PSYCHOPHYSICAL STUDIES OF THE OPTOKINETIC RESPONSE IN THE NORMAL MONKEY

by

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Abstract

The purpose of this study was to determine, by means of psychophysical and statistico-mathematical procedures, the limits of visuooculomotor capacity in the normal monkey as the basis for further studies of neural mechanisms. The absolute luminance threshold for the optokinetic response and the lower and upper optokinetic frequency thresholds as a function of the stimulus luminance were determined in 5 monkeys (*Macaca mulatta*). Stimuli were vertical bands, 21.5 cm wide, 1:9 light/dark ratio, moving across a 106 x 106 cm screen placed 25 cm in front of the animal. Eye movements were recorded by a standard electrooculographic technique. In addition, they were amplified, digitized, counted and statistically evaluated by a specially programmed digital computer. The "presence" of an optokinetic response was indicated by a significant asymmetry in the number of eye movements to the right and to the left tested with the binomial test in 3 consecutive trials. Thresholds were defined as the lowest or highest stimulus frequency which just elicited the response. It was found that the absolute luminance threshold lay at $\bar{6}.35$ log ftL. Once this threshold was surpassed, lower and upper optokinetic frequency thresholds exhibited differential characteristics. Lower threshold contours were not influenced by the stimulus luminance, whereas upper threshold contours were significantly affected and exhibited the photopic and scotopic components expected from an organism with duplex retina. On the basis of previous data and the present results, a mathematical model of the optokinetic response in the normal monkey was developed. This model allowed the prediction of the entire gamut of optokinetic reactions, i.e., their limits and supra-threshold values.

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CHAPTER I

INTRODUCTION

Eye movements elicited by optic stimuli moving in succession across the fields of vision are generically termed optokinetic responses. The most common type is optokinetic nystagmus (O.K.N.). This phenomenon is present in organisms that can move the eyes independently of the head, and is characterized by a repetitive pattern of oculomotor activity. Each unit of nystagmus consists of a "slow phase" in the same direction of the moving stimulus, and a "fast phase" in the opposite direction. In species where the independence between the movements of the head and eyes is absent or barely incipient (amphibians, reptiles, birds, and certain rodents), "head nystagmus" occurs. In most insects, moving stimuli elicit gross behavioral responses, such as changes in orientation of the entire body, which are called "optomotor reactions." In addition to these well recognized types of optokinetic responses, it is conceivable that optic stimuli moving in succession across the visual fields may give rise to oculomotor activity which does not have a characteristic repetitive pattern. Instead, the response may manifest itself as a predominance of eye movements in one direction, i.e., an asymmetric pattern which deviates from the random occurrence of spontaneous ocular deviations to either side. Comprehensive reviews of the early literature on O.K.N. may be found in Smith and Bojar (1938), Roelofs (1954), Keiner and Roelofs (1954), and Reinecke (1961).

The search for the neural basis of O.K.N. has been the object of several investigations in the monkey using the ablation technique to study the effect of circumscribed lesions of the cerebrum and brain stem upon this phenomenon. Conclusions have ranged from the delineation of specific cortical and subcortical "centers" governing O.K.N. (Crosby and Henderson, 1948; Henderson, and Crosby, 1952) to the complete denial of the existence of such centers (Pasik and Pasik, 1964a, b; Pasik, Pasik, and Bender, 1960, 1966, 1969; Pasik, Pasik, and Krieger, 1959). The latter series of experiments served to establish a general pattern of O.K.N. dysfuction which paralleled the defects in conjugate gaze caused by the same lesions. These studies did not demonstrate, however, the absolute equipotentiality of the cerebrum with regard to O.K.N.. Conclusions were based only on the presence or absence of the phenomenon when elicited by a narrow range of stimulus frequencies and no attempt was made to quantify the response.

It is well recognized that psychophysical techniques may reveal the existence of subtle deficits by placing at a premiun the sensory capacity of the organism. It appears therefore a convenient method to disclose any possible differential effect of circumscribed lesions of the central nervous system upon O.K.N.. Moreover, by relating parametrically several stimulus and response characteristics, it might be possible to separate sensory, motor, and processing components of the phenomenon as differentially affected by specific lesions. For example, changes in response characteristics resulting from variations in the luminance of the stimulus may reflect events occurring in the afferent or input component of O.K.N., whereas response features which are not affected by wide variations in the same parameter might be related to properties of the efferent or output component of the phenomenon.

Perhaps the most significant threshold studies which used optokinetic responses as indicators are those of Crozier and coworkers who determined sensitivity functions to optokinetic stimuli in species ranging from insects to man. The type of optokinetic response used varied according to the species: gross "optomotor reactions" in insects and fish (Crozier, Wolf, and Zerrahn-Wolf, 1936-1937; Wolf, and Zerrahn-Wolf, 1935-1936); "straightening reactions" in amphibians (Crozier, and Wolf, 1939); "head nystagmus" in reptiles and birds (Crozier, and Wolf, 1939-1940, 1940-1941). All of these experiments attempted to determine the highest frequency of stimulation which just elicited an optokinetic response (upper optokinetic frequency thresholds). Either the frequency of the optokinetic stimulus was decreased holding its luminance constant, or the luminance was increased, at a constant frequency, until the response became apparent. This type of stimulation was designated as "flicker," the assumption being that the stimulus frequency in cycles per sec (independently of its velocity) was *the* specific stimulus parameter which determined the response. By plotting upper optokinetic thresholds (or "critical flicker fusion" values) as a function of stimulus luminance, they attempted to islolate rod and cone (physiological) populations in each species. Since the population of receptors described probability integral curves, data were interpreted in terms of a statistical theory of visual sensitivity which is still accepted. The threshold values for fish (*Lepomis* and *Fundulus*) extended from 1 to 50 cps, with the scotopic-photopic transition point located at approximately $\bar{2}.5$ log mL in *Lepomis*, and at about $\bar{3}.5$ log mL in *Fundulus* (Crozier, Wolf, and Zerrahn-Wolf, 1936-1937; Crozier and Wolf, 1939-1940). In the frog, limens ranged from 2 to 40 cps, and the transition lay at about $\bar{3}.5$ log mL (Crozier and Wolf, 1939). The same group of investigators attempted to reproduce in human subjects the experimental situation used in lower species with at least two important differences. Firstly, humans observed the optokinetic stimulus through a telescopic tube whereas all other species were inside the rotating cylinder.

Secondly, the response indicators in man were "verbal reports": "...the speed of rotation of the cylinder was slowly reduced until the observer signalled the operator that flicker was recognized," (Crozier, Wolf, and Zerrahn-Wolf, 1937-1938, p.209). The values obtained in the latter study were 1-50 cps with the scotopic-photopic discontinuity located at about $\bar{2}.0$ log mL.

The preceding review shows that Crozier and coworkers were particularly interested in sensory processes, and to a considerable lesser degree in the nature of the optokinetic response. This is also apparent in the experiments of K.U. Smith on "visual acuity" and "perception of movement" in cats and guinea pigs after brain lesions (Smith, 1937, 1941), and in the more recent studies of Blomberg (1960) and Blomberg and Wassén (1962) in man. Smith (1937) tested cats for visual acuity following removal of the striate cortex by presenting the animals with moving, alternating black and white lines (1:1 ratio). Upper optokinetic thresholds were determined by "...observing the presence of pursuit movements of the head and the eyes made in response to the rotating striped patterns of varying widths." (Smith, 1937, p. 564). Cats were tested only postoperatively, and the stimulus luminance was not manipulated. Upper velocity thresholds for movement perception were determined in albino and pigmented guinea pigs, before and after removal of occipital areas using essentially a similar technique (Smith, 1941). In this case, "head nystagmus" was recorded by means of a mechanical arrangement. A threshold for movement perception was defined as the stimulus velocity associated with the cessation of the nystagmic pattern in the recording. Although the use of a recorded information represented a considerable improvement to define the "threshold," the method was not numerically precise since it depended only upon the appearance of the recorded pattern. The same applies to more recent threshold studies in man.

Blomberg (1960) determined "optokinetic fusion limits" in humans to study the effect of drugs, particularly alcohol (Blomberg and Wassén, 1962), using essentially the same approach of Smith (1941). The optokinetic stimuli were the shadows of a small moving cylinder made of equally-spaced ribs, projected upon the inside of a hemicylindrical screen. Subjects were placed at the axis of the half-cylinder and the eye movements were recorded electrographically. It was found that "at a low (optimal) speed the eyes could follow each vertical stripe on the screen, but when the speed was gradually decreased, the eyes jerked over more and more stripes until the speed had become too high for the subject to be able to follow... This limit...was in most cases very distinct [and when] the speed decreased, optokinetic nystagmus... re-appeared..." (Blomberg, 1960, p. 458). Group averages ranged from 254 to 284°/sec with values as high as 420°/sec. The same subjects were also examined for "critical flicker fusion" (CFF) by having them look at a screen through a tube. Optokinetic thresholds and CFF values were determined at only one luminance level. In all cases, CFF values were "considerably" higher than optokinetic threshold values (30 stripes/sec or 540°/sec). Subsequently, Blomberg and Wassén (1962) reported a statistically significant decrease in optokinetic threshold values as a result of a small dose of alcohol administered intravenously. The authors concluded that this method of obtaining optokinetic thresholds was "very objective" and suitable for studies on the effect of drugs.

It is apparent from the preceding review that psychophysical investigations on O.K.N. have dealt with the "upper thresholds" only. The determination of "lower thresholds," i.e., the lowest velocity or frequency of the stimulus which elicits the response, has not been attempted thus far. Moreover, since the optokinetic response has not been quantified, no objective criterion has been advanced to define the response at threshold. In fact, the response occurrence in some of the studies was judged by naked-eye observations of the organism's behavior (Crozier's series, see above), or by the "appearance" of the electronystagmographic record (Smith, 1941; Blomberg, 1960). Therefore, it appears important to identify response continua which would allow the definition of thresholds according to a statistical criterion of occurrence of such response characteristic.

There is general agreement that the velocity of the slow phase is one of the response features that best reflects the effect of the optokinetic stimulus in man (Dodge, Travis, and Fox, 1930; Grüttner, 1939) and in the monkey (Komatsuzaki, Harris, Alpert, and Cohen, 1969). However, this finding applies to the fully-developed suprathreshold response, i.e., optokinetic nystagmus, which has an optimal stimulus range where the slow phase velocity can be measured (Komatsuzaki, Harris, Alpert, and Cohen, 1969). Under conditions of no stimulation, as well as around the lower and upper thresholds, it is most difficult to detect slow phases if they exist altogether. Moreover, recent work in man by Körner and Dichgans (1967) suggested that slow phase velocity did not correlate with perception of real movement. Judgments of stimulus velocity showed a one-to-one correlation with the actual stimulus parameter, whereas slow phase velocity lagged behind the stimulus velocity at an ever increasing magnitude until it could no longer be measured. Thus, the slow phase velocity is of relative value for the determination of limits of response.

The frequency of the optokinetic response, defined in terms of the relative proportion of eye movements to the expected side in relation to those to the opposite side per unit time, appears to be a better behavioral indicator to determine when the optokinetic stimulus is just being detected. This measurement of oculomotor activity can be accomplished even under conditions of no stimulation or around threshold values. In addition, once a statistical criterion for significant "asymmetry" or predominance of eye movements in one direction is found, both the lower and the upper threshold, i.e., the lowest frequency that elicits the response and the highest frequency which no longer elicits the response, can be defined in a similar manner.

The asymmetry of the optokinetic response has proven to be an useful measurement of the effective stimulus in lower species. Hassenstein and Reichardt (1956) and Reichardt (1961) studied several features of information processing in the insect's nervous system (the beetle *Chlorophanus*), at suprathreshold levels. Changes in the normal walking behavior of the insect were used to evaluate the effect of optokinetic stimulation. The dorsum of the insect was glued to a piece of cardboard fixed to a stand and the beetle, thus suspended, held with its legs a Y-maze globe made of light straw. Walking movements resulted in displacements of this globe, and the number of choices to the right and to the left at the decision points were roughly equal under conditions of no stimulation. During optokinetic stimulation the beetle exhibited compensatory movements in the direction of the rotating stimulus.

A measure of asymmetry was also used in the monkey to investigate the effect of stimulus frequency on O.K.N. (Valciukas and Pasik, 1968; Valciukas, Pasik, and Pasik, 1968). In these studies, the frequency of the response was computed as the algebraic sum of the number of nystagmic beats to the right (positive) and to the left (negative) per unit time. The results made possible the formulation of a limited model of the optokinetic response which allowed the prediction of response frequencies over a wide range of stimulus frequencies. The attempt to develop a more complete mathematical model of the optokinetic response in the monkey seems premature in view of the still unknown characteristics. However, some words by Ratliff (1965) on the contribution of mathematical model to the "direct experimental analysis of the function of the nervous system" are encouraging:

> "Mathematical models...help to solve one of the major problems facing neurophysiology: how to reduce, analyse, and comprehend the enormous amount of data that can now be obtained. It is now a simple technical matter to record the activity of individual neurons simultaneously at several different points in the nervous system and to accumulate in a few seconds a permanent record of several hundred, or even several thousand, essentially identical nerve impulses. But describing the function of the nervous system in terms of a great multiplicity of essentially identical unitary processes is not unlike attempting to mete out 'the heavens with a span' or to comprehend 'the dust of the earth in a measure.' The greatest contribution any mathematical description of, or theorizing about, the function of the nervous system is likely to make is to increase the width of our 'span' and the volume of our 'measure.' (Ratliff, 1965, p. 141)

The first attempt to develop a model of optokinetic nystagmus was made by Grüttner (1939) using human subjects. This investigator outlined possible functional relationships between the amplitude, frequency, and slow phase velocity, and the velocity of the stimulus by means of free-hand curves. He also observed the influence of other stimulus parameters such as the width of the stripes, direction of movement, size of the visual field, and luminance. The attempt, however, was limited because no consistent criterion for response quantification was developed (means and standard deviations were not reported). In addition, the role of stimulus luminance as an important parameter could not be demonstrated. The same author noted that limitations of the equipment might have been responsible for this failure.

The last feature to be considered deals with the technical limitations encountered in the study of optokinetic responses. The most widely used method to record eye movements and nystagmus is electrooculography or electronystagmography. The early developments of these techniques were reviewed by Smith and Bojar (1938), Marg (1951), Henriksson (1955), and Jung and Kornhuber (1964). Recent technological advances attempted to record certain characteristics of nystagmus and/or quantify them by means of objective methods. Electronic circuitry was used to determine and graph the first derivative of the slow phase of nystagmus, i.e., changes in the amplitude of the recorded signals reflected changes in the velocity of the slow phase (Henriksson, 1955), and to count and display on polygraph paper the frequency of nystagmus (Torok and Nykiel, 1962). More recently, a computer technique for the quantitative analysis of nystagmus was developed (Herbert, Abrahamson, Einarson, Hofman, and Linder, 1968). In the latter study, the electrooculographic signal was matched to a control signal of a preset wave-length and amplitude, and incoming signals meeting the specified characteristics were stored on magnetic tape. The analog signal was then analysed and the print-out gave (a) the differentiated response under correction for spontaneous nystagmus; (b) total amplitude; (c) total number of beats within different phases of the recording; (d) duration of each phase; (e) occurrence in time of maximun response and its size; and (f) maximun frequency of the nystagmus. At the time of publication, data were still being collected for further statistical analysis. It is apparent that most quantitative studies have involved the measuremt and counting of eye movements in selected fragments of the recorded session, days or weeks after the experiment was made, i.e., none of these recent techniques processed the electrooculographic signal while it was being generated by the subject. This limitation reduced the possibilities of utilizing the techniques in animal psychophysical studies where immediate results of a certain trial are desirable to set the stimulus parameter of a subsequent trial.

Statement of Purpose

The main purpose of this investigation was to determine the limits of optokinetic responses in the normal monkey by means of psychophysical and mathematical procedures, as the basis for further studies of the neural mechanisms of this form of behavior. Specifically, attempts were made: (1) to select an objective measure of the optokinetic response which would take into account the variations in the monkey's spontaneous oculomotor activity; (2) to determine lower and upper optokinetic frequency thresholds as a function of the stimulus luminance; and (3) to develop a model of the optokinetic response describing the relationship between the frequency of the response and both the stimulus frequency and its luminance. The basic technical needs were met by constructing an optokinetic stimulator which provided for frequencies covering the entire range of optokinetic responses, and for luminances that included both photopic and scotopic levels down to the absolute luminance threshold.

The methodological requirements involved the development of a procedure which allowed the use of a small general purpose digital computer in a semi-on-line type of arrangement to count, analyse, and perform statistical tests on electrooculographic data.

CHAPTER II

MATERIAL AND METHODS

A. Subjects

Five monkeys (Macaca mulatta), 2.8 to 4.2 kg in body weight were used in the experiments. These animals were selected for the relative symmetry of their spontaneous eye movements to the right and to the left when placed in darkness. In the experience of this laboratory, 10-20% of the monkeys provided by a commercial vendor develop spontaneous nystagmus under this condition. A sixth animal was discarded for this reason.

B. Apparatus

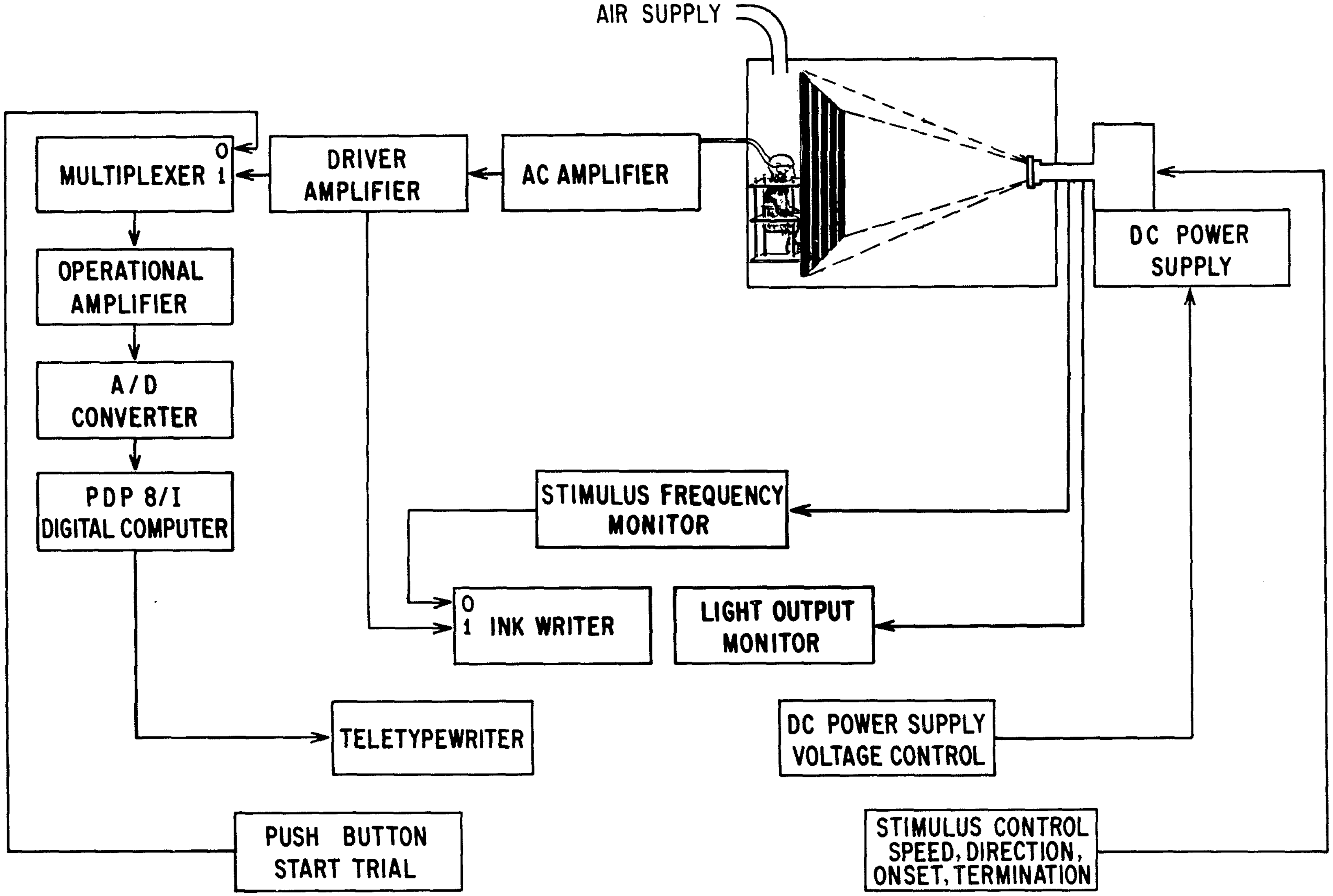
1. Optokinetic Stimulator

A diagram of the testing situation is depicted in Fig. 1. The monkey sat restrained in a special chair 25 cm behind a 106 X 106 cm rear-projection screen (Plexiglass Lenscreen, LS60PL, 1/8" thickness). The monkey's head was held relatively fixed by means of a bivalved molded acrylic holder that covered the entire surface of the head except the face and the ears.

A specially-designed 35 mm film-loop projector was used to produce luminous vertical stripes on the screen. The luminous source was a 1000-watt tungsten filament lamp operated by a Sorensen, Nobatron, DCR - 10A DC power supply. This power supply had a stability of .075% and a voltage ripple of .4%. The light output was verified on alternate days with the probe of a Gamma Scientific, Model 700, Log-Linear Photometer, connected to a jack which contained the end of a fiber optic bundle. The other end of this bundle was fixed at the edge of the light bean. Any observed decrement of the output was compensated by increasing the voltage of the power supply until a preset photometric value was obtained.

Figure 1. Diagram of the Testing Situation

The monkey sits in a special chair, behind a rear-projection screen. A film-loop projector powered by a highly stabilized DC power supply is used to expose luminous stripes on the screen. The animal, the screen, and the frontal lens of the projector are enclosed in a light-tight cubicle. Eye movements recorded by a standard electrooculographic technique are amplified, digitized, counted, and statistically evaluated by a specially programmed computer. The result of this analysis determines the frequency of stimulation to be used in the subsequent trial in a semi-on-line type of arrangement. The AC and driver amplifier and the ink writer are part of the Grass model 7 Polygraph.


