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THE EFFECT OF ROD ADAPTATION ON CONE-MEDIATED FLICKER SENSITIVITY

by

Stuart H. Goldberg

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

1983

Stuart H. Goldberg

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

6/29/83
Date

Chairman of the Examining Committee

August 31, 1983
Date

Herbert D. Saltzstein
Executive Officer

Mitchell L. Kietzman

Supervisory Committee

The City University of New York

Abstract

The Effect of Rod Adaptation on Cone-Mediated Flicker Sensitivity

by

Stuart H. Goldberg

Advisor: Dr. Thomas E. Frumkes

The present study is concerned with the influence of selective rod adaptation on the senstivity of the human observer to cone-mediated flicker. A five-channel Maxwellian view optical system was used to present an LED generated, sinusoidally flickering test stimulus of 2 20’ in diameter at 7 from fixation to the right eye of three observers. In general, this stimulus was red and had a greater influence on cones than on rods, but similar results were also obtained with flickering stimuli of other spectral compositions. In particular, red and green flicker of equal modulation depth and scotopic illuminance (but for which the photopic illuminance of the red flicker was 1.6 log units greater) were sometimes presented in counterphase, resulting in a nonflickering stimulus for rods but a flickering stimulus to cones. Sensitivity to flicker was measured during the time course of dark adaptation, or in the presence of an adapting field of variable illuminance which due to its spectral properties and illuminance respectively was shown to exert its influence on rod light adaptation. Sensitivity to flicker was usually assessed by having the observer adjust the illuminance of a flickering stimulus of constant modulation depth (87%) and frequency until flicker could just be perceived, but conclusions were verified by means of modulation thresholds.

Cone-mediated flicker sensitivity decreases throughout the rod recovery stage of dark adaptation. This effect is relatively small (0.3 log units) for flicker frequencies up to 5 Hz, but increases to about a log unit for flicker frequencies exceeding 15 Hz. Similarly, cone-mediated flicker sensitivity increases as the illuminance of a rod-stimulating adapting field increases. By varying both the size and the shape of the rod-stimulating adapting field, this influence was shown to involve a retinal area of about 1 mm (3 20’) in diameter.

The present results were discussed in terms of findings reported by other laboratories including psychophysical data from normal observers, color deficient subjects, and ophthalmological patients, as well as electrophysiological data in subhuman species. The combined findings suggest that unstimulated, dark adapted rods initiate a tonic inhibition of cone-mediated flicker signals. Several possible retinal pathways were suggested which could underly this influence.

Acknowledgements

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My mother and brothers proved that they were special throughout these past years by giving me unquestioning support whenever and however they could.

My most vital and unending sustenance has come from my wife, Judy. She was always there to provide confidence and encouragement when I needed it. Being the wife of a graduate student is a lonely existence. I dedicate this research to Judy.

I owe a special debt to my father who impressed upon me that the enlightenment which knowledge brings is always worth the effort expended to acquire it.

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Chapter 1: Introduction

According to the duplicity theory of vision, the vertebrate retina functions as a duplex processor with capabilities that are defined by the type of photoreceptors which are presently operating (for reviews see Barlow, 1972; Gouras, 1972). Although rods and cones must perform somewhat similar functions, rod-related (scotopic) vision is more oriented toward detection of dim lights, while cone-related (photopic) vision is more oriented toward keen temporal, spatial and wavelength discriminations.

Traditional interpretations (e.g., Hecht, 1937; Stiles, 1939; Wald, 1945; Rushton, 1961) stress the functional differences between the scotopic and photopic visual systems and suggest that they function independently of one another. For example, Figure 1a (Hecht & Schlaer, 1936) illustrates the influence of illuminance on the critical flicker frequency or CFF, an index of temporal sensitivity described in more detail in the next section. For various wavelength stimuli, CFF is plotted as a function of the log of stimulus illuminance in photopic trolands,[1] a unit which indicates the effect of a stimulus on the cone system. If we consider results obtained when stimulus illuminance is greater than 1.0 log trolands, all wavelengths provide data which adhere to a single function. At lower illuminances data for different wavelength stimuli describe unique functions. On the other hand, if the data are plotted in terms of rod

Figure 1a. Critical Flicker Frequency, CFF, plotted as a function of the log of the illuminance of stimuli of various wavelengths, in photopic trolands, a unit which scales stimulus effectiveness on cones. (Hecht & Schlaer, 1936)

Figure 1b. CFF replotted from above, but in scotopic trolands, a unit which scales stimulus effectiveness on rods. The legend in Figure 1a represents both plots.

Figure 1a

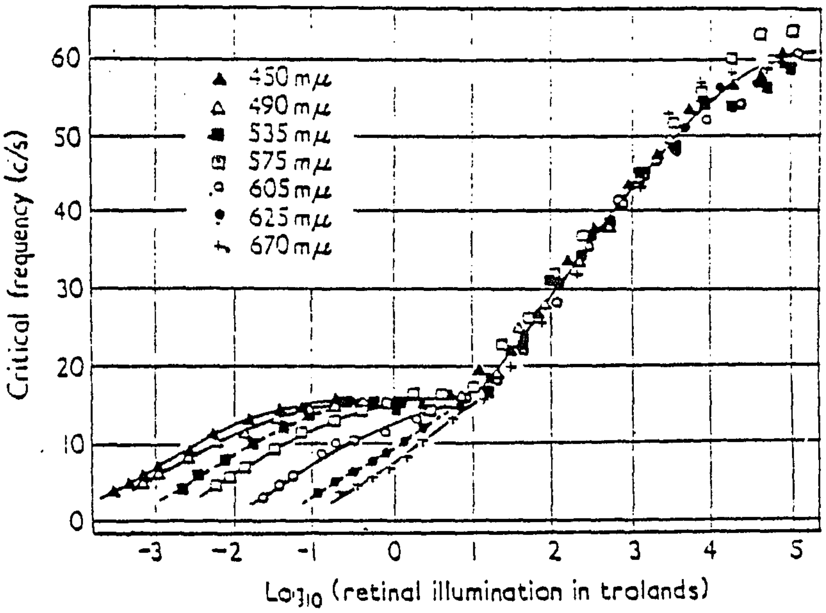
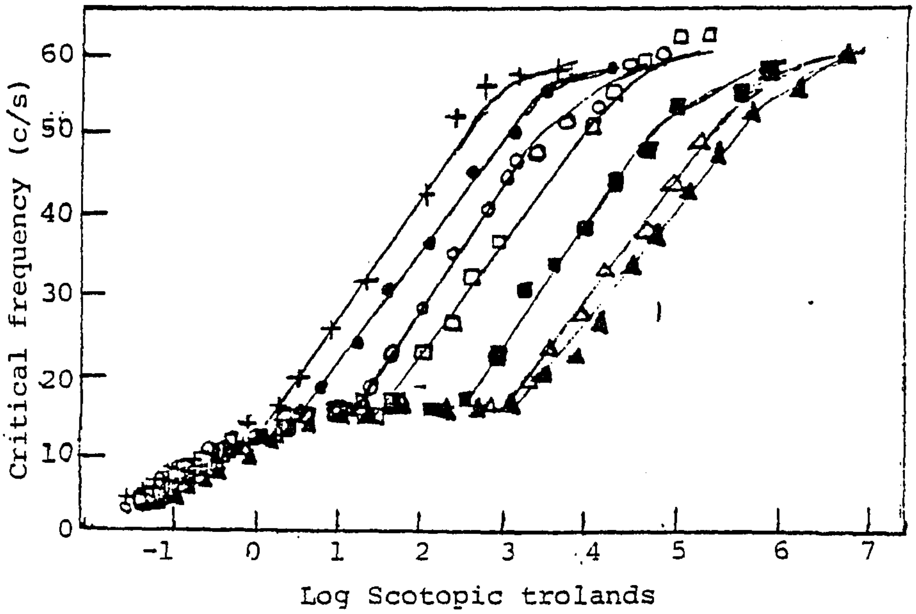


Figure 1b



sensitivity, i.e., in scotopic trolands, the data obtained when stimulus illuminance is less than 0.5 log scotopic trolands describe a common function (Figure 1b). At higher illuminance levels the data for each wavelength describe a unique function. Thus, even though the rods are capable of responding along with cones for several log units above cone threshold (Aguilar & Stiles, 1954), CFF appears to only reflect the response of the receptor type that is more sensitive to temporal changes in illuminance, the cones. Such data are typical of many which led early investigators to conclude that scotopic and photopic vision are more or less autonomous.

In recent years it has become increasingly clear that rod and cone related responses interact under many different conditions, including those which manifest flicker perception. The present investigation considers the influence of selective light and dark adaptation of rods on the ability of the cone system to mediate flicker. The following review considers some basic properties of flicker, some properties of interactions between rod- and cone-mediated vision (rod-cone interaction), and finally, one particular mechanism by which dark- adapted rods influence cone-mediated flicker perception.

Flicker

The temporal resolving or flicker-following capacity of the visual system has been the subject of a great deal of research for over 150 years (for early literature see Piéron, 1965). With some notable exceptions, studies conducted prior to the 1950s used a temporal variation technique which is referred to below as the critical flicker frequency or CFF technique. Typically, the stimulus is turned on and off successively with the interval between pulses being equal to the duration of each pulse (i.e., a square wave with a "duty cycle" of 50%). The time from pulse onset to successive pulse onset is referred to as the period, and the frequency is defined as the reciprocal of the period in seconds, designated in units called hertz (Hz, formerly called cycles per second). Typically, the observer adjusts frequency until flicker is just not perceived, at which point the CFF is reached. A number of parametric and reliable findings emerged over the years. Most notably, CFF tends to increase with the log of the stimulus illuminance (Ferry-Porter law), stimulus area (Granit-Harper law), and dark/time ratio (Ives law). In addition, the influence of the retinal position (Hecht & Verrijp, 1933), temporal waveform (Ives, 1922), and wavelength of the test stimulus (Hecht & Schlaer, 1936) were carefully investigated, as were the influence of other inducing stimuli next to the flickering test (Berger, 1954; Fry & Bartley, 1936; Ripps, Kaplan, & Siegal, 1961). In spite of the widespread use of this approach, it has several limitations. Most importantly for the present study, this technique only provides data pertaining to the fastest flicker following capacity of the subject for a given stimulus condition, and provides no information about sensitivity at slower frequencies.

Due to the influence of Ives (1922), deLange (1958), and Kelly (1961), a newer approach, delineated below as the modulation approach, has largely supplanted the CFF technique. In this approach, the observer is presented with a stimulus of fixed time-averaged illuminance which is usually sinusoidally modulated over time. A sinusoid, as illustrated in Figure 2a, can be described by four parameters: period, phase angle, mean, and amplitude (or modulation depth). The period (P) is most easily defined as the duration of time between peaks or troughs in a cycle. The period also describes the frequency ($f = 1/P$). To designate a particular time reference, the phase angle ($\emptyset$) is used. By convention the phase of the sinusoid in Figure 2a is said to "lead" the phase of a standard sine wave by 90° ($\emptyset = 90^{\circ}$). A phase difference of 0° indicates two time locked sinusoids, while a phase difference of 180° between two sinusoids indicates that the peak of one corresponds in time to the trough of the other (figure 7) in a counterphase relationship. The mean is the time-averaged or steady illuminance. The amplitude is the time varying deviation around the mean. The amplitude expressed as a percentage of the mean illuminance is often called the modulation depth.

Figure 2a. Sinusoidal illuminance waveform illustrated with the parameters that describe it: The period (P), Mean or time-average illuminance, amplitude (termed modulation depth when expressed as a percentage or proportion of the mean illuminance), and phase angle (ϕ).

Figure 2b. Typical frequency response curve obtained via the modulation approach to studying flicker sensitivity. The curves are collected at five different photopic mean illuminance levels and plotted on logarithmic coordinates, where the reciprocal of threshold modulation depth (i.e., sensitivity) is plotted on the left ordinate. (Kelly, 1961)

Figure 2c. Same as Figure 2b, but using an amplitude illuminance response measure on the ordinates. (Kelly, 1961)

Figure 2a

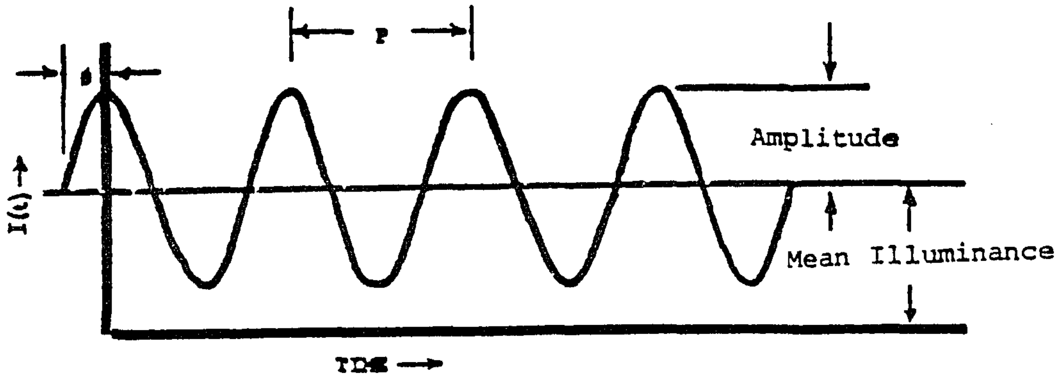


Figure 2b

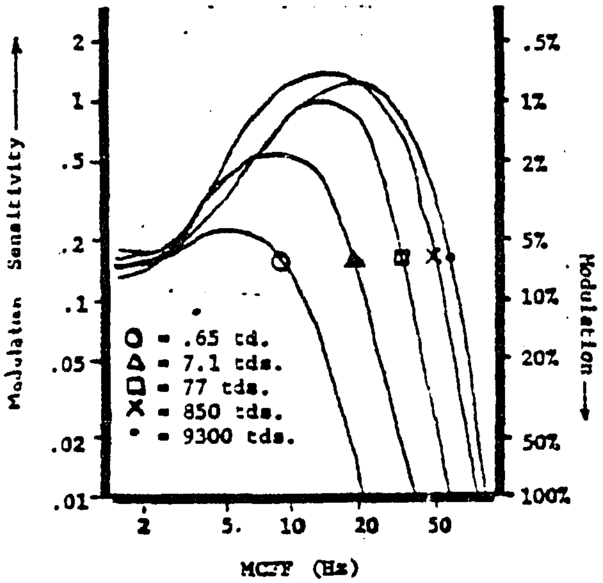
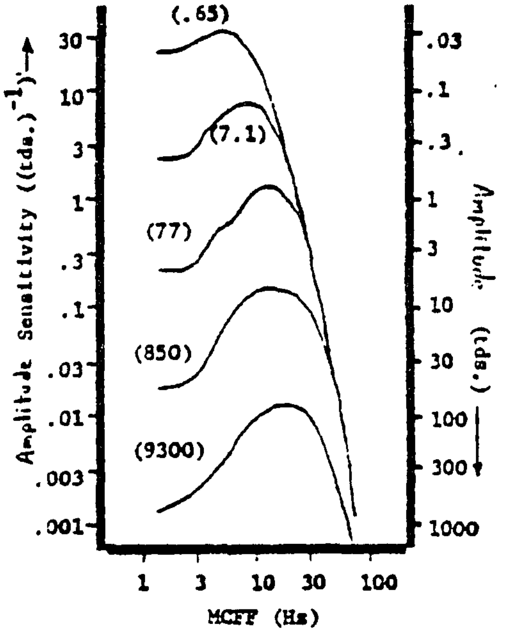


Figure 2c



In the modulation approach, for a range of flicker frequencies, the observer adjusts the modulation amplitude of the stimulus until flicker can just be perceived. Typical data obtained at many different mean illuminance levels are indicated in Figures 2b and c, with the ordinate scaled logarithmically as the reciprocal of modulation (i.e., sensitivity). This modulation approach provides two principal advantages over the older CFF technique. First, the visual system has been shown to operate in a sufficiently linear fashion to allow application of fourier analysis[2] to data such as Figures 2b and c. Application of fourier analysis to such data provides accurate predictions of the responsiveness to other temporal waveforms. For this reason, data such as Figure 2b, are often referred to as "modulation transfer functions" or MTFs (see Kelly, 1972). Second, flicker sensitivity can be assessed at any frequency, not just the highest one the observer is capable of following. Notice in Figures 2b and c that, at most mean illuminance levels, flicker sensitivity is maximal at some intermediate frequency and falls off at both higher and lower frequencies, and that low and high frequency flicker are differentially influenced by the mean illuminance of the sinusoid. Moreover, changing stimulus size, stimulus configuration, or presenting an annulus around the test stimulus has differential influences on high versus low frequency flicker (Keesey, 1970, 1972 Kelly, 1969; Nygaard, 1981; Robson, 1966; Roufs, 1972; Wisowaty, 1979). These and other observations have led some investigators (e.g., Kelly & van Norren, 1977; King-Smith & Kulikowski, 1975; Tyler, 1975) to postulate that low and high frequency flicker are mediated by somewhat distinct mechanisms.

