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THE INFLUENCE OF ROD LIGHT ADAPTATION ON ROD-CONE INTERACTION

City University of New York PH.D. 1981

THE INFLUENCE OF ROD LIGHT ADAPTATION ON ROD-CONE INTERACTION

by

Glenn M. Bauer

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1980

Glenn M. Bauer

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

11/6/80
Date

Chairman of the Examining Committee

December 16, 1980
Date

Executive Officer

Supervisory Committee

The City University of New York

Abstract

THE INFLUENCE OF ROD LIGHT ADAPTATION

ON ROD-CONE INTERACTION

by

Glenn M. Bauer

Adviser: Dr. Thomas E. Frumkes

The influence of rod stimulation on cone sensitivity was examined while the rod system was selectively light adapted. A Maxwellian view optical system was used to present all stimuli to the right eye of three observers. These stimuli included a 25 msec duration, 13' diameter, 655 nm wavelength test flash; a 500 msec duration, 40' diameter, 512 nm wavelength masking flash; and a continuously exposed, 40° diameter, 490 nm wavelength adapting field. The flashing stimuli were presented to the nasal retina, 7° from fixation along the horizontal meridian. The adapting field was concentric with a fixation target.

Experiment 1 was designed to delineate a range of adapting field illuminance over which the sensitivity of the rod system decreases while the sensitivity of the cone system is unchanged. Toward this end, the threshold of the 655 nm test flash and the threshold of the 512 nm masking flash were each determined as a function of adapting field illuminance. Experiment 1 established the masking flash illuminance values required to stimulate rods alone or rods and cones and insured that cones alone determined test flash threshold regardless of the level of adapting field illuminance. In general, there exists a 3.0 log unit range of adapting field illuminance over which rod sensitivity decreases while cone sensitivity is unchanged.

The goal of Experiment 2 was to determine the influence of rod light adaptation on rod-cone interaction. In Experiment 2a, test flash threshold was measured as a function of masking flash illuminance under dark adapted conditions and under scotopic levels of adapting field illuminance. The results were plotted as tvi curves (i.e., test flash threshold versus masking flash illuminance curves). The tvi curve obtained under dark adapted conditions can be described in four segments: Test flash threshold is constant with increases in masking flash illuminance until masking flash illuminance exceeds the absolute threshold illuminance of the masking flash (segment A). Thereafter, test flash threshold increases in proportion to the square root of increases in masking flash illuminance (segment B).until a plateau level is reached (segment C). Further increases in test flash threshold occur at still higher masking flash illuminance values. (segment D). Data corresponding to segments A and B can be described by the equation:

$$I_{c_{th}}/I_{c_o} = K\sqrt{(I_r/I_{r_{th}}) + D}$$

where $I_{c_{th}}$ is the threshold illuminance of the cone test flash, I_{c_o} is the absolute threshold of the test flash, I_r is the illuminance of the 512 nm masking flash, $I_{r_{ch}}$ is the threshold illuminance of the masking flash, D is a dark noise term, and K is a unit related constant.

The basic form of the tvi curve is preserved regardless of the scotopic level of adapting field illuminance. However, light adaptation of the rod system shifts the origin of tvi curves toward higher masking flash illuminance values by an amount equal to the increase

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$$I_{c_{th}}/I_{c_o} = K\sqrt{(I_r/I_{r_{th}}) + D}$$

where $I_{c_{th}}$ is the threshold illuminance of the cone test flash, I_{c_o} is the absolute threshold of the test flash, I_r is the illuminance of the 512 nm masking flash, $I_{r_{th}}$ is the threshold illuminance of the masking flash, D is a dark noise term, and K is a unit related constant.

The basic form of the tvi curve is preserved regardless of the scotopic level of adapting field illuminance. However, light adaptation of the rod system shifts the origin of tvi curves toward higher masking flash illuminance values by an amount equal to the increase

in masking flash threshold illuminance. In addition, the extent of the plateau level decreases as rods are light adapted.

In Experiment 2b, action spectra data were collected to elucidate the photoreceptor mechanism(s) responsible for increasing test flash threshold. The irradiance of different wavelength masking flashes required to cancel the detection of the test flash was determined when the test flash was set at a subplateau (segment B) or a supraplateau (segment D) illuminance value. Action spectra data clearly indicate that in Experiment 2a, rods alone stimulated by the 512 nm masking flash were responsible for subplateau increases in test flash threshold. However, rods and cones stimulated by the masking flash are responsible for raising test flash threshold to supraplateau levels.

The results of these experiments were related to mechanisms underlying rod-cone interaction and rod light adaptation: The effects of rod stimulation on cone sensitivity manifested in Experiment 2a were discussed in terms of an ideal detector model of rod-cone interaction. The influence of rod light adaptation on rod-cone interaction was related to changes in the responsivity of the rod photoreceptor accompanying increases in retinal illumination.

Acknowledgements

I am most indebted to Dr. Thomas E. Frumkes for his teaching, guidence, and encouragement. Deserving a special note of thanks are Jared Jacobs and Nora Nicotera for their dependable service as observer and experiemmter, Gloria Kopp for the typing of this manuscript, and Dr. Rolf Nygaard for his advice and friendship. I am also grateful to the members of the Doctoral Dissertation Defense Committee, Drs. William Battersby, James Gordon, Mitchell Kietzman, and Leonard Temme, for their constructive comments.

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Chapter 1: Introduction

The Duplicity Theory of Vision distinguishes the operations of the rod and cone systems.[1] Long, cylindrical photoreceptors, the rods, mediate vision under low (scotopic) levels of illumination while conically shaped photoreceptors, the cones, operate under high (photopic) levels of illumination.[2] The differences between the rod and cone systems becomes more apparent when one considers the modes of operation they subserve. Cones afford the acute spatial and temporal resolution and wavelength discrimination associated with daytime vision while the rod system's pronounced sensitivity to light accomodates nighttime visual performance.

The differences between scotopic and photopic vision suggest that the vertebrate visual system can be divided into two functionally independent subcomponents. This notion was advanced in many early psychophysical studies. Among those of greatest relevance to the present study are the two-color increment threshold experiments of Stiles (1939, 1949, 1959). Under dark adapted conditions, the threshold of a para-

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1. The terms rod system and cone system refer to the structural and functional connections of the rod and cone photoreceptors, respectively. These systems involve several orders of neurons. The terms rod signals and cone signals are used to denote the output of the photoreceptors and the consequent activity in the rod and cone systems following light stimulation. It is assumed that these signals can be monitored via electrophysiological and psychophysical procedures. Finally, the terms rod-cone independence and rod-cone interaction pertain to the functional interrelationships between the rod and cone systems.

2. It should be noted that under "mesopic" levels of illumination, the rod and cone systems operate simultaneously. In fact, rod-cone interactions have been demonstrated under mesopic conditions. Rod-cone interaction is discussed in detail in Chapter 2.

foveally presented test flash of variable wavelength was measured as a function of the irradiance of a continuously exposed, 10^{o} diameter adapting field also of variable wavelength. For a given wavelength combination of test and adapting stimuli, increases in adapting field irradiance were accompanied by increases in test flash threshold. For data restricted to within a few log units of test flash absolute threshold, Stiles found that a single scotopic (rod) photoreceptor mechanism was responsible for increasing the threshold of the test flash despite the fact that long wavelength adapting fields stimulated both rods and cones. Thus, Stiles assumed a functional independence between rod and cone related photoreceptor mechanisms. Rod-cone independence has also been demonstrated under conditions which yield metacontrast (Alpern, 1965) and stimulus "sensitization" (Westheimer, 1970).

Frumkes and Temme (1977) questioned the generality of the independence of the rod and cone systems. Using the two-color increment threshold procedure, they found that small (ca. 1^{o}) diameter adapting fields equated for their effects on rods differentially affect sensitivity to a rod test flash;[3] red (615-680 nm) adapting fields had a greater influence on test flash threshold indicating that cones influence the increment threshold behavior of the rod system. Large (ca. 6^{o}-8^{o}) diameter adapting fields did not differentially affect rod test flash threshold. These data suggest that the 10^{o} diameter adapting field used by Stiles was of inappropriate size to elicit rod-cone interactions.

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3. The terms rod test/masking flash and cone test flash indicate that the rod or cone photoreceptor systems subserve the detection of the appropriate stimulus.

Similarly, Temme and Frumkes (1977) reported a size dependent influence of rod stimulation on cone sensitivity. Under dark adapted conditions, they measured the threshold of a small, brief, cone test flash as a function of the illuminance of a steady, concentric, variable diameter, green adapting field. When the diameter of the adapting field was greater than 2^{o}, increment threshold data supported the notion of rod-cone independence. There exists a 3.0 log unit range beyond adapting field absolute threshold over which increases in adapting field illuminance left test flash threshold unchanged; test flash threshold did not rise until the adapting field excited cones. However, when the diameter of the adapting field was less than or equal to 40', test flash threshold increased with increases in adapting field illuminance until a plateau level was reached. Further increases in test flash threshold occured at still higher adapting field illuminances. Action spectra data obtained with a 40'diameter adapting field showed that the initial rise in cone test flash threshold was due to rods.

Recently, Frumkes, Bauer, and Nygaard (1979) provided a quantification of this type of rod-cone interaction. Specifically, they found that the initial rise in the threshold of the cone test flash was proportional to the square root of the illuminance of the rod adapting stimulus. They also present data indicating that, in terms of rod-cone interaction, the visual system behaves like an ideal detector.

Since rod activity can alter cone sensitivity, it follows that the magnitude of this interaction will increase or decreases under conditions which augment or attenuate, respectively, the magnitude of

rod generated signals. In fact, Frumkes, Bauer, and Holstein (1978) showed that the influence of a fixed illuminance rod masking flash on the threshold of a cone test flash increases during the rod recovery stage of dark adaptation. They found that test flash threshold increased in proportion to the square root of rod sensitivity to the rod masking flash. In the present study, the influence of rod stimulation on cone sensitivity is examined while the magnitude of rod signals is attenuated by light adaptation. The rationale for this study is presented in detail on pages 20-22.

Chapter 2: Literature Review

The Duplicity Theory of Vision represents a coalescence of anatomical, physiological, and behavioral observations which describe the differences between the rod and cone systems (for reviews see Hecht, 1937; Ripps and Weale, 1976). A fundamental distinction between the rod and cone systems involves the levels of illumination overwhich they operate. In general, the rod system mediates vision under low (scotopic) levels of retinal illumination while the cone system operates under high (photopic) levels of retinal illumination. As retinal illumination is gradually increased above the dark adapted level, the rod system is systematically desensitized until a transition from rod to cone mediation of visual operations is manifested.

Increment threshold procedures have provided a means for quantifying the desensitization accompanying light adaptation. In its simplest case, the increment threshold experiment measures the threshold of a test flash as a function of the illuminance of a surrounding background or adapting field. Early psychophysical investigations revealed that for parafoveally presented stimuli, the relationship between test flash threshold and adapting field illuminance is described by a two-limbed function with the lower and upper limbs being related to the rod and cone mediation of test flash threshold, respectively (Blackwell, 1946; Hecht, Peskin, & Patt, 1938). The plot of the relationship, test flash threshold as a function of adapting field illuminance is designated as a "threshold versus illuminance" or "tvi" function and is customarily plotted on log-log coordinates.

Rod Adaptation

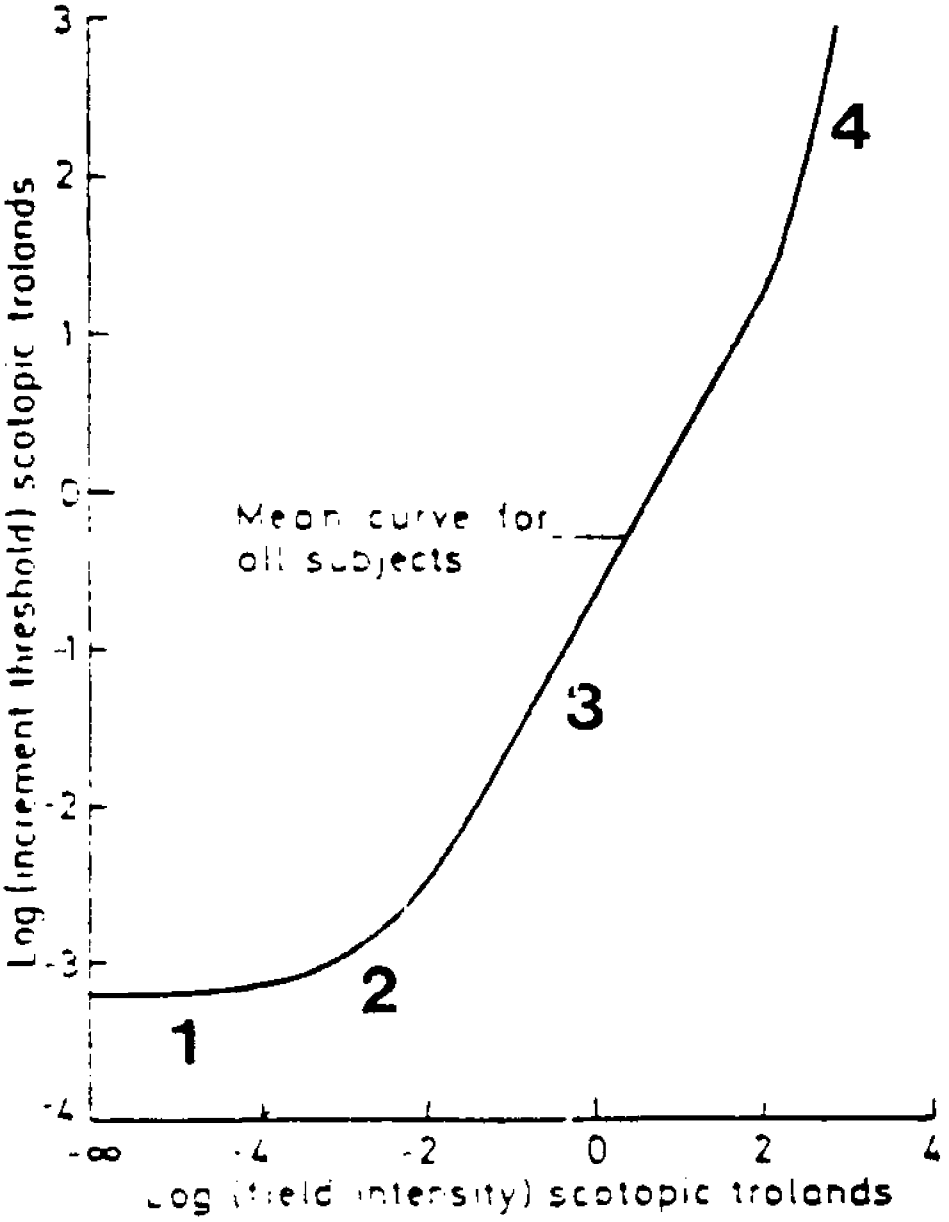
The desensitization of the rod system accompanying light adaptation

was formally addressed by Aguilar and Stiles (1954). The threshold of a 200 msec duration, 9° diameter, green test flash was measured as a function of the illuminance of a steady, concentric, red, 20° diameter adapting field. In addition, Aguilar and Stiles took advantage of the Stiles-Crawford effect to insure a functional isolation of the rod and cone systems (Flamant & Stiles, 1948; Stiles & Crawford, 1933). Since the test flash was presented through the peripheral aspect of the pupil, the threshold detection of the test flash could only be mediated through rods. The resulting tvi curve appears in Figure 1 and can be divided into four segments:

At low illuminance values the adapting field has little influence on test flash threshold (segment 1). This has been attributed to a "dark noise" within the rod system (Barlow, 1957, 1965, 1972). Dark noise can be thought of as an internal source of excitation which acts like real light and outweighs the initial increases in adapting field illuminance. Thus, at low adapting field illuminance values, test flash threshold remains constant.

In segment 2, test flash threshold rises in proportion to the square root of the increments in adapting field illuminance. These data suggest that the rod system operates according to the principles of an ideal detector over a restricted range of adapting field illuminance (see Barlow, 1957; Baumgardt, 1972; DeVries, 1943; Rose, 1948). However, at higher adapting field illuminance values (segment 3), the relationship between test flash threshold and adapting field illuminance is approximated by Weber's law, i.e., $\Delta I = KI$. Consequently, the increment threshold function bears a slope of 1.0 on logarithmic coordinates. It should be noted that the slope of segment 3 depends on the area and

Fig. 1. The theshold illuminance of a parafoveally presented, 200 msec duration, 9° diameter, green test flash as a function of the illuminance of a concentric, steady, 20° diameter, red adapting field (Aguilar & Stiles, 1954).


Log (increment threshold) scotopic trolands
3
2
1
0
-1
-2
-3
-4
Mean curve for all subjects
1
2
3
4
-∞
-4
-2
0
2
4
Log (field intensity) scotopic trolands

duration of the test flash. When these stimulus parameters are reduced, the slope of the increment threshold function decreases and approaches 0.5 for test flashes of very small area and duration (Barlow, 1957). Consequently, the range over which the rod system behaves like an ideal detector (segment 2) is expanded. It appears that the square root and Weber's laws are limits and, with most stimuli, the slope of segment 3 falls between 0.5 and 1.0. Indeed, intermediate slopes have been reported for increment threshold data when the test flash is varied in both size and duration (Barlow, 1957; Crawford, 1947; Blakemore & Rushton, 1965a, 1965b).

When adapting field illuminance approaches 2000-3000 scotopic trolands, the slope of the increment threshold function approaches infinity (segment 4); the response of the rod system appears to saturate. It has been demonstrated that this phenomenon is not due to rod photopigment bleaching or the intrusion of cones. Rushton (1956) showed that only 5% of the visual pigment is in the bleached state at the adapting field illuminance at which rod saturation occurs. Since Fuortes, Gunkel, and Rushton (1961) reported that saturation occurs at the same scotopic illuminance regardless of the adapting field wavelength, rod saturation appears to be a property of the rod system independent of any cone involvement.