AIR SUPPLY
MULTIPLEXER
0
1
DRIVER AMPLIFIER
AC AMPLIFIER
DC POWER SUPPLY
OPERATIONAL AMPLIFIER
A/D CONVERTER
PDP 8/I DIGITAL COMPUTER
STIMULUS FREQUENCY MONITOR
0
1
INK WRITER
LIGHT OUTPUT MONITOR
TELETYPEWRITER
DC POWER SUPPLY VOLTAGE CONTROL
PUSH BUTTON START TRIAL
STIMULUS CONTROL SPEED, DIRECTION, ONSET, TERMINATION

The optokinetic stimulus was provided by a 35 mm filmstrip loop obtained by photographing an artist drawn striped pattern with an Oxberry Animation Camera on high contrast film Kodak 5362. The variable aperture of the projector was set so as to project on the screen 5 vertical luminous stripes separated by dark bands. The stimulus unit or cycle consisted of a luminous stripe and a dark band with a total width of 21.5 cm (approximately 46° of visual angle at the center of the screen) and a 1:9 light/dark ratio.

The film could be driven at constant velocities, from right to left or from left to right, by means of a servomotor coupled to the transport mechanism. The motor speed control system (Electro-Craft Corporation, Minn., Series E-600) was modified by adding a helipot potentiometer and a 0 - 1,000 digital dial. The motor was found linear from 25 to 600 dial units. Two systems of gears, which could be selected with a mechanical clutch, were used to obtain a stimulus frequency range from .01 to 1 cps ("low frequency mode") and from 1-100 cps ("high frequency mode"). Monitoring of the frequency of stimulation was provided by a photocell located at the edge of the aperture in the film transport mechanism.

The frontal lens of the projector, the screen, and the monkey were inside a light-tight cubicle. Forced air circulation was provided throughout the experimental session.

2. Calibration of Stimulus Frequency

The "high frequency mode" was calibrated by replacing the light source of the projecting system by the lamp of a Grass PS 2 photostimulator which had been previously calibrated with a cathode ray oscilloscope. Measurements were made with settings from 10 to 100 flash/sec in 10 flash/sec steps. At each of these steps, the dial of the motor control unit was increased from zero until a still image of the moving stripes of the film was first seen through the projecting system. For the "low frequency mode," measurements were made from 100 to 580 dial units in 40 unit steps. At each setting, the time lapse for the passing of 10 stimulus cycles at the edge of the screen was measured with a chronometer and the stimulus frequency calculated as 10 divided by the time in seconds.

The forward and reverse directions of the motor were slightly different and separate calibrations of both modes were performed for stimuli moving from right to left and from left to right. Interpolated step values were computed for the "high" and "low frequency modes" by the method of least squares which was applicable due to the linearity of the motor in most of its range. The extreme, non-linear portions of the motor, were not used in the experiment and therefore were not included in the calculations. Fig. 2 gives the graph of these calibrations and the representative equations for the reverse direction of the motor (stimulus movement from left to right) calculated by the PDP 8/I computer with a program specially written for that purpose. A constant factor was used to correct these values for the forward direction (stimulus movement from right to left).

The stability of the calibration values was periodically checked during the experiment at selected settings of the motor control unit.

3. Calibration of Stimulus Luminance

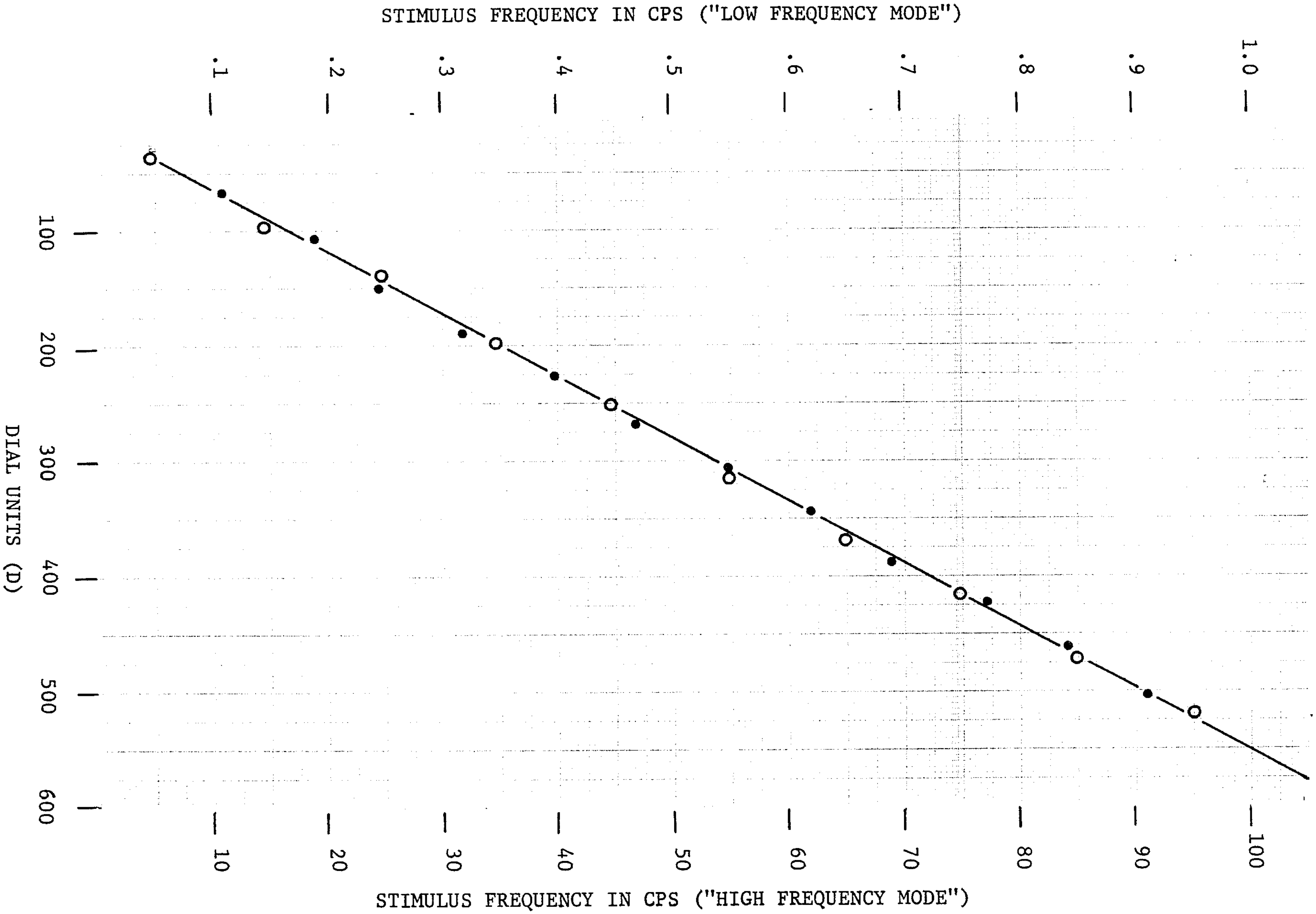
The stimulus luminance was defined as the mean luminance of the luminous stripes. The measurement was performed with a Gamma Scientific Model 700 Log-Linear Photometer equipped with a "photopic" filter which

Figure 2. Calibration of Stimulus Frequency

The motor was used in reverse direction. "Low" and "high frequency modes" indicated by solid and open circles respectively. Each point represents a determination. The linearity of the system allowed an almost perfect fit given by the equations:

$$F_s = -\ .04 + .0018\ D \quad \text{for the "low frequency mode"}$$

and $$F_s = -\ 3.43 + .19\ D \quad \text{for the "high frequency mode"}$$


STIMULUS FREQUENCY IN CPS ("LOW FREQUENCY MODE")
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
DIAL UNITS (D)
100
200
300
400
500
600
10
20
30
40
50
60
70
80
90
100
STIMULUS FREQUENCY IN CPS ("HIGH FREQUENCY MODE")

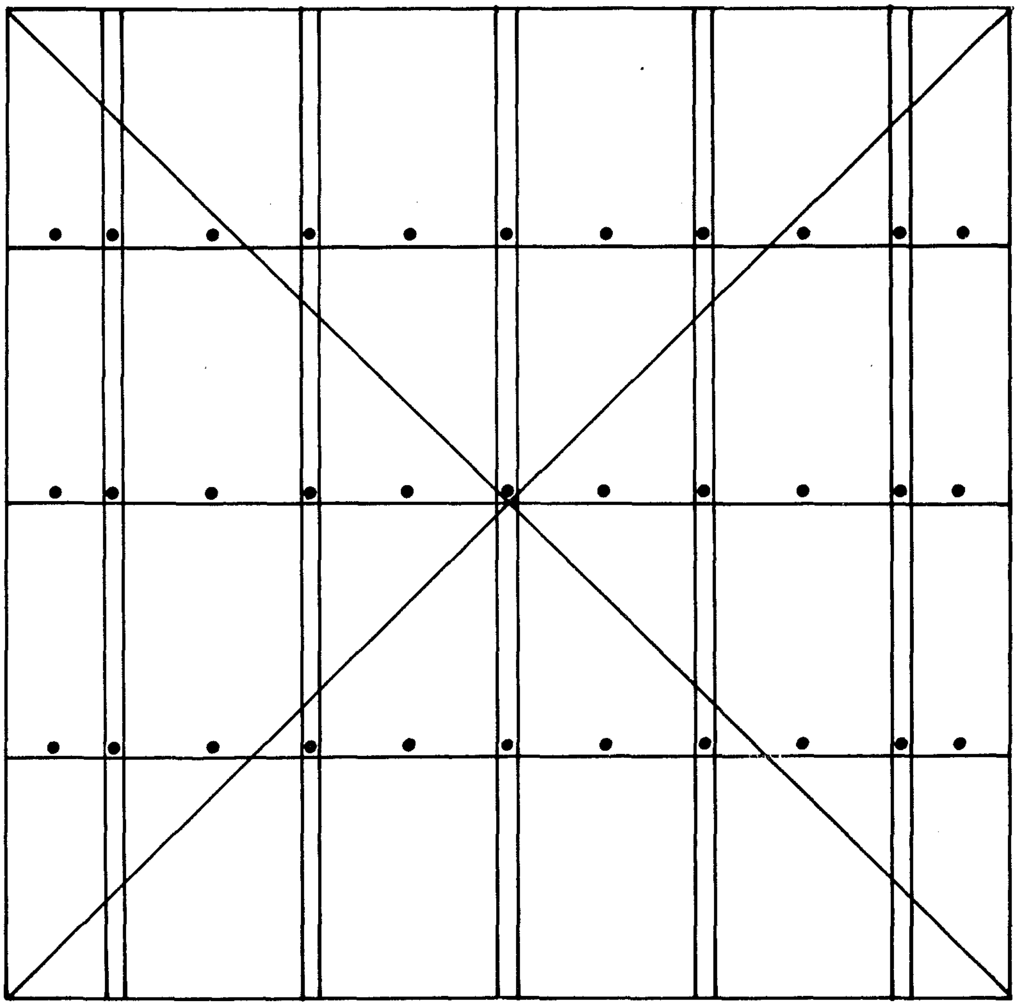
matched quite closely the spectral sensitivity of the sensing element to that of the human eye. The instrument was calibrated before each measurement with a krypton^{85} radioactive luminous standard source (I-Lite Calibration Source, American Atomic Corporation). Both, the photometer and the standard source, were certified by an independent laboratory with reference standards traceable to the National Bureau of Standards.

During the basic determination there were no filters in the projecting system. The screen was divided into four horizontal fields by means of fine silk threads as indicated in Fig. 3. The crossing point of two diagonal threads marked the center of the screen. Four photometric measurements were made just above the horizontal threads at each of the points indicated by the dots. The fiber optic probe of the photometer was held normal to the surface of the screen by placing it in the center hole of a special adaptor. Each determination was made with a different luminous stripe at the center of the screen. These measurements revealed a gradient decreasing from the periphery to the center. The mean luminance of the luminous stripes was 6.61 ftL (.82 log ftL). This value resulted from averaging the 60 measurements performed at the 15 selected points of the screen. The mean luminance of the dark bands was .0172 ftL ($\bar{2}.24$ log ftL) and derived from averaging the 72 determinations made at the 18 selected points of the screen. The contrast, defined as the ratio between the mean luminances of the luminous stripes and the dark bands, was 2.58 log units and remained constant for all levels used.

To calibrate the filters, a measurement set as 100% was made on a diffusing screen placed against the projecting lens with the film of the optokinetic pattern in place. Due to limitations of the photometer, only

Figure 3. Zoning of the Screen to Calibrate the Stimulus Luminance

The screen was divided into four horizontal fields by means of fine silk threads as indicated. The crossing point of two diagonal threads marked the center of the screen. Photometric measurements were made just above the horizontal threads at the points indicated by the dots. Four photometric determinations were made at each point. A different luminous stripe was placed at the center of the screen for each measurement.



the 1, 2, 3, and 4 neutral density filters could be calibrated directly in terms of percent transmittance. Values for combinations of filters were obtained by computing the added densities. Table 1 gives the percent transmittance of filters #1, 2, 3 and 4, and the combination of 1 + 4, 2 + 4 and 3 + 4, together with the mean luminance of the luminous stripes in ftL ($\bar{B}$), and the logarithm of $\bar{B}$. Eight values of stimulus luminance were thus obtained. The range extended from $\bar{7}.73$ to .82 log ftL in approximately one log unit steps.

4. Recording Techniques

Ocular movements in the horizontal plane were recorded in one channel of a Grass model 7 polygraph using R-C amplification with a .1 sec time constant (Fig. 1). Needle electrodes were inserted subcutaneously at the outer canthi. Polarities were adjust so that upward or downward deflections were produced by rapid eye movements to the right or to the left respectively. For all monkeys the gain was kept at 500 μV/cm. Fig. 4 illustrates a recording of spontaneous oculomotor activity under conditions of no stimulation, i.e. with stimulus stripes present but not moving. During the 6 minutes of this recording there were 115 eye movements to the right and 113 to the left. No attempt was made to identify upward or downward components of possible oblique eye movements. Blink artefacts were infrequent and in any event were cancelled out because of their consistent biphasic pattern of recording.

5. Computer, Input-Output Devices, and Programs for the Automatic Counting of Eye Movements and Statistical Analysis

A semi-on-line situation was arranged to count automatically the

TABLE 1

CALIBRATION OF FILTERS AND MEAN LUMINANCE OF LUMINOUS STRIPES AT THE SCREEN

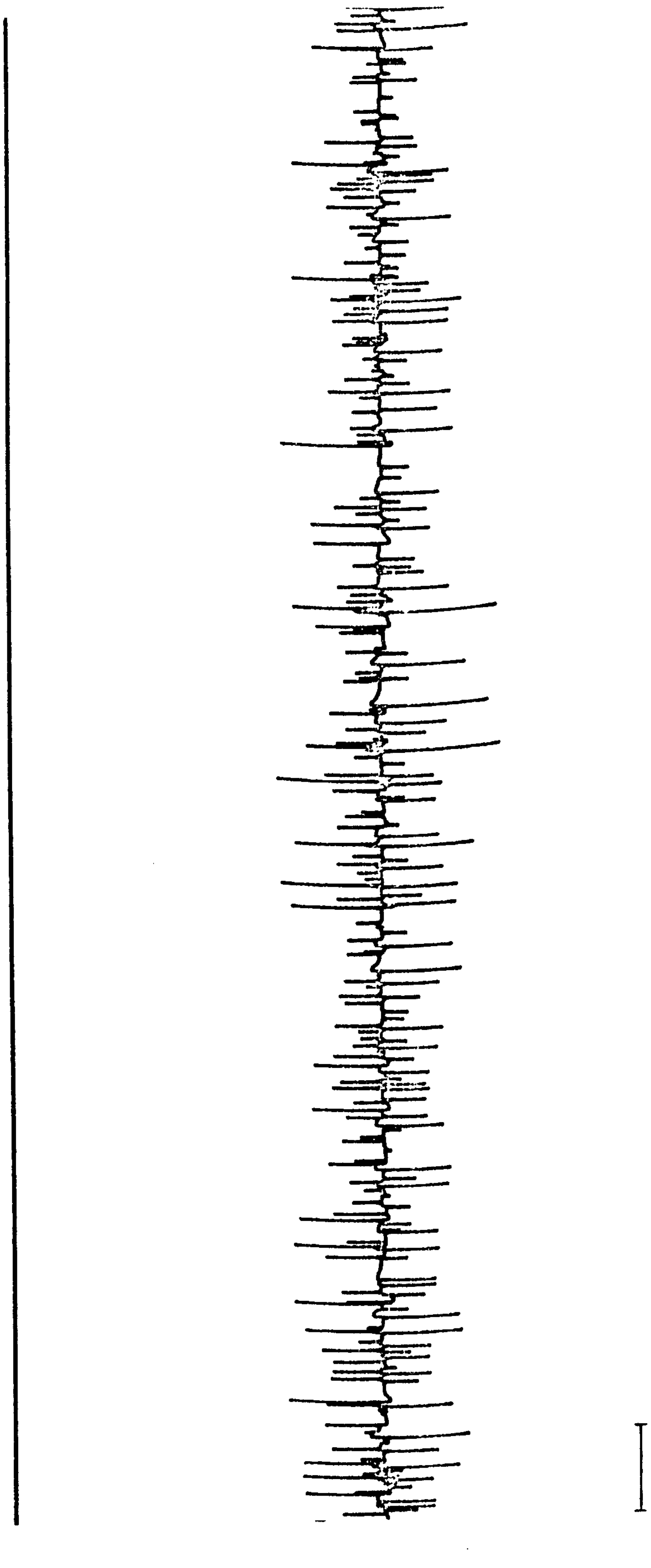
CALIBRATION OF FILTERS		STIMULUS LUMINANCE	
Density	% T	$\bar{B}$ in ftL	log $\bar{B}$
-	100 X 10^{0}	6.61 X 10^{0}	.82
1	77 X 10^{-1}	5.09 X 10^{-1}	$\bar{1}.71$
2	75 X 10^{-2}	4.96 X 10^{-2}	$\bar{2}.70$
3	86 X 10^{-3}	5.68 X 10^{-3}	$\bar{3}.75$
4	77 X 10^{-4}	5.09 X 10^{-4}	$\bar{4}.71$
1 + 4	77 X 10^{-5}	5.09 X 10^{-5}	$\bar{5}.71$
2 + 4	76 X 10^{-6}	5.02 X 10^{-6}	$\bar{6}.70$
3 + 4	82 X 10^{-7}	5.42 X 10^{-7}	$\bar{7}.73$

Notes. T : transmittance

$\bar{B}$ in log ftL: absolute measurement made only for the first value with no filters.

Figure 4. Monkey #636. Spontaneous Oculomotor Activity

Upper trace: photoelectric monitoring indicates that the stimulus is stationary. Lower trace: electrooculogram shows 115 eye movements to the right and 113 to the left occurring in a 6-minute period. $\bar{B} = \bar{1}.71$ log ftL; calibration = 20 sec.



total number of eye movements to the right and to the left, and to perform statistical analysis on the results of 40-sec trials (Fig. 1). Potential differences between the electrodes generated by eye movements were amplified by a Grass Model 7P5A preamplifier and further amplified by a Grass Model 7 DAB driver amplifier. The output from the driver amplifier was fed into an AD08-B analog-to-digital converter (Digital Equipment Corporation) via channel 1 of a multiplexer. When the starting button was depressed, a 1.5 volts DC pulse activated channel 0 of the multiplexer which in turn initiated the storage of analog-to-digital conversions. An operational amplifier was used to match the polygraph output to the converter input. A PDP 8/I digital computer (Digital Equipment Corporation) functioned as the central processor.

Analog-to-digital conversions were taken every 50 msec and stored in a table consisting of 800 memory addresses. Timing of 40-sec trials was provided by a program loop. At the completion of the 800 analog-to-digital conversions, the octal number of each conversion was subtracted from the one that followed it. The resulting octal numbers and their sign were then stored in a 799 locations table. These differences, which could be positive, negative, or zero, were analysed via a series of short programs: (1) any difference below a certain limit value was rejected; (2) the first difference greater than the limit value was counted as an eye movement, to the right if positive and to the left if negative; (3) subsequent differences were ignored until one fell below the limit value. The limit value was empirically selected so that the number of eye movements counted by the computer matched the eye movements counted visually in the electrooculograms of 254 trials. The correlation coefficient between computer and visual counting was .99.

The program also calculated the z value of the binomial test. At the end of the 40 sec trial, the teletypewriter printed out the total number of eye movements to the right and to the left, and z. By reprogramming one location, it was also possible to leave the program recycling and printing out every 40 sec. This feature was used to quantify spontaneous eye movements for various intervals without sending the signal via the pushbutton device.

In addition, the author wrote general purpose FOCAL programs for curve fitting by the method of least squares, and statistical tests which were run in the same PDP 8/I computer. Appendix B contains the write up of some of these programs.

C. Procedures

1. Control of Subject Variables

Monkeys were given an intramuscular dose of amphetamine sulphate, 1 mg/kg of body weight, 30 min before the session started in order to attain a reproducible level of alertness during the experimental session. Amphetamine does not alter the basic characteristics of the response (Cohen, Alpert, Komatsuzaki and Hyams, 1969; Komatsuzaki, Harris, Alpert and Cohen, 1969; Valciukas and Pasik, 1968; and Valciukas, Pasik and Pasik, 1968). Sixteen sessions were scheduled for each animal with at least 5-day intervals between sessions.

Binocular stimulation was used throughout. Monkeys were light adapted inside the cubicle for 30 min at each luminance level with the optokinetic stimulus stationary, before the actual session began. Auditory cues and distractions were masked by the noise of the air supply and the fans of the power supply, projector and polygraph.

Control threshold determinations were performed with both pupils either dilated by topical application of 1% cyclopentolate hydrochloride or constricted by means of .5% eserine salicylate. Results were no different than under standard conditions and will not be discussed further.

2. Quantification of Spontaneous Oculomotor Activity

Spontaneous eye movements occurring in 40-sec intervals were counted at the end of the 30-min adaptation period prior to the determination of thresholds. For each monkey, 15 to 27 of such samples were obtained at each luminance level.

