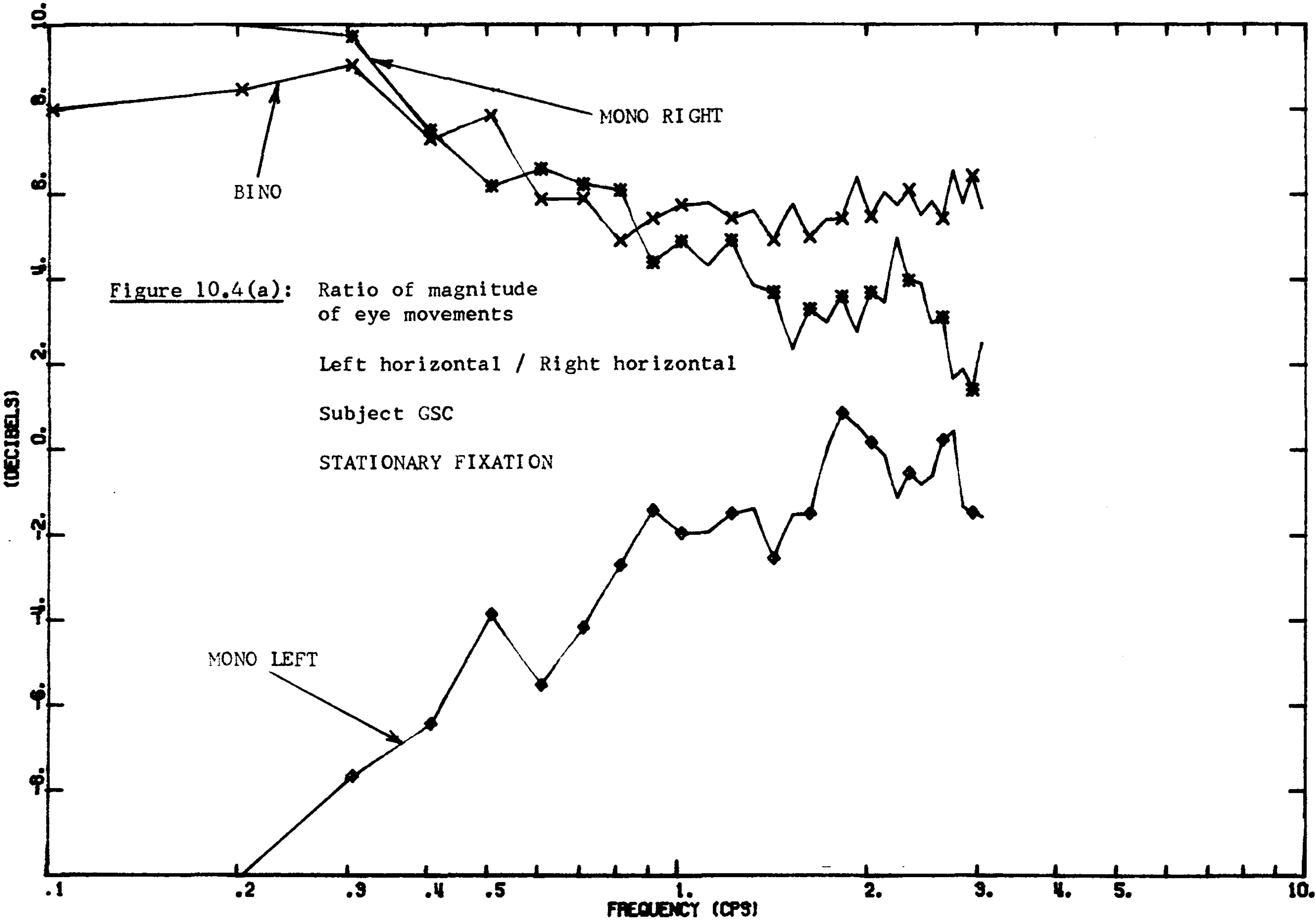
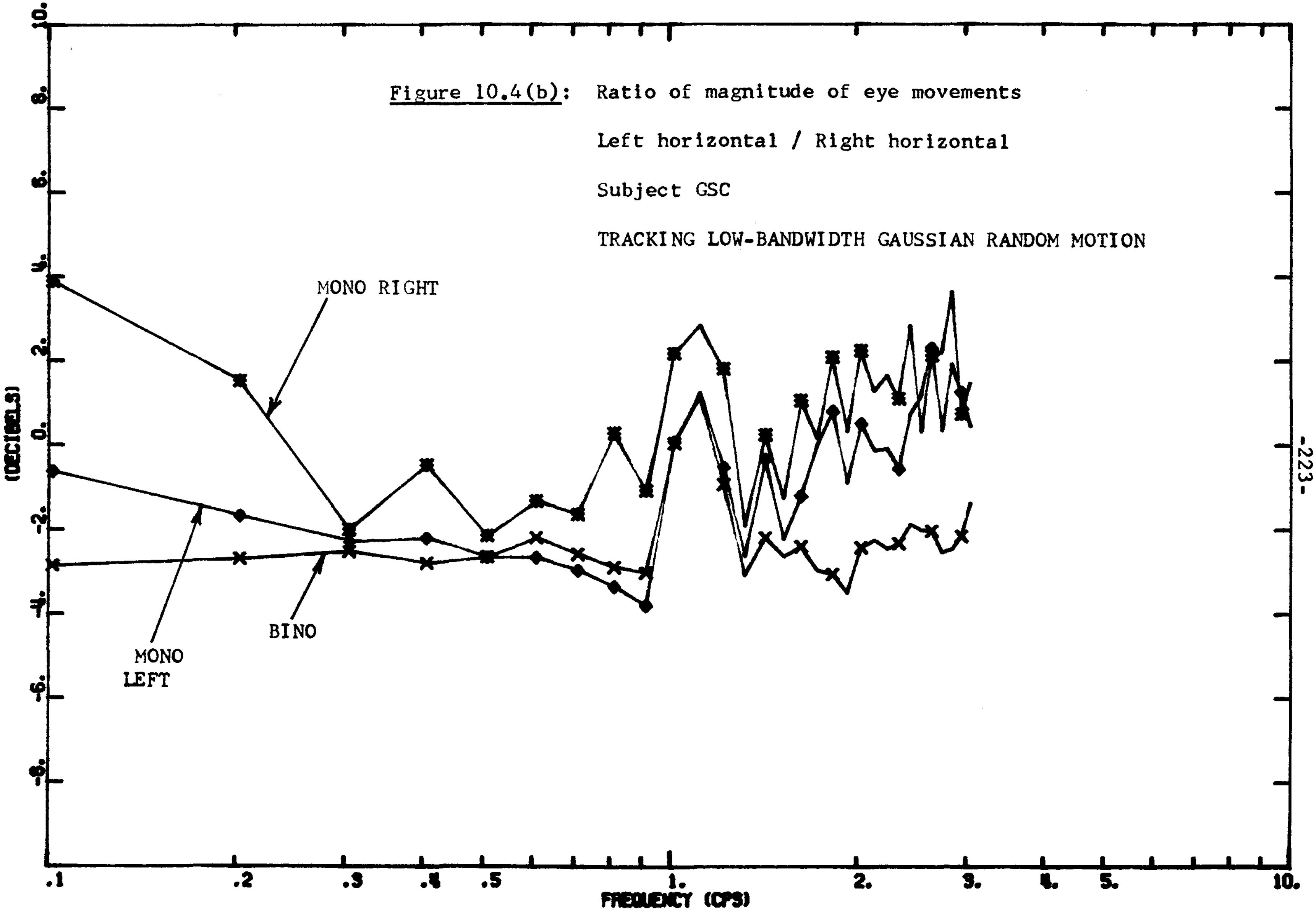


Figure 10.4(a): Ratio of magnitude of eye movements

Left horizontal / Right horizontal

Subject GSC

STATIONARY FIXATION



<u>Figure 10.4(b)</u>: Ratio of magnitude of eye movements

Left horizontal / Right horizontal

Subject GSC

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

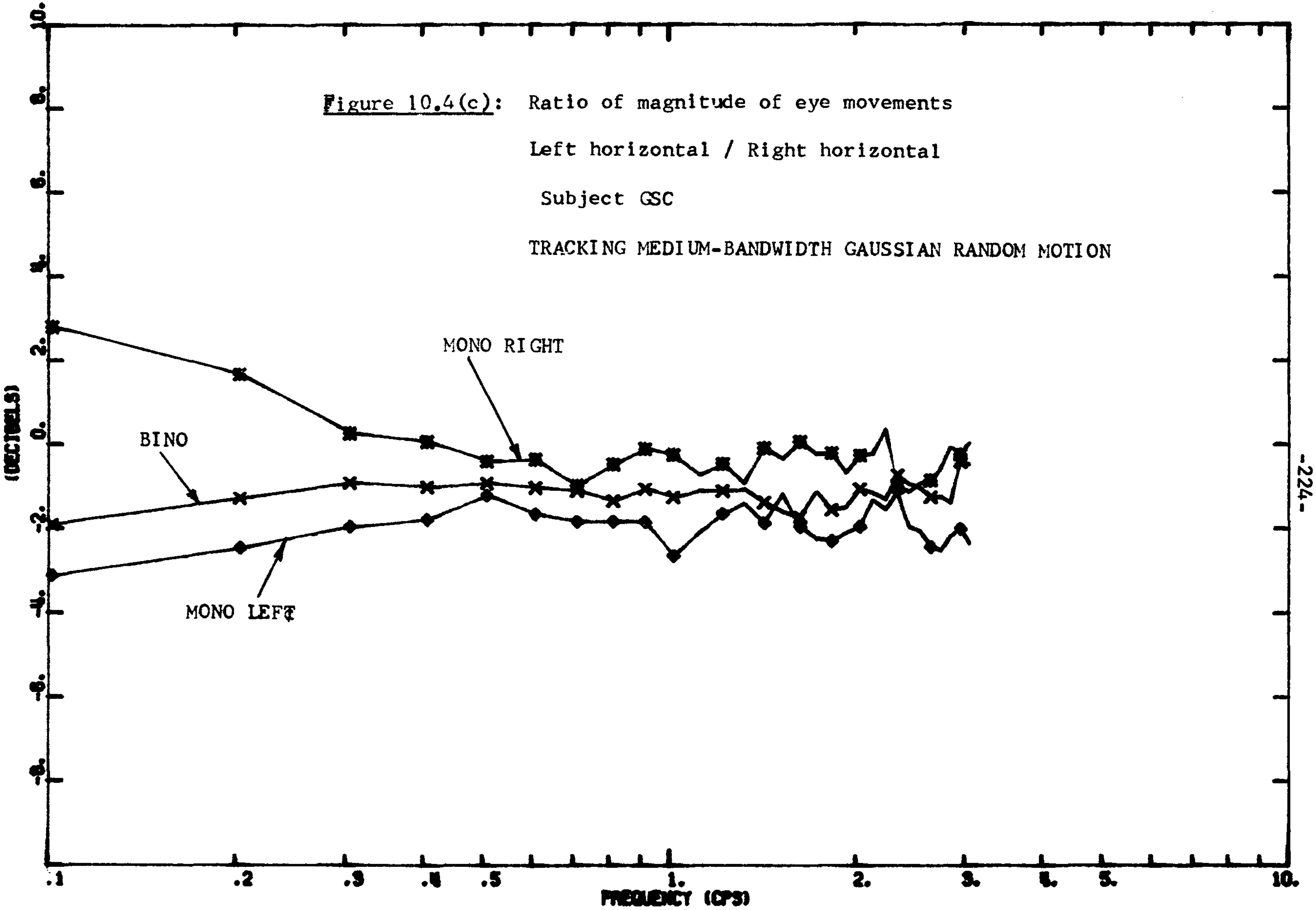


Figure 10.4(c): Ratio of magnitude of eye movements

Left horizontal / Right horizontal

Subject GSC

TRACKING MEDIUM-BANDWIDTH GAUSSIAN RANDOM MOTION

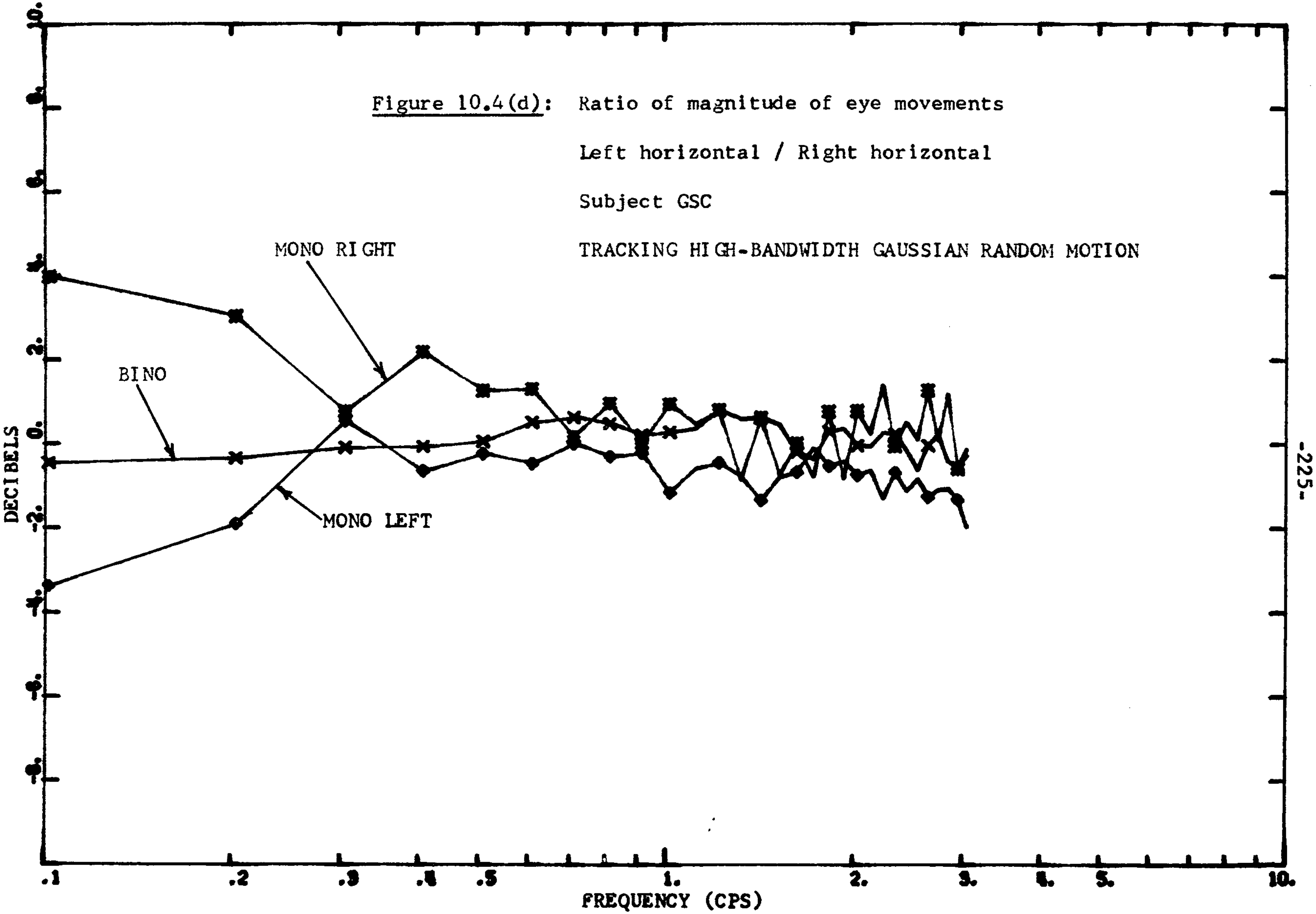


Figure 10.4(d): Ratio of magnitude of eye movements
Left horizontal / Right horizontal
Subject GSC
TRACKING HIGH-BANDWIDTH GAUSSIAN RANDOM MOTION

