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IN INCREMENT THRESHOLD EXPERIMENTS.

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INTERACTION OF SPECTRALLY TUNED MECHANISMS IN INCREMENT THRESHOLD EXPERIMENTS

by

Leonard A. Temme

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.

1975

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

August 13, 1975 — [illegible] E. Franks
date — Chairman of Examining Committee

9-3-75 — Florence L. Denmark MP.
date — Executive Officer

Mitchell L. Kietzman

William S. Battersby

Leonard Matin

Supervisory Committee

The City University of New York

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CHAPTER 1

INTRODUCTION

The most extensive studies of spectrally tuned mechanisms employing an increment threshold procedure in the human observer are those of Stiles (1949, 1953, 1959). In general, thresholds of a brief, small test flash (F_t) of light were determined as a function of the irradiance of a large, continuously exposed conditioning field (F_c). Wavelengths of both the F_t and F_c were varied parametricly. For a specific set of F_c and F_t wavelengths the curves describing the relationship between F_t threshold and F_c irradiance are called 'threshold versus irradiance curves' or tvi curves.

In interpreting his data Stiles made a number of assumptions including: 1. a patch of retina contains several different spectrally tuned mechanisms 2. threshold is determined by the most sensitive mechanism 3. there is sufficient independence among the mechanisms so as to make the concept of an individual mechanism meaningful. With these assumptions Stiles was able to account for all of his increment threshold data in terms of one spectrally tuned scotopic mechanism and several spectrally tuned photopic mechanisms. For example, in the dark adapted peripheral retina Stiles found that all tvi curves had the same shape regardless of the wavelength of either the F_t of the F_c. Changes in the F_t wavelength displaced the entire curve up or down while changes in the F_c wavelength slid the curve to the left or right. The plot of the amount of displacements of the tvi curves either left and right or up and down with changes in the F_c or F_t wavelengths produced the scotopic spectral sensitivity function. (One important exception to this result are data obtained with long wavelength F_t. This situation is considered in detail below.) Stiles concluded that the tvi curves described a single spectrally tuned mechanism related to rod functioning.

With foveal and/or photopic conditions of illumination the results were considerably different. Only with a restricted range of F_t and F_c wavelengths and F_c irradiances did one tvi curve describe the data. In fact Stiles accounted for the photopic data in terms of five independent, spectrally tuned mechanisms, not just one. Apart from some reservations about the number and relative independence of the mechanisms, a large amount of experimental evidence seems to support Stiles' psychophysical model of color vision.

Possibly one reason that Stiles' assumptions proved tenable was that the F_c was large (generally 10°). There is ample evidence, however, that the threshold of a F_t of light is dependent upon the diameter of a concentric F_c as demonstrated most cogently by Westheimer (1965, 1967). In general, as the diameter of the F_c of constant illuminance increased, thresholds of the small concentric F_t increased, then decreased. It should be noted that, firstly, the diameter of the F_c that produced maximal F_t elevation decreased as the F_c illuminance increased for both scotopic (Westheimer, 1965) and photopic (Westheimer, 1967) vision. Secondly, when both F_c and F_t affected primarily cones the diameter F_c that produce maximal F_t elevation was smaller than the diameter F_c that produce maximal threshold elevation when primarily rods were involved (Westheimer, 1965, 1967, 1970).

Westheimer's results can be restated by saying that at one illuminance level a particular sized F_c raised F_t threshold more than either a smaller or a larger F_c. Since the particular F_c that produced maximal F_t elevation was illuminance dependent, the slope of the tvi curves must be dependent upon the F_c diameter. Moreover, this suggested that tvi curves obtained with any of Stiles' spectrally tuned mechanisms must be size dependent. This dependence suggested a way of analyzing possible interactions between rod and cone systems with the increment threshold procedure.

The purpose of the present study is to determine the influence of F_c size and wavelength upon tvi functions in order to assess the posibility of rod-cone interactions using the increment threshold procedure. The rationale of the study is presented in detail on pp.39 - 43.

CHAPTER 11

LITERATURE REVIEW

TEST STIMULUS THRESHOLD AS A FUNCTION OF THE CONDITIONING FIELD ILLUMINANCE

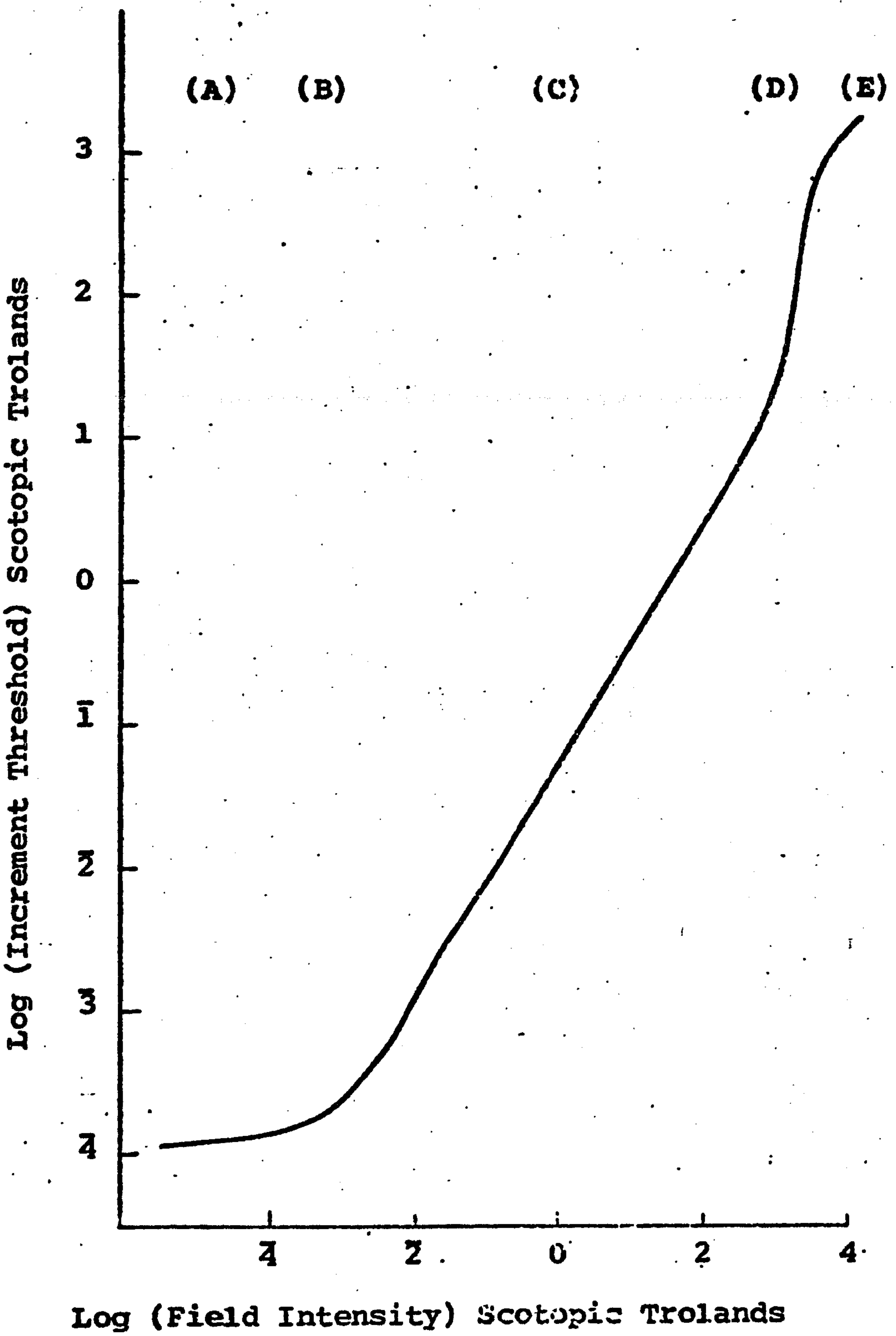
In the most basic form of the increment threshold experiment the threshold illuminance of the F_t is determined as a function of the illuminance of the F_c. The results of a classic study (Aguilar & Stiles, 1954) are exhibited in Figure 1. These data represent the increment thresholds of a 9° F_t of 200 msec. duration centered 9° from the fovea in the temporal retina. The F_c was a 20° concentric field. For several reasons (see Aguilar & Stiles. 1954) this curve is believed to reflect the threshold functioning of the rod system.

This curve has been analyzed into five different parts (Barlow, 1965). At low levels of illuminance (at A) increases in the F_c illuminance have little affect of the F_t threshold. This has been attributed to the presence of 'intrinsic noise' or 'dark noise'. Dark noise is defined as some disturbance in the visual system that outweighs whatever effects the increases in the F_c illuminance may have on the F_t threshold. As the F_c illuminance increased the F_t threshold increased as the square root of the F_c increment. This is shown at (B) and describes the activity of an 'ideal detector'.

At (C) Weber's ratio describes the relationship between the F_c illuminance and the F_t threshold. At these illuminances the F_t threshold is proportional to the illuminance of the F_c. The tvi curve at these illuminances has a slope of unity. At (D) the slope approaches infinity; this steep slope is thought to describe the typical behavior of rods at high levels of illuminance and has been called 'rod saturation'. (This behavior has not been reported for cone systems.) To generate this part of the tvi curve precautions must be taken to sufficiently desensitize the cone systems. The last part of the curve (E) is a discontinuity in the rate of change of the slope and is thought to be due to some other mechanism taking over threshold detection, in this case, one of the cone systems.

Regardless of the particular theory used to explain the tvi curve (for example see Barlow, 1965; Blackwell, 1963, 1972; Wyszecki & Stiles, 1967) the empirical relation has proved lawful and reliable. As such the tvi curve can be used as a tool to study different aspects of vision; for example: dark adaptation (Baker, 1963; Crawford, 1940, 1947), size and type of neural signals (Alpern, Rushton, & Torii, 1970a, 1970b), edge effects (Fiorentini, 1972), spatial summation

Figure 1. Threshold illuminance (in log scotopic trolands) of a 9° F_t of 200 msec duration as a function of the illuminance (also in log scotopic trolands) of a concentric 20° F_c. The F_t was centered 9° in the temporal visual field (Aguilar and Stiles, 1954).


(A)
(B)
(C)
(D)
(E)
Log (Increment Threshold) Scotopic Trolands
3
2
1
0
$\bar{1}$
$\bar{2}$
$\bar{3}$
$\bar{4}$
$\bar{4}$
$\bar{2}$
0
2
4
Log (Field Intensity) Scotopic Trolands

(Sakett, 1971; Hallett, 1968), and photopigment kinetics (Rushton, 1972b).

TEST STIMULUS THRESHOLD AS A FUNCTION OF THE CONDITIONING FIELD SIZE

The influence of the F_c diameter upon the threshold of the F_t has been the subject of considerable investigation since the time of Aubert (1860). More recent studies have shown that, providing the F_t was sufficiently small, the threshold of the F_t first increased then decreased again as the diameter of a concentric, constant illuminance F_c increased (Crawford, 1940; Frumkes & Sturr, 1968; Westheimer, 1965, 1967, 1970). This functional relationship is often referred to as the 'Westheimer effect'.

The following is a summary of the more important experimental observations about the Westheimer effect: (1) the diameter of the F_c that produced maximal F_t elevation (the peak diameter) decreased as the F_c illuminance increased for both rods and cones (Frumkes & Sturr, 1968; Westheimer, 1965, 1967). (2) When both the F_c and F_t stimulated cones the peak diameter was smaller than when only rods were involved (Westheimer, 1965, 1967, 1970). (3) The peak diameter increased with retinal excentricity (Frumkes & Sturr, 1968; Markoff & Sturr, 1971; Westheimer, 1967). (4) The Westheimer effect was obtained with stabilized retinal image conditions; therefore, the effect was not due to uncontrolled eye movements (Teller, Andrews, & Barlow, 1966). (5) There was a relationship between the F_t size and the peak diameter of the F_c (Alexander, 1974b). (6) In studies of Westheimer (1967) there was no evidence of any dichoptic effects. However, other studies have shown that if the F_t and F_c were flashed in different eyes an appreciable dichoptic threshold effect was obtained (Battersby & Wagman, 1962). If the F_c was not flashed the dichoptic threshold effects were not obtained (Fiorentini, Bayly, & Maffei, 1972; Markoff & Sturr, 1971; Sturr & Teller, 1973).

An immediate extension of the basic Westheimer effect is the sensitization paradigm. In this situation a F_t is presented in the center of a F_c. A flashing annulus is presented around the F_c. When the annulus is not present the F_c diameter is such that it raises the F_t threshold maximally, but, when the annulus is present the F_c is extended beyond the peak diameter and the F_t threshold falls. The annulus is usually thought to sensitize or disinhibit the central patch of retina detecting the F_t.

With the sensitization approach the afterimage of a flashing annulus (dark light) did not affect the threshold of the F_t imaged upon the F_c of peak diameter. Therefore, signals from bleached patches of retina do not cause sensitization (Westheimer, 1968).

A limited spatial summation of a sensitizing annulus has been found (Teller, Matter, & Phillips, 1970); a dim annulus was more affective in sensitization than a part of that annulus regardless of the illuminance of that partial annulus. The time course of sensitization was found to be similar to the time course found in the Crawford-Baker type studies of early dark adaptation (Teller, Matter, Phillips, & Alexander, 1971).

Models of the Westheimer Effect

There are two general classes of theories that are used to explain the Westheimer effect. One type uses concepts of edge effects and spatial summation; the other theory uses concepts of receptive fields and size-tuned channels.

(a) Edge effects and spatial summation - As the diameter of the constant illuminance F_c increased up to some peak diameter, the threshold of the F_t increased. This observation was explained in terms of spatial summation and/or neural convergence. Increasing the diameter of the F_c was thought to increase 'neural noise' which in turn elevated F_t threshold. This hypothesis (see Frumkes & Sturr, 1968) is consistent with two observations:

First, the peak diameter was greater for rods than for cones, which is as expected since rods have a greater area of neural summation than do cones. Second, the peak diameter increased with retinal eccentricity, as does neural summation.

More difficult to explain is the fall in the F_t threshold as the F_e increased in diameter beyond the peak diameter. There are thought to be two factors involved with the fall in threshold. Firstly, increases in the F_c diameter removes an edge from the vicinity of the F_t which is known to reduce the threshold of the F_t (Fry & Bartley, 1935). This edge effect hypothesis is supported by the observation that an edge produced by an annulus whose illuminance was greater than the F_c had the same threshold elevating effect as did an edge produced by a dark annulus (Lennie & MacLeod, 1973; Wyatt, 1972). Therefore, it was not the illuminance, or the direction of the illuminance change, but the presence of an edge that affected the threshold of the F_t. Secondly, it has been suggested that sensitization plays a role (Mathews, 1971; Pirenne, 1962; Ratoosh & Graham, 1951). The outlying part of the F_c inhibits the central parts with the resulting decrease in the inhibitory action exerted by these parts on the F_t. This model is another form of disinhibition.

(b) Receptive field models and size-tuned models -

There are many forms of this type of model. For example, Enoch and his coworkers (Enoch, Birger, & Birns, 1970a, 1970b; Enoch, Sunga, & Bachmann, 1970a, 1970b) and Teller, Andrews, and Barlow (1966) suggest that the Westheimer effect reflects directly the activity of ganglion cells. The primary evidence for this suggestion is that the threshold of the small F_t imaged in the excitatory center of the ganglion cell receptive field changes as the diameter of the larger F_c changes (Barlow, Fitzhugh, & Kuffler, 1957; Burkhardt & Berntson, 1972; Enroth-Cugell & Robson, 1968). The obtained threshold versus diameter functions are similar to the psychophysically obtained Westheimer functions.

Related explanations of the Westheimer effect are often given in terms of 'size-tuned channels' or 'spatially tuned mechanisms'. There have been several models for constructing size-tuned mechanisms all of which can account for the Westheimer effect (Bagrash, 1973; Blakemore & Campbell, 1968; Thomas, 1970). For example, a size-tuned channel can be modelled from an array of fixed sized, center-surround antagonistic receptive fields. Thus, when a F_c falls on the array, the greatest excitation occurs where the edge of the F_c falls within the center parts of the receptive fields but only partially fills the antagonistic surround. The receptive fields in which both the center and surround are completely illuminated by the F_c are more sensitive than those that are partially illuminated. This is so since the center and surround are antagonistic, and the sum excitation of total center and surround stimulation is less than the sum of excitation of total center stimulation and partial surround stimulation (Bagrash, 1973). Thus the peak diameter of the F_c would then be dependent upon the size of the F_t. In fact the peak diameter was found to be dependent upon the F_t diameter (Alexander, 1974b).

Another theory (Lennie & MacLeod, 1973) stems from the observation that increases of illuminance of a F_c on which a small F_t was presented first light adapts ganglion cells with larger receptive fields. The flux (area X luminance) falling on a receptive field center determined the sensitivity, not illuminance alone (Enroth-Cugell & Shapely, 1973). Thus in the psychophysical situation used to study the Westheimer effect, when diameter is varied, it is the receptive fields with small centers that determine the F_t threshold.

It is obvious that all the many models used to explain the Westheimer effect are similar; and to some extent they may all have some validity. What is important for the present study is that the F_t threshold is dependent upon the F_c size. This observation is crucial to the rationale developed below for demonstrating a size dependent interaction between spectrally tuned mechanisms.

The present experiments used the increment threshold technique to study interaction between photopic and scotopic mechanisms. Therefore, it is necessary first to define these mechanisms.

RECEPTORS MEDIATING VERTEBRATE VISION

The Duplicity Theory, Rods and Cones

The duplicity theory was first stated by Max Schultze in 1866 as a consequence of his comparative anatomical studies of retinae. As it is usually stated, for example by Hecht (1937), there are two families of photoreceptors; those that are long and cylindrical, the rods, which mediate vision at low levels of illuminance; those that are conical in shape, the cones, which are active at higher levels of illuminance. Schultze and many later proponents of the duplicity theory (Alpern, 1965; Hecht, 1937) are explicit in stating that these two classes of receptors do not interact with one another.

In general, it can be said that scotopic vision is mediated by rhodopsin in rods, has low spatial and temporal resolution, has a high Weber ratio, gives no sense of color, is best a few degrees from the fovea, and has a spectral sensitivity curve that peaks at 506 nm (see Wyszecki & Stiles, 1967). Photopic vision is mediated by three types of cones that contain different photopigments. Photopic vision has a high spatial and temporal resolution, is best in the fovea, mediates color perception, has generally a lower Weber ratio, and its spectral sensitivity function peaks at approximately 560nm.

It is generally accepted today that there are both photochemical and neural reasons for the differences between photopic and scotopic vision. However, the question of rod-cone independence is far from answered.

Three cone vision - There is now much evidence that color vision is a consequence of three functionally distince cone channels; this is basically the trichromatic theory. The evidence for this theory can be divided into three classes.

(a) Electrophysiological - Intracellular recording from teleost fish have demonstrated three different types of cones with peak sensitivity around 462, 529, and 611nm (Tomita, 1972). Unit recording from a number of different neurons within the teleost retina, and at the ganglion cell, lateral geniculate, and cortical level of primate (see Gouras, 1972) are consistant with the hypothesis that there are three different cone types, although most neurons receive input from at least two different cone types.

(b) Photochemical - Michrospectrophotometric techniques have enabled a number of different investigators to record action spectra of individual cones in a number of species (see Liebman, 1972). In the human retina, Marks, Dobelle, and MacNichol (1964) and Wald and Brown (1965) have noted three different cone types with peak sensitivity at 445, 535, and 670nm.

Measurements of photopigments in situ in the intact human, using retinal densitometry (Campbell & Rushton, 1955; Ripps & Weale, 1964) showed two of the three photopigments (peaking at 540 and 570nm). Although a short wavelength photopigment has yet to be isolated, there is good agreement between these photochemical data from the human and the psychophysical data of Wald (1964) and Stiles (1959).

(c) Psychophysical - There are three types of psychophysical data directly relevant to trichromatic theory. (a) Color matching experiments in which a normal observer adjusts individually the intensities of three lights so as to make the mixture of these three lights identical in appearance with some arbitrarily chosen standard light (see Wright, 1972). (b) Color deficit experiments which indicate that there are three types of color blindness or color weakness, tritanopia, protanopia, deuteranopia. These color deficits are often thought to be caused by the individual having an unusually small amount, or missing respectively the short, middle, or long wavelength photopigment. Color mixing and densitometry seem to support the hypothesis that these individuals are deficient in a photopigment. Estimates of spectral sensitivity functions from these dolor deficient individuals have been made, with peak sensitivities estimated at 440nm (Blackwell & Blackwell, 1961), 530-540nm and 560-570nm (Hsia & Graham, 1957; Willmer, 1955). (c) Bleaching experiments in which an intense background light of an appropriately chosen wavelength is used to bleach preferentially a specific cone pigment. In essence this induces an artificial color blindness (Brindley, 1954; Wald, 1964). This approach is the limiting case of the more general increment threshold approach developed by Stiles to study color vision discussed in depth below on pp

INTERACTION BETWEEN DIFFERENT RECEPTOR MECHANISMS

There is controversy as to the extent of independence between the different receptor mechanisms mediating vertebrate vision.

Interaction Between Different Cone Types

All vertebrates known to have color vision are known to have spectrally opponent cells somewhere in their visual system (Abramov, 1972). Spectrally opponent cells must receive input from receptors with at least two different spectral sensitivities. It is therefore trivial to conclude that the information from different receptor mechanisms is combined somewhere in the visual system.