3. Response at Threshold

In the course of a threshold determination, the optokinetic response was considered as "present" if (1) there was a significant asymmetry in the number of eye movements to the right and to the left as determined by the binomial test (Siegel, 1956) at a probability of .05 in a 40-sec trial; and (2) such an asymmetry was sustained for three consecutive trials. The response was defined as "absent" if no significant asymmetry was detected as a result of the same test in three consecutive trials.

In the early stages of the experiment, the possibility of using a more classic criterion of 75% of eye movements in the expected direction was considered. However, it was found that when the total number of movements per trial was relative large, this estimate became unrealistic because the response on such trial resembled too closely a frank optokinetic nystagmus. For instance, in a trial with 80 eye movements, the 75% criterion would call for 60 movements in the expected direction, whereas the .05 level in the binomial test would be satisfied with only

48. In this latter case, the appearance of the electrooculogram was more of a predominance of eye movements in the expected direction than that of optokinetic nystagmus. In any event, the result of the binomial test had the additional advantage of keeping constant the probability of occurrence of an asymmetry of eye movements regardless of the magnitude of the sample.

4. Binomial Test

The binomial test was computed for each trial by:

$$z = \frac{(R - .5) - (NP)}{\sqrt{NPQ}}$$

where R is the number of eye movements to the expected side, .5 is a correction factor for continuity, N is the total number of eye movements to both sides, P and Q are the probabilities of occurrence of a movement to the right or to the left respectively. P and Q were calculated by:

$$P = \frac{R}{R + L} \;; \quad Q = \frac{L}{R + L}$$

where R and L are the number of eye movements to the right and to the left respectively. The z value at the .05 level of confidence is 1.64.

In a pilot experiment, analysis of 192 samples of spontaneous eye movements of three of the monkeys, with a stationary optokinetic pattern at .82 log ftL revealed that P and Q distributed normally with a mean of .5 and a *SD* of .05. Based on that information, limits of significance of P were found to be .42 and .58 by the formula:

$$\pm P = z\ SD \pm \bar{P}$$

where z was set equal to 1.64 (p = .05), SD = .05, and $\bar{P}$ = .5.

5. Stimulus Threshold

Fig. 5 gives examples of oculomotor activity of various frequencies of stimulation holding the stimulus luminance constant at $\bar{1}.71$ log ftL, and with movement of the stripes from right to left. At the top left, luminous stripes are present but not moving. The electrooculogram shows spontaneous oculomotor activity which is symmetrical, the z value being .20. The top center illustrates a trial at low frequency of stimulation (.11 cps) where there is no significant predominance of eye movements to the right and consequently this is a subthreshold trial. At top left, there is already a significant asymmetry as a result of optokinetic stimulation with a z equal to 1.74. This is the type of behavior observed at threshold. The bottom left tracing depicts a trial where stimulation is frankly suprathreshold and is associated with such an asymmetrical response that the probability of occurring by chance alone is less than 10-^{4}. This is the pattern of typical optokinetic nystagmus. The next recording results from a stimulus delivered at a higher frequency of stimulation. Here, behavior is characteristic of an upper threshold and quite similar to that shown for the lower threshold. Finally, in the last tracing, a higher frequency of stimulation results again in a random pattern of eye movements as evidenced by a z lower than 1.64.

According to the procedures used, four types of frequency thresholds could be defined. The lower ascending threshold was the lowest stimulus

Figure 5. Monkey #636. Oculomotor Activity Under Several Stimulus Conditions

Top: stimulus present but not moving (left); subthreshold trial (center); lower threshold trial (right). Bottom: suprathreshold trial (left); upper threshold trial (center); beyond upper threshold trial (right).

R: number of rapid eye movements to the right; L: number of rapid eye movements to the left; z: result of binomial test; B: stimulus luminance; R→L: direction of stimulus movement from right to left.

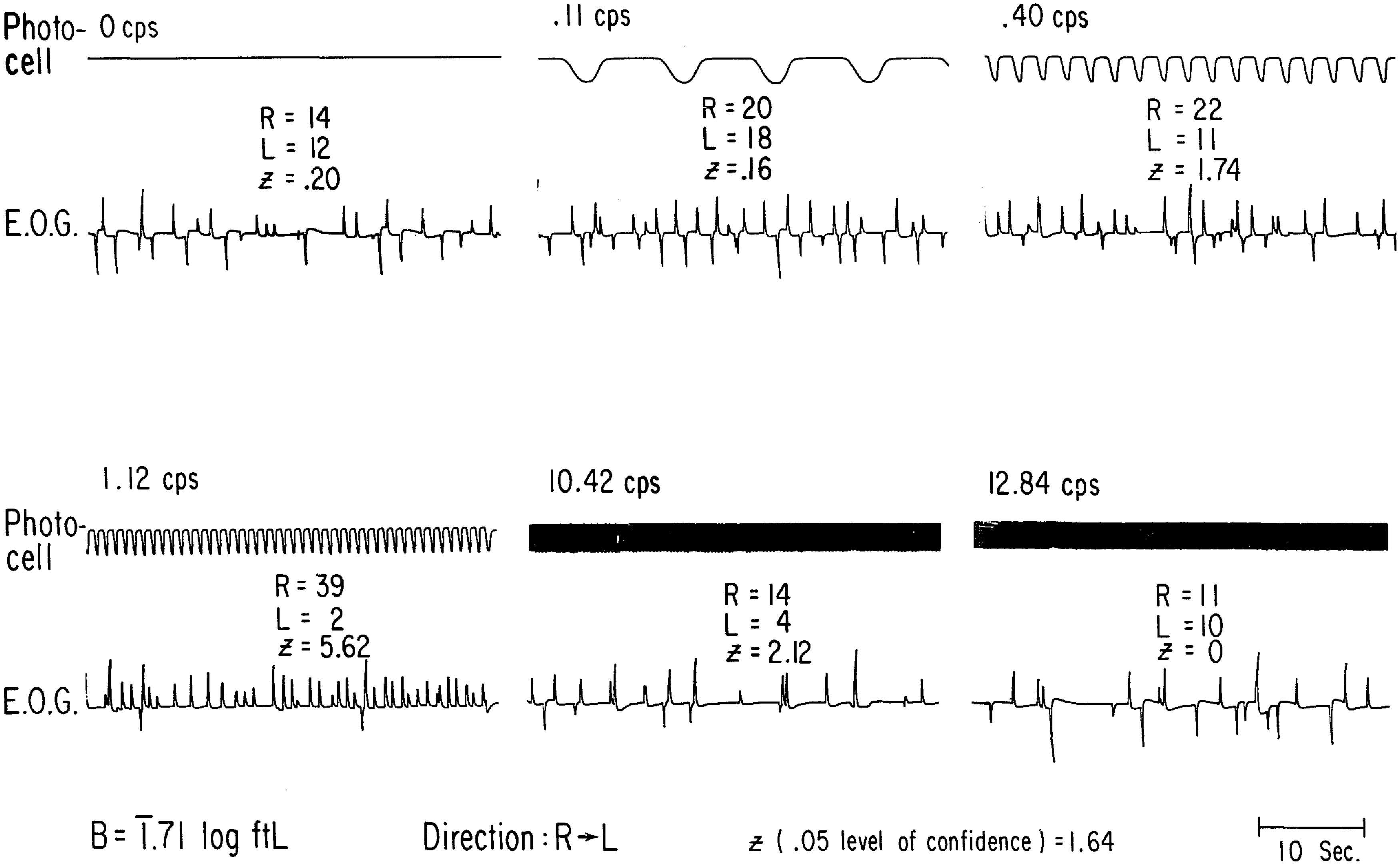


Photo-cell
0 cps
R = 14
L = 12
z = .20
E.O.G.
.11 cps
R = 20
L = 18
z = .16
.40 cps
R = 22
L = 11
z = 1.74
1.12 cps
Photo-cell
R = 39
L = 2
z = 5.62
E.O.G.
10.42 cps
R = 14
L = 4
z = 2.12
12.84 cps
R = 11
L = 10
z = 0
B = $\bar{1}$.71 log ftL
Direction : R → L
z (.05 level of confidence) = 1.64
10 Sec.

frequency which just elicited the response, whereas the lower descending threshold was the lowest frequency of stimulation which no longer elicited the response. The lower threshold was considered as the average of these ascending and descending thresholds. The upper ascending threshold was the highest stimulus frequency which no longer elicited the response. The upper descending threshold was the highest frequency of stimulation which just elicited the response. The upper threshold was obtained by averaging these ascending and descending thresholds.

6. Method and Program of Stimulus Presentation

Stimulation was delivered in 40 sec trials. The dùration of the intertrial interval which ranged from 2 to 40 sec, allowed for the necessary changes of stimulus conditions. Since in pilot experiments lower and upper thresholds were found to lie approximately one logarithmic unit apart, the step values were set at .05 cps for lower thresholds determinations and at .5 cps for upper thresholds determinations. This resulted in similar $\Delta F_S/F_S$ units being used to plot both thresholds (F_S: stimulus frequency). Thresholds were determined by a modified method of limits. Figs. 6 and 7 depict diagrams of the steps followed for the determination of the lower and upper optokinetic frequency thresholds respectively. Each determination was preceded by an exploratory test to estimate the range within which the threshold would possibly be found. In the few occasions when the response on the first trial was significantly asymmetrical the procedure was restarted a step lower or higher depending on whether the determination belong to an ascending or descending series.

Table 2 presents the programs of stimulus presentation used in each

Figure 6. Diagram of the Method to Determine Lower Optokinetic Frequency Thresholds

The squares represent serial stages of the procedure. The diamonds represent choice points.

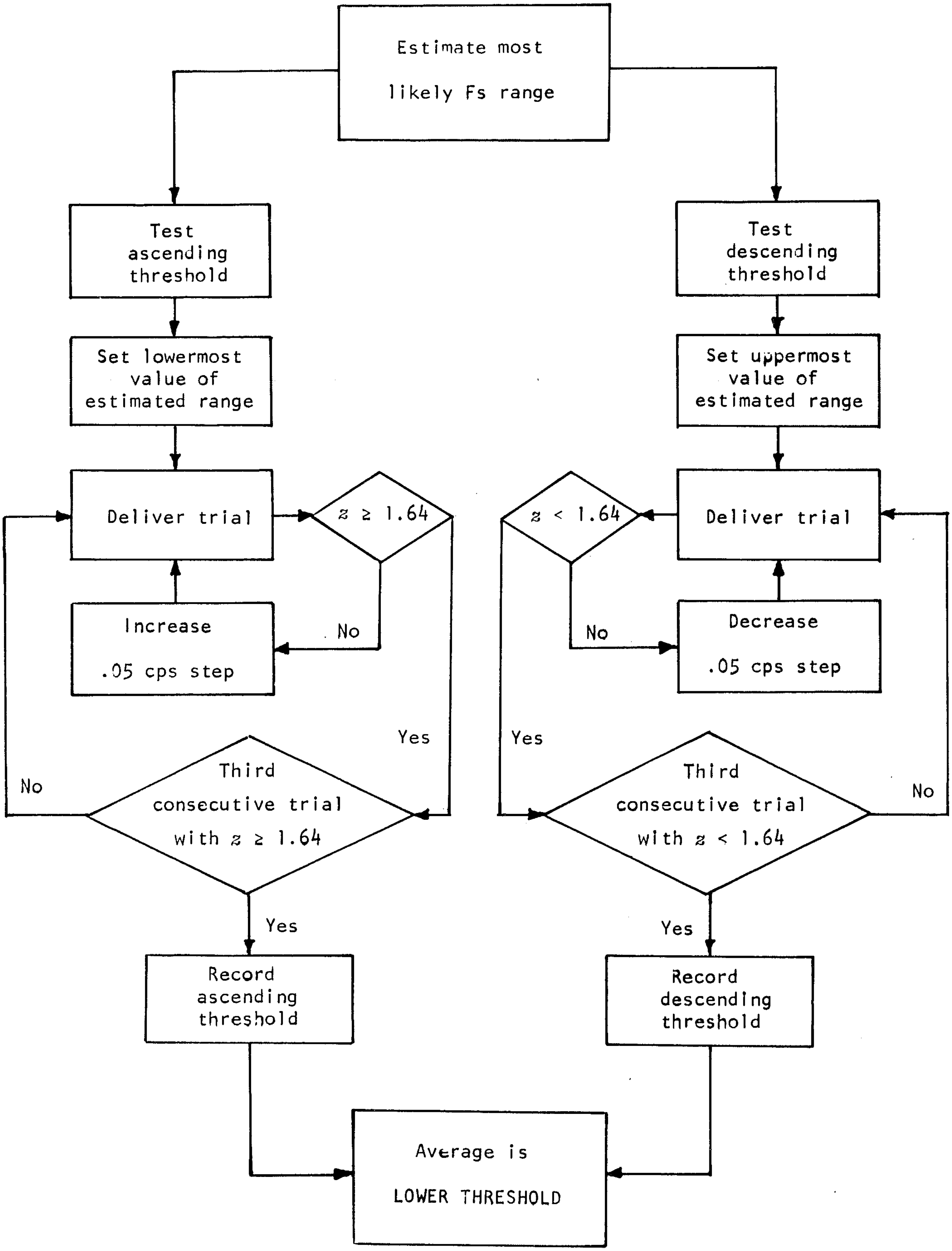

Estimate most likely Fs range
Test ascending threshold
Set lowermost value of estimated range
Deliver trial
$z \geq 1.64$
No
Increase .05 cps step
Yes
No
Third consecutive trial with $z \geq 1.64$
Yes
Record ascending threshold
Test descending threshold
Set uppermost value of estimated range
Deliver trial
$z < 1.64$
No
Decrease .05 cps step
Yes
No
Third consecutive trial with $z < 1.64$
Yes
Record descending threshold
Average is LOWER THRESHOLD

Figure 7. Diagram of the Method to Determine Upper Optokinetic Frequency Thresholds

The squares represent serial stages of the procedure. The diamonds represent choice points.

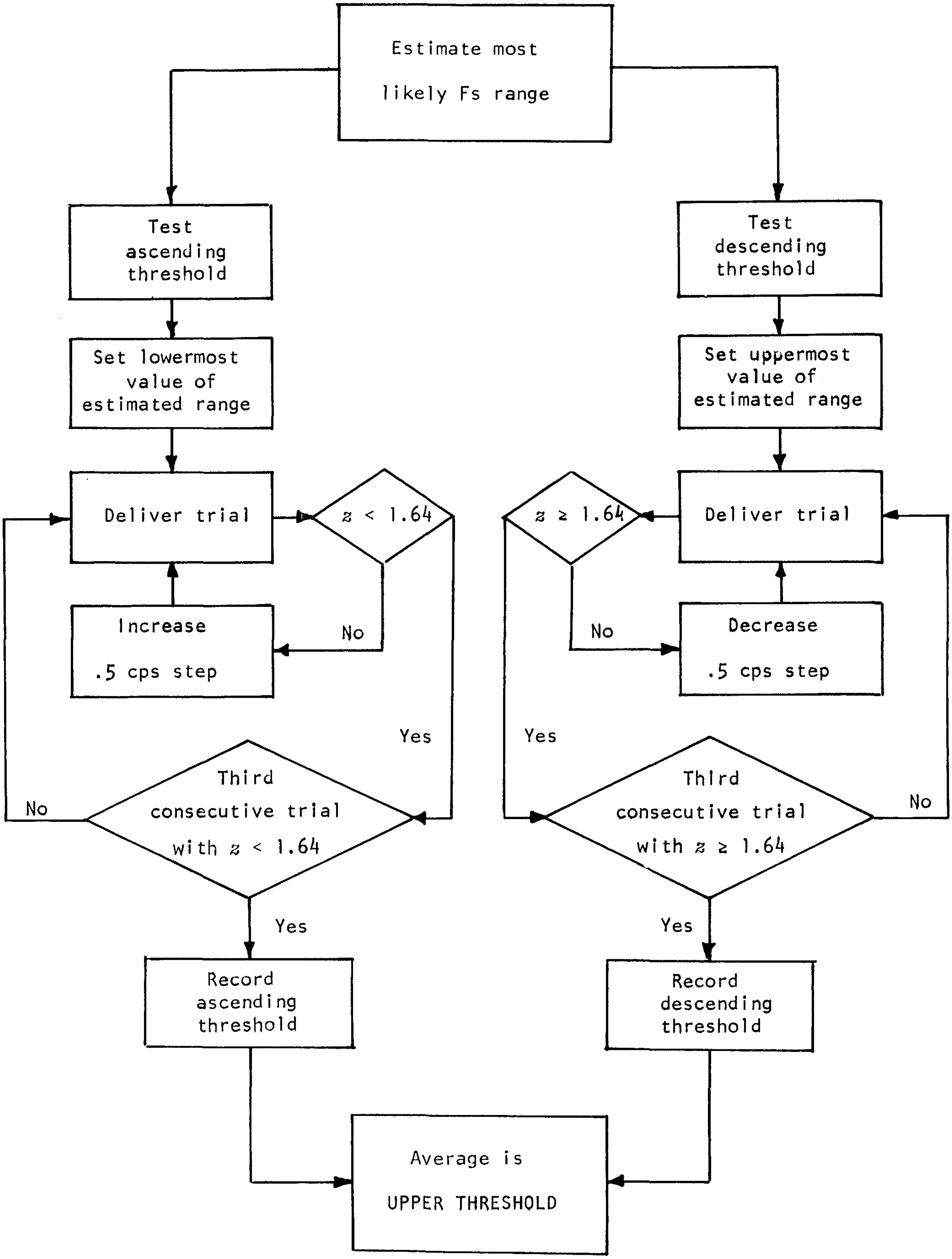

Estimate most likely Fs range
Test ascending threshold
Test descending threshold
Set lowermost value of estimated range
Set uppermost value of estimated range
Deliver trial
$z < 1.64$
$z \geq 1.64$
Deliver trial
Increase .5 cps step
Decrease .5 cps step
No
No
Yes
Yes
No
Third consecutive trial with $z < 1.64$
Third consecutive trial with $z \geq 1.64$
No
Yes
Yes
Record ascending threshold
Record descending threshold
Average is UPPER THRESHOLD

TABLE 2

PROGRAM OF STIMULUS PRESENTATION FOR EACH MONKEY

SESSION

1	2	3	4	5	6	7	7
14URA	15URA	11ULA	14ULA	22URA	21URA	26ULA	20ULA
14URD	15URD	11ULD	14ULD	22URD	21URD	26ULD	20ULD
14LLA	15LLA	11LRA	14LRA	22LLA	21LLA	26LRA	20LRA
14LLD	15LLD	11LRD	14LRD	22LLD	21LLD	26LRD	20LRD
10LLD	11LLD	15LRD	13LRD	20LLD	25LLD	21LRD	23LRD
10LLA	11LLA	15LRA	13LRA	20LLA	25LLA	21LRA	23LRA
10URD	11URD	15ULD	13ULD	20URD	25URD	21ULD	23ULD
10URA	11URA	15ULA	13ULA	20URA	25URA	21ULA	23ULA
12URA	13URA	17ULA	16ULA	24URA	27URA	27ULA	24ULA
12URD	13URD	17ULD	16ULD	24URD	27URD	27ULD	24ULD
12LLA	13LLA	17LRA	16LRA	24LLA	27LLA	27LRA	24LRA
12LLD	13LLD	17LRD	16LRD	24LLD	27LLD	27LRD	24LRD
16LLD	17LLD	12LRD	10LRD	23LLD	26LLD	25LRD	22LRD
16LLA	17LLA	12LRA	10LRA	23LLA	26LLA	25LRA	22LRA
16URD	17URD	12ULD	10ULD	23URD	26URD	25ULD	22ULD
16URA	17URA	12ULA	10ULA	23URA	26URA	25ULA	22ULA

9	10	11	12	13	14	15	16
33URA	37URA	37ULA	33ULA	45URA	44URA	40ULA	46ULA
33URD	37URD	37ULD	33ULD	45URD	44URD	40ULD	46ULD
33LLA	37LLA	37LRA	33LRA	45LLA	44LLA	40LRA	46LRA
33LLD	37LLD	37LRD	33LRD	45LLD	44LLD	40LRD	46LRD
34LLD	36LLD	35LRD	30LRD	47LLD	42LLD	42LRD	47LRD
34LLA	36LLA	35LRA	30LRA	47LLA	42LLA	42LRA	47LRA
34URD	36URD	35ULD	30ULD	47URD	42URD	42ULD	47ULD
34URA	36URA	35ULA	30ULA	47URA	42URA	42ULA	47ULA
30URA	31URA	36ULA	32ULA	41URA	40URA	43ULA	45ULA
30URD	31URD	36ULD	32ULD	41URD	40URD	43ULD	45ULD
30LLA	31LLA	36LRA	32LRA	41LLA	40LLA	43LRA	45LRA
30LLD	31LLD	36LRD	32LRD	41LLD	40LLD	43LRD	45LRD
32LLD	35LLD	31LRD	34LRD	46LLD	43LLD	44LRD	41LRD
32LLA	35LLA	31LRA	34LRA	46LLA	43LLA	44LRA	41LRA
32URD	35URD	31ULD	34ULD	46URD	43URD	44ULD	41ULD
32URA	35URA	31ULA	34ULA	46URA	43URA	44ULA	41ULA

Notes. In each condition, the first figure indicates the presentation (1 to 4), followed by the luminance level (0 to 7). The first letter represents upper (U) or lower (L) threshold determination, followed by the direction of the stimulus movement (to the right: R or to the left: L) and by the type of series used (ascending: A or descending: D). Within a session each luminance level (4 presentations) is preceded by 30 min. adaptation.

of the 16 sessions. During each session, 4 of the 8 luminance levels were presented in a random order. Only 2 determinations were made at each level: one for upper threshold (ascending and descending) and one for lower threshold (ascending and descending). At each luminance level the direction of the stimulus movement was opposite for upper and lower threshold determination. For instance, when the upper threshold was determined for movement of the stripes from left to right, the lower threshold was obtained for stimuli moving from right to left. This procedure was followed to balance out any possible effect resulting from recurrent stimulation with stimulus movement to one side only. Each condition for ascending and descending thresholds was presented 4 times to each monkey. Fig. 8 illustrates the experimental design for each monkey according to the program outlined above. Table 3 gives the various levels of averaging used in the course of the experiment.

Figure 8. Experimental Design

Upper and lower thresholds were determined at each of the 8 luminance levels. Four ascending and 4 descending thresholds were obtained with the stimuli moving to the right and an equal number of times with stimuli moving to the left.