The results of Aguilar and Stiles (1954) have since been substantiated (Alpern, Rushton, & Torii, 1970a, 1970b; Blakemore & Rushton, 1965a; Hallet, 1969), but the mechanisms underlying rod desensitization to light remain unclear. Although interocular desensitization effects which require the participation of cerebral mechanisms have clearly been demonstrated (Battersby & Wagman, 1962; LeGrand, 1968), retinal processes

are generally assumed to underly most of the changes in sensitivity to light (Barlow, 1972; Gouras, 1972; Ripps & Weale, 1976). In fact, recent electrophysiological data indicate that changes in the responsivity of the rod photoreceptors can largely account for psychophysically derived rod increment threshold data (Arden, 1976; Fain, 1976; Kleinschmidt & Dowling, 1975).

As shown by intracellular recordings from a number of vertebrate species, the rod photoreceptor response to light stimulation can be described by the equation

$$V/V_{max} = I/(I+\sigma) \qquad (1)$$

where V is the change in membrane potential, V_{max} is the maximum observable change, I is the intensity of the light stimulus, and σ is the intensity of the light stimulus for which $V = \frac{1}{2}V_{max}$ (Dowling & Ripps, 1972; Fain, 1976; Grabowski & Pak, 1975; Hagins, Penn, & Yoshikami, 1970; Kleinschmidt & Dowling, 1975; Normann & Werblin, 1974). Increasing the level of background illumination reduces the maximum observable response ("response compression") and/or changes the value of σ which, in effect, shifts the response function horizontally along the intensity axis toward higher stimulus intensities. Response compression restricts the range over which incremental responses can be obtained while increasing the value of σ results in more light being required to elicit a criterion (threshold) response. Fain (1976) and Kleinschmidt and Dowling (1975) have demonstrated that rod desensitization is primarily derived from a shifting of the response function although psychophysical procedures suggest that response compression underlies rod desensitization accompanying light adaptation (Alpern, Rushton, & Torii, 1970a, 1970b). In any event, the magnitude of these indices of rod desensitization has

been found to be proportional to the decrease in rod sensitivity reported by Aguilar and Stiles (1954). Thus, it appears that light adaptation serves to modify the gain of rod generated signals.

Although desensitization to light is a pronounced effect of rod light adaptation, other aspects of scotopic vision also change as the level of retinal illumination increases. For example, there is an improvement in the rod system's ability to accommodate spatial and temporal resolutions (Daitch & Green, 1969; Kelly, 1969). This suggests that light adaptation affects a functional reorganization of the rod system such that the nature of spatial and temporal interactions within the rod system are altered (see also Westheimer, 1965). The present study examines the influence of rod light adaptation on interactions between the rod and cone systems.

Rod-Cone Interaction

The differences between scotopic and photopic vision suggest that the vertebrate visual system can be divided into two functionally independent subcomponents. This notion was advanced by psychophysicists during the first half of this century. On the other hand, under "mesopic" conditions when the rod and cone systems operate simultaneously, there lies a potential for rod-cone interactions; i.e., changes in the activity of one photoreceptor system systematically alters the responsivity of the other system. In fact, there is a substantial body of anatomical, physiological, and psychophysical data which supports the notion of such interaction.

Anatomical and physiological evidence for rod-cone interaction- The results of recent anatomical and physiological studies suggest that the rod and cone systems interact at several retinal loci. In the cat, gap

junctions, which represent the anatomical substrate for electrical coupling between cells, have been found between rod amacrine and cone bipolar cells (Nelson, Kolb, Famiglietti, & Gouras, 1976) while Raviola and Gilula (1973) observed gap junctions between rod sphericles and cone pedicles in a variety of vertebrate species including monkeys. Moreover, it has been reported that horizontal cells have dendrites which contact cones and axons which contact rods (Kolb, 1970). These connections may underly the intracellularly recorded rod-like signals from cones (Nelson, 1977), cone-like signals from rod amacrine cells (Nelson et al., 1976) and may account for the rod and cone signals recorded from horizontal cells (Neimeyer & Gouras, 1973; Nelson, Lutzow, Kolb, & Gouras, 1975; Steinberg, 1969).

Interactions between the rod and cone systems are also apparent at the level of the ganglion cell. Extracellular unit recordings indicate that mammalian ganglion cells receive both rod and cone generated signals which add together (Andrews & Hammond, 1970; Enroth-Cugell, Hertz, & Lennie, 1977; Gouras & Link, 1965; Rodieck & Rushton, 1976). These findings corroborate those anatomical reports indicating that rod and cone bipolar cells converge on the same ganglion cell (Dowling & Boycott, 1966; Kolb & Famiglietti, 1974).

In summary, anatomical and physiological investigations have identified several proximal and distal retinal loci at which rod and cone pathways converge in the mammalian retina.

Psychophysical evidence for rod-cone interactions- Traditionally, the rod and cone systems were assumed to be functionally autonomous (Hecht, 1937; Rushton, 1961; Stiles, 1939); however, rod-cone interactions have been demonstrated using a variety of psychophysical procedures:

color mixing and color additivity studies have shown that rod activity contributes to the perceptions of hue and saturation when large or extrafoveal stimuli are employed (McCann, 1972; McCann & Benton, 1969; Stabell, B. & Stabell, U., 1973, 1974, 1979; Stabell, U. & Stabell, B., 1973, 1975, 1978, 1979; Trezona, 1970, 1973, 1974), while the results of several dark adaptation experiments suggest that the rod and cone systems interact during the recovery from photopigment bleaching (Drum, 1979; Hough & Ruddock, 1969; Lythgoe, 1932; Spillman & Conlon, 1972; Wooten & Butler, 1976). Additionally, it has been demonstrated that rod and cone signals engage in temporal summatory interactions (Frumkes, Sekular, Barris, Reiss, & Chalupa, 1973) which enhance the perception of flicker (MacLeod, 1972; Van den Berg & Spekreisje, 1977).

The application of increment threshold procedures to study the interrelationship between the rod and cone systems is predicated on the two-color increment threshold experiments of Stiles (1939, 1949, 1959). Under dark adapted conditions, the threshold of a 200 msec duration, 1^{o} diameter test flash of variable wavelength was determined as a function of the irradiance of a continuously exposed, 10^{o} diameter adapting field also of variable wavelength. Stiles obtained tvi durves using many wavelength combinations of test and adapting field stimuli. For parafoveal data restricted to irradiance values within a few log units of test flash absolute threshold, the tvi functions were invariant in shape but shifted vertically (parallel to the ordinate) or horizontally (parallel to the abscissa) depending upon whether the wavelength of the test flash or the adapting field was varied, respectively. With test flash wavelength fixed and adapting field wavelength varied, the horizontal shifts served as an index of the spectral sensitivity of the

photoreceptor mechanism responsible for increasing test flash threshold. When the adapting field wavelength was fixed and test flash wavelength varied, the vertical shifts represented the spectral sensitivity of the photoreceptor mechanism subserving test flash threshold detection. By extrapolation, Stiles constructed spectral sensitivity curves of these mechanisms. The resulting spectral sensitivity curves were nearly identical to the spectral sensitivity of the CIE scotopic observer despite the fact that long wavelength adapting field stimuli influenced both rods and cones (Stiles, 1939). Consequently, Stiles concluded that cones do not influence the increment threshold behavior of the rod system.

Using increment threshold procedures, a number of studies have since tested the generality of the independence between the rod and cone systems. In agreement with Stiles, Alpern (1965) and Westheimer (1970) reported that cone activity does not influence the metacontrast of, or the sensitization to a rod test flash respectively. More recently, however, cone influences on rod determined thresholds have been demonstrated under conditions which yield metacontrast (Barris & Frumkes, 1978; Foster, 1976), stimulus sensitizations (Blick & MacLeod, 1978; Buck, Peeples, & Makous, 1979; Frumkes & Temme, 1977; Lennie & MacLeod, 1973; Makous & Booth, 1974), and Crawford-type masking (Frumkes & Holstein, 1979). These studies indicate that the duration of the interval between the onsets of test and masking stimuli in the contrast experiment and the diameter of the adapting stimulus in the sensitization experiment determine the extent to which cone activity will influence the threshold behavior of the rod system.

Considerably less attention has been focused on the manner in which rod activity influences the increment threshold behavior of the cone

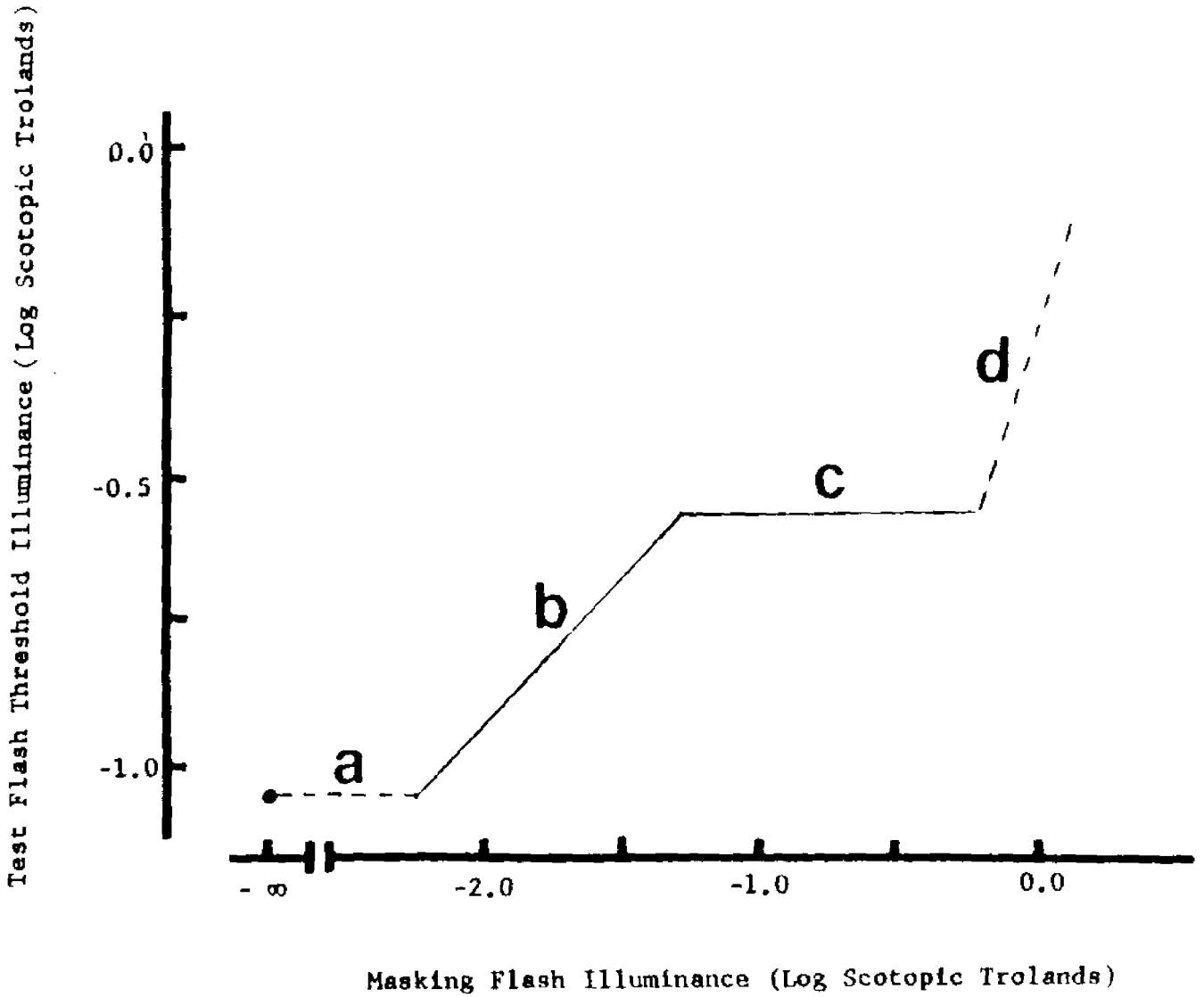
system. Those investigations addressing this issue, including the present study, typically measure the threshold of a long wavelength test flash ($\geq$ 615 nm) as a function of the illuminance of a concentric adapting field. Implicit is the assumption that test flash threshold is determined by cones. The validity of this assumption rests on a variety of experimental evidence: At absolute threshold, cones are equal to or greater than rods in their sensitivity to small, brief stimuli greater than 615 nm in wavelength (Hecht & Hsia, 1945; Wald, 1945). Additionally, increasing the illuminance of an adapting field will depress the sensitivity of rods more so than cones. For example, Stiles (1959) notes that under conditions where Weber's law holds true, the Weber fraction for rods is 15-20 times greater than the Weber fraction for the long wavelength photopic mechanisms. Insofar as the most sensitive photoreceptor mechanism determines threshold, cones alone are responsible for the threshold detection of a long wavelength test flash regardless of the adapting field illuminance.

Using the two-color increment threshold procedure, Temme and Frumkes (1977) found a size dependent influence of rod stimulation on cone sensitivity. In the dark adapted eye, the threshold of a parafoveally presented, 25 msec duration, 15' diameter, 655 nm wavelength cone test flash was measured as a function of the illuminance of a steady, concentric, variable diameter, 512 nm wavelength adapting field. Data obtained with large ($>$ 2^{o}) diameter adapting field stimuli corroborated the notion of independence between the rod and cone systems. There exists a 3.0 log unit range beyond adapting field absolute threshold over which increases in adapting field illuminance left test flash threshold unaffected. Test flash threshold did not rise until the adapting field excited cones. In

contrast, when the adapting field diameter was $\leq$ 40', test flash threshold increased with increments in adapting field illuminance until a plateau level was reached. Further increases in test flash threshold occurred at still higher adapting field illuminance values. Action spectra data obtained with a 40' diameter adapting field indicated that the initial rise in test flash threshold was dependent upon the scotopic illuminance of the adapting field. Similar spatial constraints have been reported by Latch and Lennie (1977). These data suggest that the 10^{o} diameter adapting field used Stiles (1939, 1949, 1959) was of inappropriate size of elicit rod-cone interactions.

Recently, Frumkes, Bauer, and Nygaard (1979) provided a quantification of the type of rod-cone interaction reported by Temme and Frumkes (1977). In this experiment, a 500 msec duration, 40' diameter, 512 nm wavelength masking flash was employed as opposed to a steady adapting stimulus. The results of this experiment, performed under dark adapted conditions, are illustrated in Figure 2 where the log of cone test flash threshold is plotted as a function of the log of masking flash illuminance. This tvi curve can be described in four segments: In segment A, increases in masking flash illuminance have little influence on test flash threshold. However, when the mask illuminance is approximately -2.5 log scotopic trolands, test flash threshold increases with increments in masking flash illuminance (segment B) until a plateau level is achieved (segment C). Further increases in test flash threshold occur at still higher masking flash illuminances (segment D). On this log-log plot, segment B is described by a straight line with a slope of 0.5. In fact, Frumkes et al. (1979) found that segments A and B can be described by the equation

Fig. 2. The threshold illuminance of a parafoveally presented, 25 msec duration, 13' diameter, 655 nm wavelength test flash as a function of the illuminance of a concentric, 500 msec duration, 40' diameter, 512 nm wavelength masking flash (Frumkes, Bauer, & Nygaard, 1979). This function represents data collected under dark adapted conditions.


Test Flash Threshold Illuminance (Log Scotopic Trolands)
0.0
-0.5
-1.0
a
b
c
d
- ∞
-2.0
-1.0
0.0
Masking Flash Illuminance (Log Scotopic Trolands)

$$I_{c_{th}}/I_{c_o} = K\sqrt{(I_r/I_{r_{th}}) + D} \qquad (2)$$

where $I_{c_{th}}$ is the illuminance of the cone test flash at threshold, I_{c_o} is the absolute threshold of the test flash, I_r is the illuminance of the rod detected masking flash, $I_{r_{th}}$ is the threshold illuminance of the rod detected masking flash, D is a dark noise term, and K is a unit related constant.[4]

Having established that rod activity can modify cone determined thresholds (and visa versa), it follows that the magnitude of this interaction will increase or decrease under conditions which augment or attenuate, respectively, rod generated signals. Recently, Frumkes, Bauer, and Holstein (1978) employed a modification of the two-color increment threshold procedure to demonstrate a growing influence of rod stimulation on cone sensitivity during recovery from photopigment bleaching. The threshold of a 25 msec duration, 13' diameter, 655 nm wavelength test flash was measured at various times in the dark following photopigment bleaching. The test flash was presented 250 msec after the onset of a concentric, 500 msec duration, 40' diameter, 512 nm wavelength, fixed illuminance "rod" masking flash. The illuminance of the masking flash was fixed so that it was only visible during the rod recovery stage of dark adaptation. Under these conditions, test flash threshold first decreased until cone absolute threshold was achieved. However, soon after the masking flash became visible, test flash threshold rose until a plateau level was reached, concommitant with full recovery from photopigment bleaching. When test flash threshold was plotted as a function of rod sensitivity, (i.e., the ratio between the fixed illuminance of the

4. Frumkes et al. (1979) also provide data suggesting that, in terms of rod-cone interaction, the visual system behaves like an ideal detector. This is discussed in more detail on pages 77-79.

masking flash and the threshold illuminance of the masking flash at a given time in the dark), a linear function with a slope of 0.5 was obtained on logarithmic coordinates. Thus, cone test flash threshold was proportional to the square root of rod sensitivity to the rod masking flash. This square root relationship was obtained providing that the fixed illuminance masking flash was within 2.0 log units of masking flash absolute threshold.

The results of Frumkes et al. (1978) suggest that their rod-cone interaction paradigm provides a useful tool for studying changes in rod sensitivity accompanying dark adaptation; the cone increment threshold function obtained during the rod recovery stage of dark adaptation provides an index for quantifying changes in rod sensitivity concommitant with dark adaptation. Unfortunately, the dark adaptation experiment does not permit an analysis of rod functioning at a particular state of adaptation; one simply cannot hold time constant! This problem can be surmounted by observing the behavior of the rod system (viz. the effects of rod stimulation on cone sensitivity) under various levels of light adaptation. This approach is adopted in the present study.

Rationale of the Present Study

The present study employs the procedures used by Temme and Frumkes (1977) and Frumkes et al. (1979). The threshold of a 25 msec duration, 13' diameter, 655 nm wavelength test flash is measured as a function of the illuminance of a concentric, 500 msec, 40' diameter, 512 nm masking flash, while the rod system is selectively light adapted by varying the illuminance of a third stimulus: a steady, large (40^{o} diameter), 490 nm wavelength, adapting field.