The locus of interaction from a physiological standpoint and the degree of interaction between these receptors in various behavioral situations, however, is a matter of dispute. Granit (1947), in species representing every vertebrate class recorded ganglion cell activity that indicated input from many types of cones, a finding that has been since augmented by subsequent observations (see Gouras, 1972). For example, spectrally opponent bipolar cells (Kaneko, 1973) and horizontal cells (Svaetchin & MacNichol, 1958) have been shown in the goldfich. In the turtle, cones seem to effect the sensitivity of neighboring cones either directly (Baylor, Fuortes, & O'Brian, 1971) or via horizontal cells (Fuortes, Schwartz, & Simon, 1973).

Human psychophysical data seem to suggest interaction or independence between different cone systems under some conditions but not other conditions. For example Boynton, Stiles, and Ikeda (1964) have shown that both inhibition as well as summation occur between the cone systems. The hetrochromatic threshold reduction factor (HTRF) is a measure of the extent to which the F_t threshold is lower when the spectral composition of the F_t is different from the spectral composition of the F_c then when both the F_t and F_c are spectrally the same (Boynton, Scheibner, Yates, & Rinalducci, 1965). The HTRF as a measure of the interaction between spectral mechanisms reflected significant departures from independence between the spectral mechanisms. Apparent motion has been demonstrated between stimuli that were selective for different chromatic mechanisms (Foster & Indris, 1974). That apparent motion was observed implies some form of convergence of information from the different spectral systems at a locus within the visual system. Guth (1971) has reported both subthreshold summation and inhibition between chromatic channels.

On the other hand, independence between chromatic mechanisms has been suggested in the metacontrast situation (Alpern & Rushton, 1965) and the sensitization paradigm (McKee & Westheimer, 1970). Since these are similar to the studies reported to demonstrate rod-cone independence, the methodological considerations will be discussed later (on pp. 29-31). Finally Stiles' (1959) work with the increment threshold procedure has generally been interpreted as demonstrating independence between the chromatically tuned mechanisms.

Rod-Cone Interaction

The question of rod-cone interactions in the retinae of higher mammels is much debated. At the anatomical level the work of Cajal and more recently that of Kolb (1969) and Boycott and Dowling (1969) are clear in showing that : (1) cone and rod bipolar cells may converge upon the same ganglion cell; (2) horizontal cells receive input from both cones and rods; (3) no direct conventional synaptic connections have been noted between rods and cones.

The anatomical and physiological literature do not always support each other. For example, it is clear that rod and cone signals may interact with each other in a reciprocally inhibitory manner. This was shown in the ganglion cell of the Macaque (Gouras & Link, 1966) which is congruent with the anatomical demonstration of rod and cone bipolar cells converging upon the same ganglion cell. However, two separate electrophysiological studies (Neimeyer & Gouras, 1973; Steinberg, 1966) have shown both rod and cone input into the same hroizontal cell of cat although anatomical data do not indicate such connections. Moreover, there are now some electrophysiological data suggesting direct rod input onto cones in the cat (Nelson, 1975).

Psychophysical data are also far from clear cut. There is some psychophysical evidence for independence between rod and cone systems in the human retina. The increment threshold data of Stiles have been interpreted as showing independence between the rod system (his π_0 mechanism) and the various cone mechanisms. Stiles' increment threshold procedure is discussed in detail below (pp 34-39). Independence of rod and cone systems has reportedly been demonstrated in two important studies, one a metacontrast study (Alpern, 1965) and the other a sensitization study (Westheimer, 1970).

In the metacontrast study of Alpern the F_t was presented 50 msec. before the contrast flash. It was found that if the F_t affected the rod system, the contrast flash affected the F_t threshold only to the extent that it also affected the rod system. If the F_t affected the long wavelength cone system, the contrast flash affected the F_t threshold only to the extent that it directly affected the long wavelength cone system. Therefore there was a functional independence between the rod and cone systems.

However, the interstimulus interval was kept constant at 50 msec. It is now known that the temporal interval between the stimuli is an important variable (Frumkes, Sekuler, Barris, Reiss, & Chalupa, 1973). It is well established that the rod system has a longer latency than does the long wavelength cone system. Gouras and Link (1966) showed electrophysiologically that the reciprocal occlusion of rod and cone signals at the ganglion cell was dependent upon the interval between the stimuli. Therefore, before the independence of rod and cone systems in the metacontrast situation can be considered conclusive, the temporal parameter must be explored.

Westheimer (1970) demonstrated independence between the rod system and the long wavelength cone system with a sensitization paradigm. His experiment involved three steps. Firstly, in the dark adapted eye Westheimer curves characteristic of the long wavelength cone system and the rod system were obtained. This was done with a long wavelength F_c and either a long wavelength F_t to test the long wavelength cone system or a middle wavelength F_t to test the rod system. As expected, the peak diameter obtained when testing the rod system was larger than the peak diameter obtained when testing the cone system. Secondly, Westheimer chose an annulus whose inner diameter was so large that it would affect the rod F_t and have little, if any, affect on the long wavelength cone F_t. Thirdly, Westheimer tested to see if the annulus affected the rod F_t as a consequence of stimulating the rod system or the cone system or both. Since the middle and long wavelength annuli had equal affects on the rod F_t when they were scotopically matched, Westheimer concluded: (1) only the rod F_t was affected by the annulus, (2) the affect on the rod F_t was mediated only by the rods directly stimulated by the annulus. Therefore, rods sensitize rods in the Westheimer situation and cones did not sensitize rods; interactions between the rod and cone systems did not occur.

There is a major problem with the Westheimer study. If a cone system could in fact sensitize a rod threshold, the experiment was designed so that it could not detect the sensitization. As Westheimer mentions, the annulus size chosen was beyond the range that cone system influences can express themselves. The inner diameter of the annulus was 64'. But in Westheimer's experiment the cone F_c of 40' and larger had no affect upon the F_t threshold. Therefore, this experiment was so designed that it was impossible for cone sensitization to express itself.

However, several other types of data suggest interactions of rod and cone systems.

Firstly, there are indications that rods do contribute to the perception of color (see Stabell & Stabell, 1973). Much of this work is in terms of large field colorimetry (Clarke, 1963; Nimeroff, 1964a, 1964b; Stiles & Burch, 1959; Stiles & Wyszecki, 1962). This work has led to the development of a large field tetrachromatic metric (Trezona, 1973, 1974) in an effort to quantify the chromatic effects of rods. Other experiments (McCann, 1972; McCann & Benton, 1969) related to the retinex theory of Land (1964) have shown that the rod system can mediate the perception of hue for all spectral as well as nonspectral colors (as the retinex theory predicts).

The second type of data comes from dark adaptation studies. There are indications that the threshold for color rises after the rod-cone break in the classical dark adaptation curve (Lie, 1963; Lythgoe, 1932; Spillman & Conlon, 1972). This observation has been attributed to either the rod system's supression of the activity of the cone systems or neuroretinal activity being determined by the rod system to the exclusion of the cone systems. Related studies have shown that the rate of dark adaptation as measured by the threshold of a short wavelength F_t is speeded in the presence of a long wavelength stimulus (Brown, Kuhns, & Adler, 1957; Brown, 1971). In a set of studies comparing the Purkinje shift in normals with that of a tritanope, it was concluded that the short wavelength cone system inhibits the rod system thereby determining the luminance at which the Purkinje shift occurs (Hough, 1968; Hough & Ruddock, 1969a, 1969b).

Another class of data suggesting rod-cone interactions comes from increment threshold determinations. Using a Stiles-Crawford effect to ensure the selectivity of the stimulus for either rods or cones, a cone system has been shown to raise the threshold of the rod system by more than a log unit (Makous & Boothe, 1974). With the Westheimer sensitization paradigm described above (pp 17) a stimulus affecting predominately the cone system has been shown to sensitize the rod system in situations where a stimulus affecting predominately rods had no affect upon the sensitivity of the rod system (Lennie & MacLeod, 1973). In a Crawford type masking experiment involving measurement of the F_t threshold, rod-cone masking has been indicated when the time delay between the stimuli was varied parametrically (Frumkes _et al_. 1973). If certain assumptions are made about the relative sensitivity of rod and cone systems to long and short wavelength stimuli, the activity of the long wavelength cone system has been shown to affect the threshold of the rod system detecting a 502nm F_t (Sternheim & Glass, 1975). Recently a technique developed from the HTRF (see pp 27) of Boynton et. al. (1965) to study changes in wavelength sensitivity at different retinal loci showed that the rod system elevated the threshold of the long wavelength cone system (Martinez & Sturr, 1975).

The above review suggests that the literature pertaining to interaction between different spectrally tuned mechanisms and between rods and cones specifically, is large and at least at the psychophysical level these data are still not conclusive.

One of the sources of the hypothesis of independence of rod and cone systems is Stiles' work in color vision. His system is influential and successful in explaining a large amount of data. Therefore his model shall be used as a basis to test the hypothesis that different spectrally tuned mechanisms (more specifically rods and the long wavelength cone system) are independent.

INCREMENT THRESHOLD AS A TECHNIQUE FOR STUDYING COLOR VISION

The increment threshold technique has been extended to the study of color vision most notably by

Stiles (Enoch, 1972; Marriott, 1962; Wyszecki & Stiles, 1967). Since the F_t and F_c are often of different wavelengths this procedure is often called the <u>two color method</u>.

Stiles explicitly made several assumptions about the mechanisms of color vision (Wyzecki & Stiles, 1967):

(a) a patch of retina contains several different spectrally tuned mechanisms. Suprathreshold stimulation of any one would result in a visual experience.

(b) each of these individual mechanisms is conceived to be an association of a selected proportion of receptors (rods and cones) that are functionally associated via the neural system.

(c) it is not assumed that a single spectrally tuned mechanism is composed of a single kind of receptor type containing a single photopigment, nor is it assumed that a single receptor belongs to a single mechanism.

(d) mechanisms function with sufficient independence so that the concept of independent mechanisms is meaningful.

(e) the F_t threshold illuminance observed in the increment threshold is determined by the most sensitive mechanism, regardless of the specific wavelength of either the F_t or F_c.

(f) each mechanism has its individual spectral sensitivity function. Thus for a specific mechanism a stimulus of one wavelength and luminance can be exactly matched by another stimulus of different wavelength and luminance. The luminance of these two wavelength stimuli would have to be adjusted so as to have equal affects on the mechanism as determined by its spectral sensitivity function.

Stiles generated increment threshold curves (tvi curves) with the F_c illuminance and wavelength and F_t wavelength as parameters. He concluded that all his data can be explained if the existence of five independent photopic mechanisms and one scotopic mechanism is postulated. The photopic mechanisms are thought to describe cone functioning and subserve color perception. the scotopic mechanism is thought to describe rod functioning.

Stiles' method of analysis will be illustrated in the simplest case. In the dark adapted retina a single mechanism is thought to be operative, the rod mechanism or π_0. In these experiments a 1°, 200 msec. F_t was imaged in the center of a 10° F_c centered 5° in the periphery. For a F_t and F_c both of the same wavelength, a tvi curve was obtained. For a large range of illuminances a single smooth curve with no breaks described the data. This is consistent with the assumption that a single mechanism was responsible for the data. A discontinuity was found in the function when the F_t exceeded a certain illuminance. This discontinuity was taken as evidence that another mechanism, one of the five photopic mechanisms, has become operative and taken over threshold detection.

When the F_c wavelength was changed but the F_t wavelength remained unchanged; and a second tvi curve generated; this second curve was identical to the first curve since at dim illuminances only a single mechanism, π_0, mediated threshold. However, this second curve was shifted laterally, parallel to the abscissa. The sensitivity of π_0 to the different F_c wavelengths determined the amount of lateral shift that occurred with changes in the F_c wavelength. In the case where a single scotopic mechanism mediated threshold a plot of the relative lateral displacements as a function of F_c wavelength yielded a scotopic spectral sensitivity function nearly identical to the CIE scotopic observer.

The same analysis applied to changes in the F_t wavelength. If a single mechanism mediated threshold and the F_c wavelength remained unchanged but the F_t wavelength was varied, then the obtained tvi curves all described a single mechanism and consequently had all the same shape. However, changes in the F_t wavelength shifted the curves up or down, parallel to the ordinate, by an amount indicative of the underlying π mechanism's sensitivity to the different wavelengths. (One important exception to this is data obtained with long wavelength F_t. This situation is considered in detail below.) A plot of the vertical displacements as a function of the wavelength yielded the scotopic spectral sensitivity function of the underlying π_0 mechanism.

This method of analysis follows directly from the Principle of Univariance (Naka & Rushton, 1966a, 1966b; Rushton, 1972) which states that for a single photopigment, light stimuli of different wavelengths differ only in the number of quanta that are absorbed by that pigment. The pigment responds to the number of quanta, not to the kind of quanta.

With foveal and/or photopic conditions of illumination, the results were considerably different. Only with a restricted range of F_t and F_c wavelengths and F_c illuminances did one mechanism describe the data. In fact, Stiles accounted for the photopic data in terms of five independent π mechanisms, not just one. Apart from some reservations about the number and relative independence of the mechanisms a large amount of experimental evidence seems to justify Stiles' psychophysical model of color vision.

In the present study of rod-cone interrelationships, the threshold of a brief, small F_t was determined as a function of the illuminance of a larger F_c with F_c size and the wavelength of both the F_c and F_t parameters. In essence, this study combines elements of the two color threshold technique of Stiles with the Westheimer paradigm. Because many of the recent studies cited as evidence of rod-cone independence have incorporated the theory of Stiles' it is from his theoretical approach that the rationale of the present study is developed.

RATIONALE OF THE STUDY

Cones Affect Rods

A particular wavelength F_t can be chosen so that its detection is primarily the work of the rod system. With this F_t a tvi curve can be generated with a large F_c of a wavelength that also stimulates primarily the rod system. (For example, if both stimuli are approximately 512nm there should be at least a 1.5 log unit range of illuminance in which light flashes are visible but below cone threshold.) A second tvi curve can be obtained using a F_c wavelength that affects both rods and cones. All the other parameters of the situation unchanged. If the F_t detection is dependent upon one mechanism and the individual mechanisms are independent, the the second tvi curve should be superposable upon the first tvi curve simply by shifting one of the tvi curves to the left of right. The spectral sensitivity of the rod system to the two different F_c wavelengths would determined the amount of displacement. This result, if obtained, would be a partial replication of some early work of Stiles.

The F_c can then be changed to a smaller diameter and in a similar manner two more tvi curves can be obtained. There are two possible outcomes:

(a) Rod-Cone independence - the tvi curves obtained with the smaller diameter F_c should also be superposable with themselves but not necessarily with the pair of tvi curves obtained with the larger Fc. However, the amount of lateral displacement necessary to superpose the first pair of tvi curves should be the same as the lateral displacement necessary to superpose the second pair of tvi curves. Thus the exact amount of displacement should again be predictable from the scotopic sensitivity curves. These results would be consistent with, but do not prove, the hypothesis of independence between rod and cone systems.

(b) Rod-Cone interaction - if for different size F_c

the curves obtained with different wavelengths are not superposable (that is, if they have different shapes, or the amount of relative displacement for superposition differs for different size F_c) then the hypothesis of independence of rod and cone systems is not tenable. In this case something other than stimulation by the F_c of the rod system must be affecting the sensitivity of the rod system. The threshold of the rod system as measured by the F_t is modulated by cone system as well as the rod system stimulated by the F_c.

Rods Affect Cones

Consider the following three factors: firstly, in the Stiles' increment threshold experiments the most sensitive spectrally tuned mechanism determines F_t threshold. Secondly, a variety of data indicate that for wavelengths greater than 625nm cone sensitivity is equal or greater than rod sensitivity. (This exact relationship is unimportant for the present study providing that the sensitivity of rods is not appreciably greater than cones.) Thirdly, if tvi curves are plotted on linear (non-logarithmic) coordinates, the slope for the rod system is much steeper than for the middle or long wavelength cone systems. For example, Stiles (1959) reports that with his specific parameters, at the range where Weber's law held true, the Weber constant for rods was 30 while for π_4 (middle wavelength cones) and π_5 (long wavelength cones) it was 1.9 and 1.8 respectively.

The foregoing considerations suggest that if a tvi curve is obtained with a large F_c and if both F_t and F_c wavelengths are greater than 625nm this curve would reflect primarily cone activity. When the F_c is of an extremely dim illuminance, F_c threshold may be determined by either the rod system, the cone system, or both systems. As the F_c illuminance increases, the sensitivity of both receptor systems will decrease, but the rod system will decrease faster than the cone system. (that is the rod Weber fraction is much greater). Since the most sensitive mechanism determines threshold, at illuminances at which the F_c raises threshold, the tvi curves will reflect the activity of the more sensitive cone system (probably the π_5 system of Stiles).

With the same long wavelength F_t a second tvi curve can be generated with a F_c wavelength such that it affects the rod system much more than it does the cone system. All other parameters will remain the same. Independence of spectrally tuned mechanisms would be indicated (but not proved) if the two tvi curves could be superposed by a lateral shift. The amount of this shift would be determined by the sensitivity of the appropriate chromatic mechanisms to the F_c wavelength (in this case presumably π_5).

The F_c can then be changed to a smaller diameter and in a similar manner two more tvi curves can be generated. There are again several possible outcomes:

(a) Rod-Cone independence - the tvi curves obtained with the smaller diameter F_c should again be superposable; but not necessarily with the pair of tvi curves obtained from the larger F_c. However, the amount of lateral displacement necessary to superpose the tvi curves obtained from the large F_c should be the same as the amount of displacement necessary to superpose the tvi curves obtained with the smaller F_c. This result if obtained would be consistent with the hypothesis of independence between the spectrally tuned mechanisms; this result would not prove the hypothesis.

(b) Rod-Cone interaction - if, however, for different size F_c the tvi curves obtained with different wavelength F_c are not superposable, then the hypothesis of independence is not tenable. This could be evidenced by a number of possible results: for example, the tvi curves could have different shapes, or the F_c affects the F_t 655nm threshold at illuminances below cone threshold, or the amount of lateral displacement for superposition of tvi curves differs for different diameter F_c.

CHAPTER 111

APPARATUS

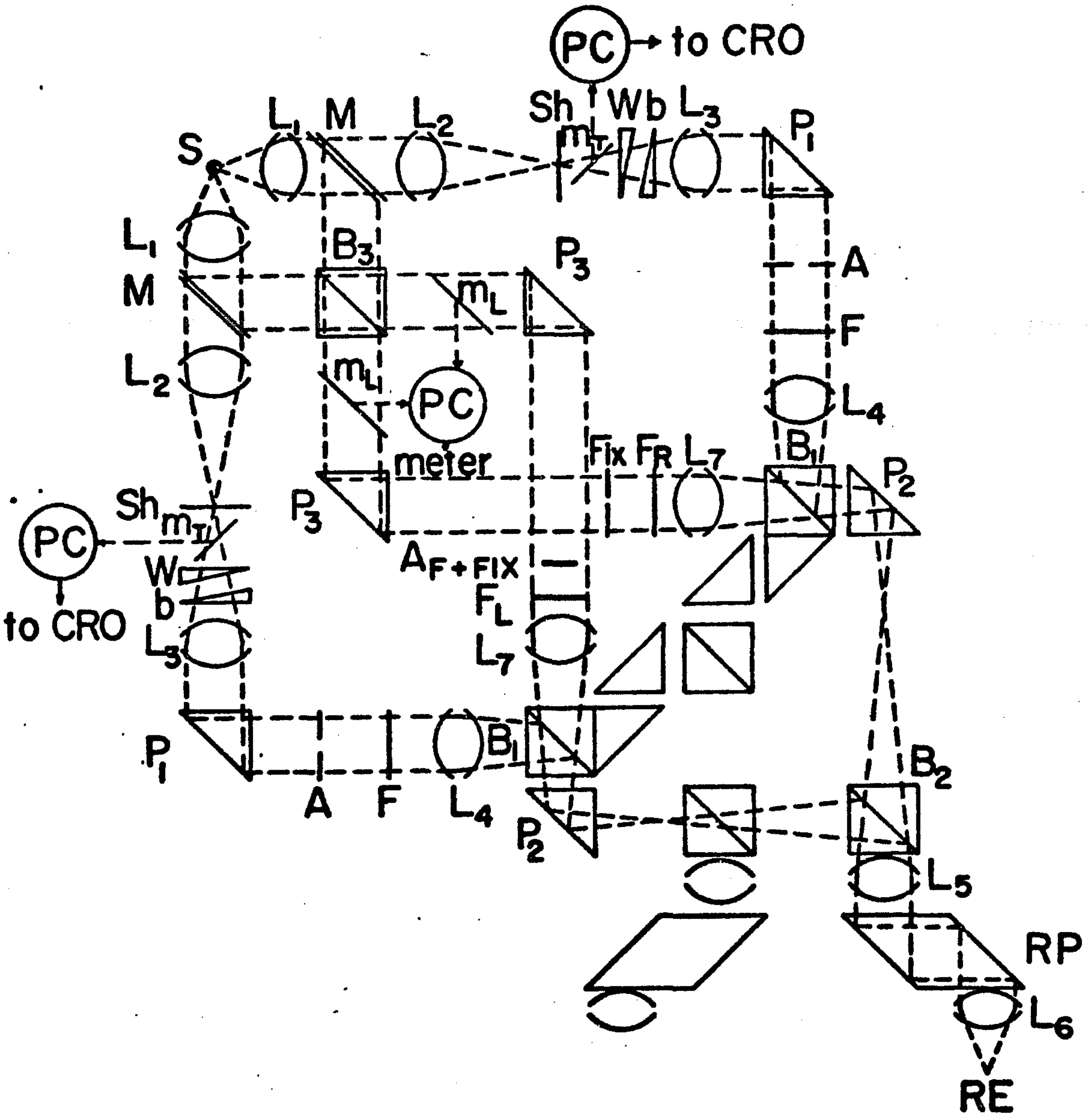
Visual stimuli were presented in Maxwellian view with a four channel optical stimulator described in detail below and depicted in Figure 2 (Frumkes & Sturr, 1968). Only the channels that were used are outlined with dotted lines in Figure 2.