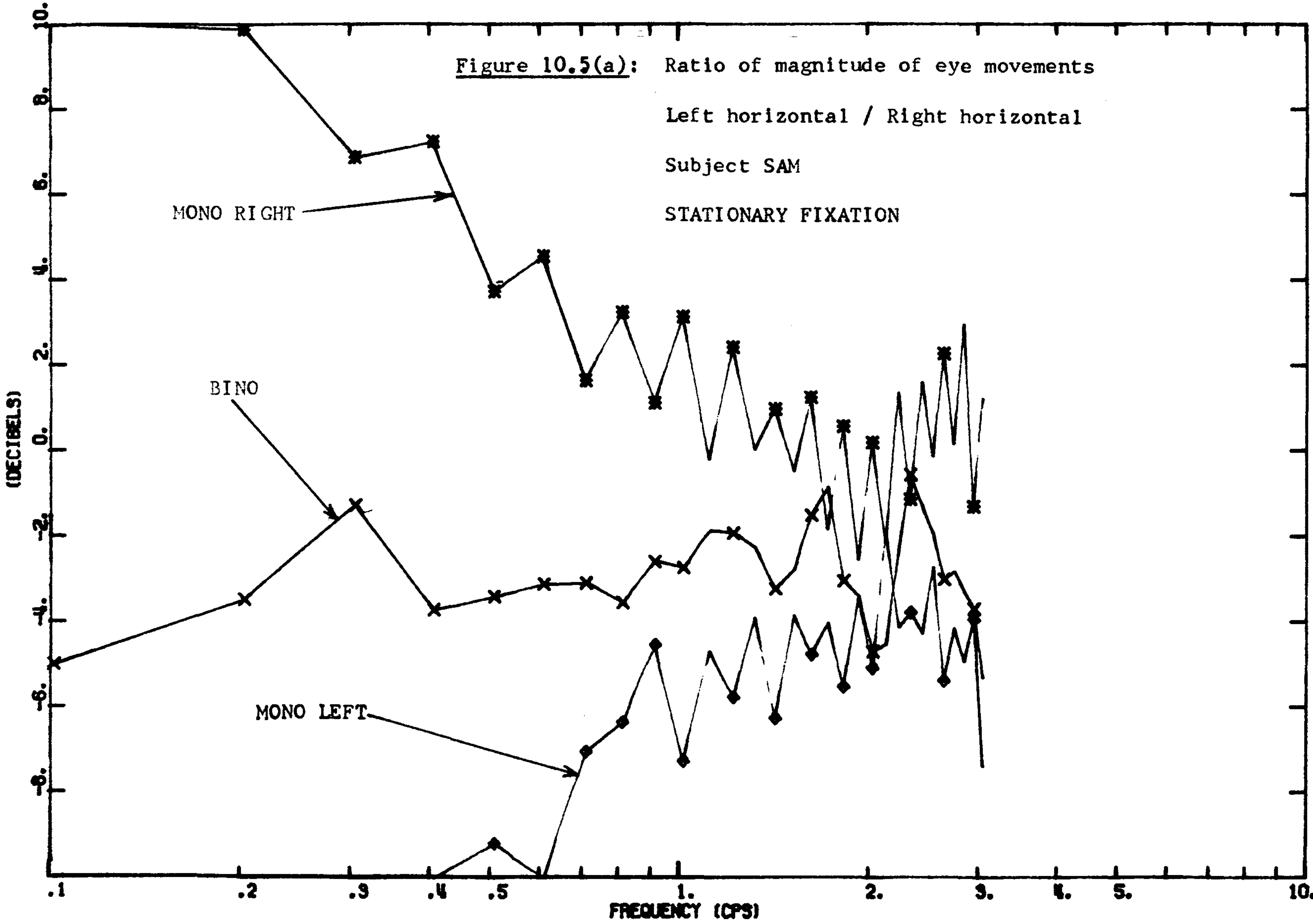


Figure 10.5(a): Ratio of magnitude of eye movements

Left horizontal / Right horizontal

Subject SAM

STATIONARY FIXATION

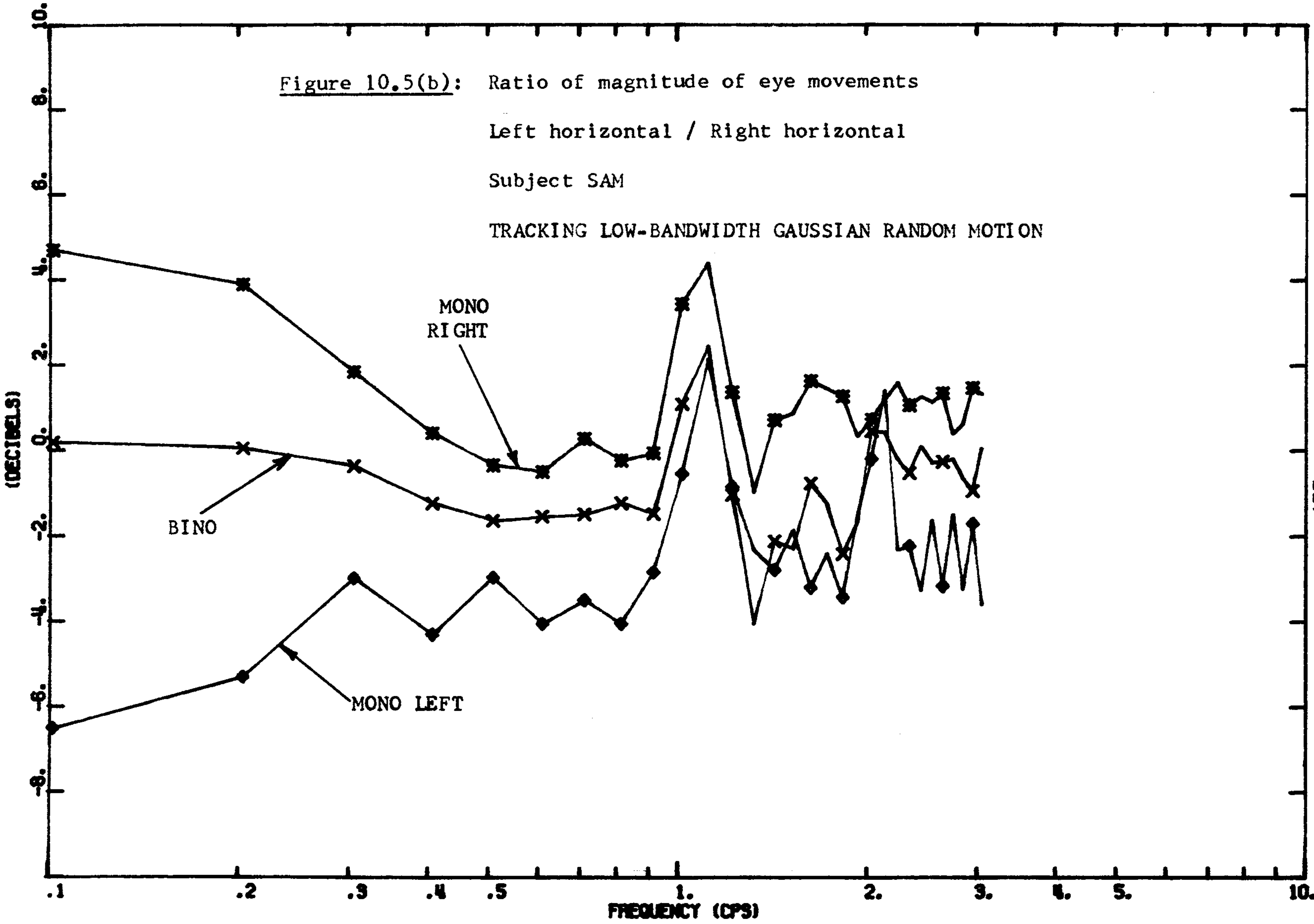


Figure 10.5(b): Ratio of magnitude of eye movements

Left horizontal / Right horizontal

Subject SAM

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

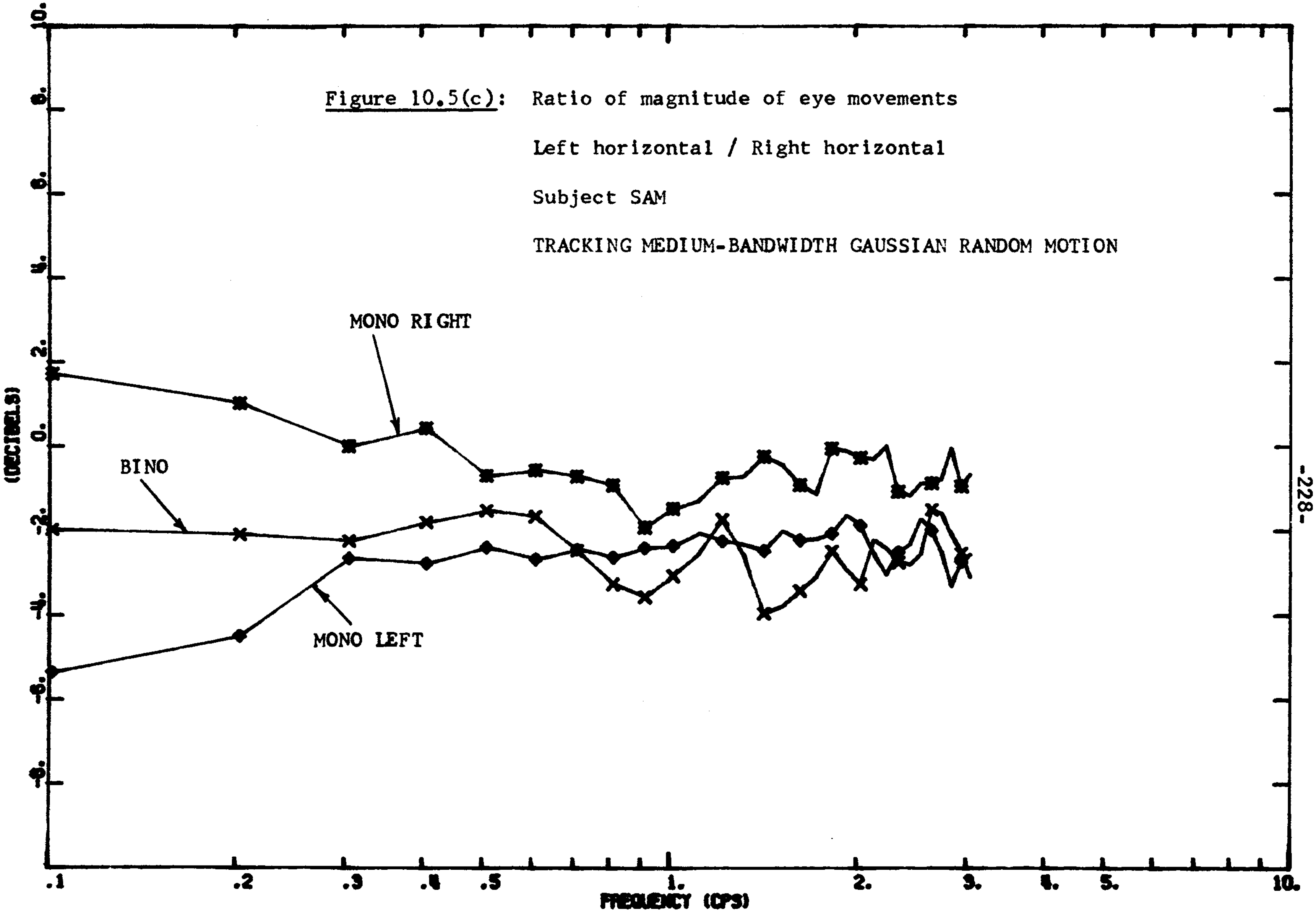


Figure 10.5(c): Ratio of magnitude of eye movements

Left horizontal / Right horizontal

Subject SAM

TRACKING MEDIUM-BANDWIDTH GAUSSIAN RANDOM MOTION

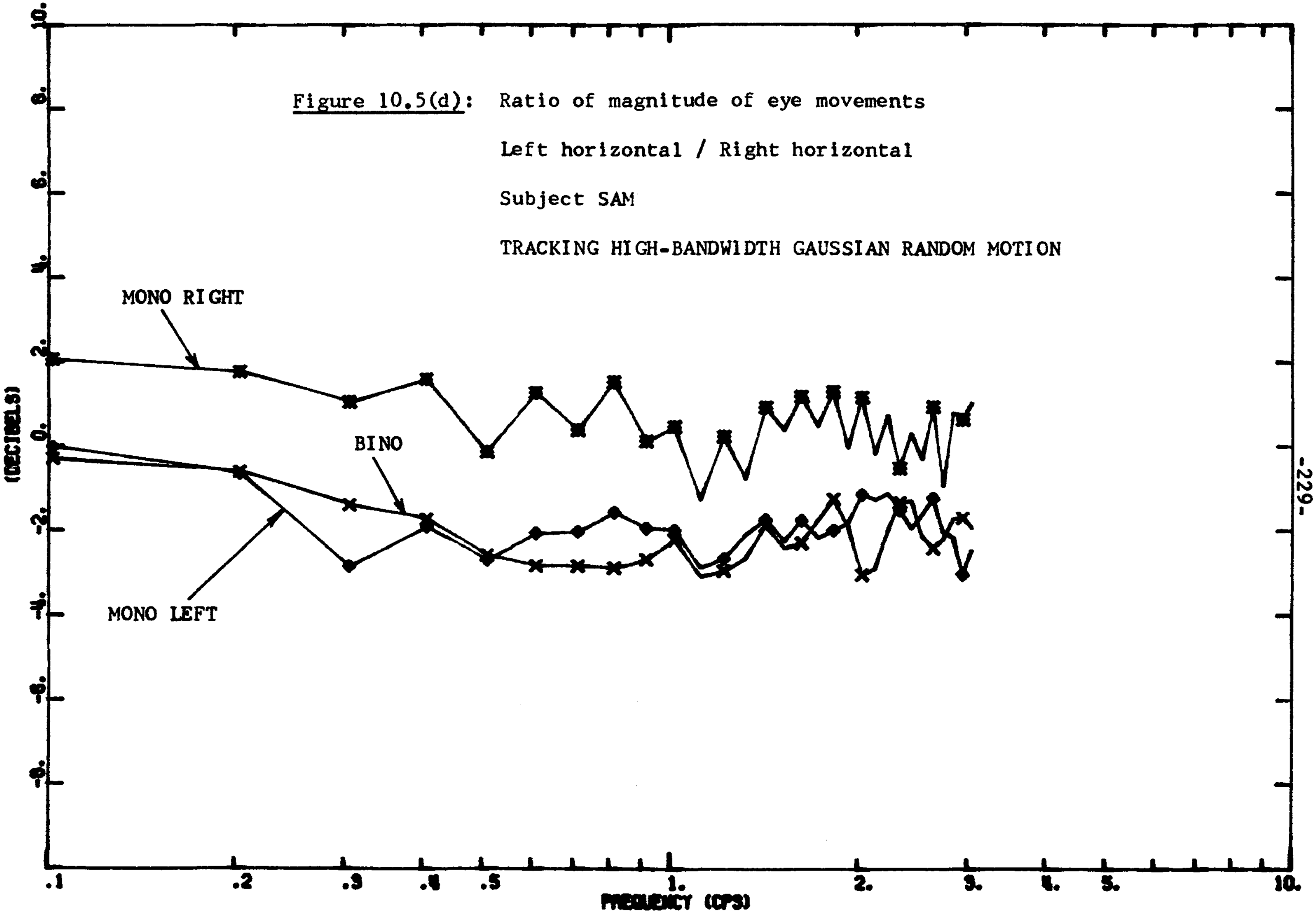


Figure 10.5(d): Ratio of magnitude of eye movements

Left horizontal / Right horizontal

Subject SAM

TRACKING HIGH-BANDWIDTH GAUSSIAN RANDOM MOTION

We can draw the same conclusions from these results for horizontal movements that we have drawn previously for vertical motions in section 2. 2; the evidence here is much more conclusive. Moreover, for all cases except for one out of eight, the curve for binocular fixation falls between those for monocular viewing. However, in contrast to vertical movements, horizontal motions of the two visual axes are not at all synchronous as we shall find in the following sections.

3. 2 Conjugate eye movements. As we have discussed in section 1 of this chapter, to describe the relative lead/lag of the visual axes in the horizontal direction by means of phase shifts is not particularly enlightening. Instead, we will define the combined left and right eye movements to be the sum of a conjugate and a vergent part, equally shared by motions of the two visual axes. In this section we will discuss the conjugate part, and in the next one, the vergent part. Finally, in section 3. 4, we will discuss the ratio between the two.

Figures 10. 6a through 10. 6d show the power spectra C(f) for conjugate eye movements for subject GSC; Figures 10. 7 are the corresponding diagrams for subject SAM. For the tracking tasks, Figures b, c, and d, the viewing condition has little effect on the power spectra of conjugate motion. The curves for monocular and binocular tracking are equal for all practical purposes. This is not the case for stationary fixation as exhibited by Figures a. For subject GSC, the power spectra for binocular viewing are considerably higher than those for monocular; precisely the opposite is true for subject SAM. On the other hand, for SAM, the curves for monocular and binocular

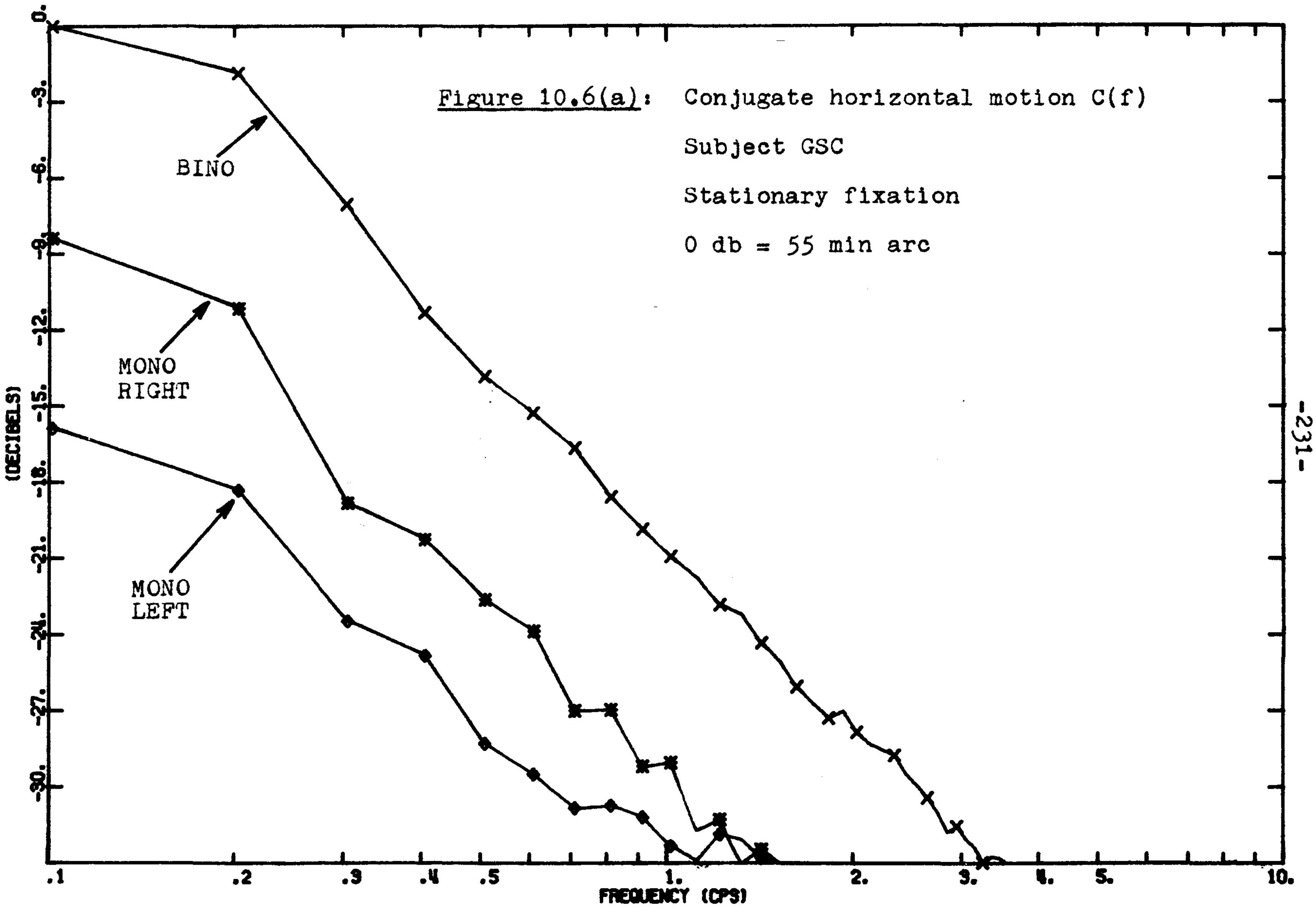


Figure 10.6(a): Conjugate horizontal motion C(f)

Subject GSC

Stationary fixation

0 db = 55 min arc

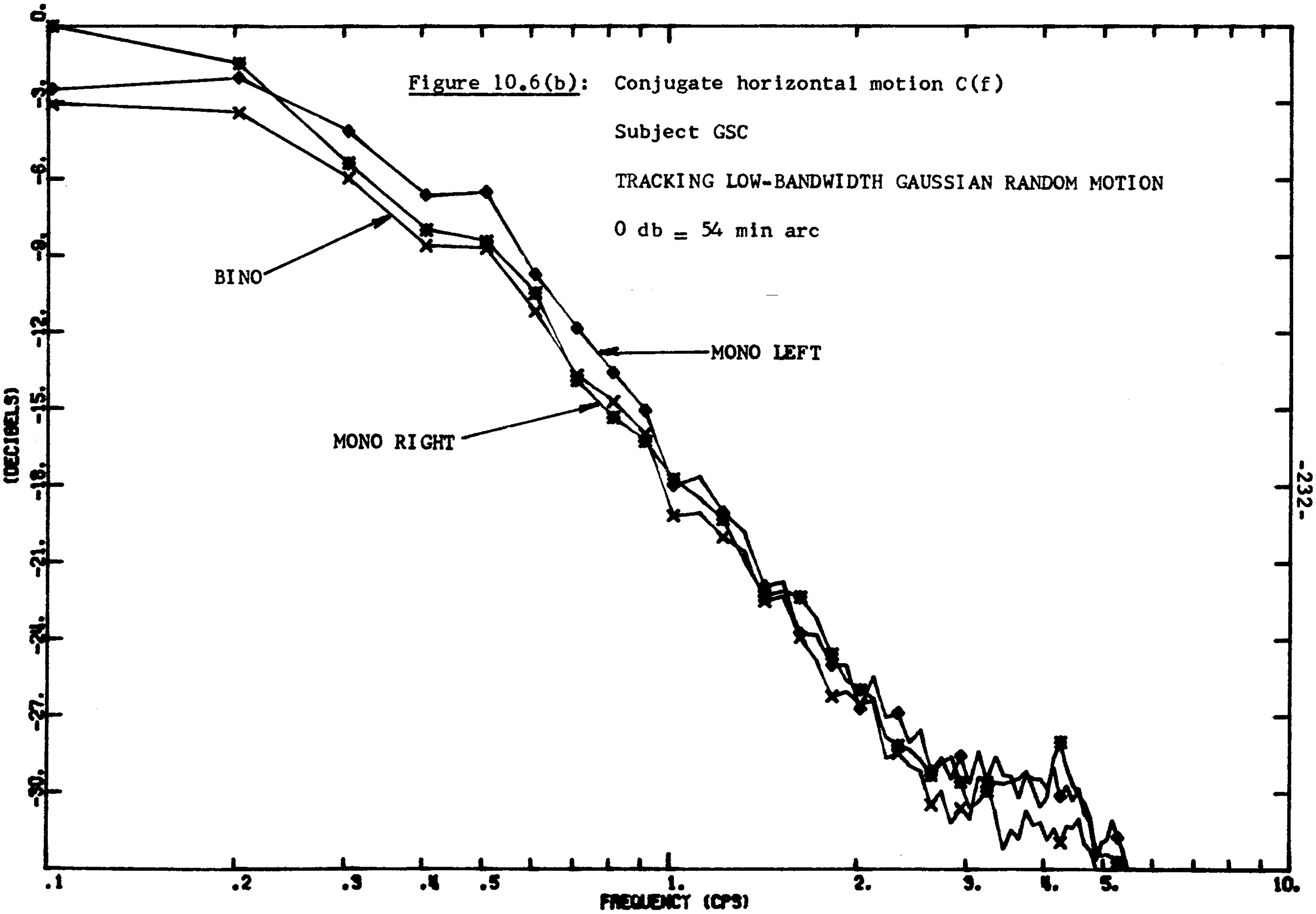


Figure 10.6(b): Conjugate horizontal motion C(f)

Subject GSC

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 54 min arc

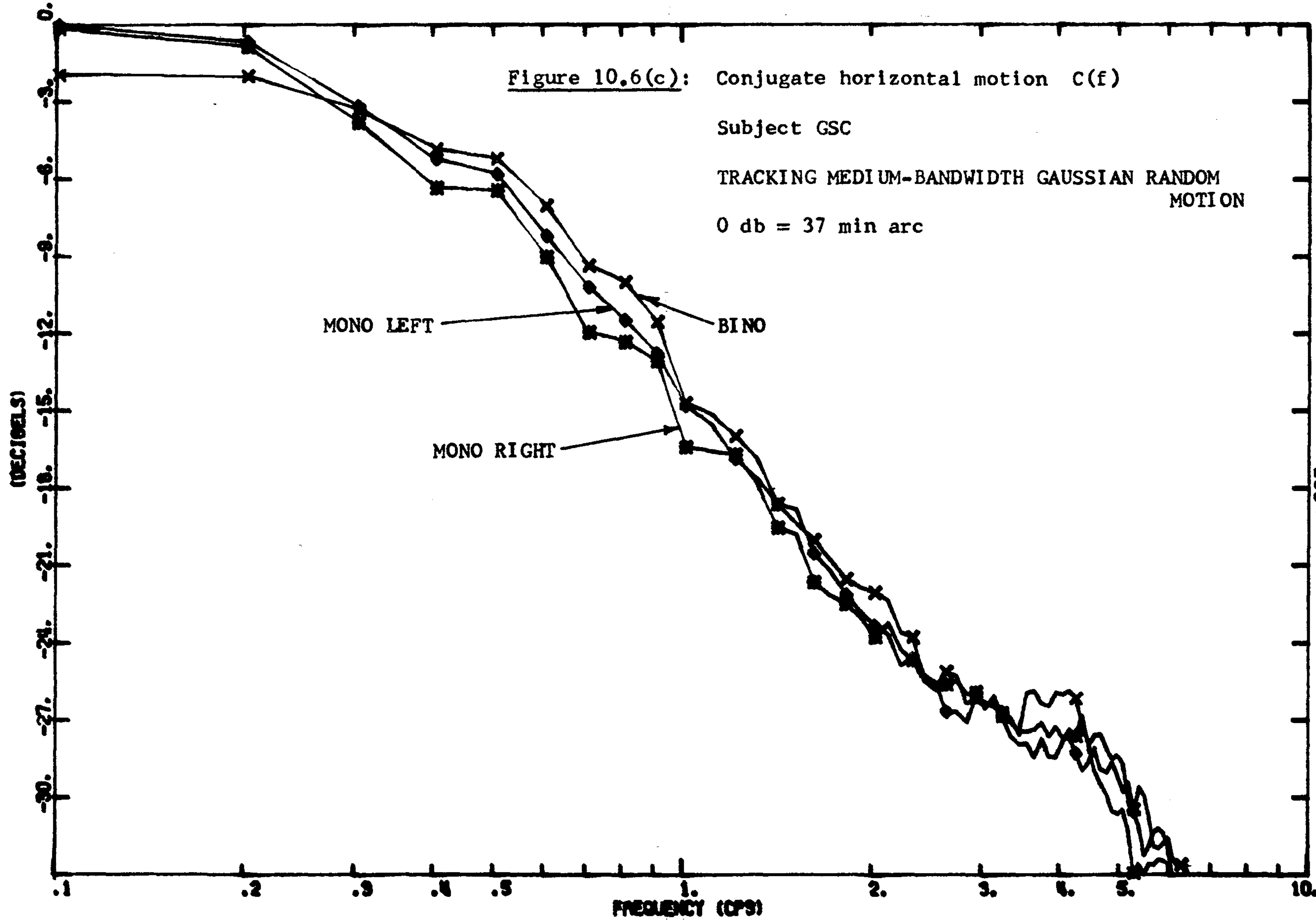


Figure 10.6(c): Conjugate horizontal motion C(f)