The influence of adapting field illuminance on test and masking

flash thresholds- The rationale of the present study is predicated on the assumption that the threshold of the long wavelength test flash is determined by cones while the threshold of the shorter wavelength masking flash is determined by rods or cones at low and high levels of adapting field illuminance, respectively. Therefore, tvi curves can be generated to delineate the range of increasing adapting field illuminance over which sensitivity to the masking flash decreases while sensitivity to the test flash is unchanged. Subsequently, the effects of rod stimulation on cone sensitivity can be examined over this "scotopic" range of adapting field illuminance values.

The influence of masking flash illuminance on test flash threshold- Under dark adapted conditions, the tvi curve describing the relationship between test flash threshold and masking flash illuminance should correspond to the data reported by Frumkes et al. (1979) (see Figure 2). The log of test flash threshold should increase linearly with the log of masking flash illuminance until a plateau level is achieved; further increases in test flash threshold are expected at still higher masking flash illuminance values. Additionally, the initial linear segment of the tvi function should bear a slope of 0.5.

Increasing the adapting field illuminance is expected to shift the tvi curve horizontally, parallel to the abscissa, toward higher masking flash illuminance values. Insofar as these shifts are indicative of the adapting field attenuation of rod sensitivity (see pages 5-9), the shifts should be equal to the difference between the log of masking flash threshold in the dark adapted eye and the log of masking flash threshold at a given level of adapting field illuminance. The magnitude of these shifts can be predicted from the masking flash threshold versus adapting

field illuminance tvi function.

If equation (2) is robust, the square root relationship between test flash threshold and masking flash illuminance should hold regardless of the scotopic level of adapting field illuminance. This equation only applies to the initial rise in test flash threshold and does not predict the characteristics of the plateau and supraplateau segments of the tvi function under dark or light adapted conditions.

Verification of rod-cone interaction- To the extent that the influence of the masking flash is mediated through the rod system, action spectra data should conform to the spectral sensitivity function of the CIE scotopic observer. Deviations from that function indicate that cones contribute to the masking influence.

Chapter 3: Methodology

Apparatus

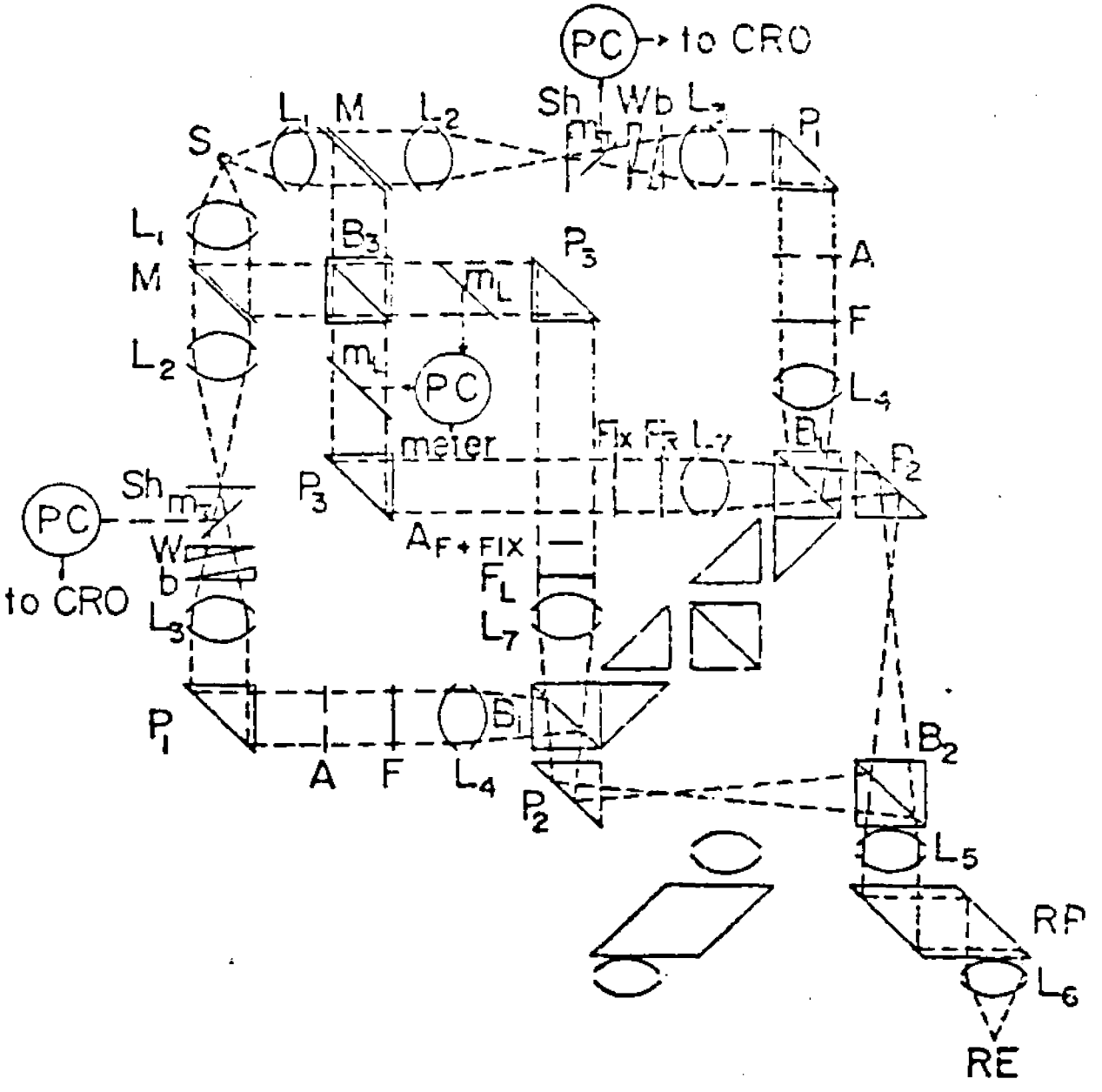
All stimuli were presented via a four-channel Maxwellian view optical system. The optics of an identical system have been described by Frumkes and Sturr (1968) while Battersby and Schuckman (1970) have described the electronic controls.

Optical System

A schematic diagram of the optical system appears in Figure 3. Since the system was designed to provide monocular and binocular presentation of stimuli, only the channels used in the present monocular study are indicated with dotted lines.

Test and masking stimuli channels- Two symmetrical channels provided the test and masking stimuli. Light from source S was collimated into two beams by lenses L_1. In general, the horizontal beam formed the mask stimulus channel while the vertical beam formed the test stimulus channel. The beams were brought into focus by lenses L_2 to form a filament image on the plane of the shutters Sh. Two 4.0 log unit circular neutral density wedges, W, which were balanced by fixed wedges, b, precisely controlled illuminance. The light beams were recollimated by lenses L_3 and deflected by right angle prisms P_1. The size of the mask and test stimuli were determined by various apertures located at A. The horizontal and vertical positions of these apertures were controlled by micromanipulators. The wavelengths of the test and mask stimuli were controlled by placing chromatic filters into filter racks F_1. These filter racks also accommodated neutral density filters which provided gross illuminance control of test and mask stimuli. Light beams were refocused by lenses L_4, passed

Fig. 3. Schematic diagram of the four-channel Maxwellian view optical system discussed in the text.


PC
to CRO
Sh
Wb
L7
P1
S
L1
M
L2
B3
P3
A
F
L4
mL
PC
meter
Fix
Fr
L7
B1
P2
Sh
m7
W
b
L3
to CRO
AF + FIX
FL
L7
P1
A
F
L4
B1
P2
B2
L5
RP
L6
RE

through beamsplitters B_1 and deflected by right angle prisms P_2. The mask and test channel beams were recombined by beamsplitter B_2. At L_5 the combined beams were recollimated, then passed through rhomboid prism RhP, and finally focused by lens L_6 at the nodal point of the observer's right eye, RE.

Adapting and fixation channels- Two symmetrical channels provided the adapting field and fixation target. Light beams collimated by lenses L_1 were deflected 90° by partially reflecting front surface mirrors M. The two collimated beams were then combined by beamsplitter B_3 and deflected 90° by prisms P_3. The beams passed through aperture Af + Fix or Fix which determined the spatial configurations of the adapting field and fixation target. The illuminance and wavelength of these stimuli were controlled by neutral density and chromatic filters placed into filter racks Fr and Fl. The adapting field and fixation target beams were refocused by lenses L_7 and passed into beamsplitters B_1 where they were combined with the mask and test channels.

Fixation- The observer's head was stabilized by means of a full mouth bite bar, the position of which could be adjusted in three planes. Focus was obtained with a diopter adjustment on the final eye lens L_6. When the observer was correctly positioned, the filament image was formed at the nodal point of the right eye. Consequently, the observer saw the final lens, L_6, filled with light in Maxwellian view. The filament image of the final eye lens was 0.5 x 2.0 mm which was much smaller than the diameter of the observer's pupil during any phase of the present scotopic study.

Spatial control of stimuli- The size of each stimulus was determined by apertures of various diameters. A projection technique showed than an

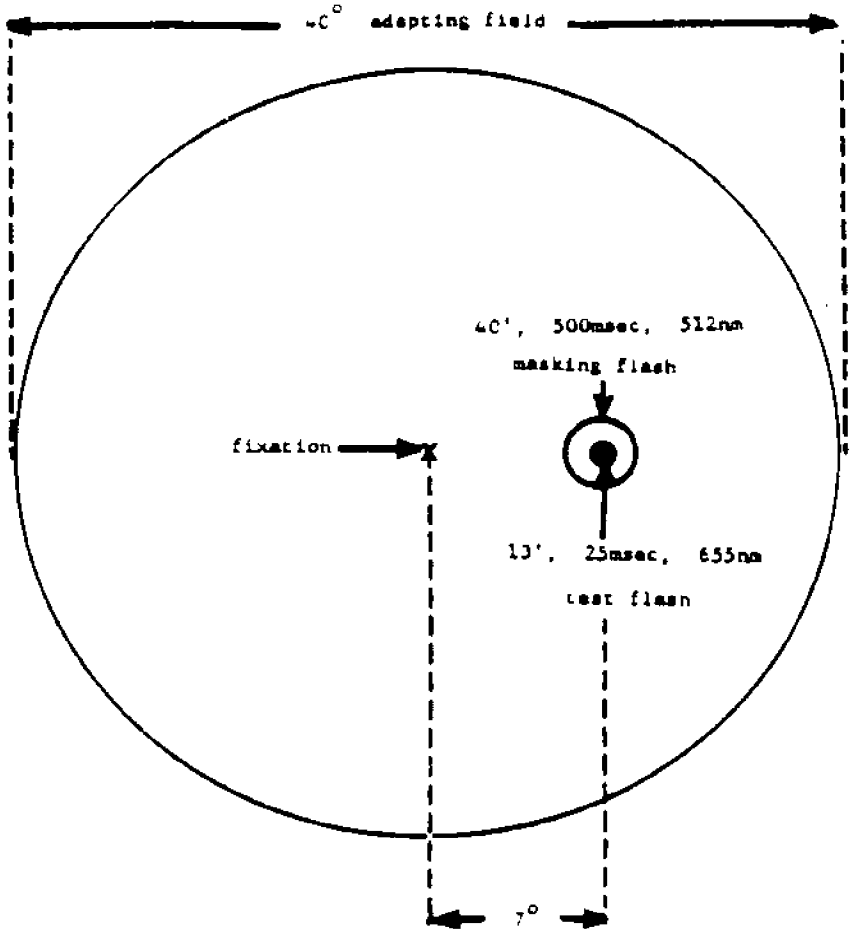
aperture of 1 mm in diameter placed at A projected a retinal image of 1.8°; when all apertures were removed from the optical system, any channel provided a 40° field. With this knowledge, the size and retinal position of all stimuli were determined. Specifically, the test stimulus was 13' in diameter, the masking stimulus was 40' in diameter, the adapting field was 40° in diameter, and the fixation target consisted of four dots, each 15' in diameter placed as a 3° square. The fixation target was centered in the adapting field. The masking and test stimuli were presented to the nasal retina, 7° from fixation along the horizontal meridian of the right eye. The spatial configuration of the stimuli are illustrated in Figure 4a.

Temporal control of stimuli- The adapting field and fixation target were continuously exposed. The durations of the test and masking stimuli were controlled by shutters, Sh, which were driven by electromagnets modified from a Grass polygraph. The shutters were powered by two Tektronix 161 Pulse Generators and amplified by specially constructed power amplifiers. One pulse generator controlled the duration, onset, and waveform of the test stimulus and the second pulse generator governed these parameters for the masking stimulus. Specifically, the masking stimulus was a 500 msec duration square wave flash. The test stimulus was a 25 msec duration square wave flash and was presented 250 msec after the onset of the masking flash (see Figure 4b). The rise and fall times of these flashes were approximately 1.0 msec.

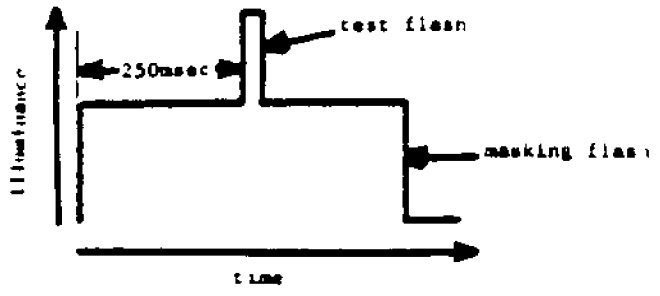
A Tektronix 162 Waveform Generator provided an adjustable recycling rate and triggered the pulse generators. During all phases of the present study, the recycling rate was once every four seconds. A second waveform generator provided a time base for a stimulus monitoring Tektronix 360

Fig. 4a. Spatial arrangement of the stimulus array. The test flash is a 13' diameter disk located 7° from the fixation point along the horizontal meridian in the temporal field of the right eye. The masking flash is a 40' diameter disk concentric with the test flash. The adapting field is 40° in diameter and concentric with the fixation target.

Fig. 4b. Temporal arrangement of the test and masking flashes. The 25 msec duration test flash is presented 250 msec after the onset of the 500 msec duration masking flash.


40° adapting field
40', 500msec, 512nm
masking flash
fixation
13', 25msec, 655nm
test flash
7°

a


test flash
250msec
masking flash
time

b

oscilliscope, CRO. Light passing through an open shutter was partially deflected by mirror M_1 into photocell circuit PC whose output fed into the 360 oscilloscope. Thus, flashing stimuli durations, rise times, and onsets could be continuously monitored.

Light source- The light source was tungsten filament incandescent General Electric CPR Projector Lamp. The lamp was powered by a 6-volt power supply (Electro Products Model H). The output of the power supply was controlled by a rheostat and the current was monitored by an ammeter. The lamp was designed to operate at 18 amperes, however, the lamp was underpowered at approximately 16.5 amperes in order to increase its life. Two lamps were used during the course of the present study. Threshold measurements obtained with various chromatic filters insured that the output of the two lamps were equivalent in all channels of the optical system.

Source intensity was continuously monitored by means of a photocell, PC, which received input from partially reflecting mirrors, m_L, and whose output was connected to a milliammeter. The source intensity was regulated such that the output of the photocell was always 0.8 milliamperes.

Illuminance control- The illuminance of the test and masking stimuli were controlled by 4.0 log unit circular and balanced neutral density wedges. The position of the wedges were governed by a series of gears connected to indicator dials such that forty revolutions of the indicator dial resulted in one revolution of the wedge. Thus, one revolution of the indicator dial resulted in an illuminance change of 0.1 log units. Additional illuminance control was achieved by adding Kodak Wratten 96 neutral density filters into the two main beams at F. The illuminance of the

adapting field and the fixation target was achieved by placing neutral density filters into Fl and Fr.

Wavelength control- The wavelength of the test and masking stimuli were governed by Baird-Atomic or Ditric Optics interference filters (with half bandwidths between 6-12 nm) inserted into the appropriate beams at F. Specifically, the peak wavelengths of the test and masking stimuli were 655 and 512 nm, respectively. In Experiment 2b, interference filters with peak wavelengths of 420,472,540,577,600,620, and 680 nm were also used in the masking flash channel.

The wavelength of the adapting field was determined by a Kodak Wratten 44 broadband filter which has a peak transmission of photons 490 nm in wavelength. The wavelength of the fixation target was determined by a Kodak Wratten 29 broadband filter which partially passes all photons of wavelengths greater than 610 nm.

Illuminance calibration- The illuminance of spectrally unfiltered channels was determined by a procedure outlined by Westheimer (1966). A perfectly diffusing surface with a specific reflectivity was placed 1 mm beyond the filament image. The luminance of the surface, in millilamberts, was measured with a Macbeth illuminometer. Retinal illumination in trolands, I, was determined by the formula $I = 10^7(\bar{B})X^2/r$ where $\bar{B}$ is the surface luminance in millilamberts, X is the distance between the filament image and the diffusing surface in meters, and r is the reflectivity of the diffusing surface. From here on, the term illuminance will be used to denote retinal illuminance.