OPTICAL SYSTEM

Conditioning and Test Channels

Light from source S was collimated into two beams by lenses, L_1. The horizontal beam formed the conditioning channel; the vertical beam formed the test channel. Lenses L_2 focused these beams so that the filament image was formed onto the shutter, Sh, for the test channel. (Since the F_c was a steady unpulsed stimulus, the shutter was removed from the horizontal channel.) A circular neutral density wedge, W, with a density range of 3.8 log units and a balancing wedge, b, were used for precise control of luminances. The beams were collimated by lenses, L_3 and deflected 90° by prism, P. The size and retinal position of the visual stimuli were controlled by various size apertures inserted onto a microscope stage that was positioned by micromanipulators located at A. Extra neutral density filters and chromatic filters were added as needed to either the

Figure 2. Schematic diagram of the optical system. See text for explanation.


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

conditioning or test channels by inserting them into filter racks, F. The beams were focused by lenses, L_4, passed through a beam splitter, B_1. and deflectted 90° by prism, P_2. The test and conditioning beams were recombined at beam splitter, B_2. The combined channel was recollimated by lens, L_5, and passed through rhomboid prism, RP, and focused at the nodal point of the observer's right eye (RE) by lenses, L_6.

Adapting and Fixation Channels

The light collimated by L_1 passed a 20% partially reflecting mirror, M_1. These two separate beams were combined by beamsplitter, B_3 and were deflected 90° by prism, P_3. At A_f & Fix, one channel passed through a photographic plate of an etched cross hair which presented a fixation target for photopic illuminances. Luminances were controlled by neutral density filters placed into filter rack, F_1. At Fix F_r, another channel passed through a photographic negative which contained four circular holes, the wavelength of which were controlled by a red (wratten 29) filter. This arrangement supplied the scotopic fixation target. The observer saw four dim red circules so positioned so as to form the corners of a 3° square. These adapting and fixation channels were refocused and joined the test and conditioning channels via beam splitter, B_1.

Fixation

The observer's head was positioned by a Bausch and Lomb chin and head rest which provided adjustment in three planes. Focus was obtained with a diopter adjustment at the final eye lens. When the observer was correctly positioned, the filament image was formed at the nodal point of the eye. Thus the observer saw the final eye lens filled with light in Maxwellian view. The filament image at the final eye lens was 0.5 X 2.0 mm, and therefore was smaller than the iris of the observer at any time during the present experiment, since this experiment was run under dark adapted conditions.

Size and Retinal Position of the Stimulus

The size of the various apertures was determined by a projection technique. (For example, an aperture of 1 mm placed at A was determined to project a retinal image of 1.8°.) With all apertures removed from the optical system, any of the channels provided a 40° field as determined by projection. With this knowledge, retinal position was calibrated on the micromanipulator. By changing aperture size, the F_t and F_c could be altered in size. By changing aperture position by means of the micromanipulator, retinal position of the stimuli was changed with respect to the center of the 40° field.

Duration Control

The F_c and the fixation and adaptation fields were continually exposed. The duration of the F_t was controlled by a shutter (Sh in Figure 2) which was driven by an electromagnet modified from use in a Grass polygraph. This was powered by pulses obtained from a Tektronix 161 pulse generator and amplified by specially constructed power amplifiers.

A Tektronix 162 waveform generator was used to determine recycling rate. This triggered both a Tektronix 360 oscilloscope and the pulse generator controlling the shutter.

Light passing through the open shutter in the F_t channel was partially reflected by the mirror, m_t (Figure 2) into a photocell, PC, whose output was read onto the 360 oscilloscope. Thus, F_t duration and rise and fall time were constantly monitored. Both rise and fall times were approximately 1 msec.

LIGHT SOURCE

A tungsten filament lamp (G. E. CPR Projection Lamp) was the common source for all four channels of the optical system. This bulb was supplied with current from a 6 volt power supply (Electro Products Model H.). The current operating the power supply was controlled by a rheostat and measured by an ammeter. In general, the bulb was underpowered (at approximately 16.5 amps) below the rated value of 18 amps in order to increase the life of the source. Most of the present study was performed with one bulb.

Light from a partially deflecting mirror ($\underline{m}_1$) in Figure 2 was deflected to a photocell in order to monitor the source of illumination. The output of the photocell was continuously monitored by a sensitive milliammeter. During all phases of the study the experimenter would adjust the current to the power supply as necessary in order to keep the photocell output constant.

Stimulus Wavelength and Illumination

Luminance of the test and conditioning channels was controlled by circular neutral density wedges ($\underline{W}$ in Figure 2) of 4 log unit range. The position of these wedges was governed by a dial (designed to be used in a Beckman spectrophotometer) and by a series of gears. The wedge was reliably moved through 360° by 40 turns of the dial. Measuring with a photovolt photometer, it was determined that one turn of the dial changed stimulus luminance 0.1 log units with an error of less than 0.01 units. Luminance of the F_t and F_c could be further reduced by inserting neutral density filters (wratten 96) into the two main beams (at $\underline{F}$ in Figure 2). The wavelengths of the F_t and F_c were determined by inserting Baird Atomic interference filters (half bandwidth of 6 nm) at F. Luminance of the fixation and adapting channels was determined with neutral density filters inserted in these channels at F_1 (Figure 2).

Calibration of Achromatic Stimulus Illumination

Absolute illuminance calibration of the two main channels was done in two different manners. In the first technique, a monocular bipartite field was set up so that a diffuse field of known illuminance (30.00 mL) was presented to half of the bipartite field, the other half of the field was of unknown illuminance from the optical system to be calibrated (in Maxwellian view). The observer adjusted the wedge position controlling the F_t or F_c channel until it matched the diffuse field The procedure was carried out with several different observers for both channels. It was determined that maximal illuminance in the channel providing the F_t was approximately 3.8 log mL. The maximal illuminance in the channel providing the F_c was approximately 4.1 log mL. Illuminance of the adapting and fixation fields was determined by brightness matches between these channels and the test channel.

In the second procedure illuminance of the fields was determined according to the procedure described by Westheimer (1966). A diffusing surface was placed

1 mm beyond the filament image. Illuminance of the surface was determined in mL. Retinal illuminance in trolands, I, was determined by formula (1), where $\bar{\bar{B}}$ is mL, X is distance of the surface from the filament

$$I = 10^7 (\bar{\bar{B}}) x^2/r \qquad (1)$$

image, and r is the reflectance of the surface.

If all light from a Maxwellian view stimulator passed through the pupil, a stimulus of 10 trolands should equal 1 mL. According to our calibrations, 7.45 trolands was equivalent to 1 mL. This error was consistently obtained, but it represented a reliable error of approximately 0.13 log units.

Spectral Calibration of Stimulus Illuminance

The calibration of the test and conditioning channels when the chromatic interference filters were employed was obtained in three different ways: scotopic trolands (units which presumably reflect rod vision), photopic trolands (units which presumably reflect cone vision) and radiometric units.

(a) Photopic trolands - One of the main channels (test or conditioning) presented a 1° field of 1.78 log photopic trolands white light. The other channel presented the chromatic light, also a 1° field vertically adjacent to the white light. Two observers then adjusted the brightness of the colored light to match the brightness of the white light. Although brightness is not the best way to equate illuminance, photopic trolands have this meaning throughout this report.

(b) Scotopic trolands - A similar procedure was used to determine the illumination of the colored stimuli in units that are considered to reflect primarily rod activity. This time the two 1° stimuli were placed 7° from fixation, vertically adjacent to one another. Two dark adapted observers then adjusted the chromatic light to match the brightness of the white light of 1.35 log scotopic trolands. In the present report, scotopic trolands are based on the calibrations using this procedure.

(c) Relative irradiance of the chromatic channels - With the conditioning field channel set at maximal illumination and the appropriate chromatic filter inserted, the filament image of the optical stimulator was focused onto the head of an EG & G Spectral radiometer (580-12). The output of the channel with each filter successively in place was determined. Since the sensitivity of the spectral radiometer to different wavelengths is known, the relative power (Irradiance) of the different chromatic stimuli was determined. The relative power was converted to relative quanta with formula (2) in which

Q is relative quanta, E_λ is relative power, λ is the

$$Q = E_\lambda\ (\lambda/1243) \qquad (2)$$

peak wavelength of the stimulus, and 1243 is a constant.

Table 1 is a comparison of the three different calibrations of the spectral stimuli.

TABLE 1

	Log Photopic trolands	Log Scotopic trolands	Log Relative Power/ unit area/unit time	Log Relative Quanta
		CONDITIONING FIELD		
512nm	2.00	2.37	0.00	0.00
680nm	2.00	0.28	1.05	1.53
		TEST FIELD		
512nm	2.00	2.52	NOT CALIBRATED	
655nm	2.00	0.64		

CHAPTER 1V

PROCEDURE

OBSERVERS

Three observers were used in this study: CLS (21 year old female), TEF (33 year old male) and LAT (29 year old male). TEF had 20/20 vision; CLS wore contact lenses to correct myopia, while the diopter adjustment in the final eye lens was used to corredt the myopia of LAT.

All phases of the present study were performed completely on observers LAT and CLS. Subsequently, the major aspects of this study were replicated with observer TEF.

STIMULUS PARAMETERS

Fixation and Adapting Fields

The F_c and F_t were presented concentrically against a continuously exposed adapting field which consisted of a tungsten filament lamp white light (color temperature of approximately 2400° K), 40° in diameter and of $\bar{4}.6$ log scotopic tds. illuminance. It was previously established that this adapting field only slightly elevated F_t threshold, however, it reduced threshold variability and stabilized adaptation. A dim red (wratten 29 filter) tarfet (4 dots, each 30' in diameter, spaced as a 3° square) placed in the center of the field served as a fixation target. It is unlikely that the threshold of the F_t imaged 7° temporally was significantly affected by the fixation targets, the nearest of which was more than 5.7° distant.

Test Stimulus

In the increment threshold studies of Stiles, the F_t had a 1° diameter and a 100 msec duration. In the studies of Westheimer,the F_t was generally much shorter and smaller (1' to 5' in diameter and of 1 msec duration). Ideally, in the present study, F_t would have been of a size and duration similar to Westheimer's. But, in fact, it was 25 msec in duration and 15' in diameter. These values were chosen since preliminary data showed that: (1) the qualitative nature of the Westheimer effect was obtained with F_t of these dimentions, and (2) the additional dynamic range obtained with these larger and longer stimuli compensated for the limited energy of the luminance source of the optical stimulator.

The F_t was presented in the 7° temporal visual field (nasal retina). All F_c were concentric with the F_t.

For the most part, the F_t wavelength was determined with Baird-Atomic interference filters (half bandwidth of approximately 6 nm). Filter transmission peaked either at 512nm or 655nm. Providing that the 512nm F_t was at an illuminance no greater than 1.0 log units above its threshold when no F_c was present it probably stimulated primarily rods. Several types of evidence support this assumption

(1) When the F_t was presented 7° in the periphery a long term dark adaptation curve indicated both rod and cone branches (see Figure 3). The rod plateau was over 1 log unit below the cone plateau.

(2) Threshold determinations of the 512nm F_t in the rod free fovea were over one log unit higher than threshold determinations in the peripheral retina.

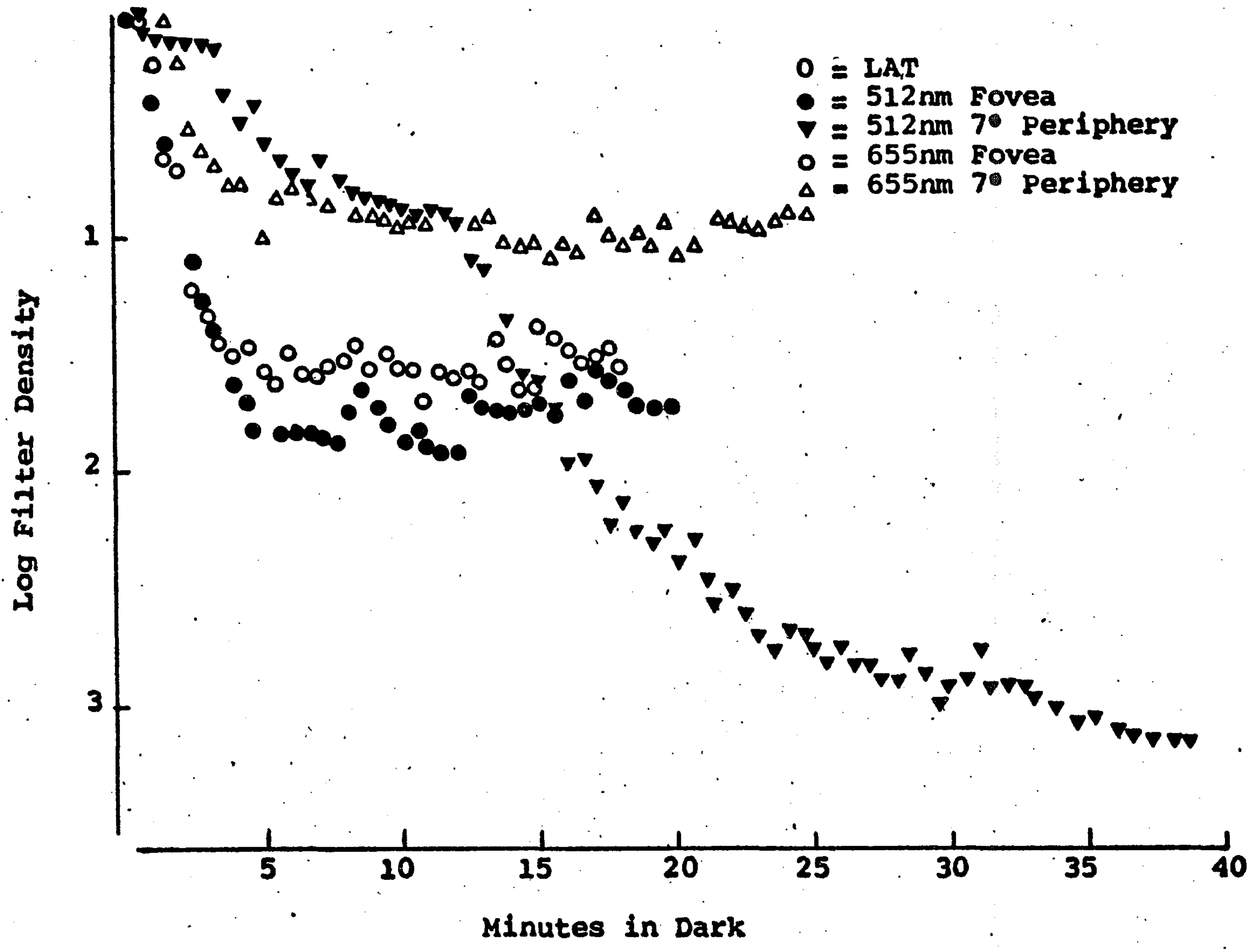
(3) These stimuli always appeared colorless

(4) With stimuli similar to the 512nm F_t used in the present study, other workers (Makous & Boothe, 1974) have failed to observe a Stiles-Crawford effect, a cone specific phenomena.

(5) Using stimuli identical to those used in the present study, the action spectrum of an 8° diameter F_c necessary to raise the 512nm F_t threshold 0.5 log units above its detection threshold was found (Temme & Frumkes, 1975). The action spectrum obtained described the action spectrum of the scotopic CIE standard observer (Figure 4).

When no F_c was present the 655nm F_t probably

Figure 3. Observer LAT. Dark adaptation function of a 25 msec F_t of either 512nm (closed symbols) or 655nm (open symbols) in wavelength. Thresholds were determined either in the fovea (circles) or 7° in the temporal visual field (triangles).


O = LAT
● = 512nm Fovea
▼ = 512nm 7° Periphery
o = 655nm Fovea
△ = 655nm 7° Periphery
Log Filter Density
1
2
3
5
10
15
20
25
30
35
40
Minutes in Dark

influenced cones to an equal or greater extent than rods as indicated by the following evidence:

(1) Long term dark adaptation curves obtained with the 655nm F_t presented 7° in the peripheral retina showed no evidence of a rod-cone break. Adaptation was complete within 10 minutes (Figure 3).

(2) Thresholds for the 655nm F_t were lower in the fovea than in the periphery (Figure 3).

(3) These stimuli always appeared red.

(4) With long wavelength stimuli similar to the 655nm F_t of the present experiment, other workers (Westheimer, 1970; Makous & Boothe, 1974) observed a Stiles-Crawford effect, a cone specific phenomenon.

(5) Using stimuli identical to those used in the present study, the action spectrum of an 8° diameter F_c necessary to raise the threshold of the 655nm F_t 0.5 log units was determined (Temme & Frumkes, 1975). The action spectrum obtained described the action spectrum of Stiles π_5 mechanism, the long wavelength chromatic mechanism (Figure 4).

Thus in all tvi functions the 655nm F_t threshold was probably determined by the cone system. This conclusion directly follows the rationale presented in the introduction (pp 39-43).

Conditioning Stimulus

The F_c was continuously exposed and was either 512nm or 680nm in wavelength. At any level of illumination the 512nm F_t probably affected the rod system to a much greater extent than the cone systems (Wald, 1949), while the 680nm F_c probably affected the cone systems to an equal or greater extent than the rod system.

A previous study suggested the size of the F_c to be employed in the present study (Temme & Frumkes, 1975). In brief, the F_t threshold was determined as a function of the diameter of the equal luminance F_c. The luminance was chosen so that 2° F_c were approximately 1 log unit above their own threshold. When both F_t and F_c were approximately 660nm in wavelength the increment threshold was greatest for a 40' F_c. When both stimuli were approximately 500nm in wavelength the F_t threshold was maximal with a 2° F_c. On the basis of these data the F_c diameters chosen for the present study were:

8° - There are no data in the literature to indicate that an increase in the diameter of the F_c of constant illuminance beyond 6° has an effect on the F_t threshold. Thus, the 8° F_c served as an approximation of an 'infinitely' large field and an approximation to the stimulus conditions of Stiles.

<u>2</u>° - The 500nm F_t threshold was approximately maximally elevated with the 2° F_c whereas the 655nm F_t threshold was only slightly elevated above the 8° F_c threshold level.

<u>1</u>° - With the 500nm F_t a F_c of 1° produced threshold elevation intermediate between that produced with an 18' and a 2° F_c. Thus the 1° F_c diameter was used only with the 512nm F_t.

<u>40</u>' - With a 655nm F_t a F_c of approximately 40' diameter produced maximal F_t threshold elevation whereas the 500nm F_t threshold was lower than the threshold obtained with the 1° F_c. The 40' F_c was used with both 655nm and 512nm F_t.

<u>18</u>' - With the 655nm F_t a F_c of approximately 18' diameter produced no effect upon the F_t threshold. The 18' F_c diameter was used with the 655nm F_t only and not with the 512nm F_t.

The stimulus conditions used in the present study are summarized in Table 11.

It should be noted that with the F_t of 15' in diameter, 25 msec duration and with the F_c range of illuminance available, the tvi curves obtained may not be similar to the classical tvi curve shown in Figure 1 which used a F_t of 9° in diameter, 200 msec duration and a range of F_c illuminances of approximately 10 log units.

Figure 4. Observer TEF. Spectral sensitivity of a F_c necessary to raise either a 655nm (open symbols) or a 512nm (closed symbols) F_t 0.5 log units above its threshold measured with no F_c present.

The F_c diameter was either 8° (circles) or 40' (triangles) with the 655nm F_t; with the 512nm F_t the F_c was either 8° (circles) or 1° (triangles). The F_t was presented 7° in the temporal visual field; the F_c was concentric with the F_t. The displayed functions (solid lines) are the CIE scotopic spectral sensitivity function and the π_5 spectral sensitivity function as defined by Stiles (1959).