		$\bar{7}.73$ log ftL		$\bar{6}.70$ log ftL		...	.82 log ftL	
		Direction		Direction			Direction	
		Right	Left	Right	Left		Right	Left
Upper Threshold	Ascending	N = 4	N = 4	N = 4	N = 4	...	N = 4	N = 4
	Descending	N = 4	N = 4	N = 4	N = 4		N = 4	N = 4
Lower Threshold	Ascending	N = 4	N = 4	N = 4	N = 4	...	N = 4	N = 4
	Descending	N = 4	N = 4	N = 4	N = 4		N = 4	N = 4

TABLE 3

NOTATION USED TO DESIGNATE LEVELS OF AVERAGING

$\bar{X}.$	Mean of ascending and descending thresholds per individual monkey.
$\bar{X}..$	Mean of four $\bar{X}.$ to the right, or of four $\bar{X}.$ to the left, per individual monkey.
$\bar{X}...$	Mean of $\bar{X}..$ to the right and to the left per individual monkey.
$\bar{X}....$	Mean of $\bar{X}...$ at a given stimulus luminance over the group.
$\bar{X}.....$	Grand mean of $\bar{X}....$ of all luminance levels over the group (used in lower threshold only).

CHAPTER III

EXPERIMENTAL RESULTS

A. Spontaneous Oculomotor Activity

The main purpose of quantifying spontaneous eye movements was to find out whether the assumption of right-left symmetry of oculomotor activity could be maintained in the presence of the stationary stimuli at each luminance level. As indicated in Methods (page 31), to perform the binomial test on each trial, the probabilities of occurrence of eye movements to the right (P) and to the left (Q) were both set equal to .5 on the basis of pilot data obtained at only one stimulus luminance. Table 4 shows the values of P at each luminance level per individual monkey. Only 2 out of 40 of these values exceeded slightly the limits of significance previously established (.42 - .58). This occurred in Monkey #616 at the two lowest luminances tested. The results also show that the mean value of P for the group ($\bar{P}$) was practically .5 for all luminance levels. In addition, the variability tended to be greater as the stimulus luminance decreased. These increases in variability may be interpreted as a "release" of individual patterns of asymmetry in spontaneous oculomotor activity at lower luminance levels.

B. Absolute Luminance Threshold for Elicitation of an Optokinetic Response

1. Individual Data. The attempts to determine lower and upper thresholds were not always successful. Occasionally, the entire range of available stimulus frequencies was delivered without resulting in significant asymmetries. Such attempts, designated as *RM* for random movements, were opposed to the "positive" attempts which were always associated with a numerical value. The number and percentage of positive

TABLE 4

PROBABILITY OF OCCURRENCE OF A SPONTANEOUS EYE MOVEMENT TO THE RIGHT (*P*) AT EACH LUMINANCE LEVEL

$\bar{B}$	MONKEY #					$\bar{X}$	*SD*
	612	616	617	636	637		
$\bar{7}.73$	.55	.39	.61	.53	.45	.51	.086
$\bar{6}.70$	.50	.41	.56	.51	.51	.50	.054
$\bar{5}.71$	.53	.48	.54	.52	.51	.52	.023
$\bar{4}.71$	.51	.44	.51	.55	.48	.50	.041
$\bar{3}.75$	.48	.43	.51	.55	.50	.49	.044
$\bar{2}.70$	.46	.49	.52	.51	.50	.50	.023
$\bar{1}.71$	.47	.49	.53	.50	.49	.50	.022
.82	.53	.51	.51	.52	.53	.52	.010

Notes. $\bar{B}$: luminance in log ftL

Each value per individual monkey is the average of 15 to 27, 40-sec samples.

attempts for both lower and upper thresholds determinations per individual monkey are shown in Table 5. In all animals, there were close to 100% positive attempts at luminances down to $\bar{5}.71$ ftL. A drop in percentage occurred at $\bar{6}.70$ log ftL in monkey #617 and 637, and at $\bar{7}.73$ log ftL in #612, 616 and 636.

The absolute luminance threshold (B_Θ) was considered as the level at which at least 50% of positive attempts occurred. By this criterion, B_Θ lay between $\bar{6}.70$ and $\bar{7}.73$ log ftL for all the monkeys except #637. In the latter animal B_Θ was between $\bar{5}.71$ and $\bar{6}.70$ log ftL.

The percentage of positive attempts at lower luminance levels was smaller for upper than for lower thresholds. This was possibly due to the poor resolution of the luminance steps used in the experiment (1 log).

2. <u>Group Data</u>. Table 5 also contains the group means of positive attempts and their percentages, and the standard deviations around the means. According to the criterion for B_Θ previously set, the group B_Θ lay between $\bar{6}.70$ and $\bar{7}.73$ log ftL. Fig. 9 depicts the percentage of positive attempts as a function of the stimulus luminance over the group. The mean B_Θ was estimated by graphic interpolation to lie at about $\bar{6}.35$ log ftL. It is interesting to note that the stimulus luminance closest to this mean ($\bar{6}.70$ log ftL) was associated with the largest standard deviation. In fact, this *SD* was 4 times greater than the next closest value observed. Standard deviations may be considered as indicators of stimulus uncertainty, and it is clear that $\bar{6}.70$ log ftL elicited the greatest uncertainty in the group.

TABLE 5

NUMBER AND PERCENTAGE OF POSITIVE ATTEMPTS TO DETERMINE AN OPTOKINETIC FREQUENCY THRESHOLD AS A FUNCTION OF STIMULUS LUMINANCE

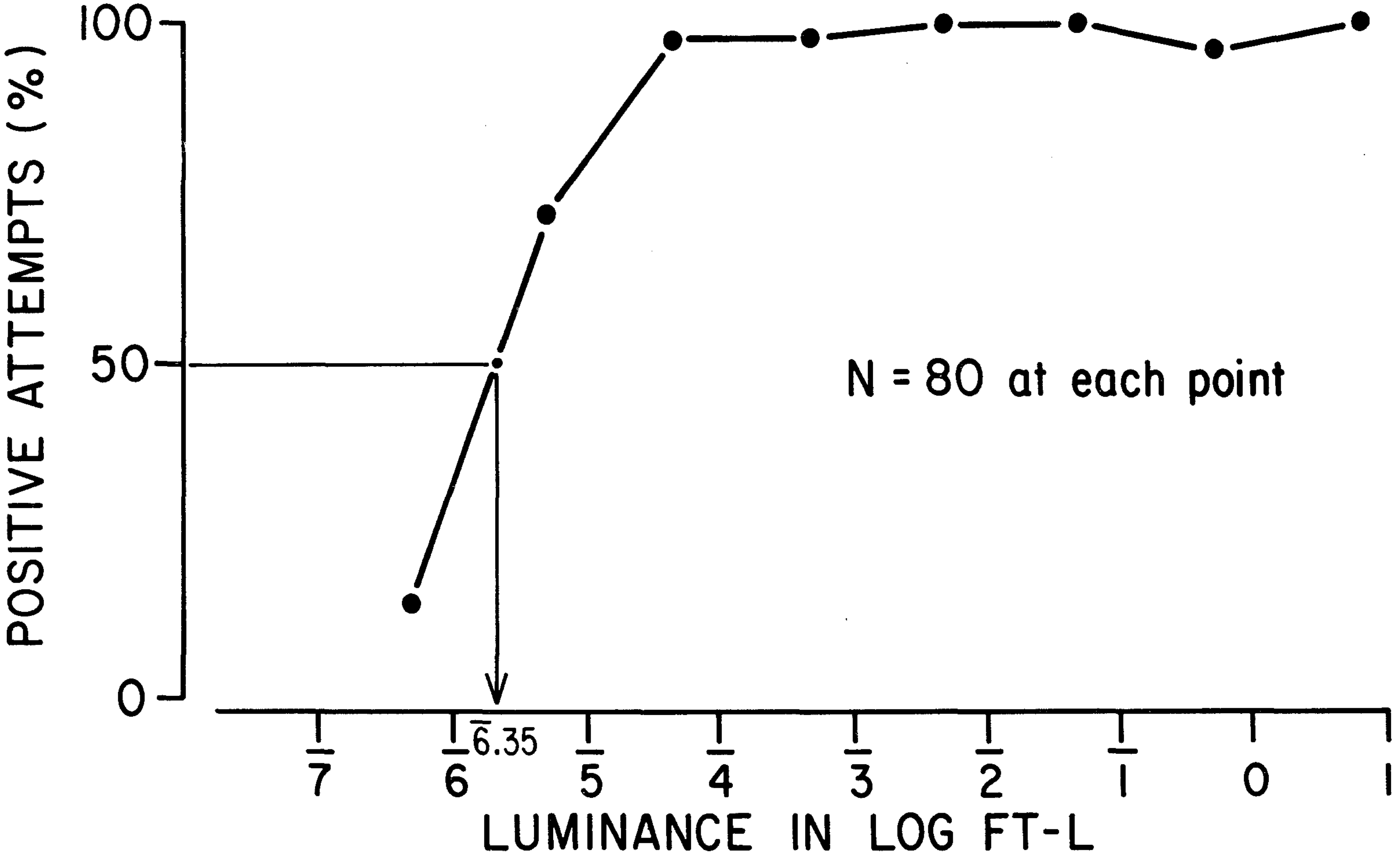
$\bar{B}$	MONKEY #					$\bar{X}$	*SD*
	612	616	617	636	637		
$\bar{7}.73$	3.0	0.0	4.0	4.0	0.0	3.7	.58
	18.8	0.0	25.0	25.0	0.0	13.8	
$\bar{6}.70$	14.0	15.0	9.0	13.0	6.0	11.4	3.78
	87.5	93.8	56.2	81.2	37.5	71.2	
$\bar{5}.71$	16.0	14.0	16.0	16.0	16.0	15.6	.89
	100.0	87.5	100.0	100.0	100.0	97.5	
$\bar{4}.71$	16.0	16.0	15.0	15.0	16.0	15.6	.55
	100.0	100.0	93.8	93.8	100.0	97.5	
$\bar{3}.75$	16.0	16.0	16.0	16.0	16.0	16.0	.00
	100.0	100.0	100.0	100.0	100.0	100.0	
$\bar{2}.70$	16.0	16.0	16.0	16.0	16.0	16.0	.00
	100.0	100.0	100.0	100.0	100.0	100.0	
$\bar{1}.71$	16.0	14.0	16.0	15.0	16.0	15.4	.89
	100.0	87.5	100.0	93.8	100.0	96.3	
.82	16.0	16.0	16.0	16.0	16.0	16.0	.00
	100.0	100.0	100.0	100.0	100.0	100.0	

Notes. $\bar{B}$: luminance in log ftL.

For each luminance level and for each monkey, the upper figure indicates the number of positive trials and the lower figure their percentage from a total of 16 combined lower and upper threshold determinations.

Figure 9. Percentage of Positive Attempts to Determine Optokinetic Frequency Thresholds (both Lower and Upper Combined)

The absolute luminance threshold was estimated by graphic interpolation to lie at about $\bar{6}.35$ log ftL.


100
50
0
POSITIVE ATTEMPTS (%)
N = 80 at each point
6̄.35
7̄
6̄
5̄
4̄
3̄
2̄
1̄
0
1
LUMINANCE IN LOG FT-L

C. Optokinetic Frequency Thresholds as a Function of Stimulus Luminance

1. Lower Thresholds

a. Individual Data. Appendix A, Section 1 presents the results in tables per individual monkey. The thresholds obtained with stimulus movement to the right and to the left are given separately. Each numerical value (positive attempt) is the threshold determination resulting from the average ($\bar{X}.$) of ascending and descending series. *RM* indicates random eye movements, that is an unsuccessful attempt to obtain a threshold. Means of 4 attempts ($\bar{X}..$) and standard deviations are also given. The notation of the level of averaging is given in Table 3.

Statistical evaluation of the differences between the mean thresholds obtained with stimulus movement to the right and to the left (t tests for independent samples) revealed that no animal, at any luminance level, exhibited a significant right-left difference at a probability level of .05. Therefore, thresholds for stimulus movement to the right and to the left ($\bar{X}..$) were combined and the results, given under $\bar{X}...$, showed no trend as a function of luminance consistent for all animals. Moreover, analyses of variance performed to determine whether stimulus luminance had any effect on the lower threshold values ($\bar{X}...$) of individual monkeys, showed that only one animal (#636) exhibited a significant difference among the means at $p < .05$ (Appendix A, Section 2).

b. Group Data. Table 6 contains lower thresholds ($\bar{X}...$) for each monkey and the group means ($\bar{X}....$) and standard deviations. Fig. 10 depicts these data as a graphical display with the stimulus luminance in log ftL on the abscissa, and the mean lower thresholds in cps on the

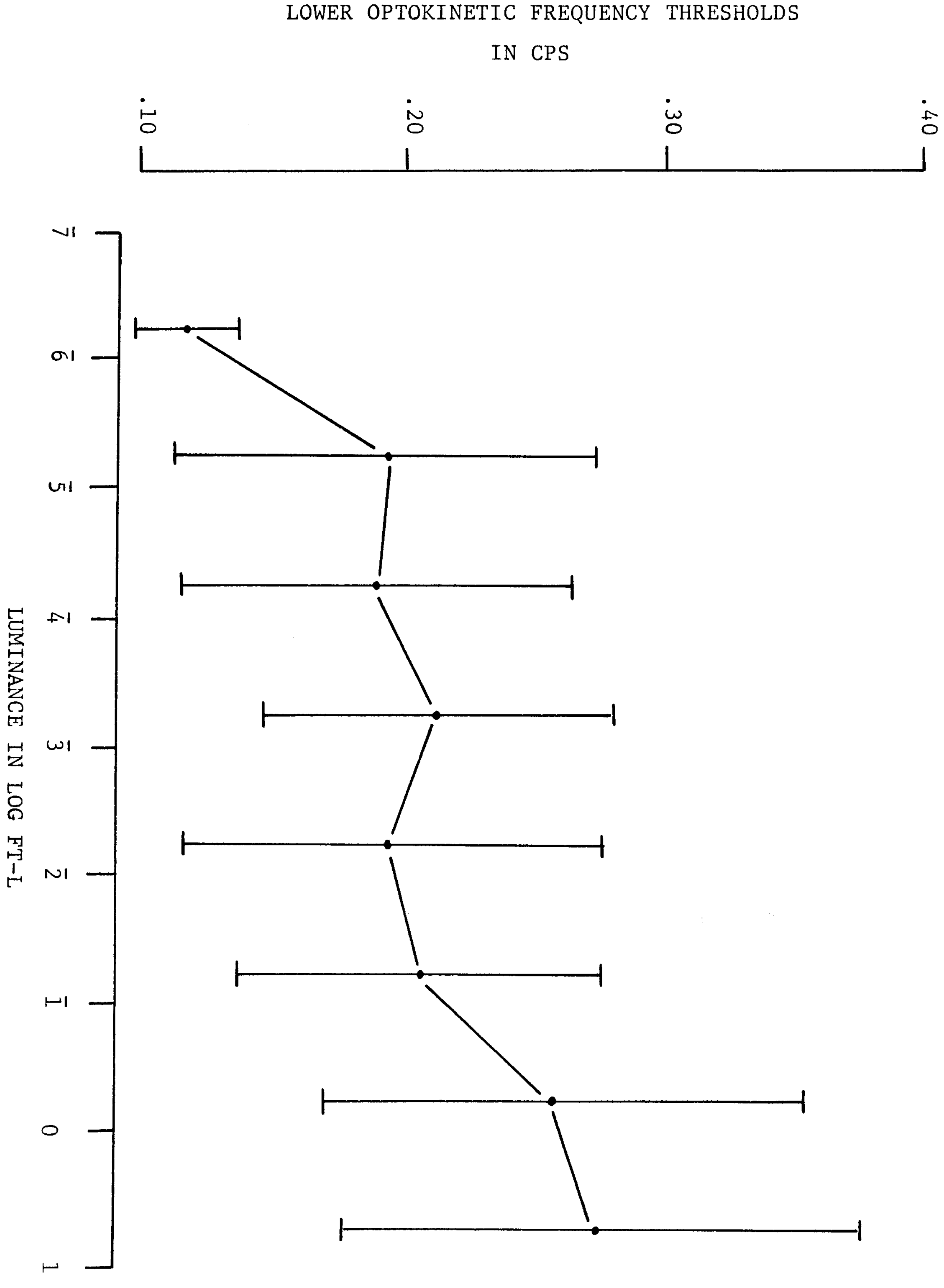
TABLE 6

LOWER OPTOKINETIC FREQUENCY THRESHOLDS AT EACH STIMULUS LUMINANCE

$\bar{B}$	MONKEY #					$\bar{X}$....	*SD*
	612	616	617	636	637		
$\bar{7}.73$	.137	*RM*	.115	.095	*RM*	.116	.021
$\bar{6}.70$	.176	.302	.099	.128	.261	.193	.086
$\bar{5}.71$	.116	.218	.123	.186	.301	.189	.076
$\bar{4}.71$	.102	.260	.210	.200	.296	.214	.074
$\bar{3}.75$	.103	.191	.170	.180	.328	.194	.082
$\bar{2}.70$	.143	.205	.168	.229	.316	.212	.067
$\bar{1}.71$	.139	.345	.192	.331	.286	.258	.090
.82	.177	.426	.159	.319	.291	.274	.110

Notes. $\bar{B}$: luminance in log ftL.

Figure 10. Lower Optokinetic Frequency Thresholds as a Function of Stimulus Luminance. Group Data.


LOWER OPTOKINETIC FREQUENCY THRESHOLDS
IN CPS
.10
.20
.30
.40
$\bar{7}$
$\bar{6}$
$\bar{5}$
$\bar{4}$
$\bar{3}$
$\bar{2}$
$\bar{1}$
0
1
LUMINANCE IN LOG FT-L

ordinate. A large magnification of the ordinate was used to show a possible trend of the means; as a consequence, the standard deviations seemed large when in fact they were not. Mean lower thresholds tended to increase with the luminance level of the stimulus. Although some discontinuity of the trend seemed to occur around $\bar{3}$ log ftL, a double contour was not outlined because no such trends were observed in individual monkeys.

An analysis of variance was performed to determine whether stimulus luminance had any effect on the group mean lower threshold values ($\bar{X}$....). Table 7 (top) summarizes the results. Conditions in which no thresholds were obtained were not included. It was found that the group mean thresholds ($\bar{X}$....) were not significantly different from each other and therefore, no significant influence of stimulus luminance upon lower optokinetic frequency thresholds could be demonstrated.

c. Other Findings. The grand mean for lower thresholds at all the luminance levels ($\bar{X}$.....) was .21 cps (*SD* = .05). This value was equivalent to a velocity of 4.5 cm/sec or of 10°/sec at the center of the screen. The lowest value found in individual determinations was .013 cps, or a velocity of approximately 3 mm/sec, or 30'/sec at the center of the screen. The latter value was obtained 3 times in different monkeys as a descending threshold and it was not associated with any particular portion of the luminance range used. Another finding of interest was that ascending thresholds were always higher than descending thresholds.

TABLE 7

ANALYSIS OF VARIANCE OF THE EFFECT OF STIMULUS LUMINANCE ON OPTOKINETIC FREQUENCY THRESHOLDS

LOWER THRESHOLDS

Source of Variation	Sum of Squares	d.f.	Mean Square	*F*
$\bar{B}$	.0647	7	.0092	1.37
Error	.1997	30	.0067	
Total	.2644	37		

UPPER THRESHOLDS

Source of Variation	Sum of Squares	d.f.	Mean Square	*F*
$\bar{B}$	88.05	6	14.68	3.99*
Error	99.30	27	3.68	
Total	187.35	33		

* $p < .01$

2. Upper Thresholds

a. Individual Data. The results of each determination are given in tables per individual monkey in Appendix A, Section 3. The organization and notations of the tables are identical to those for lower thresholds (page 52). Similarly to the treatment of lower threshold data, t tests for independent samples were performed to determine whether there was a significant difference between thresholds obtained with stimulus movement to the right and to the left. It was found that only one animal (#636), in a single condition ($\bar{6}.70$ log ftL) showed a significant right-left difference at a probability level of .05. This condition was unusual in that there were only two positive attempts with identical values and therefore the standard deviation was zero. Thus, it was considered justified to combine the thresholds for stimulus movements to the right and to the left ($\bar{X}..$) into a common value ($\bar{X}...$).

A graph of mean upper thresholds ($\bar{X}...$) of individual monkeys is depicted in Appendix A, Section 4. A consistent pattern was found in all monkeys. Upper threshold contours consisted of two segments: a "low" and a "high luminance contour." For all monkeys, except #637, the "low luminance contour" extended from the absolute luminance threshold to approximately $\bar{3}.75$ log ftL; and the "high luminance contour" extended from $\bar{3}.75$ log ftL to the highest luminance level manipulated (.82 log ftL). In monkey #637 the discontinuity between the two contours was located at about $\bar{4}.71$ log ftL.

Analyses of variance were performed to determine whether the luminance of the stimulus had any influence on the mean upper threshold values ($\bar{X}...$) of individual monkeys. As in the case of lower thresholds, due to the presence of negative attempts, degrees of freedom varied over the group. It was found that only two monkeys exhibited significant differences among the means at a probability level of .05. (Appendix A, Section 5).

b. Group Data. Table 8 contains the mean ($\bar{X}$...) upper thresholds for each monkey at each stimulus luminance, the group means ($\bar{X}$....) and standard deviations. Fig. 11 depicts the group data in graphical form with the stimulus luminance in log ftL on the abscissa and the mean upper thresholds in cps on the ordinate. It was apparent that upper thresholds tended to increase with the luminance of the stimulus. The pattern observed in the group data was consistent with that of individual monkeys. Upper threshold contours consisted of two segments: a "low" and a "high luminance contour." The former extended from the absolute luminance threshold to $\bar{3}.75$ log ftL, and the latter from $\bar{3}.75$ log ftL to the highest luminance level tested (.82 log ftL).