Rod-Cone Interaction

Neural Substrate- In recent years, a large body of evidence has indicated that rod and cone related signals interact within the vertebrate visual system. Recent anatomical evidence suggests that such interaction results principally from two sorts of mechanisms. In the distal retina, gap junctions, the anatomical substrate for electrical coupling between cells, have been observed between rod spherules and cone pedicles in a variety of different species including primates (Raviola & Gilula, 1973). Along these lines, electrophysiological evidence for electrical coupling between rods and cones has been obtained in many different vertebrate species including mammals (Nelson, 1977). In the mammalian retina, these connections provide the only known distal retinal mechanism for rod-cone interaction since no functional second order process (either of the bipolar cells, the somatic ending of horizontal cells, or the axonal ending of B-type horizontal cells) receives both rod and cone input. This mechanism is sufficient to permit rod and cone input to be evident in all types of second order neurons (Nelson, Kolb, Robinson, & Marianni, 1981). Rod-cone interaction is also anatomically evidenced in the inner retina by a number of electrical and conventional synapses between rod- and cone-related bipolar, amacrine, and ganglion cell processes (Dowling & Boycott, 1966; Kolb & Nelson, 1981). Therefore, it should come as no surprise that rod-cone interaction has been observed at the ganglion cell level by means of extracellular recording in virtually every species that has been so examined including cat (Rodieck & Rushton, 1976) and Rhesus monkey (Gouras & Link, 1966).

In general, electrophysiological studies of rod-cone interaction involving single unit recording have shown two similarities. First, photic stimulation of rods or cones leads to a response of the same polarity (either hyperpolarizing or depolarizing) at some common neural locus. Thus, these interactions can be described as "summatory" as has been emphasized by Rodieck and Rushton (1976) and Nelson et al., (1981). Therefore, joint stimulation of rods and cones leads to a larger response than stimulation of either type of photoreceptor alone. One exception to this has been noted in the mudpuppy retina by Fain (1975) who found a c-type s potential (the response presumably of a horizontal cell) which was hyperpolarized by rod stimulation and depolarized by cone stimulation. A second and unanimous feature of single unit studies is that rod-cone interaction is most evident when both types of photoreceptors are stimulated. This is somewhat surprising since both types of photoreceptors release neurotransmitter at a maximal rate in the dark (Dowling, 1979; Miller, Slaughter, & Massey, 1982; Trifanov & Byzov, 1965). Therefore it is plausible that the inhibitory action (Miller, Frumkes, Slaughter, & Dacheux, 1981) of at least some rod- or cone-related amacrine cells types should therefore be evident in the dark.

ERG studies in the frog have suggested that cones are inhibited by rod pathways in the dark. Therman (1939) found responses to long wavelength flashes of light to decrease while responses to a short wavelength stimulus increased as time in the dark continued (also see Fatechand, 1979). Similarly Dodt & Jessen (1960) showed that the intensity at which a threshold response occurred for a long wavelength (652 nm) stimulus decreased at first, then increased at precisely the time during which a rod phase, increase in sensivity, was evident for shorter wavelength stimuli. Several studies (Gordon, 1967; Hood, 1972a, 1972b) have found that the ERG response to an intense white flickering stimulus increases, in magnitude as time in the dark progresses. Hood (1972b) studied this phenomenon in some detail. He found that for long wavelength (636 nm) flicker the response decreases, as much as 10 fold, and the time course of the change was proportional to the scotopic intensity of the bleaching stimulus used. The results were attributed to an increasing, tonic inhibitory influence of rods on cone flicker performance with time in the dark. Since this effect can be blocked by picrotoxin but not by other pharmacological agents, it is likely that this last finding results from a tonic release of GABA in the dark by rod pathways (Goldberg & Frumkes, 1983; Frumkes & Eysteinsson, personal communication).

Psychophysical Studies- In recent years, rod-cone interaction has been manifested by a variety of psychophysical procedures. Color mixing and additivity studies have shown that rod activity contributes to hue and saturation judgements when large or extrafoveal stimuli are employed (Mc Cann, 1972; Stabell, B. & Stabell, U., 1971, 1973, 1979a, 1979b; Stabell, U. & Stabell, B., 1973, 1977, 1979; Trezona, 1970, 1976). Dark adaptation experiments have shown that this interaction grows with rod recovery from a photopigment bleaching (Hough & Ruddock, 1969; Lythgoe, 1932; Spillman & Conlon, 1972). Additionally, it has been demonstrated that rod and cone signals interact in a temporally summatory fashion to change threshold (Frumkes, Sekuler, Barris, Reiss, & Chalupa, 1973; Drum, 1982).

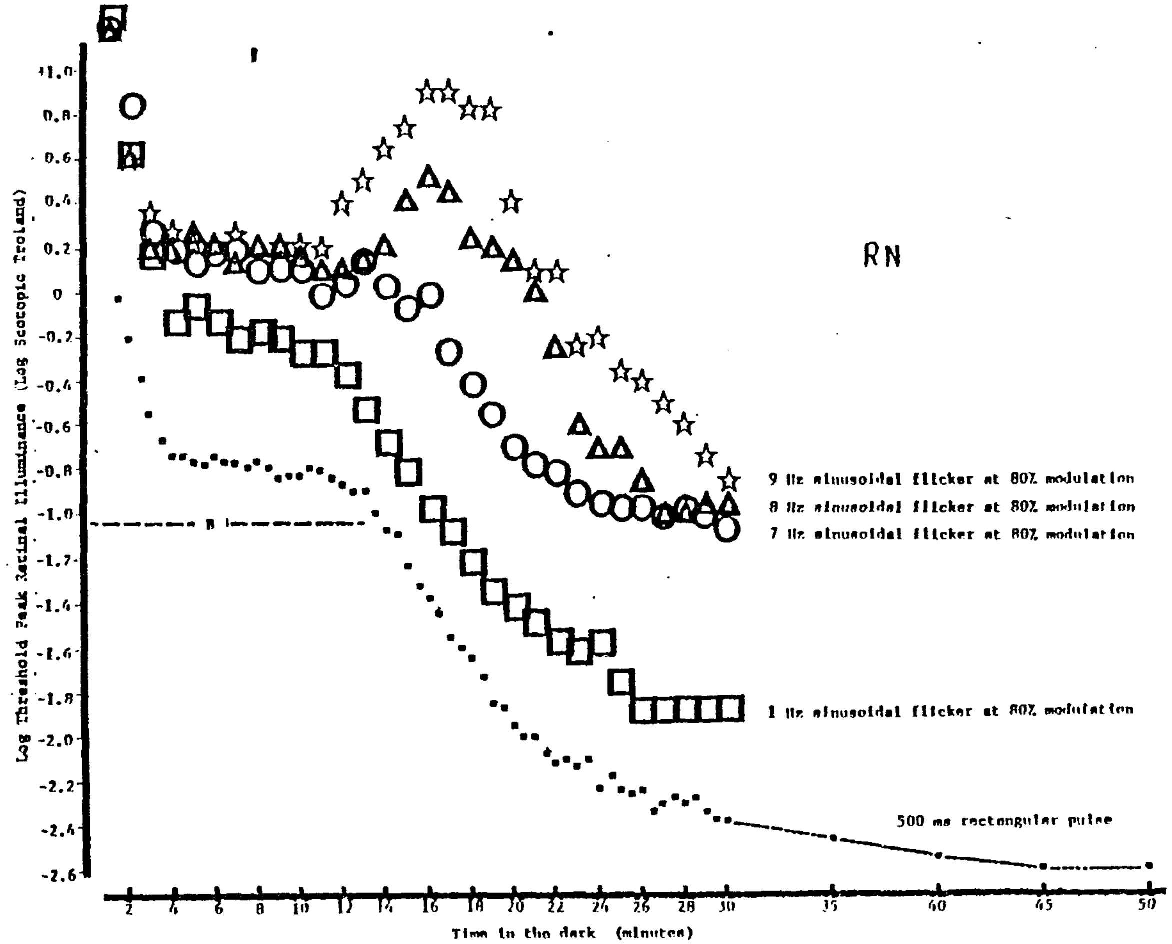
Rod-cone interactions have been most clearly evidenced by means of increment threshold procedures in a variety of psychophysical situations, including sensitization (Blick & MacLeod, 1978; Frumkes & Temme, 1977; Makous & Boothe, 1974), metacontrast (Barris & Frumkes, 1978; Foster, 1976) and Crawford masking (Frumkes & Holstein, 1979). In the most detailed of these studies appropriately presented rod stimulation was shown to elevate cone-mediated thresholds by as much as one log unit (Bauer, Frumkes, & Nygaard, 1983; Bauer, Frumkes, & Holstein, 1983). Several features, reminiscent in many respects of the single unit studies cited above, highlight the quantitative model describing these interactions (Bauer, Frumkes, & Holstein, 1983; Bauer, Frumkes, & Nygaard, 1983). First, the rod signal which influences cone thresholds is proportional to the rod-related photic stimulus. Since the rod influence is on cone-detected thresholds, rod-cone interaction is again most evident when both rods and cones are photically stimulated. Second, the model posits that rods and cones have an excitatory influence at some common locus leading to the perception of light.

Although not always explicitly stated, the majority of psychophysical studies of rod-cone interaction imply such a summatory interaction. For example, MacLeod (1972) and van den Berg and Speckreisje (1977) have studied the influence of the temporal phase between long and short wavelength flickering stimuli on the ability to detect flicker. The illuminance and wavelength of the two stimuli were fixed such that a long wavelength stimulus had a greater influence on cones, a short wavelength stimulus on rods. MacLeod (1974) suggested that rod and cone- related flicker signals algebraically sum at a common locus, but that there is a constant latency difference between the more sluggish rod system and faster cone system. Therefore, depending upon the response phase, the separate signals would sum or cancel each other. For example, with 7 Hz stimuli, flicker sensitivity was maximal when a red and green stimulus were 180° out of phase, and minimal when they were in phase. This suggests that rods have a 72 msec longer latency than cones. For flicker frequencies between 1 and 19 Hz, van den Berg and Speckreisje suggested a constant latency difference of 75 msec. Rodieck and Rushton (1976) came to essentially the same conclusions by extracellularly recording flicker-type responses from ganglion cells. Collectively, these flicker observations constitute powerful evidence for a summatory mechanism for rod-cone interaction.

Over the years, the clearest evidence for an inhibitory influence of rods on cone related vision have involved dark adaptation. Some workers have relied on color perception rather than threshold. For example, some investigators have shown that the threshold for color identification increases after the rod-cone break of the traditional dark adaptation curve (Lythgoe, 1932; Spillman & Conlon, 1972). Still other workers have employed threshold tasks, and have shown that as rods become dark adapted, the threshold for a long wavelength cone-detected test stimulus increases slightly, (Drum, 1981; Wooten & Butler, 1976). In general, all these observations have been explained by assuming that the rod system inhibits cone system sensitivity, as rods dark adapt.

Rod suppression of cone activity, not to be confused with the cancellation effect first described by MacLeod (1972), has also been suggested on the basis of flicker studies. Using a red stimulus of a constant illuminance, such that flicker would be principally detected by cones, Lythgoe and Tansley (1929) found CFF to decrease during the time course of dark adaptation. During dark adaptation and for many different flicker frequencies, Nygaard (1981) determined the illuminance of a 565 nm, flickering stimulus of constant modulation depth which was necessary to detect intermittence. His data are illustrated in Figure 3. For all flicker frequencies less than 7 Hz, data are reminiscent of usual two-limbed dark adaptation curves in that threshold for a flicker sensation decreases throughout adaptation. For 8 and 9 Hz flicker, the required illuminance also decreases during the cone limb of adaptation, but during the initial period of rod recovery the threshold for flicker detection increases before it decreases. At 13 Hz (Nygaard, personal communication), the threshold illuminance increased throughout the rod phase of dark adaptation. The most parsimonious explanation for these findings is that dark adapted, unstimulated rods initiate an inhibitory influence which has little effect on the neural apparatus concerned with cone threshold or low frequency flicker detection, but has a strong effect on the cone mediated detection of higher flicker frequencies. It is this possibility which led to the present study.

Figure 3. Dark adaptation curves obtained for two threshold response tasks: Pulse (500 msec) detection (small filled squares) and flicker detection at 1 Hz (open squares), 7Hz (circles), 8 Hz (triangles), and 9 Hz (stars). (Nygaard, 1981)


RN
Log Threshold Peak Retinal Illuminance (Log Scotopic Troland)
+1.0
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
-1.4
-1.6
-1.8
-2.0
-2.2
-2.4
-2.6
B
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
35
40
45
50
Time in the dark (minutes)
9 Hz sinusoidal flicker at 80% modulation
8 Hz sinusoidal flicker at 80% modulation
7 Hz sinusoidal flicker at 80% modulation
1 Hz sinusoidal flicker at 80% modulation
500 ms rectangular pulse

Rationale for the Present Study

The present study is an in-depth follow-up of the observations of Lythgoe and Tansley (1929) and Nygaard (1981). A sinusoidally flickering stimulus of constant size and wavelength, was presented to the parafoveal retina. Such a stimulus can be varied in three different parameters: the mean illuminance, the modulation depth, and the frequency. In the course of the study different threshold procedures were employed to assess flicker sensitivity by keeping two of these parameters as independent variables while the observer varied the third such that flicker was just detected. All conclusions are based on the results from at least two of these operational procedures. Sensitivity to flicker was assessed throughout the time course of dark adaptation, and at different illuminances of a large scotopically effective adapting field, i.e., at different steady levels of rod light adaptation. A wide variety of stimulus conditions were investigated to determine a range of stimuli for which rod-adaptation could be selectively altered while flicker remained cone-mediated. Furthermore, to make absolutely certain that only cones were detecting flicker, a counterphase situation was designed such that only cones could conceivably be responding to flicker. The main focus of the study was to determine if rod dark and light adaptation does, in fact, effect cone-mediated flicker sensitivity.