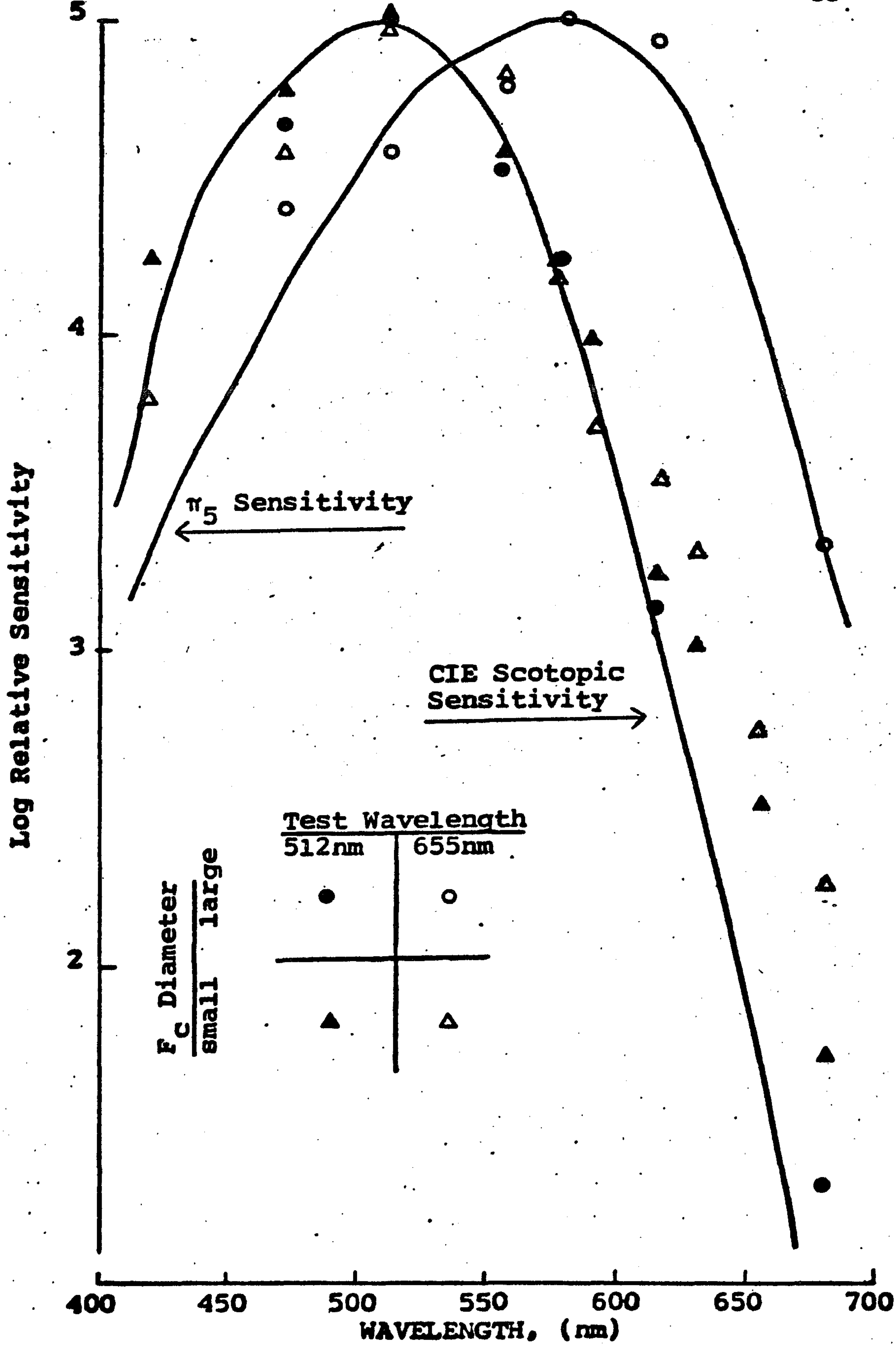

5
4
3
2
Log Relative Sensitivity
π5 Sensitivity
CIE Scotopic Sensitivity
Test Wavelength
512nm
655nm
F_C Diameter
large
small
400
450
500
550
600
650
700
WAVELENGTH, (nm)

TABLE 2

STIMULUS PARAMETERS

Retinal Position

7° temporal visual field on the horizontal meridian

Test Flash

duration	25 msec.
size	15'
wavelength	655nm or 512nm
recycling rate	4 sec.

Conditioning Field

duration	continuous
wavelength	680nm or 512nm
size	a) with the 512nm F_t: 8°, 2°, 1°, 40'
	b) with the 655nm F_t: 8°, 2°, 40', 18'

Adapting Field

duration	continuous
size	40°
wavelength	white light (color temperature 2400° K)
illuminance	4.6 log scotopic trolands

Fixation Target

duration	continuous
size	4 30' circles outlining a 3° square
wavelength	wratten 29 filter

Experimental Procedure

The main purpose of the present study was to compare tvi curves obtained with one particular wavelength F_t and one particular F_c diameter of two different wavelengths. Since some of the data were variable and some of the effects were small, two data collection procedures were used.

(a) Procedure one - The particular wavelength F_t and the size and wavelength of the F_c to be used in a given experimental session were determined according to a prearranged randomized schedule. The observer first dark adapted for 25 minutes, and for two minutes to the adaptation and fixation fields. The F_t was then presented with no F_c present once every four seconds. The observer varied the F_t illuminance by adjusting the setting of the neutral density wedge for threshold. Three F_t thresholds were determined in succession with the experimenter varying the wedge setting nonsystematically between each threshold determination. The F_c was then introduced with no F_t present, and F_c detection threshold was then determined five times in succession in a similar manner. After these control data were obtained, increment thresholds were determined (F_t threshold superimposed upon a particular illuminance F_c). Thus the method of adjustment was used throughout this study with F_t always recycled once every four seconds.

The order of presentation of F_c illuminances within a session was in accordance with a prearranged schedule. This schedule was semirandom in that (1) thresholds with the same F_c illuminance were not determined more than three times in succession, and (2) from trial to trial F_c illuminance was not decreased more than one log unit. Within an experimental session, increment thresholds were obtained with six different F_c illuminances. At each illuminance level four different threshold determinations were made. Finally, the data reported in the results were obtained in at least two different experimental sessions.

(b) Procedure two - Increment threshold curves obtained with the 8° F_c of both wavelengths (according to the above procedure) were plotted. For a particular wavelength F_t, the amount of lateral shift of the two curves necessary for superposition was obtained. Thus, a particular illuminance of the 512nm F_c and the 680nm F_c was found that would have equal effects upon the one wavelength F_t. According to the rationale of the study, the crucial question is whether this equivalence applies to all F_c diameters.

The first procedure outlined above was now modified in two notable ways. First, within a single experimental session data were collected with two F_c wavelengths. In the first half of an experimental session, data were collected with a particular F_t and a particular size and wavelength F_c of three illuminances. In the second half of the experimental session, data were collected with the other wavelength F_c also at three different illuminance. The three illuminances used with the two different wavelength F_c were always such that if they were of the 8° diameter, they would have equal effects on the F_t threshold. In the next experimental session the same experimental conditions were run, only backwards. Thus the two sessions were counterbalanced.

Little data were collected with this second procedure. This procedure served only to verify the results obtained with the first procedure. In fact, the two procedures yielded data that were in substantial agreement.

DATA TREATMENT

In order to compare the influence upon the tvi curves of two F_c of the same diameter but different wavelengths, it is necessary to equate the different wavelengths in some reasonable fashion. For reasons developed in the Introduction the method of Stiles served as a basis for the analysis used in the present study.

This method suggests that the operation of one spectral mechanism is reflected in some range of a tvi function obtained with a single F_t wavelength. Therefore, some lateral shift of two tvi functions should provide superposition of the functions, if, in fact, only one type of spectral mechanism is determining threshold. Moreover, the displacement obtained with any diameter F_c should yield superposition of the tvi functions obtained with other sized F_c if the different spectral mechanisms are independent of each other.

To illustrate this technique, Figure 5 shows the thresholds for the 512nm F_t (on the ordinate in log scotopic tds.) as a function of the scotopic illuminance of an 8° F_c of either 512nm (closed circles) or 680nm (open circles) for observer LAT. The tvi curves obtained with the different wavelength F_c do have a similar shape. However, the function obtained with the 680nm F_c lie to the right of the function obtained with the 512nm F_c.

The amount of lateral displacement necessary to superpose the two tvi functions was determined by two different procedures.

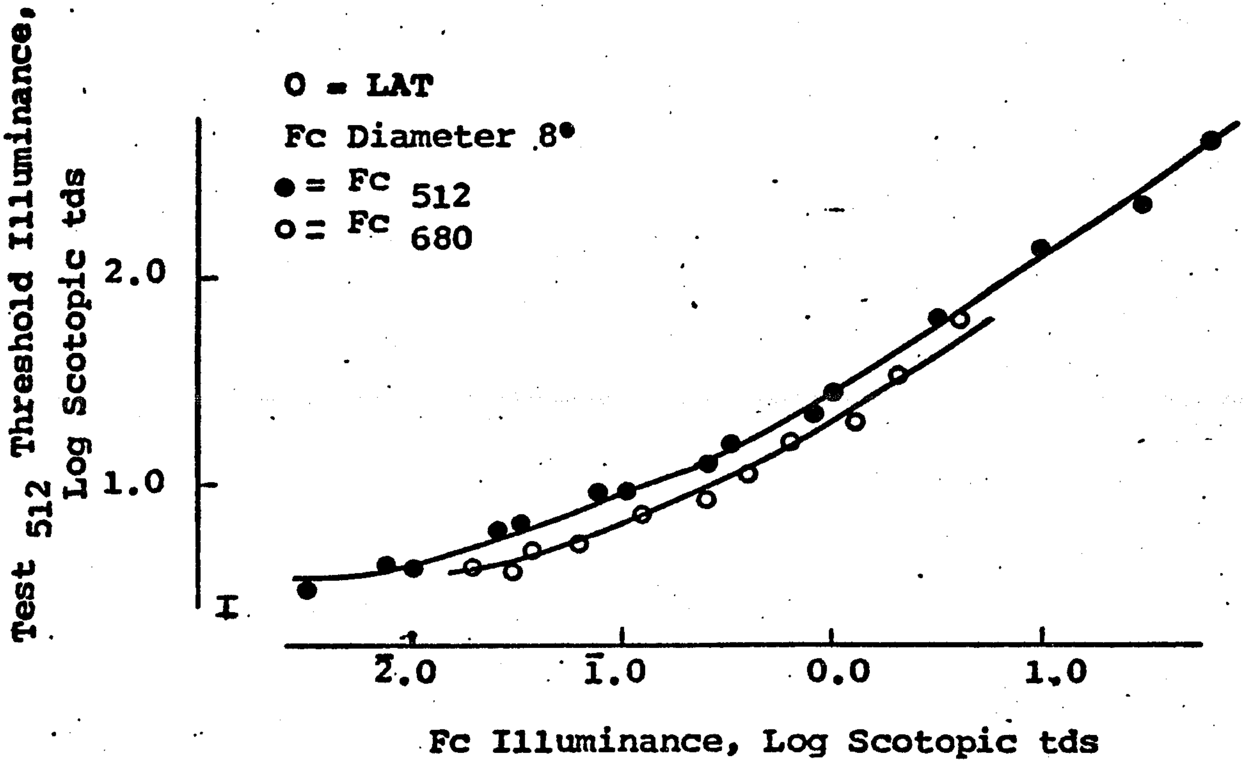
(a) A linear least squares regression procedure (Hays, 1963) was used to fit a function to the portion of the tvi function that appeared linear on log-log co-ordinates. This was done for data obtained with both the 512nm and 680nm F_c. Since the slopes of the functions fitted to the data with the two F_c were in substantial agreement (within 0.04) the difference in the y-intercepts of the tvi functions directly suggested the amount of lateral shift necessary to superpose the functions.

(b) The threshold of the 512nm F_t was plotted as a function of the illuminance of the 8° 512nm F_c on a piece of transparent graph paper. Similarly, the threshold of the 512nm F_t was plotted as a function of the illuminance of the 8° 680nm F_c on another piece of transparent paper. Four different individuals were instructed to superpose the two tvi curves by shifting the functions along the abscissae in respect to one another. The arithmetic mean of the displacements of the four different individuals was computed.

The two procedures yielded essentially the same displacement (within 0.15 log units). All obtained tvi functions were plotted in accordance with the second procedure since first, it made use of the linear and non-linear portions of the data, and second, for observers LAT and CLS exactly the same lateral displacement was obtained.

According to the rationale developed in the Literature Review, the displacement that yielded superposition of the two tvi functions obtained with either wavelength F_c of 8° should also yield superposition of the two tvi curves obtained with the same two wavelengths but other diameter F_c if the mechanisms are independent. Thus, the displacements obtained by this procedure to superpose the 8° functions are used in plotting the data obtained with the 512nm F_t for all three observers (in Figures 6 through 10). When a 655nm F_t was used, the tvi functions obtained with both wavelength 8° F_c were superposed according to the same procedures. This displacement was used in plotting the data presented in Figures 11 through 16.

Figure 5. Observer LAT. Increment threshold illuminance, in log scotopic tds. as a function of the illuminance, also in log scotopic tds., of an 8° 512nm (closed circles) or 680nm (open circles) F_c.


O = LAT
Fc Diameter 8°
● = Fc_{512}
○ = Fc_{680}
Test 512 Threshold Illuminance, Log Scotopic tds
2.0
1.0
$\bar{2}$.0
$\bar{1}$.0
0.0
1.0
Fc Illuminance, Log Scotopic tds

CHAPTER V

RESULTS

A. Influence of F_c size and wavelength upon tvi curves

1. 512nm F_t

Figures 6 through 10 show the increment thresholds of the 512nm F_t in log scotopic tds. as a function of the illuminance, in log scotopic tds. of either a 680nm F_c (open circles and upper abscissae) or 512nm F_c (closed circles and lower abscissae) for all three observers. In the upper portions of Figures 6 (observer CLS) and 7 (observer LAT) are the data generated with an F_c of 8° in diameter. Following the procedures outlined in the section on Data Treatment (pp 69-73), the 512nm and 680nm functions were laterally shifted 0.4 log units so as to superpose them at the lower levels of illuminance. This same lateral displacement of 0.4 log units was used to plot Figures 8 and 9 for all F_c diameters used.

Inspection of the upper portions of Figure 6 (observer CLS) showed that as the illuminance of the 8° diameter F_c increased, F_t threshold increased monotonically. The functions obtained with either wavelength F_c were virtually identical at most levels of illuminance.

The lower portions of Figure 6 showed tvi curves obtained with an F_c of 2° in diameter. The 2° diameter F_c had a different effect upon the F_t threshold than the 8°

Figure 6. Observer CLS. Increment thresholds of the 512nm F_t (on the ordinates in log scotopic tds.) as a function of the illuminance of an 8° (upper co-ordinates) or 2° (lower co-ordinates) F_c. Open circles are data obtained with the 680nm F_c and correspond to the upper abscissae (in log scotopic tds.); closed circles are data obtained with the 512nm F_c and correspond to the lower abscissae (in log scotopic tds.). Curves were displaced laterally 0.4 log units for superposition of the 8° functions. The bracket on the extreme left of the abscissae shows 95% confidence interval for the F_t threshold obtained with no F_c present.

Detection thresholds of the F_c are: 8° 512nm = $\bar{3}.50$ log scotopic tds.; 2° 512nm = $\bar{3}.70$ log scotopic tds.; 8° 680nm = $\bar{3}.86$ log scotopic tds.; 2° 680nm = $\bar{2}.06$ log scotopic tds.

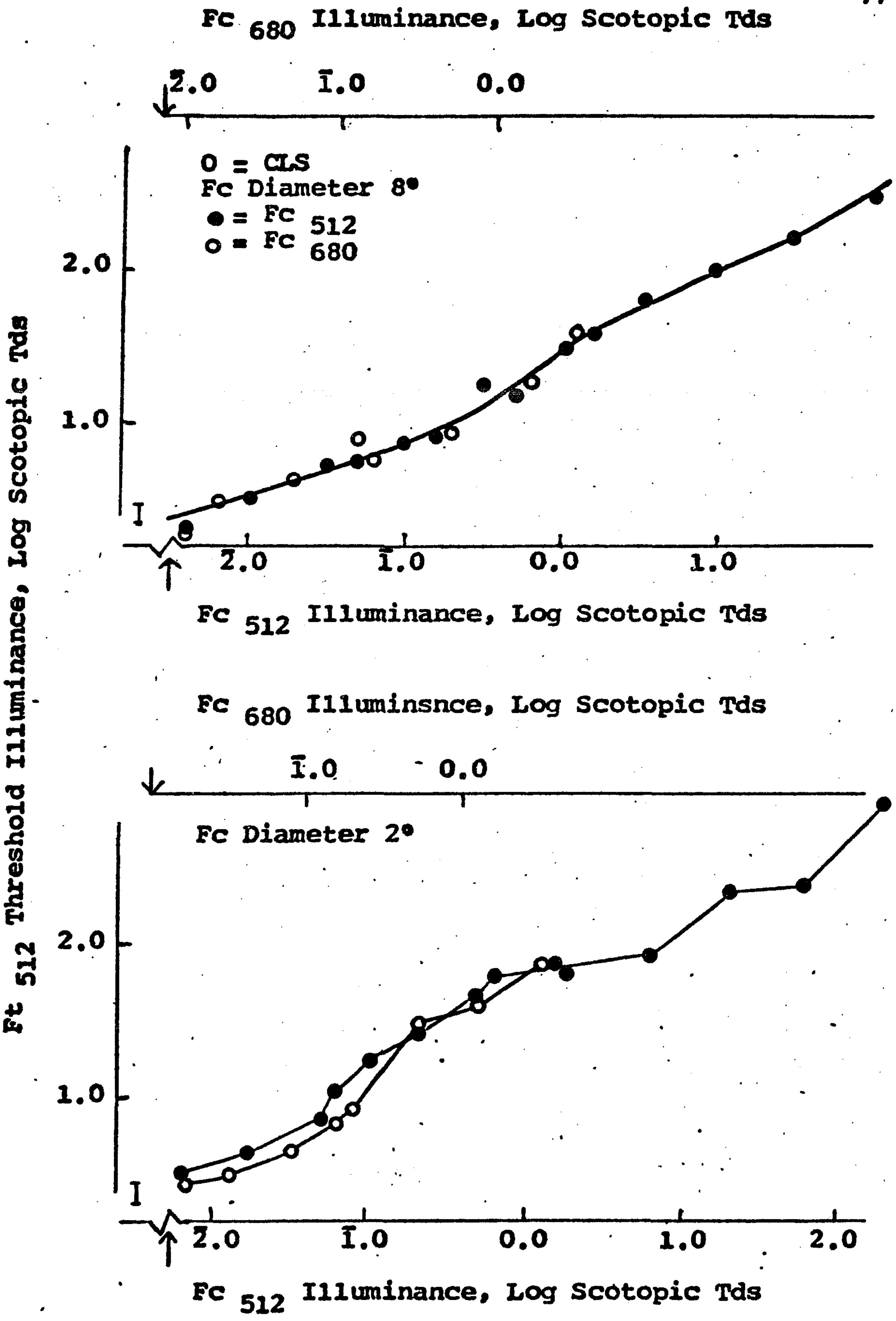
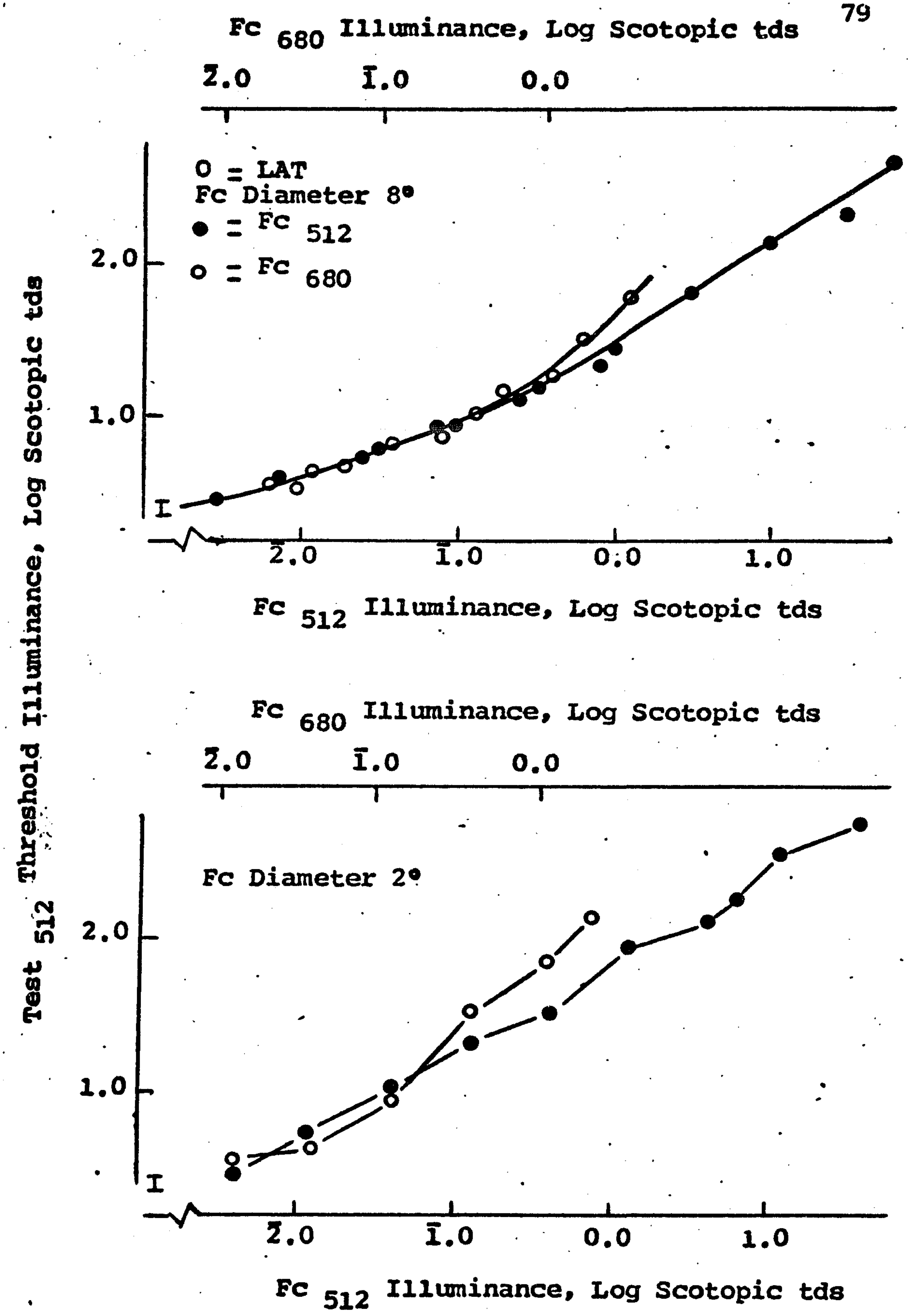

Fc 680 Illuminance, Log Scotopic Tds
2̄.0
1̄.0
0.0
O = CLS
Fc Diameter 8°
● = Fc 512
o = Fc 680
2.0
1.0
I
2̄.0
1̄.0
0.0
1.0
Fc 512 Illuminance, Log Scotopic Tds
Ft 512 Threshold Illuminance, Log Scotopic Tds
Fc 680 Illuminsnce, Log Scotopic Tds
1̄.0
0.0
Fc Diameter 2°
2.0
1.0
I
2̄.0
1̄.0
0.0
1.0
2.0
Fc 512 Illuminance, Log Scotopic Tds

Figure 7. Observer LAT. Increment thresholds of the 512nm F_t as a function of the illuminance of the 8° or 2° F_c. See legend in Figure 6.