Subject GSC

TRACKING MEDIUM-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 37 min arc

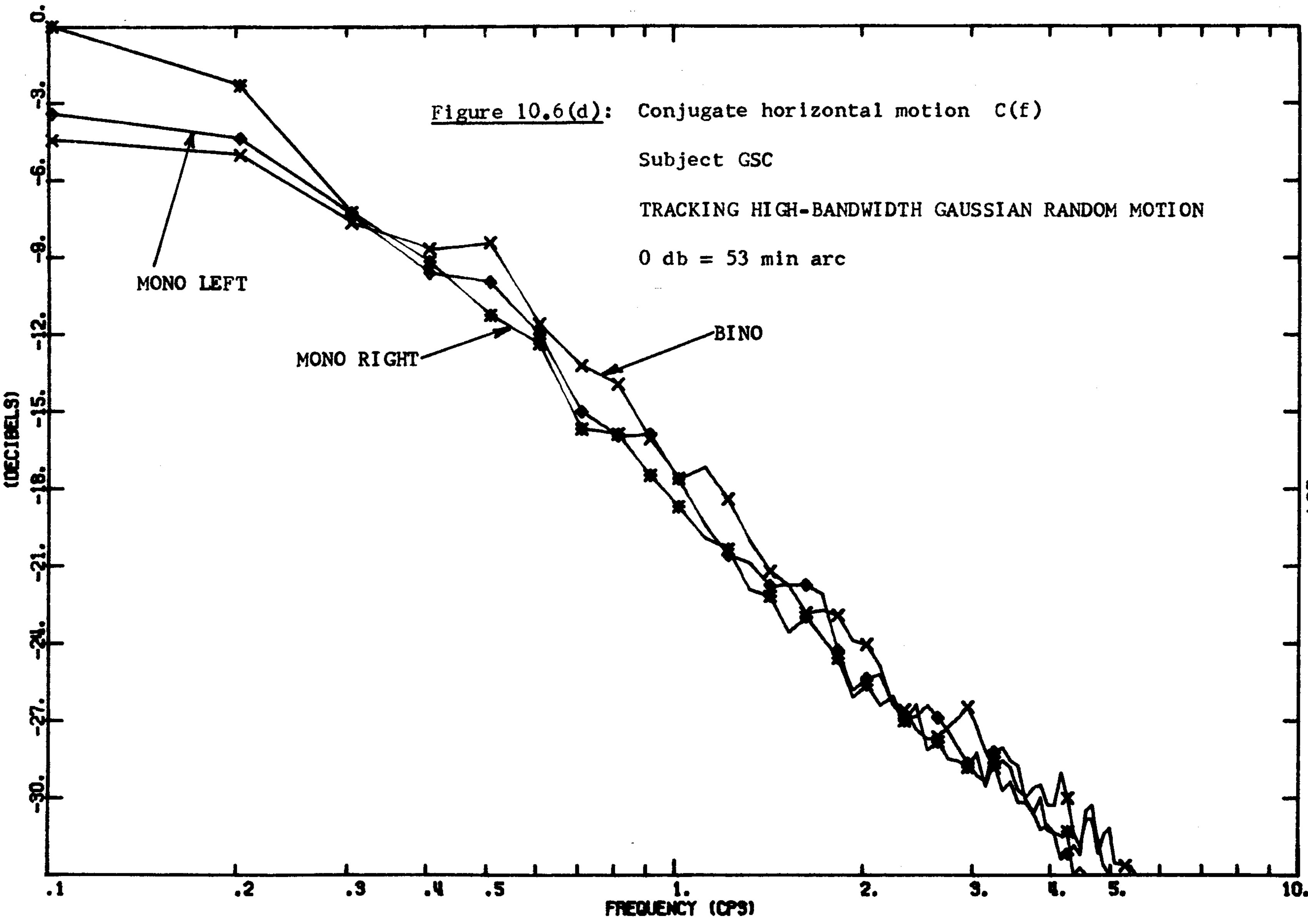


Figure 10.6(d): Conjugate horizontal motion C(f)

Subject GSC

TRACKING HIGH-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 53 min arc

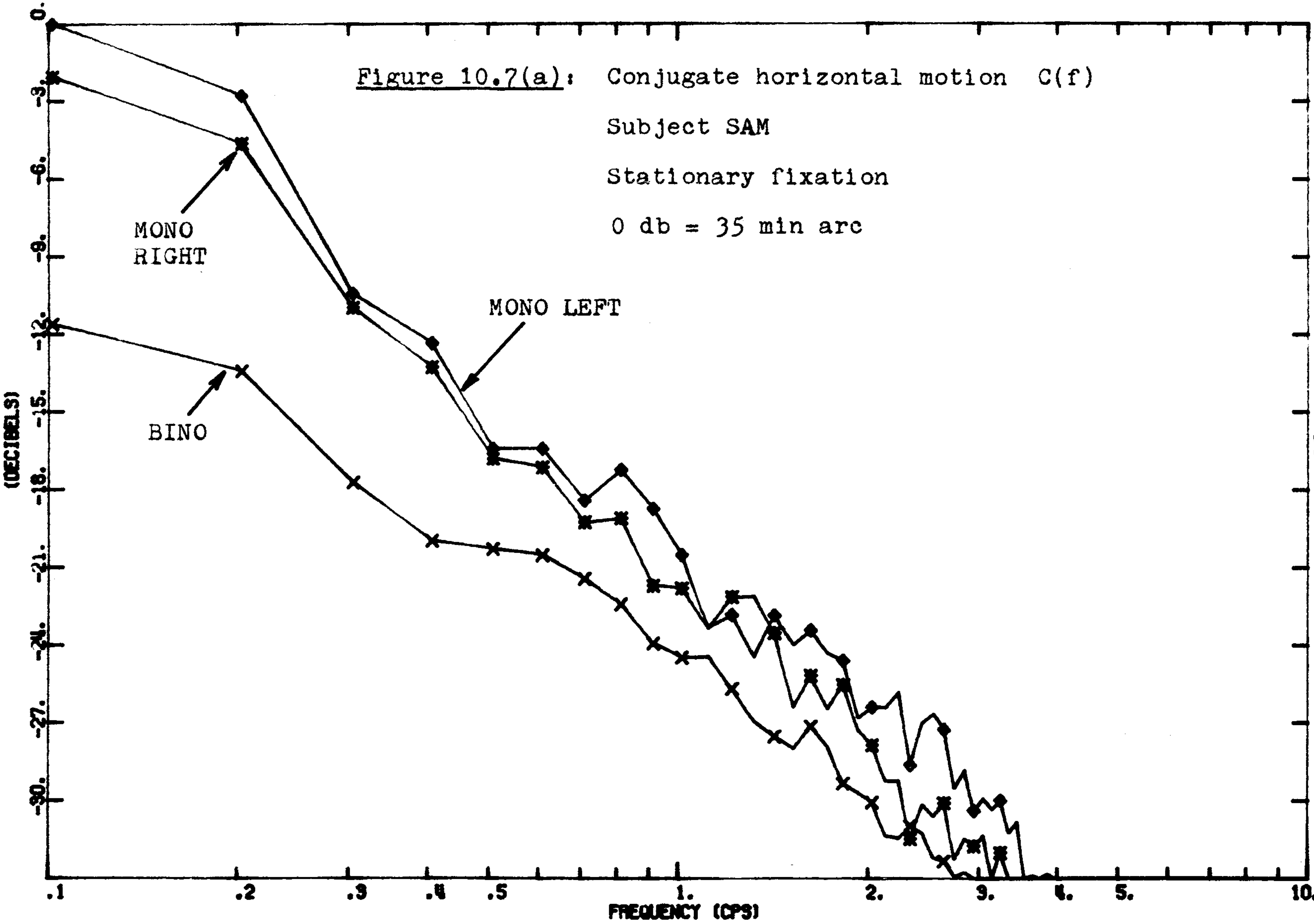


Figure 10.7(a): Conjugate horizontal motion C(f)

Subject SAM

Stationary fixation

0 db = 35 min arc

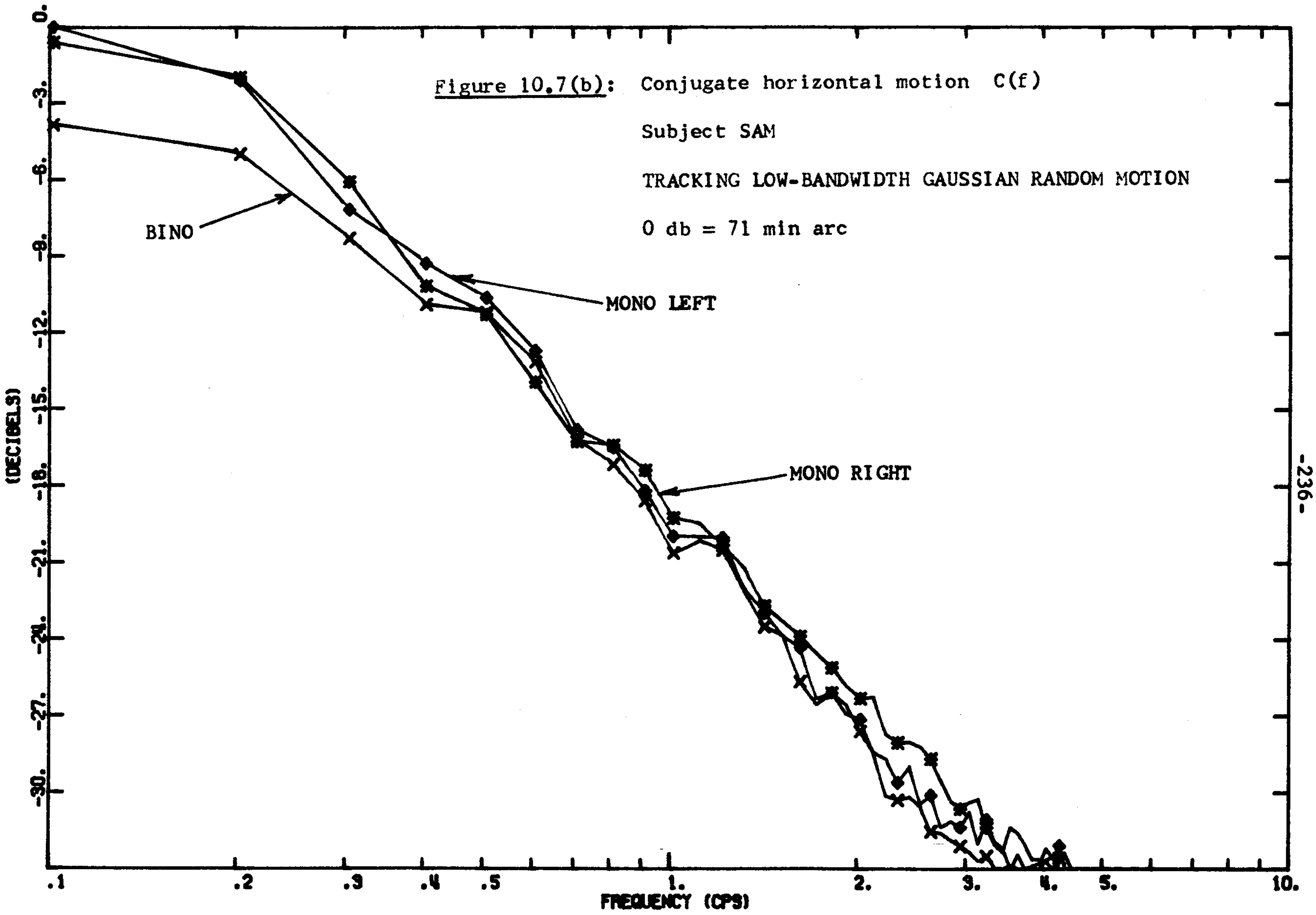


Figure 10.7(b): Conjugate horizontal motion C(f)

Subject SAM

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 71 min arc

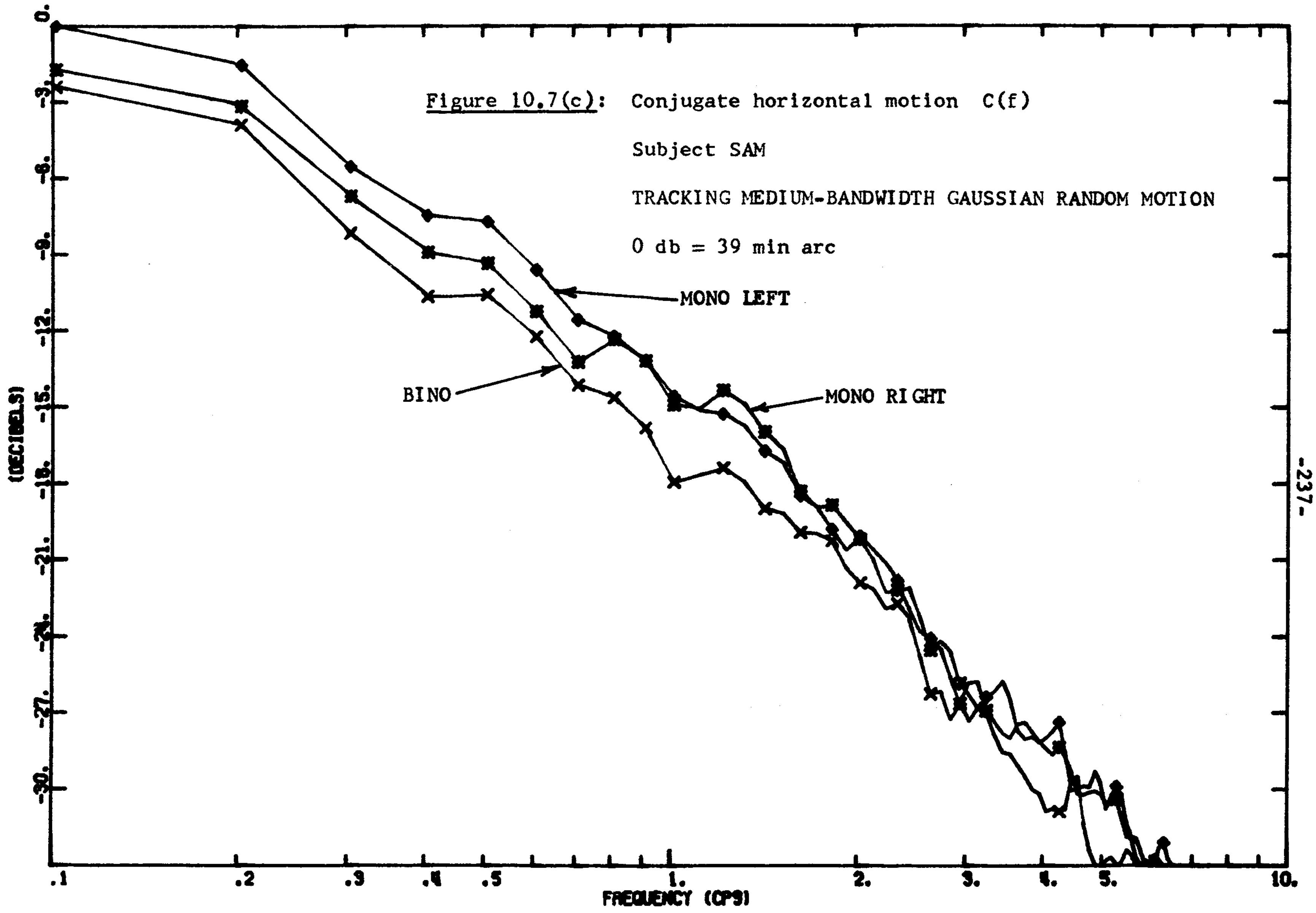


Figure 10.7(c): Conjugate horizontal motion C(f)

Subject SAM

TRACKING MEDIUM-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 39 min arc

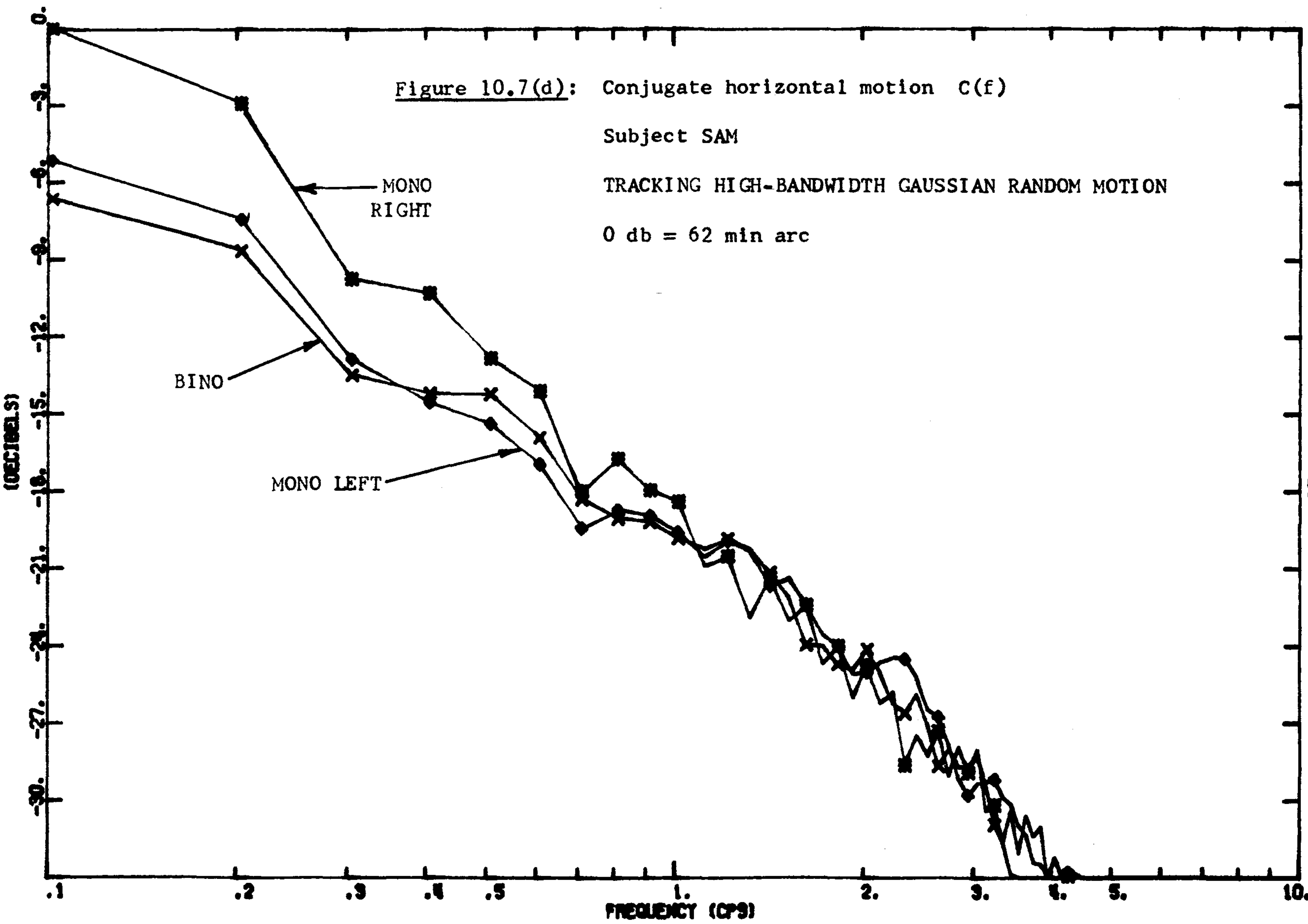


Figure 10.7(d): Conjugate horizontal motion C(f)

Subject SAM

TRACKING HIGH-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 62 min arc

viewing become nearly equal at frequencies above 1 cps, while for subject GSC, the 9-db difference is constant throughout the bandwidth of the system.

It is perhaps not surprising that conjugate motion should be relatively independent of viewing condition for tracking tasks. However, we shall reserve further comments until we have examined the out-of-phase component of horizontal motion, what we shall call "vergence."

3.3 Vergence. There is no stimulus for vergence movements in any of these experiments. In all cases, the target is located at a constant distance from the subject and is viewed directly. Hence, there is no stimulus for accommodation and none for fusional vergence. Therefore, the quantity which we describe in this section and call vergence may be interpreted in two ways. First, it may be regarded as the output of some "vergence control center" as noise superimposed on the conjugate motion. Alternatively, it may be viewed simply as a mathematical consequence of the fact that horizontal motions of the left and right visual axes are unequal and unsynchronized. There is no logical way of distinguishing between these two interpretations; we can only correlate this information with other known facts about the oculomotor system and appeal to intuition. This question will be taken up again in the Discussion section.

Figures 10.8 and 10.9 show the vergence power spectra for subjects GSC and SAM, respectively. In 7 out of 8 cases, the curve corresponding to binocular viewing is lower than those for monocular, particularly at low frequencies. The sole exception is for subject

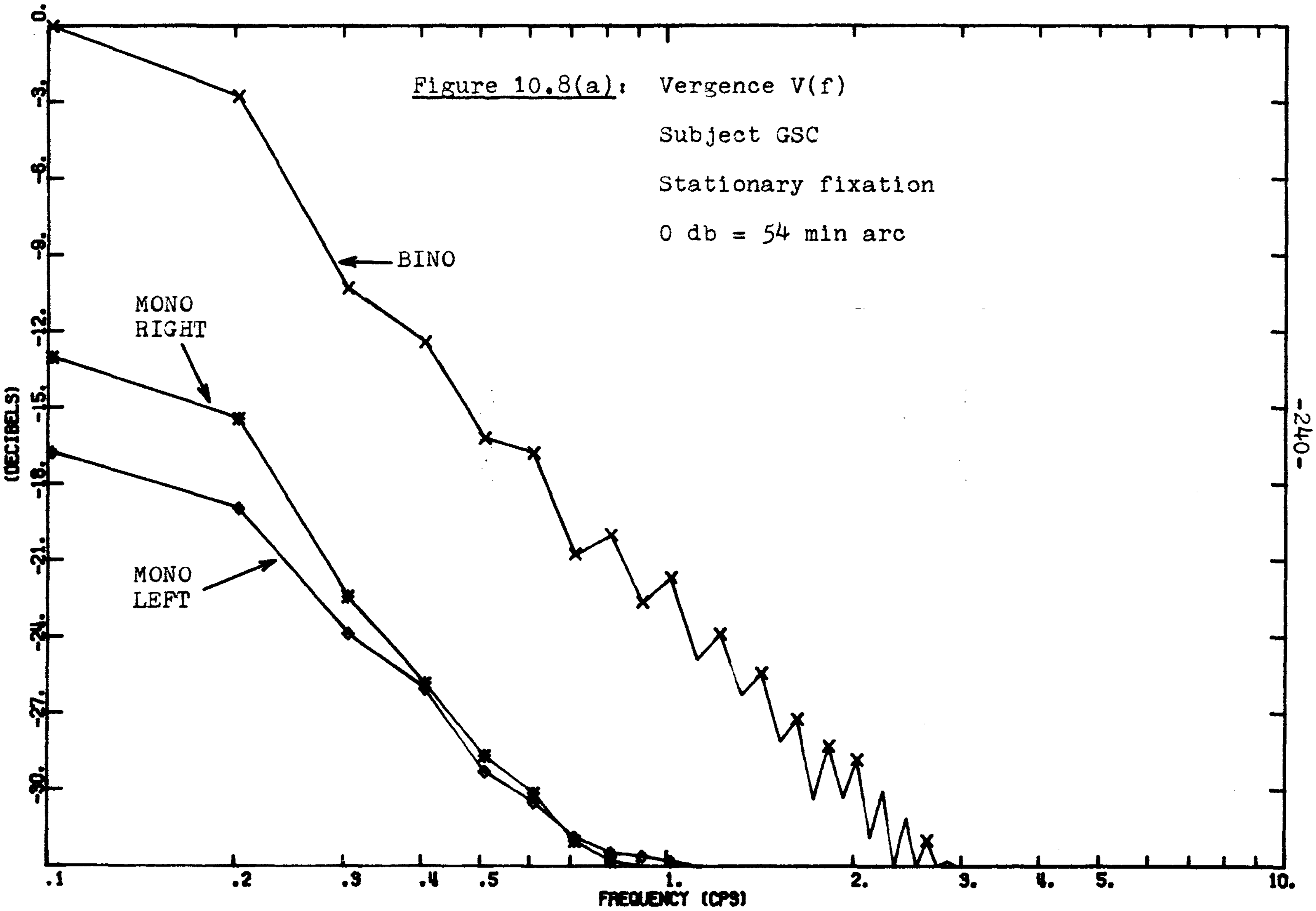


Figure 10.8(a): Vergence V(f)