Footnotes

(1) Light is measured in terms of radiometric units (physical energy) or in terms of photometric units (the influence on the human visual system). Photopic units are scaled in terms of the overall sensitivity of human cones. Scotopic units are scaled in terms of the sensitivity of human rods. Retinal illuminance, the measure of light used throughout this thesis, can be expressed in terms of photopic trolands (tds.) or scotopic trolands. When no adjective modifier is indicated, photometric units are assumed to be photopic. Two stimuli which have the same scotopic or photopic troland value are equally effective on rods or cones, respectively.

(2) According to Fourier's theorm (Gaskill, 1978) any waveform can be decomposed into or synthesized, to any degree of accuracy, from a superimposition of a sufficient number of sine waves of appropriate frequencies, amplitudes, and with the proper phase relationship. For an expanded but simple presentation of the requirements for use of, and the analytic techniques involved in fourier analysis, see Cornsweet (1970).

Chapter 2: Methods

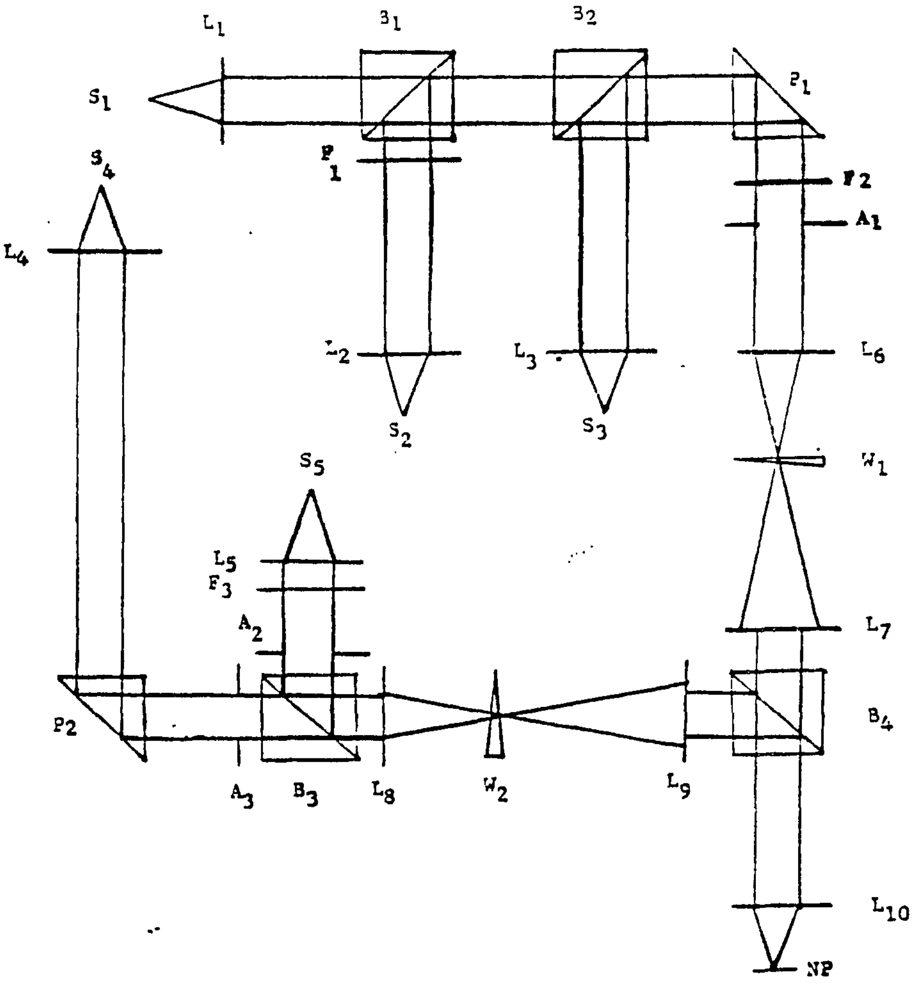
Apparatus and Calibration

A. Optical System

All stimuli were presented to the observer's right eye via a 5-channel Maxwellian view optical system with a separate source for each channel, as indicated in Figure 4. Four sources were LEDs. S1 was "red-orange" (General Instruments 5152), S2 and S3 were "green" (Stanley EBG 5504), and S4 was "yellow" (General Instruments MV 5352) with respectively peak wavelengths of 630, 540, and 585 nm and half bandwidths of about 40 nm. One of these sources, (usually S4) was filtered by a Wratten 29 filter which only passed wavelengths more than 610 nm and served as a red fixation target. S1 and S2, either separately or in combination, served as the sinusoidally flickering stimuli in all but one of the experiments. S5 was a 28 volt, 1 amp, tungsten bulb (CP21) which was underpowered at 24.5 volts and was used as a preadapting or adapting field for dark and light adaptation experiments, respectively.

As illustrated in Figure 4, the output of S1 was first collimated by L1. After passing through two beam splitters (B1 and B2), the collimated beam was deflected 90° by a reflecting prism (P1), passed by a series of attenuating filters (F2) and truncated by an aperture stop (A1). The collimated beam from S1 was then refocused by L6 onto the

Figure 4. Schematic of the 5-channel, Maxwellian view optical system used in the present study, with ray paths from all sources illustrated. See text for details.


L1
B1
B2
S1
P1
F1
F2
S4
A1
L4
L2
L3
L6
S2
S3
W1
S5
L5
F3
L7
A2
P2
B4
A3
B3
L8
W2
L9
L10
NP

plane of absorbance of a Kodak 4 log unit circular neutral density wedge (W1) after which it was recollimated by L7. After passing through another beamsplitter (B4), the recollimated beam was refocused by L10 onto the nodal plane of the observer's eye.

Light from the other four sources (S2-S5) followed similar types of paths. By means of a series of beam splitters and reflecting prisms, these ray paths were superposed in the nodal plane of the observer's right eye and if all apertures were removed completely filled L10, producing a 28° diameter, circular visual field, in Maxwellian view. The focused, superposed images of all five sources, measured at the position of the observer's nodal plane, was under 3 mm in diameter, considerably smaller than the observer's pupil in the low illuminance conditions comprising this study.

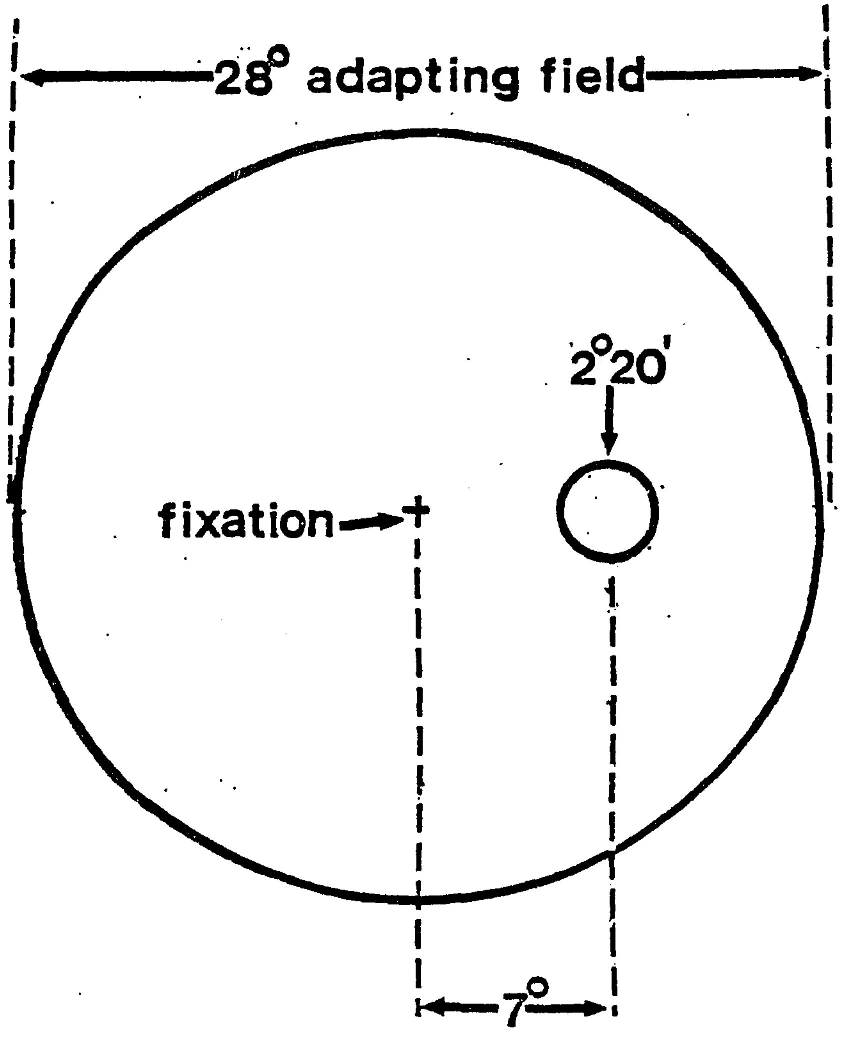
Apertures (A1-A3), whose position was controlled by means of two dimensional micromanipulators, were used to determine both the spatial configuration and visual field locus of all stimuli presented to the observer's right retina. By a projection technique, it was determined that a 1.6 mm diameter aperture produced a retinal image of about 2° diameter. With this information, the exact size of stimuli associated with each source could be specified. Aperture-stopped and other stimuli were made by precision drilling into 1/10 inch aluminum, or were photographically produced with high contrast (> 3 log units) film.

As indicated separately below, the illuminance and wavelength of all stimuli were controlled by a combination of electronic controls, spectral and neutral density filtering. Neutral density filtering was usually accomplished by means of circular 4 log unit neutral density filter wedges. These were controlled by a 40 turn, calibrated dial. Further neutral density and spectral filtering were accomplished by means of fixed filters placed at F1, F2, or F3.

Figure 5 illustrates the field of view used throughout this study. The observers always fixated with their right eye on a red cross subtending 1 of visual angle. The 2° 20', flickering test stimulus (S1 and/or S2) was always centered 7°from the cross center in the right visual field. The only exception to this was a control procedure (see page 32), where S1 and S4 switched roles. The full 28°adapting field was provided by S5.

The observer's head was stabilized with a full mouth bite bar, the position of which could be adjusted in three planes. When the observer was correctly positioned the Maxwellian lens (L10) appeared fully and homogeneously illuminated. This position corresponded with placement of the Maxwellian image in the center of, and entirely passing through, the observer's pupil.

Figure 5. Field of view used in the present study showing positions and dimensions of the 2°20' flickering stimulus, fixation crosss, and adapting field (which also served as the bleaching field).

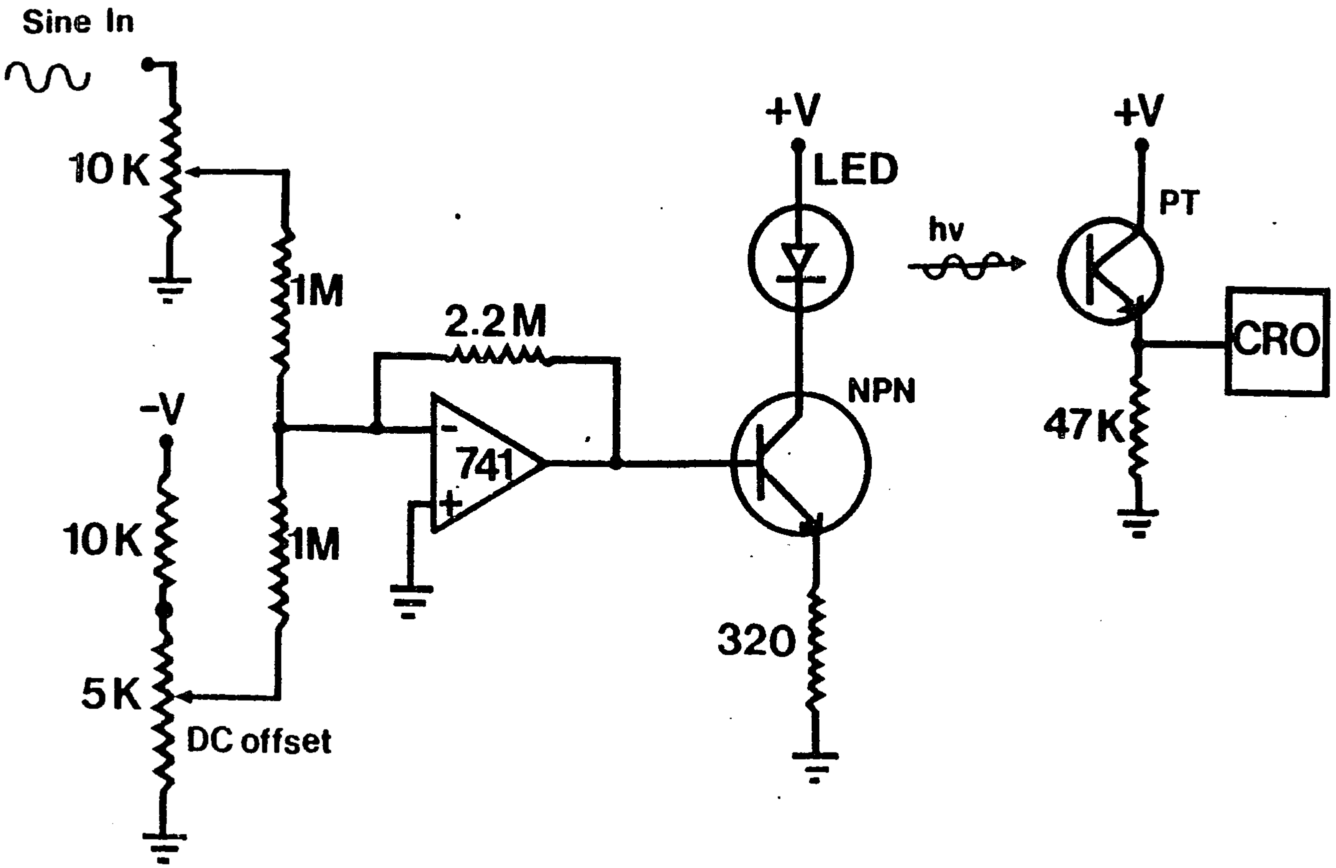

28° adapting field
2°20'
fixation
7°

B. Control of Illuminance and Illuminance Calibration

Figure 2a illustrates the type of sinusoidal stimulus used throughout this study. As indicated in the introduction, such a stimulus has three variable parameters: Its period (or frequency), its time averaged or mean illuminance, and its modulation depth. In addition, if there is an additional sinusoidal stimulus of the same frequency (as in the counterphase control condition), phase angle is a fourth variable parameter.