Detection thresholds of the F_c are: 8° 512nm = $\bar{3}.68$ log scotopic tds.; 2° 512nm = $\bar{3}.66$ log scotopic tds.; 8° 680nm = $\bar{2}.03$ log scotopic tds.; 2° 680nm = $\bar{2}.30$ log scotopic tds.


Fc 680 Illuminance, Log Scotopic tds
2̄.0
1̄.0
0.0
O = LAT
Fc Diameter 8°
● = Fc 512
○ = Fc 680
2.0
1.0
I
2̄.0
1̄.0
0.0
1.0
Fc 512 Illuminance, Log Scotopic tds
Fc 680 Illuminance, Log Scotopic tds
2̄.0
1̄.0
0.0
Fc Diameter 2°
2.0
1.0
I
2̄.0
1̄.0
0.0
1.0
Fc 512 Illuminance, Log Scotopic tds
Test 512 Threshold Illuminance, Log Scotopic tds

F_c in that the slope of the 2° tvi function appeared steeper. None the less, the 2° 512nm and 680nm tvi curves still superposed. These results are in agreement with the predicted results if independence between rod and cone systems is assumed.

With observer LAT similar trends were seen in that tvi curves obtained with 8° F_c were largely superposed at the lower levels of illumination. With the 2° F_c, however, at illuminance levels greater than $\bar{1}.0$ log scotopic tds. the 680nm F_c seemed to affect the F_t threshold more than would be predicted from the 8° data. This lack of superposition can be more clearly seen with tvi curves obtained with smaller diameter F_c.

Figures 8 and 9 show tvi curves obtained from the same observers when F_c diameter was either 1° (upper portions of the figures) or 40' (lower portions of the figures). The lateral displacement that superposed the 8° tvi curves of different F_c wavelengths was used to displace these data. With these smaller diameter F_c and with this displacement of 0.4 log units, the 680nm F_c consistently produced a greater elevation of the F_t threshold than did the 512nm F_c. According to the rationale of this study, this lack of superposition was inconsistent with the notion of independence of spectrally tuned mechanisms. Moreover, the 680nm F_c always appeared red in

Figure 8. Observer CLS. Increment thresholds of the 512nm F_t as a function of the illuminance of a 1° (upper co-ordinates) or 40' (lower co-ordinates) F_c. See legend, Figure 6.

Detection thresholds of the F_c are: 1° 512nm = $\bar{2}.10$ log scotopic tds.; 40' 512nm = $\bar{2}.38$ log scotopic tds.; 1° 680nm = $\bar{2}.31$ log scotopic tds.; 40' 680nm = $\bar{2}.64$ log scotopic tds.

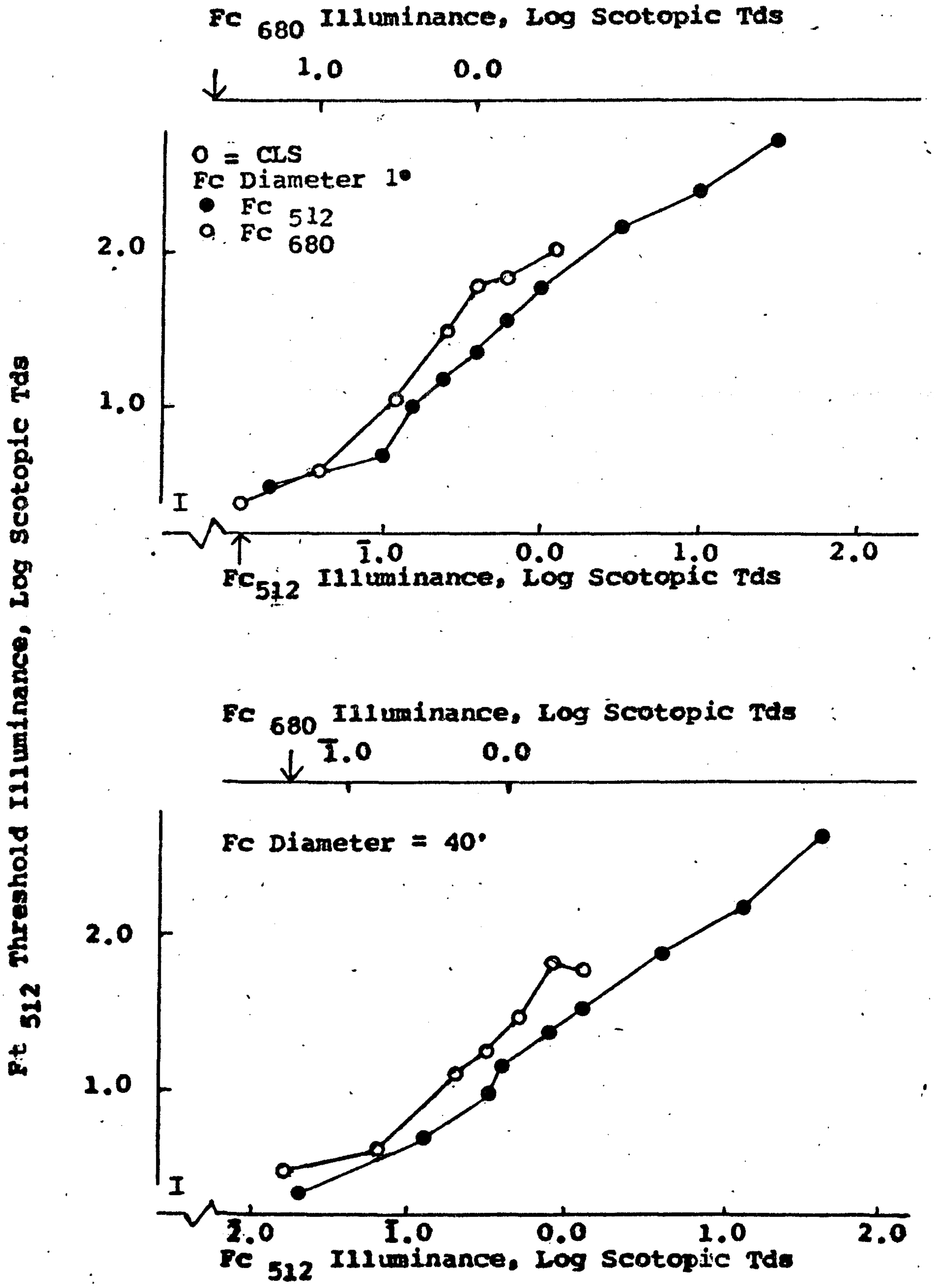
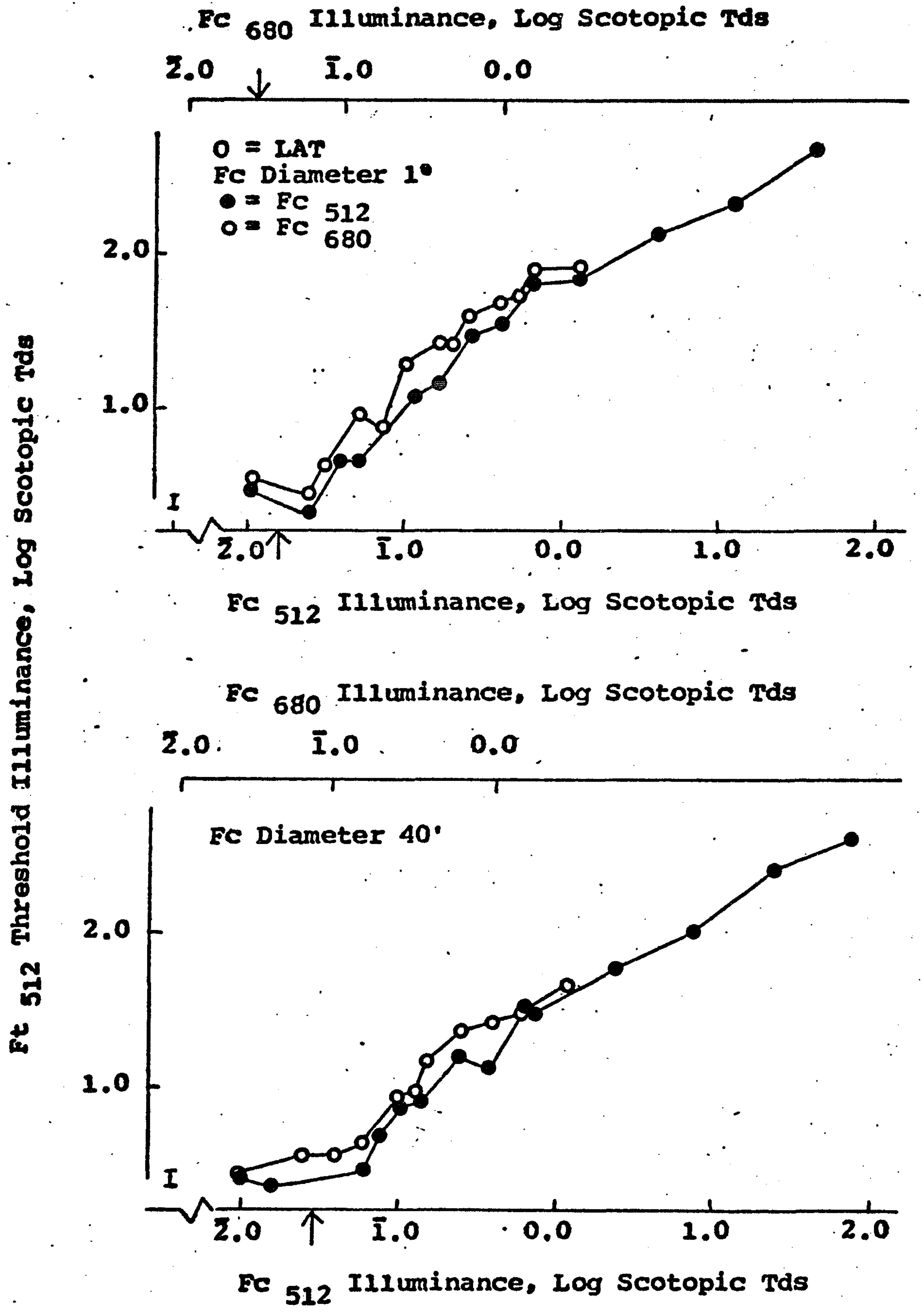

Fc 680 Illuminance, Log Scotopic Tds
1.0
0.0
O = CLS
Fc Diameter 1°
● Fc 512
○ Fc 680
2.0
1.0
I
1̄.0
0.0
1.0
2.0
Fc512 Illuminance, Log Scotopic Tds
Ft 512 Threshold Illuminance, Log Scotopic Tds
Fc 680 Illuminance, Log Scotopic Tds
1̄.0
0.0
Fc Diameter = 40'
2.0
1.0
I
2̄.0
1̄.0
0.0
1.0
2.0
Fc 512 Illuminance, Log Scotopic Tds

Figure 9. Observer LAT. Increment thresholds of the 512nm F_t as a function of the illuminance of a 1° (upper co-ordinates) or 40' (lower co-ordinates) F_c. See legend in Figure 6.

Detection thresholds of the F_c are: 1° 512nm = $\bar{2}.21$ log scotopic tds.; 40' 512nm = $\bar{2}.45$ log scotopic tds.; 1° 680nm = $\bar{2}.54$ log scotopic tds.; 40' 680nm = $\bar{2}.72$ log scotopic tds.


Fc 680 Illuminance, Log Scotopic Tds
2̄.0
1̄.0
0.0
O = LAT
Fc Diameter 1°
● = Fc 512
o = Fc 680
2.0
1.0
I
2̄.0
1̄.0
0.0
1.0
2.0
Fc 512 Illuminance, Log Scotopic Tds
Fc 680 Illuminance, Log Scotopic Tds
2̄.0
1̄.0
0.0
Fc Diameter 40'
2.0
1.0
I
2̄.0
1̄.0
0.0
1.0
2.0
Fc 512 Illuminance, Log Scotopic Tds
Ft 512 Threshold Illuminance, Log Scotopic Tds

color and probably stimulated the cone system as well as the rod system, while the 512nm stimulus appeared colorless and probably stimulated the rod system. To the extent that the 512nm and 680nm 8° F_c were equated for their influence upon the rod system, these results indicated that something other than the rod system was affecting the threshold of the 512nm F_t with the smaller diameter F_c.

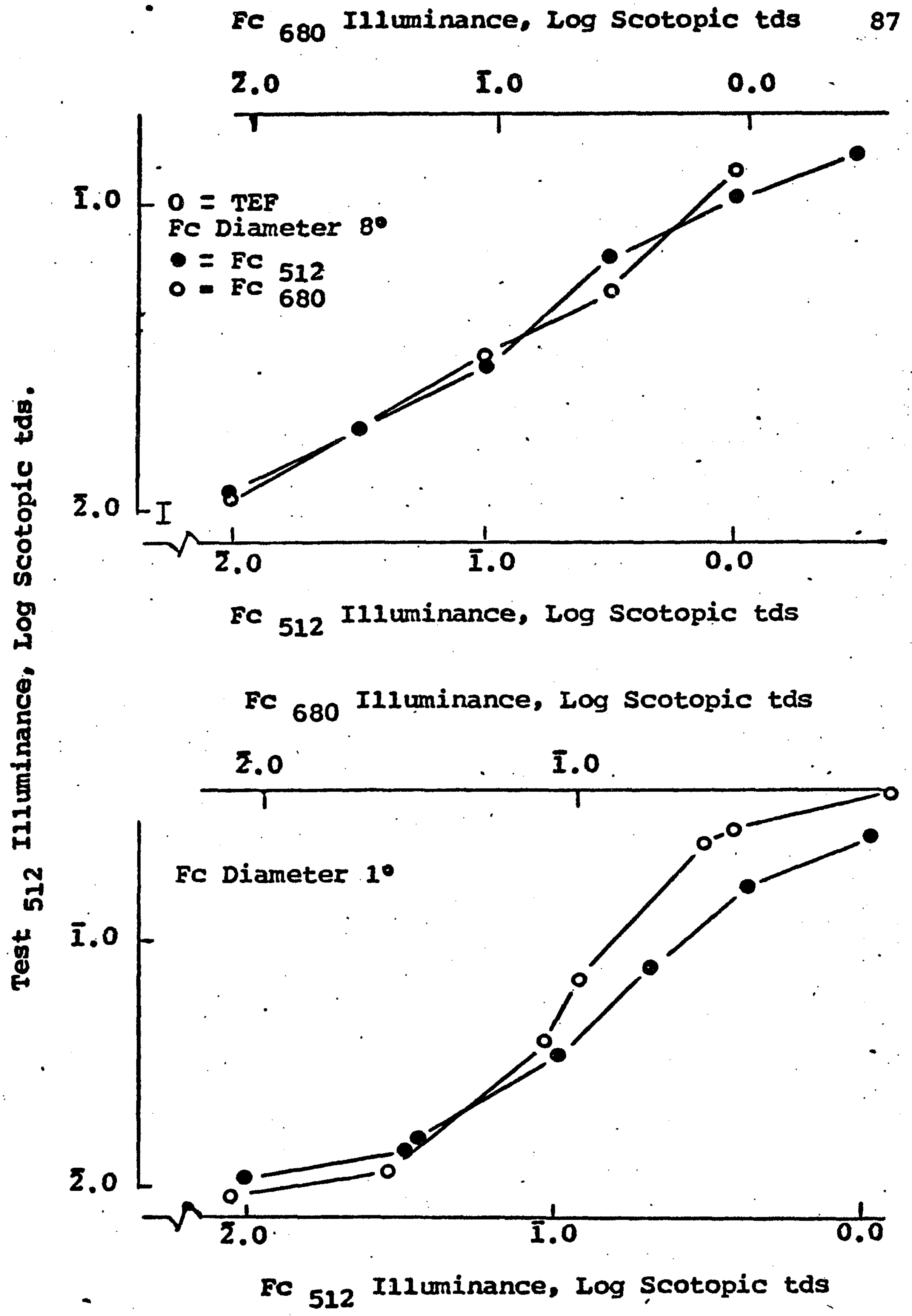
Figure 10 shows comparable data obtained from observer TEF. The upper set of curves of Figure 10 show the superposed tvi curves obtained with the 8° F_c of either 680nm or 512nm. It should be noted that the displacement obtained with observer TEF was approximately 0.1 log units, which was different from that found with the other two observers. In general TEF was about 0.5 log units more sensitive to 512nm light than were the other two observers.

The lower set of functions of Figure 10 shows tvi curves obtained with the 1° F_c of either 512nm or 680nm. It should be noted that for illuminances of about $\bar{1}.0$ log scotopic tds. and more, the lateral displacement that superposed the 8° functions did not superpose the functions generated with the smaller F_c. This was in agreement with data obtained from the other two observers.

Figure 10. Observer TEF. Increment thresholds of the 512nm F_t (on the ordinates in log scotopic tds.) as a function of the illuminance of an 8° (upper co-ordinates) or 1° (lower co-ordinates) F_c. Open circles are data obtained with 680nm F_c and correspond to the upper abscissae (in log scotopic tds.); closed circles are data obtained with the 512nm F_c and correspond to the lower abscissae (in log scotopic tds.). The curves have been laterally displaced relative to each other 0.2 log units for superposition of the 8° functions.

The bracket on the extreme left of the abscissae shows the 95% confidence interval of the F_t threshold obtained with no F_c present.

Detection thresholds of the F_c are: 8° 512nm = $\bar{3}.21$ log scotopic tds.; 1° 512nm = $\bar{2}.01$ log scotopic tds.; 8° 680nm = $\bar{3}.46$ log scotopic tds.; 1° 680nm = $\bar{2}.15$ log scotopic tds.


Fc 680 Illuminance, Log Scotopic tds
2̄.0
1̄.0
0.0
1̄.0
2̄.0
O = TEF
Fc Diameter 8°
● = Fc 512
○ = Fc 680
2̄.0
1̄.0
0.0
Fc 512 Illuminance, Log Scotopic tds
Test 512 Illuminance, Log Scotopic tds.
Fc 680 Illuminance, Log Scotopic tds
2̄.0
1̄.0
Fc Diameter 1°
1̄.0
2̄.0
2̄.0
1̄.0
0.0
Fc 512 Illuminance, Log Scotopic tds

2. 655nm F_t

Figures 11 through 15 show the threshold of the 655nm F_t (in log photopic tds.) as a function of the illuminance (also in log photopic tds.) of either a 512nm (closed circles and lower abscissae) or 680nm (open circles and upper abscissae) F_c for all three observers[1]. In the upper portions of Figures 11 and 12 (observers LAT and CLS respectively) are shown the tvi curves obtained with the 8° F_c. In these figures, the 512nm and 680nm functions were laterally displaced approximately 0.2 log units so as to superpose the two functions. This same displacement was used throughout Figures 11 to 15 regardless of the F_c diameter.

Inspection of the upper portions of Figures 11 and 12 shows that, first, as the illuminance of the 8° diameter F_c increased, F_t threshold increased. Second, for both observers, the 680nm F_c affected F_t threshold within one log unit of its own detection threshold. In contrast, 512nm F_c did not influence F_t threshold until it was more than 3 log units above its detection threshold (see the figure legends for the detection thresholds of

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[1] Photopic illuminance was used to plot the data obtained with the 655nm F_t since the lateral shift was less than if scotopic illuminance was used. This is consistent with the notion that the photopic system mediated the 655nm F_t threshold.

Figure 11. Observer LAT. Increment thresholds of the 655nm F_t (on the ordinates in log photopic tds.) as a function of the illuminance of an 8° (upper co-ordinates) or 2° (lower co-ordinates) F_c. Open circles are data obtained with the 680nm F_c and correspond to the upper abscissae (in log photopic tds.); closed circles are data obtained with the 512nm F_c and correspond to the lower abscissae (in log photopic tds.). The curves were laterally displaced relative to each other 0.2 log units for superposition of the 8° functions. The brackets on the extreme left indicate 95% confidence interval for the F_t threshold obtained with no F_c present.

Detection thresholds of the F_c are: 8° 512nm = $\bar{3}.41$ log photopic tds.; 2° 512nm = $\bar{3}.39$ log photopic tds.; 8° 680nm = $\bar{1}.75$ log photopic tds.; 2° 680nm = 0.02 log photopic tds.