An analysis of variance was performed to determine whether the luminance of the stimulus influenced the group mean upper thresholds ($\bar{X}$....). Results showed a highly significant difference among these means ($F = 3.99$, $p < .01$) (Table 7, bottom).

c. Other Findings. The highest upper threshold ever observed was 30.54 cps, or a velocity of 637 cm/sec or 1496°/sec at the center of the screen. This value was found as an ascending threshold in the first determination attempted in monkey #636 at .82 log ftL. Moreover, this animal showed several upper threshold values over 20 cps not associated with any particular trial or luminance level of the stimulus. As in the case of lower thresholds, ascending thresholds were always higher than

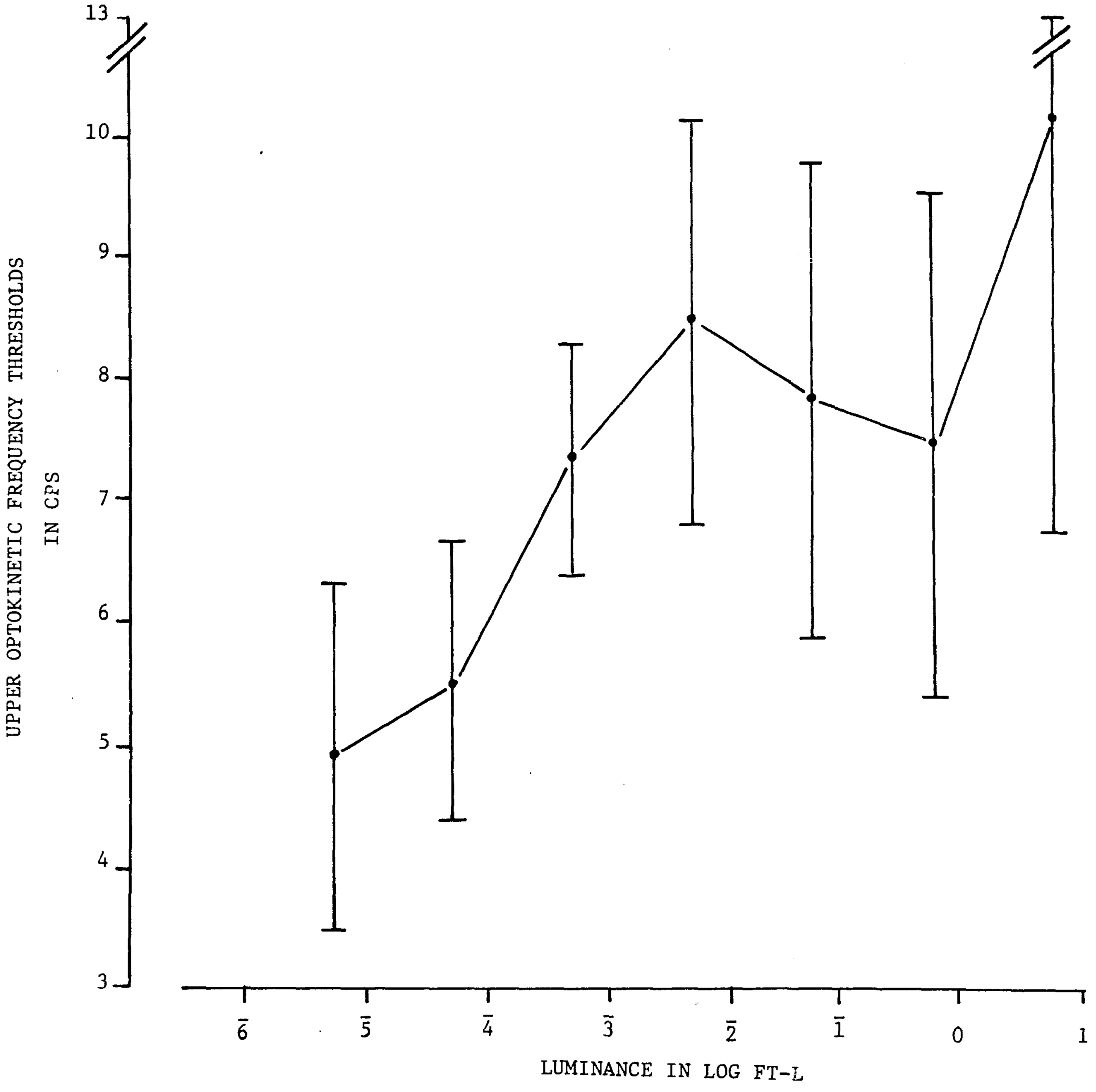
TABLE 8

UPPER OPTOKINETIC FREQUENCY THRESHOLDS AT EACH STIMULUS LUMINANCE

$\bar{B}$	MONKEY #					$\bar{X}$....	*SD*
	612	616	617	636	637		
$\bar{7}.73$	*RM*	*RM*	*RM*	*RM*	*RM*	*RM*	--
$\bar{6}.70$	3.46	6.60	5.39	4.08	*RM*	4.88	1.40
$\bar{5}.71$	4.99	5.33	7.30	5.60	4.10	5.47	1.17
$\bar{4}.71$	7.46	5.74	8.22	7.94	7.43	7.36	.96
$\bar{3}.75$	7.77	6.90	10.43	10.21	6.89	8.46	1.74
$\bar{2}.70$	6.73	6.52	9.76	9.65	6.43	7.82	1.73
$\bar{1}.71$	6.70	5.92	10.50	9.34	5.56	7.60	2.19
.82	9.36	7.36	12.78	14.15	7.07	10.14	3.19

Notes. $\bar{B}$: luminance in log ftL.

Figure 11. Upper Optokinetic Frequency Thresholds as a Function of Stimulus Luminance. Group Data.


UPPER OPTOKINETIC FREQUENCY THRESHOLDS
IN CPS
13
10
9
8
7
6
5
4
3
$\bar{6}$
$\bar{5}$
$\bar{4}$
$\bar{3}$
$\bar{2}$
$\bar{1}$
0
1
LUMINANCE IN LOG FT-L

descending thresholds.

D. Integration and Summary of Experimental Results

Thus far, lower and upper optokinetic frequency threshold contours have been analysed separately. However, it is apparent that both contours limit an "area" of optokinetic reaction. Fig. 12 is a graph which attempts to illustrate the concept summarizing at the same time the main results of the study.

It is shown that the shapes of lower and upper threshold contours were differentially affected by the luminance of the stimulus. Lower thresholds remained at a relatively constant height with respect to the stimulus luminance, whereas upper thresholds showed a marked upturn once the absolute luminance threshold was surpassed, and exhibited a "low" and a "high luminance" segment. Although lower and upper threshold contours must converge at some point in the luminance axis, the determination of this point, which probably requires finer luminance steps, was beyond the scope of the present work.

The experimental results of this investigation may be summarized as follows:

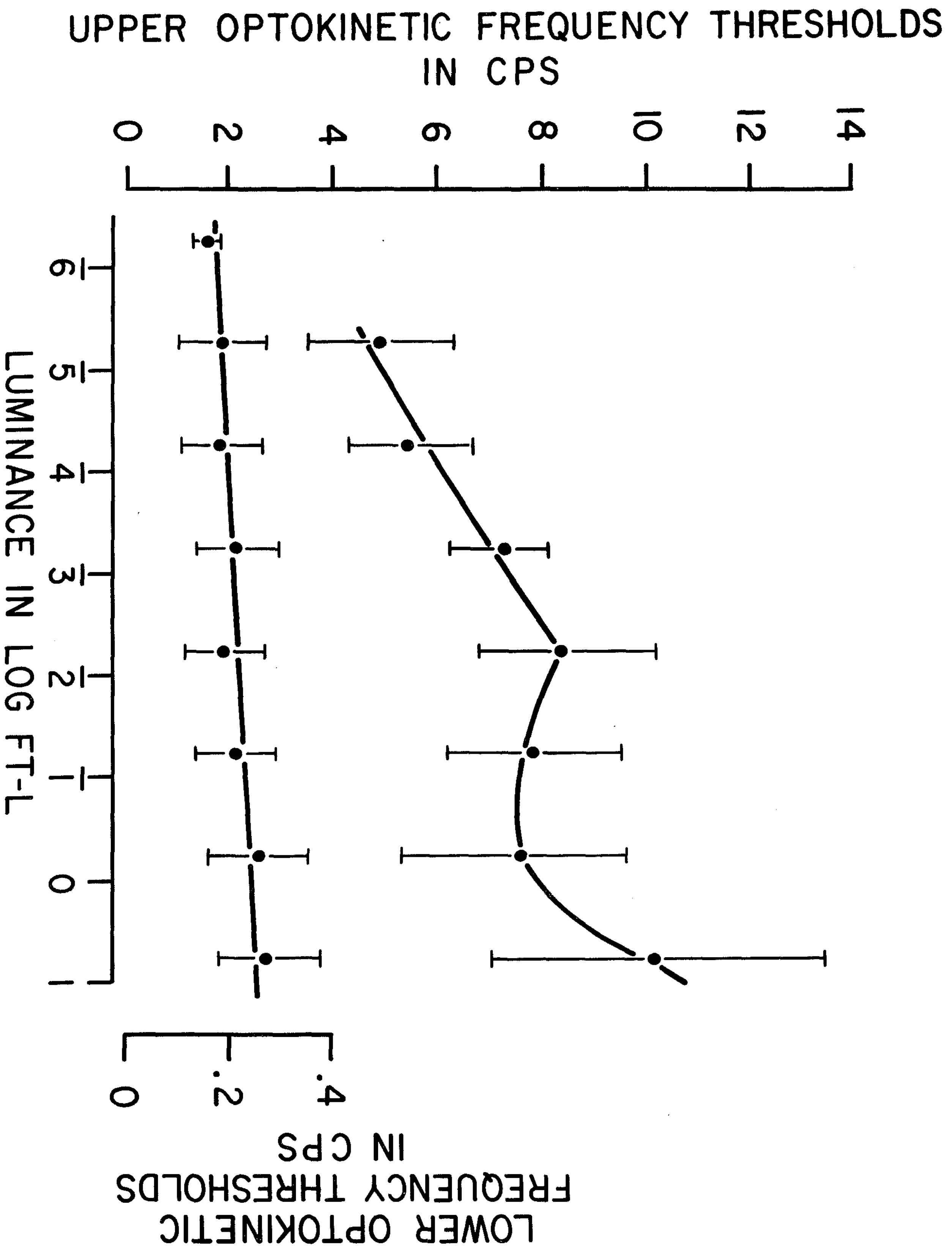
1. Spontaneous eye movements to the right and to the left were symmetrical at all luminance levels of the stationary stimulus.

2. Lower and upper optokinetic frequency thresholds were similar for stimulus movement to the right and to the left.

3. The estimated absolute luminance threshold for the elicitation of an optokinetic response lay at about $\bar{6}.35$ log ftL.

4. The luminance of the stimulus did not significantly affect lower optokinetic frequency thresholds. Once the absolute luminance threshold was surpassed, lower thresholds tended to increase slightly but not

Figure 12. Lower and Upper Optokinetic Frequency Thresholds as a Function of Stimulus Luminance. Group Data.


UPPER OPTOKINETIC FREQUENCY THRESHOLDS
IN CPS
0
2
4
6
8
10
12
14
LUMINANCE IN LOG FT-L
6
5
4
3
2
1
0
-1
0
.2
.4
LOWER OPTOKINETIC
FREQUENCY THRESHOLDS
IN CPS

significantly with the stimulus luminance.

5. Stimulus luminance affected significantly upper optokinetic frequency thresholds. "Low" and "high luminance contours" were present in all animals and in the group. The discontinuity between the contours was found at approximately $\bar{3}.75$ log ftL.

6. A "dynamic area" of optokinetic response was defined as being delimited by the lower threshold contour, the absolute luminance threshold and the upper threshold contour.

CHAPTER IV

TENTATIVE MATHEMATICAL MODEL OF THE OPTOKINETIC RESPONSE

This chapter is an attempt at synthesis. The main purpose is to show how the psychophysical data on limits of optokinetic reaction found in the present experiment may be integrated with above-threshold data of an earlier study (Valciukas and Pasik, 1968; Valciukas, Pasik and Pasik, 1968) into a coherent picture of the optokinetic response of the normal monkey. Specifically, the attempt will be made to show that: (1) this response can be described by means of a mathematical model; (2) optokinetic frequency threshold values may be predicted from such a model; (3) the threshold data from the present study may be used to correct the model and predict some properties of the optokinetic response at suprathreshold values.

A. Frequency of the Optokinetic Response Between Lower and Upper Thresholds (Frequency of Optokinetic Nystagmus)

Some quantitative properties of the optokinetic response within its dynamic range have been recently defined by Valciukas and Pasik (1968) and Valciukas, Pasik, and Pasik (1968). In these investigations, the frequency of the optokinetic response (F_r) was parametrically studied as a function of stimulus frequency (F_s) and of stimulus luminance (B). The value of F_r derived from:

$$F_r = \frac{R - L}{t} \qquad (1)$$

where R is the number of nystagmic beats to the expected side; L, the beats to the opposite side; and t, the trial duration which was constant and equal to 20 sec. The same formula was used to quantify spontaneous oculomotor activity when the optokinetic stimulus was present but not moving.

In addition, the "efficiency ratio" (E) was defined as the number of nystagmic beats per stimulus cycle:

$$E = \frac{F_r}{F_s} \tag{2}$$

Fig. 13 shows results of this earlier study. The abscissa is F_s in log cps and the ordinate is F_r in nystagmic beats/sec. F_r was shown to be dependent on both F_s and B. In addition, it was shown that when B increased, the peak response $F_{r(max)}$ became greater and its location, $F_{s(max)}$, was displaced toward higher values of F_s. When E ratios were plotted against the logarithm of F_s, a straight line was obtained (Fig. 14). This finding allowed to relate E and log F_s by a logarithmic function of the general type:

$$E = a + b \log F_s \tag{3}$$

The values of the constants a and b were calculated by the method of least squares and the empirical equations of the "efficiency ratio" for the two luminance levels were found to be:

$$E_{(.56)} = 1.236 - 1.073 \log F_s \tag{3'}$$

$$E_{(\bar{4}.56)} = .964 - 1.033 \log F_s \tag{3''}$$

where the subscript of E indicates the level of B in log ftL. All values of F_r could then be calculated by a simple algebraic manipulation of equations (2) and (3):

Figure 13. Frequency of the Optokinetic Response (F_r) as a Function of the Stimulus Frequency (F_s) at Two Luminance Levels (B)

Group data from Valciukas and Pasik (1968). Shaded areas indicate standard deviation values.

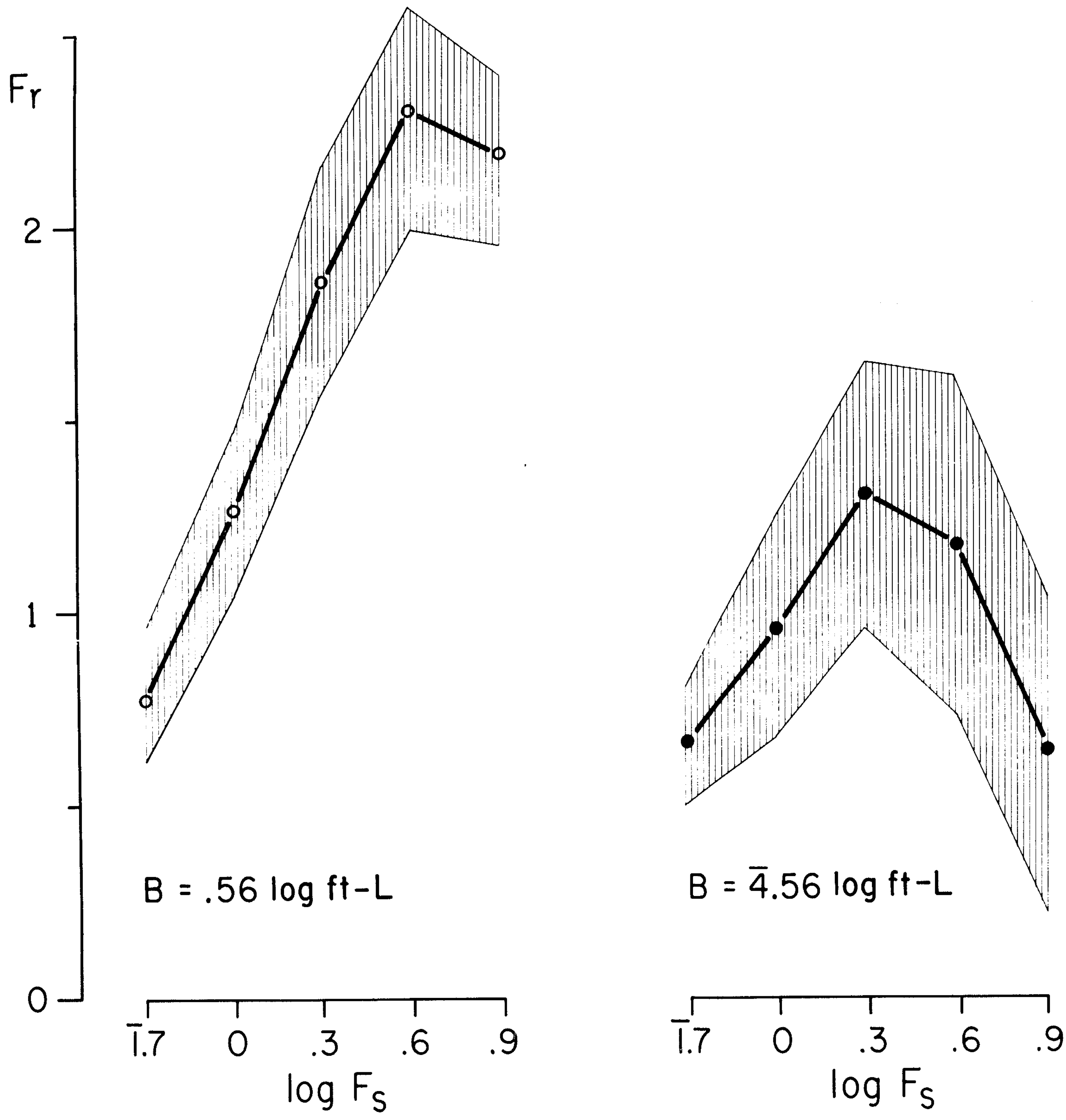
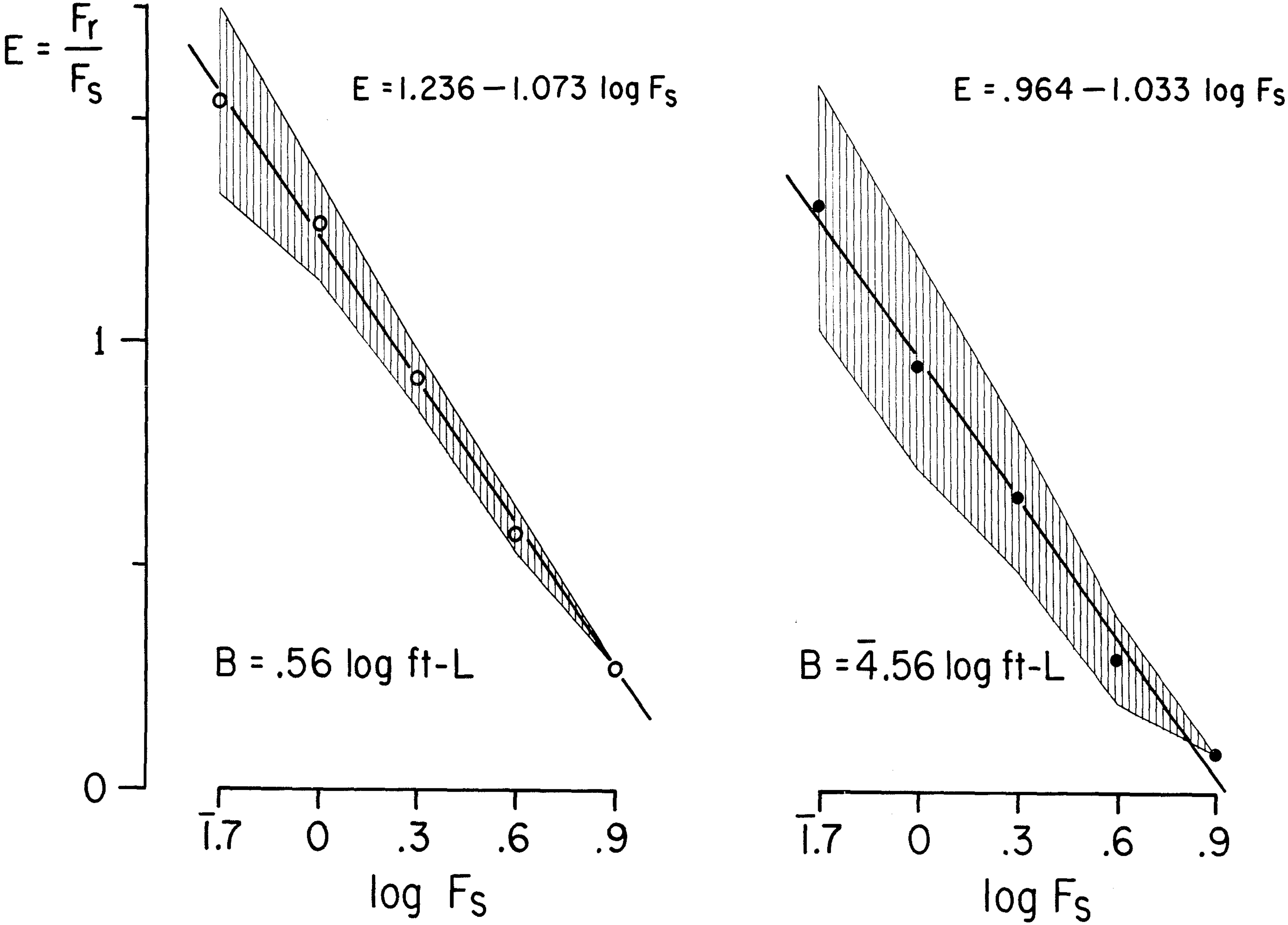

F$_r$
2
1
0
B = .56 log ft-L
$\bar{1}$.7
0
.3
.6
.9
log F$_s$
B = $\bar{4}$.56 log ft-L
$\bar{1}$.7
0
.3
.6
.9
log F$_s$

Figure 14. The Efficiency Ratio (*E*) as a Function of the Logarithm of Stimulus Frequency (F_S) at Two Luminance Levels (*B*).

Group data from Valciukas and Pasik (1968). The shaded areas are the standard deviation values. The constants of the equations were obtained by the method of least squares.