Subject GSC

Stationary fixation

0 db = 54 min arc

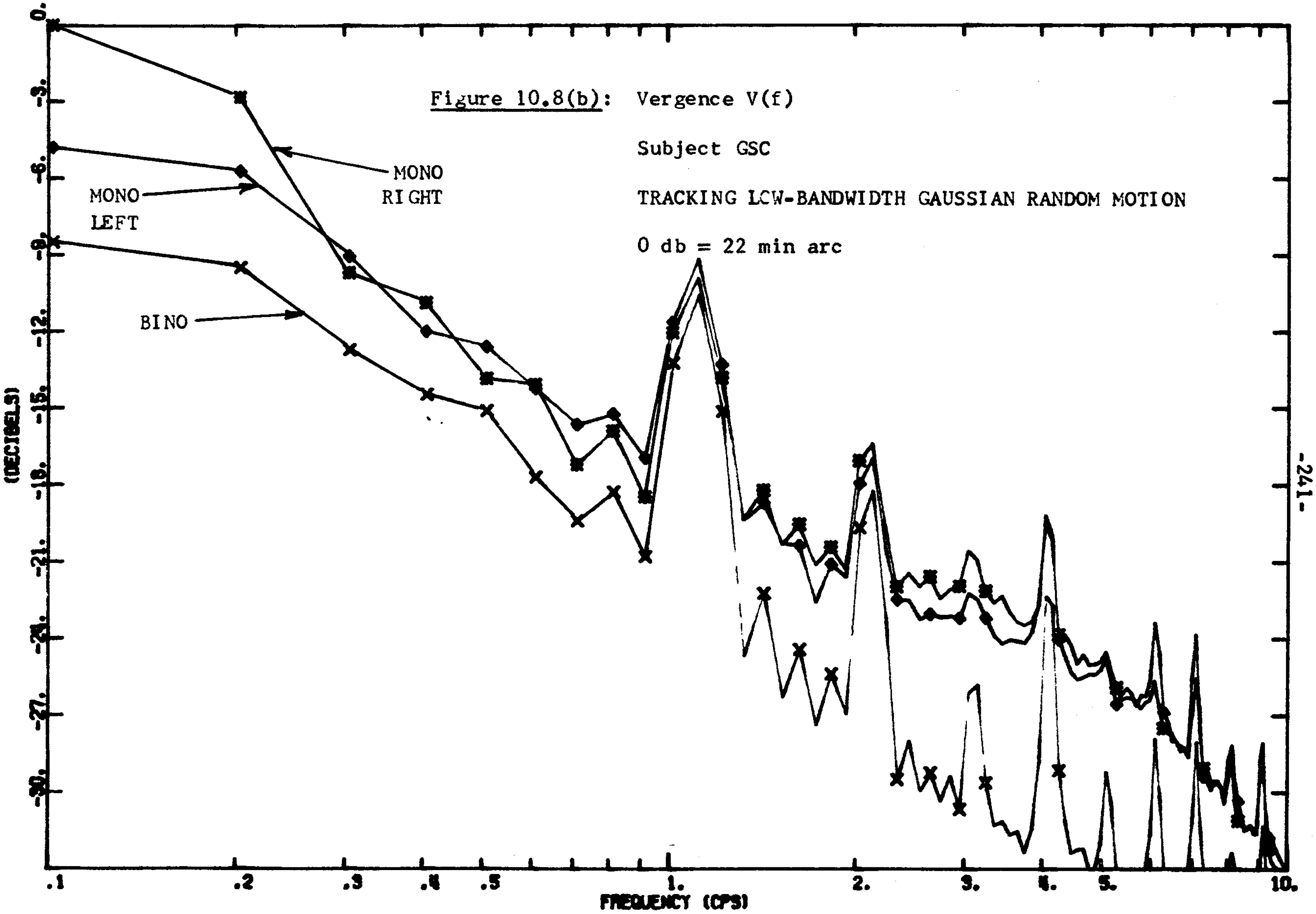


Figure 10.8(b): Vergence V(f)

Subject GSC

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 22 min arc

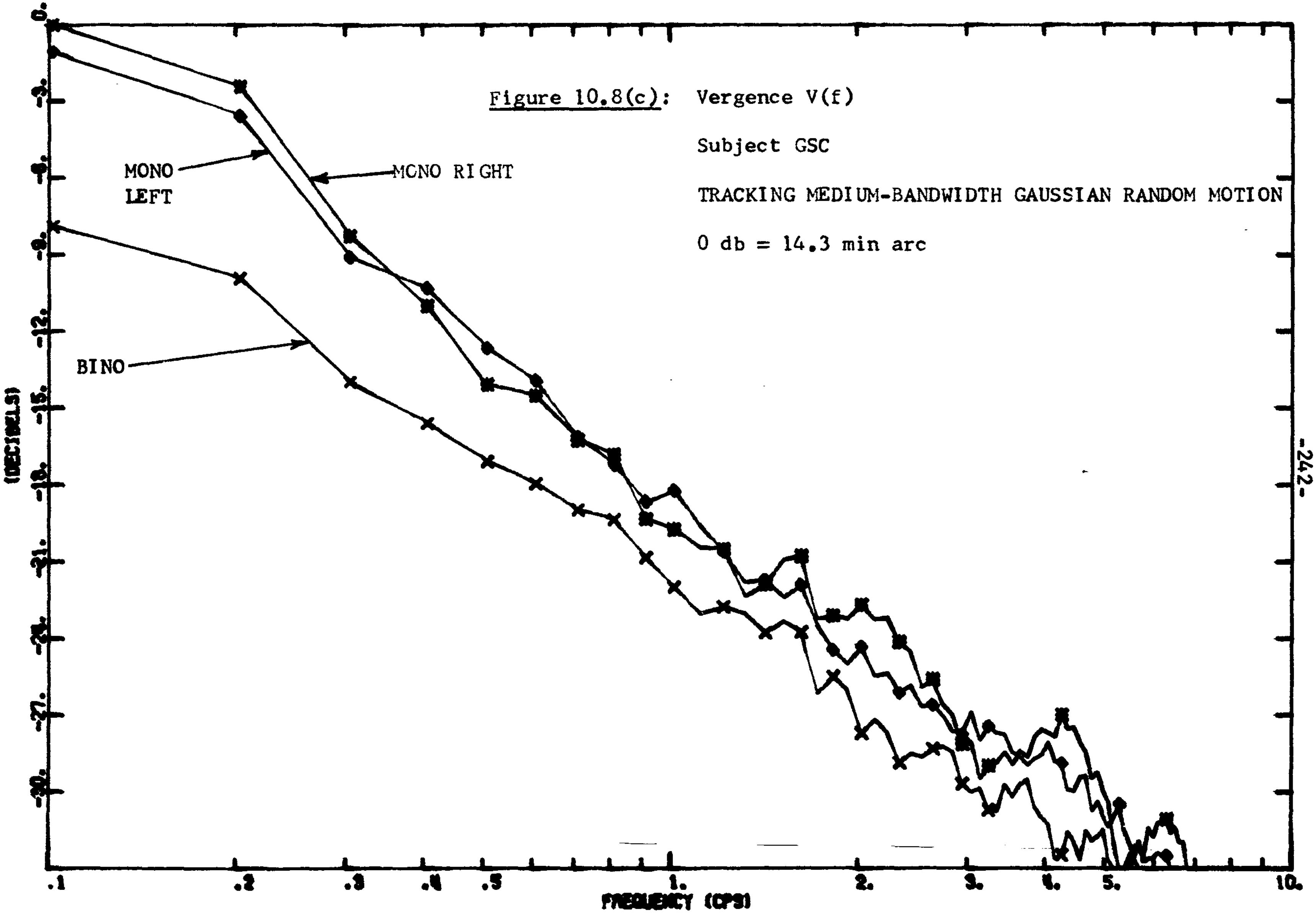


Figure 10.8(c): Vergence V(f)

Subject GSC

TRACKING MEDIUM-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 14.3 min arc

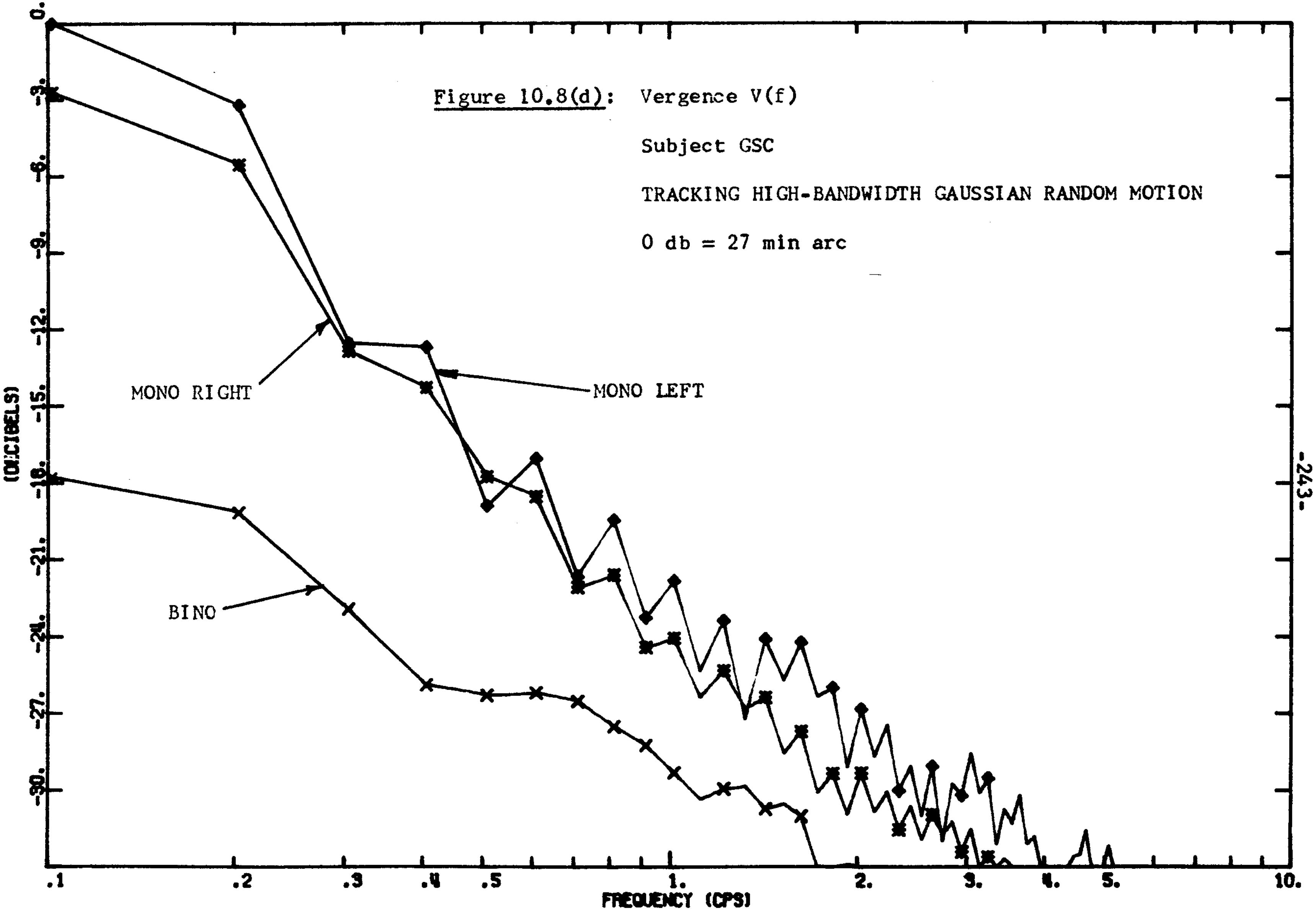


Figure 10.8(d): Vergence V(f)

Subject GSC

TRACKING HIGH-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 27 min arc

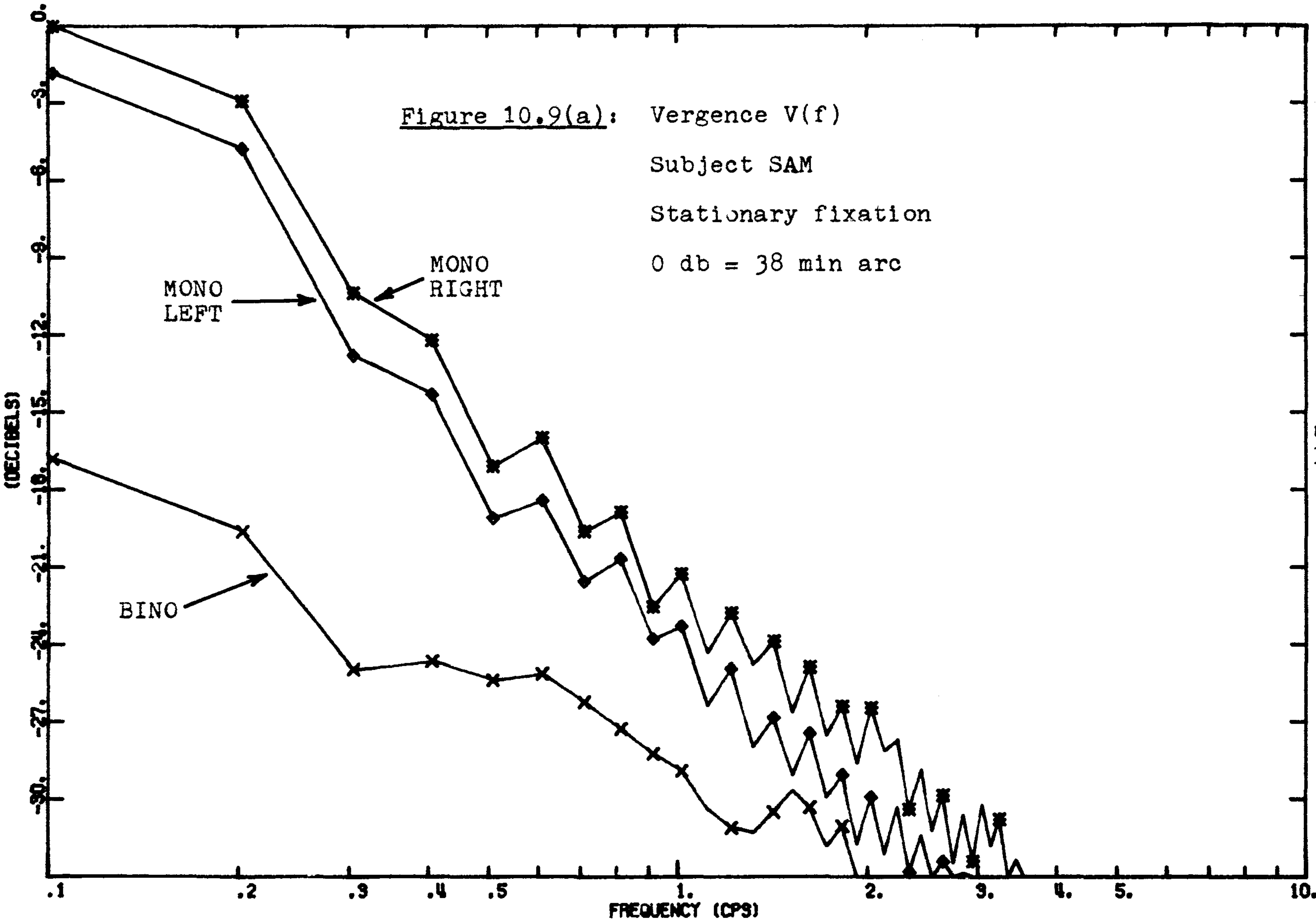
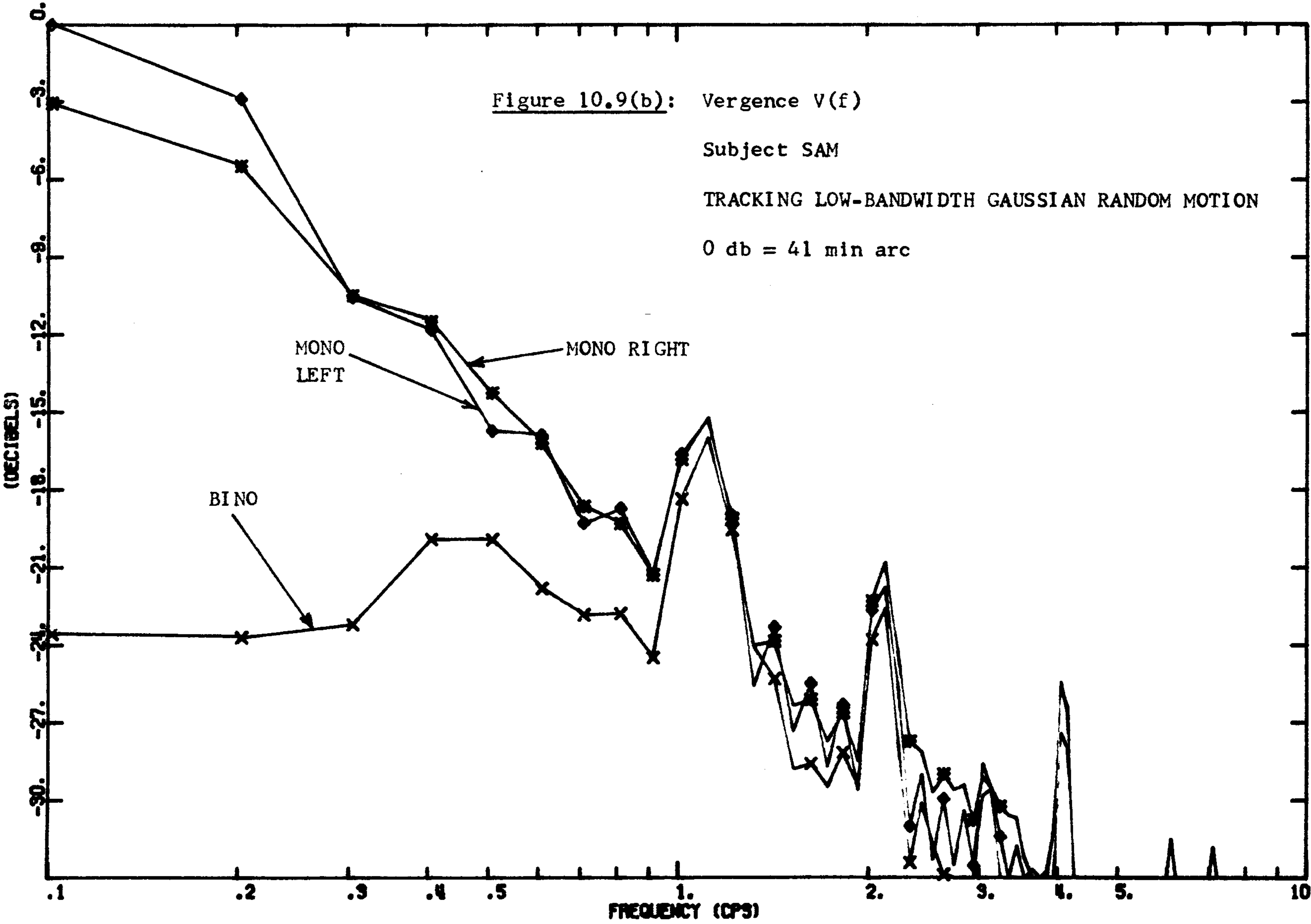


Figure 10.9(a): Vergence V(f)

Subject SAM

Stationary fixation

0 db = 38 min arc



<u>Figure 10.9(b)</u>: Vergence V(f)

Subject SAM

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 41 min arc

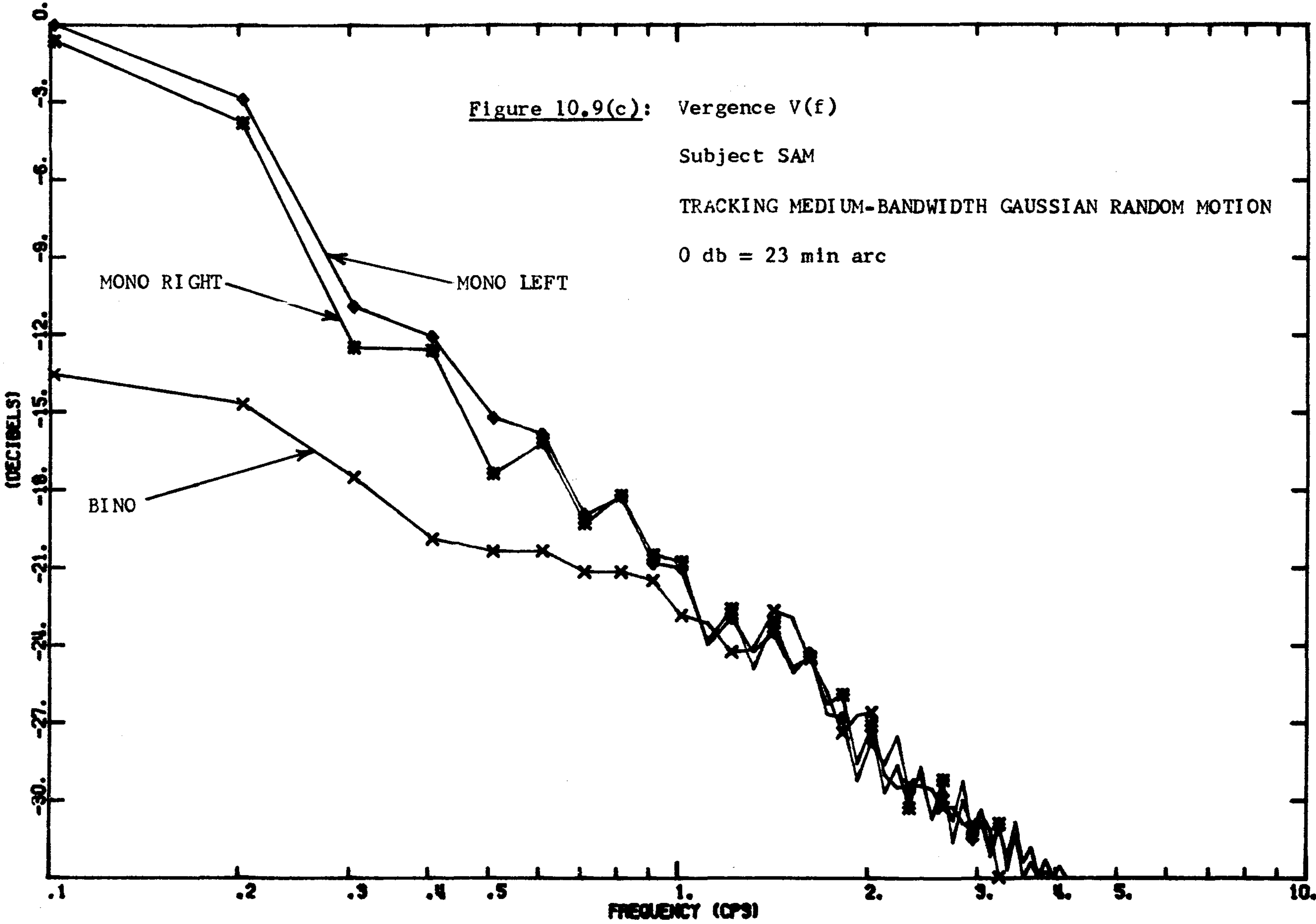


Figure 10.9(c): Vergence V(f)