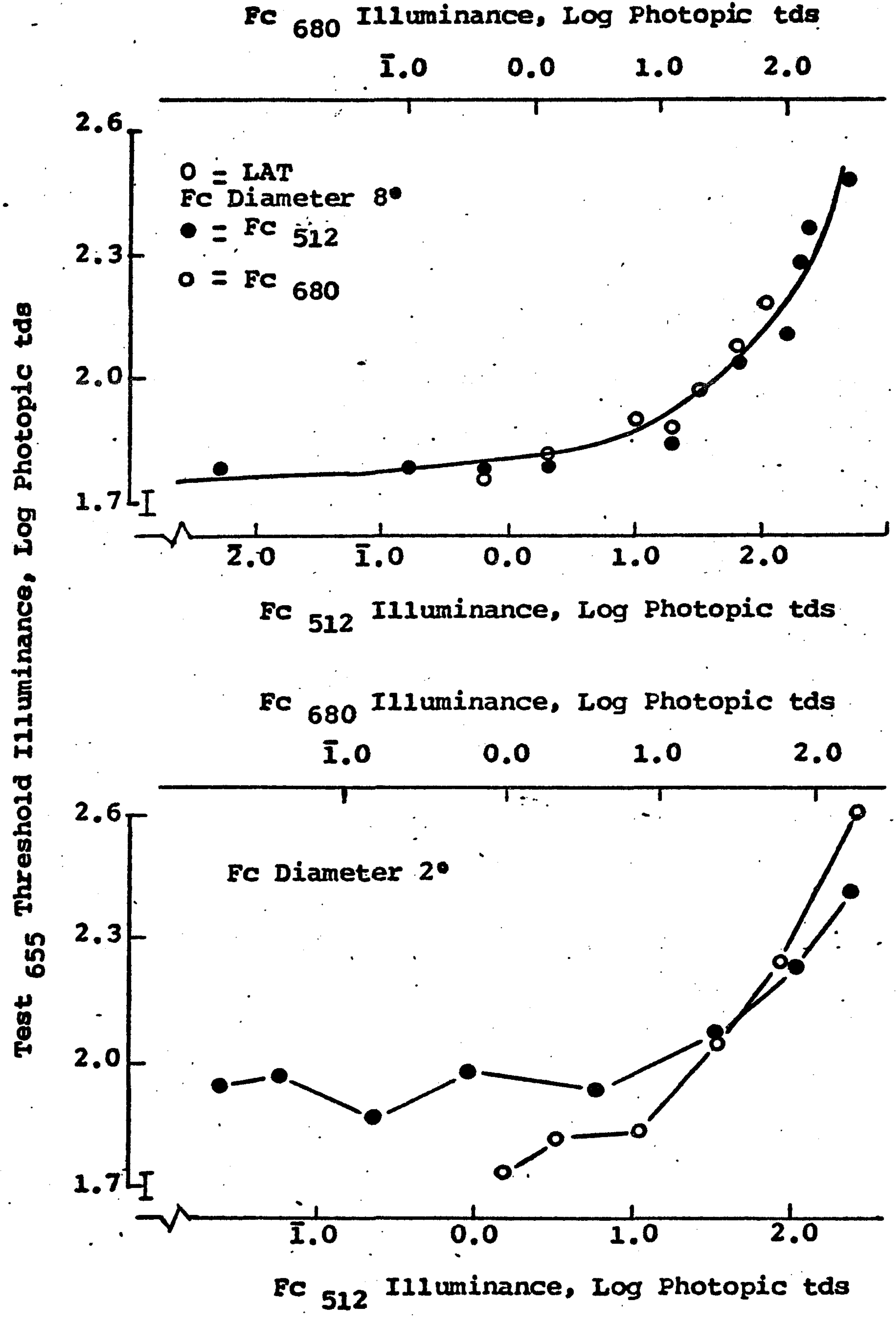
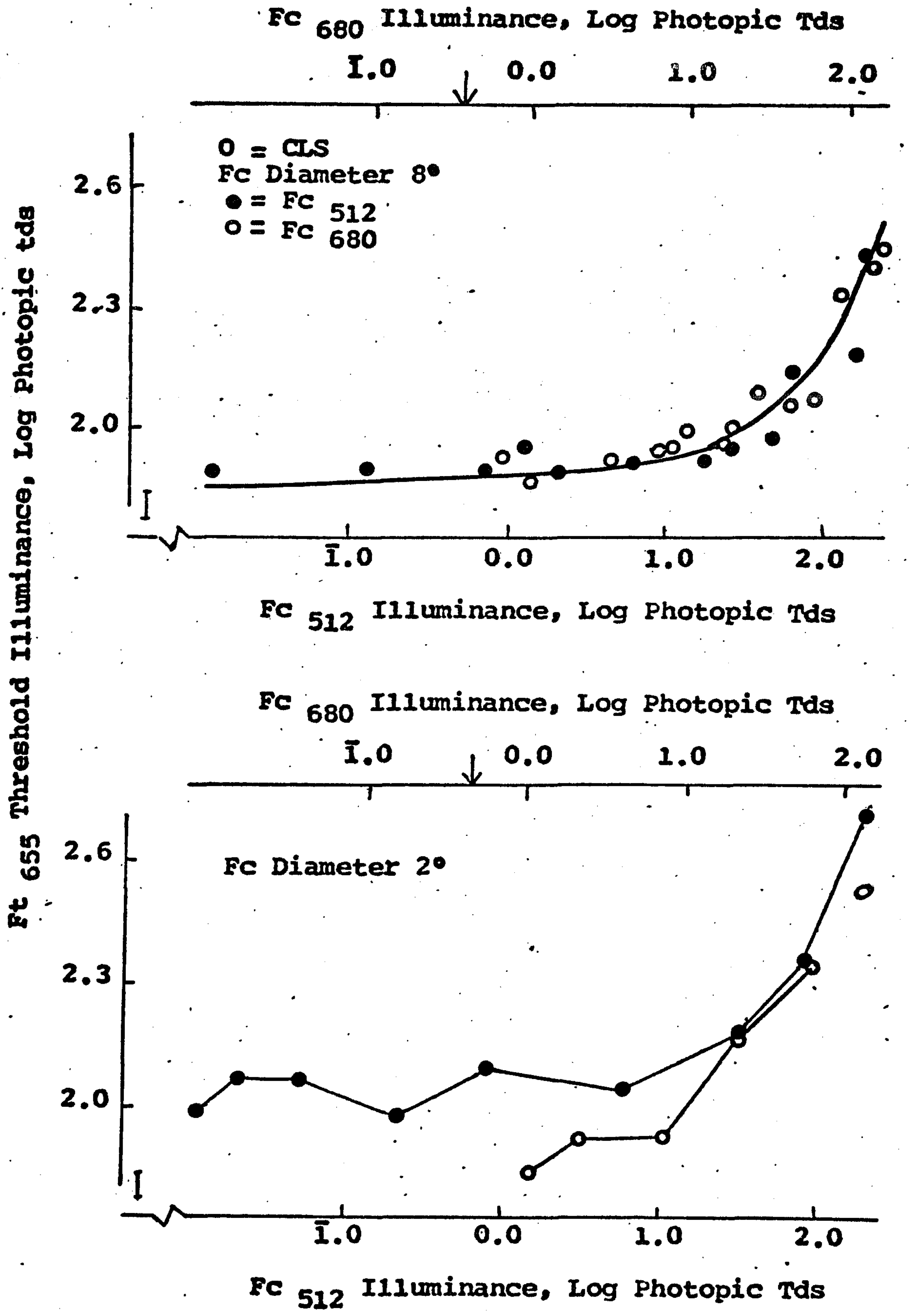

Fc 680 Illuminance, Log Photopic tds
1̄.0
0.0
1.0
2.0
2.6
2.3
2.0
1.7
O = LAT
Fc Diameter 8°
● = Fc 512
o = Fc 680
2̄.0
1̄.0
0.0
1.0
2.0
Fc 512 Illuminance, Log Photopic tds
Fc 680 Illuminance, Log Photopic tds
1̄.0
0.0
1.0
2.0
2.6
2.3
2.0
1.7
Fc Diameter 2°
1̄.0
0.0
1.0
2.0
Fc 512 Illuminance, Log Photopic tds
Test 655 Threshold Illuminance, Log Photopic tds

Figure 12. Observer CLS. Increment thresholds of the 655nm F_t as a function of the illuminance of an 8° (upper co-ordinates) or 2° (lower co-ordinates) F_c. See legend, Figure 11.

Detection thresholds of the F_c are: 8° 512nm = $\bar{3}.28$ log photopic tds.; 2° 512nm = $\bar{3}.43$ log photopic tds.; 8° 680nm = $\bar{1}.58$ log photopic tds.; 2° 680nm = $\bar{1}.78$ log photopic tds.


Fc 680 Illuminance, Log Photopic Tds
1̄.0
0.0
1.0
2.0
O = CLS
Fc Diameter 8°
● = Fc 512
○ = Fc 680
2.6
2.3
2.0
1̄.0
0.0
1.0
2.0
Fc 512 Illuminance, Log Photopic Tds
Ft 655 Threshold Illuminance, Log Photopic tds
Fc 680 Illuminance, Log Photopic Tds
1̄.0
0.0
1.0
2.0
Fc Diameter 2°
2.6
2.3
2.0
1̄.0
0.0
1.0
2.0
Fc 512 Illuminance, Log Photopic Tds

the F_c). Yet, the functions obtained with both wavelength F_c were virtually identical. These data were therefore consistent with the notion of independence of spectrally tuned mechanisms.

The lower half of Figures 11 and 12 show tvi curves obtained with F_c of 2° diameter. With this diameter F_c, there was an indication of differences between the different wavelengths. The 512nm F_c seemed to have an affect upon the F_t threshold whereas, at comparable illuminances, the 680nm F_c had no affect. This difference between the tvi curves produced by the different wavelength F_c was even more apparent with still smaller F_c diameters as illustrated in Figures 13 and 14. The upper portions of Figure 13 (observer LAT) showed that 40' F_c yielded functions that were clearly not superposed. At illuminances slightly above detection threshold, the 680nm F_c produced a tvi curve with a steep slope. In contrast, as the 512nm F_c increased above its detection threshold, F_t threshold increased gradually, up to a plateau. At still greater levels of illumination, F_t threshold began to rise again.

Similar trends were seen with the 18' diameter F_c (bottom Figure 13) and with observer CLS (Figure 14) in that the 680nm functions were clearly not super-

Figure 13. Observer LAT. Increment thresholds of the 655nm F_t as a function of the illuminance of a 40' (upper co-ordinates) or 18' (lower co-ordinates) F_c. See legend in Figure 11.

Detection thresholds of the F_c are: 40' 512nm = $\bar{2}.18$ log photopic tds.; 18' 512nm = $\bar{2}.99$ log photopic tds.; 40' 680nm = 0.46 log photopic tds.; 18' 680nm = 0.99 log photopic tds.

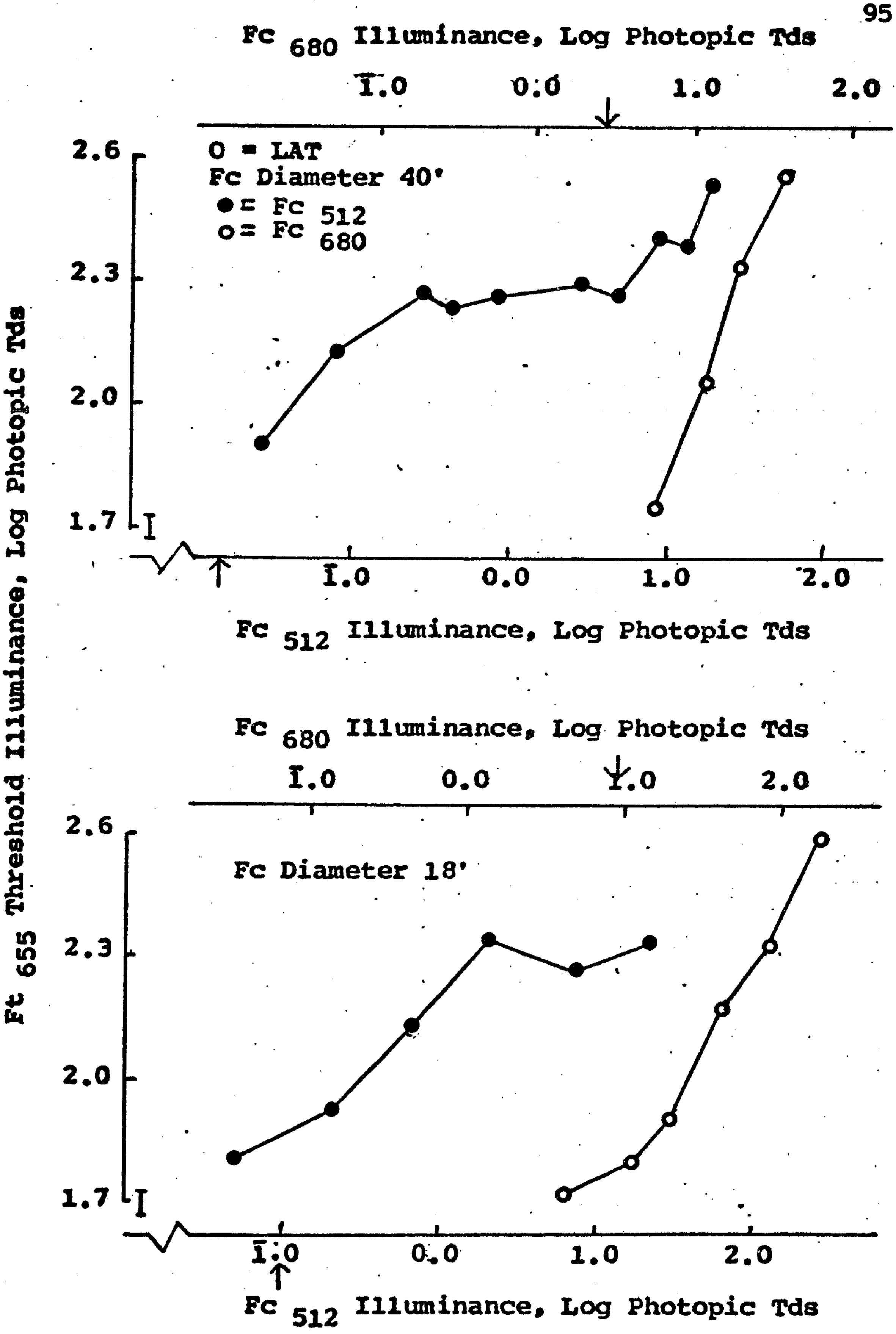
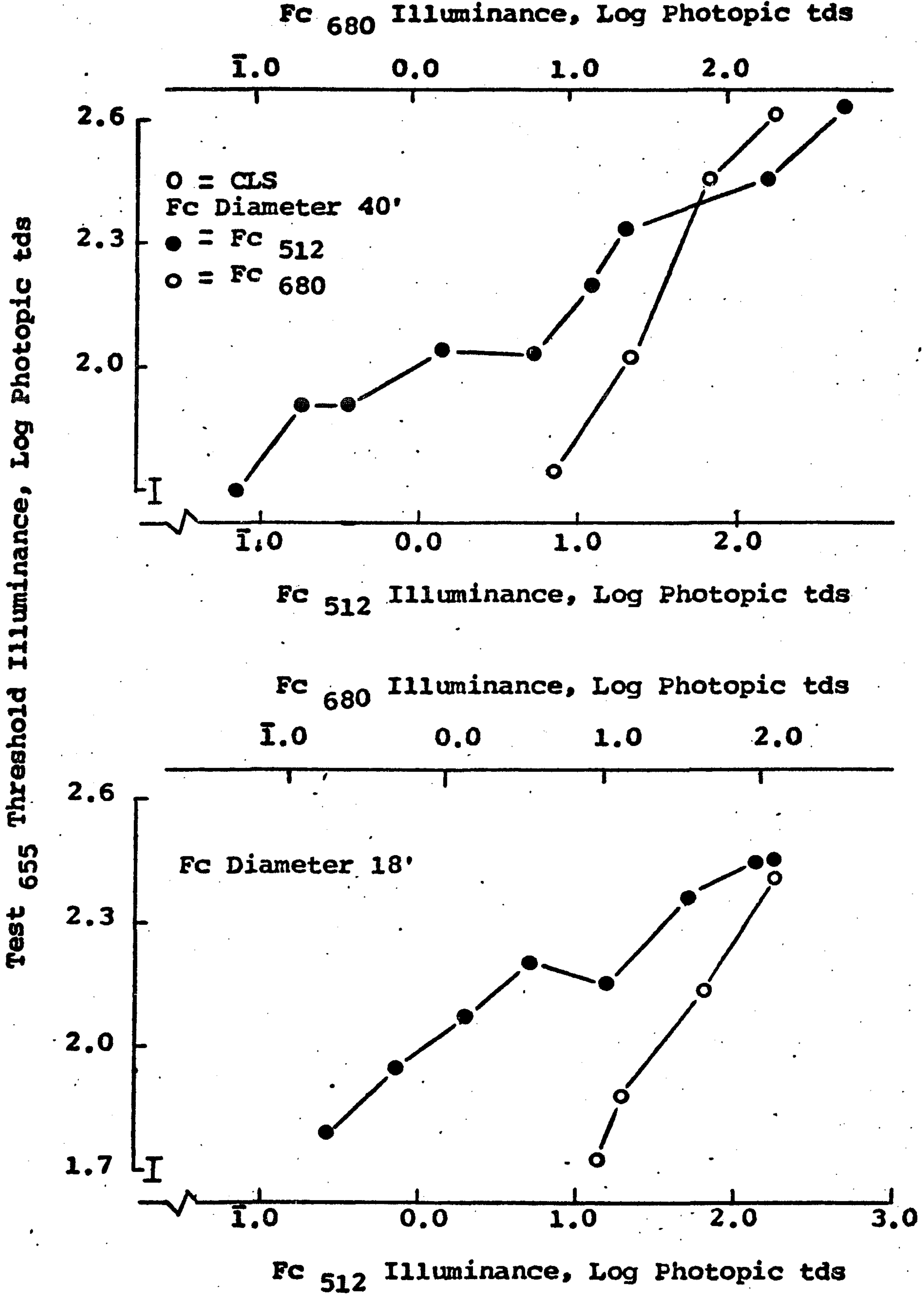

Fc 680 Illuminance, Log Photopic Tds
1̄.0
0.0
1.0
2.0
O = LAT
Fc Diameter 40'
● = Fc 512
o = Fc 680
2.6
2.3
2.0
1.7
Fc 512 Illuminance, Log Photopic Tds
Fc 680 Illuminance, Log Photopic Tds
Fc Diameter 18'
Ft 655 Threshold Illuminance, Log Photopic Tds
Fc 512 Illuminance, Log Photopic Tds

Figure 14. Observer CLS. Increment thresholds of the 655nm F_t as a function of the illuminance of a 40' (upper co-ordinates) or 18' (lower co-ordinates) F_c. See legend in Figures 11.

Detection thresholds of the F_c are: 40' 512nm = $\bar{2}.11$ log photopic tds.; 18' 512nm = $\bar{2}.70$ log photopic tds.; 40' 680nm = 0.36 log photopic tds.; 18' 680nm = 0.75 log photopic tds.


Fc $_{680}$ Illuminance, Log Photopic tds
$\bar{1}$.0
0.0
1.0
2.0
2.6
2.3
2.0
O = CLS
Fc Diameter 40'
● = Fc $_{512}$
o = Fc $_{680}$
$\bar{1}$.0
0.0
1.0
2.0
Fc $_{512}$ Illuminance, Log Photopic tds
Fc $_{680}$ Illuminance, Log Photopic tds
$\bar{1}$.0
0.0
1.0
2.0
2.6
2.3
2.0
1.7
Fc Diameter 18'
$\bar{1}$.0
0.0
1.0
2.0
3.0
Fc $_{512}$ Illuminance, Log Photopic tds
Test $_{655}$ Threshold Illuminance, Log Photopic tds

posed upon the 512nm functions. The 680nm and 655nm stimuli always appeared colored and were probably always affecting the cone system as well as the rod system. The small 512nm F_c were affecting F_t threshold at illuminance levels at which they appeared colorless and at which they were probably producing minimal affects upon any cone related mechanisms. To the extent that the F_t threshold was dependent upon the cone system, these results obtained with the small diameter F_c indicate that the rod system can influence the sensitivity of the cone system.