$E = \frac{F_r}{F_s}$
1
0
$E = 1.236 - 1.073 \log F_s$
$B = .56$ log ft-L
$\bar{1}.7$
0
.3
.6
.9
log F_s
$E = .964 - 1.033 \log F_s$
$B = \bar{4}.56$ log ft-L
$\bar{1}.7$
0
.3
.6
.9
log F_s

$$F_r = (a + b \log F_s)\, F_s \tag{4}$$

and therefore:

$$F_{r(.56)} = (1.236 - 1.073 \log F_s)\, F_s \tag{4'}$$

$$F_{r(\bar{4}.56)} = (.964 - 1.033 \log F_s)\, F_s \tag{4''}$$

Equation (4') is depicted in graphical form in Fig. 15 together with empirical determinations for the entire spectrum of F_s in two different monkeys. The empirical data confirmed that an equation of this sort could satisfactorily describe the optokinetic nystagmus of the normal monkey, at least at this luminance level.

Equations (4') and (4") showed that the constants a and b changed with stimulus luminance B. As B increased, a became more positive and b more negative. Although only two values of each constant were available, it was assumed that the equations of the constants could be defined by logarithmic functions of B of the type:

$$a = c + d \log B \tag{5}$$

$$b = e + f \log B \tag{6}$$

By the method of least squares, these equations were found to be:

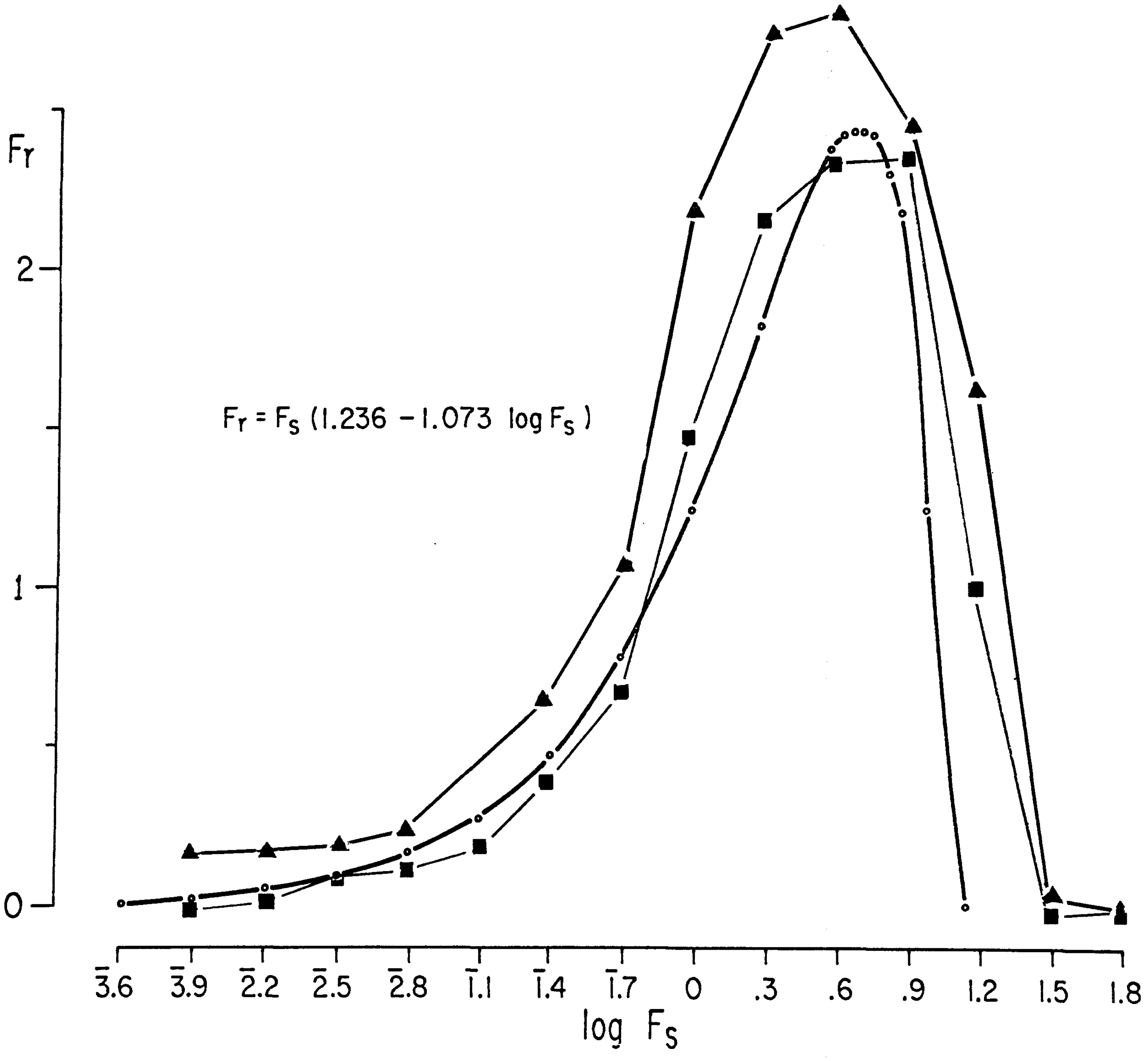
$$a = 1.1979 + .068 \log B \tag{5'}$$

$$b = -1.0674 - .01 \log B \tag{6'}$$

Equations (5) and (6) served to transform equation (4) into a more general expression where F_r was a function of the parameters F_s and B:

Figure 15. Graphical Representation of Equation (4') with Empirical Determinations for the Entire Spectrum of F_S.

Open circles: predicted values of F_S; triangles and squares: empirical values from two different monkeys (from Valciukas, Pasik and Pasik, 1968).


Fr
2
1
0
$F_r = F_s\,(1.236 - 1.073 \log F_s)$
$\bar{3}.6$
$\bar{3}.9$
$\bar{2}.2$
$\bar{2}.5$
$\bar{2}.8$
$\bar{1}.1$
$\bar{1}.4$
$\bar{1}.7$
0
.3
.6
.9
1.2
1.5
1.8
log Fs

$$F_r = [(c + d \log B) + (e + f \log B) \log F_s] F_s \qquad (7)$$

Inserting in (7) the values from (5') and (6') the expression became:

$$F_r = [(1.1979 + .068 \log B) + (- 1.0674 - .01 \log B) \log F_s] F_s \qquad (7')$$

This equation was fed into the computer (Appendix B, Program No. 1) and values of F_r were calculated for as many values of F_s as necessary to obtain a smooth curve, varying B in one log steps. Fig. 16 is a two-dimensional representation of equation (7'). The abscissa is the logarithm of F_s, and the ordinate, the predicted values of F_r at each level of B.

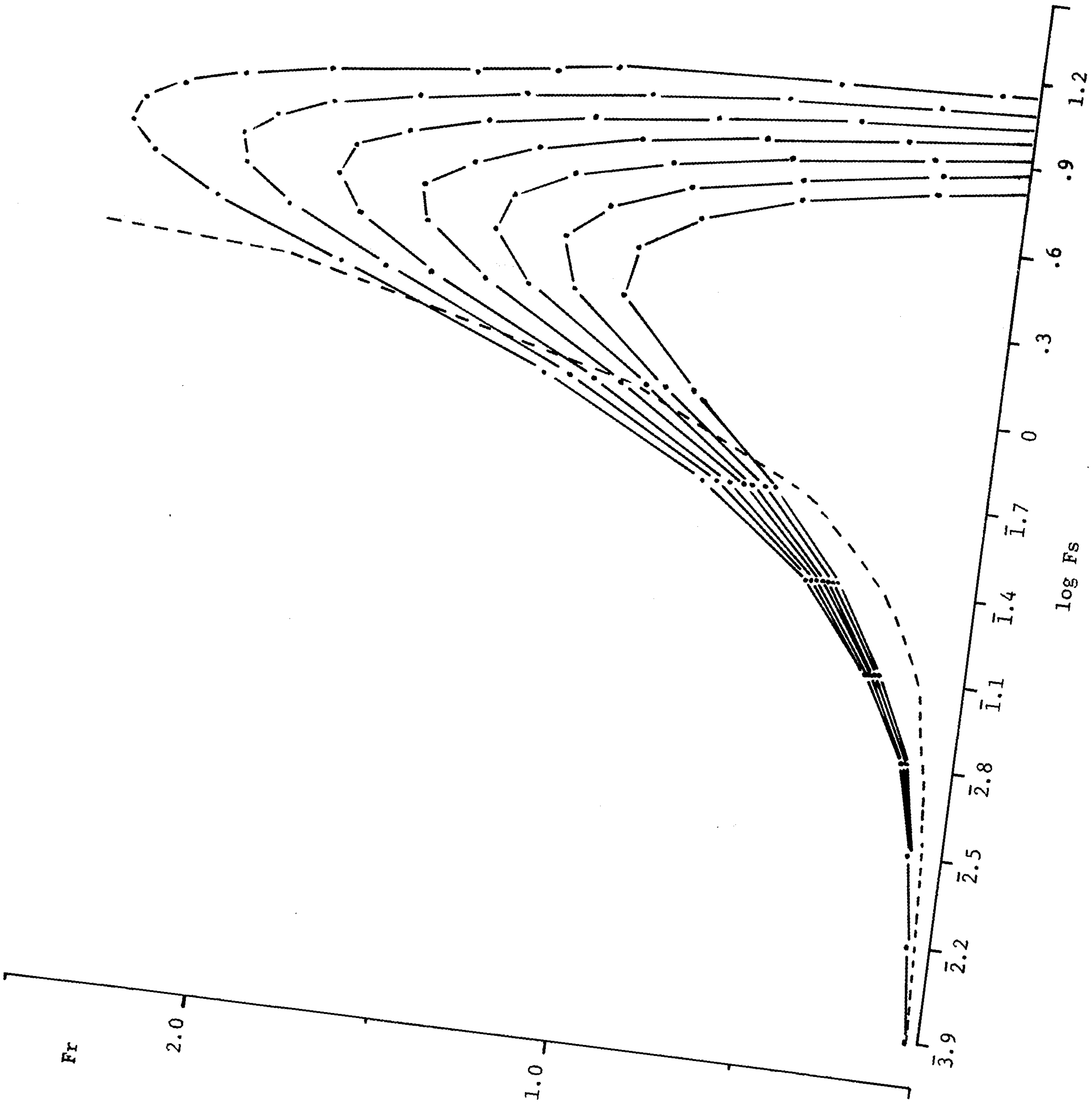
Equation (7') may be considered as a mathematical model of changes of the dependent variable F_r as a function of two independent variables: F_s and B.

B. Frequency of the Optokinetic Response at Lower and Upper Thresholds (Limits of Reaction)

The mathematical model as developed above, described the entire range of F_r as a function of F_s and B. In the attempt to predict from this same model the lower and upper optokinetic frequency thresholds ($F_{s\Theta lo}$ and $F_{s\Theta up}$) at each stimulus luminance, it was necessary to find the F_r values at threshold ($F_{r\Theta}$). Using equation (1) on the raw data of the present study, at .82 log ftL, it was found that the group mean $F_{r\Theta}$ was .30 nystagmic beats/sec (*SD* = .03). Inspection of the rest of the data allowed the preliminary assumption that this value was relatively constant over all the other luminance levels tested. It was then possible to calculate $F_{s\Theta lo}$ and $F_{s\Theta up}$. A computer program was written for

Figure 16. The Frequency of the Optokinetic Response (F_r) as a Function of Stimulus Frequency (F_s) and Luminance (B) as Predicted from Equation (7).

From inside out B values in log ftL are: $\bar{6}.56$, $\bar{5}.56$, $\bar{4}.56$, $\bar{3}.56$, $\bar{2}.56$, $\bar{1}.56$, and .56. Dashed line designates the one-to-one relationship between the frequency of the stimulus and the frequency of the response.


Fr
2.0
1.0
log Fs
$\bar{3}.9$
$\bar{2}.2$
$\bar{2}.5$
$\bar{2}.8$
$\bar{1}.1$
$\bar{1}.4$
$\bar{1}.7$
0
.3
.6
.9
1.2

that purpose (Appendix B, Program No. 2) and Fig. 17 illustrates the method in graphical form. The curve represents equation (7') for a given stimulus luminance. Successive values of F_s (increasing in .01 cps steps) were inserted in the equation and when the result was $F_r = .30$, the F_s value was printed out. Table 9 gives the computer print out with B values extending approximately from the absolute luminance threshold to 4.5 log B. It is evident that there was very little variation in $F_{s\Theta lo}$, whereas $F_{s\Theta up}$ increased rapidly with log B. The table values corresponding to the luminance range used in the present study were plotted in Fig. 18 together with the thresholds obtained empirically. Although there was close agreement between both sets, the mathematical model failed to predict scotopic and photopic components of the upper threshold contour. This failure of the model derived most probably from the assumed relationship between the constant a and log B as expressed in equation (5), since constant b varied little as a function of B [compare equations (4') and (4")]. Thus, the attempt was made to retrieve the values of the constant a from the upper threshold data obtained in the present study in order to "correct" the model.

C. Correction of the Optokinetic Response Frequency Function from Properties of Upper Threshold Contours

The constant b was first determined from equation (6') and, as stated above, remained relatively unchanged over wide ranges of B (Table 10). The constant a for each luminance level was calculated from the equation:

$$F_{r\Theta} = (a + b \log F_{s\Theta up})\, F_{s\Theta up} \tag{8}$$

Figure 17. Diagram of the Method for Theoretical Calculation of Stimulus Thresholds

The frequency of response at threshold is set on the ordinate, and the values of both the lower and the upper thresholds are read on the abscissa.

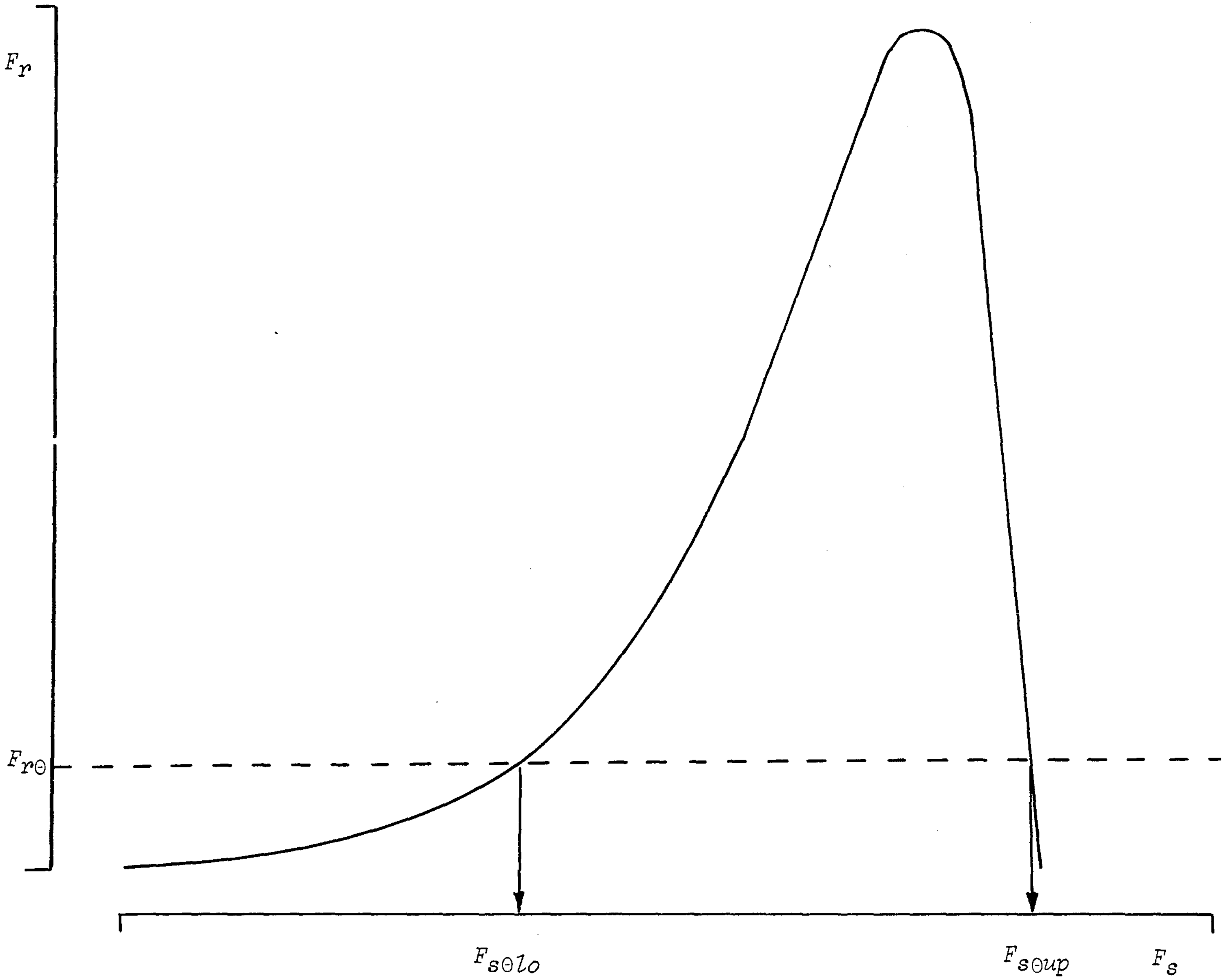

F_r
$F_{r\Theta}$
$F_{s\Theta lo}$
$F_{s\Theta up}$
F_s

TABLE 9

COMPUTER PRINT OUT OF THEORETICAL OPTOKINETIC FREQUENCY THRESHOLD VALUES

```
               B                   Fsθlo                  Fsθup

=+      4.5000          =+      0.1000          =+      21.9675
=+      4.0000          =+      0.1000          =+      20.7277
=+      3.5000          =+      0.1000          =+      19.5479
=+      3.0000          =+      0.1100          =+      18.4181
=+      2.5000          =+      0.1100          =+      17.3382
=+      2.0000          =+      0.1100          =+      16.3184
=+      1.5000          =+      0.1100          =+      15.3486
=+      1.0000          =+      0.1100          =+      14.4187
=+      0.5000          =+      0.1200          =+      13.5389
=+      0.0000          =+      0.1200          =+      12.7090
=-      0.5000          =+      0.1200          =+      11.9092
=-      1.0000          =+      0.1200          =+      11.1593
=-      1.5000          =+      0.1300          =+      10.4394
=-      2.0000          =+      0.1300          =+       9.7595
=-      2.5000          =+      0.1300          =+       9.1196
=-      3.0000          =+      0.1400          =+       8.5097
=-      3.5000          =+      0.1400          =+       7.9298
=-      4.0000          =+      0.1400          =+       7.3899
=-      4.5000          =+      0.1500          =+       6.8699
=-      5.0000          =+      0.1500          =+       6.3799
=-      5.5000          =+      0.1600          =+       5.9200
=-      6.0000          =+      0.1600          =+       5.4900
```

Figure 18. Theoretical and Empirical Lower and Upper Optokinetic Frequency Thresholds

•——•Theoretical thresholds calculated from the mathematical model of the optokinetic response.

▲---▲Empirical thresholds determined in the present study.

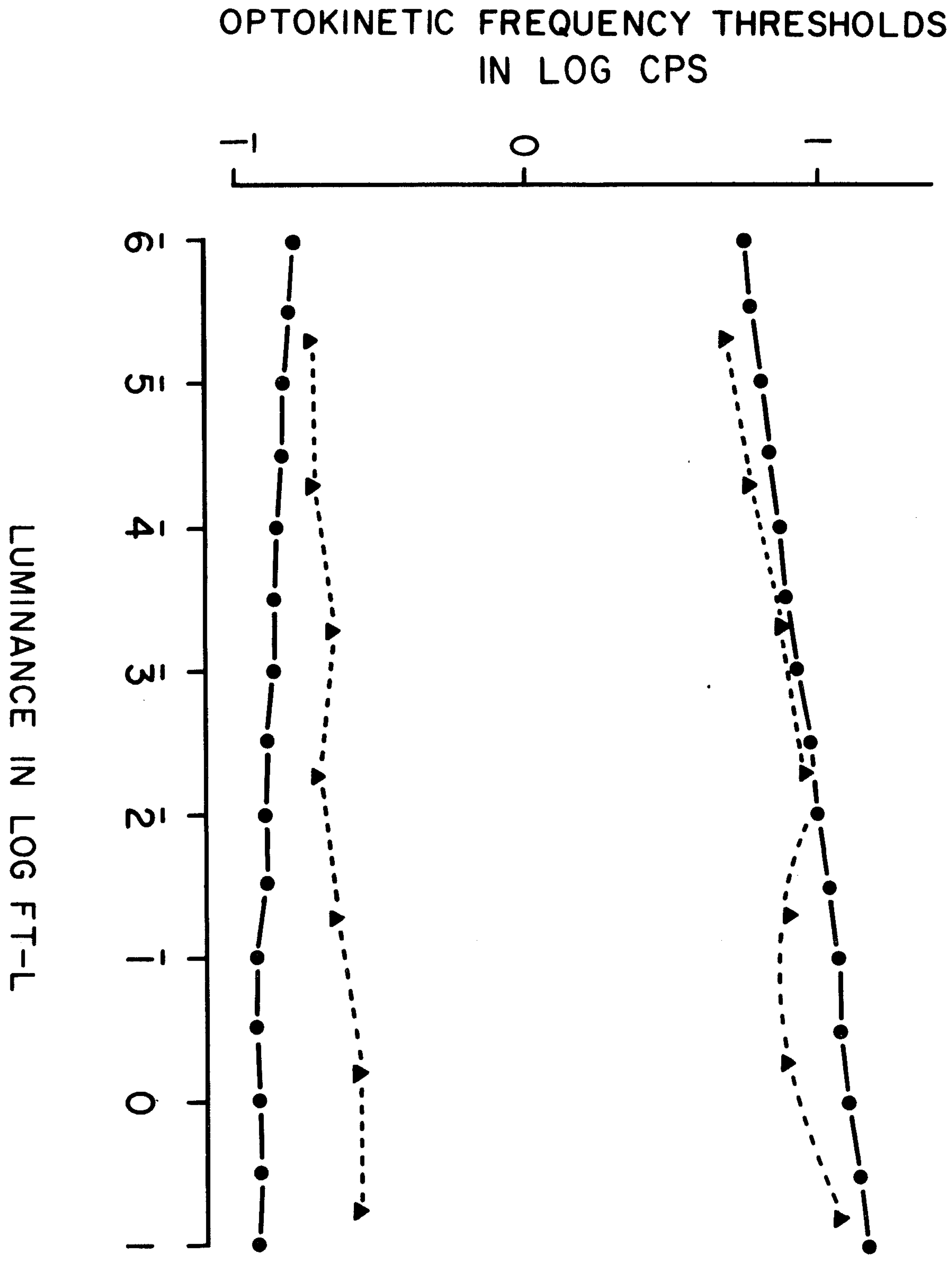

OPTOKINETIC FREQUENCY THRESHOLDS
IN LOG CPS
1̄
0
1
LUMINANCE IN LOG FT-L
6̄
5̄
4̄
3̄
2̄
1̄
0
1

TABLE 10

CONSTANTS b AND a, AND PEAK RESPONSE AND ITS LOCATION AS PREDICTED FROM UPPER THRESHOLDS AT EACH STIMULUS LUMINANCE

$\bar{B}$	$F_{s\Theta up}$	b	a	$F_r(max)$	$F_s(max)$
$\bar{7}.73$	RM	-1.0045	-	-	-
$\bar{6}.70$	4.884	-1.0144	.6475	.79	1.61
$\bar{5}.71$	5.466	-1.0245	.8015	.99	2.24
$\bar{4}.71$	7.357	-1.0345	.9306	1.31	2.93
$\bar{3}.75$	8.458	-1.0449	.9985	1.51	3.33
$\bar{2}.70$	7.818	-1.0544	.9737	1.41	3.09
$\bar{1}.71$	7.603	-1.0645	.9707	1.39	3.01
.82	10.144	-1.0756	1.1069	1.86	3.94

Notes. $\bar{B}$: luminance in log ftL

$F_{s\Theta up}$: upper optokinetic frequency threshold

$F_r(max)$: peak response

$F_s(max)$: location of peak response.

which is similar to equation (4), therefore:

$$a = \frac{F_{r\Theta}}{F_{s\Theta up}} - b \log F_{s\Theta up} \tag{9}$$

The values of F_r for the entire range of F_s at each luminance level were recalculated with the new corrected constants a and b using equation (4) and computer program No. 3 (Appendix B). In addition, peak responses and their location were determined with computer program No. 4 (Appendix B) where F_s was increased in .01 cps steps and F_r calculated from equation (4). In the latter procedure, the computer printed out the values of F_s and F_r only when the difference between two successive F_r values, i.e., the velocity of the function, was zero. Table 10 gives the results of this latter manipulation at each luminance level together with the empirical $F_{s\Theta up}$, and the calculated values of the constants b and a. It is interesting to note that the ratio:

$$E_{(max)} = \frac{F_{r\,(max)}}{F_{s\,(max)}} \tag{10}$$

is fairly constant for all luminance levels, the mean values being .46 (SD = .01).