Subject SAM

TRACKING MEDIUM-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 23 min arc

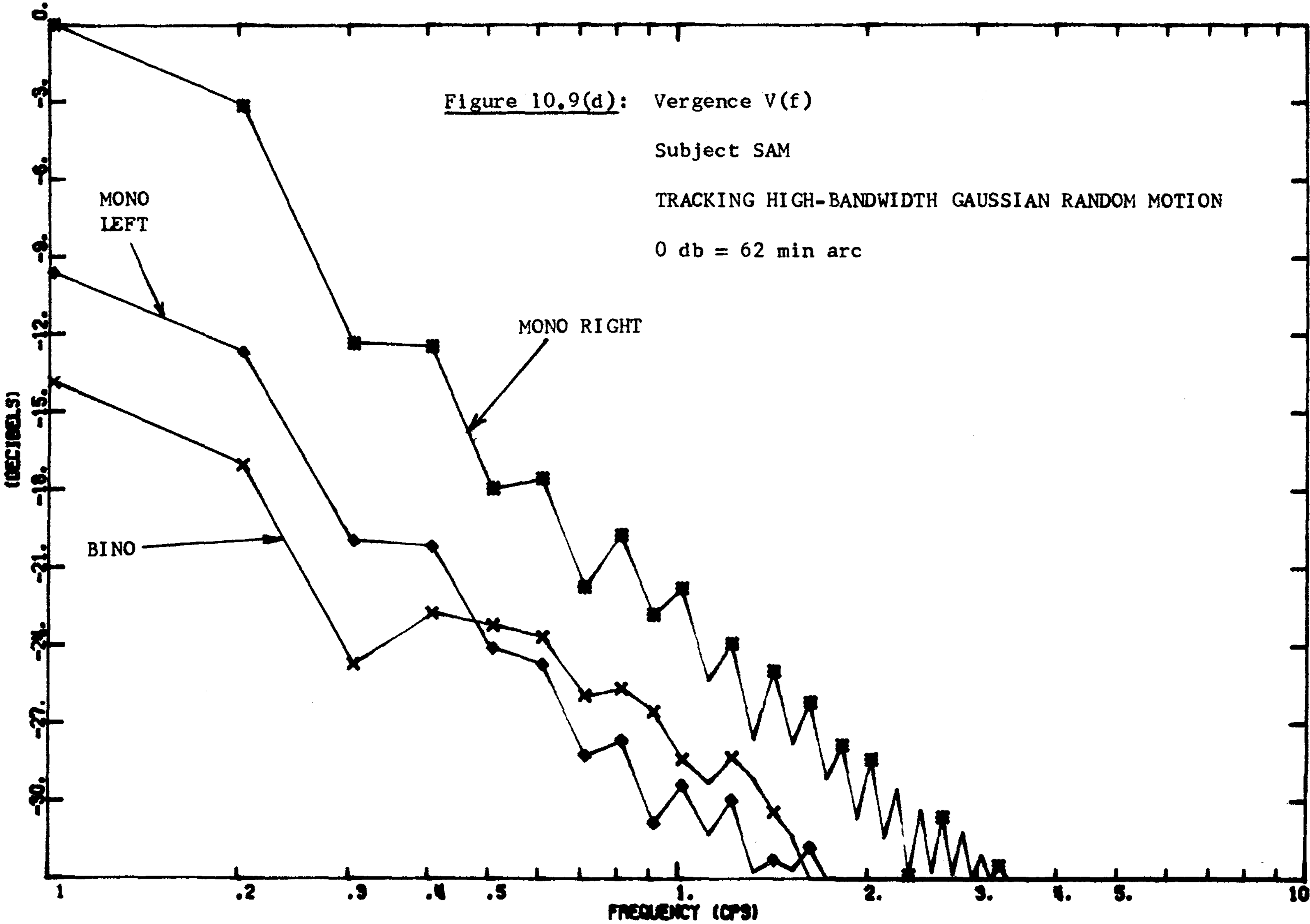


Figure 10.9(d): Vergence V(f)

Subject SAM

TRACKING HIGH-BANDWIDTH GAUSSIAN RANDOM MOTION

0 db = 62 min arc

GSC, stationary fixation, where just the opposite holds true. In all 7 cases where the binocular curve is lower than the others, the difference decreases with increasing frequency and disappears by about 1 - 2 cps. For GSC stationary fixation where the binocular curve is higher, the difference remains constant at about 12 db throughout the whole bandwidth. Referring to section 3. 2 above, the corresponding conjugate motion power spectra also exhibited a constant difference between the binocular and the monocular curves. In short, for subject GSC, both the conjugate and the vergent components are larger for binocular stationary fixation, while for subject SAM, both components are smaller for binocular viewing. Moreover, comparison of Figures 10. 6 with 10. 8 and Figures 10. 7 with 10. 9 shows that the fall-off with frequency is comparable for corresponding conjugate and vergence power spectra. Therefore, while conjugate and vergent power spectra are of interest, their ratio is the most meaningful quantity.

3. 4 Ratio of vergence/conjugate motions. Figures 10. 10 and 10. 11 show the ratios of vergence/conjugate components of horizontal eye movements for subjects GSC and SAM, respectively. The graphs may be considered valid up to about 2 - 3 cps, beyond which the components of motions are so small that their ratio is meaningless. Disregarding the artifact in Figures b, there are no peaks in relative vergence power. There is, however, a minimum for the tracking tasks. This is particularly apparent for subject GSC, where, for all three viewing conditions, there is a broad minimum in relative vergence power at about 0. 5 cps. For SAM, the minima are

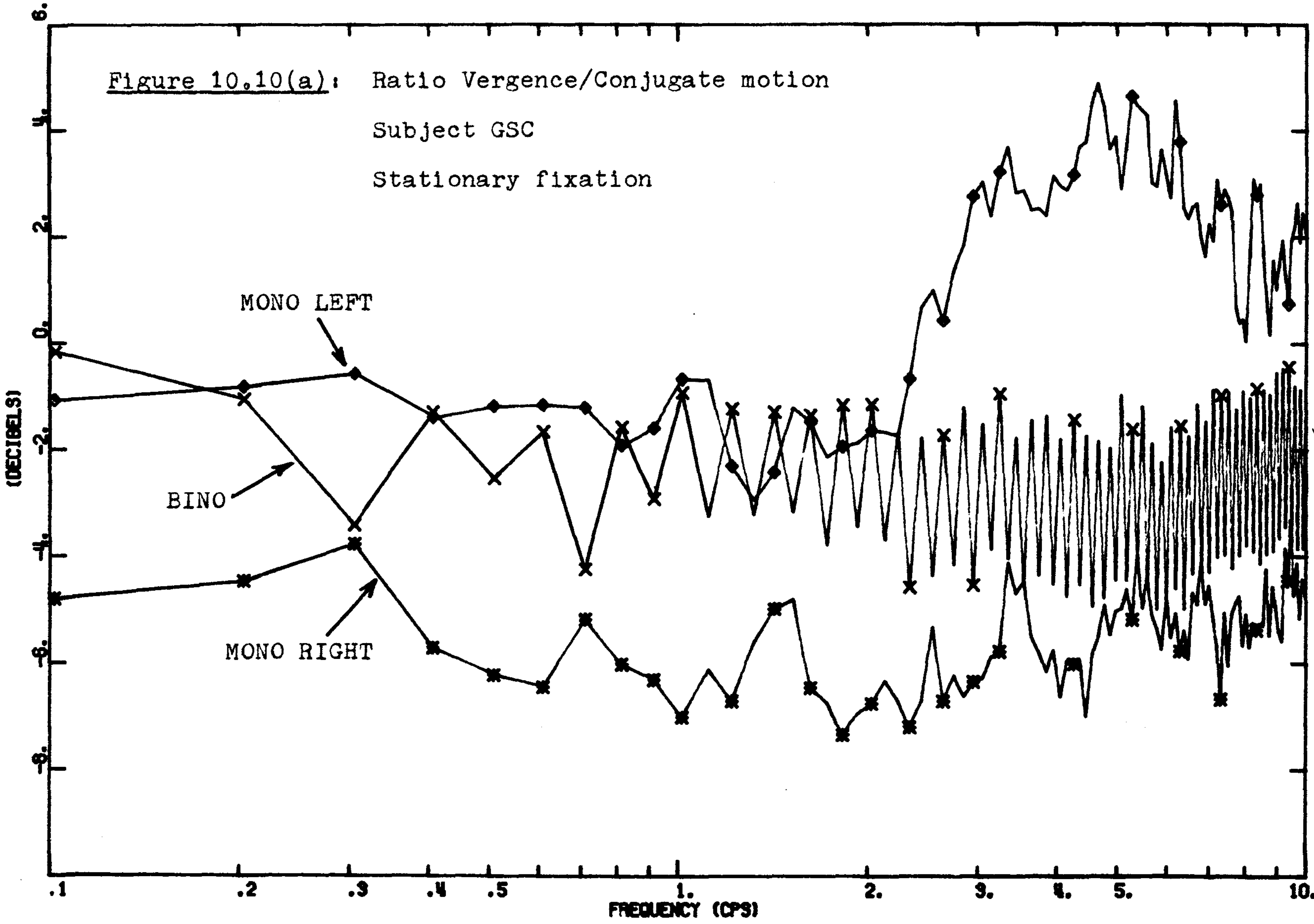


Figure 10.10(a): Ratio Vergence/Conjugate motion

Subject GSC

Stationary fixation

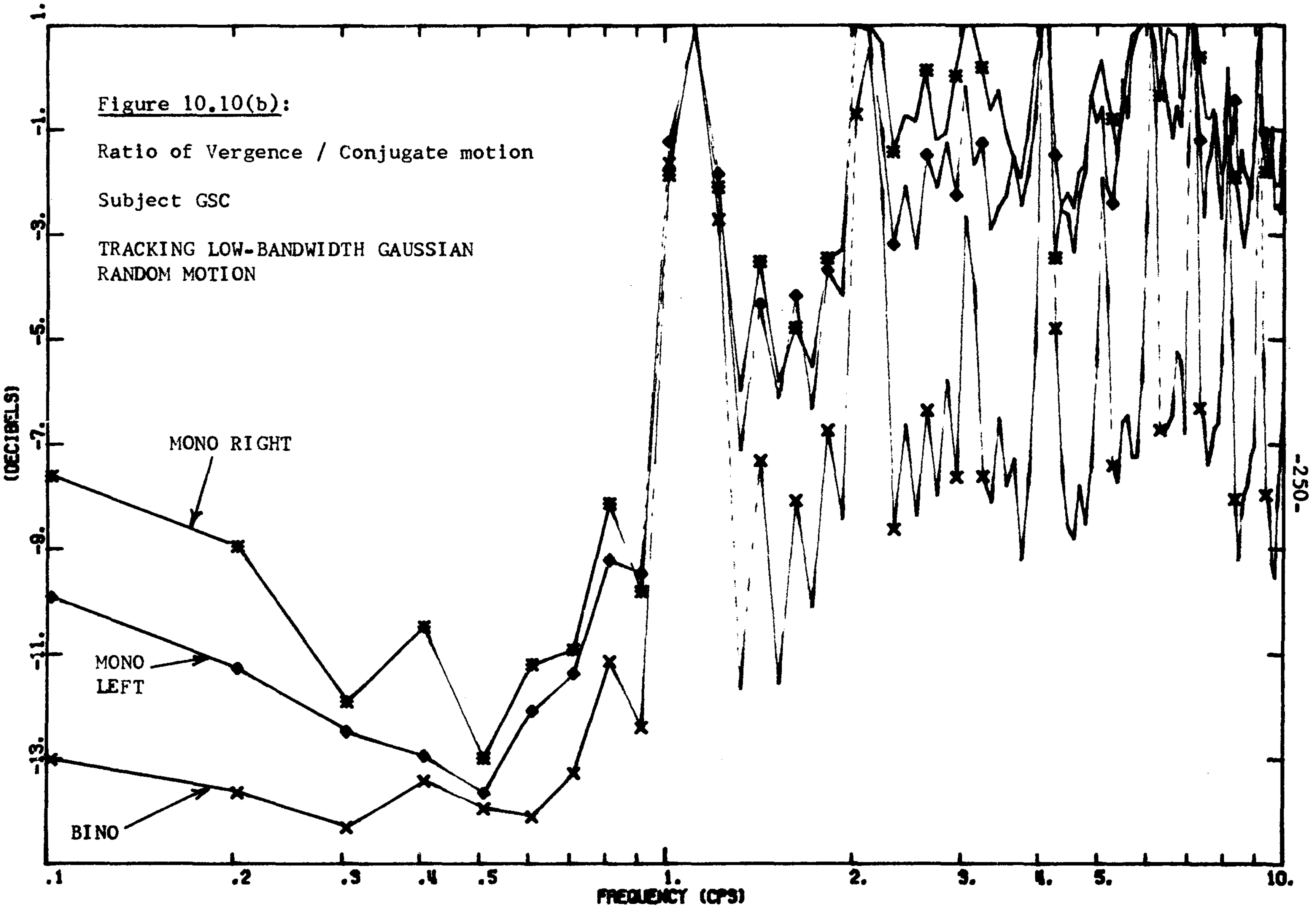


Figure 10.10(b):