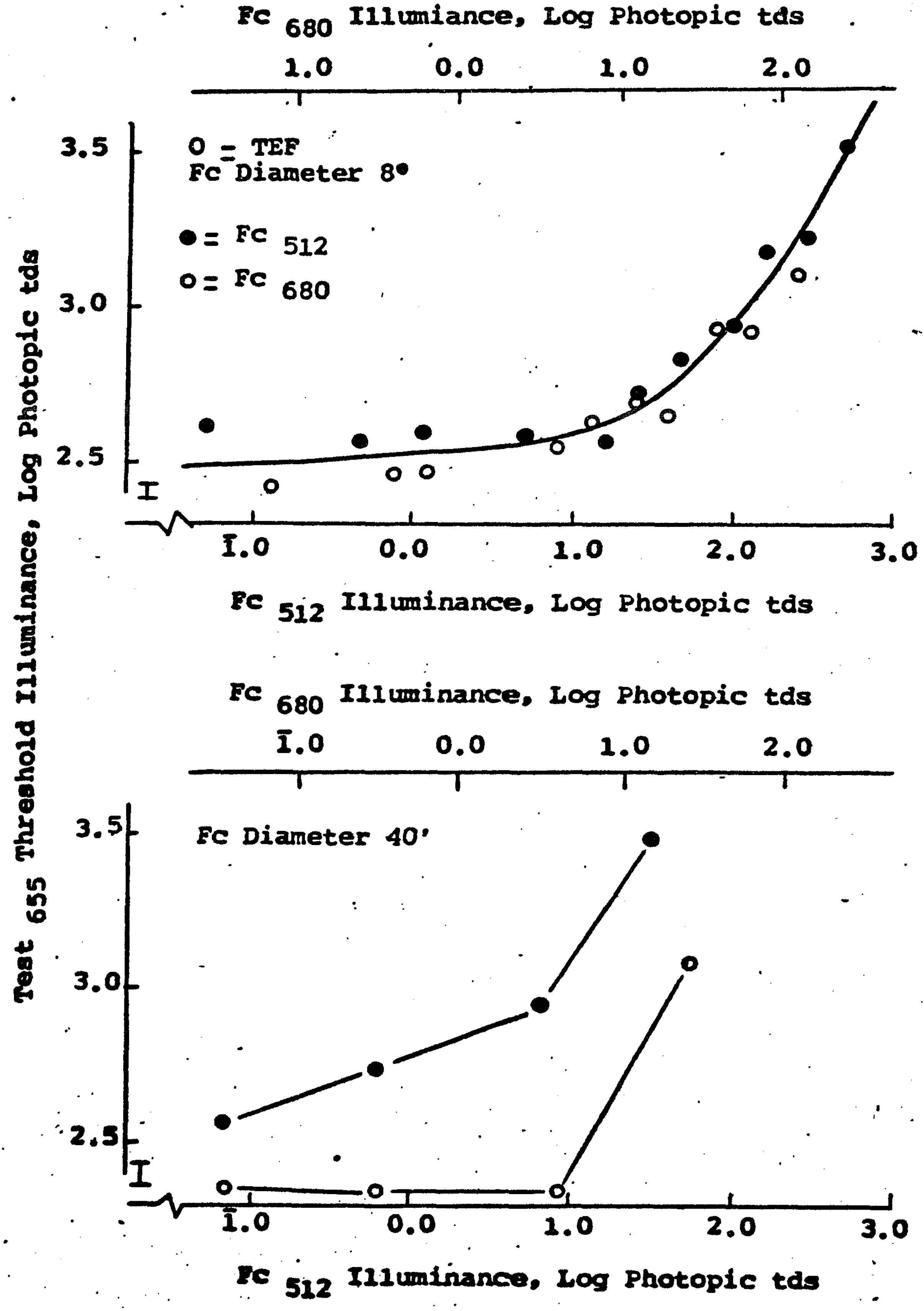
The upper set of functions in Figure 15 shows the tvi curves obtained with the 655nm F_t as a function of the illuminance (in log photopic tds.) of the 8° F_c for observer TEF. The tvi functions obtained with the two different F_c wavelengths were superposed by a lateral displacement of 0.3 log units. This displacement was different from the displacement obtained from the other two observers. As mentioned above, observer TEF was more than 0.5 log units more sensitive to 512nm light than were the other two observers.

The lower set of functions in Figure 15 shows the tvi curves obtained with a 40' F_c. These tvi functions were displaced the same as the 8° functions in the upper portion of the figure. As found with the other two observers

Figure 15. Observer TEF. Increment thresholds of the 655nm F_t (on the ordinates in log photopic tds.) as a function of the illuminance of an 8° (upper co-ordinates) or 40' (lower co-ordinates) F_c. Open circles are data obtained with the 680nm F_c and correspond to the upper abscissae (in log photopic tds.); closed circles are data obtained with the 512nm F_c and correspond to the lower abscissae (in log photopic tds.).

The functions have been displaced laterally relative to each other 0.3 log units for superposition of the 8° functions. The brackets on the extreme left of the abscissae show the 95% confidence interval of the F_t threshold determined with no F_c present.

Detection thresholds of the F_c are: 8° 512nm = $\bar{4}.94$ log photopic tds.; 40' 512nm = $\bar{3}.91$ log photopic tds.; 8° 680nm = $\bar{1}.18$ log photopic tds.; 40' 680nm = $\bar{1}.72$ log photopic tds.


Fc 680 Illuminance, Log Photopic tds
1.0
0.0
1.0
2.0
3.5
3.0
2.5
O = TEF
Fc Diameter 8°
● = Fc 512
○ = Fc 680
Ī.0
0.0
1.0
2.0
3.0
Fc 512 Illuminance, Log Photopic tds
Test 655 Threshold Illuminance, Log Photopic tds
Fc 680 Illuminance, Log Photopic tds
Ī.0
0.0
1.0
2.0
3.5
3.0
2.5
Fc Diameter 40'
Ī.0
0.0
1.0
2.0
3.0
Fc 512 Illuminance, Log Photopic tds

the displacement necessary to superpose the functions obtained with the large diameter F_c did not superpose the tvi functions obtained with the smaller F_c.

B. Effictiveness of different size and wavelength conditioning fields upon F_t threshold

Collectively, the results presented in Figures 6 through 15 showed that the relative influence of different wavelength F_c upon F_t threshold was dependent upon the diameter of the F_c. This interaction between size and wavelength was more directly analyzed with the following procedure. From Figures 6 to 15 that F_c illuminance which elevated F_t threshold 0.6 log units above its detection threshold was determined for all wavelength and size combinations. Thus regardless of the size and wavelength, all the different F_c produced an equivalent affect upon the visual system.[2]

Figures 16 (observer LAT) and 17 (observer CLS) plot the F_c illuminances necessary to raise the F_t threshold o.6 log units above its threshold as a function of the F_c diameter with wavelength of the stimuli the parameter. The F_c illuminance is plotted both in terms

[2] Note that the criterion of 0.6 log unit was chosen only because the best Westheimer functions were then obtained with the present data. With perfect tvi functions any criterion should be appropriate. There is nothing theoretically significant about the 0.6 log unit criterion that was used.

Figure 16. Observer LAT. F_c illuminance (on the left in log scotopic tds., on the right in log photopic tds.) needed to raise the F_t threshold 0.6 log units as a function of the F_c diameter in log minutes. Wavelength is the parameter. Triangles are 512nm F_t, circles are 655nm F_t, open symbols are 680nm F_c , closed symbols are 512nm F_c. The dashed line on the lower left of the left hand set of functions shows a slope of minus one.

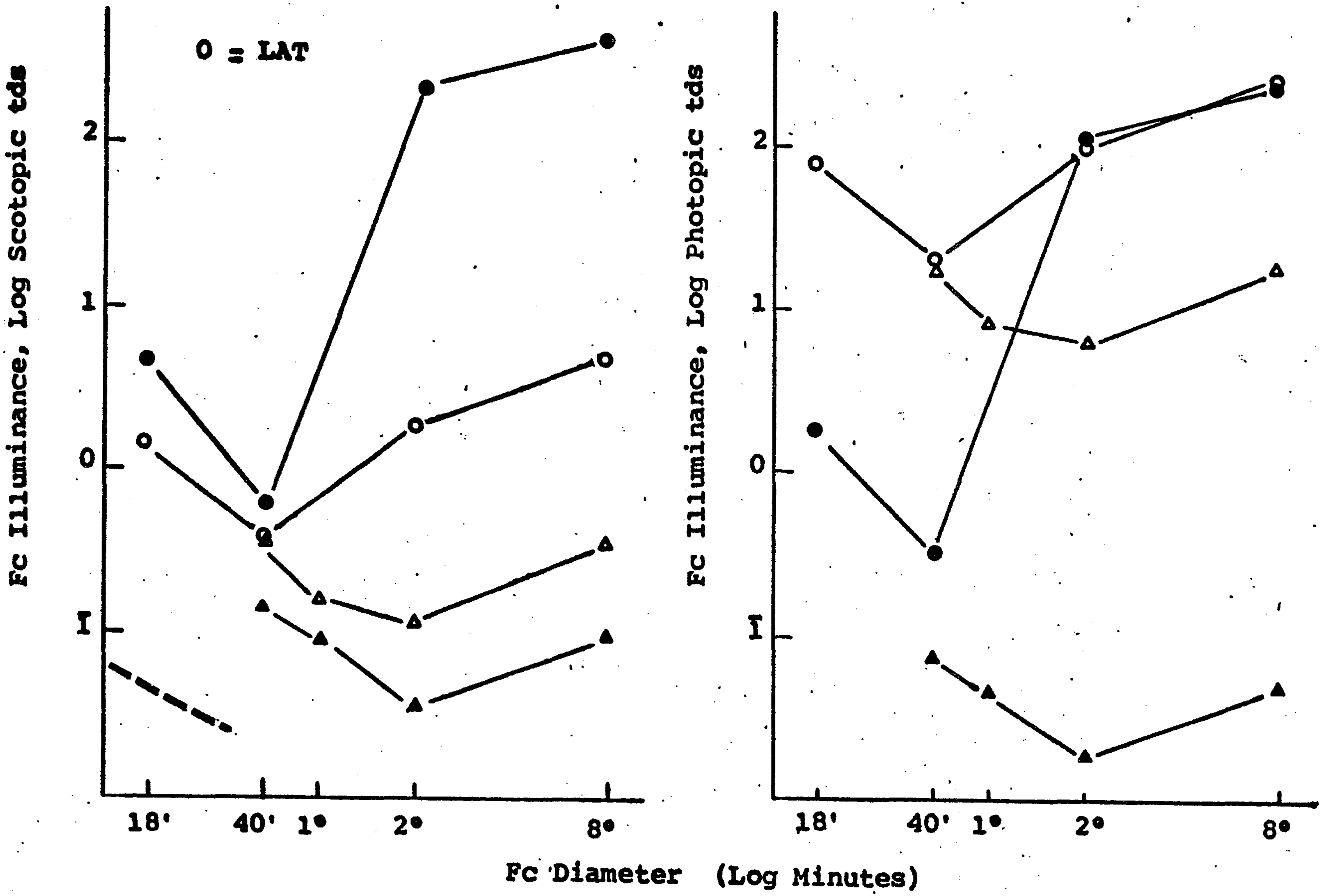
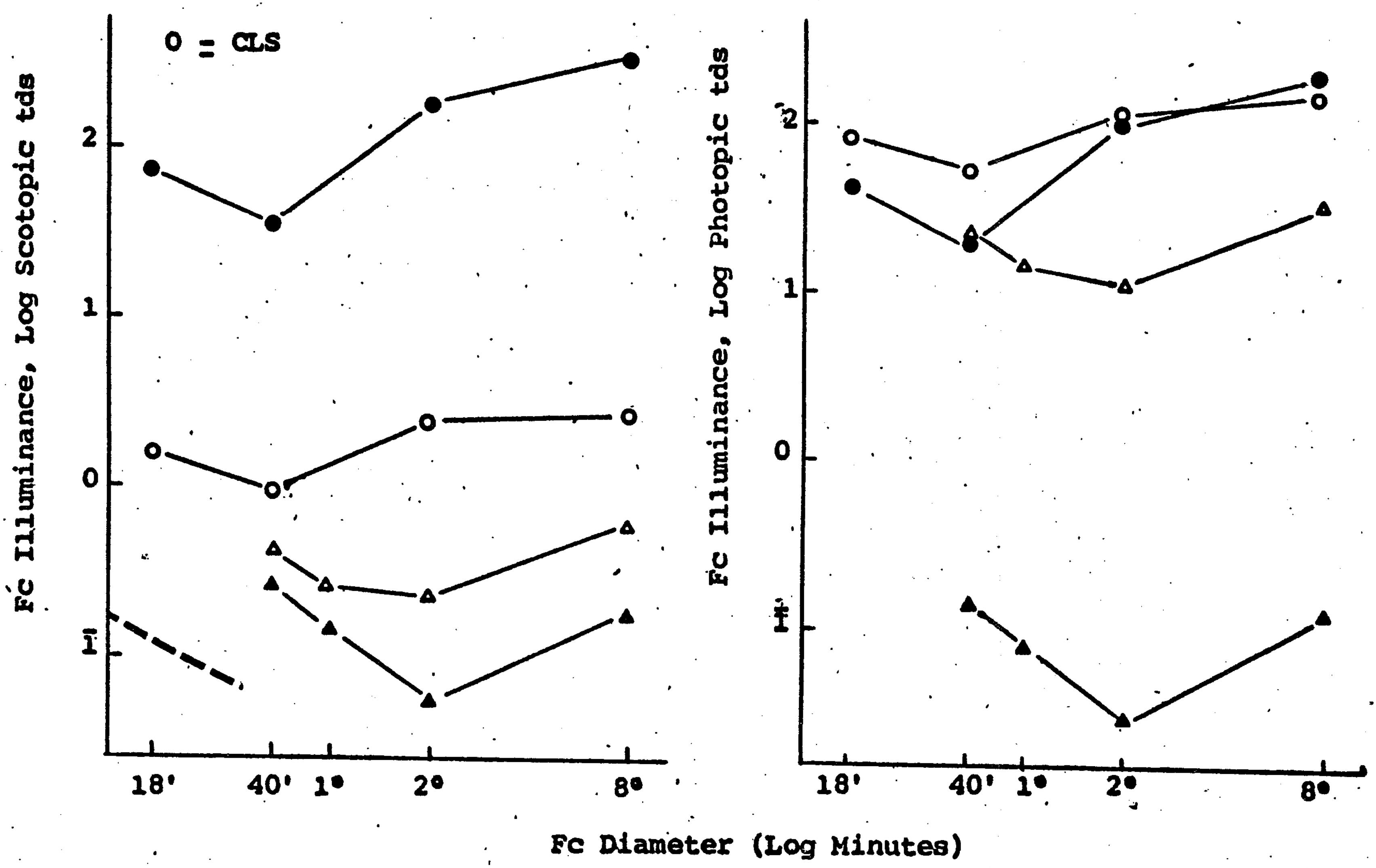

O = LAT
Fc Illuminance, Log Scotopic tds
Fc Illuminance, Log Photopic tds
2
1
0
$\bar{1}$
18'
40'
1°
2°
8°
Fc Diameter (Log Minutes)

Figure 17. Observer CLS. F_c illuminance needed to raise the F_t 0.6 log units as a function of the F_c diameter. See legend in Figure 16.


O = CLS
Fc Illuminance, Log Scotopic tds
2
1
0
Ī
Fc Illuminance, Log Photopic tds
2
1
0
Ī
18'
40'
1°
2°
8°
Fc Diameter (Log Minutes)

of log scotopic (left co-ordinates) and log photopic (right co-ordinates) trolands. These data show that as the F_c diameter increased the illuminance necessary to bring the F_t to threshold at first decreased then increased. With the 655nm F_t, the nadir of these 'U' shaped functions occurred with smaller diameter F_c than with the 512nm F_t. Moreover, the curves obtained with the 512nm F_t were more similar to each other in shape than to either of the 655nm functions. The functions obtained with the 655nm F_t were also more like each other than like either of the two 512nm functions. This was consistent with the arguement that the different wavelength F_t reflected the activity of different spectral mechanisms.

The dotted line at the lower left of each set of co-ordinates in Figures 16 and 17 had a slope of minus one. While the slope of the right hand limb of each 'U' shaped function was variable, the falling limb of most of the functions approximately paralleled the dotted line. This suggested that if these data were replotted in terms of F_c flux, all the functions would appear flat initially, then monotonically increase.

Figures 18 and 19 (observers LAT and CLS respectively) replot the data shown in Figures 16 and 17 respectively. Here, the F_c flux necessary to raise the

F_t threshold 0.6 log units above its detection threshold were plotted as a function of the F_c diameter. Flux was plotted in terms of both scotopic (left co-ordinates) and photopic (right co-ordinates) units. With the one exception (the 655nm F_t upon the 512nm F_c for observer LAT), all the resultent function were monotonically increasing. As F_c diameter increased, the flux necessary to mask F_t at first increased slightly, then more rapidly, The four functions (especially for observer CLS) were more similar to each other when they were plotted in this fashion then when they were plotted in terms of illuminance. This may be important in understanding the Westheimer effect.

Figure 18. Observer LAT. F_c flux necessary to raise the F_t threshold 0.6 log units as a function of the F_c diameter in log minutes. Scotopically equated flux on the left; photopically equated flux on the right. Wavelength is the parameter. Triangles are 512nm F_t, circles are 655nm F_t, open symbols are 680nm F_c, closed symbols are 512nm F_c.

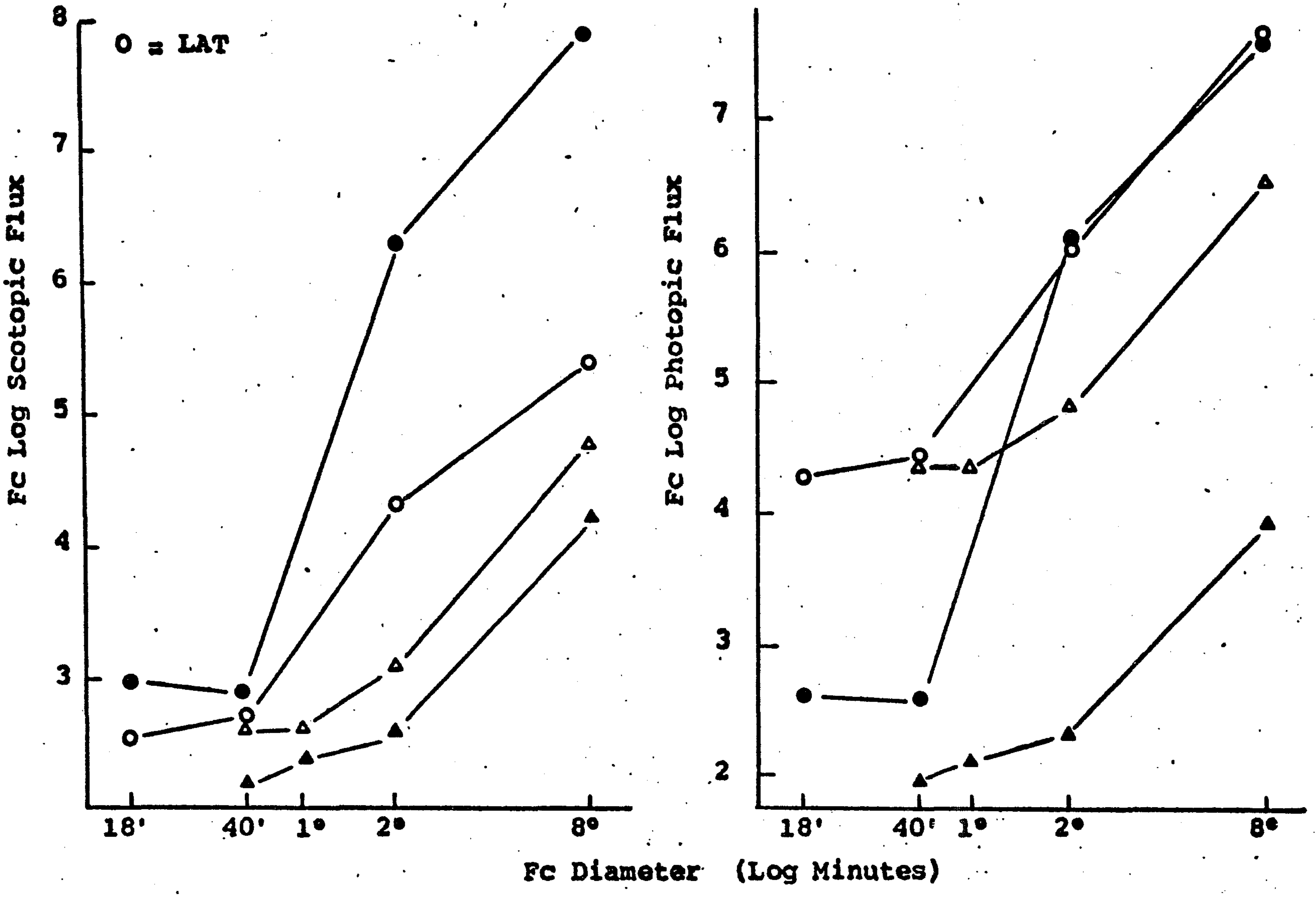
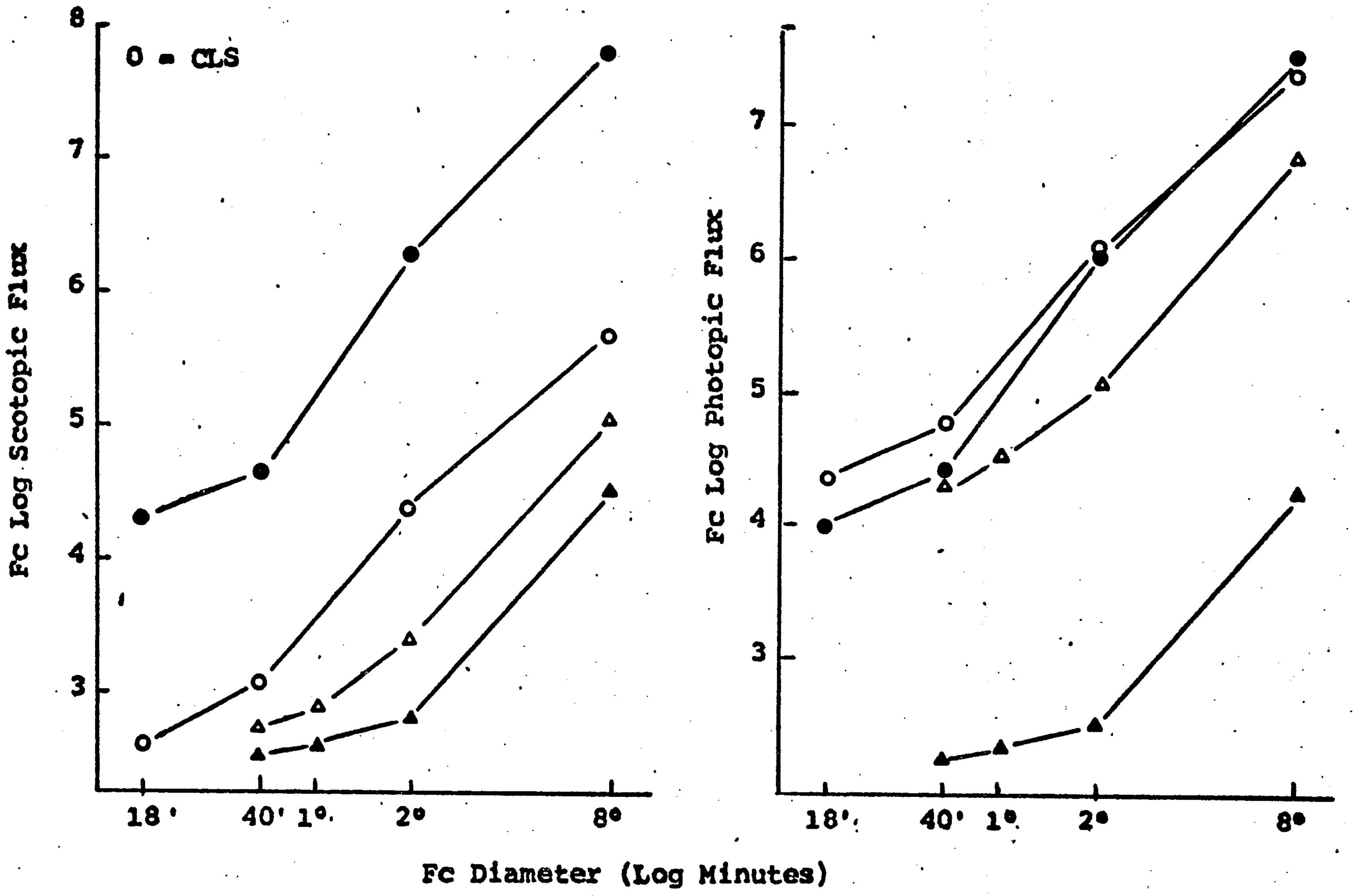

O = LAT
Fc Log Scotopic Flux
8
7
6
5
4
3
Fc Log Photopic Flux
7
6
5
4
3
2
18'
40'
1°
2°
8°
18'
40'
1°
2°
8°
Fc Diameter (Log Minutes)

Figure 19. Observer CLS. F_c flux necessary to raise the F_t threshold 0.6 log units as a function of the F_c diameter. See legend in Figure 18.