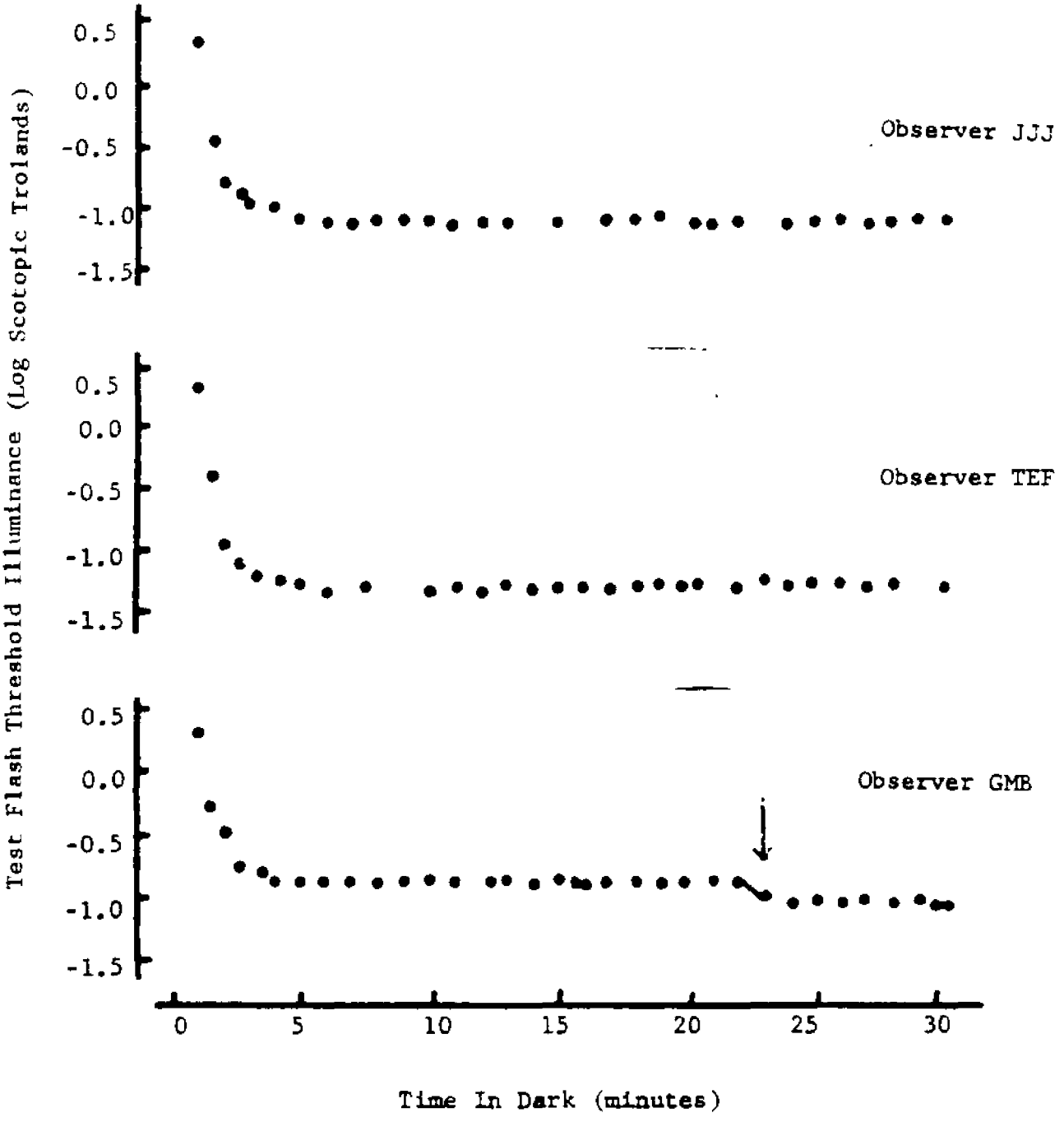
The illuminance of the 512 nm wavelength stimulus was calibrated by performing a brightness match between a spectrally unfiltered stimulus

-1.5 log scotopic trolands in illuminance and a 512 nm stimulus. Both stimuli were 1^{o} in diameter and 1 second in duration. The stimuli were presented vertically adjacent to one another 7^{o} from fixation. Under dark adapted conditions, two observers adjusted the illuminance of the 512 nm stimulus until it matched the brightness of the unfiltered stimulus. Since the match was made with a spectrally filtered stimulus of an illuminance well below cone threshold, this procedure provided a good measure of scotopic illuminance. Subsequently, the illuminance of the 490 nm stimulus was calibrated by performing a brightness match with the calibrated 512 nm stimulus.

A different procedure was used to calibrate the illuminance of the 655 nm stimulus. The absolute thresholds of a calibrated 512 nm, 2^{o} diameter, 500 msec duration stimulus and a 655 nm, stimulus of the same size and duration were determined under dark adapted conditions. The absolute threshold of the 655 nm stimulus was arbitrarily equated with the absolute threshold illuminance of the 512 nm stimulus. This procedure assumes that the absolute thresholds of both stimuli are determined by the rod system. Although cones may be more sensitive than rods to long wavelength stimuli (Wald, 1945), spectral sensitivity often varies among observers; long term dark adaptation curves can exhibit rod-cone breaks with stimuli of all wavelengths (Hecht, Haig, & Chase, 1937). This proved to be the case with GMB, the observer used for this calibration procedure. Observers JJJ and TEF did not show this effect (see Figure 5).

Irradiance calibration- An E.G. and G. Model 580/585 Spectroradiometer was used to measure the relative irradiance of all narrow band chromatic stimuli. The filament image of the optical system was focused

Fig. 5. Long term dark adaptation curves of a 25 msec duration, 13' diameter, 655 nm wavelength test flash for observers JJJ, TEF, and GMB. The test flash was presented to the temporal field, 7^{o} from fixation. An arrow marks the rod-cone break manifested in the dark adaptation function for observer GMB.


Test Flash Threshold Illuminance (Log Scotopic Trolands)
0.5
0.0
-0.5
-1.0
-1.5
Observer JJJ
Observer TEF
Observer GMB
0
5
10
15
20
25
30
Time In Dark (minutes)

onto the head of the spectroradiometer. The output of each channel with each filter in place was determined. Since the sensitivity of the spectroradiometer was known, the relative power (irradiance) of the different chromatic stimuli could be determined. The relative power was converted into log relative quanta, Q, by the formula $Q = E_\lambda \lambda/1243$ where E_λ is relative power, λ is the peak wavelength of the filter, and 1243 is a constant.

Method

The general goal of this research was to determine the influence of rod light adaptation on the type of rod-cone interaction described by Temme and Frumkes (1977) and later quantified by Frumkes et al. (1979). Toward this end, three experiments were performed. The purpose of Experiment 1 was to delineate a scotopic range of retinal illumination over which the sensitivity of the rod system is attenuated while the sensitivity of the cone system is unchanged. In Experiment 2a, the effects of rod stimulation on cone sensitivity are examined over this range of retinal illumination. This experiment incorporates the procedures employed by Frumkes et al. (1979) in the dark adapted eye. Experiment 2b was designed to verify that, in Experiment 2a, it is in fact the rod system which influences the increment threshold behavior of the cone system. The stimulus parameters used in these experiments are summarized in Table 1.

Observers

Two observers, JJJ and GMB, participated in all phases of the present study. JJJ was a myopic male, 29 years of age, and GMB was a myopic male, 27 years of age. A 38 year old emmetropic male, TEF, was used as a third observer to replicate key aspects of the present study. No corrective

Table 1

Stimulus parameters common to all experiments

	Test flash	Masking flash	Adapting field
Duration	25 msec	500 msec	continuously exposed
Diameter	13'	40'	40^{o}
Wavelength	655 nm	512 nm	490 nm

Stimulus parameters specific to experiment 1

	Test flash	Masking flash	Adapting field
Illuminance	Adjusted to threshold	Adjusted to threshold	Varied

Stimulus parameters specific to experiment 2a

	Test flash	Masking flash	Adapting field
Illuminance	Adjusted to threshold	Varied	Varied parametrically

Stimulus parameters specific to experiment 2b

	Test flash	Masking flash	Adapting field
Illuminance	Fixed at 0.4 or 1.0 log units above absolute threshold	Adjusted to mask the test flash	Varied parametrically
Wavelength	655 nm	420, 477, 512, 540, 577, 600, 620, 655, 680 nm	490 nm

lenses were worn by any observer during experimentation since the diopter adjustment of the final eye lens was sufficient to correct for the myopia of observers JJJ and GMB.

General procedure

At the beginning of each experimental session, the observer aligned his right eye with the adapting field which was set at an illuminance of 2.0 log scotopic trolands. He adjusted the position of the full mouth bite bar until the adapting field was in full view. The observer also adjusted the position of the final eye lens so that the fixation target was in sharp focus. (Frequent checks showed that this procedure produced a sharply focused source filament image in the plane of, and centered with the pupil.) The observer then dark adapted for 25 minutes. Subsequently, the appropriate experimental procedures were initiated. In the experiments to be described, threshold illuminance values were determined by the observer adjusting the position of the neutral density wedge controlling stimulus illuminance. An experimenter nonsystematically varied the position of the wedge setting after each threshold determination.

A set of rules governed all data collection. First, no experimental session lasted more than 90 minutes after dark adaptation was complete. Second, within each experimental session, three threshold values were determined consecutively with a specific set of stimulus parameters. If the range of threshold values exceeded 0.2 log units, at least one additional threshold value was determined. Third, every data point reported was based on observations obtained in at least two experimental sessions, and, consequently, involves a minimum of six threshold determinations. Fourth, to facilitate threshold determinations, the observers were

instructed to use a blanking procedure when they were approaching threshold; the observers pushed a button which cancelled either the test flash or the masking flash for one presentation. This afforded a comparison of the stimulus array with and without the test flash or masking flash.

Chapter 4: Experiment 1

Procedure

The goal of Experiment 1 was to delineate a range of retinal illumination over which the sensitivity of the rod system decreases while the sensitivity of the cone system is unchanged. Toward this end, the threshold illuminance of the 655 nm test flash and the threshold illuminance of the 512 nm masking flash were determined as a function of adapting field illuminance.[5] In a particular experimental session, the threshold of only the test flash or the masking flash was measured. Initially, the threshold of a flashing stimulus was measured with no adapting field present. Subsequently, the adapting field illuminance was increased in 0.5 log unit steps from an initial value of -3.0 log scotopic trolands. At each level of adapting field illuminance, the observer viewed the fixation target and the adapting field for two minutes before a flashing stimulus was presented. This was to insure that light adaptation was complete before the collection of data.

Results and discussion

Figures 6,7, and 8 show the mean threshold illuminance values, in log scotopic trolands, of the 655 nm test flash (open circles) and the 512 nm masking flash (closed circles) as a function of adapting field illuminance, in log scotopic trolands, for observers JJJ,

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5. As used in Experiment 1, the term masking flash is somewhat of a misnomer since the threshold of this stimulus is being measured. However, this stimulus is used to mask the detection of the test flash in Experiment 2.

Fig. 6. Observer JJJ: The threshold illuminance of the 655 nm test flash (open symbols) and the 512 nm masking flash (closed symbols) as a function of adapting field illuminance. The crossbars represent the 95% confidence limits.

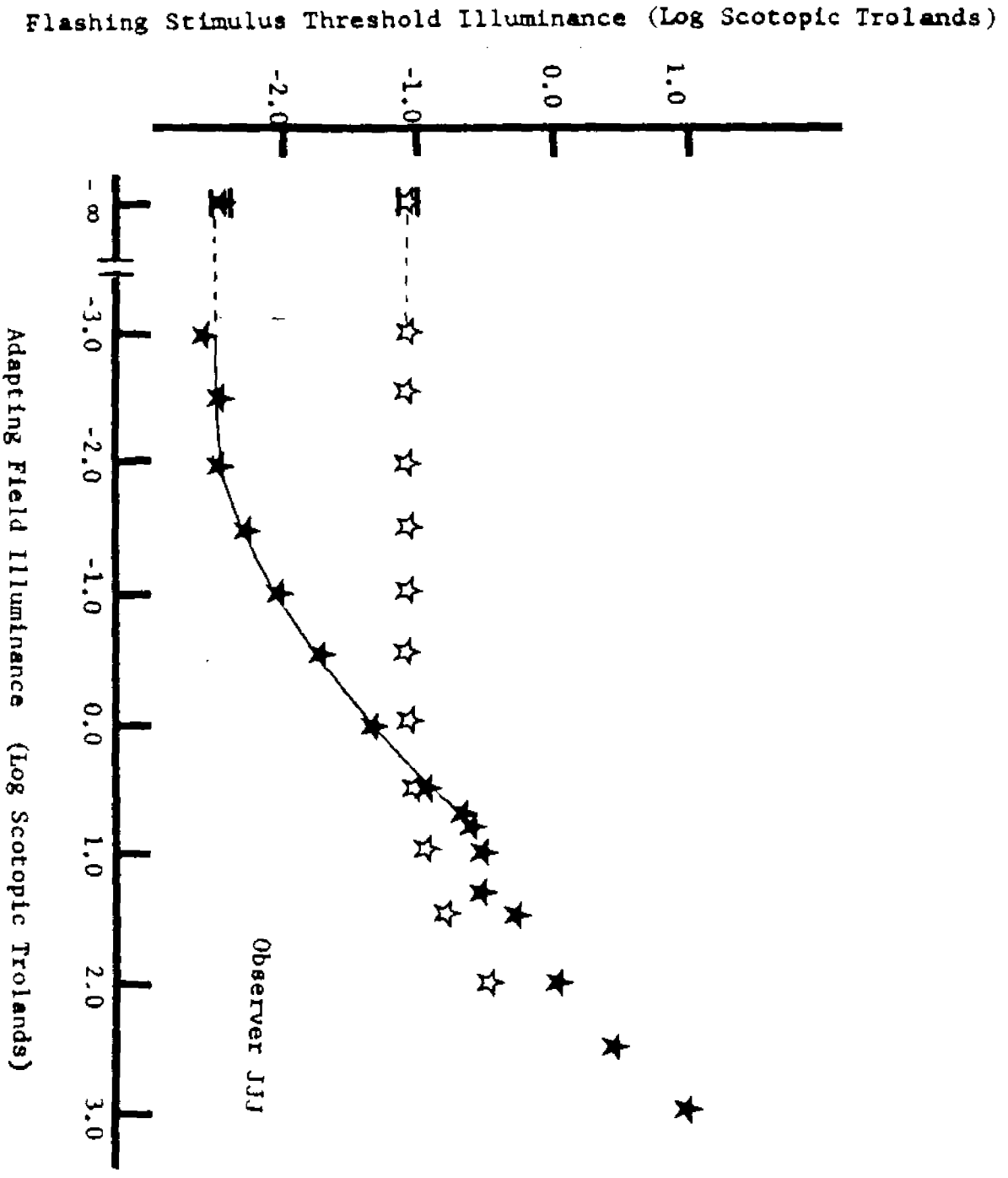

Flashing Stimulus Threshold Illuminance (Log Scotopic Trolands)
-2.0
-1.0
0.0
1.0
- ∞
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
Adapting Field Illuminance (Log Scotopic Trolands)
Observer JJJ

Fig. 7. Observer TEF: The threshold illuminance of the 655 nm test flash (open symbols) and the 512 nm masking flash (closed symbols) as a function of adapting field illuminance. The cross-bars represent the 95% confidence limits.

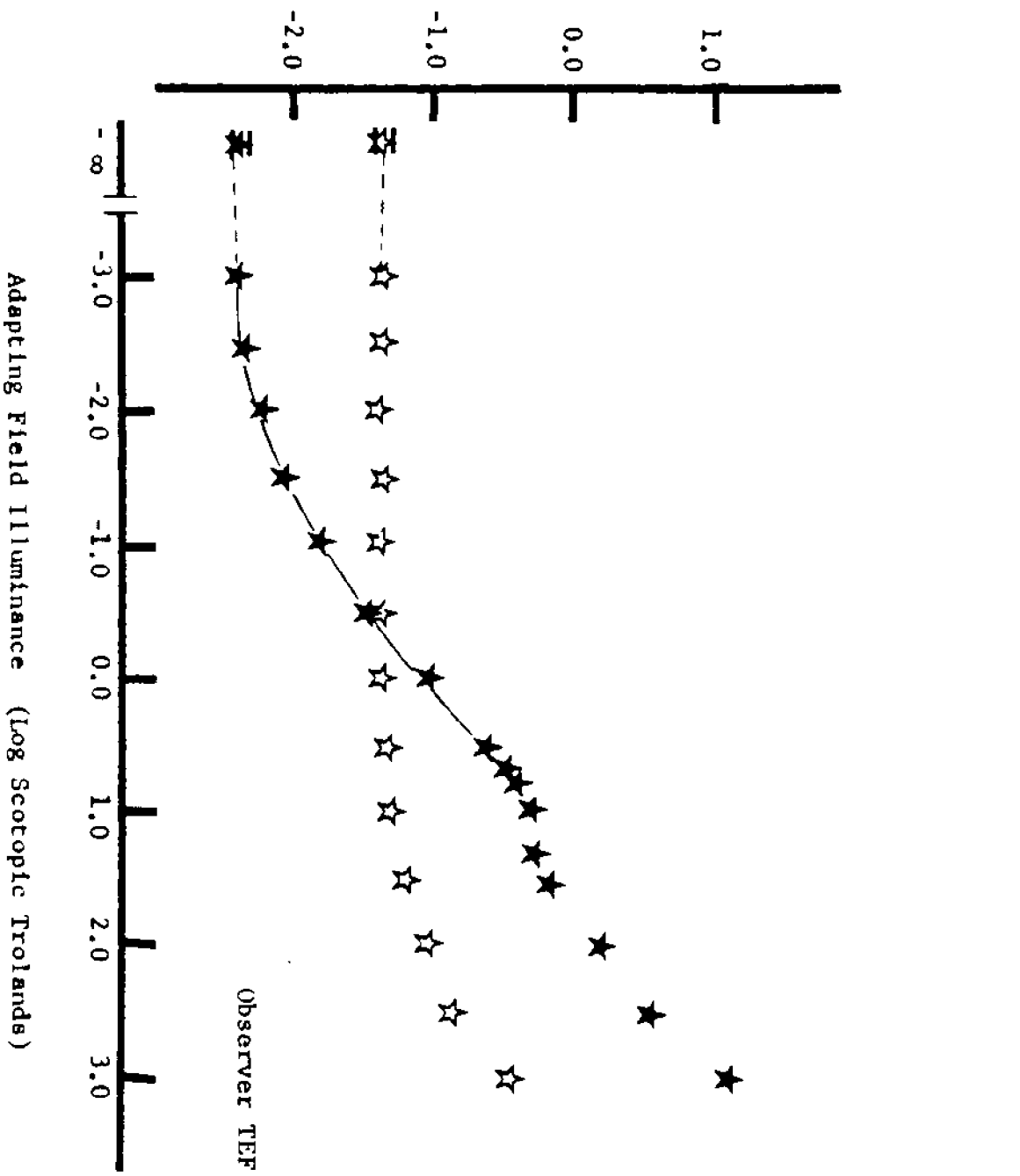
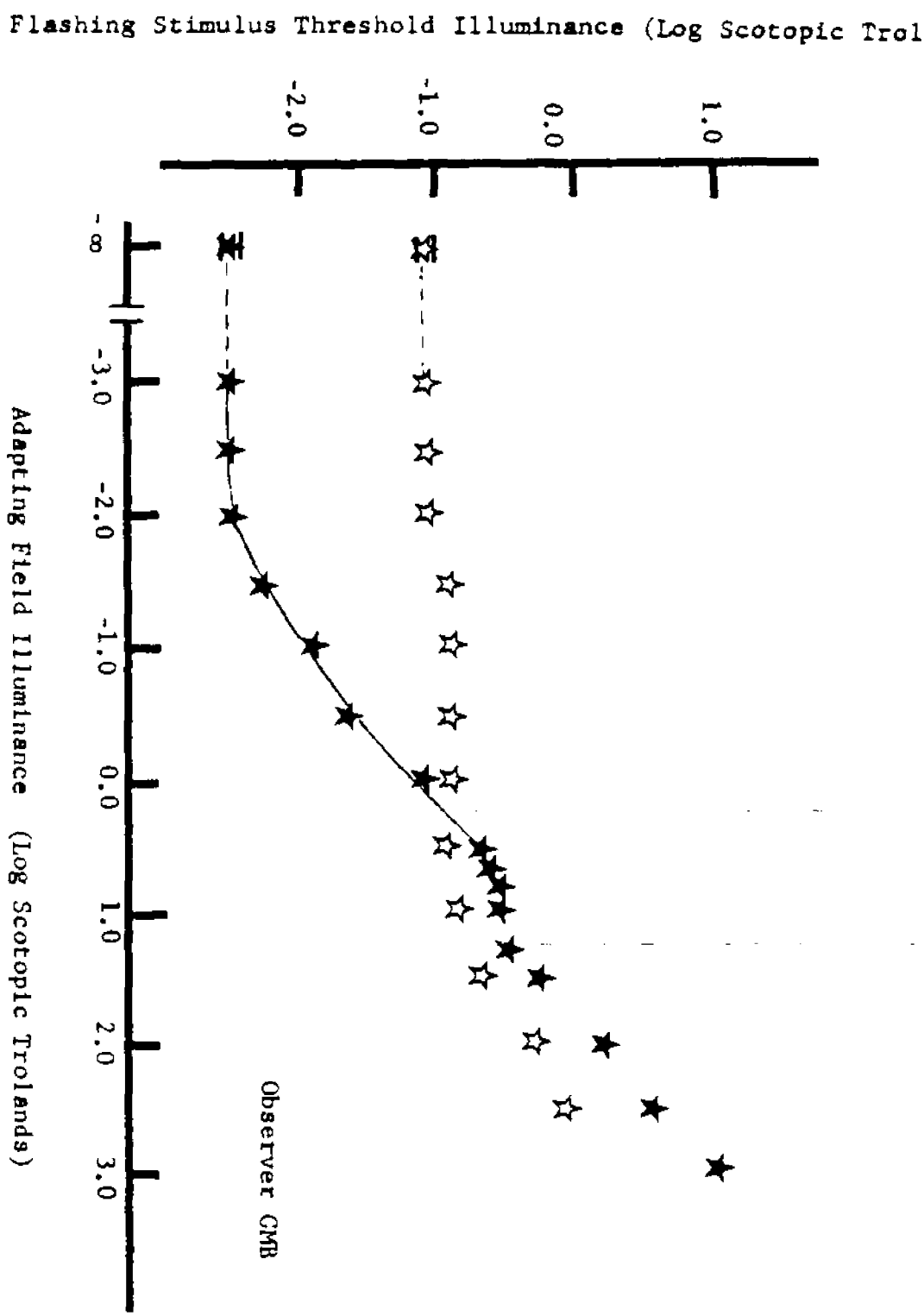