Ratio of Vergence / Conjugate motion

Subject GSC

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

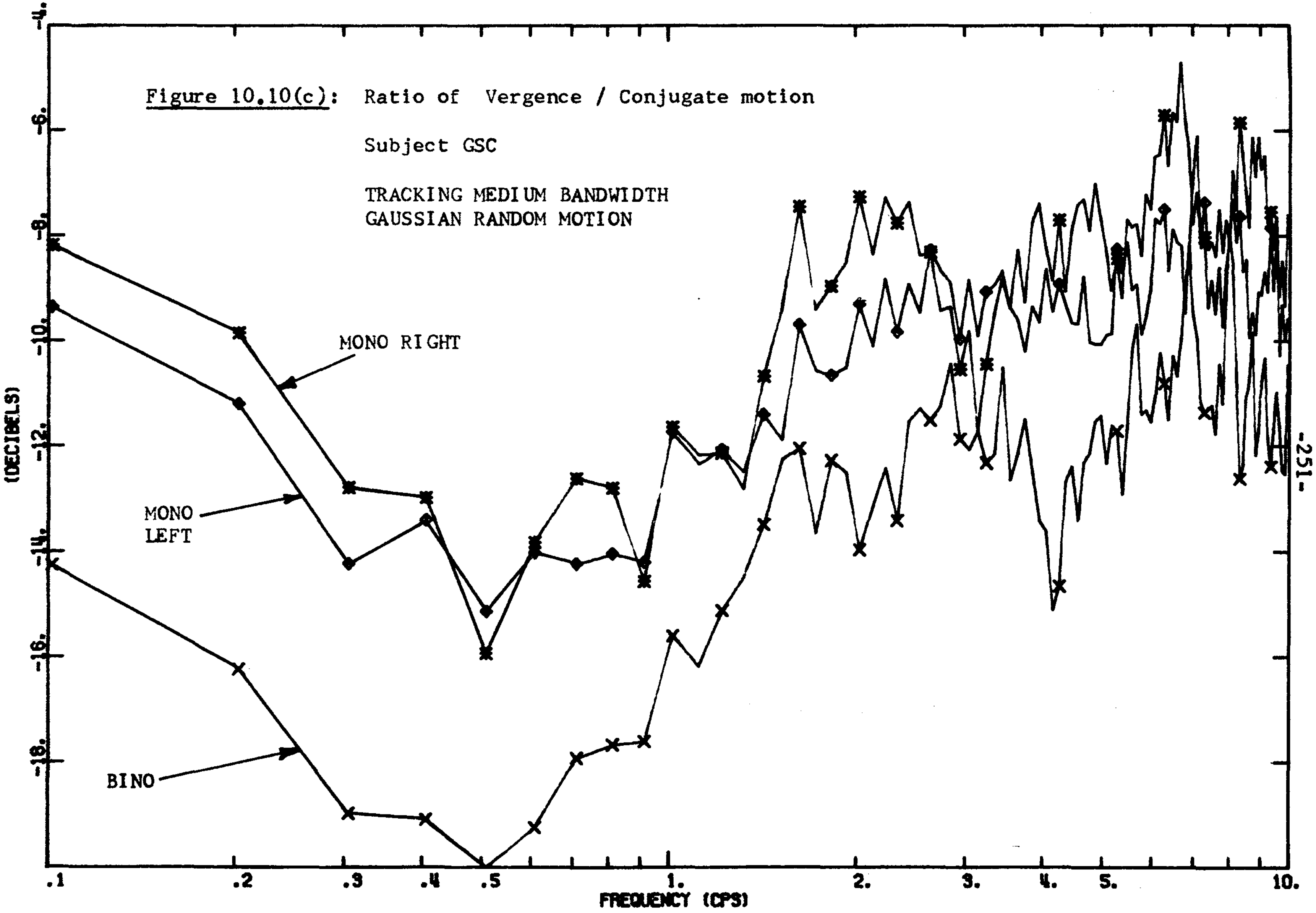


Figure 10.10(c): Ratio of Vergence / Conjugate motion

Subject GSC

TRACKING MEDIUM BANDWIDTH
GAUSSIAN RANDOM MOTION

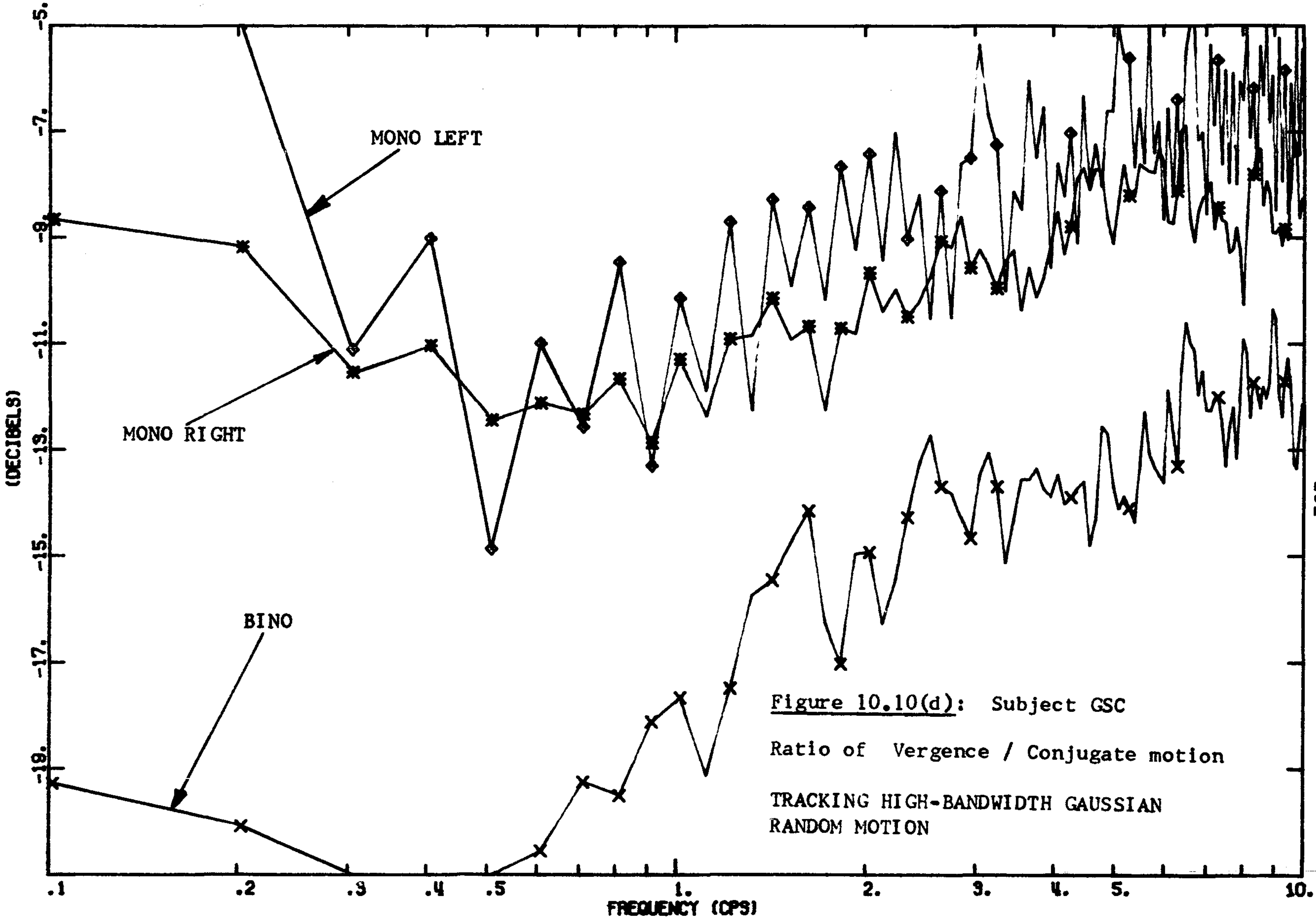


Figure 10.10(d): Subject GSC

Ratio of Vergence / Conjugate motion

TRACKING HIGH-BANDWIDTH GAUSSIAN RANDOM MOTION

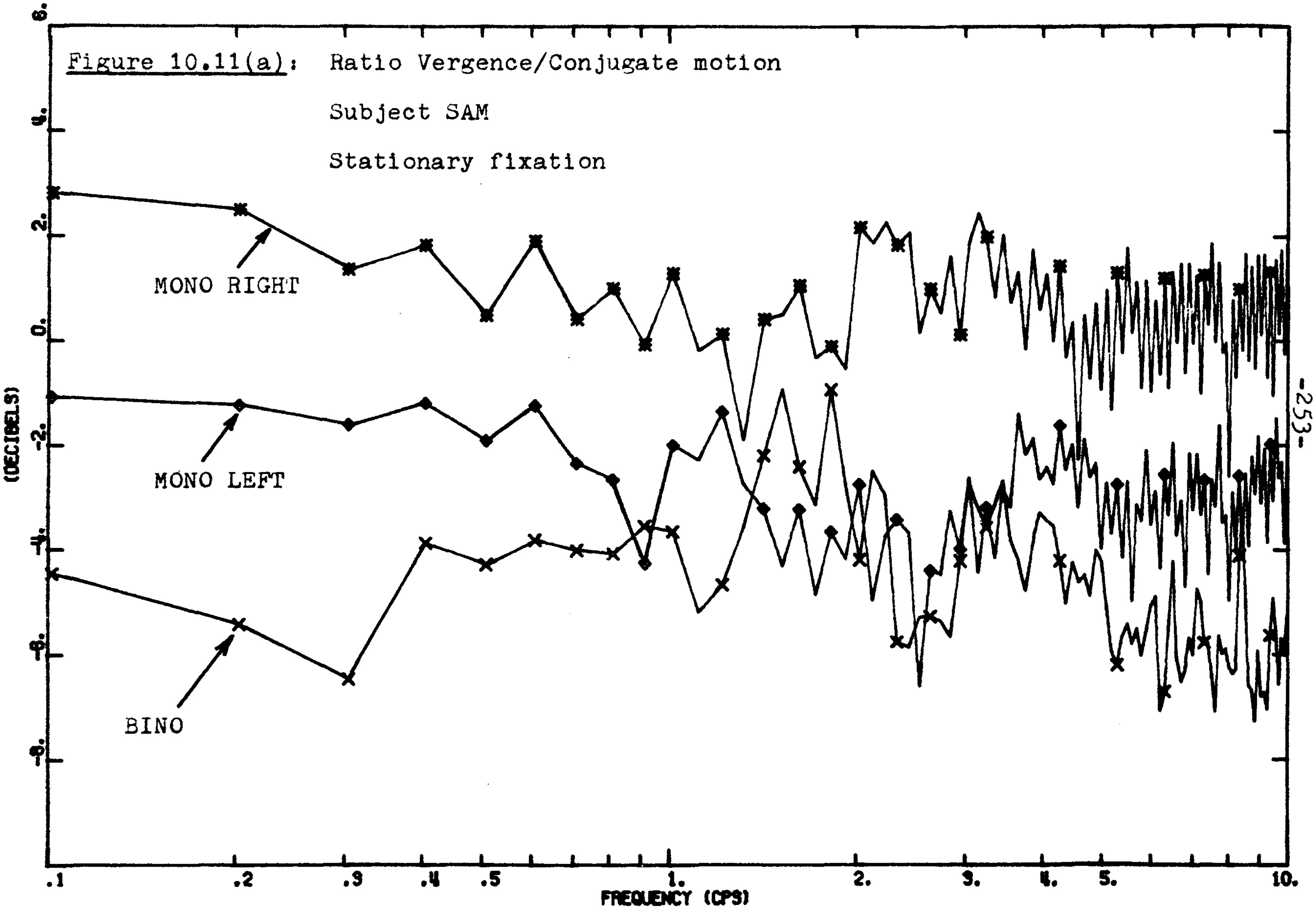


Figure 10.11(a): Ratio Vergence/Conjugate motion

Subject SAM

Stationary fixation

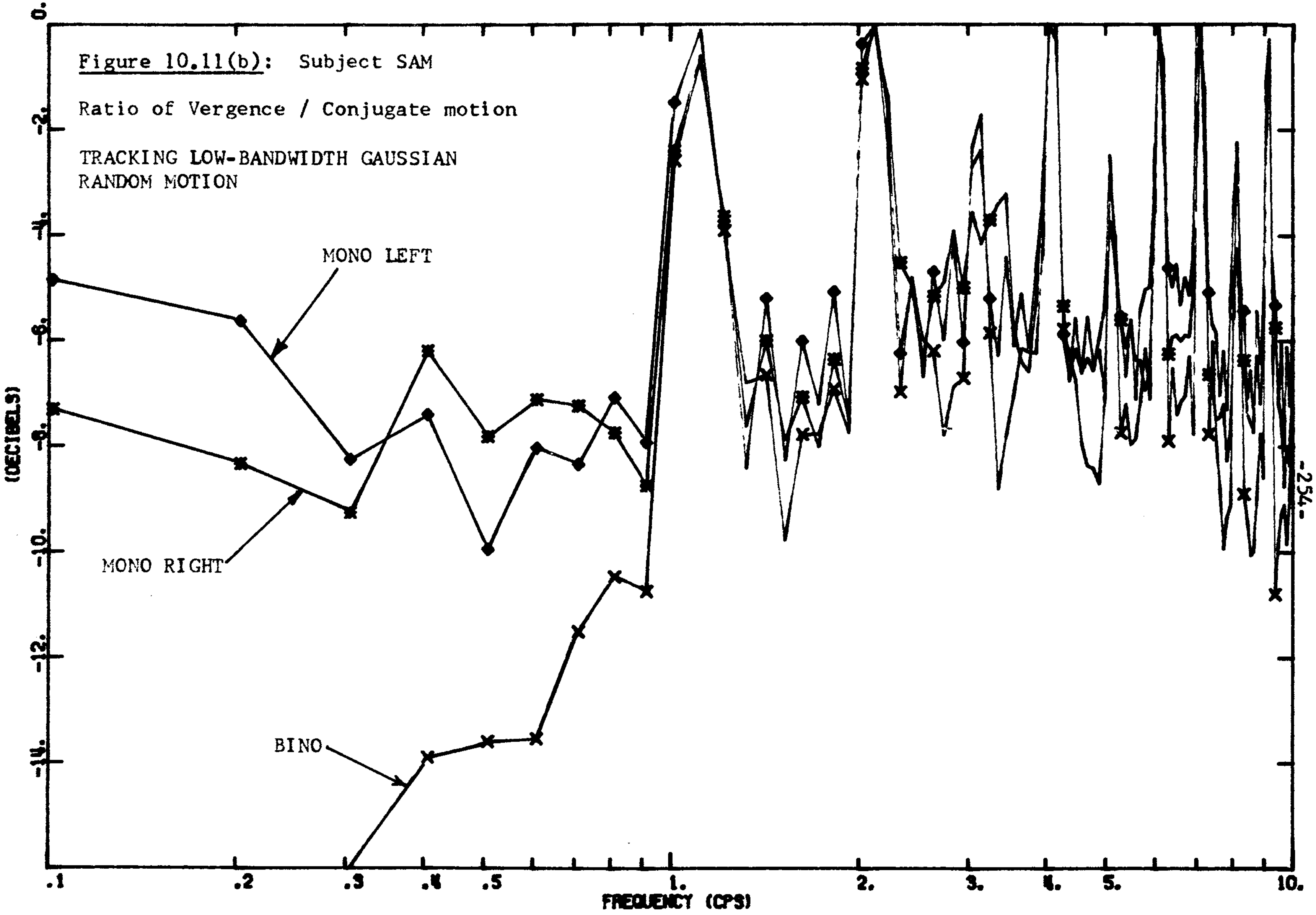


Figure 10.11(b): Subject SAM

Ratio of Vergence / Conjugate motion

TRACKING LOW-BANDWIDTH GAUSSIAN RANDOM MOTION

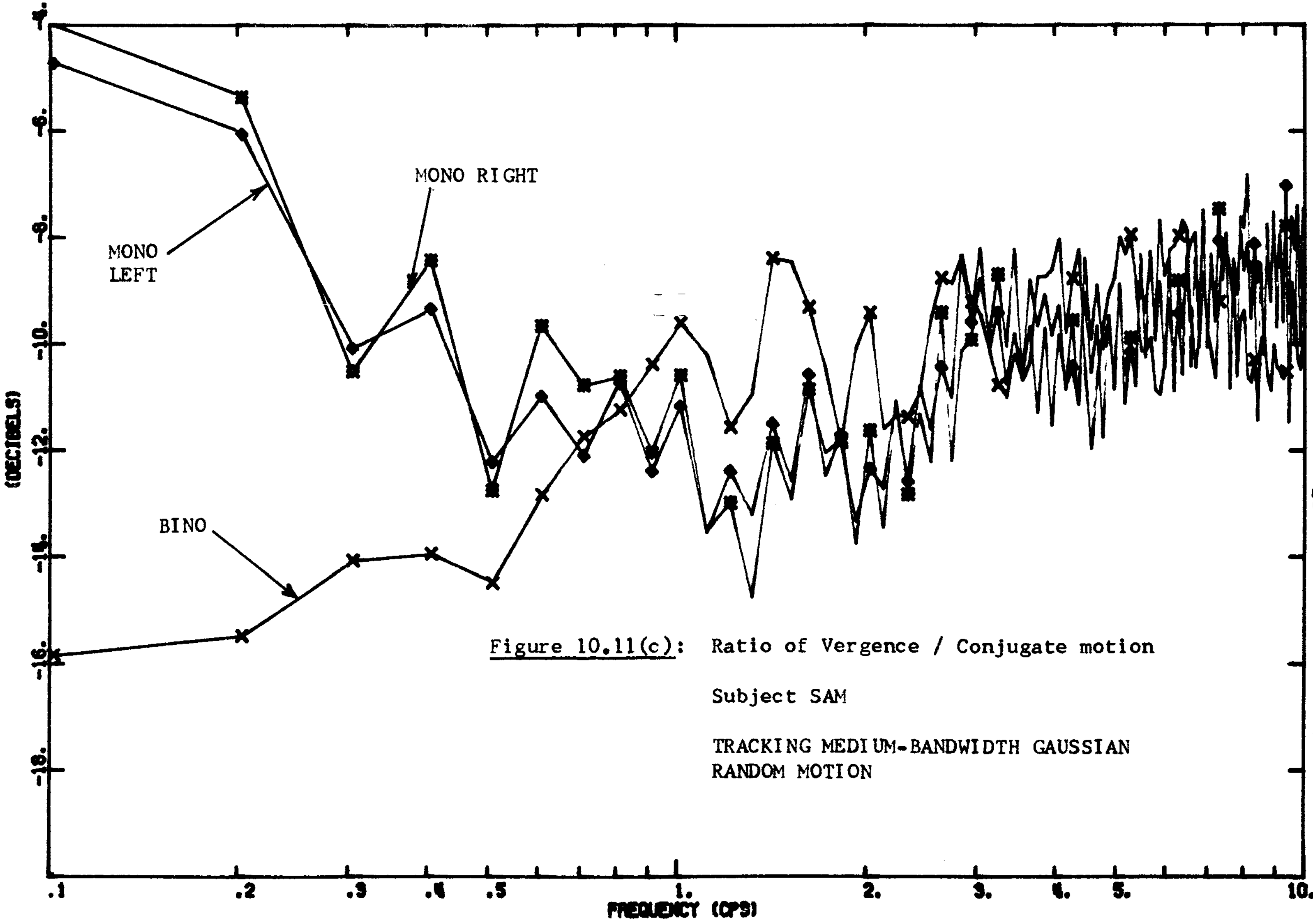


Figure 10.11(c): Ratio of Vergence / Conjugate motion

Subject SAM

TRACKING MEDIUM-BANDWIDTH GAUSSIAN
RANDOM MOTION

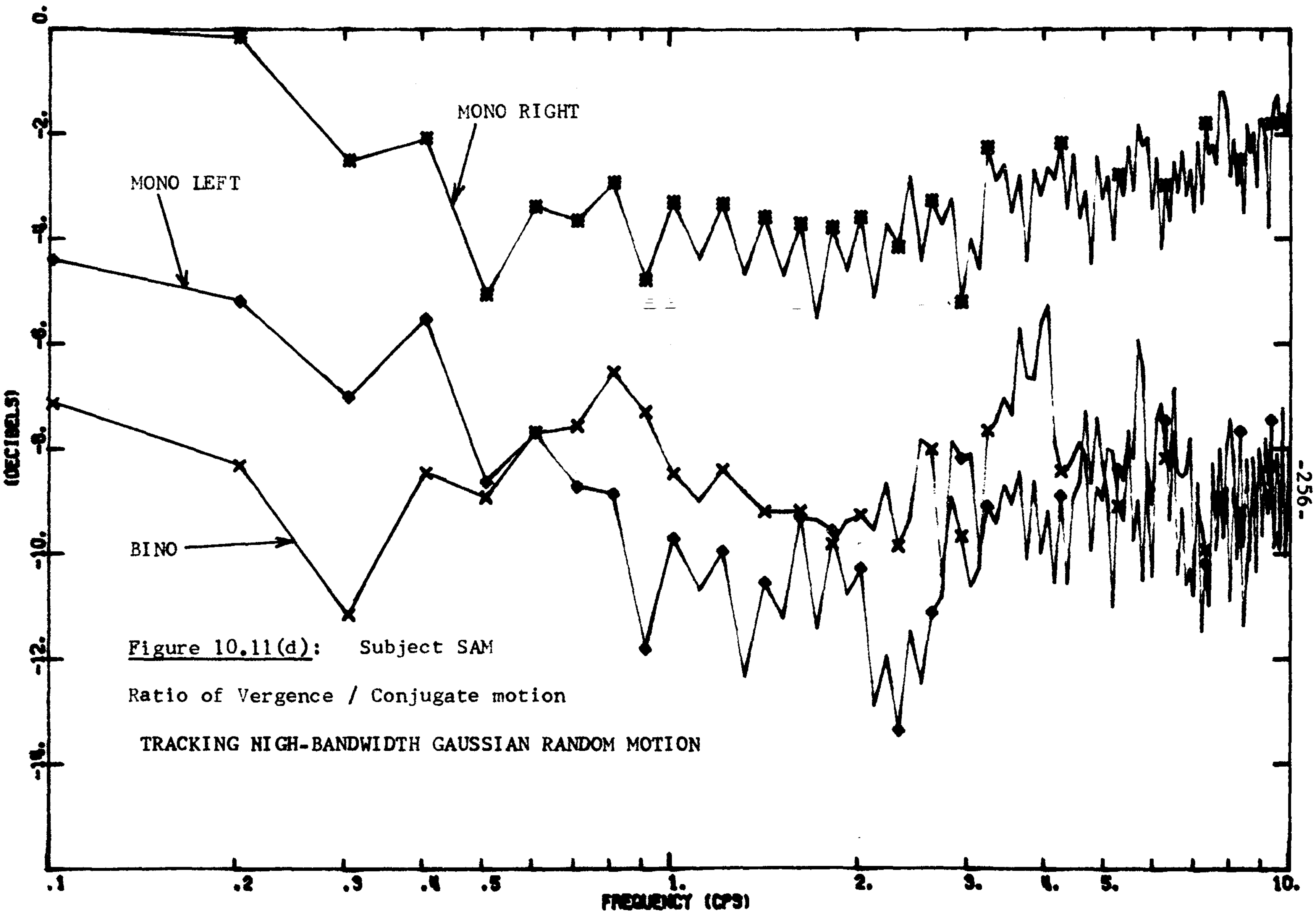


Figure 10.11(d): Subject SAM

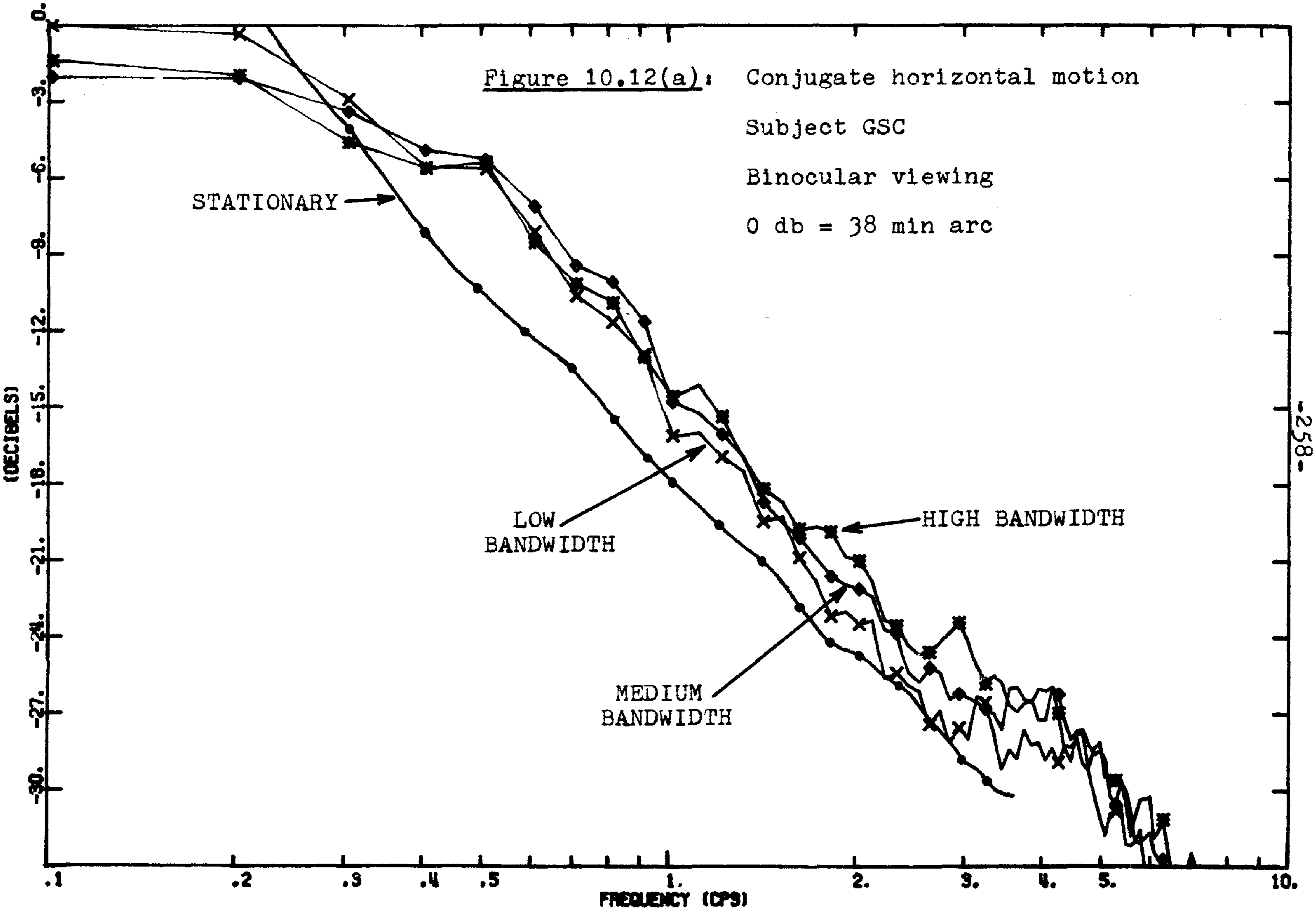
Ratio of Vergence / Conjugate motion

TRACKING NIGH-BANDWIDTH GAUSSIAN RANDOM MOTION shallower and occur at roughly 1 cps. In contrast, stationary fixation produces no such minima: most of the curves remain on the average constant with frequency.

For the tracking tasks, the relative vergence power for binocular viewing is lower than that for monocular at all frequencies for GSC and below 0.7 - 1 cps for SAM. Moreover, for GSC the difference increases as the bandwidth of the stimulus increases. For stationary fixation, no such generalizations can be made. For SAM the binocular curve is lower than the monocular ones, but for GSC it is not. Again, the mono-right curve is the lowest one for GSC, but it is the highest one for SAM. The only observation which we can make from the stationary fixation results is that, in general, the ratios are fairly constant with frequency and are higher in value than for the tracking tasks. In other words, there is a higher percentage of vergence power in stationary fixation than in tracking.

3.5 Effect of the various stimuli on horizontal motions. In order to more readily compare the effect of the various stimuli on horizontal motions, we have presented on one graph the four curves corresponding to stationary fixation and to the three tracking tasks. Figures 10.12a, b, and c show the power spectra for conjugate motion, for vergence motion, and the vergence/conjugate ratio, respectively, for subject GSC. Figures 10.13 are the corresponding diagrams for subject SAM. The viewing condition is binocular.

We have previously found (Chapter VIII) that the individual power spectra for overall horizontal motion were fairly equal for all stimuli in either eye. We would now like to determine whether this



<u>Figure 10.12(a)</u>: Conjugate horizontal motion

Subject GSC

Binocular viewing

0 db = 38 min arc

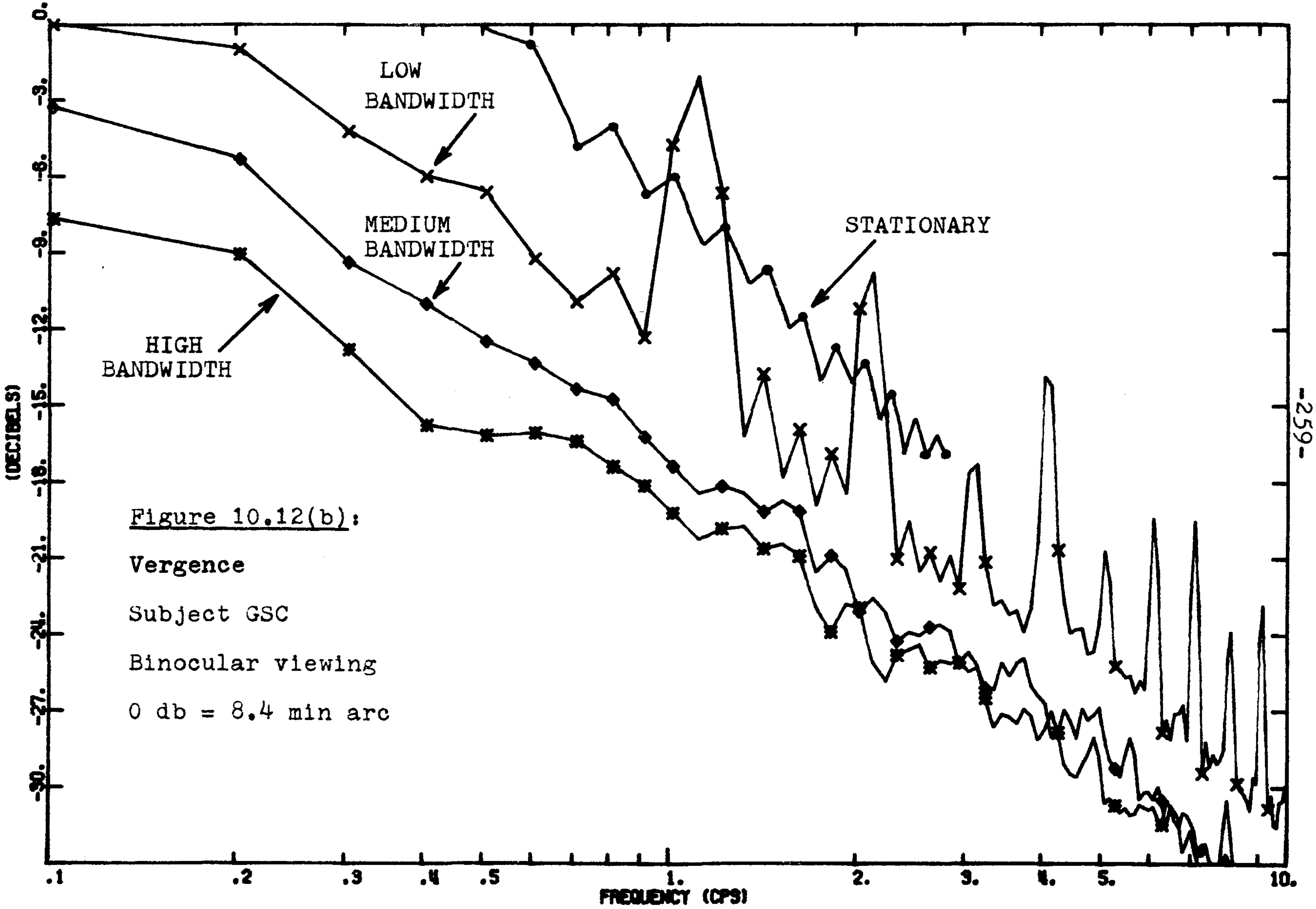


Figure 10.12(b):