In order to achieve precise control over frequency and modulation, the control circuit illustrated in Figure 6, described by Nygaard and Frumkes (1982b) was used. The ground alternating sinusoidal voltage of a single function generator (Hewlett-Packard 202A, labelled "Sine In" in Figure 6) was divided across a ten-turn potentiometer (10K in the Figure 6) which determined the modulation amplitude of the time varying signal to be fed into all of the LEDs. A positive bias upon the LED, which was provided by the DC offset potentiometer in Figure 6 and fed into the 741 operational amplifier (opamp), maintained the LED within a linear current-voltage range of operation. All sources of DC voltage were obtained from a ±12 volt power supply. Optical filtering was used to control the mean illuminance. Finally, stimuli could be presented in counterphase with each other by insertion of opamp(s), in an inverting configuration and with unity gains, in the control circuit

Figure 6. Schematic of the electrical circuit used to sinusoidally drive the LEDs. (Nygaard & Frumkes, 1982b)


Sine In
10 K
1M
2.2 M
-V
741
10 K
1M
5 K
DC offset
+V
LED
NPN
320
hv
+V
PT
CRO
47 K

for any one of the LEDs.

The control knob for the 10K potentiometer was placed so that it could be readily adjusted by the observer. The influence of the potentiometer setting on the amplitude of modulation was determined every 1/4 turn by measuring the sinusoidal irradiance, (EG&G 560 series radiometer) on an oscilloscope (Tektronix series 5103N) display. As long as the irradiance modulation was no greater than 90% of the mean level, the relationship between potentiometer dial setting and amplitude irradiance of modulation was found to be quite linear and reliable.

The inputs from the DC offset and 10K potentiometer were added by using the opamp (741) in a summing configuration with appropriate resistance values to achieve unity gain. A portion of the low impedance output of the opamp was captured by the base-emitter junction of a common NPN transistor that provided current gain to the electrical waveform. The radiant output of the LED was controlled by the emitter current which was limited to a level just under specification maximum (35 mA) by a current-limiting resistor coupling the emitter to ground. A phototransistor (PT) with its base lead removed was positioned in the rear of each LED. Its emitter current followed the LED output linearly and the proportionally related voltage drop from emitter to ground (across the 47K resistor) was captured by an oscilloscope ("CRO", Tektronix series 5103N, model D10 single beam). The oscilloscope was used to monitor LED output continuously during all sessions.

Some modification of the general circuitry illustrated in Figure 6 was required for steady presentation of a fixation target, two control procedures, and a scotopic calibration procedure. S4 was usually presented as a fixation target. In this operating mode, a 50K ohm ten-turn rheostat coupled the 12.2 volt power supply directly to the S4 current-limiting resistor-ground combination. By varying the position of the rheostat the observer, could vary the illuminance of the fixation target.

One control procedure required the presentation of S4 (yellow) as the flickering test stimulus for comparison with S1 (red) and S2 (green), in terms of photopic flicker sensitivity. For this procedure a toggle switch reversed all circuits prior to the S1 and S4 LEDs. Thus, S1 became a steady, rheostat controlled, fixation target, while S4 was now driven by the circuit in Figure 6. A second control procedure involved presentation of S1 and S2 in counterphase. The scotopic calibration procedure required presentation of S1 and S2 as pulses instead of flickering sinusoids. The modifications necessary to accomplish these last two procedures are covered later in this chapter.

Although, for LEDs, the relationship between foward-biased current and luminous emission is highly linear, the relationship between voltage and current is nonlinear. The deviation of the electro-optical system response from perfect linearity was analyzed by use of oscilloscope-coupled radiometry (EG&G 560 series radiometer) according to the technique described in detail by Nygaard and Frumkes (1982b). The resulting measurements from use of this technique indicated that there were identical distortions for all flicker frequencies from 1-50 Hz (which includes all those in the present study). Modulation depth was defined with the formula $m = L_1 - L_2)/(L_1 + L_2)$, where "$L_1$" and "$L_2$" are the positive-going and negative-going peaks respectively and "m" is the modulation depth (expressed as a percentage). No distortion was observed for stimuli modulated less than 40%. At 90% modulation, the time-averaged illuminance changed less than 6% (equivalent to less than a .05 log unit change) , and all other types of nonlinearities were estimated to be less than 5%. These small stimulus nonlinearities were considered tolerable for the experiments to be performed. Finally, the 10K potentiometer, which was used to control modulation depth, was calibrated, at every quarter turn of its 10 turn range, by aid of inspection of an oscilloscope display.

In the actual experiments the maximum modulation depths for S1 and S2 were set to within 1% of each other (approximately 87%). This was necessary since there is some small difference in the linear responses of different LEDs, and S1 and S2 were presented in counterphase with their mean levels scotopically matched in some control procedures.

The retinal illuminance of each source at its mean level, with no neutral density filtering in the beam path, was determined by a procedure outlined by Nygaard and Frumkes (1982a). The limitations of the procedure require that for maximum accuracy the source image be smaller than the observer's pupil (which it was, see page 24), that the plane of reference of the measuring device be filled with light, and that it be placed at a distance at least 10 times the radius of the source image. This was accomplished by placing the detector head of the radiometer, with a photometric filter in place, 30 mm from the Maxwellian image (which was under 3.0 mm in diameter), on a plane normal to the optical axis of the final eye lens (L10). By appropriate calculations the expression of Nygaard and Frumkes (1982a)

$$E_R = 10^6 Ed^2$$

where E is the the readout from a photopically filtered radiometer, d is the distance from the detector head to the source image, provided the measure of photopic retinal illuminance (E_R , expressed in photopic trolands in this paper). This procedure was repeated for each source specified in Figure 4. For tungsten source S5 this procedure was repeated many times with narrow band interference filters (Baird-Atomic or Ditric Optics, with half bandwidths of 6-12 nm) placed in the beam path at F3. An adapting field of 512 nm peak wavelength, was used in the light adaptation experiments of chapter 4.

The scotopic illuminance of S5, with the above interference filters in place, was calculated by employing the equation

$$\log T_s = \log T_\rho + \Delta$$

from Wyzecki and Stiles (1967, page 226), where T_ρ is the relevant value in photopic trolands, $\Delta = \log (2.567(V'_\lambda / V_\lambda))$; a measure of the difference between the C.I.E. photopic and scotopic spectral luminosity functions, and T_s is the calculated retinal scotopic illuminance (in scotopic trolands).

The scotopic illuminance of sources S1 and S2 were calculated by matching them, at absolute threshold, with S5 (512 nm interference filter placed in F3). For this procedure the circuit in Figure 6 was modified as described on page 42. After 30 minutes of dark adaptation absolute thresholds, via the method of adjustment, for S1, S2, and 512 filtered S5 were determined for all three observers used in this study. All sources were presented as $2^\circ 20'$ discs viewed 7° parafoveally. S1 and S2 were pulsed for 500 msec once every 4 seconds and 512 filtered S5 was uncovered by the experimenter once every 4 seconds for approximately 500 msec. Given the scotopic illuminance calculation done for S5 with a 512 nm filter and the mean neutral density filtering required of all observers, it was determined that the mean absolute threshold was .00044 scotopic trolands (range of 0.15 log units among observers), a threshold value which corresponds quite well to published values (e.g., Hecht, Haig, & Chase, 1937). The absolute threshold for S1 and S2 were treated as 0.00044 scotopic trolands throughout the experiments. This procedure assumes that the absolute thresold for all stimuli was determined by rods, as suggested in the classical literature (Hecht & Hsia, 1945; Wald, 1945). Since the attenuation of each stimulus by either fixed filters or by wedges was known, it was therefore a straightfoward calculation to determine the illuminance of each of the various stimuli presented.

C. Methods

Observers- Three observers, two females (CMT and KJL), and one male (SHG, the author) were used in this study. SHG, who served in all aspects of this study, was 28 years old, emmetropic and an experienced psychophysical observer. CMT, who served in the dark adaptation and one aspect of the light adaptation experiments was 21 years old and myopic. She wore contact lenses during the testing. KJL, who served in the light adaptation experiments, was 28 years old and emmetropic.

General Procedures- Prior to each experimental session, the observer lined up with the full 28° adapting field set at 3.2 log scotopic trolands, then briefly checked the focus and position of the test stimulus and fixation cross. Three types of flicker threshold were determined in the experiments to be reported; illuminance, modulation depth, and CFF. To avoid either light or flicker adaptation all three employed an ascending method of adjustment. During dark adaptation experiments, after each threshold, the observer increased the wedge density to decrease illuminance. During both light adaptation and CFF sessions after the observer completed an adjustment the experimenter turned the appropriate control dial to decrease flicker amplitude (wedge or potentiometer knob) or frequency (function generator dial) before the next trial. One should note that in adjusting the wedge the observer is manipulating the mean illuminance and modulation amplitude of flicker, while in adjusting modulation depth only amplitude is changed.

Several constraints were imposed on data collection. First, no session lasted more than 90 minutes after the 25 minutes of dark adaptation was complete. For dark adaptation experiments the rule was no more than three, 30 minute runs in a day. Second, within each steady state experimental session at least two threshold values were determined with a specific set of stimulus parameters. If the range of values exceeded a certain minimum (0.2 log units for illuminance, 8% for modulation, and 2 Hz for CFF thresholds), at least one additional reading was taken. In dark adaptation procedures the independent variable was time and one determination was made every 30 seconds. Third, every data point reported was based on observations in at least three experimental sessions, and consequently, involves a minimum of six threshold determinations. Fourth, to facilitate threshold determinations, the observers were instructed to use a flicker blanking switch which cancelled the "flicker" in the test stimulus, leaving it steady at the mean illuminance of the flickering sinusoid. The blanking switch was placed in the LED driving circuit (Figure 6) so that the time varying, "Sine In," input to the LED could be disconnected from the circuit, but not the steady input from the power supply. The comparison, between the flickering and steady stimulus, made for increased confidence, by the observers in their adjustment. This was especially true with mesopic adapting fields where the detection and flicker illuminance thresholds converged.

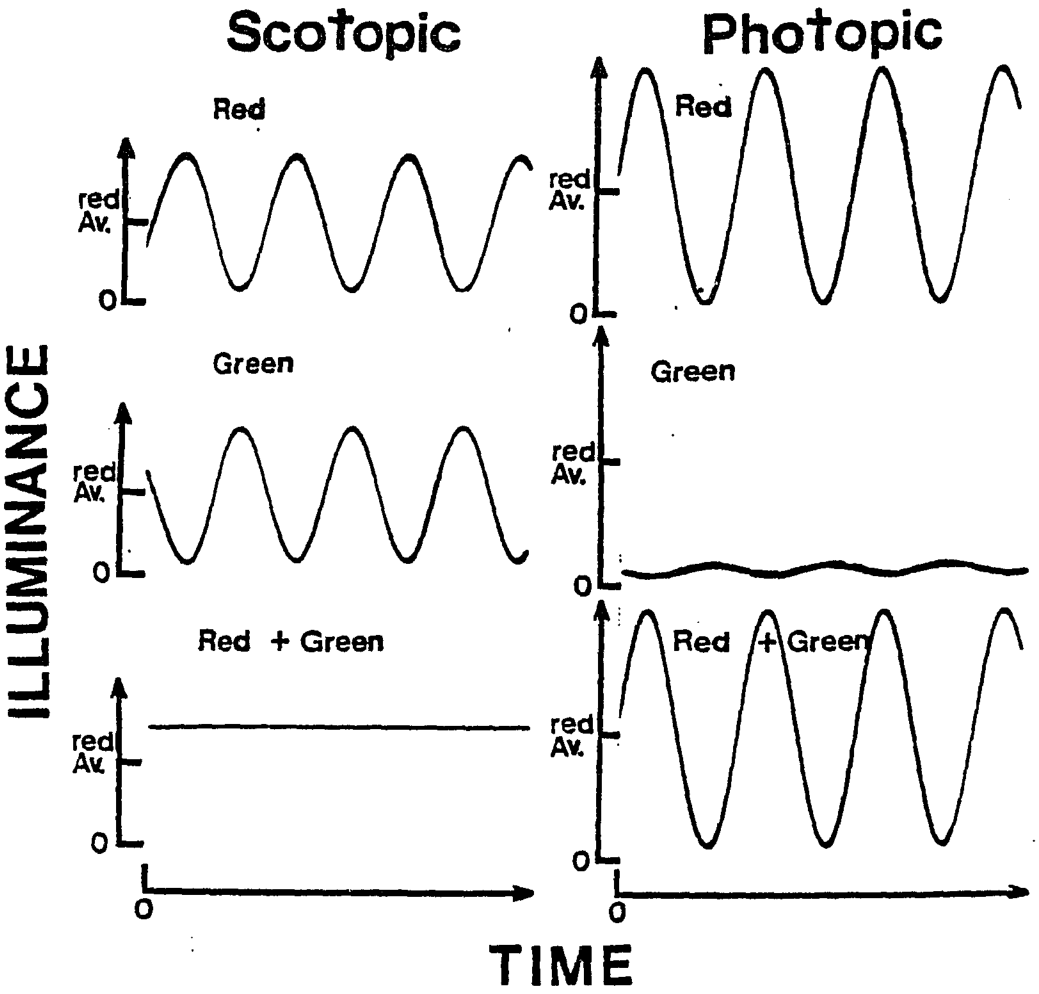
Counterphase Control Conditions

The presumed explanation for the psychophysical examples of rod-cone interaction, that have been studied in the most detail has been a summation of rod and cone signals at a common locus. In order to control for any effect that summating rod and cone flicker signals might have, in these experiments, a special procedure was derived, involving the "silent" substitution paradigm of Rushton (e.g., Rodieck and Rushton (1976). As illustrated on the left of Figure 7, if red and green scotopically equivalent sinusoids are presented in counterphase their sum, or effective scotopic illuminance, is steady at twice the mean illuminance of either, alone. But the illuminances required for a such a red-green scotopic match would create a gross photopic mismatch. Thus, as illustrated on the right of Figure 7, the combination of scotopically matched red and green flickering sinusoids in counterphase results in a photopically flickering stimulus with little change from red alone. Thus, the aim of this control procedure was to present counterphase sinusoids with scotopically identical mean illuminances and modulation depths.

To accomplish the required 180° phase difference the driving circuit of Figure 6 was modified. A second opamp, in an inverting configuration with a gain of 1, was imposed prior to the NPN transistor, in the driving circuit for S1 (red).

This control procedure also required that the S1 (red) and S2 (green) stimuli be matched in terms of their scotopic effectiveness. This was accomplished by measuring absolute thresholds for each, presented as a 2° 20' disc, placed 7° parafoveally in the form of 500 msec pulses, after 30 minutes in the dark. In the driving circuits for S1 and S2, the electrical components which preceded the NPN transistor

Figure 7. Schematic description of the rod effective illuminances (scotopic), cone effective illuminances (photopic), and temporal relationship between the red and green stimuli used to produce the red-green counterphase stimuli described in the text.