0 = CLS
Fc Log Scotopic Flux
8
7
6
5
4
3
Fc Log Photopic Flux
7
6
5
4
3
18'
40'
1°
2°
8°
Fc Diameter (Log Minutes)

CHAPTER V1

DISCUSSION

The present results confirm the general findings of previous increment threshold studies (Barlow, 1965; Stiles, 1959) in showing that, as the F_c illuminance increased, F_t threshold increased in a monotonic fashion. The tvi functions shown in Figures 6 through 15 are different from the classic results of Aguilar and Stiles (1954) for at least two reasons. Firstly, the F_t of the present study was much smaller and briefer than that used by Aguilar and Stiles. Secondly, the range of illuminances employed in the present study was about 4 log units less than used by Aguilar and Stiles. Thus it is not surprising that the slopes of the functions of the present study were never unity (Weber's Law).

The present study also confirms previous reports (Westheimer, 1965) showing that the shape of the tvi function was markedly influenced by the size of the F_c. Moreover, the influence of the F_c upon the tvi function differed for the two F_c wavelengths, as would be suggested by the data of Westheimer (1970).

The most striking and novel result of the present study was that each of the four wavelength combinations employed produced unique tvi functions with the smaller sized F_c. This result was apparent in the tvi functions plotted in Figures 6 through 15, but more apparent in the Westheimer functions plotted in Figures 16 through 19.

Increment Threshold Functions

Different wavelength F_c were compared with a method of analysis derived from the two color increment threshold procedure of Stiles[1]. This method of analysis was chosen over other possible methods of comparing the different wavelength F_c since the theory of Stiles has been most influencial in the field of color vision and is consistent with a large body of experimental data.

The present experiment explicitly made a number of assumptions of which some were similar to the assumptions

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[1] There are several ways to compare the F_c of different wavelengths other than with a Stiles type of approach. The different F_c wavelengths can be equated for (a) equal energy (b) the detection threshold of the F_c (c) equal illuminance effects measured photopically (d) equal illuminance effects measured scotopically The data were analyzed with each of these methods but were not included because of limitations of space. No method gave information about the data that was not obtained with the present analysis. Moreover, each of these methods yielded meaningful comparisons for about half of the data. For example, when the data were plotted in terms of photopic tds. the tvi curves obtained with the 655nm F_t approximately superposed the 512nm and 680nm functions. However, the tvi curves of the 512nm F_t plotted in terms of scotopic tds. seperated the 512nm F_c data from the 680nm F_c data by about 5 log units, yielding meaningless comparisons. Similar problems occurred with the other possible methods of comparison.

of Stiles. These assumptions are supported by some experimental data.

(1) There are several different spectrally tuned mechanisms (rods and cone systems or π mechanisms) mediating human vision. This assumption is validated by the data supporting the duplicity theory and trichromatic theories of color vision.

(2) The 512nm stimuli in the present study stimulated the rod system to a greater extent than any of the cone related systems. This assumption is supported by the relative sensitivity of the photopic and scotopic spectral sensitivity functions.

(3) The 655nm and 680nm stimuli used in the present study probably stimulated cone related mechanisms to a greater or equal extent than they stimulated the rod related mechanism. This assumption was supported by the classic data of Hecht *et al*. (1937) and Wald (1945).

(4) The behavior of an individual spectrally tuned mechanism is not dependent upon the wavelength of of the stimuli; but depends upon the number of quanta that are absorbed by the mechanisms. This is a statement of the photochemical concept of Univariance, which has been shown by a combination of photochemical and psychophysical techniques to apply to human vision (Naka & Ruchton, 1966a; Rushton, 1972). A corollary of this assumption is that, if

the two tvi curves differ in shape and only the wavelengths of the stimuli were different, then they cannot be describing the operation of a single spectrally tuned mechanism. The converse is not necessarily true.

(5) The threshold of a F_t is determined by the most sensitive mechanism. This last assumption is implicit in most increment threshold studies and made by most workers.

One of the reasons the model of Stiles was used in this present study was that it made specific predictions about the outcome of the present experiments. As developed in the Rationale section (pp 39-43), a single wavelength F_t on a F_c of the same diameter but different wavelength should be superposable by some lateral displacement. The obtained tvi functions describe the operation of one of the spectral mechanisms. The F_t determines which one. The extent of the lateral displacement is an indication of the relative sensitivity of the spectral mechanism to the two different wavelength F_c. The lateral displacement of one pair of tvi functions obtained with one diameter F_c should yield superposition of the tvi functions obtained with another F_c diameter.

Increment threshold functions of the 512nm F_t obtained with the 8° F_c of either 512nm or 680nm did superpose by a lateral shift for all three observers. Thus these data were in agreement with the theory. The same lateral shift that superposed the 8° functions largely superposed the tvi functions obtained with the 2° F_c. Thus the large diameter F_c yield data that were in agreement with the data of Stiles.

Comparable data were obtained with the 655nm F_t. Similar conclusions were reached. With the 8° F_c, the tvi functions obtained with the 512nm and 680nm F_c did superpose when displaced an amount predicted by the relative photopic spectral sensitivity to the 512nm and 680nm F_c. This was approximately true with the 2° fields as well.

However, with the 512nm F_t, the lateral shift that superposed the tvi functions with the 8° and the 2° F_c did not superpose the tvi functions obtained with the 1° F_c nor the functions obtained with the 40' F_c. With these diameter F_c, the 680nm F_c affected the 512nm F_t more than did the 512nm F_c. All three observers showed this effect. The crucial point is that the particular displacement needed to superpose the 8° F_c was insufficient with either the 1° or the 40' F_c. That is, the spectral sensitivity of the mechanism affected by the F_c had changed with a change in the F_c diameter.

Moreover, Temme and Frumkes (1975) using stimuli identical to those used in the present study determined the action spectrum of a 1° F_c necessary to raise the 512nm F_t 0.5 log units above its detection threshold. The obtained action spectrum described the action spectrum of the scotopic CIE standard observer, except at the long wavelength end of the spectrum where small F_c fields had an effect greater than would be predicted by the rod sensitivity alone (Figure 4). Therefore, the small 'excess effect' of the small F_c upon the threshold of the 512nm F_t in some way reflected the activity of a cone related mechanism.

Comparable observations and conclusions were made with the data obtained with the 655nm F_t. With this F_t the lateral shift that superposed the tvi functions obtained with the 8° and 2° F_c did not superpose the tvi functions obtained with the 40' F_c nor with the 18' F_c.

The 512nm F_c raised the threshold of the 655nm F_t at illuminances where the 680nm F_c had no effect. Again, the point is that the particular displacement that superposed the 8° functions did not superpose the functions obtained with the smaller F_c diameters; the spectral sensitivity of the mechanism affected by the F_c had changed with a change in the F_c diameter.

Note, the 40' and 18' diameter F_c 512nm affected the threshold of the 655nm F_t at illuminances probably below the threshold of any cone related mechanism. Moreover, Temme and Frumkes (1975), using stimuli identical to those used in the present study, determined the action spectrum of a 40' F_c necessary to raise the 655nm F_t 0.5 log units above its threshold. The obtained action spectrum described the action spectrum of the scotopic CIE standard observer (Figure 4). Therefore, this effect must reflect the activity of some rod related mechanism.

This effect of the 18' and 40' 512nm F_c must be neural and not due to some optical artifact (e.g. stray light) since the same illuminance of the same wavelength F_c had no effect upon the F_t threshold when the F_c diameter was large. That is, with the larger fields there was more light on the retina, but the F_t threshold was lower.

Therefore, the tvi functions are consistent with the hypothesis that there is at best a limited independence among the spectral mechanisms in the increment threshold situation. The hypothesis of independence is consistent with the data of the large F_c or the small F_c diameters; but not both large and small F_c diameters simultaneously.

Westheimer Functions

The data in Figures 15 through 18 confirmed the general findings of Westheimer (1965, 1967, 1970) and others in showing that as the size of the F_c increased, the F_c illuminance necessary to mask a constant illuminance F_t at first decreased than increased again. These data also showed that the diameter F_c most affective in masking the 512nm F_t was larger than the diameter most affective in masking the 655nm F_t. This observation is consistent with the hypothesis that the 655nm F_t threshold was determined by a cone related mechanism and the threshold of the 512nm F_t was determined by a rod related mechanism. The F_c diameters that were most affective in masking the F_t were in the present study, considerably larger than those diameters reported by Westheimer. None the less, the F_t used in the present study were considerably larger and longer than those used by Westheimer. It has been shown that the larger the diameter of the F_t the larger the peak diameter of the F_c (Frumkes & Kraft, 1972; Alexander, 1974 b). Thus these findings were consistent with the literature.

The results presented in Figures 15 to 18 extend the observations of Westheimer (1970) in that the influence of the diameter of two different wavelength

F_c were investigated. The results run counter to Westheimer's suggestion that in the increment threshold situation rod and cone systems independently adapt. Providing that the 512nm F_t was detected by a rod related mechanism and the 655nm F_t was detected by a cone related mechanism, independence between the receptor mechanisms would suggest that the F_t wavelength would not effect the Westheimer functions. Since the heterochromatic functions showed greater effects on F_c size than did the homochromatic combinations, then the prediction based upon independence was not born out. Moreover, no Westheimer function obtained with one pair of wavelengths described the function obtained with another pair of wavelengths. If univariance were obeyed, one would expect that some of these functions would be superposable; which they were not. It is unlikely that univariance breaks down as a photochemical principle (at these levels of illuminance); but rather there are neural events occurring with the smaller F_c which differentially affect one spectrally tuned mechanism and not the other.[2]

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[2] The retina is not a homogeneous structure. Rod/cone ratio changes as a function of retinal locus. Thus the peripheral aspect of a large F_c fell onto a patch of retina with a larger rod/cone ratio than the peripheral aspect of a smaller diameter F_c. This observation, not adequately treated in any study of the Westheimer effect is an important consideration here because the results are analyzed in terms of rod-cone interaction. It is unlikely, however, that the results are a <u>continued</u>

Westheimer originally demonstrated the influence of F_c diameter upon the threshold of the F_t in two ways (1965). According to the procedure adapted by most later investigators, the F_t threshold illuminance is obtained as a function of the diameter of a constant illuminance F_c. He also obtained the illuminance of a varying diameter F_c necessary to mask a constant illuminance F_t. The latter procedure was used to generate the curves shown in Figures 15 and 16.

There were three reasons that this latter procedure seemed more reasonable than the common procedure. First, there is no photometric or radiometric unit of light that described the effects of lights simultaneously upon the rod and cone systems. Since the comparison involved two different wavelength F_c there was no <u>a priori</u> way to choose a comparable illuminance for the two different F_c wavelengths. Second, in the traditional way of generating the Westheimer function the

consequence of the change in rod/cone ratio alone for two reasons. First, there was evidence of the rod-cone interaction only with the small diameter F_c; that is, when the F_c fell onto the most homogeneous patch of retina. Secondly, since (a) the locus of the F_t was mot moved and (b) it is assumed that the most sensitive mechanism determined threshold, then attempts to explain the present results as changes in rod/cone ratio stimulated by different size F_c must include some form of neural interaction between the rod and cone systems.

F_t threshold is measured as the diameter of the constant illuminance F_c is varied. To the extent that the F_t threshold reflects the state of sensitivity of the patch of retina, changes in the F_t reflect changes in the visual sensitivity. Comparing changes in F_t threshold as a function of the diameter of the F_c means that different states of visual sensitivity are compared. Therefore, the usual way of generating a Westheimer function results in comparing the effects of different stimuli upon a retina whose sensitivity is changing (Guth, 1973). Third, by plotting Westheimer functions in the fashion we chose, it was possible to determine the effects of flux. In the traditional way of generating the Westheimer function these factors remain unmeasured.

Physiological Speculations

Westheimer Functions

There is evidence that the state of adaptation of individual ganglion cells is determined by the total flux falling on a summative center of the ganglion cell receptive field. One would then expect that, as the diameter of equal flux F_c increased to some critical diameter, F_t threshold should be constant. This, in fact, has been observed in ganglion cells of the cat (Enroth-Cugell and Shapely, 1973). The Westheimer functions in terms of F_c (Figures 18 and 19) flux showed curves with two branches. The first part of the curves were either flat or rose relatively slowly. The second part rose rapidly. Thus the physiological prediction was consonant with the observed data; but too few F_c sizes were used to adequately test such a hypothesis.

Recently, both Kaneko (1973 and Werblin (1974) suggested that the ganglion cell receptive field center reflects bipolar cell receptive fields. _If_ (a) this is true, and _if_ (b) the Westheimer function directly reflects the receptive field of the ganglion cell, _then_ the falling limb of the 'U' shaped Westheimer functions would be established by the layer of the bipolar cell. In a series of papers Westheimer functions have been generated from pathological retinas (Enoch _et_ _al_. 1969, 1970a, 1970b). In all cases in which Westheimer functions were generated regardless of the level of pathology in the visual system the falling arm of the 'U' shaped function was found intact (with a slope of minus unity; perfect spatial reciprocity). Thus, if the outer plexiform layer was maintained, the falling limb of the Westheimer function was found.

Rod-Cone Interaction

Many of the foregoing considerations strongly suggested that in the increment threshold situation, rod and cone systems exerted an influence upon each other , provided that the spatial parameters of the stimuli were appropriately chosen. What are the mechanisms of this interaction?

Electrophysiological evidence collected over the past few years (reviewed in the second chapter) suggested means for this interaction at virtually every level of the retina; at the receptor cell itself (Schwartz, 1975), horizontal cell (Whitten & Brown, 1974) amacrine cell (Fatechand, 1975) ganglion cell (Gouras and Link, 1965). However, since these results were obtained from a wide variety of species, it is difficult to make any definite extrapolations to the present data. At whatever locus the initial interactions occur, it is likely that by the level of the ganglion cell there are reciprocal, inhibitory interactions between rod and cone systems.

There is psychophysical evidence that a cone mediated edge will effect the sensitivity of the rod system (Lennie & MacLeod, 1973). This observation is consistent with the results of the present experiment which indicated that interactions between rod and cone systems occur only with small diameter F_c. This would imply that the salient edge signals from one receptor system would effect the threshold of the other system. (To say that the effects are due to edges is not an adequate explanation since the mechanism or mechanisms by which edge effects occur are not known.)

If (1) Werblin and Kaneko are correct in suggesting that the ganglion cell receptive field center reflects the interactions occurring at the level of the outer plexiform layer, and (2) the Westheimer function reflects ganglion cell activity directly, as has been suggested by several researchers, <u>then</u> it is tempting to conclude that the site of interactions between rods and cones evidenced in the present results is at the level of the outer plexiform layer. This would be the case since rod-cone interactions were evidenced only with the small diameter F_c (the initial limb of the Westheimer function).

However, this is all clearly speculative; the available data do not locate the site of interactions of the spectral mechanisms. The evidence indicated only that there was such an interaction and that it occurred clearly with the small stimuli. There was no comparable evidence suggesting interactions with the large diameter F_c.

CHAPTER V11

SUMMARY AND CONCLUSIONS

The present study was an assessment of the influence of the diameter, illuminance, and wavelength of a conditioning field (F_c) of light upon the threshold of a test flash (F_t). Stimulus parameters were chosen to assess the interrelationships between rod and cone systems in the increment threshold situation.

A four channel Maxwellian view optical system presented all stimuli to the dark adapted right eye of three well trained psychophysical observers. In all cases F_c and F_t were concentrically presented 7° in the temporal field against a $\bar{4}.6$ log td. (white light) field. The F_t was 15' in diameter, and 25 msec in duration and either 512nm or 655nm in wavelength. The continually exposed F_c was either 512nm or 680nm in wavelength and varied in diameter from 18' to 8°. Regardless of specific parameters, F_t threshold was determined as a function of the F_c illuminance. Results were plotted either as tvi curves (log F_t threshold as a function of log F_c illuminance) or as Westheimer functions (F_c illuminance necessary to mask the presence of a fixed illuminance F_t as a function of the F_c diameter).

The increment threshold curves obtained with different wavelength combinations were compared with a technique suggested by the two color increment threshold procedure of Stiles (1959). According to this analysis:

1. F_t threshold increased as F_c illuminance increased.

2. Regardless of the stimulus wavelength, F_c diameter always influenced the shape of the tvi curve.

3. With a 512nm F_t and F_c diameter of 2° or more, tvi functions obtained with either wavelength F_c could be superposed by a lateral displacement of the functions predicted by the relative sensitivity of the rod system to the two different wavelengths. This agreed with the hypothesis that primarily the rod system determined the 512nm F_t threshold and that the F_c affected F_t threshold only to the extent that it affected the rod system.

4. With F_c diameter of 1° or less and a 512nm F_t tvi functions obtained with the different wavelength F_c could be approximately superposed but the lateral displacement was not predictable by the spectral sensitivity of the spectrally tuned mechanism that superposed the large 8° functions. The 680nm F_c had an effect upon the F_t threshold greater than predicted by the sensitivity of the rod system alone. This suggested that the cone system affected the threshold of the rod system.

5. With a 655nm F_t and F_c diameter of 2° or more, tvi functions obtained with either wavelength F_c could be

superposed by a lateral displacement predictable by the relative sensitivity of Stiles π_5 mechanism to the two different F_c wavelengths. This agreed with the notion that cones determined the threshold of the 655nm F_t, and that the F_c affected the 655nm F_t threshold only to the extent that the F_c influenced the same spectrally tuned mechanism.

6. With a 655nm F_t and F_c diameter equal or less than 40' tvi curves obtained with the different wavelength F_c were not superposable. Furthermore, the 512nm F_c affected the F_t threshold at illuminance levels that were probably below the threshold of the cone mechanisms. To the extent that the 655nm F_t threshold was determined by the cone system, these results indicate that the rod system can influence the threshold of the cone system.

The Westheimer functions showed that:

1. Regardless of the stimulus wavelengths, as the F_c diameter increased, the illuminance of the F_c necessary to mask the perception of the F_t first increased then decreased.

2. The F_c most effective in masking the F_t was smaller in diameter when a 655nm F_t was used than when a 512nm F_t was used. These results suggested that the 512nm F_t threshold was probably determined by the rod system while the 655nm F_t threshold was determined by the cone system.

3. With either wavelength F_t, the two different F_c wavelengths did not produce equivalent Westheimer functions. The influence of the 680nm F_c diameter was more marked than the influence of the 512nm F_c diameter upon 512nm F_t threshold. The influence of the 512nm F_c diameter was more marked than the influence of the 680nm F_c diameter upon the 655nm F_c. These results were interpreted in terms of rod-cone interaction.

4. The data were interpreted as showing that F_c flux, not illuminance, is the variable which should be considered when studying the Westheimer effect.

The above results were discussed in terms of the mechanisms underlying the observed spatial and chromatic interactions.

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