Vergence

Subject GSC

Binocular viewing

0 db = 8.4 min arc

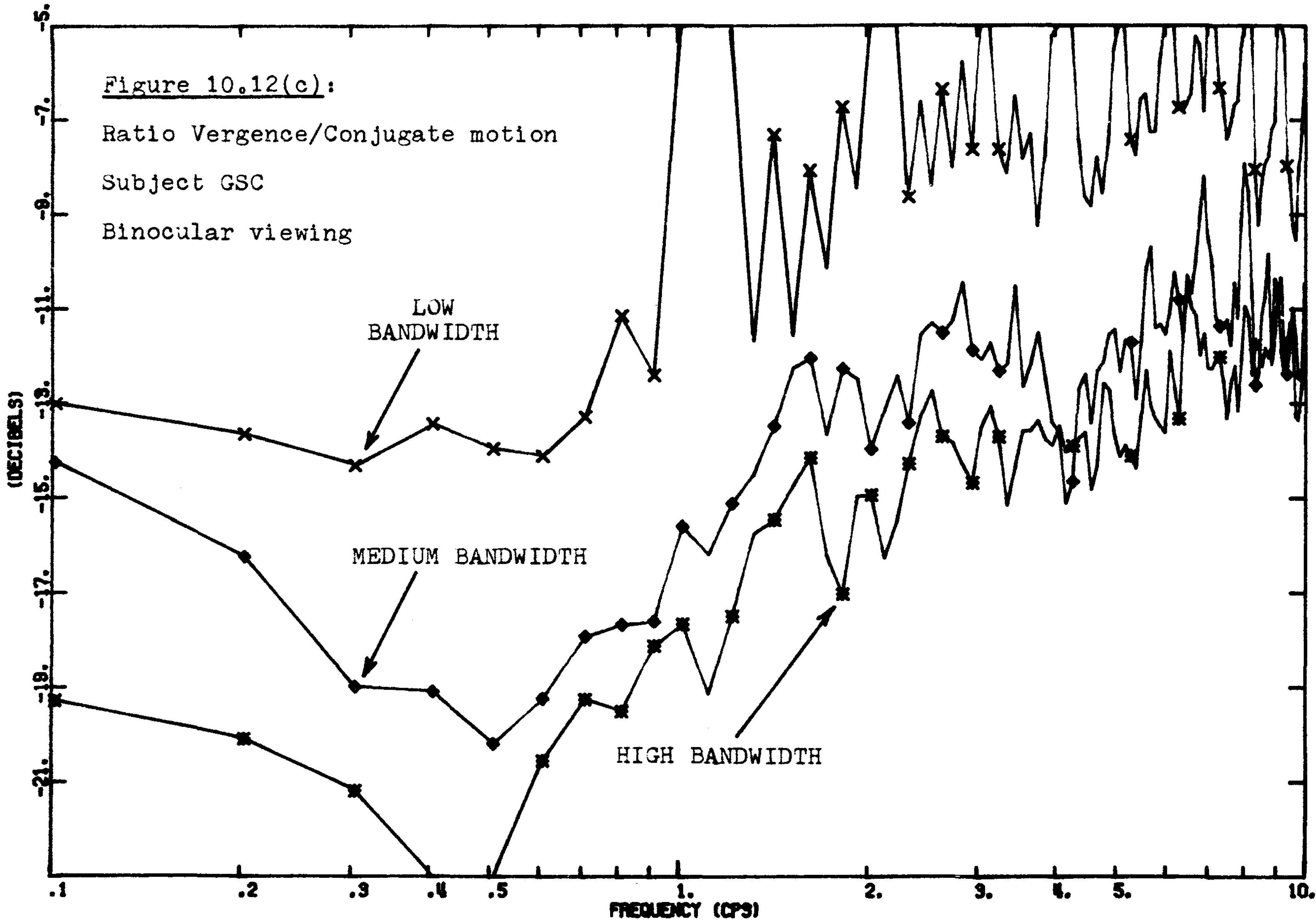


Figure 10.12(c): Ratio Vergence/Conjugate motion

Subject GSC

Binocular viewing

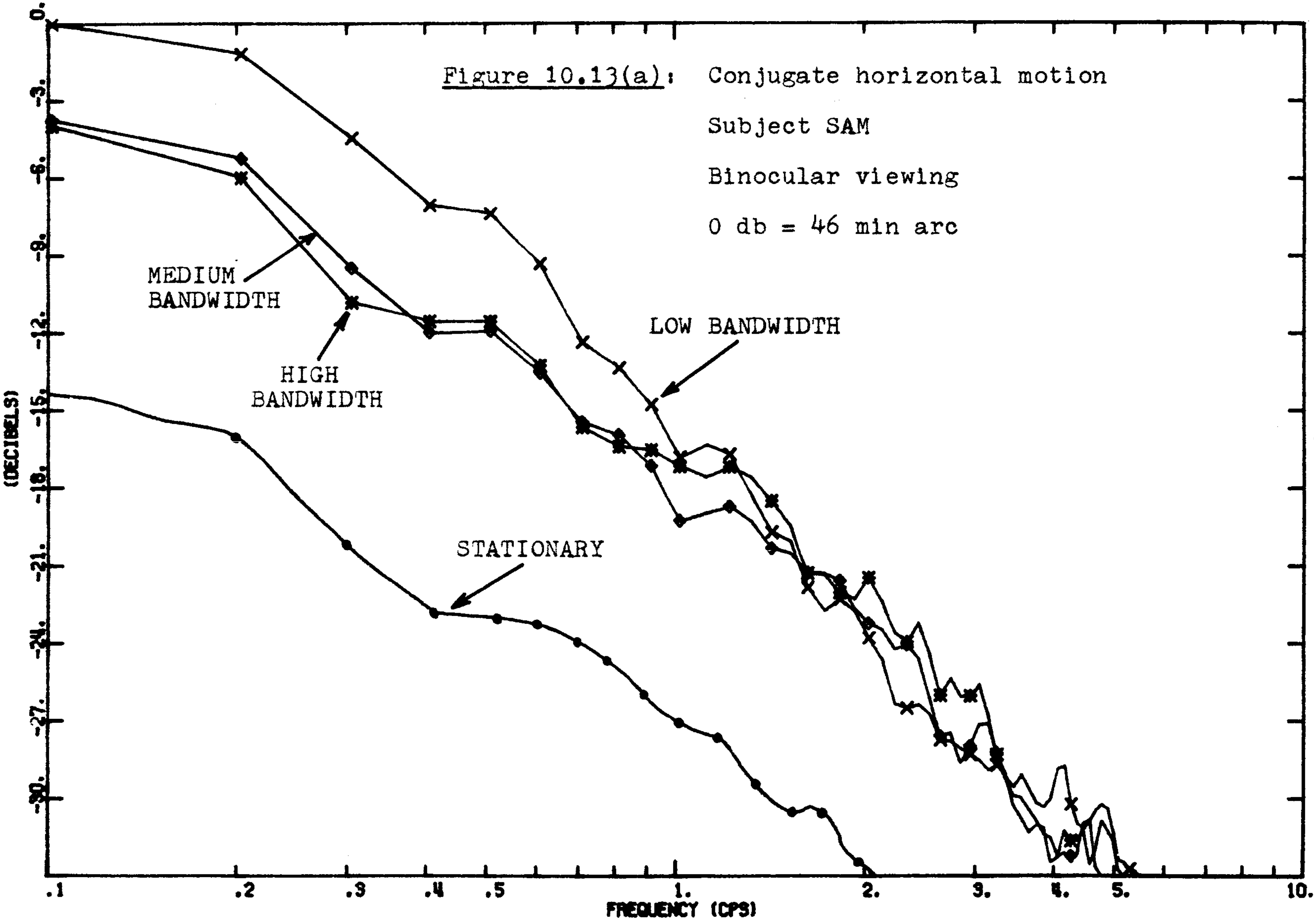


Figure 10.13(a): Conjugate horizontal motion

Subject SAM

Binocular viewing

0 db = 46 min arc

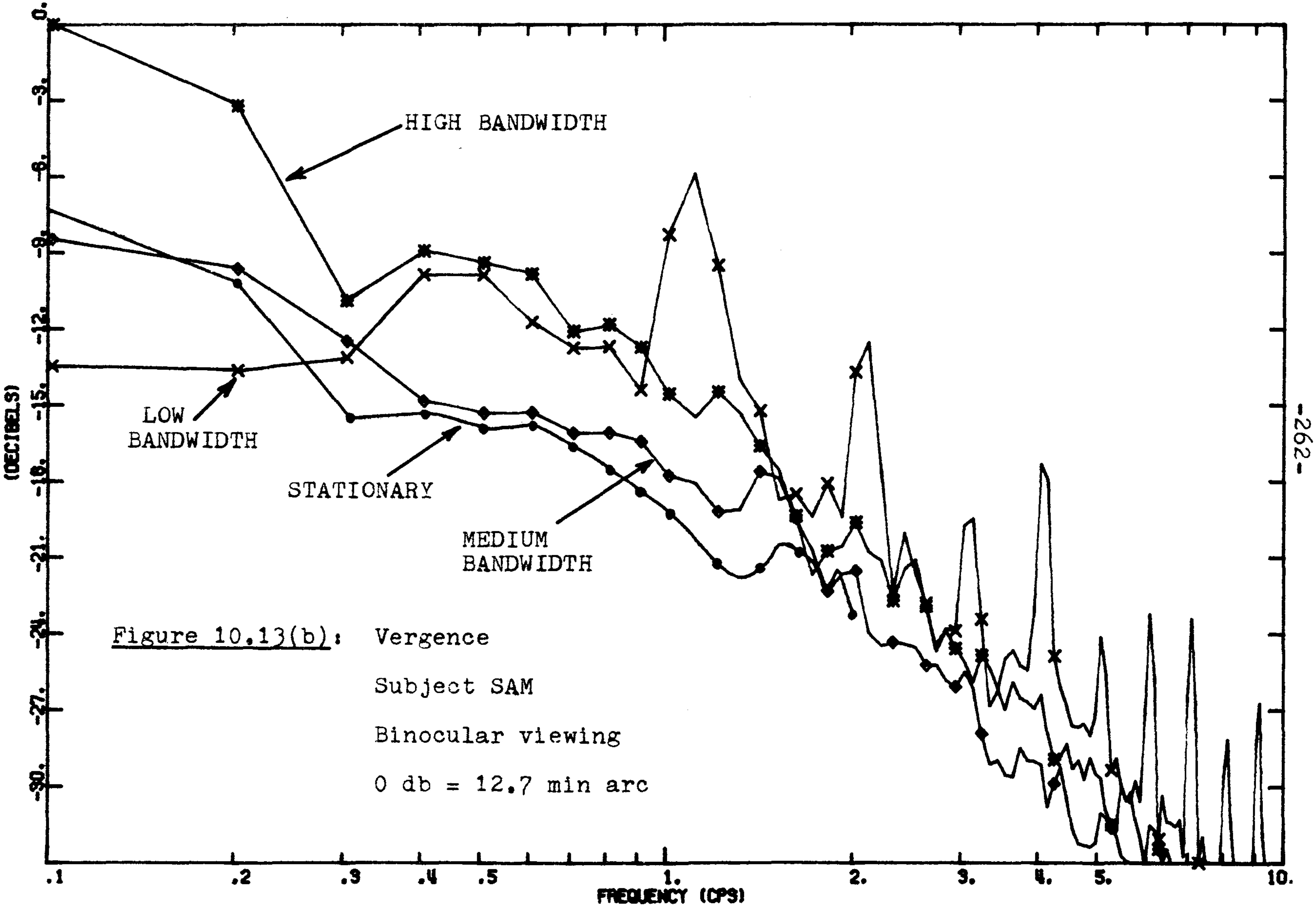
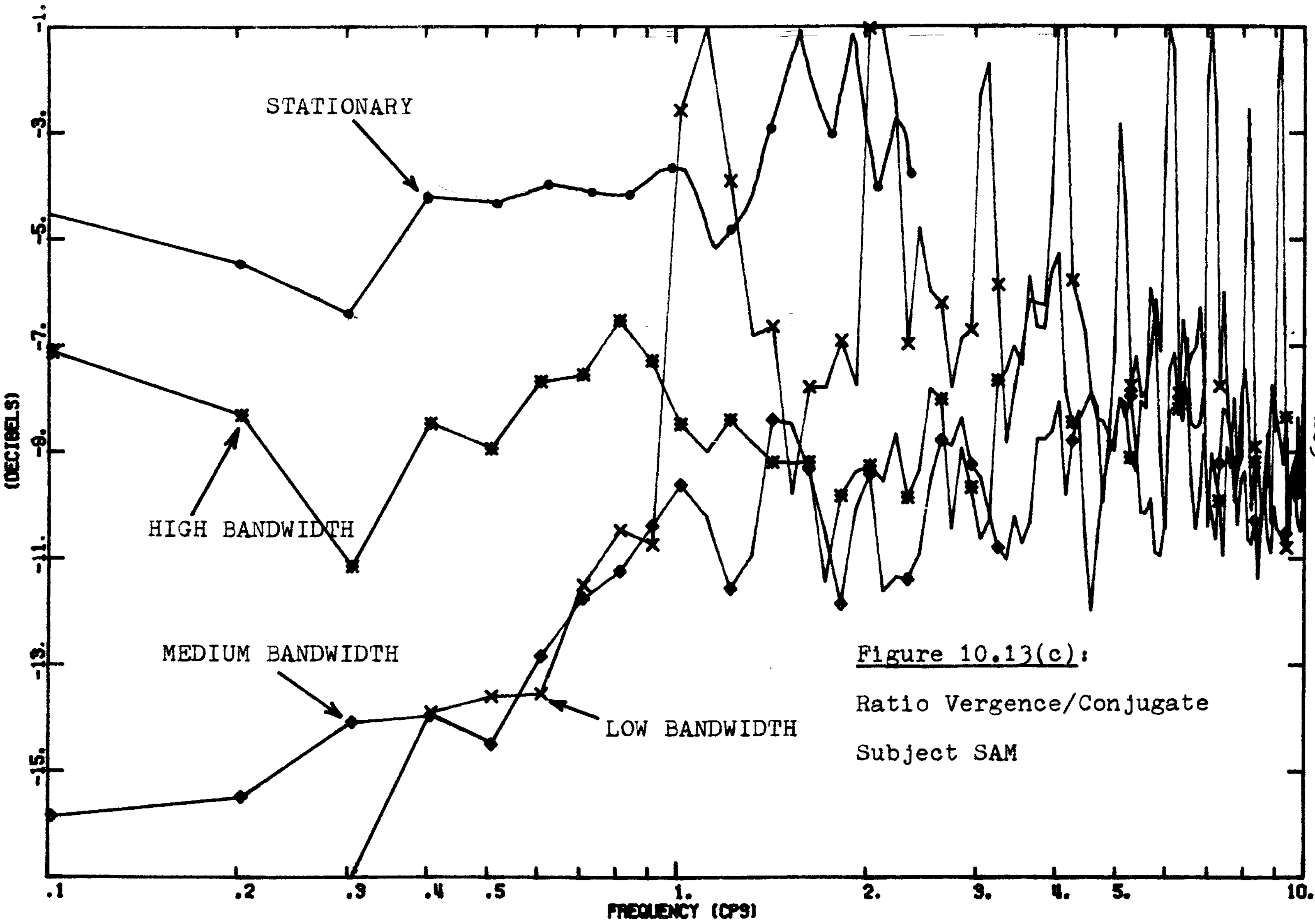


Figure 10.13(b): Vergence

Subject SAM

Binocular viewing

0 db = 12.7 min arc



<u>Figure 10.13(c)</u>:

Ratio Vergence/Conjugate

Subject SAM

equality of overall horizontal eye movements applies equally to the conjugate and vergent components. From Figure 10.12a we see that the conjugate power spectra are essentially the same for stationary fixation and for the three tracking experiments for subject GSC. On the other hand, from Figure 10.12b, we see that this is definitely not the case for the vergence component. In fact, there is a very logical order: as the average speed of the target increases, the vergence power decreases at any given frequency. Figure 10.12c, vergence/conjugate ratio, further confirms this observation: the low-bandwidth Gaussian motion stimulus yields a ratio curve which is higher than that of the medium-bandwidth stimulus at all frequencies, and in turn the medium-bandwidth curve is higher than that of the high-speed curve. The ratio curve for stationary fixation is not shown for it falls above the graph at roughly -2 db. In other words, for this subject, the relative out-of-phase "vergence" noise is strongly reduced by the increasing bandwidth of the moving stimuli.

For subject SAM the results are not as clear-cut. The conjugate component for stationary fixation is lower than that for the three tracking experiments. On the other hand, the vergence component is about the same. Figure 10.13c shows the vergence/conjugate ratio: the ratio curve corresponding to stationary fixation is higher than those for the moving stimuli. However, the curves for the tracking tasks are not as well-ordered as for subject GSC.

In summary, then, a moving target reduces the relative amount of vergence power in horizontal fixation, and for one subject, the amount of reduction is proportional to the bandwidth of the stimulus motion. Furthermore, the extent of this reduction does not seem to be frequency-dependent.

4. Discussion

To summarize the results of this chapter, we will first compare voluntary tracking eye movements to those involuntary spontaneous motions which occur during stationary fixation. For simplicity, we will first consider binocular viewing conditions only.

Since horizontal motions of the left and right visual axes are generally unequal and unsynchronous, we must choose some measure to describe their relative movements. The most obvious method would be simply to measure the relative phase, but this metric is not particularly enlightening. Instead, we have chosen to describe horizontal motion as the sum of a conjugate and a vergent component. It is true that there is no stimulus for vergence in any of the experiments, but for stationary fixation there is no stimulus for conjugate motions either, so that both of these measures are reasonable ones to use in describing spontaneous involuntary movements. Likewise, in the tracking experiments, we may consider the vergence to be simply a measure of the noise superimposed on the conjugate tracking eye movements.

The proportion of vergence to conjugate motions is much higher for stationary fixation than for tracking. Moreover, for voluntary eye movements, the vergence ratio exhibits a minimum at about 0.5 - 1 cps, while for spontaneous movements the fraction of vergence seems to be relatively independent of frequency. In addition, for one subject

(GSC), the amount of vergence power is roughly inversely proportional to the bandwidth of the stimulus motion. Thus, although the individual power spectra of tracking eye movements resemble those of spontaneous motions, the synchronization of the two axes is quite different in the horizontal direction.

Let us now examine the consequences of occluding one eye. First, the two visual axes always move vertically in perfect synchronization at all frequencies, for all stationary or moving stimuli, and for both monocular and binocular viewing conditions. However, in spite of this, vertical movements of the occluded eye are larger than those of the seeing eye; this discrepancy diminishes almost monotonically with increasing frequency. This relative increase in the size of movements of the occluded eye is much more pronounced for horizontal motions than for vertical and also much more significant for stationary fixation than for tracking. In fact, for spontaneous horizontal movements, this ratio is significantly different from unity at frequencies up to 2 cps.

The fraction of vergence power does not depend on the monocular or binocular viewing condition for stationary fixation. For one subject (SAM) it appears as if fractional vergence is less for binocular fixation, at least up to 1 cps; but for the other subject, it is the curve for right-mono fixation which has the least vergence ratio. In contrast, for tracking tasks, binocular fixation significantly reduces the proportion of vergence power from the monocular values.

Another way to examine the relative leads or lags between movements of the two visual axes is to compute the average delay between motions of each visual axis and those of the target being tracked. This has been discussed in section 3 of Chapter VII: the average delay T is computed such that the phase lag (relative to target motion)

$$\phi(f) = 360 f T \qquad (9)$$

fits the experimentally determined values by the root-mean-square criterion. Table 10-1 lists the net "computing" times T_c after the transit time has been subtracted. It may be noted that the right vertical channel is missing from certain cases for subject SAM.

For both subjects, motions of the right visual axis tend to lead those of the left. However, there is no evidence to show that movements of the occluded eye lag the target by a greater amount than those of the seeing eye in monocular fixation. Any differences between corresponding lag times of the two visual axes appear to be small and purely random. Moreover, differences for the vertical channels are on the average no smaller than those for horizontal movements.

On the other hand, in all but one case out of 22, the lag times for binocular viewing conditions are smaller than the corresponding values for monocular tracking. In Chapter VII, section 3, we have shown that delay time was proportional to the inverse of the rate of information transfer from target motion to tracking eye movements. Moreover, we found that the computing time T_c was just that amount of time required to allow the retinal image to sweep across that number of receptors necessary to produce a "quantum" of afferent information; this "quantum" was operationally defined as the minimum

TABLE 10-1. Delay Times (ms) of Eye Movements Relative to Target Motion

(A) Subject GSC

Bandwidth of stimulus motion	Viewing condition	LV	RV	LV-RV	LH	RH	LH-RH
Low	bino	64	63	+ 1	79	80	- 1
	left	112	117	- 5	113	108	+ 5
	right	95	100	- 5	97	99	- 2
Medium	bino	146	140	+ 6	164	152	+ 12
	left	167	162	+ 5	173	184	- 11
	right	154	152	+ 2	165	168	- 3
High	bino	227	212	+ 15	266	197	+ 69
	left	231	260	- 29	330	304	+ 26
	right	292	290	+ 2	303	296	+ 7

(B) Subject SAM

Low	bino	108	98	+ 10	85	79	+ 6
	left	110	107	+ 3	109	113	- 4
	right	144	144	0	98	103	- 5
Medium	bino	157	-	-	161	155	+ 6
	left	176	-	-	161	153	+ 8
	right	172	-	-	164	160	+ 4
High	bino	94	-	-	182	179	+ 3
	left	268	-	-	199	185	+ 14
	right	263	-	-	203	206	- 3

amount necessary to elicit corrective eye movements.

Under binocular viewing conditions, the active retinal area is of course twice that for monocular tracking. If the left and the right channels were independent and simply additive, the rate of afferent information would consequently be doubled and the computing time would therefore be halved. It is known that half of the optic nerve fibers decussate at the optic chiasma; thus, the lateral geniculate of of either side receives an equal amount of afferent signals from corresponding points of the left and the right retina. If the neural connections at the lateral geniculate were simply additive, the computing delay times T_c for binocular viewing would be half the corresponding values for monocular tracking. On the other hand, if the neural connections served only to measure retinal discrepancy, the computing times should not change. The fact that T_c is reduced but not halved shows that the actual mechanism is a combination of these two extremes.