Scotopic
Photopic
Red
Red
red Av.
red Av.
0
0
Green
Green
red Av.
red Av.
0
0
Red + Green
Red + Green
red Av.
red Av.
0
0
0
0
ILLUMINANCE
TIME

in Figure 6 were replaced by Tektronix pulse (series 161) and waveform (series 162) generators. By manipulating the timing controls on the 161 and 162 units, S1 and S2 were driven as pulses cycled once every 4 seconds. By manipulating the variable voltage controls on the pulse generators, the pulsed S1 and S2, optically unattenuated, illuminances were set to that of their respective mean sinusoidal levels, while monitoring the oscilloscope display of a radiometer output. These procedures were also used to make the scotopic calibrations mentioned on page 35.

These threshold procedures were carried out on all observers. The results determined the neutral density filtering required to equate the S1 (red) and S2 (green) stimuli in scotopic illuminance. The equation was carried out, during the control experiments, by placing the appropriate neutral density filtering in F1 (see Figure 4). These values turned out to be 0.8 for SHG and 0.9 log units for the other two observers.

By setting the modulation depths for these red and green stimuli to within 1% of each other, reasonably scotopically identical sinusoids could be presented in counterphase, regardless of wedge position. This is the case since an adjustment of W1 would change both sinusoidal mean and amplitude equally for both stimuli and not alter the original match.

To verify that this stimulus was steady for rods CFF thresholds were taken on these red-green counterphase, and also the red (S1), and the green (S2) stimuli for a wide range of stimulus illuminances. These data are plotted, with stimulus illuminance scaled in terms of photopic trolands, in Figure 8 for SHG and Figure 9 for CMT. For the red (Figure 8) and green (Figures 8 and 9) functions there are plateaus at low illuminances which indicates rod flicker following. The counterphase function does not plateau at all. When SHG was presented with counterphase stimuli less than -1.0 log photopic trolands, in illuminance, and 5 Hz, in frequency, flicker was never visible. CMT never saw flicker for red or red-green stimuli below -1.0 log photopic trolands. Figure 10 is a plot of the same data, with stimulus illuminance scaled in scotopic trolands, for SHG. In this plot the red and green functions correspond very well with each other until approximately -2.0 log scotopic trolands and about 5 Hz, when counterphase flicker becomes visible. Taken together these observations indicate that the counterphase stimulus is, in fact, a steady stimulus for rods but time varying for cones. Furthermore, the facts that counterphase flicker was not visible below 5 Hz for either observer and the red and green functions overlapped below 5 Hz (Figure 10) indicate that rods are more sensitive than cones to frequencies below 5 Hz in dark adapted conditions.

Figure 8. CFF thresholds as a function of the log of the stimulus illuminance (photopic trolands) for the green, alone; red, alone; and red-green (counterphase) stimuli described in the text. Note the rod-limbs of the red-alone and green-alone functions and correspondence of the red and red-green functions in the photopic illuminance range. (observer SHG)

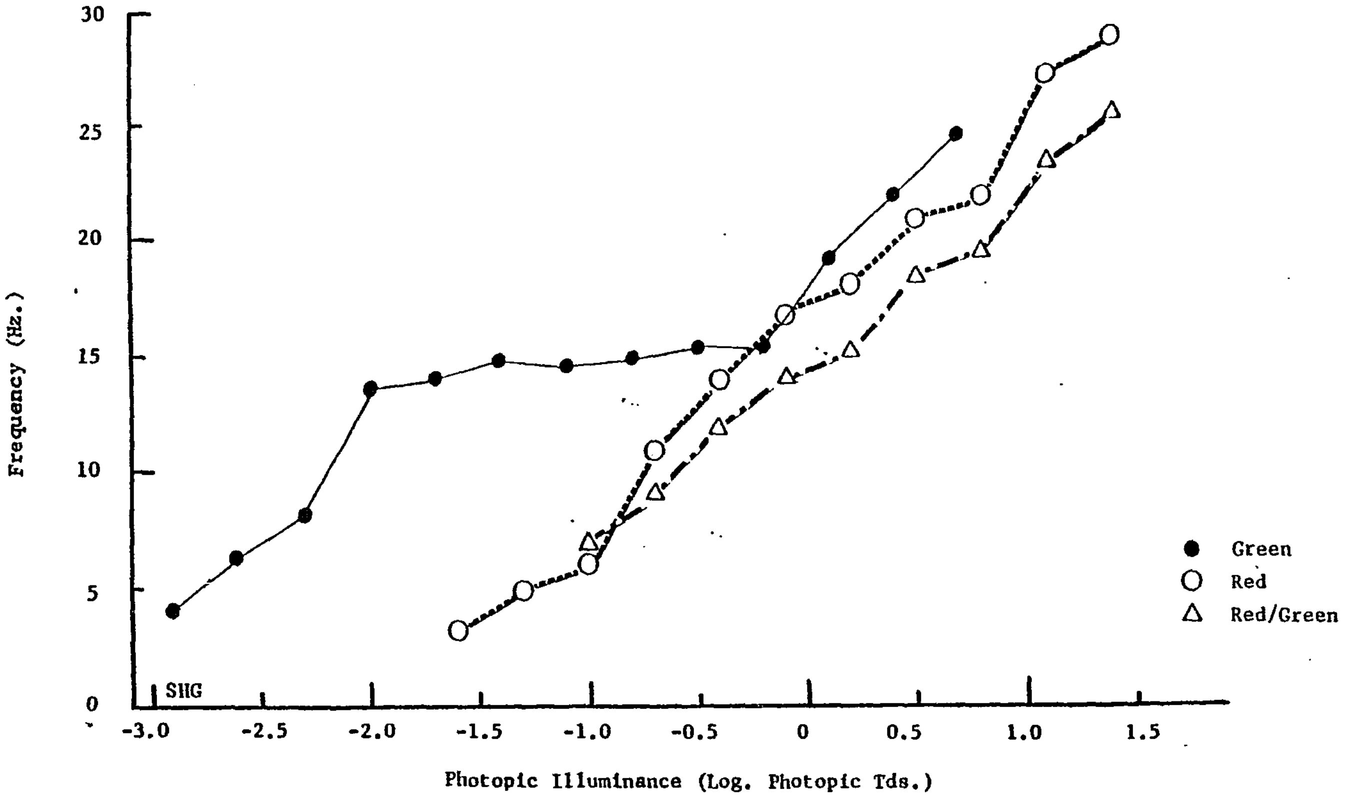

30
25
20
15
10
5
0
Frequency (Hz.)
SHG
-3.0
-2.5
-2.0
-1.5
-1.0
-0.5
0
0.5
1.0
1.5
Photopic Illuminance (Log. Photopic Tds.)
● Green
○ Red
△ Red/Green

Figure 9. Same as Figure 8, but for observer CMT.

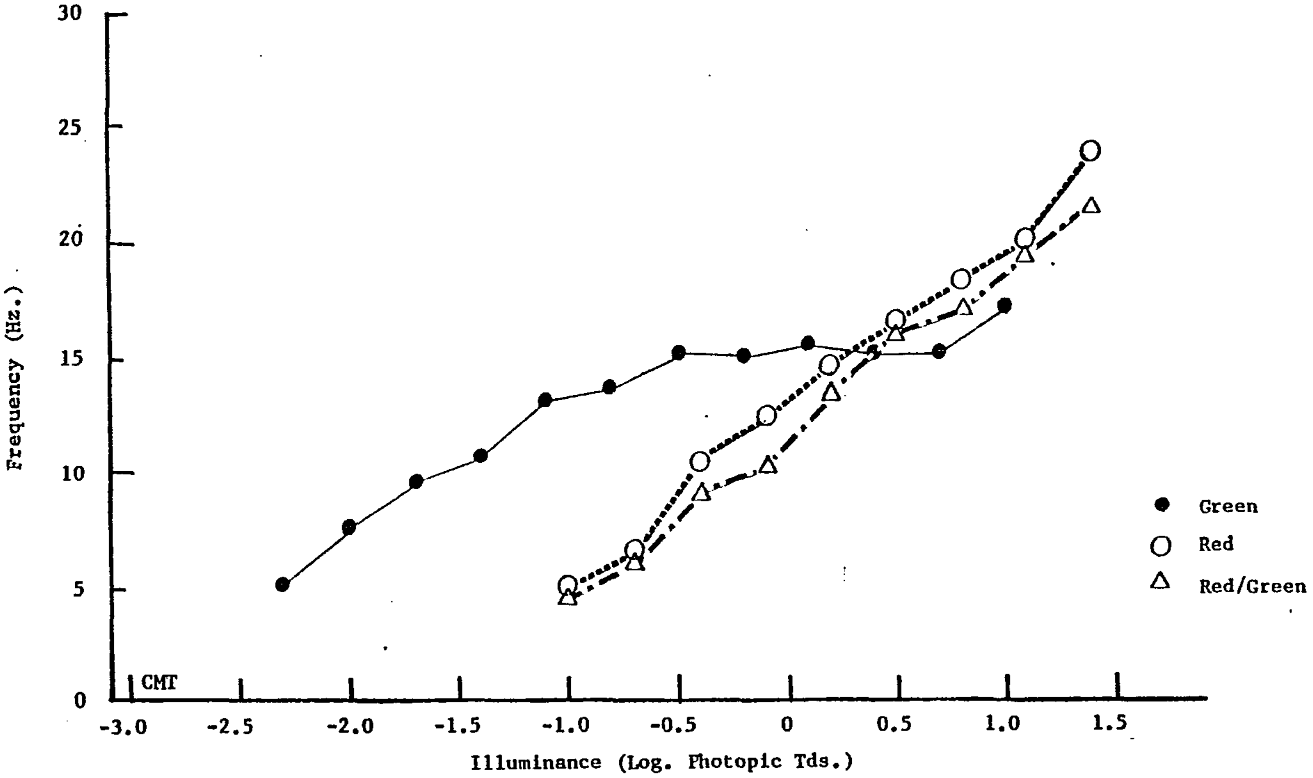
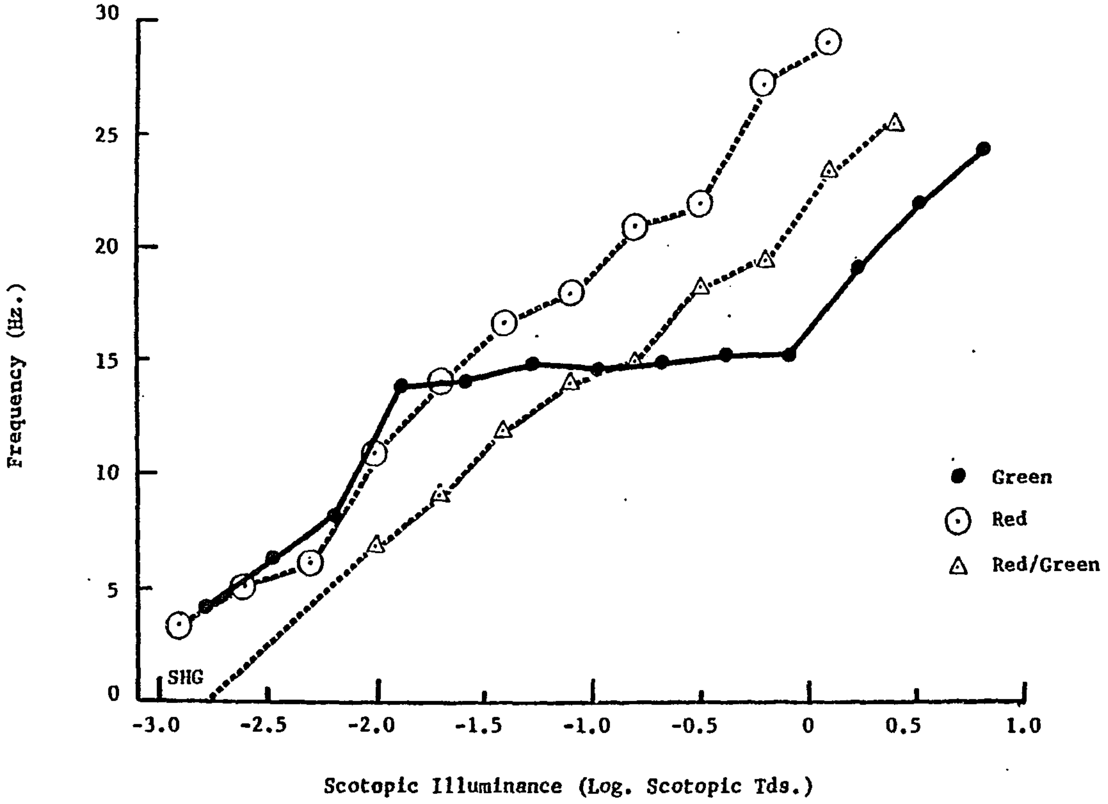

30
25
20
15
10
5
0
Frequency (Hz.)
CMT
-3.0
-2.5
-2.0
-1.5
-1.0
-0.5
0
0.5
1.0
1.5
Illuminance (Log. Photopic Tds.)
● Green
○ Red
△ Red/Green

Figure 10. Same as Figures 8 and 9, but with the abscissa scaled in scotopic trolands for observer SHG. Note the close correspondence between the red and green functions until approximately -2.0 log scotopic trolands.


30
25
20
15
10
5
0
Frequency (Hz.)
SHG
-3.0
-2.5
-2.0
-1.5
-1.0
-0.5
0
0.5
1.0
Scotopic Illuminance (Log. Scotopic Tds.)
● Green
⊙ Red
△ Red/Green

In comparing the red and counterphase functions one notes that counterphase CFF is always slightly lower, almost throughout the whole range of illuminances. This is partially a result of the modulation depth for the counterphase stimulus being slightly less than that for the red stimulus. If one refers back to the right side of Figure 7, it becomes obvious that the added green, compared to red alone, makes for a combination stimulus with a slightly higher mean and lower amplitude illuminance. Therefore, lower CFF values are to be expected. Kelly (1972) has demonstrated that it is the amplitude of modulation that is most crucial in determining CFF. In both the dark and light adaptation experiments, presented in the two following chapters, the illuminance necessary to detect the same frequency of flicker was slightly greater for counterphase than for red stimuli i.e., the counterphase function generally ran slightly above the red function. But the shift is greater than would be expected on the basis of a small (0.7 troland, calculated at 87% modulation of S1 and S2) difference in amplitude. Some other factor must also be operating here.

One should also note the long plateau (1.8 log units) in the green CFF functions of both observers. Similar plateaus have been noted for rod CFF functions by Conner and MacLeod (1977) and Nygaard (1981). A similar plateau is also evident in Figure 1 for stimuli shorter, in wavelength, than 575 nm.

Chapter 3: The Influence of Dark Adaptation on Flicker Sensitivity

The present series of experiments are an extension of the findings of Lythgoe and Tansley (1929) and, particularly, Nygaard (1981). The present experiments examine a decrease in sensitivity to flicker which can sometimes be observed during the time course of rod dark adaptation. The results show that this represents a decrease in cone-mediated sensitivity to flicker which is dependent on the state of rod adaptation.

Procedure

The same basic procedure was used for all the experiments reported in this chapter. After the observer was aligned with the optical system, a preadapting stimulus was presented for 60 seconds. This was generally a "white light" (spectrally unfiltered tungsten source S5) of 46,000 photopic trolands (tds.). In the case of one control experiment, the bleaching light was 480, 540, 580, or 600 nm in wavelength (determined by interference filters) and 150 scotopic trolands in illuminance. After the bleaching light was extinguished, the observer was presented with a flickering test stimulus of a constant modulation depth (87%). As determined by the LEDs which served as sources, the flickering test stimulus was either red, green, yellow, or red and green of equal scotopic illuminance in counterphase. For each observer, the conditions were randomly picked for any particular day's testing with one provision. No stimulus condition was run more than twice in a day.