D. Dynamic Volume of the Optokinetic Response

From the evidence of threshold and suprathreshold data it was possible to construct a tentative model of the optokinetic response in terms of two independent variables (luminance and frequency of the stimulus), and one dependent variable (frequency of the response). As depicted in Fig. 19, this model may be defined as a "volume" of reaction. The

Figure 19. Dynamic Volume of the Optokinetic Response in the Normal Monkey as a Function of Frequency and Luminance of the Stimulus

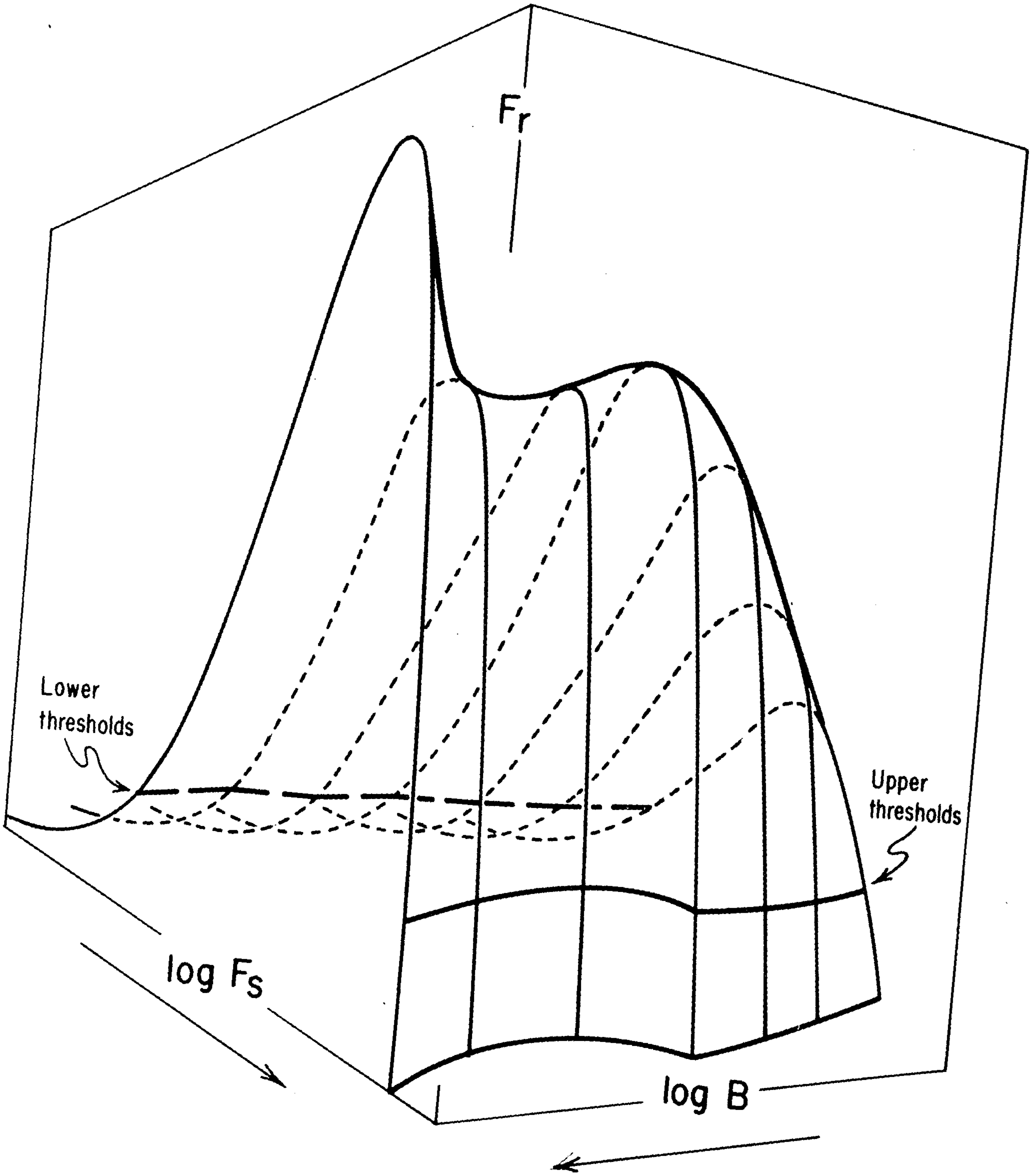

F_r
Lower thresholds
Upper thresholds
log F_s
log B

illustration is a three-dimensional display of the corrected mathematical model (see above) with log F_s and log B on the abscissae, and F_r on the ordinate. The zero level of response corresponds to the base of the solid, and F_r at threshold is indicated by a heavy line elevated .30 units over the base (the lower threshold contours in the back of the solid figure and the upper threshold contours in the front).

The significance of this concept lies in its ability to capture at least a fragment of the complex relationship between stimulus parameters and optokinetic response characteristics. Moreover, the concept of volume of reaction puts under a common frame of reference the apparent distinction between threshold and suprathreshold studies of visuo-oculomotor behavior.

CHAPTER V

DISCUSSION

A. Optokinetic Thresholds

Optokinetic frequency thresholds were defined in the present study on the basis of statistical properties of spontaneous eye movements. This specification de-emphasized the seemingly basic distintion between spontaneous oculomotor activity and fully-established optokinetic nystagmus. Both were seen as part of a continuum with the transition point, i.e., the response at threshold, only arbitrarily, although consistently specified. The present definition seems to be a better alternative to the subjective criteria used by other investigators, such as the visual observation of the optomotor reflex (Crozier and coworkers, see page 4), or the gross inspection of the electrooculographic record (Smith, 1941; Blomberg, 1960). It should be noted that the upper optokinetic threshold as defined by Blomberg in humans (the "optokinetic fusion limit") could not be applied in the present study. This investigator considered the threshold as the velocity of the stimulus at which the eyes ceased to move. In the monkey, oculomotor activity was usually continuous, so that when the stimulus was delivered at a value above the upper threshold, random eye movements invariably occurred. It is noteworthy that the use of a small general-purpose digital computer for the counting and statistical evaluation of the eye movements in fractions of a second made possible the interplay between the psychophysical preparation and the experimenter. During the threshold determination, a minimal time elapsed for organismic variables to operate and the experimenter was free to control the rather complex configuration of the procedure.

The values of lower optokinetic frequency thresholds obtained in the present investigation may be compared with data available on perception of movement in the monkey (Ross, 1943). In the latter study, thresholds for perception of real movement were determined in the monkeys *Cebus capucina* and *Cercocebus fuliginosus* at 6 luminance levels ranging from $\bar{3}.33$ log mL to 1.44 log mL. The animals were trained to discriminate a rotating vs. a stationary maltese cross, and the liminal values were considered as those resulting in 75% correct responses. When thresholds were plotted against the logarithm of the stimulus luminance, it was found that the contour was relatively flat over the photopic range, began to raise as the scotopic level was approached, and showed a fairly sharp upturn thereafter. The actual values ranged from 4 mm/sec in the flat portion to a maximun of 5.5 mm/sec in the ascending portion. These figures are difficult to interpret since no angular velocities were given. Moreover, no statistical evaluation of the results were offered. An analysis of variance performed on Ross' data revealed that the influence of the stimulus luminance upon the thresholds for perception of movement was not significant. This finding is in agreement with the results of the present study. Thus, it seems that stimulus luminance does not affect the lower thresholds either for perception of movement or for elicitation of an optokinetic response. Once a slowly moving stimulus is detected by the monkey, an increase in luminance does not enhance the sensitivity to the stimulus.

The characteristic features of the monkey's upper optokinetic frequency threshold contours are comparable to those of other species including man as reported by Crozier and coworkers (see page 4). These investigators succeeded in identifying rod and/or cone physiologic populations by plotting threshold contours for "critical flicker fusion" as a function of luminance using optokinetic stimuli. These contours were in agreement with the structural composition of the retina of each species. In summarizing these experiments, Bartley (1951) classified the subjects as those having (1) rods only (gecko, horned lizard); (2) cones only (turtle,bird); (3) both types of receptors (duplex retina) (frog, fish, man); (4) three groups of receptors (cones and two kinds of rods (newt); and (5) compound eyes (crayfish, dragonfly, bee).

Photopic ("cone") and scotopic ("rod") components were also apparent in the present determination of upper optokinetic frequency thresholds in the monkey. Although Blough and Schrier (1963) have demonstrated the duplex function of the monkey's retina by plotting the dark adaptation curve with a behavioral technique, the results are difficult to compare since they were reported in terms of relative values. The transition point between the two components found in the present study is consistent with the luminance level of the discontinuity obtained for man using a similar procedure (Crozier, Wolf, and Zerrahn-Wolf, 1937-1938), and with that illustrated by Bartley (1951). The value is also in general agreement with the point where Ross (1943) observed an upturn of the threshold contour for perception of real movement, and with the data on brightness discrimination in the monkey (Crawford, 1935). The latter study determined this value by plotting fractional brightness differences ($\Delta I/I$) as a function of stimulus luminance.

Although the general shape of the upper optokinetic frequency threshold contours in the monkey is that of an organism with duplex retina, it differs in certain features from the results of Crozier and coworkers. Firstly, the values of the entire contour were lower, and secondly, the "cone" component exhibited an unusual depression before the initiation of the "rod" component. Important differences in the techniques of stimulation might explain the comparatively lower values. In the present investigation, the period of the pattern was much wider, the light-dark ratio was smaller, and the contrast was low, all factors possibly associated with an overall reduction in the stimulus effectiveness to elicit an optokinetic response. Moreover, the contrast was not only low but also constant over all luminance steps used, and this factor may account for the narrower range of the obtained threshold values. The very large spread of values (usually from 2 to 50) found by Crozier and associates could be due also to the variety of optokinetic patterns utilized to obtain higher frequencies of stimulation. For example, in the case of the dragonfly larvae (Crozier, Wolf, and Zerrahn-Wolf, 1936-1937), these investigators used a 5-stripe cylinder to obtain a frequency of 2 cps; a 10-stripe cylinder for 3.3 to 10 cps; a 20-stripe cylinder for 12.5 to 16 cps; and a 40-stripe cylinder for 20 to 61 cps. This change in pattern characteristics may be a confounding factor which is now difficult to evaluate. It is known that keeping the luminance and speed of rotation constant, doubling the number of stripes will not result in doubling the frequency of optokinetic response (Komatsuzaki, Harris, Alpert, and Cohen, 1969). It is not unlikely that in the case of "critical flicker fusion" determinations with an optokinetic stimulus, the larger the number of stripes, the higher the thresholds obtained.

Finally, no supporting literature could be obtained for the finding of the depression exhibited by the photopic component before reaching the scotopic segment. It can only be tentatively advanced that the monkey's sensitivity to an optokinetic stimulus seems to increase at the site where cones and rods overlap, compared to surrounding areas where greater proportions of cones and rods are found.

The present experiment allowed the determination of lower and upper optokinetic frequency thresholds as well as the estimate of the absolute luminance threshold for eliciting an optokinetic response in the normal monkey. No data on this absolute luminance threshold in the monkey or man could be found in the literature. The finding therefore may be compared only to the values of absolute thresholds for light perception in man. Bartley (1951) reports a value of $\bar{7}.5$ log mL. In the present study, B_θ for optokinetic response in the monkey was estimated to lie at about $\bar{6}.35$ log ftL. The technique used, however, was not designed to determine absolute visual thresholds and some differences were to be expected. Similarly, the present experimental design did not include the actual determination of this threshold. It is apparent that as the luminance of the stimulus is reduced, the difference between upper and lower thresholds becomes progressively smaller until a value should be reached where the distinction between upper and lower threshold is no longer valid. More discrete steps in the luminance continuum were probably needed for this determination.

B. Symmetry of Spontaneous Oculomotor Activity and Directional Effects of Optokinetic Stimulation

The existence and significance of an axis of behavioral symmetry in species of symmetrical organization have been discussed over a half century ago by Jacques Loeb. This author elaborated an entire theory of animal behavior based on just that concept.

> "The starting point for a scientific and quantitative analysis of animal conduct is the symmetry relations of the animal body. The existence of these symmetry relations reduce the analysis to a comparatively simple problem... The importance of this symmetrical structure lies in the fact that the morphological plane of symmetry is also the dynamical plane of symmetry of the organism." (Loeb, 1918, p. 19).

Since deviations from the symmetry of spontaneous oculomotor activity were considered the basis for evaluating *when* the monkey detected a stimulus change in its surroundings, the core of the present study following the formulation of Loeb's fundamental behavioral property. The assumption of symmetry of spontaneous oculomotor activity was confirmed at all luminance levels. It is important to emphasize that this condition is a prerequisite for threshold determinations. In studies on possible threshold alterations as a result of brain lesions, special consideration must be given to transient or long lasting asymmetries produced by the damage. An extreme situation would be spontaneous nystagmus in one direction. In addition, the probability of asymmetrical oculomotor activity in brain-damaged monkeys increases when the subjects are placed in darkness. In these cases there may be an inverse relationship between the luminance of the stimulus and the degree of asymmetry of spontaneous oculomotor activity. In fact, even in the normal animal it is shown (Table 4) that the group standard deviation of $\bar{P}$ (mean probability of occurrence of eye movements to the right) is inversely proportional to the luminance of the stationary stimulus. It appears as if higher luminance levels "clamp" spontaneous oculomotor activity into symmetrical patterns, whereas lower luminance levels "release" individual patterns of non-significant, but individually consistent, asymmetries.

In all the situations mentioned above, the data will have to be corrected to compensate for the original asymmetry. This correction will involve the selection of P and Q values in the binomial test according to the existing asymmetry. It isrecalled that P and Q are the probabilities of eye movements to the right and to the left respectively during spontaneous oculomotor activity, both set equal to .5 on the basis of data for the normal monkey.

C. Model of the Optokinetic Response in the Normal Monkey

The specification of the stimulus frequency (F_s) as *the* optokinetic stimulus throughout this study does not imply that this is the only determinant of the response. The total optokinetic stimulus contains so many other variables that it is probably deceiving at present to select just one as the significant parameter. The same reservations apply to the response features chosen for study, i.e., its frequency (F_r), since this is one of many that can change as a function of stimulus parameters. Therefore, the three-dimensional model (see Fig. 19) developed from the present and previous data should be considered as a preliminary attempt which relates only two independent variables (the luminance and the frequency of the stimulus) and one dependent variable (the frequency of the response). Moreover, the significance of some of its features can be discussed only at a descriptive level since experimental tests of the model has not yet been conducted. However,the present attempt can be contrasted with previous efforts where optokinetic functions were postulated by means of idealized free-hand curves (Grüttner, 1939) or studies where the data were not fitted to mathematical equations (Komatsuzaki, Harris, Alpert, and Cohen, 1969).

The proposed model provides a systematic framework from which neural investigations of the effect of brain lesions on this response could be evaluated. This type of studies demand finer experimental tests where subtle deficits produced by brain lesions could be detected and the relative involvement of different areas of the brain could be contrasted.

It is clear from the model that there are response features which change along the "luminance axis" and others that vary along the "frequency axis." The changes along the B axis must derive from properties of the monkey's visual system. The most obvious is the presence or absence of the response as determined by the absolute luminance threshold. Similarly, the existence of scotopic and photopic segments, which are present at least in the upper threshold contours and in the contour shown by the peak F_r, also favors the sensorial interpretation of these changes. Finally, the peak F_r and its location in the F_s axis, may be considered also as indicators of sensory capacities since they vary along the B axis. The shift in location of the peak F_r as a function of the stimulus luminance may reflect a higher probability of detecting more of the moving stimuli as the luminance is increased.

Response characteristics that vary along the F_s axis may result from visual, oculomotor, and/or processing factors. The most conspicuous sensory components are defined by the optokinetic frequency thresholds. The lower and upper thresholds are probably related to detection of movement and to critical flicker fusion respectively. The values of the upper frequency thresholds, however, were relatively lower than the CFF values given for the monkey (Symmens, 1962). The characteristics of the stimulus pattern and the use of the eye movements as response indicators might explain the differences.

At each luminance level, there is an optimal range of F_s which elicits the optokinetic response in the normal monkey. This dynamic range is probably dependent on processing mechanisms of unique characteristics. Ordinarily, there is no ideal one-to-one relationship between F_s and F_r. Fig. 16 shows that, at low frequencies of stimulation, the system overreacts to the incoming visual information, i.e., F_r tends to be greater than F_s up to a value at which the relationship becomes one-to-one. Thereafter, F_r lags behind F_s up to a peak. This peak F_r may be the result of limitations in the oculomotor system which cannot respond with higher frequencies. However, if only motor factors were at play, one might expect a plateau at the peak F_r level. The decay of F_r after this peak may be interpreted, therefore, in sensory terms as a reflection of the decreased probability of perceiving the passing stripes.

Finally, two characteristics of the optokinetic response appear to be exclusively related to properties of the oculomotor system since they remain relatively constant in the presence of great variations in the stimulus luminance. These features are the frequency of the response at threshold, and the efficiency ratio F_r/F_s at the peak F_r.

It is expected that the application of the psychophysical techniques described in this investigation to studies of the effect of restricted cerebral lesions will reveal specific alterations in one or several characteristics of the optokinetic response. It may be possible, therefore, to attribute the deficits to the visual, oculomotor, and/or processing components of the phenomenon as outlined above.

APPENDIX A

INDIVIDUAL DATA

Section 1. Tables of lower optokinetic frequency thresholds at each stimulus luminance ($\bar{B}$ in log ft-L).

Section 2. Analyses of variance of the effect of stimulus luminance on lower optokinetic frequency thresholds.

Section 3. Tables of upper optokinetic frequency thresholds at each stimulus luminance ($\bar{B}$ in log ftL).

Section 4. Graph of upper optokinetic frequency thresholds.

Section 5. Analyses of variance of upper optokinetic frequency thresholds.

APPENDIX A, SECTION 1

MONKEY #612

B	Direction	Attempts				Statistics			
		1	2	3	4	$\bar{X}..$	*SD*	*t*	$\bar{X}...$
$\bar{7}.73$	R	.064	*RM*	.038	*RM*	.051	--	--	.136
	L	*RM*	.222	*RM*	*RM*	.222	--		
$\bar{6}.70$	R	.064	.116	.142	.064	.097	.049	1.094	.177
	L	.086	.086	.167	.685	.256	.299		
$\bar{5}.71$	R	.116	.142	.142	.082	.120	.039	.309	.117
	L	.086	.082	.113	.167	.113	.049		
$\bar{4}.71$	R	.126	.064	.090	.090	.090	.021	1.487	.102
	L	.086	.113	.113	.140	.113	.022		
$\bar{3}.75$	R	.090	.142	.090	.064	.097	.032	.652	.103
	L	.113	.122	.086	.113	.100	.026		
$\bar{2}.70$	R	.142	.090	.142	.142	.129	.036	.778	.143
	L	.113	.249	.113	.150	.156	.064		
$\bar{1}.71$	R	.177	.194	.168	.090	.158	.056	1.083	.139
	L	.086	.195	.086	.113	.120	.052		
.82	R	.116	.160	.220	.194	.173	.045	.368	.177
	L	.167	.167	.195	.195	.181	.026		

APPENDIX A, SECTION 1 (cont.)