The actual rate of information transfer from target motion to eye movements was computed in section 3 of Chapter VII. Let us consider the very simplified model for information flow shown in Figure 10. 14. Let R_1 and R_2 be the rate of information transfer in the left and the right channels of the oculomotor system under monocular viewing conditions. Let B_1 and B_2 be the corresponding values for binocular tracking; assume that, when both eyes see the target, a fraction α of the information in the left channel is added to that of the right; let β be the corresponding fraction for the right-to-left flow. Then:

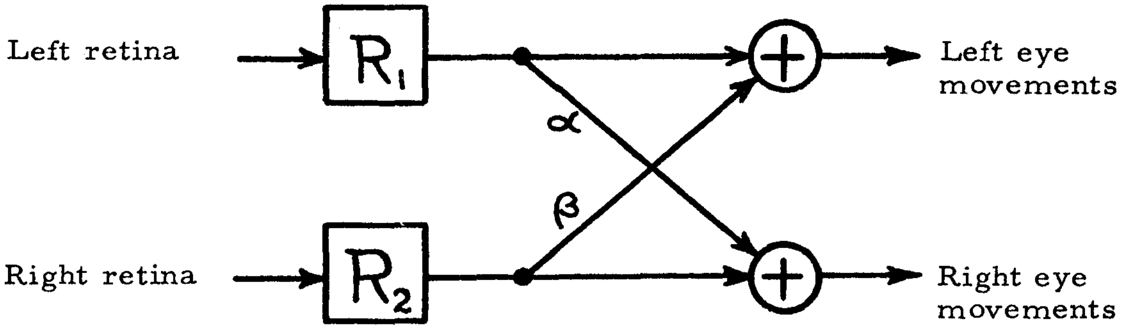


Figure 10. 14. Simplified schematic for information flow in the oculomotor system.

$$B_1 = R_1 + \beta R_2 \ ,$$
$$B_2 = R_2 + \alpha R_1 \ . \tag{10}$$

Table 10-2(a) lists the rate of information transfer between the left and the right channels, that is, B_i minus R_i. Since the computing times T_c are shorter for binocular viewing than for monocular, we expect, from the results of section 3 of Chapter VII, that B_i should be greater than R_i. In fact, in 20 out of 22 cases, the values in Table 10-2(a) are positive. Table 10-2(b) lists the actual fractions of information transfer α and β. All values are less than unity and, except for 2 cases, greater than zero. Hence, the simple flow diagram of Figure 10. 14 is at least a first approximation to a realistic model. The values α and β fluctuate widely as may be expected from this over-simplified model. In spite of this, however, some general trends may be observed. First, the fraction of information transfer α from left to right tends to be greater than the corresponding value β for the right-to-left transfer. Moreover, the maximum of the cross-

TABLE 10-2(a). Rate of Information Transfer (bits/sec) between the Left and the Right Channels of the Oculomotor System

	Subject GSC				Subject SAM			
Bandwidth of stimulus motion	Vertical		Horizontal		Vertical		Horizontal	
	→	←	→	←	→	←	→	←
Low	0.319	0.232	0.151	0.201	0.249	0.165	0.214	0.362
Medium	0.231	-0.436	0.204	0.086	-	0.007	-0.219	0.024
High	0.167	0.116	0.290	0.087	-	0.141	0.308	0.196

TABLE 10-2(b). Fractional Rate of Information Transfer between the Left and the Right Channels of the Oculomotor System

	Subject GSC				Subject SAM			
Bandwidth of stimulus motion	Vertical		Horizontal		Vertical		Horizontal	
	α	β	α	β	α	β	α	β
Low	0.218	0.126	0.090	0.088	0.180	0.161	0.148	0.182
Medium	0.217	-0.366	0.143	0.061	-	-	-0.149	0.015
High	0.438	0.179	0.309	0.133	-	-	0.651	0.603

correlation function between movements of the left and of the right visual axes is greater for monocular fixation with the left eye than for that with the right eye. This is in marked contrast to the case for fixation of a stationary target, where we observed that the fixation pattern of the occluded right eye was much greater than that for the occluded left eye. Second, in a majority of cases (6 out of 8), the fraction of cross information flow is greater for vertical than for horizontal motion. This, of course, is in agreement with the fact that vertical motions of the two visual axes are in phase at all frequencies. Third, as the bandwidth of the target motion increases, both α and β tend to increase. This is quite consistent with the results of the previous section, where it was found that, at least for one subject, the fraction of "vergence noise" decreased monotonically with increasing stimulus bandwidth.

In summary, if eye movements made under binocular tracking conditions are compared with the corresponding monocular motions, we find that the movements are more nearly equal for the two visual axes, that the amount of superimposed "vergence noise" is considerably less, that the computing time T_c is reduced, and finally, that the rate of information transfer between target and eye motions is increased.

XI. CONCLUSIONS

1. Gain and Phase of the Oculomotor System: a New Interpretation

Construction of a model for the oculomotor system can be approached in the following way. We postulate that the error is the retinal distance between the fovea and the image of the object which is to be tracked. A measure of this error is relayed to certain nerve networks in the lateral geniculate, in the cerebral cortex, and at the mid-brain level,which process it in some way and then send the appropriate innervation to the extra-ocular muscles. The eyeball itself is an easily identifiable physical entity which can be quite accurately described as a linear second-order system. This presents no difficulty. However, it is quite another matter to describe the aggregate of nerve networks which process the error information and mediate the proper sequence of innervation to the extra-ocular muscles. Physically, their location can only be vaguely described as somewhere in the lateral geniculates or in the frontal and occipital regions of the cerebral cortex, and in the brain stem. Ultimately, we would like to derive a mathematical model for this processor which would describe how the error information is computed and which would enable us to predict the response of the system to any target motion. Considering the lack of available information on the subject, it is quite natural that investigators in this field attempted to describe the oculomotor system by a linear model. The technique for determining the parameters of linear systems is quite straightforward; the target is moved sinusoidally at various frequencies and the amplitude and phase of the tracking eye movements are measured. From the gain curve, a transfer function is constructed with the appropriate poles and zeros. In turn, this transfer function dictates a specific minimum phase function of frequency, which in general is greater than the measured values. The difference is attributed to a cortical predictor whose efficiency depends on the degree of complexity of target motion. Subsequently, complexity is found to be a function of spectral content or bandwidth of the stimulus. Some heroic efforts have been made to derive the predictor transfer function, which was found to consist of a low-pass filter with larger-than-unity gain in series with a phase-lead network. Interestingly, the phase-lead proved to be a linear function of frequency (7) ; this can be interpreted as a constant delay. In fact, all phase curves which have been published (and those in this work) can be fitted quite nicely by postulating a constant delay rather than an increasing phase lag. From Dallos and Jones (7) and Fender and Nye (8) , we derive 36 ms for single sine waves; from Stark, et al. (11), we obtain 157 ms for the "sum of sinusoids" stimulus; and from Dallos and Jones (7) , we calculate 246 ms for a Gaussian noise target. In this thesis, nine stimuli were used -- 6 sums of sinusoids and 3 Gaussian random processes -- and the resulting delay times were found to be linearly related to the inverse of the rate of information transfer between target motion and tracking eye movements. Because of the small number of data points available, we do not claim that the measure of information we have used is necessarily the best choice, but we have demonstrated that a significant relationship can be found between oculomotor system computing time and some measure of retinal image motion information.

Basically, a predictor had to be postulated in order to reconcile the discrepancies between the measured gain and phase curves. However, we have found that these discrepancies vary considerably for the various "unpredictable" stimuli. Responses to the narrow-band 4-frequencies stimuli are particularly striking. The gain goes up with frequency while the phase decreases. To reconcile this by means of a cortical predictor is an exercise in which we do not wish to indulge. There is no a priori reason to expect that the aggregate of neurons should process retinal error information in such a manner that the phase and gain should be related in a way which we find mathematically pleasant. It is much more reasonable and intuitively clear to postulate that the computing delay times are determined by the rate of retinal information and that the magnitude of the resultant eye movements is a function of biological constraints.

The evidence in this work supports this hypothesis. Thus, when target motion is restricted to a narrow band of frequencies, the oculomotor system chooses to respond preferentially to the fastest component of motion; this behavior has obvious survival value. On the other hand, if the stimulus contains power at all frequencies within the oculomotor system bandwidth, then the available muscular energy is distributed equally within the band. In fact, the power spectra for spontaneous eye movements made during fixation of a stationary target do not differ significantly from those spectra corresponding to tracking eye movements if the target motion consists of band-limited Gaussian random motion. This may be interpreted to mean that, at least for tracking small continuous Gaussian target motions, the oculomotor control system does not increase the average rate of impulses in the oculomotor nerves above the spontaneous rate. Rather, the impulses in the oculomotor nerves of opposite recti muscles (such as the medial and lateral) are simply coordinated so that the visual axis follows the target motions instead of performing purely random motions. In this manner, the efferent portion of the system operates at full output at all times; there is no need for a warm-up period. A most ingenious device!

The results of this work also show that, for smooth target motions other than trivial predictable simple sinusoids, the average delay is determined by the average speed of the retinal image. Enough photo-receptors in a given receptive field must be excited so that their integrated output can produce a quantum of afferent signal information sufficient to trigger corrective eye movements. It has been shown that at least one or two (depending on the subject) photo-receptors must be excited, and that the retinal image must spend at least 3/4 milliseconds on one photoreceptor. In spite of the scatter of the data points, the remarkable agreement between corresponding parameters for the two subjects strongly indicates that the lag of the oculomotor system can be understood simply by considering basic physiological constraints. There is no need to appeal to mystical predictors or analyzers which are presumably buried somewhere in the aggregate of nerve networks of the lateral geniculates or the cerebral cortex. Moreover, sampled data systems such as that postulated by Young (13) are now more readily understandable. Instead of a mysterious sampler whose sampling period appears to be the result of a stochastic process, we now understand that the sampling time is simply that delay necessary to integrate the required retinal signal so as to elicit tracking eye movements. There is of course nothing wrong with simply presenting a "stochastic sampled data" model of the oculomotor system. However, since it is now clear that the so-called sampling time must be determined by the target motion, it is obvious that such a model cannot be used to predict oculomotor response to stimuli other than the specific one used for testing.

Linear models have been useful in describing the gross response characteristics of the oculomotor system and can still be used to predict the response to a very limited class of inputs. However, we believe that it is now a futile exercise to attempt to refine these models by adding increasingly complex predictors or other mysterious black boxes. It would be much more fruitful to attempt to determine precisely just what measure of retinal image motion (in addition to the basic metric described above) is considered as useful information by the oculomotor system.

2. Corrective Role of Spontaneous Eye Movements During Fixation

It had previously been thought that, during fixation of a stationary point, instabilities of the oculomotor system were exhibited as smooth eye movements -- drifts -- which tended to drive the visual axis away from the fixation mark. The resulting fixational errors -- defined as the distance between the retinal image and the center of the fovea -- were then supposed to be corrected by the sudden, step-like eye movements: the flicks.

The results of Chapter IV show that this is clearly not the case. Both flicks and drifts subserve the same function; they drive the visual axes so that the retinal image of the target describes an apparently random trajectory on a finite region of the fovea. If the retinal image wanders too far from the center of fixation, either a flick or a drift drives the visual axis back on target, although flicks are somewhat more efficient in this respect. The motion of the retinal image can be regarded as a space-limited and band-limited Gaussian random process.

The function of such a mechanism which keeps the retinal image in constant motion may be to prevent adaptation of photoreceptors. Moreover, as pointed out in section 1, if the efferent portion of the oculomotor system is maintained at a high dynamic state at all times, the difficulties of sudden power surges are avoided. The average number of efferent impulses is not changed; only the correlation between discharges in opposite motoneutrons of a pair of muscles is affected when it is desired to track a moving target.

In addition to the mechanism which prevents the retinal image from wandering too far from the center of fixation, there exists a binocular error sensor which measures horizontal retinal disparity between the two eyes. Such vergence errors are then corrected solely by means of smooth movements, the so-called drifts. It must be emphasized that such correction of binocular errors is above and beyond that amount of correction to be expected from two monocular corrective feedback loops operating in parallel.

In contrast, vertical discrepancies of the visual axes do not trigger corrective eye movements of either type. Retinal disparities in the vertical direction are corrected solely by means of two parallel monocular corrective feedback loops. However, since all vertical eye movements are synchronous for the two visual axes, correction of vertical retinal errors poses a special problem: the left visual axis is not allowed to move up while the right moves down. In the next section, we will describe how such a corrective scheme might operate.

3. Corrective Feedback Loops of the Oculomotor System

If a subject fixates monocularly on a stationary target, the fixation pattern of the visual axis of the occluded eye is much larger than that of the seeing eye. For both subjects studied (GSC and DSG), this effect is particularly pronounced if the right eye is occluded. However, since the occluded eye can furnish no retinal information regarding fixational error, the surprising fact is not that its fixational pattern is large, but rather that it is finite. Clearly, there must exist a feedback loop other than the visual one. In fact, there are spindles in the extra-ocular muscles which can provide measures of muscle tone (3). It has been shown (9) that the information provided by these muscle spindles is not enough to give the subject a reliable indication of the direction of his visual axis. Thus, in a dark room, a person could not estimate better than 75 percent of the time whether a spot of light was 6 prism-diopters to the left or to the right. Consequently, it has been suggested (9) that these spindles might provide information regarding gross differences in eye position as well as differences in muscle tonus and metabolism. It was postulated that such information could be used as parametric feedback so as to modulate the effectiveness of efferent discharges in the oculomotor neurons in order to compensate for metabolic differences between corresponding extra-ocular muscles. In this manner, movements of the left and right visual axes could be made more nearly equal.

We shall return shortly to the problem of the relative magnitude of eye movements in the two visual axes. For the moment, let us observe that the muscle spindles must provide quite accurate information about differences in eye position. Thus, in some cases (such as DSG fixating the horizontal bar with the right eye, Figure 4. 5e), the fixation pattern of the occluded eye is not much bigger than that of the seeing eye. It is, in fact, quite irrelevant that the muscle spindles do not provide the subject with conscious information regarding the orientation of his visual axes. It is only necessary that such information be used to modulate the effectiveness of the motoneurons so as to maintain the two visual axes fairly parallel.

This feedback loop need not necessarily be short. In fact, it has been found (4, 5) that stretching the extra-ocular muscles in the goat produced afferent discharges as far as the superior colliculus and the posterior commissure. If the same conditions hold true in humans, there may very well be a binocular mechanism which compares afferent signals from spindles of the left and right muscles.
In any case, the fixation patterns (Figures 4. 4 and 4. 5) clearly show that the orientation of the visual axis of the occluded eye does not deviate drastically from that of the seeing eye. These results imply that extra-ocular muscle spindles are much more accurate indicators of visual axis direction than had previously been assumed.

Let us now compare the sizes of eye movements in the seeing eye with those of the occluded eye. It might be expected that one way to limit the wander of the visual axis for the occluded eye might be to simply attenuate all eye movements in that eye. Such a scheme would thus put less stringent demands on the proprioceptive qualities of the muscle spindles. Surprisingly, just the opposite holds true: the results of Chapter IV clearly show that both flicks and drifts for a given eye increase in magnitude when that eye is occluded. Moreover, the power spectra of spontaneous and of tracking eye movements (Chapter X) show that this size discrepancy holds true in tracking tasks as well as in fixation of stationary targets, although it is more pronounced in the latter case. Furthermore, even though the two visual axes always move vertically in synchronization at all frequencies, vertical motions of the occluded eye are again larger than those of the other eye, although the size ratio approaches unity at frequencies higher than about 0. 5 cps. Consequently, there must exist a retinal feedback loop whose main function is to attenuate efferent discharges from the cortical levels.

The usefulness of such a mechanism becomes apparent when we consider the following facts: flicks or saccades always occur simultaneously and in the same direction for the two eyes; all vertical motions are synchronous in the two visual axes; and finally, in dichoptic tracking tasks, the average lag of eye movement responses in the seeing eye is not significantly different from that in the occluded eye. Thus, in normal binocular viewing conditions, information from either retina may trigger corrective eye movements, which then occur simultaneously for the two visual axes. Clearly, since fixational errors are in general not equal for the two retinae, there must be some provision for modulating efferent discharges from cortical levels. Our results show that this modulation manifests itself as an attenuation of efferent signals.

It is interesting to speculate on the location of this retinal feedback loop. Of course, it is quite possible that it may simply be the same as that for the flow of retinal information which triggers corrective eye movements: from the retina to the lateral geniculate, then to the occipital cortex, and finally to the midbrain and to the oculomotor nuclei in the brain stem (see Figure 1. 2). Such a scheme, however, lacks elegance and does not do justice to the faith we have in the evolution of the oculomotor system. In the lower vertebrates, the principal center for vision is the optic tectum. With increasing encephalization, its functions have been gradually taken over by the occipital cortex. In humans, the homologue of the optic tectum, the superior colliculus, has been considerably reduced in size and importance. Neurophysiologists have been very active in trying to find meaningful tasks for this center. From his studies of pathological human subjects, Cogan (2) has concluded that there exists a center for vertical eye movements in the superior colliculus. On the other hand, Pasik and Pasik (10)and Bender and Shanzer (1) have examined the oculomotor system of the monkey by means of lesions and stimulation and have concluded that there are no centers for eye movements in the superior colliculi. However, considering the evolutionary changes of this particular center, extrapolation of results from one specie to another should be done with more than the usual degree of caution. In any case, it is generally agreed (6) that the superior colliculus receives afferents from the retina either directly or via the lateral geniculate, and sends efferents to the pretectal nuclei and possibly to the brain stem. Moreover, this center is also a relay station between the occipital cortex and the pretectal nuclei (midbrain), although it can be bypassed via the internal corticotectal tracts (12). In short, while the superior colliculus is perhaps not essential for the mediation of ocular movements, it is nevertheless in an ideal position to receive afferent information directly from the retina and to modulate efferent signals from the cortical levels. Moreover, if Cogan is right and there is a control center for vertical eye movements in the superior colliculus, then our theory becomes increasingly attractive. There is no center for the correction of vertical retinal disparity; the visual axes are constrained to move vertically in synchrony. Consequently, it is extremely important that the required attenuation of efferent cortical signals for vertical eye movements should occur in the most efficient way possible. What could be more ingenious than to place the "modulator" and vertical control center in the same aggregate of nerve cells?

4. Signal, Noise, and Information Flow in the Oculomotor System

The determination of signal and noise and the measurement of information flow in biological control systems present basic difficulties which are not inherent in manmade systems. In artificial servomechanisms, the task is well defined and the performance is therefore quite straightforward to measure. In communication systems, the nature of the signal is known in advance and, in many cases, the noise statistics can be estimated. In short, we can use such terms as "error," "signal-to-noise ratio," "rate of information transfer," and "channel capacity" in a meaningful and precise manner. However, to describe nerve networks by means of such terms can, in some cases, be quite misleading.

Consider, for example, the concept of noise in the oculomotor system. It had previously been thought that the spontaneous involuntary eye movements made during fixation were the result of "instabilities" in the oculomotor system; "noisy drifts" were supposedly corrected by flicks. However, we have shown that this is not the case: neither flicks nor drifts play the major corrective role. Mathematically, we can describe such eye movements as a stochastic (Gaussian) process. However, to classify such a process as noise is totally inadequate, because if this were the case, then a moving target would elicit tracking eye movements superimposed on spontaneous motions of constant average amplitude. This does not happen; the power spectrum of the ocular motion does not change; the efferent discharges are simply reorganized so that the visual axis follows the fixation mark. As the bandwidth of the target motion increases, the spectra of the tracking eye movements remain the same, but the ratio of vergence to conjugate horizontal motions decreases. Since there is no stimulus for vergence, are we thus justified in construing this behavior to be an increase in signal-to-noise ratio? I think not; a more reasonable interpretation is that the oculomotor system simply reorganizes its constant power output so as to perform the visual tasks demanded of it.

Another concept which demands judicious interpretation is that of information transfer in the oculomotor system. We determined the rate of information flow essentially by a measure of the correlation between Gaussian target motion and the tracking eye movements. Such a metric is useful in describing the degree of control exerted in various parts of the system, but the use of the work "information" may be misleading in that it implies that the oculomotor system performs some complex analysis of the retinal image motion. We have found, in fact, that the computing delay time T_c was determined not by "complexity" or spectral content of target motion, but by the very basic biological fact that a minimum afferent signal had to be generated by the retina in order to produce a meaningful signal. Nevertheless, when used with other values such as the correlation between left and right eye movements, the measure of information transfer between target and eye motions can indicate the amount of communication that takes place within the oculomotor system. Thus, we have determined that, as the bandwidth of the target motion gets larger, the degree of bilateral control also increases. Moreover, the amount of left-to-right control is greater than that of right-to-left. This is exactly the reverse of the situation for stationary fixation. These asymmetries lead us to postulate the following hypothesis. When a subject fixates a stationary target monocularly, the visual axes are kept in parallel orientation only by means of feedback from the extraocular muscle spindles since discharges of the oculomotor nerves are uncoordinated. In contrast, for a tracking task, this function is performed mainly by coordinated efferent signals mediated by the central nervous system.

The results of this work show that the techniques of engineering analysis can be used with profit in the study of biological systems only by constantly and judiciously relating the abstract systems analysis concepts to the underlying biological principles.

REFERENCES FOR CHAPTER XI

1. Bender, M. B. and Shanzer, S., "Oculomotor Pathways Defined by Electric Stimulation and Lesions in the Brainstem of Monkey," The Oculomotor System, Chapter IV, edited by M. B. Bender, Harper and Row Publishers, New York (1964).

2. Cogan, D. G., Neurology of the Ocular Muscles, Charles C. Thomas Publisher, Springfield, Illinois (1956).

3. Cooper, S. and Daniel, P. D., "Muscle Spindles in Human Extrinsic Eye Muscles," Brain 72 (March 1949), pp. 1-24.

4. Cooper, S., Daniel, P. D., and Whitteridge, D., "Nerve Impulses in the Brain Stem of the Goat. Responses with Long Latencies Obtained by Stretching the Extrinsic Eye Muscles," J. Physiol. 129 (1953), pp. 491-513.

5. Cooper, S., Daniel, P. D., and Whitteridge, D., "Nerve Impulses in the Brain Stem of the Goat. Spontaneous Discharges and Responses to Visual and Other Afferent Stimuli," J. Physiol. 120 (1953), pp. 514-527.

6. Crosby, E. C. and Henderson, J. W., "The Mammalian Midbrain and Isthmus Region. Part II: Fiber Connections of the Superior Colliculus. B: Pathways concerned in automatic eye movements," J. Comp. Neurology 88 (1948), pp. 53-91.

7. Dallos, P. J. and Jones, R. W., "Learning Behavior of the Eye Fixation Control System," IEEE Trans. Automatic Control, AC-8 (July 1963), pp. 218-227.

8. Fender, D. H. and Nye, P., "An Investigation of the Mechanisms of Eye Movement Control," Kybernetik 1 (July 1961), pp. 81-88.

9. Ludvigh, E., "Possible Role of Proprioception in the Extraocular Muscles," A. M. A. Arch. Ophthal. 48 (1952), pp. 436-441.

10. Pasik, P. and Pasik, T., "Oculomotor Functions in Monkeys with Lesions of the Cerebrum and the Superior Colliculi," The Oculomotor System, Chapter III, edited by M. B. Bender, Harper and Row, Publishers, New York (1964).

11. Stark, L., Vossius, G., and Young, L. R., "Predictive Control of Eye Tracking Movements," IRE Trans. Human Factors in Electronics, HFE-3 (Sept. 1962), pp. 52-57.

12. Whitteridge, D., "Central Control of Eye Movements," Handbook of Physiology; Section 1: Neurophysiology, Vol. II, edited by J. Field, American Physiological Society, Washington, D.C. (1960), pp. 1089-1109.

13. Young, L.R., Van Houtte, N., and Forster, J.D. "A Hybrid Model for Eye Tracking Movements," Proc. of Annual Conference on Engineering in Medicine and Biology, Vol. 10 (1968), p. 25.7.