Flashing Stimulus Threshold Illuminance (Log Scotopic Trolands)
-2.0
-1.0
0.0
1.0
- 8
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
Adapting Field Illuminance (Log Scotopic Trolands)
Observer TEF

Fig. 8. Observer GMB: The threshold illuminance of the 655 nm test flash (open symbols) and the 512 nm masking flash (closed symbols) as a function of adapting field illuminance. The cross-bars represent the 95% confidence limits.


Flashing Stimulus Threshold Illuminance (Log Scotopic Trolands)
-2.0
-1.0
0.0
1.0
-8
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
Adapting Field Illuminance (Log Scotopic Trolands)
Observer CMB

TEF, and GMB, respectively. The threshold illuminance values of the test and masking flashes when no adapting field was present are indicated on the abscissa at the point labeled "minus infinity". The 95% confidence limits for these data points are indicated by the crossbars. In general, the 95% confidence limits for other data points throughout the study are less than $\pm$ 0.1 log units.

Masking flash threshold as a function of adapting field illuminance- For all observers, a two-limbed tvi curve describes the relationship between masking flash threshold and adapting field illuminance. In Figure 6 (observer JJJ), it can be seen that increasing adapting field illuminance from $-\infty$ to -2.0 log scotopic trolands has little influence on masking flash threshold; masking flash threshold remains stable at approximately -2.5 log scotopic trolands. However, further increases in adapting field illuminance are accompanied by increases in masking flash threshold until a plateau level of threshold illuminance is reached as adapting field illuminance approaches 1.0 log scotopic trolands. Additional increases in masking flash threshold occur when the illuminance of the adapting field exceeds 1.5 log scotopic trolands. Similar tvi curves were obtained for observers TEF and GMB. It should be noted that when the illuminance of the adapting field is less than 1.0 log scotopic trolands, all observers reported that the masking flash appeared without hue at threshold.

The present results are consistent with classical increment threshold data indicating that the detection of a parafoveally presented short wavelength stimulus is mediated through the rod and cone systems at low

and high levels of retinal illumination, respectively (Blackwell, 1946; Hecht et al., 1938; Stiles, 1949). Insofar as the photoreceptor mechanism most sensitive to the masking flash determines the threshold illuminance of this stimulus (Stiles, 1959), light adaptation desensitizes the rod system until a point is reached which finds cones more sensitive to the masking flash. The transition from rod to cone mediation of masking flash threshold occurs when the illuminance of the adapting field approaches 1.0 log scotopic trolands. Consequently, there exists a 3.0 log unit range of adapting field illuminance, from -2.0 to 1.0 log scotopic trolands, over which the rod system determines the threshold of the masking flash.

Test flash threshold as a function of adapting field illuminance- For observers JJJ (Figure 6) and TEF (Figure 7) it is clear that a single-limbed tvi curve describes the relationship between test flash threshold and adapting field illuminance. Test flash threshold remains stable until the illuminance of the adapting field exceeds 1.0 log scotopic trolands. Additionally, observers JJJ and TEF reported that the test flash always appeared punctate and red in hue at threshold. These These data indicate that cones and only cones determine test flash threshold at all levels of adapting field illuminance.

Inspection of Figure 8 reveals a "kink" in the test flash threshold versus adapting field illuminance tvi curve for observer GMB. As adapting field illuminance is increased from -2.0 to -1.5 log scotopic trolands, test flash threshold rises approximately 0.1 log units, an increase which is statistically significant. It is important to recognize that this "kink" appears at the adapting field illuminance which marks the onset of increases in masking flash threshold. Thereafter

test flash threshold remains stable until adapting field illuminance exceeds 1.0 log scotopic trolands. Consequently, for observer GMB cones alone determine test flash threshold when adapting field illuminance exceeds -2.0 log scotopic trolands. Indeed, observer GMB reported that, at threshold, the test flash appeared punctate and red in hue only when the level of adapting field illuminance exceeded -2.0 log scotopic trolands.

In summary, the results of Experiment 1 indicate that for observers JJJ and TEF there exists a 3.0 log unit range of adapting field illuminance, from -2.0 to 1.0 log scotopic trolands, over which sensitivity of the rod system decreases while the sensitivity of the cone system is unchanged. This range is somewhat attenuated for observer GMB. For this observer, the range is restricted to adapting field illuminance values between -1.5 and 1.0 log scotopic trolands.

Chapter 5: Experiment 2

The goal of Experiment 2 was to determine the influence of rod light adaptation on rod-cone interaction. Experiment 2a examined the relationship between test threshold and masking illuminance under dark adapted conditions, thus replicating the results Frumkes et al. (1979). Subsequently, this relationship was examined under scotopic levels of adapting field illuminance. In accordance with the results of Experiment 1, the values of adapting field illuminance used span the range of adapting field illuminance over which rod sensitivity decreases while cone sensitivity is unaffected. In Experiment 2b action spectra data were collected to elucidate the photoreceptor mechanism(s) repsonsible for increases in test flash threshold.

Experiment 2a

Procedure

In Experiment 2a each of the three observers were treated slightly differently. For observer JJJ, test flash threshold was initially measured as a function of masking flash illuminance with under dark adapted conditions, i.e., with no adapting field present, and then when the illuminance of the adapting field was set at -2.0, -1.5, -1.0, -0.5, 0.0, and 0.5 log scotopic trolands. In each experimental session only one value of adapting field illuminance was employed according to a prearranged randomization schedule.

Prior to the collection of experimental data, test flash and masking flash threshold illuminance values were determined separately in the dark adapted eye. These data provided an index of intersession variability. Subsequently, test flash threshold was measured in the presence of the masking flash. At least eight masking flash illuminance values in 0.4

log unit increments were used. This range of masking flash illuminance values was sufficient to replicate the test flash threshold versus masking flash illuminance tvi curve described by Frumkes et al. (1979). The order in which different illuminance masking flashes were presented was randomized before each experimental session.

The same general procedure was employed for observer GMB, but data were only collected when the illuminance of the adapting field was set at -1.5, -1.0, -0.5, 0.0, and 0.5 log scotopic trolands. The results of Experiment 1 showed that for observer GMB, cones alone mediate the threshold detection of the test flash at these levels of adapting field illuminance.

Experiment 2a was only performed under dark adapted conditions with observer TEF. Additionally, masking flash illuminance was varied in 0.2 log unit steps. This provided a precise description of the test flash threshold versus masking flash illuminance increment threshold relationship.

Results

Figures 9 and 10 show the relationship between test flash threshold and masking flash illuminance in the dark adapted eye for observers JJJ and TEF, respectively. Accordingly, the log of test flash threshold illuminance is plotted as a function of the log of masking flash illuminance. The threshold illuminance values of the test flash when no masking flash was present are indicated on the abscissa at the point labeled "minus infinity;" an arrow denotes the absolute threshold illuminance values of the masking flash. These tvi curves can be described in four segments. For example, using the data of observer JJJ (Figure 9), it can be seen that increasing masking flash illuminance has no effect on test flash threshold until masking flash illuminance exceeds -2.5 log scotopic

Fig. 9. Observer JJJ: The threshold illuminance of the 655 nm test flash as a function of the illuminance of the 512 nm masking flash. The threshold of the test flash with no masking flash present is indicated on the abscissa at the point labeled "minus infinity". An arrow marks the absolute threshold illuminance of the masking flash. These data were collected under dark adapted conditions.

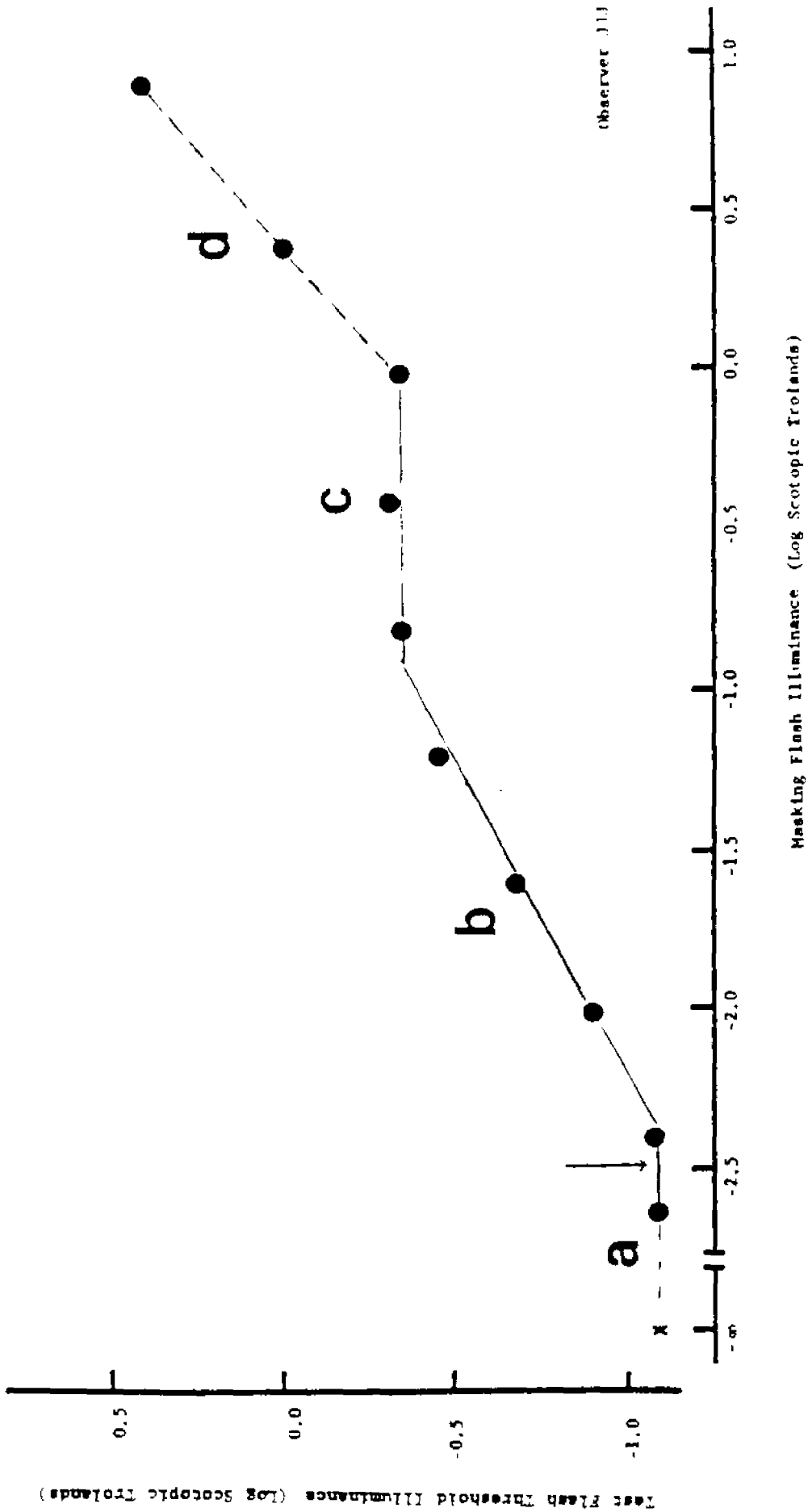
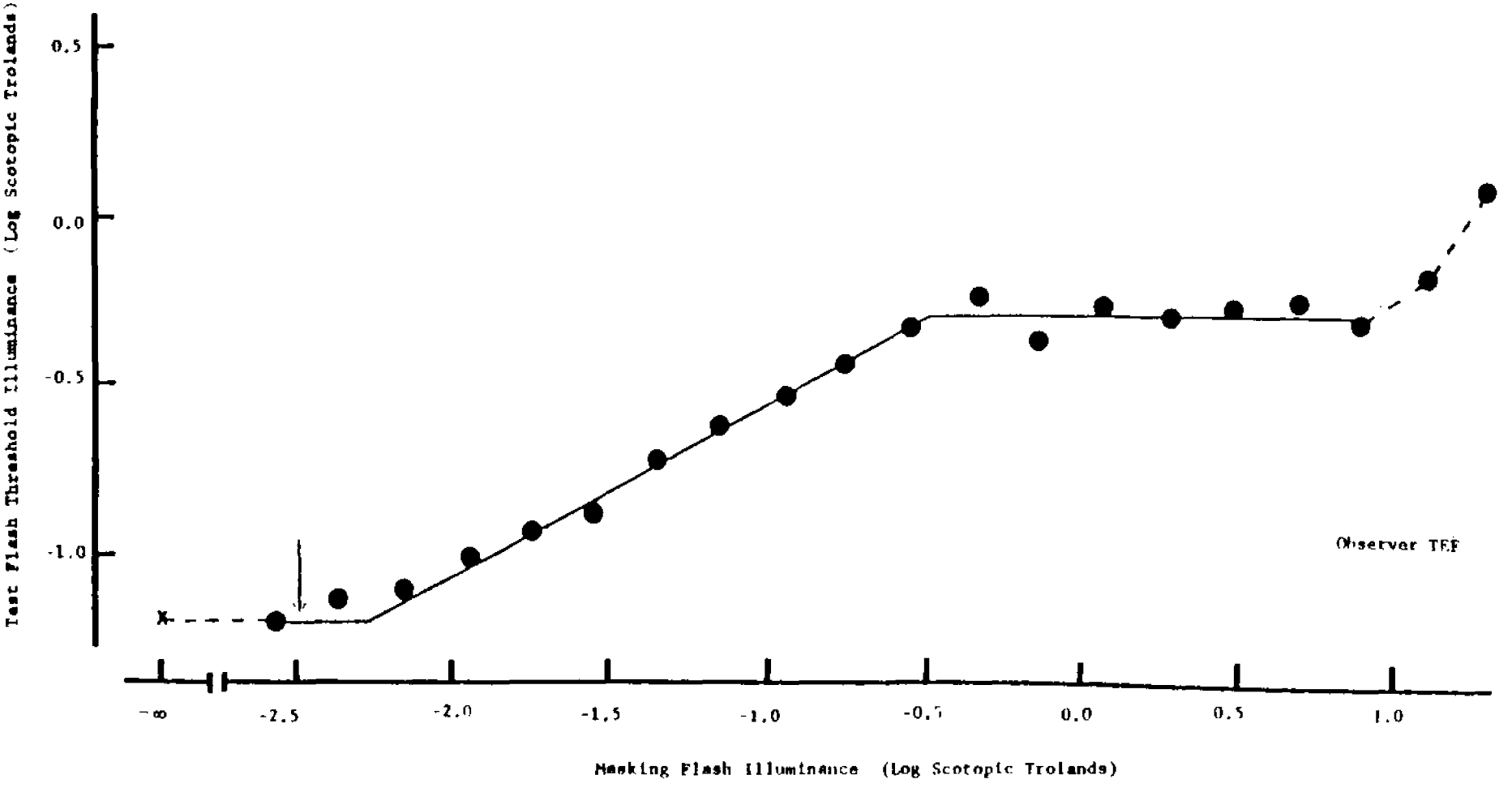

Observer JJH
a
b
c
d
x
-∞
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
Masking Flash Illuminance (Log Scotopic Trolands)
-1.0
-0.5
0.0
0.5
Test Flash Threshold Illuminance (Log Scotopic Trolands)

Fig. 10. Observer TEF: The threshold illuminance of the 655 nm test flash as a function of the illuminance of the 512 nm masking flash. The threshold of the test flash with no masking flash present is indicated on the abscissa at the point labeled "minus infinity". An arrow marks the absolute threshold illuminance of the masking flash. These data were collected under dark adapted conditions.