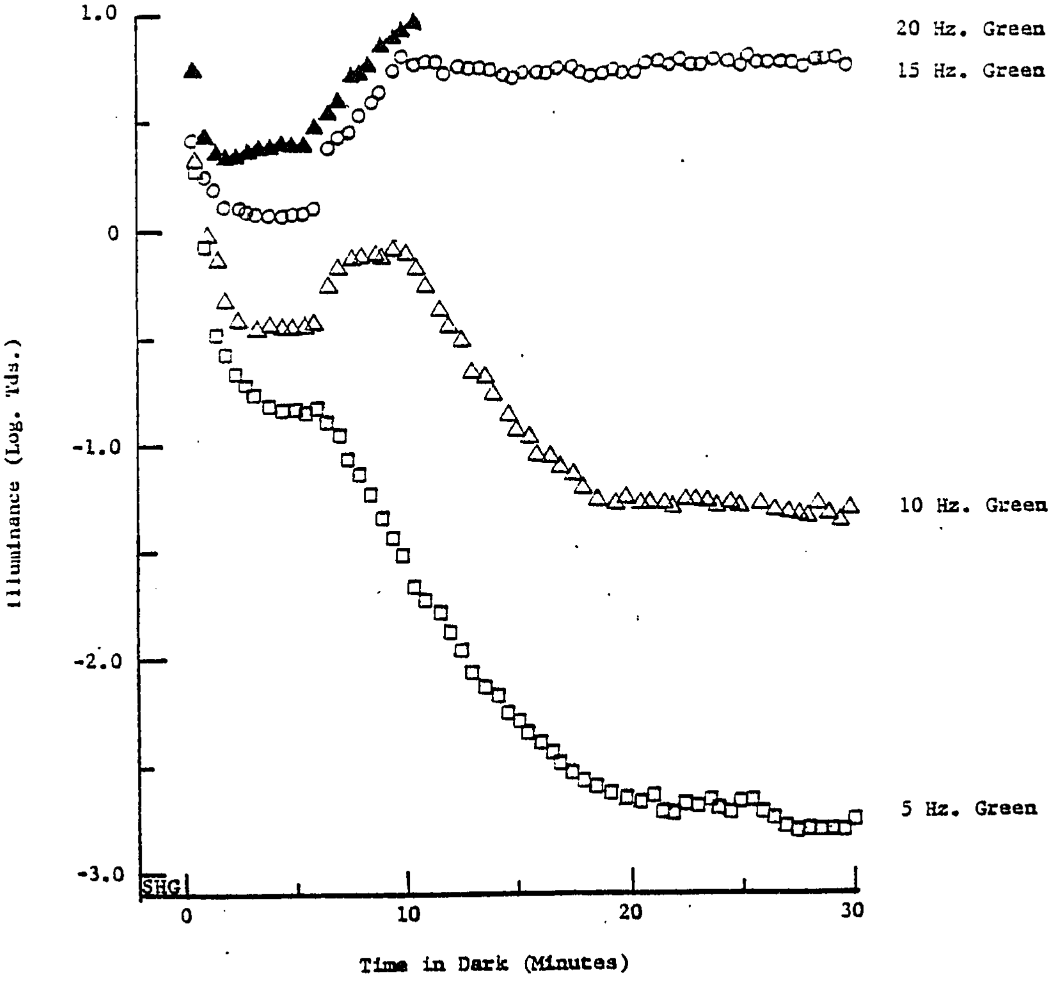
Throughout dark adaptation, the observer continually adjusted the illuminance of this stimulus so that flicker was barely perceptible. In making the adjustments, the observer always approached threshold in an ascending manner to minimize any adaptation effects (see Granit & von Ammon, 1930; Smith, 1970, Pantle, 1971). The wedge position controlling the test stimulus illuminance was recorded every 30 seconds.

Results and Discussion

The Influence of Dark Adaptation on Sensitivity to Green Flicker

Figure 11 (observer SHG) illustrates sensitivity changes to green flicker as a function of time in the dark, in minutes, for four different frequencies. In this figure (and except for Figure 20, all figures in this chapter), the illuminance necessary to detect flicker is plotted on the ordinate in log photopic tds. Hence, an increase in sensitivity is indicated by a lowering of the ordinate position. Notice that as flicker frequency increases, overall sensitivity to green flicker decreases.

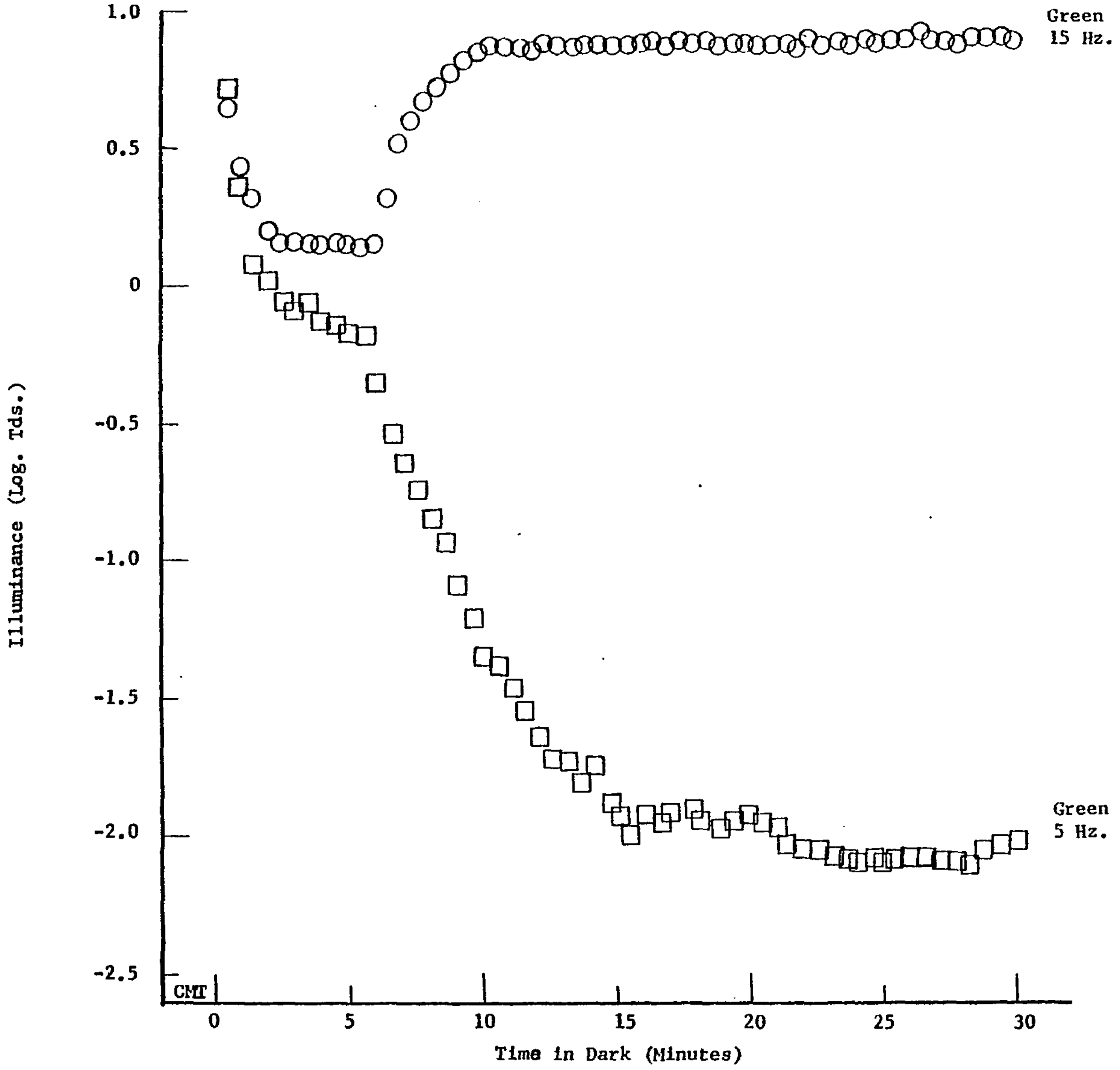
Figure 11. Green flicker sensitivity as a function of time in the dark. Sensitivity was measured at four frequencies; 5 Hz (open squares), 10 Hz (closed triangles), 15 Hz (circles), and 20 Hz (closed triangles). After about 11 minutes of dark adaptation, for 20 Hz, the observer did not perceive flicker with the stimulus adjusted to its maximum intensity (as illustrated). Thus, no further data are plotted for this function. Each point represents the median of at least six runs. Observer's initials generally appear in the lower left hand corner of each Figure presented, SHG in this case. The range of thresholds over runs for SHG, for these and all succeeding dark adaptation data was always between 0.1 and 0.4 log units.


1.0
0
-1.0
-2.0
-3.0
Illuminance (Log. Tds.)
SHG
0
10
20
30
Time in Dark (Minutes)
20 Hz. Green
15 Hz. Green
10 Hz. Green
5 Hz. Green

Inspection of Figure 11 shows that the influence of dark adaptation on green flicker sensitivity is highly dependent on frequency . For example, the 5 Hz data describe a two-limbed function which is reminiscent of a classical dark adaptation curve. According to usual interpretations (Hecht, 1937), the upper limb can be attributed to the sensitivity of cones, the lower limb to rods. Cone limbs are also apparent in the 10, 15, and 20 Hz functions but depending on frequency, the course of sensitivity changes during the latter phase of adaptation i.e., during the "rod-limb" or from about 5-30 minutes in the dark. For 10 Hz flicker, sensitivity first decreases then increases during the rod-limb. For 15 Hz, sensitivity to flicker decreases to a plateau level at about 10 minutes in the dark and then remains fairly constant. For 20 Hz, sensitivity decreases until about 11 minutes in the dark, after which, flicker was not visible even at the maximum stimulus intensity possible (final datum point illustrated on 20 Hz function). Similar trends can be seen for 5 and 15 Hz flicker in the data of observer CMT in Figure 12.

The influence of flicker frequency on the sensitivity changes observed during the latter phase of dark adaptation most probably reflects a number of different factors including the relative sensitivities of the cone and rod systems to different flicker frequencies and the influence of dark adaptation on these sensitivities. Recall that Figures 8 and 10 showed that under dark adapted conditions,

Figure 12. Same as Figure 11, but for CMT and two Green flicker frequencies. The range of thresholds over runs for CMT, for these and all succeeding dark adaptation data was always between 0.2 and 0.5 log units.


Illuminance (Log. Tds.)
1.0
0.5
0
-0.5
-1.0
-1.5
-2.0
-2.5
CMT
0
5
10
15
20
25
30
Time in Dark (Minutes)
Green
15 Hz.
Green
5 Hz.

the scotopic system is more sensitive than the photopic system to 5 Hz flicker. Hence, it is likely that the 5 Hz function (from 5-30 minutes) represents the recovery of the rod system to flicker during adaptation. On the other hand the usual upper limit of rod flicker-following capability is about 15 Hz (Figures 1 and 8, but see Conner & MacLeod, 1977). Accordingly, it would seem that the 15 and 20 Hz functions reflect cone system sensitivity to flicker throughout dark adaptation and that some feature of rod dark adaptation suppresses cone-mediated sensitivity to flicker. The 10 Hz data most probably reflect a combination of these factors and is described in more detail later (Appendix on page 123).

Three different types of evidence are necessary to substantiate the above tentative explanation for the 15 and 20 Hz data of Figures 11 and 12. First, it must be shown that cones are mediating flicker sensations during the latter stages of dark adaptation. Second, it must be shown that all sensitivity changes occurring during the rod-limb of adaptation can be attributed, in fact, to rod adaptation. Third, it must be shown that rod adaptation, not an interfering rod-mediated flicker signal is suppressing flicker sensitivity during the latter period of dark adaptation.

1. The effect of stimulus wavelength on flicker sensitivity during dark adaptation

According to the tentative explanation given for the data of Figures 11 and 12, one would expect that if a stimulus were used which favored cone-mediated sensitivity at the expense of rod-mediated sensitivity, the data would always reflect cone-mediated flicker sensitivity. By considering the relative spectral sensitivities of the rods and cones as established by classical data (Stiles, 1939, Wald, 1945) and as shown more directly for flicker by the data of Figures 8-10, a cone-mediated flicker sensitivity function could be accomplished by repeating the above experiments with a long wavelength (630 nm) flickering test stimulus. Such data are shown in Figures 13 and 14. These Figures illustrate the influence of dark adaptation and frequency on sensitivity to flicker. (For illustration purposes, the data obtained with the 5 Hz green flicker are replotted as open squares). During the "cone-limb" of dark adaptation, data obtained with a red flickering stimulus appear very similar to the counterpart green data of Figures 11 and 12. During the rod-limb of dark adaptation, however, notice that there is a decrease in sensitivity, a result which was also obtained at 2 Hz (not illustrated). Note in Figure 13 that as frequency increases, the decrease in sensitivity during the rod-limb, grows with flicker frequency. This trend repeats itself in all of the data in the present study.