MONKEY #616

B	Attempts				Statistics			
	1	2	3	4	$\bar{X}..$	*SD*	*t*	$\bar{X}...$
$\bar{7}.73$	*RM*	*RM*	*RM*	*RM*	*RM*	--	--	*RM*
	RM	*RM*	*RM*	*RM*	*RM*	--		
$\bar{6}.70$	.116	.298	.557	.454	.356	.192	.758	.302
	.077	.513	.067	.331	.247	.215		
$\bar{5}.71$	.194	.540	.116	*RM*	.284	.226	.878	.218
	.059	.413	.077	.059	.152	.174		
$\bar{4}.71$	.168	.350	.428	.514	.365	.148	2.330	.261
	.059	.204	.277	.086	.156	.102		
$\bar{3}.75$	.142	.168	.333	.462	.276	.150	2.234	.191
	.086	.140	.086	.113	.106	.026		
$\bar{2}.70$	.220	.186	.194	.090	.173	.057	.855	.205
	.113	.277	.421	.140	.238	.142		
$\bar{1}.71$	.168	.194	.618	*RM*	.327	.253	.200	.345
	.258	.140	.658	.395	.363	.222		
.82	.246	.385	.679	.419	.432	.181	.101	.426
	.322	.231	.594	.531	.420	.171		

APPENDIX A, SECTION 1 (cont.)

MONKEY #617

B	Direction	Attempts				Statistics			
		1	2	3	4	$\bar{X}..$	*SD*	*t*	$\bar{X}...$
$\bar{7}.73$	R	.142	*RM*	.090	*RM*	.116	.031	.083	.115
	L	.086	*RM*	.140	*RM*	.113	.038		
$\bar{6}.70$	R	.116	.064	*RM*	.116	.099	.030	.021	.099
	L	.086	*RM*	*RM*	.113	.100	.019		
$\bar{5}.71$	R	.064	.168	.064	.064	.090	.052	2.035	.123
	L	.140	.204	.113	.168	.156	.039		
$\bar{4}.71$	R	.056	.246	.318	.090	.177	.125	.783	.210
	L	.168	.231	.331	*RM*	.243	.082		
$\bar{3}.75$	R	.090	.116	.116	.177	.125	.037	1.159	.170
	L	.113	.167	.140	.439	.215	.151		
$\bar{2}.70$	R	.082	.160	.142	.168	.138	.039	1.450	.168
	L	.231	.113	.167	.277	.197	.072		
$\bar{1}.71$	R	.125	.142	.160	.194	.155	.030	1.902	.192
	L	.168	.222	.195	.331	.229	.072		
.82	R	.090	.142	.090	.168	.123	.039	1.831	.159
	L	.113	.231	.168	.268	.195	.068		

APPENDIX A, SECTION 1 (cont.)

MONKEY #636

B	Direction	Attempts				Statistics			
		1	2	3	4	$\bar{X}_{..}$	*SD*	*t*	$\bar{X}_{...}$
$\bar{7}.73$	R	*RM*	.090	.064	*RM*	.077	.018	2.782	.095
	L	*RM*	.113	.113	*RM*	.113	.000		
$\bar{6}.70$	R	.142	.090	.168	.090	.123	.039	.359	.128
	L	.113	.177	.168	.077	.134	.047		
$\bar{5}.71$	R	.220	.255	.168	.116	.199	.060	.192	.186
	L	.195	.122	.140	.267	.181	.065		
$\bar{4}.71$	R	.168	.229	.246	.168	.203	.041	.121	.200
	L	.313	.195	.168	.113	.197	.084		
$\bar{3}.75$	R	.177	.134	.220	.116	.162	.046	.657	.180
	L	.331	.204	.113	.140	.197	.097		
$\bar{2}.70$	R	.168	.289	.272	.203	.233	.057	.207	.228
	L	.249	.222	.286	.140	.224	.062		
$\bar{1}.71$	R	.255	.402	.359	.350	.341	.062	.421	.331
	L	.286	.259	.440	.295	.320	.082		
.82	R	.307	.480	.324	.220	.332	.108	.429	.319
	L	.231	.286	.340	.367	.306	.060		

APPENDIX A, SECTION 1 (cont.)

MONKEY #637

B	Direction	Attempts				Statistics			
		1	2	3	4	$\bar{X}..$	*SD*	*t*	$\bar{X}...$
$\bar{7}.73$	R	*RM*	*RM*	*RM*	*RM*	*RM*	--	--	*RM*
	L	*RM*	*RM*	*RM*	*RM*	*RM*	--		
$\bar{6}.70$	R	*RM*	*RM*	.142	.194	.168	.037	.924	.261
	L	.313	.740	.140	.222	.354	.267		
$\bar{5}.71$	R	.385	.514	.229	.194	.330	.148	.688	.301
	L	.258	.367	.295	.167	.272	.083		
$\bar{4}.71$	R	.410	.333	.471	.194	.353	.120	1.782	.297
	L	.286	.231	.249	.195	.240	.039		
$\bar{3}.75$	R	.437	.255	.333	.359	.346	.075	.562	.328
	L	.313	.449	.222	.258	.311	.100		
$\bar{2}.70$	R	.410	.410	.583	.090	.374	.206	.906	.316
	L	.476	.140	.195	.222	.258	.149		
$\bar{1}.71$	R	.255	.255	.281	.428	.305	.083	.523	.286
	L	.150	.431	.237	.249	.267	.118		
.82	R	.281	.272	.324	.298	.294	.023	.090	.290
	L	.449	.285	.140	.277	.288	.126		

APPENDIX A, SECTION 2

Analyses of Variance of the Effect of Stimulus Luminance on Lower Optokinetic Frequency Thresholds

	Source of Variation	Sum of Squares	d.f.	Mean Square	F
# 612	$\bar{B}$	.0262	7	.0037	1.00
	Error	.0861	23	.0037	
	Total	.1123	30		
# 616	$\bar{B}$	.1960	6	.0327	1.49
	Error	.4609	21	.0219	
	Total	.6569	27		
# 617	$\bar{B}$	.0310	7	.0044	1.02
	Error	.0897	21	.0043	
	Total	.1207	28		
# 636	$\bar{B}$	.1659	7	.0237	12.47*
	Error	.0417	22	.0019	
	Total	.2076	29		
# 637	$\bar{B}$	.0129	6	.0022	.13
	Error	.3474	21	.0165	
	Total	.3603	27		

Notes. * $p < .01$

d.f.: only treatments ($\bar{B}$) with 50% of positive attempts (or greater) were considered.

APPENDIX A, SECTION 3

MONKEY #612

B	Direction	Attempts				Statistics			
		1	2	3	4	$\bar{X}$..	*SD*	*t*	$\bar{X}$...
$\bar{7}.73$	R	*RM*	*RM*	*RM*	*RM*	*RM*	--	--	
	L	*RM*	*RM*	*RM*	*RM*	*RM*	--		
$\bar{6}.70$	R	3.06	2.50	2.78	3.53	2.97	.46	1.427	3.46
	L	2.83	6.06	*RM*	*RM*	4.44	2.28		
$\bar{5}.71$	R	4.74	3.90	3.25	8.37	5.06	2.29	.115	4.99
	L	5.77	5.96	3.69	4.25	4.22	1.12		
$\bar{4}.71$	R	6.69	4.46	9.95	9.30	7.60	2.52	.180	7.46
	L	10.14	5.77	6.44	6.91	7.32	1.94		
$\bar{3}.75$	R	5.76	7.06	10.51	7.63	7.74	2.00	.033	7.77
	L	8.43	8.91	9.29	4.54	7.79	2.20		
$\bar{2}.70$	R	4.74	7.44	5.48	5.58	5.77	1.11	1.320	6.73
	L	11.09	6.06	8.34	5.20	7.67	2.63		
$\bar{1}.71$	R	6.51	6.14	6.97	4.74	6.09	.96	1.310	6.70
	L	9.67	6.06	6.91	6.63	7.32	1.61		
.82	R	5.58	8.46	11.07	8.46	8.39	2.24	1.000	9.36
	L	9.29	11.09	14.22	6.72	10.33	3.15		

APPENDIX A, SECTION 3 (cont.)

MONKEY #616

B	Direction	Attempts				Statistics			
		1	2	3	4	$\bar{X}_{..}$	*SD*	*t*	$\bar{X}_{...}$
$\bar{7}.73$	R	*RM*	*RM*	*RM*	*RM*	*RM*	--	--	*RM*
	L	*RM*	*RM*	*RM*	*RM*	*RM*	--		
$\bar{6}.70$	R	3.34	3.06	*RM*	4.46	3.62	.74	2.39	6.60
	L	13.65	6.63	12.60	5.39	9.57	4.16		
$\bar{5}.71$	R	3.90	3.34	3.06	4.92	3.81	.82	1.71	5.32
	L	6.06	3.78	10.71	*RM*	6.85	3.53		
$\bar{4}.71$	R	12.38	3.62	2.97	5.02	6.00	4.34	.22	5.74
	L	4.92	3.78	6.34	6.91	5.49	1.41		
$\bar{3}.75$	R	6.14	5.02	5.86	3.90	5.23	1.00	1.73	6.90
	L	14.03	6.06	7.86	6.34	8.57	3.72		
$\bar{2}.70$	R	8.74	2.50	5.30	5.20	5.44	2.56	1.44	6.52
	L	6.91	7.86	5.96	9.67	7.60	1.58		
$\bar{1}.71$	R	6.14	3.62	5.58	7.16	5.62	1.48	.66	5.92
	L	6.15	6.53	5.96	*RM*	6.22	.29		
.82	R	14.98	4.55	4.09	7.16	7.70	5.04	.25	7.36
	L	5.49	9.00	5.87	7.77	7.03	1.65		

APPENDIX A, SECTION 3 (cont.)

MONKEY #617

B	Direction	Attempts				Statistics			
		1	2	3	4	$\bar{X}$..	*SD*	*t*	$\bar{X}$...
$\bar{7}.73$	R	*RM*	*RM*	*RM*	*RM*	*RM*	--	--	*RM*
	L	*RM*	*RM*	*RM*	*RM*	*RM*	--		
$\bar{6}.70$	R	5.30	*RM*	*RM*	4.09	4.69	.86	1.30	5.39
	L	6.99	5.20	*RM*	*RM*	6.10	1.26		
$\bar{5}.71$	R	9.58	8.18	6.42	6.79	7.74	1.44	.58	7.30
	L	10.42	7.10	5.67	4.25	6.86	2.64		
$\bar{4}.71$	R	9.86	9.95	10.61	5.30	8.93	2.44	.73	8.21
	L	11.85	6.44	4.82	6.91	7.50	3.03		
$\bar{3}.75$	R	14.42	12.75	13.30	6.79	11.82	3.42	1.36	10.43
	L	11.91	9.10	8.53	6.63	9.05	2.20		
$\bar{2}.70$	R	14.98	11.35	10.79	6.97	11.02	3.28	1.11	9.76
	L	13.08	7.86	6.63	6.44	8.50	3.12		
$\bar{1}.71$	R	13.03	11.35	11.63	7.52	10.88	2.36	.30	10.50
	L	16.57	7.96	9.10	6.82	10.11	4.44		
.82	R	17.50	11.91	8.74	6.42	11.14	4.80	.74	12.77
	L	25.04	10.62	13.37	8.62	14.41	7.35		

APPENDIX A, SECTION 3 (cont.)

MONKEY #636

B	Direction	Attempts				Statistics			
		1	2	3	4	$\bar{X}..$	*SD*	*t*	$\bar{X}...$
$\bar{7}.73$	R	*RM*	*RM*	*RM*	*RM*	*RM*	--	--	*RM*
	L	*RM*	*RM*	*RM*	*RM*	*RM*	--		
$\bar{6}.70$	R	2.50	3.90	3.34	*RM*	3.25	.70	3.188*	4.08
	L	4.92	4.92	*RM*	*RM*	4.92	.00		
$\bar{5}.71$	R	8.93	5.76	4.18	3.81	5.67	2.33	.090	5.60
	L	7.29	7.01	3.97	3.88	5.54	1.87		
$\bar{4}.71$	R	7.07	10.98	6.69	5.30	7.51	2.44	.259	7.94
	L	15.36	6.06	*RM*	3.68	8.37	6.17		
$\bar{3}.75$	R	15.54	13.59	8.46	9.02	11.65	3.46	.839	10.21
	L	17.16	8.81	4.92	4.16	8.76	5.96		
$\bar{2}.70$	R	19.92	14.42	6.97	5.86	11.79	6.62	.875	9.65
	L	18.30	3.97	3.12	4.63	7.51	7.23		
$\bar{1}.71$	R	10.23	10.29	3.34	5.58	7.36	3.47	.981	9.34
	L	18.87	10.42	4.63	*RM*	11.31	7.16		
.82	R	29.05	23.37	9.86	8.46	17.68	10.13	1.139	14.15
	L	19.16	13.84	3.68	5.77	10.62	7.18		

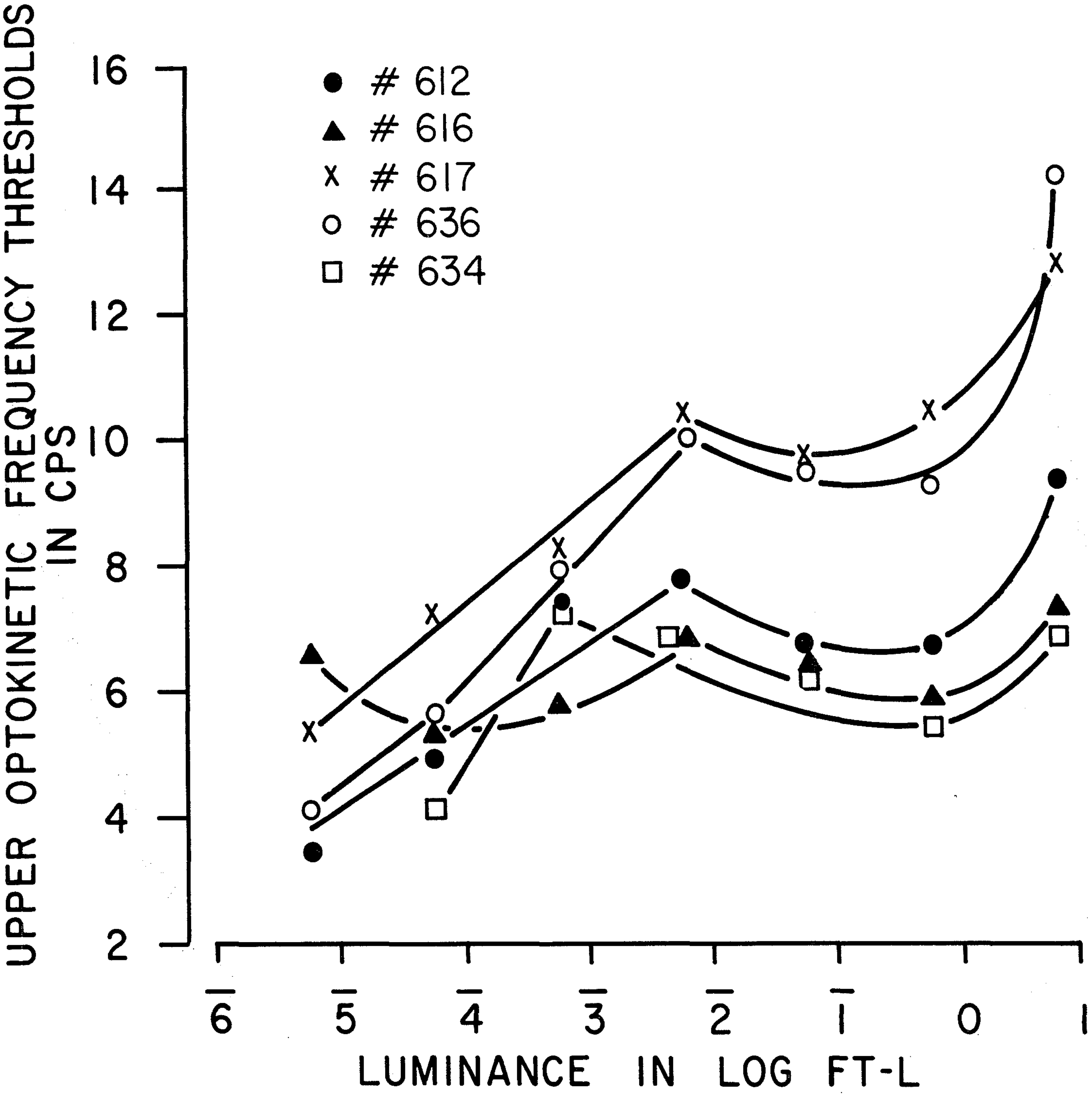
* $p < .05$

APPENDIX A, SECTION 3 (cont.)

MONKEY #637

B	Direction	Attempts				Statistics			
		1	2	3	4	$\bar{X}..$	*SD*	*t*	$\bar{X}...$
$\bar{7}.73$	R	*RM*	*RM*	*RM*	*RM*	*RM*	--	--	*RM*
	L	RM	RM	RM	RM	RM	--		
$\bar{6}.70$	R	*RM*	*RM*	*RM*	*RM*	*RM*	--	--	*RM*
	L	*RM*	*RM*	*RM*	*RM*	*RM*	--		
$\bar{5}.71$	R	4.18	2.04	4.46	3.25	3.48	1.09	1.918	4.10
	L	4.35	5.77	4.25	4.54	4.72	.71		
$\bar{4}.71$	R	7.53	5.58	5.30	5.58	6.00	1.03	1.678	7.43
	L	13.37	8.81	7.48	5.77	8.86	3.25		
$\bar{3}.75$	R	8.18	4.46	7.16	4.74	6.14	1.83	.976	6.89
	L	11.37	6.82	6.06	6.34	7.65	2.50		
$\bar{2}.70$	R	6.42	7.90	4.74	4.92	6.00	1.48	.499	6.43
	L	11.37	4.63	4.73	6.72	6.86	3.16		
$\bar{1}.71$	R	5.76	6.14	6.14	4.09	5.53	.98	.058	5.56
	L	7.86	4.54	5.39	4.54	5.58	1.57		
.82	R	7.63	8.00	6.79	7.90	7.58	.55	1.828	7.07
	L	6.91	5.20	8.34	5.77	6.56	1.38		

Appendix A, Section 4. Graph of Upper Optokinetic Frequency Thresholds.


UPPER OPTOKINETIC FREQUENCY THRESHOLDS IN CPS
16
14
12
10
8
6
4
2
● # 612
▲ # 616
x # 617
○ # 636
□ # 634
6̄
5̄
4̄
3̄
2̄
1̄
0
1
LUMINANCE IN LOG FT-L

APPENDIX A, SECTION 5

Analyses of Variance of the Effect of Stimulus Luminance on Upper Optokinetic Frequency Thresholds

	Source of Variation	Sum of Squares	d.f.	Mean Square	F
# 612	$\bar{B}$	90.72	6	15.12	7.03**
	Error	45.20	21	2.15	
	Total	135.92	27		
# 616	$\bar{B}$	20.69	6	3.45	.75
	Error	96.88	21	4.61	
	Total	117.57	27		
# 617	$\bar{B}$	132.53	6	22.09	2.09
	Error	211.92	20	10.56	
	Total	344.45	26		
# 636	$\bar{B}$	245.09	6	40.85	1.56
	Error	523.53	20	26.18	
	Total	768.62	26		
# 637	$\bar{B}$	30.32	5	6.06	2.83*
	Error	38.44	18	2.14	
	Total	68.76	23		

Notes. * $p < .05$

** $p < .01$

d.f.: only treatments ($\bar{B}$) with 50% of positive attempts (or greater) were considered.

APPENDIX B

COMPUTER PROGRAMS IN FOCAL 1968

Program No. 1.	Mathematical model of the optokinetic response.
Program No. 2.	Procedure to calculate lower and upper optokinetic frequency thresholds from the mathematical model of the optokinetic response.
Program No. 3.	Optokinetic function.
Program No. 4.	Procedure to calculate peak response and its location from the mathematical model of the optokinetic response.

Program No. 1

```
02.10 A ?BB? ; A ?       SF?
02.20 S A=1.1979+.0680*BB
02.30 S B=-1.0674-.01*BB
02.40 S E=A+B*FLOG(SF)*.4343
02.50 S R=E*SF
02.60 T "       " R
02.70 T ! ; G 2.1
```

Program No. 2

```
01.40 S SF=0 ; S BB=0
01.50 S BB=5
01.60 S BB=BB-1

02.10 T ! ?BB?
02.11 S SF=SF+.01
02.20 S A=1.1979+.0680*BB
02.30 S B=-1.0674-.01*BB
02.40 S E=A+B*FLOG(SF)*.4343
02.50 S R=E*SF
02.60 I (.25-R)5.1,5.1,2.11

05.10 T "        " SF

06.11 S SF=SF+.01
06.20 S A=1.1979+.0680*BB
06.30 S B=-1.0674-.01*BB
06.40 S E=A+B*FLOG(SF)*.4343
06.50 S R=E*SF
06.60 I (R-.25)7.1,7.1,6.11

07.10 T "          " SF
07.20 S SF=0 ; G 1.6
```

Program No. 3

```
02.10 ASK ! "ENTER A" A ; ASK "     ENTER B" B

03.10 ASK ! "ENTER FS" X ; TYPE "     FR" X*[A+B*FLOG(X)*.4343]
03.20 GOTO 3.1
```

Program No. 4

```
01.50 S X=0 ;  S Y2=0
01.60 A ?A? ;  A ?      B?

02.10 S X=X+.01
02.20 S Y1=(A-B*FLOG(X)*.4343)*X
02.30 S D=Y1-Y2
02.40 I (Y1-Y2)3.1,3.1,2.5
02.50 S Y2=Y1 ;  G 2.1

03.10 T "           FS"  X ; T "          FK" Y1
```

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AUTOBIOGRAPHICAL STATEMENT

The author was born in Argentina where he completed his B.A. and M.A. in Psychology at the Universidad Nacional de Rosario. There he taught several subjects before coming to the United States. In 1963 he was Research Assistant in the Department of Psychiatry at the Albert Einstein College of Medicine of Yeshiva University. He entered the doctoral program in Psychology at the City University of New York in the specialization of Neuropsychology in 1964. On that year he also was appointed Research Fellow in the Department of Neurology at the Mount Sinai Hospital. In 1966 he became Assistant in Neurology at the newly created Mount Sinai School of Medicine of the City University of New York. In 1970 he was Lecturer in Psychology at Bronx Community College of C.U.N.Y. He participated in several national and international meetings where he reported studies in monkeys on effects of temporal lobe lesions, oculomotor dysfunctions in split-brain preparations, parametric studies of optokinetic nystagmus and nystagmus elicited by monocular stroboscopic stimulation. After graduation he plans to pursue quantitative studies on visuo-vestibulo-oculomotor interactions.