Test Flash Threshold Illuminance (Log Scotopic Trolands)
0.5
0.0
-0.5
-1.0
Observer TEF
-∞
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
Masking Flash Illuminance (Log Scotopic Trolands)

trolands, the absolute threshold illuminance of the masking flash (segment A). Thereafter, test flash threshold increases with increases in masking flash illuminance (segment B) until a plateau level is reached when masking flash illuminance is -1.0 log scotopic trolands (segment C). On this log-log plot segment B is well fitted by a straight line with a slope of 0.5 indicating that test flash threshold is proportional to the square root of masking flash illuminance. Further increases in test flash threshold only occur when masking flash illuminance exceeds 0.0 log scotopic trolands (segment D). The four segments are even more apparent in the tvi curve for observer TEF (Figure 10) where data were collected in finer increments. (Paradoxically, both observers reported that over the plateau segment, the masking flash appeared increasingly brighter although test flash threshold remained stable.)

It is most important to recognize that the initial increments in the threshold of the cone detected test flash (segment B) are manifested when the masking flash only stimulates rods. The results of Experiment 1 show that rods alone are stimulated when masking flash illuminance is less than -0.5 log scotopic trolands. This illuminance is greater than any mask illuminance value corresponding to segment B for either observer JJJ or TEF. Consequently, rods and only rods stimulated by the masking flash are responsible for subplateau increments in the threshold of the cone detected test flash. The results of Experiment 1 also show that rods and cones are stimulated by the masking flash at illuminances corresponding to supraplateau increments in test flash threshold.

Figures 11 and 12 show the influence of rod light adaptation on this type of rod-cone interaction for observers JJJ and GMB, respectively. In

Fig. 11. Observer JJJ: The threshold illuminance of the 655 nm test flash as a function of the illuminance of the 512 nm masking flash with adapting field illuminance as a parameter. The threshold of the test flash with no masking flash present is indicated on the abscissa at the point labeled "minus infinity". Data collected under dark adapted conditions (closed circles) are a replot of the data appearing in Figure 7.

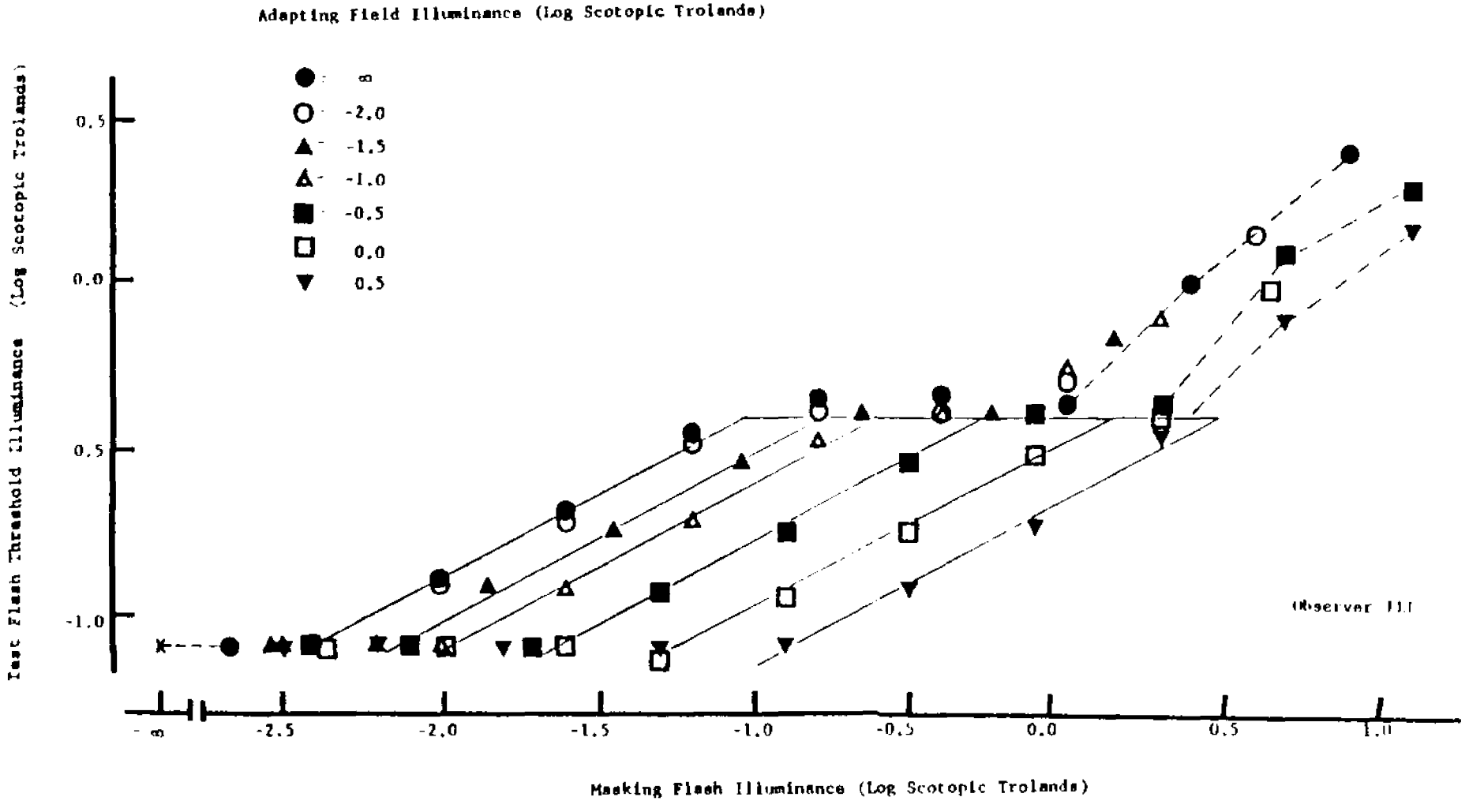

Adapting Field Illuminance (Log Scotopic Trolands)
∞
-2.0
-1.5
-1.0
-0.5
0.0
0.5
Test Flash Threshold Illuminance (Log Scotopic Trolands)
0.5
0.0
0.5
-1.0
- ∞
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
Masking Flash Illuminance (Log Scotopic Trolands)

Fig. 12. Observer GMB: The threshold illuminance of the 655 nm test flash as a function of the illuminance of the 512 nm masking flash with adapting field illuminance as a parameter. The threshold of the test flash with no adapting field present is indicated on the abscissa at the point labeled "minus infinity".

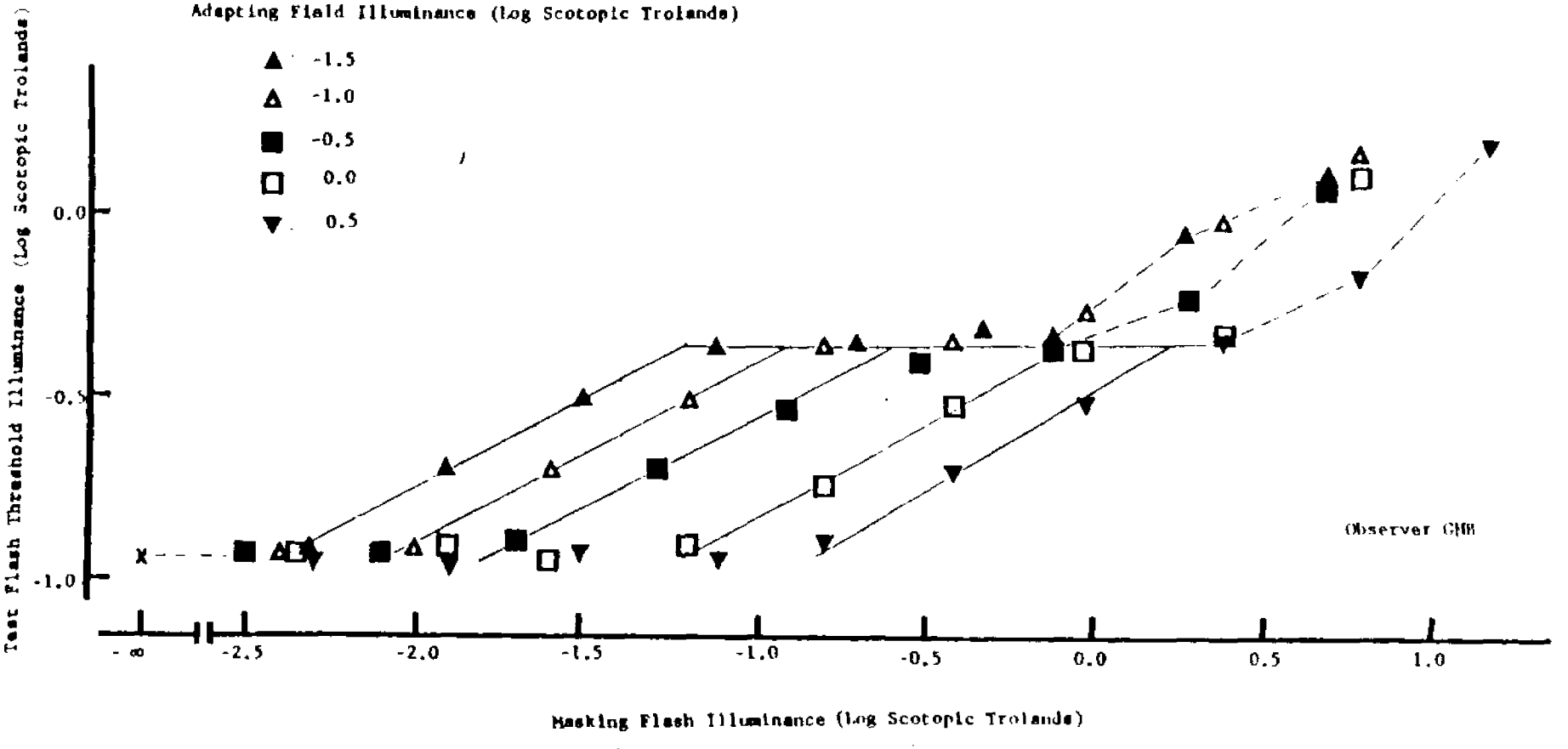

Adapting Field Illuminance (Log Scotopic Trolands)
-1.5
-1.0
-0.5
0.0
0.5
Test Flash Threshold Illuminance (Log Scotopic Trolands)
0.0
-0.5
-1.0
Observer GHB
- ∞
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
Masking Flash Illuminance (Log Scotopic Trolands)

Figure 11, data obtained in the absence of the adapting field are a replot of the data presented in Figure 9. Clearly, these tvi curves display the four segments described above. Note that the initial rises in test flash threshold are well fitted by straight lines with slopes of 0.5. Thus, over a restricted range of masking flash illuminance, test flash threshold is proportional to the square root of masking flash illuminance regardless of the scotopic level of adapting field illuminance. Interestingly, the range over which the square root relationship holds is fixed. That is, the ordinate value at which the plateau level is reached is the same regardless of the scotopic level of adapting field illuminance. For all observers, the plateau level occurs when test flash threshold illuminance was approximately -0.3 log scotopic trolands.

A striking feature of Figures 11 and 12 involves the shifting of the origin of the tvi curves toward higher masking flash illuminance values as the level of adapting field illuminance increases. In fact, these shifts are equal to the log difference between masking flash threshold at a particular level of adapting field illuminance and masking flash threshold in the dark adapted eye. For example, Figure 11 (observer JJJ) shows that the tvi curve obtained adapting field illuminance was set at -1.0 log scotopic trolands is shifted 0.4 log units to the right of the tvi curve obtained with no adapting field present. Figure 6 shows that when adapting field illuminance is increased to -1.0 log scotopic trolands, masking flash threshold rises approximately 0.4 log units. All the data corresponding to segments A and B in Figures 11 and 12 readily collapse into one function when masking flash threshold is taken into account. This is illustrated in Figures 13 (observer JJJ) and 14 (observer

Fig. 13. Observer JJJ: The log of the ratio between test flash threshold illuminance and test flash absolute threshold illuminance as a function of the log of the ratio between masking flash illuminance and masking flash threshold illuminance at different scotopic levels of adapting field illuminance. These data are a replot of the data appearing in Figure 11.

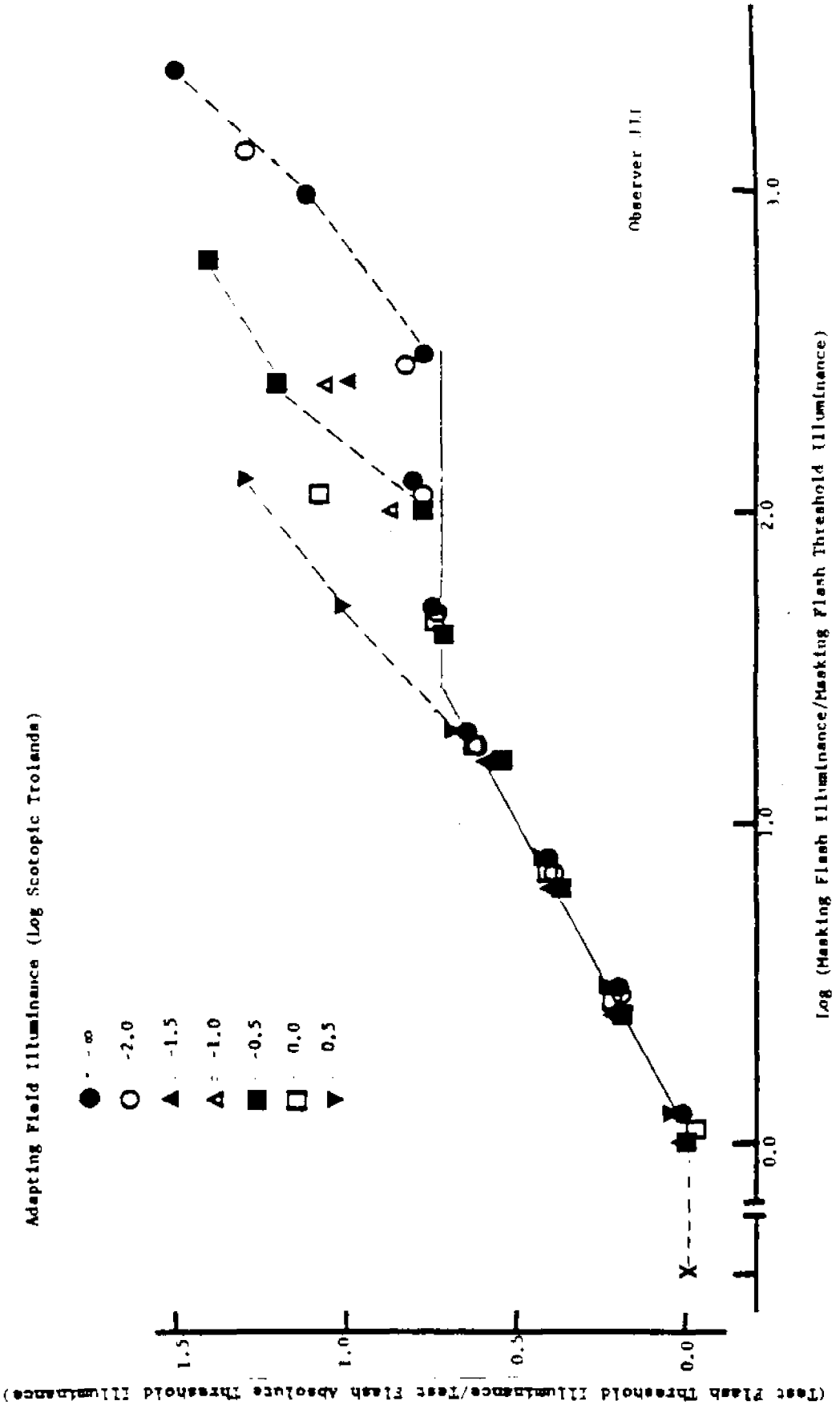
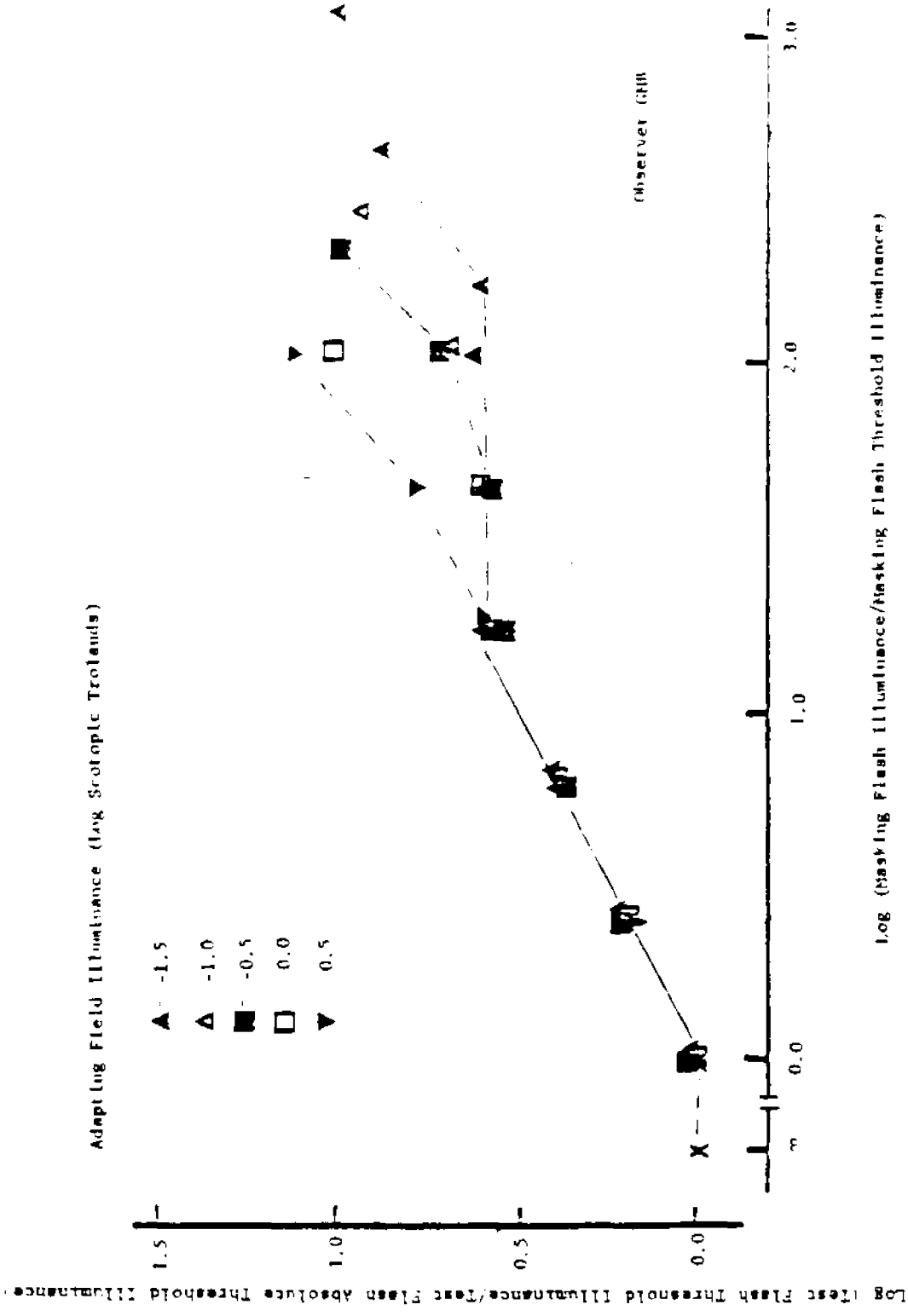