Figure 13. Red (630 nm) flicker sensitivity as a function of time in the dark for 5 Hz (closed circles), 10 Hz (open triangles), 15 Hz (open circles), 20 Hz (closed triangles), and 5 Hz green (open squares). (observer SHG)

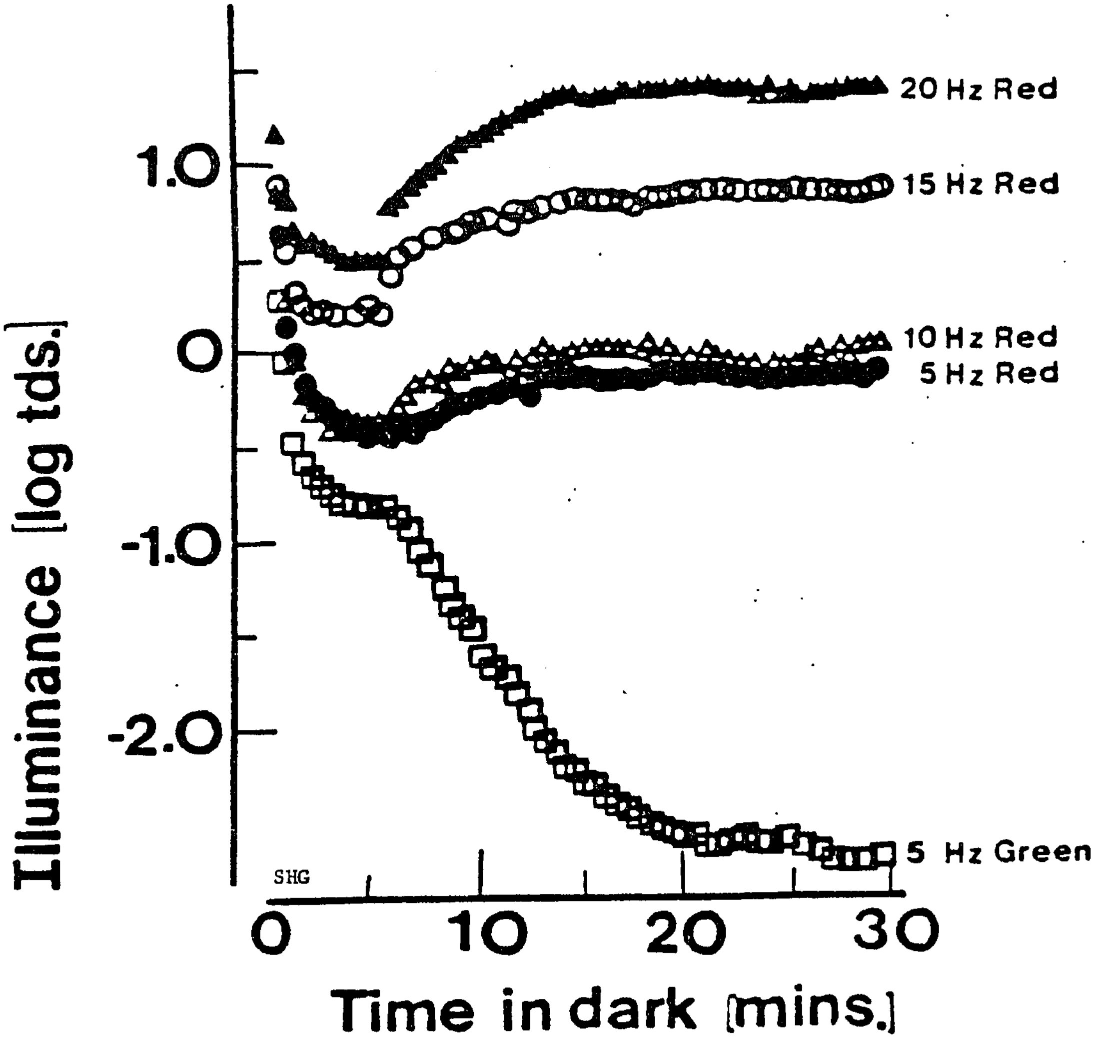
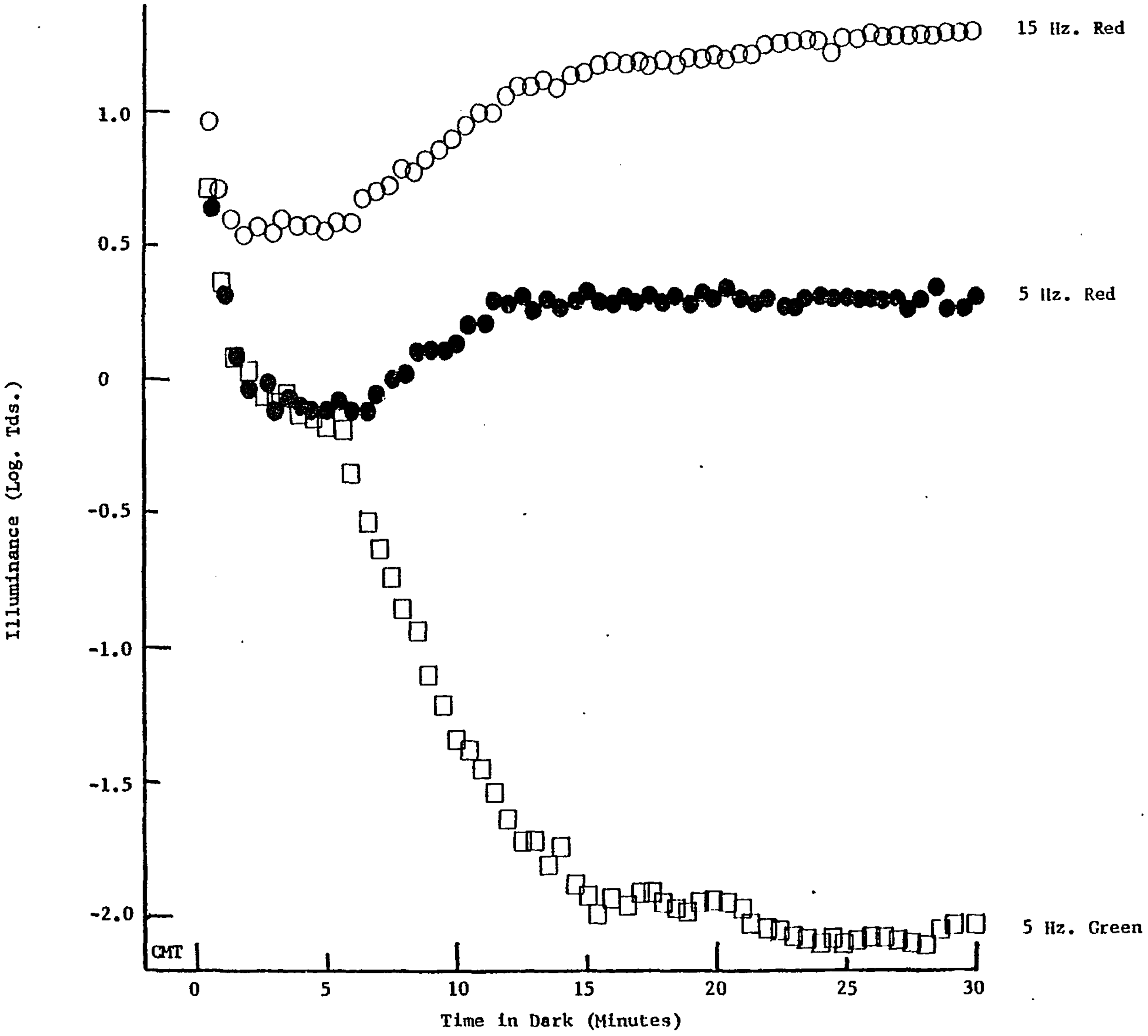

Illuminance [log tds.]
1.0
0
-1.0
-2.0
20 Hz Red
15 Hz Red
10 Hz Red
5 Hz Red
5 Hz Green
SHG
0
10
20
30
Time in dark [mins.]

Figure 14. Same as Figure 13 for observer CMT and only 5 and 10 Hz red flicker.

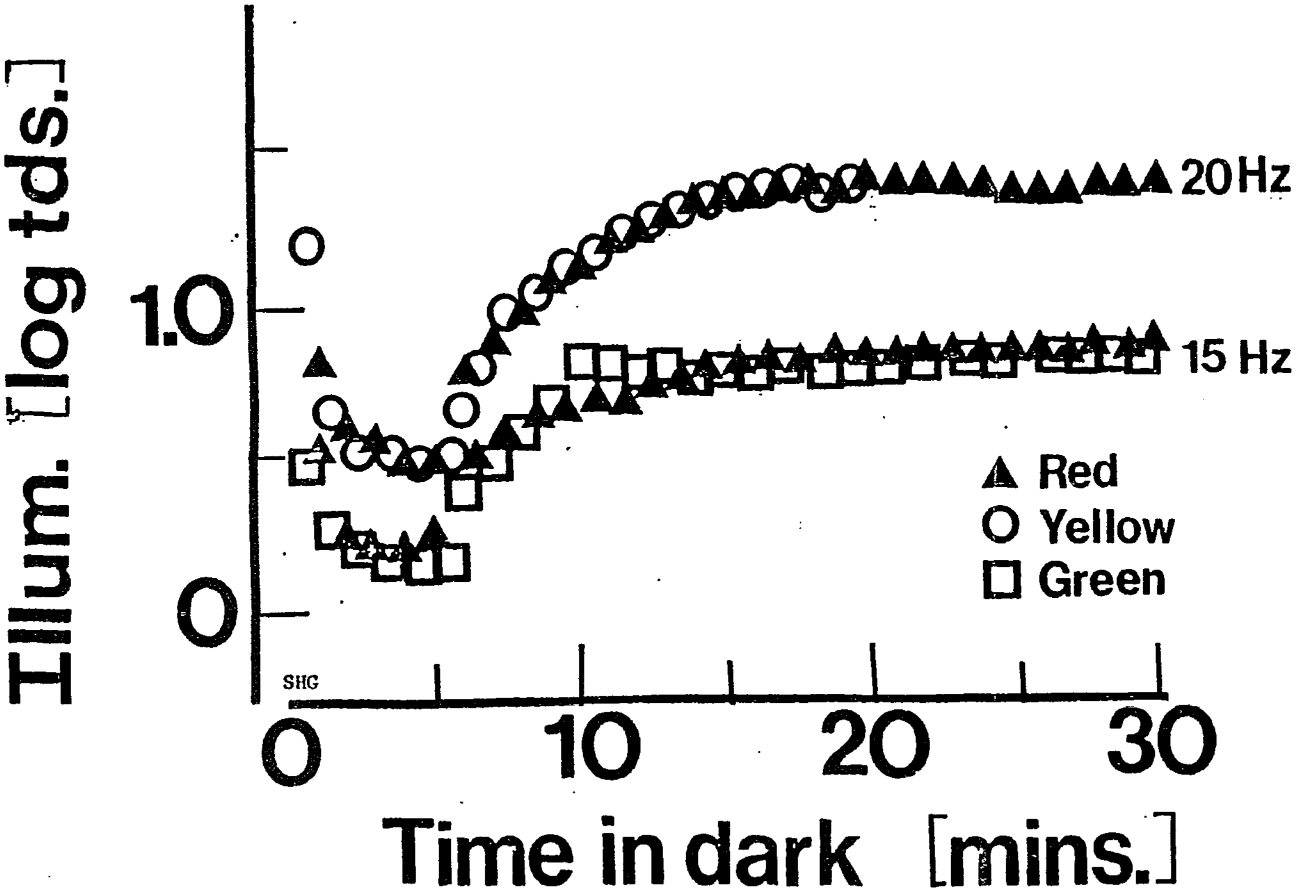

15 Hz. Red
5 Hz. Red
5 Hz. Green
Illuminance (Log. Tds.)
1.0
0.5
0
-0.5
-1.0
-1.5
-2.0
CMT
0
5
10
15
20
25
30
Time in Dark (Minutes)

Providing that cones are in fact mediating the flicker perceptions obtained with the red stimulus, the data of Figures 13 and 14 are entirely consistent with the working hypothesis proposed above. In order to ascertain that, in fact, cones were mediating the flicker, the same experiment was repeated with a yellow flickering stimulus for comparison with the red and green functions on photopically scaled coordinates. Figure 15 is a plot of the sensitivity changes to 15 and 20 Hz flicker as a function of dark adaptation for all three (green, yellow, and red) stimuli. The unit on the ordinate, log photopic trolands, scales flicker thresholds for all stimuli in terms of the sensitivity of human cones. Note again that the frequency exerts an influence on the shape of these functions, but stimulus color has no effect. It can be concluded that the indicated functions represent the sensitivity of the cone system throughout the entire period of dark adaptation. Thus, the first of the three types of evidence has been presented.

2. The effect of bleach wavelength on the time course of cone flicker sensitivity during dark adaptation

In order to determine whether the changes in flicker sensitivity observed after 5 minutes in the dark were attributable to the dark adapted state of rods, the 20 Hz red flicker experiment, whose results are illustrated in Figure 13, was repeated after preadapting the eye with light

Figure 15. Flicker sensitivity as a function of time in the dark for red (triangles), yellow (circles), or green (squares) flicker of 15 or 20 Hz. (Observer SHG)

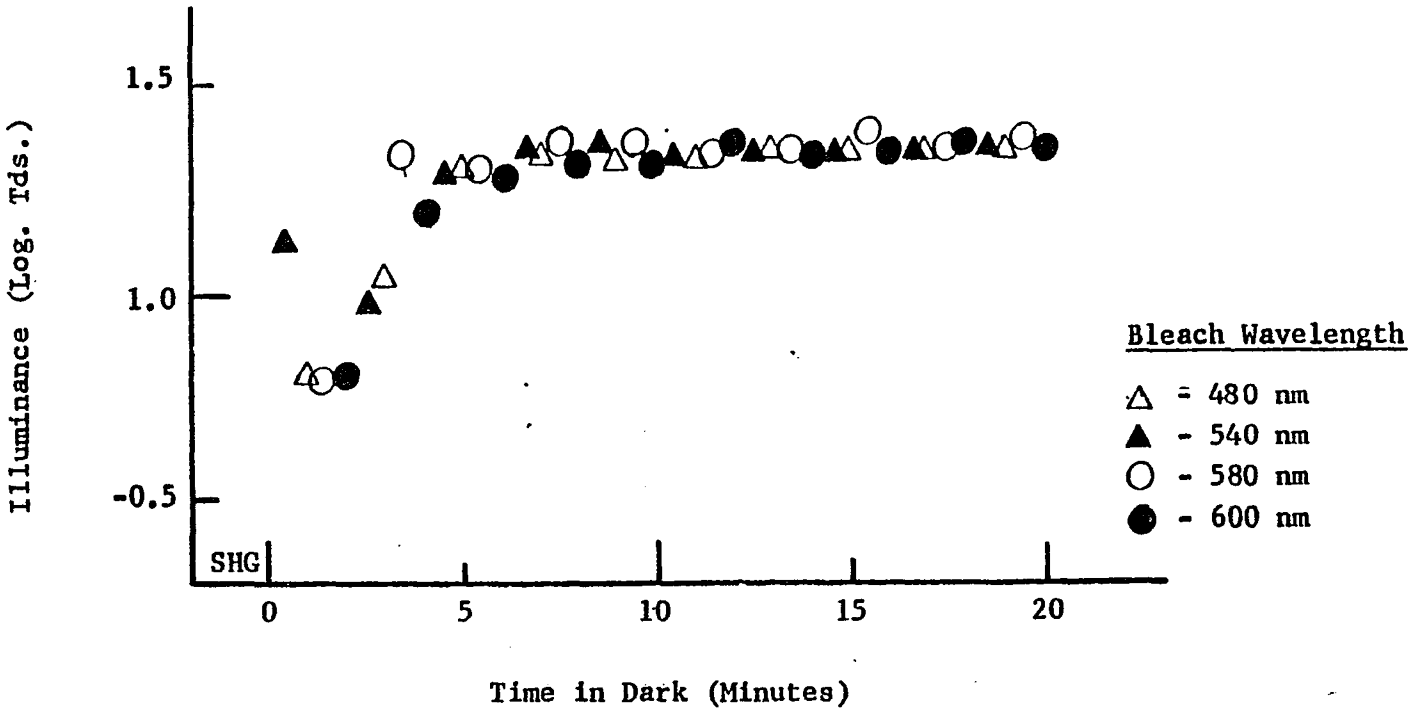

Illum. [log tds.]
1.0
0
20 Hz
15 Hz
▲ Red
○ Yellow
□ Green
SHG
0
10
20
30
Time in dark [mins.]

of either 480, 540, 580, or 600 nm. These bleaches were always 150 scotopic trolands, which was the most intense that could be achieved with the 600 nm filtered tungsten source. The photopic illuminance of these bleaches were respectively 16, 126, 500, or 1600 photopic trolands which differ by as much as 2 log units. Thus, all had an identical effect on rods but widely varying effects on cones. With few exceptions, all four sets of data (Figure 16) fall along exactly the same function. Therefore, the second type of evidence for accepting the tentative hypothesis proposed above has been presented. Accordingly we are left with the conclusion that the changes in cone-mediated flicker sensitivity that occur during the rod-limb of dark adaptation are attributable to the dark adapted state of rods.