Observer III
Adapting Field Illuminance (Log Scotopic Trolands)
-∞
-2.0
-1.5
-1.0
-0.5
0.0
0.5
Log (Masking Flash Illuminance/Masking Flash Threshold Illuminance)
Log (Test Flash Threshold Illuminance/Test Flash Absolute Threshold Illuminance)
0.0
1.0
2.0
3.0
0.0
0.5
1.0
1.5

Fig. 14. Observer GMB: The log of the ratio between test flash threshold illuminance and test flash absolute threshold illuminance as a function of the log of the ratio between masking flash illuminance and masking flash threshold illuminance at different scotopic levels of adapting field illuminance. These data are a replot of the data appearing in Figure 12.


Adapting Field Illuminance (log Scotopic Trolands)
-1.5
-1.0
-0.5
0.0
0.5
Observer GHH
1.5
1.0
0.5
0.0
0.0
1.0
2.0
3.0
Log (Test Flash Threshold Illuminance/Test Flash Absolute Threshold Illuminance)
Log (Masking Flash Illuminance/Masking Flash Threshold Illuminance)

GMB) where the log of the ratio between test flash threshold illuminance and test flash absolute threshold illuminance is plotted as a function of the log of the ratio between masking flash illuminance and masking flash threshold illuminance at a particular level of adapting field illuminance. It can be seen that following such a manipulation, all subplateau adhere to the same straight line function with a slope of 0.5. Inspection of Figures 13 and 14 also show that the extent of the plateau segment is dependent upon the level of adapting field illuminance. The range of masking flash illuminances which give rise to the plateau segment is attenuated as adapting field illuminance is increased. In fact, tvi curves obtained when adapting field illuminance was 0.5 log scotopic trolands do not display a plateau.

Insofar as rods subserve the influence of the masking flash, all subplateau data can be described by equation 2:

$$I_{c_{th}} / I_{c_o} = K \sqrt{(I_r / I_{r_{th}}) + D}$$

The results of Experiment 1 show that rods alone are stimulated when masking flash illuminance is less than -0.5 log scotopic trolands. Thus, with no adapting field present, rods alone are responsible for subplateau increments in test flash threshold. However, rods and cones are stimulated by all supraplateau masking flashes. Since equation 2 describes all subplateau data, it would seem that a single (rod) photoreceptor mechanism is responsible for all subplateau increments in test flash threshold. However, different mechanisms may underly supraplateau masking effects. The nature of the photoreceptor mechanism(s) responsible for raising the threshold of the cone detected test flash is addressed in Experiment 2b.

Experiment 2b

Procedure

Following the period of dark adaptation, the threshold of the test flash was determined four times in succession with no adapting field present for observer JJJ and with the illuminance of the adapting field set at -1.5 log scotopic trolands for observer GMB. The results of Experiment 1 insure that under these conditions, cones alone mediate test flash threshold. The test flash was then presented at an illuminance 0.4 or 1.0 log units above the mean threshold illuminance value. These values correspond to test flash threshold illuminance values below and above the plateau segment described in Experiment 2a. The observer's task was to adjust the irradiance of different wavelength masking flashes (420, 477, 512, 540, 577, 600, 620, 655, and 680 nm) until the test flash could no longer be detected. The order in which the different wavelength masking flashes were presented was randomized before each experimental session. Mask irradiance values were subsequently converted into log relative quanta using the formula described on page 35 .

With observer JJJ, Experiment 2b was performed with no adapting field present and when the illuminance of the adapting field was set at -1.0 and 0.0 log scotopic trolands. With observer GMB, the adapting field was always present and set at an illuminance of either -1.5, -0.5, or 0.5 log scotopic trolands. In collecting action spectra data, only one level of test flash illuminance and one level of adapting field illuminance was used in each experimental session as prescribed by a randomization schedule.

Results

Figures 15 and 16 show action spectra data obtained when test flash

Fig. 15. The log relative quanta of the masking flash required to cancel the detection of the 655 nm test flash raised 0.4 log units above its absolute threshold as a function of masking flash wavelength for observers JJJ (right coordinates) and GMB (left coordinates). Adapting field illuminance serves as a parameter. The solid curve indicates the CIE scotopic luminosity function (Wyszecki & Stiles, 1967).

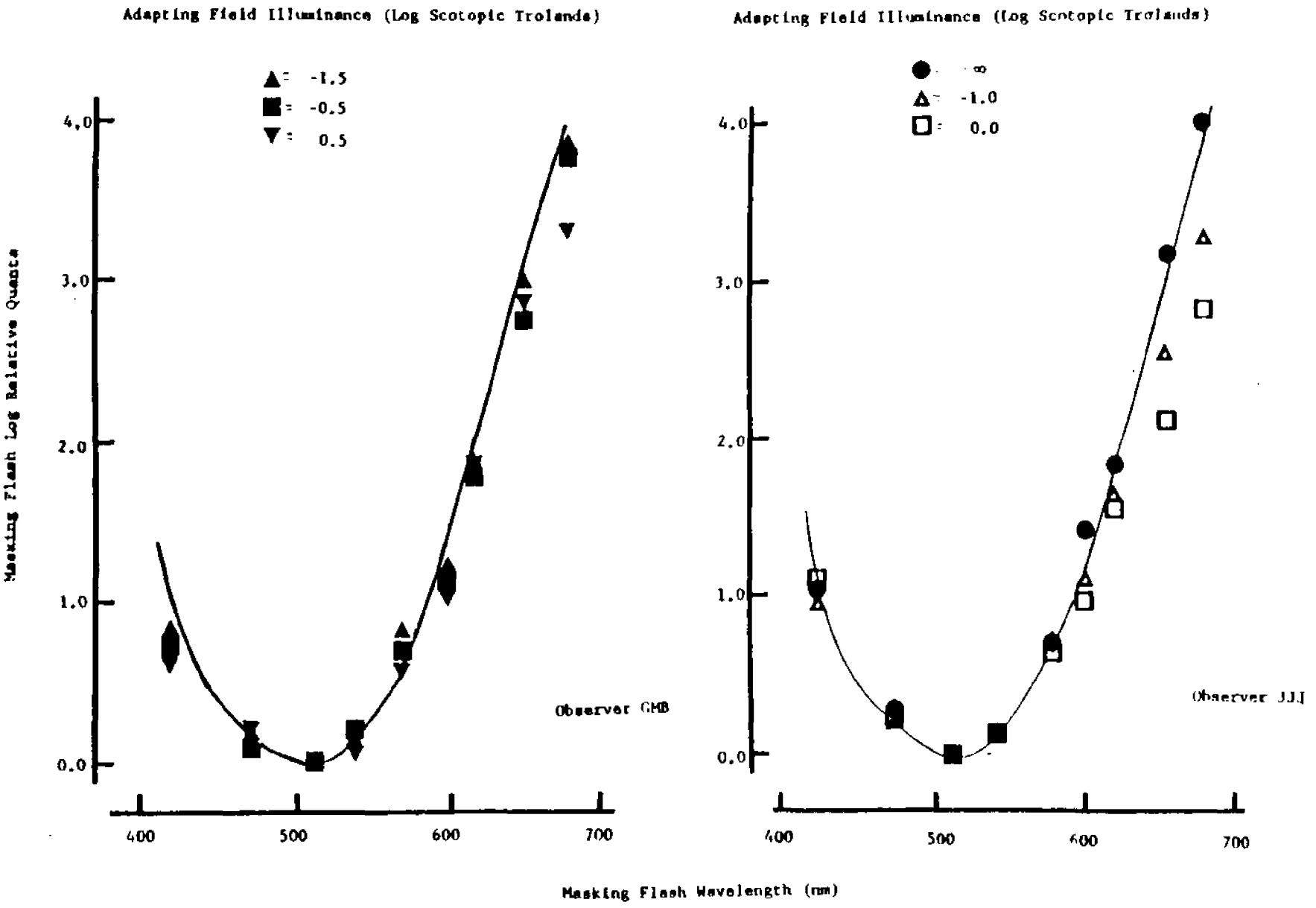
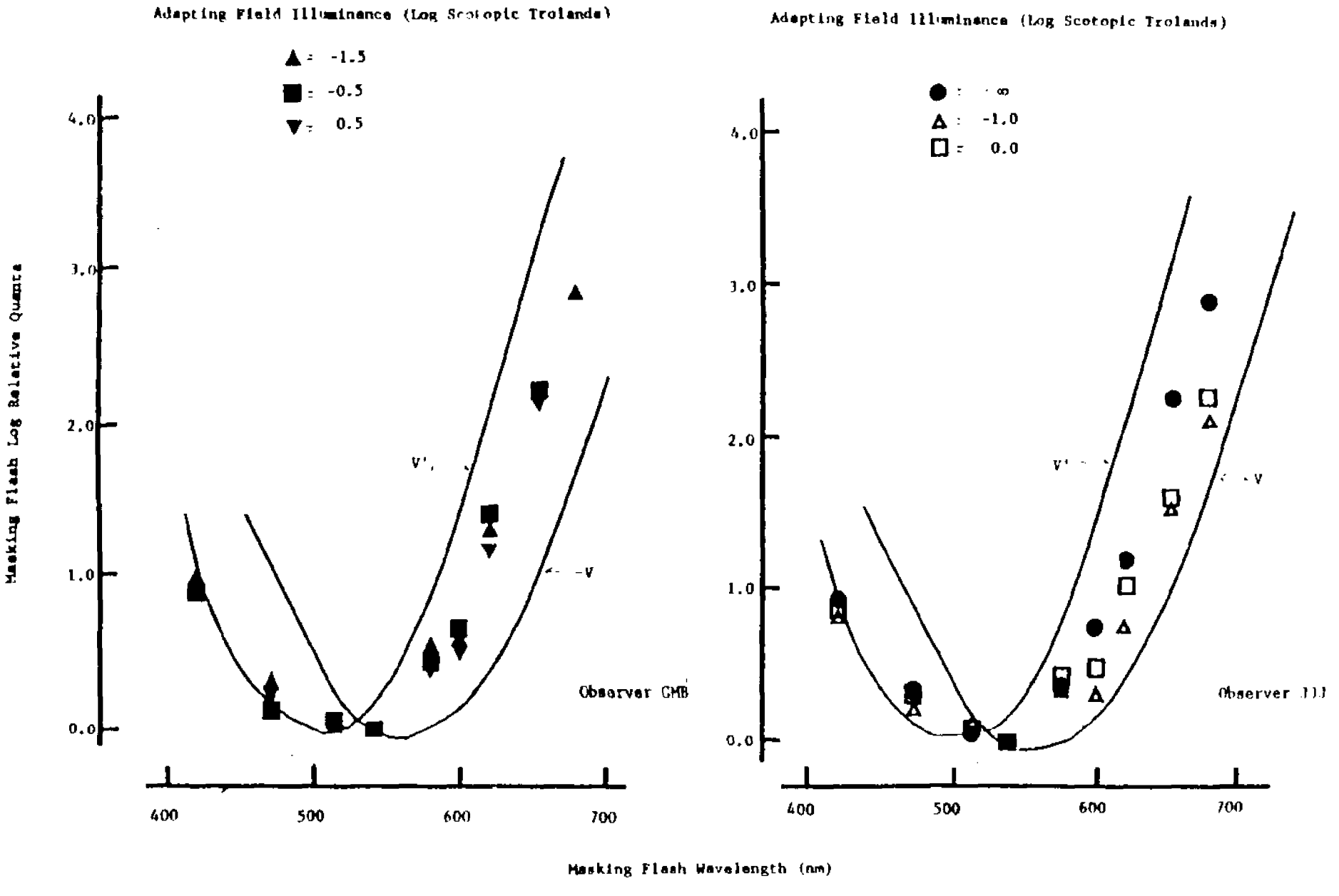

Adapting Field Illuminance (Log Scotopic Trolands)
▲ = -1.5
■ = -0.5
▼ = 0.5
Masking Flash Log Relative Quanta
4.0
3.0
2.0
1.0
0.0
400
500
600
700
Observer GMB
Adapting Field Illuminance (Log Scotopic Trolands)
● = ∞
△ = -1.0
□ = 0.0
4.0
3.0
2.0
1.0
0.0
400
500
600
700
Observer JJL
Masking Flash Wavelength (nm)

Fig. 16. The log relative quanta of the masking flash required to cancel the detection of the 655 nm test flash raised 1.0 log units above its absolute threshold as a function of masking flash wavelength for observers JJJ (right coordinates) and GMB (left coordinates). Adapting field illuminance serves as a parameter. The solid curves labeled V' and V indicate the CIE scotopic and photopic luminosity functions, respectively (Wyszecki & Stiles, 1967).


Adapting Field Illuminance (Log Scotopic Trolands)
▲ = -1.5
■ = -0.5
▼ = 0.5
4.0
3.0
2.0
1.0
0.0
V'
-V
Observer GMB
400
500
600
700
Masking Flash Log Relative Quanta
Adapting Field Illuminance (Log Scotopic Trolands)
● = ∞
△ = -1.0
□ = 0.0
4.0
3.0
2.0
1.0
0.0
V'
-V
Observer JJJ
400
500
600
700
Masking Flash Wavelength (nm)

illuminance was set at 0.4 and 1.0 log units above absolute threshold, respectively, for observers JJJ (right coordinates) and GMB (left coordinates). Accordingly, the log relative quanta of the masking flash required to cancel the detection of the test flash was plotted as a function of masking flash wavelength with adapting field illuminance as a parameter. The solid curves labeled V' and V indicate the CIE scotopic and photopic luminosity functions, respectively (Wyszecki and Stiles, 1967). In Figures 15 and 16 the vertical position of each set of data points and the CIE functions were shifted vertically until their minima corresponded. This was the only curve fitting manipulation.

Action spectra data obtained when the test flash was set at the subplateau illuminance value (Figure 15) agree well with the CIE scotopic luminosity function when the adapting field was absent or of minimal illuminance. This indicates that rods alone are responsible for masking the cone detected test flash. At higher adapting field illuminances, data points systematically deviate from the scotopic luminosity function when long wavelength masking flashes are employed; less log relative quanta are required to mask the test flash. This trend is most obvious for observer JJJ. Nevertheless, a good fit is always preserved when masking flash wavelength is less than 620 nm. Since the increment threshold data of Experiment 2a were collected with a 512 nm masking flash, these action spectra data strongly suggest that a single rod photoreceptor mechanism was responsible for subplateau increases in test flash threshold regardless of the scotopic level of adapting field illuminance.

Inspection of Figure 16 reveals that when the test flash illuminance was set at a supraplateau level, action spectra data do not conform to the

CIE scotopic luminosity function. For both observers a 540 nm masking flash is most effective in cancelling the detection of the test flash. Additionally, action spectra data markedly deviate from the V' function when long wavelength masking flashes are employed and a "hump" or shoulder appears at abscissa values between 577 and 600 nm. These deviations are accentuated as the illuminance of the adapting field is increased and action spectra data approach the CIE photopic luminosity function. These data strongly suggest that the combined activity of rods and cones stimulated by the masking flash are responsible for raising test flash threshold to supraplateau illuminance values.

Discussion of Experiments 2a and 2b

The results of Experiment 2 show the influence of rod light adaptation on the type of rod-cone interaction described by Temme and Frumkes (1977) and subsequently quantified by Frumkes et al. (1979). For the sake of clarity, these results will be discussed in terms of the four segments of the test flash threshold versus masking flash illuminance tvi curve.

Segments A and B: subplateau increments in test flash threshold- Using stimuli identical to those employed in the present study, Frumkes et al. (1979) found that under dark adapted conditions, subplateau increments in test flash threshold could be described by equation 2:

$$I_{cth} / I_{co} = K \sqrt{(I_r / I_{rth}) + D}$$

The results of Experiment 2 show that equation 2 obtains under all scotopic levels of retinal illumination: the initial rise in the threshold of the cone detected test flash was proportional to the square root of the illuminance of the rod detected, 512 nm masking flash regardless

of the acotopic level of adapting field illuminance.[6] Light adaptation of the rod system shifts the origins of the tvi curves toward higher masking flash illuminance values by an amount equal to the decrease in rod sensitivity to the masking flash. In terms of equation 2, this amounts to resetting the value of the variable, $I_{r_{th}}$. Consequently, all subplateau data obtained with different scotopic adapting fields collapse into one function when the value of $I_{r_{th}}$ is taken into account.

Equation 2 predicts an attenuation of the influence of a fixed illuminance masking flash on test flash threshold as the rod system is light adapted: Holding the value of masking flash illuminance (I_r) constant and increasing the threshold illuminance value of the masking flash ($I_{r_{th}}$) should cause test flash threshold ($I_{c_{th}}$) to <u>decrease</u> by an amount proportional to the square root of increases in masking flash threshold illuminance. The results of Experiment 2 substantiate this prediction. Figure 17 shows a replot of the data appearing in Figure 11 (observer JJJ). The log of test flash threshold in the presence of a -1.0 log scotopic troland masking flash, at different levels of adapting field illuminance, is plotted as a function of the log of masking flash threshold at these different levels of adapting field illuminance. (The corresponding values of adapting field illuminance appears next to each data point.) As predicted, these data are well fitted by a straight line with a slope of -0.5. This indicates that the influence of a fixed

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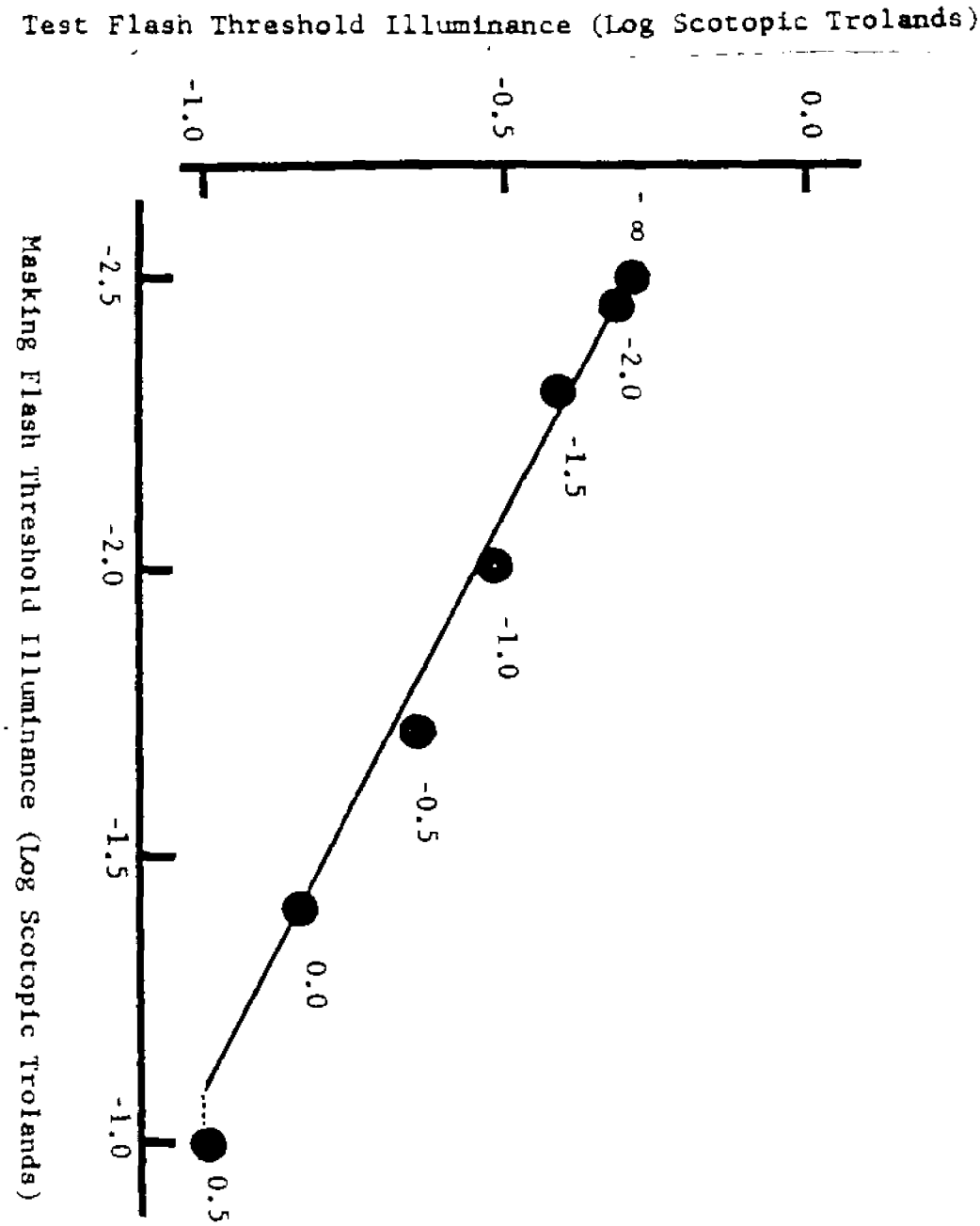
6. It is important to recognize that equation 2 only describes the influence of rod stimulation on cone sensitivity. However, action spectra data collected in Experiment 2b clearly show that rod <u>and</u> cone photoreceptor mechanisms contribute to subplateau increments in the threshold of the cone detected test flash when long wavelength masking flashes are employed. Equation 2 does not take this into account.

Fig. 17. The threshold illuminance of the 655 nm test flash in the presence of a -1.0 log scotopic troland , 512 nm masking flash under different scotopic levels of adapting field illuminance as a function of the threshold illuminance of the masking flash at these different levels of adapting field illuminance. The corresponding values of adapting field illuminance, in log scotopic trolands, appears next to each datum point.


Test Flash Threshold Illuminance (Log Scotopic Trolands)
-1.0
-0.5
0.0
-∞
-2.0
-1.5
-1.0
-0.5
0.0
0.5
Masking Flash Threshold Illuminance (Log Scotopic Trolands)
-2.5
-2.0
-1.5
-1.0

illuminance masking flash on test flash threshold decreases in proportion to the square root of increases in masking flash threshold. These data compliment the findings of Frumkes, Bauer, and Holstein (1978) who reported that during the course of dark adaptation, test flash threshold increased in proportion to the square root of rod sensitivity to a fixed illuminance masking flash. In terms of equation 2, this amounts to holding the value of I_r constant and <u>decreasing</u> the value of $I_{r_{th}}$ as dark adaptation progresses.

Taken together, the results of the present study and the results of Frumkes et al. (1978) suggest that, in terms of rod-cone interaction, real light and bleached rhodopsin have equivalent influences on the sensitivity of the rod system. In terms of equation 2, they both serve to set the value of $I_{r_{th}}$. In fact, such an equivalence was recently demonstrated by Bauer and Frumkes (1980). They found that the same equivalent background function (Crawford, 1947) describes the effects of background illuminance and recovery from photopigment bleaching on rod sensitivity when rod sensitivity is measured directly, as in Experiment 1, or when rod sensitivity is measured indirectly by observing the influence of rod stimulation on cone threshold, as in Experiment 2.

It is quite likely that changes in the responsivity of the rod photoreceptor underly the effects of rod light adaptation manifested in the present study. As noted in the introduction, the photoreceptor response to light is described by equation 1:

$$V/V_{max} = I/(I+\sigma)$$

As long as the stimulus illuminance is within a few log units of absolute threshold, equation 1 can be reduced to $V = (V_{max})\ (I)/\sigma$ or more simply

$V = QI$ (Rodieck, 1972) where Q is equivalent to σ/V_{max}.

It has been demonstrated that Q provides an index of rod desensitization. The value of Q increases directly with the level of retinal illumination (Kleinschmidt & Dowling, 1975; Fain, 1976). In fact, Fain obtained a curve approximating the rod increment threshold function of Aguilar and Stiles (1954) w' en the value of Q was plotted as a function of background illuminance. In terms of the present study, the sensitivity factor Q is proportional to the sensitivity factor $I_{r_{th}}$ of equation 2. Indeed, both Q and $I_{r_{th}}$ determine the stimulus intensity required to produce a threshold response: Q determines the stimulus intensity (I) which elicits a threshold membrane voltage change while $I_{r_{th}}$ determines that masking flash illuminance at which subplateau increments in test flash threshold originate.

The significance of the square root relationship between test flash threshold and masking flash illuminance remains to be addressed. In the increment threshold situation, a square root relationship implies that the visual system operates according to the principles of an ideal detector (Barlow, 1972). The efficiency of an ideal detector is limited only by random fluctuations in the magnitude of successive input signals.[7] These fluctuations obey the Poisson law such that the variance of successive input signals increases directly with the magnitude of the mean input signals. Additionally, for an increment in the input signal to be detected, the change must be proportional to the square root of the

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7. The variability of the input signal has been attributed to random fluctuations in the visual stimulus (Hecht, Schlaer, & Pirrene, 1942: Rose, 1948; Bouman, Vos, & Walraven, 1963) and fluctuations in neural discharge (Barlow, 1965; McGill, 1976).

mean input signal (McGill, 1976).

Frumkes, Bauer, and Nygaard (1979) proposed that the present rod-cone interaction occurs at a "common neural locus" which behaves like an ideal detector. According to their model, the masking flash produces a rod signal which is introduced to the common neural locus. The magnitude of the rod signal fluctuates with successive masking flash presentations according to the Poisson law. The test flash produces a cone signal which is also introduced to the common neural locus. However, the variability of the cone signal at threshold is considered to be small and can be discounted. For the test flash to be detected against the concentric masking flash, the magnitude of the cone signal must be proportional to the square root of the mean rod signal. Frumkes et al. (1979) assume that the rod and cone signals are linearly related to the illuminance of masking and test flashes, respectively. Consequently, the illuminance of the test flash, at threshold, will be proportional to the square root of masking flash illuminance.[8]

The ideal detector model of rod-cone interaction proposed by Frumkes et al. (1979) will account for the square root relationship between test flash threshold and masking flash illuminance manifested in the present study. Interestingly, this model predicts that the threshold of a rod test flash will increase in proportion to the square root of increases in the illuminance of a cone masking flash. However, experimental

8. Frumkes et al. (1979) provide data in support of their model. Using stimuli identical to those employed in the present study, the probability of seeing the cone detected test flash was measured as a function of test flash illuminance with masking flash illuminance serving as a parameter. These data were well fitted by normal approximations of Poisson distributions with means which were proportional to the square root of the illuminance of the masking flash.

verification of this prediction is most difficult; it is impossible to construct test and masking flashes which selectively stimulate the rod and cone systems, respectively.

Segment C: the plateau level of test flash threshold- As noted in the introduction, equation 2 does not pertain to the plateau segment of the test flash threshold versus masking flash illuminance tvi curve. Although a quantitative analysis of plateau level data was not performed, the results of Experiment 2 suggest a mechanism responsible for these data.

Several lines of evidence indicate that the manifestation of the plateau is solely a rod related phenomenon: First, under dark adapted conditions, the plateau begins when masking flash illuminance is approximately -1.0 log scotopic trolands. Rods alone are stimulated by the masking flash at this illuminance. Secondly, the extent of the plateau is dependent upon the adapted state of the rod system; the plateau decreases as rods are light adapted. Thirdly, Bauer and Frumkes (1980) found that the origin of the plateau is dependent upon the scotopic illuminance of the masking flash. That is, the masking flash illuminance demarking the onset of the plateau is the same when masking stimuli of different wavelengths are equated for their influence on rods. Therefore, the onset of the plateau appears to be independent of any cone involvement. This finding parallels the results of Fuortes et al. (1961) who reported that the scotopic illuminance of the adapting stimulus determines the point at which rod signals saturate in the rod desensitization experiment of Aguilar and Stiles (1954).

It appears that the magnitude of the rod signal responsible for

masking the test flash has an upper limiting value; i.e., the rod signal "saturates." However, this apparent saturation differs from the rod saturation reported by Aguilar and Stiles (1954) in several respects: the rod signal saturates at an illuminance that can be more than 3.0 log units below traditional measures of rod saturation (Aguilar & Stiles, 1954; Blakemore & Rushton, 1965; Hallet, 1969). In addition, the present saturation effect does not appear to be a direct consequence of rod desensitization accompanying light adaptation: that the ordinate value marking the onset of the plateau is fixed regardless of the scotopic level of adapting field illuminance suggests that, in terms of equation 2, the saturation effect is dependent upon the value of I_r, not the value of $I_{r_{th}}$ as Aguilar and Stiles (1954) would have it.

The paradox that over the plateau segment the masking flash appears brighter with increases in masking flash illuminance despite the fact that test flash threshold remains stable suggests that the rod signal responsible for altering cone sensitivity is independent of the rod signal contributing to the apparent brightness of the masking flash. This paradox implies that these two rod related phenomena are mediated through separate pathways within the rod system. Presently, there is little evidence to support the notion of multiple rod channels (see, however, Conner & MacLeod, 1977; Green & Siegel, 1975).

Segment D: supraplateau increments in test flash threshold- The results of Experiment 2b indicate that rods and cones stimulated by the masking flash are responsible for raising test flash threshold to supraplateau illuminance values. Action spectra data approximate mesopic luminosity functions (Bridgman, 1953; Hough, 1968; Kinney,

1955, 1957). Kinney (1957) found that mesopic luminosity functions are basically scotopic in shape but show increased sensitivity to long wavelengths. Mesopic luminosity functions also show shoulders and depressions at 470, 530, and 610 nm which represent cone sensitivity superimposed on the scotopic luminosity function. In the present study, supraplateau action spectra deviate from the CIE scotopic luminosity function in the same manner. Action spectra show an increased sensitivity at long wavelengths and a shoulder appears at abscissa values between 577 and 600 nm.

If the rod signal responsible for subplateau increments in test flash threshold saturates, then supraplateau increments are due to cones alone. Supraplateau action spectra would then reflect the addition of separate subplateau (rod) and supraplateau (cone) masking influences. If this is true, supraplateau action spectra should deviate from the CIE scotopic luminosity function at <u>all</u> wavelengths. However, this is not the case. The results of Experiment 2b show that supraplateau action spectra do not deviate from the scotopic function at the short wavelength end of the spectrum.

It appears that a complex interaction of rods and cones stimulated by the masking flash underlies supraplateau increases in the threshold of the cone detected test flash.[9] Clearly, more research is required to elucidate the nature of the photoreceptor mechanism(s) responsible for these data.

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9. Bridgman (1953) notes that mesopic luminosity functions do not simply represent rod <u>or</u> cone function at a particular wavelength depending upon which system is more sensitive. If this were the case, it would be easy to predict the shape of mesopic luminosity functions by knowing the relative sensitivities of the rod and cone systems. Instead, Bridgman (1953) suggests that the shape of mesopic luminosity functions result from summatory interactions between the rod and cone systems.

Chapter 6: Summary and Conclusions

The influence of rod stimulation on cone sensitivity was examined while the rod system was selectively light adapted. A Maxwellian view optical system was used to present all stimuli to the right eye of three observers. These stimuli included a 25 msec duration, 13' diameter, 655 nm wavelength test flash; a 500 msec duration, 40' diameter, 512 nm wavelength masking flash; and a continuously exposed, 40° diameter, 490 nm wavelength adapting field. The flashing stimuli were presented to the nasal retina, 7° from fixation along the horizontal meridian. The adapting field was concentric with a fixation target.

Experiment 1 was designed to delineate a range of adapting field illuminance over which the sensitivity of the rod system decreases while the sensitivity of the cone system is unchanged. Toward this end, the threshold of the 655 nm test flash and the threshold of the 512 nm masking flash were each determined as a function of adapting field illuminance. In general, there exists a 3.0 log unit range of adapting field illuminance over which rod sensitivity decreases while cone sensitivity is unchanged. Experiment 1 also established the masking flash illuminance values required to stimulate rods alone or rods and cones and insured that cones alone determined test flash threshold regardless of the level of adapting field illuminance.

The goal of Experiment 2 was to determine the influence of rod light adaptation on rod-cone interaction. In Experiment 2a, test flash threshold was measured as a function of masking flash illuminance under dark adapted conditions and under scotopic levels of adapting field illuminance. The results were plotted as tvi curves (i.e., test flash

threshold versus masking flash illuminance curves). The tvi curve obtained under dark adapted conditions can be described in four segments: Test flash threshold is constant with increases in masking flash illuminance until masking flash illuminance exceeds the absolute threshold illuminance of the masking flash (segment A). Thereafter, test flash threshold increases in proportion to the square root of increases in masking flash illuminance (segment B) until a plateau level is reached (segment C). Further increases in test flash threshold occur at still higher masking flash illuminance values (segment D). Data corresponding to segments A and B can be described by the equation:

$$I_{c_{th}}/I_{c_o} = K\sqrt{(I_r/I_{r_{th}}) + D}$$

where $I_{c_{th}}$ is the threshold illuminance of the cone test flash, I_{c_o} is the absolute threshold of the test flash, I_r is the illuminance of the 512 nm masking flash, $I_{r_{th}}$ is the threshold illuminance of the masking flash, D is a dark noise term, and K is a unit related constant.

The basic form of the tvi curve is preserved regardless of the scotopic level of adapting field illuminance. However, light adaptation of the rod system shifts the origin of tvi curves toward higher masking flash illuminance values by an amount equal to the increase in masking flash threshold illuminance. In addition, the extent of the plateau level decreases as rods are light adapted.

In Experiment 2b, action spectra data were collected to elucidate the photoreceptor mechanism(s) responsible for increasing test flash threshold. The irradiance of different wavelength masking flashes required to cancel the detection of the test flash was determined when the test flash was set at a subplateau (segment B) or a supraplateau

(segment D) illuminance value. Action spectra data clearly indicate that in Experiment 2a, rods alone stimulated by the 512 nm masking flash were responsible for subplateau increases in test flash threshold. However, rods and cones stimulated by the masking flash are responsible for raising test flash threshold to supraplateau levels.

The results of these experiments were related to mechanisms underlying rod-cone interaction and rod light adaptation: The effects of rod stimulation on cone sensitivity manifested in Experiment 2a were discussed in terms of an ideal detector model of rod-cone interaction. The influence of rod light adaptation on rod-cone interaction was related to changes in the responsivity of the rod photoreceptor accompanying increases in retinal illumination.

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