3. Red-green counterphase flicker experiments

The sensitivity changes in cone-mediated 15 and 20 Hz flicker that are concommitant with rod dark adaptation could be attributed to a number of mechanisms. One possibility involves an interaction between a putative rod flicker signal and a cone flicker signal such as that studied by MacLeod (1972) and van den Berg and Speckreisje (1977). Although classical data would suggest that rods are unable to follow these high frequencies, recent evidence (Conner & MacLeod, 1977, Skootun, Nordby, & Magnussen, 1980) shows that at higher illuminance levels, rods discriminate flicker

Figure 16. 20 Hz red flicker sensitivity as a function of time in the dark for equal scotopic bleaches of 480 (open triangles), 540 (closed triangles), 580 (open circles), or 600 nm (closed circles). (observer SHG)


Illuminance (Log. Tds.)
1.5
1.0
-0.5
SHG
0
5
10
15
20
Time in Dark (Minutes)
Bleach Wavelength
△ = 480 nm
▲ - 540 nm
○ - 580 nm
● - 600 nm

up to 30 Hz. Since rod dark adaptation may well be expected to increase the size of this rod flicker signal a cancellation explanation must be considered. To examine this possibility, sensitivity to flicker was assessed throughout the time course of dark adaptation with a red-green counterphase stimulus presented as illustrated in Figure 7. This stimulus presented a steady light of double the time-averaged illuminance of red flicker alone, to the rods, while simultaneously presenting cones with a flicker stimulus similar to red, alone.

For observers SHG and CMT, Figures 17-19 compare changes in flicker sensitivity occurring during dark adaptation obtained with red alone and red-green counterphase flickering stimuli. For all frequencies tested, it can be seen that the elimination of any putative rod signal has negligible influence on cone-mediated flicker sensitivity. Since doubling the time-averaged photon catch of the rods barely influences sensitivity these results indicate that the steady effect of the test light on rods is negligible in determining sensitivity changes in the "dark" and rule out a cancellation explanation for the above results. We are left with the conclusion that cone-mediated flicker sensitivity depends more directly on the dark adapted state of rods.

Figure 17. Comparison of red (closed circles) and red-green counterphase (open circles) flicker sensitivity as a function of time in the dark for 5, 15, and 20 Hz stimuli. (Observer SHG)

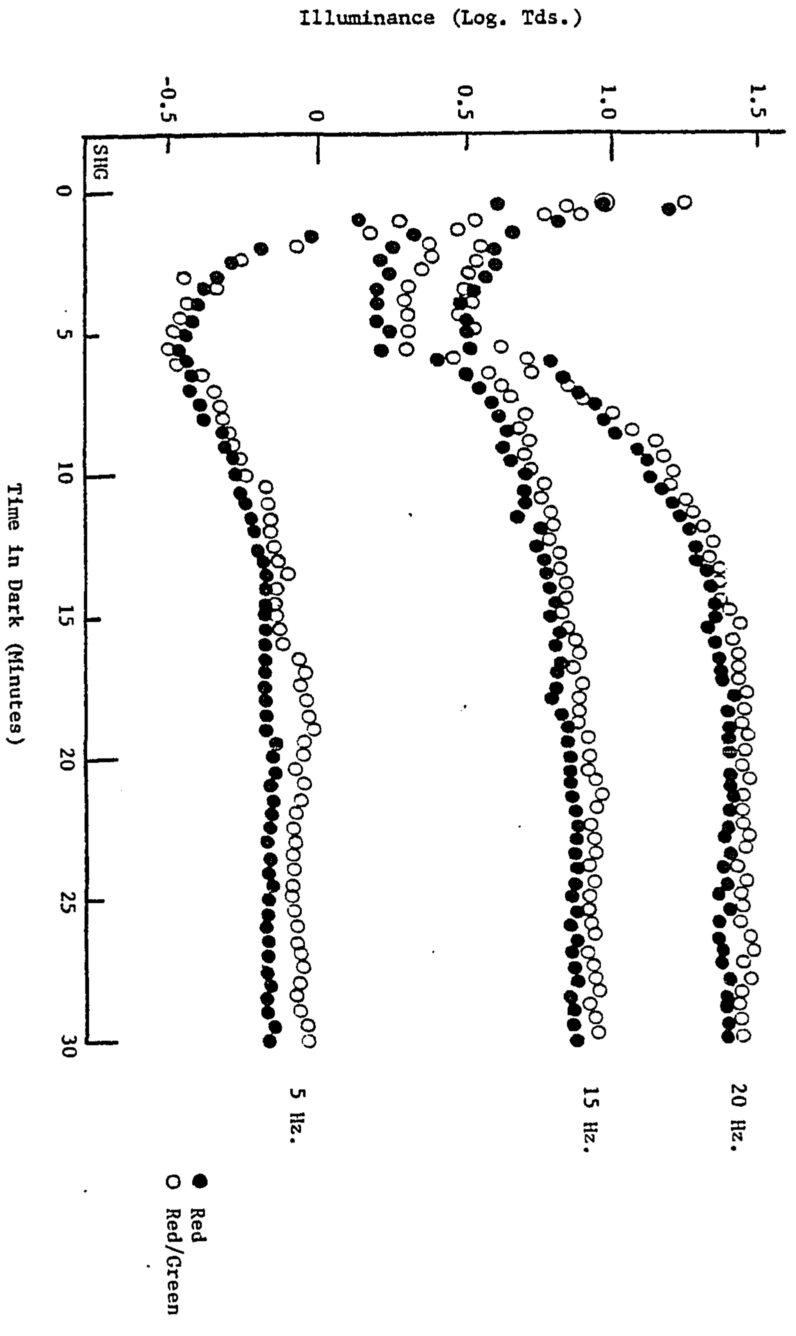

Illuminance (Log. Tds.)
1.5
1.0
0.5
0
-0.5
SHG
0
5
10
15
20
25
30
Time in Dark (Minutes)
20 Hz.
15 Hz.
5 Hz.
● Red
○ Red/Green

Figure 18. Same as Figure 17, but for 10 Hz flicker. A seperate plot was necessary, for illustration of this data, since for this observer the 5 and 10 Hz functions overlapped to a large degree.

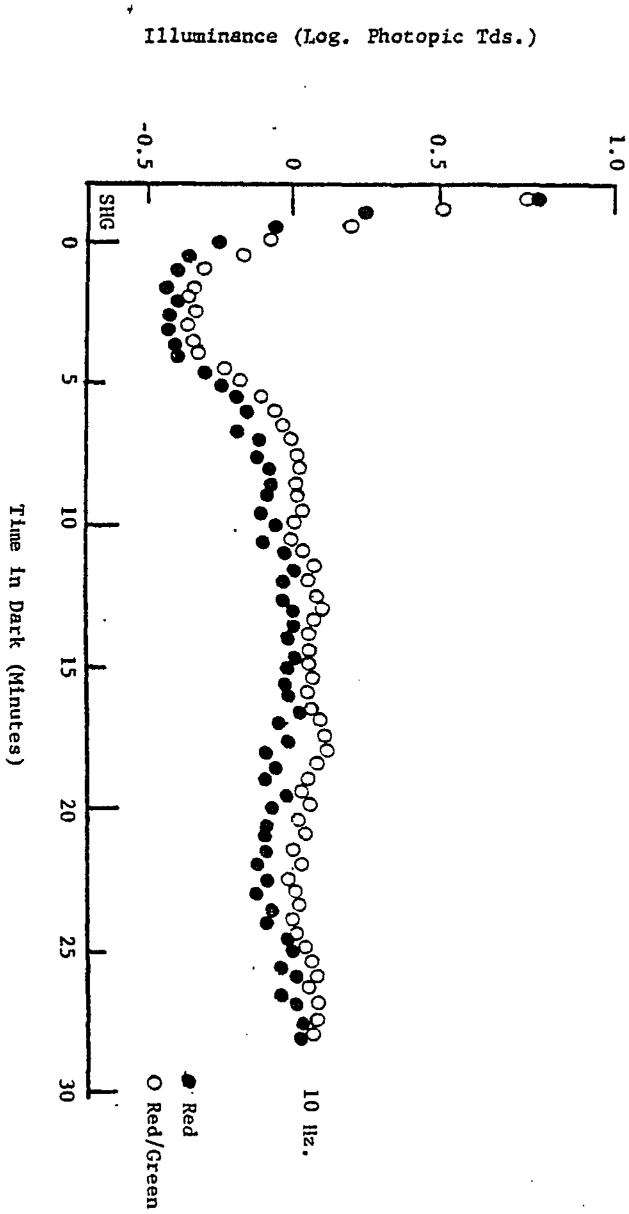
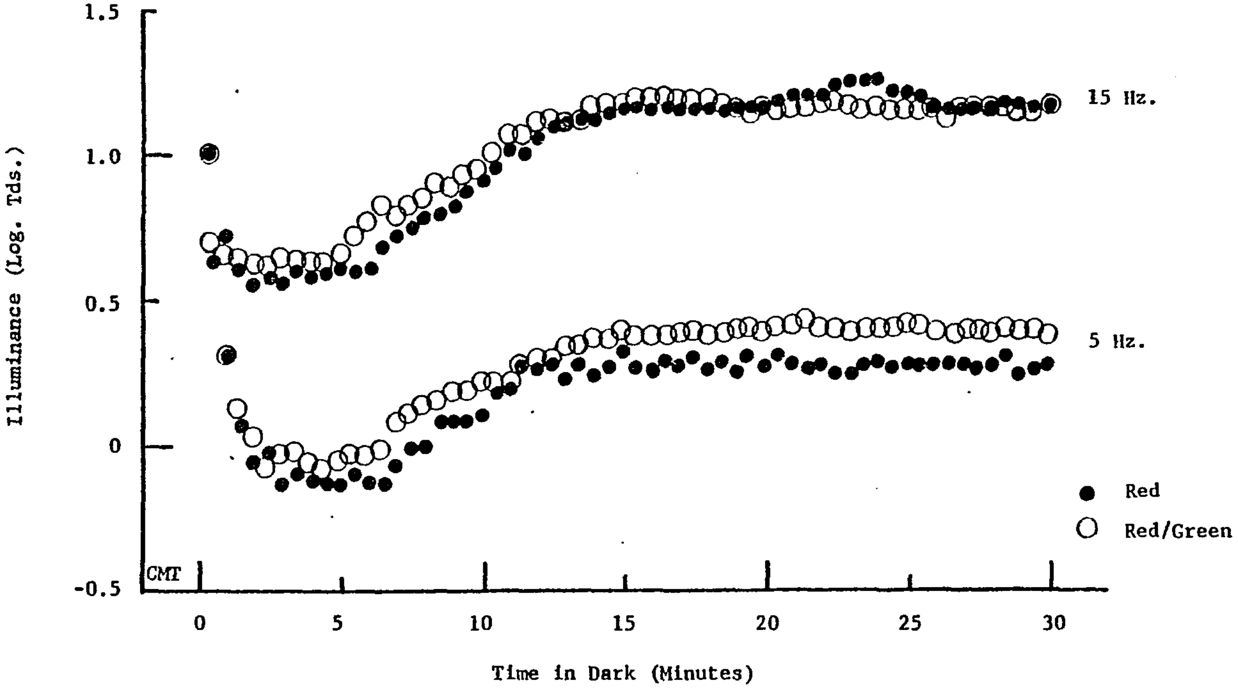

Illuminance (Log. Photopic Tds.)
1.0
0.5
0
-0.5
SHG
0
5
10
15
20
25
30
Time in Dark (Minutes)
10 Hz.
● Red
○ Red/Green

Figure 19. Same as Figure 17, but for observer CMT and 5 and 15 Hz flicker.

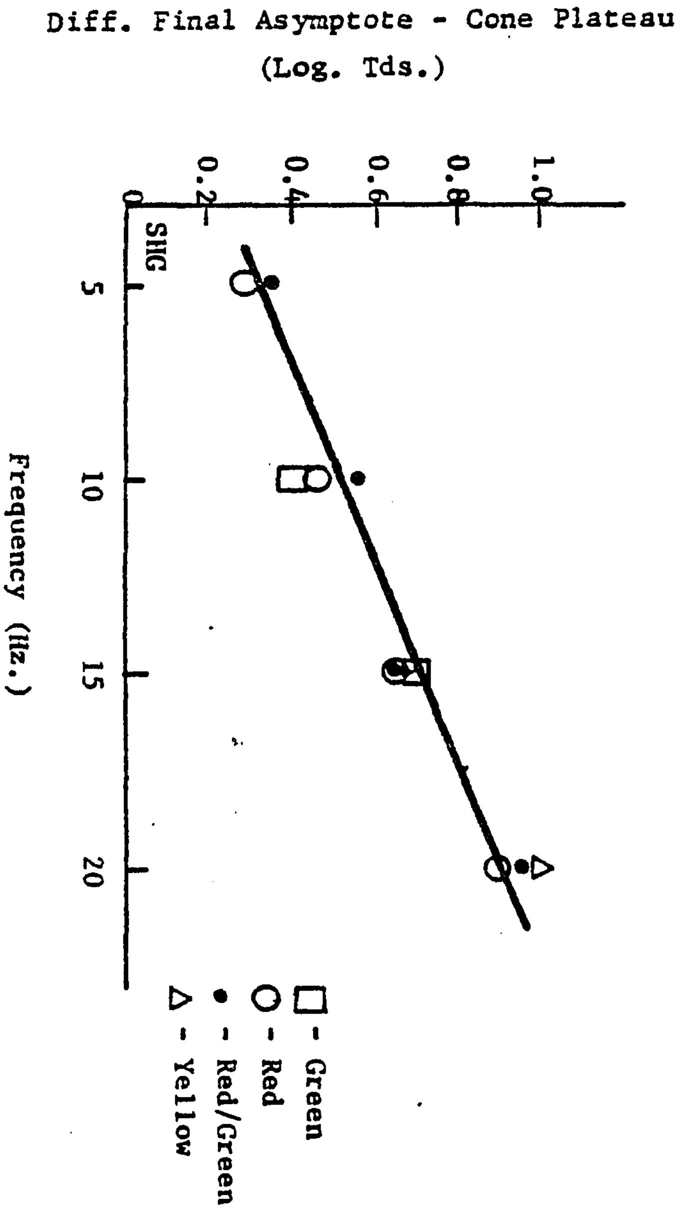

1.5
1.0
0.5
0
-0.5
Illuminance (Log. Tds.)
CMT
0
5
10
15
20
25
30
Time in Dark (Minutes)
15 Hz.
5 Hz.
● Red
○ Red/Green

One also notes, in the functions presented in Figures 17-19 that frequency, again, seems to be influential in determining the size of the decrease in sensitivity, that occurs during the rod-limb of dark adaptation. For observer SHG, the difference between the log illuminance necessary for flicker perception, for all of the different color stimuli whose results were presented in this chapter, at the end of the "cone plateau" and after dark adaptation is plotted as a function of frequency in Figure 20. These results seem to fit a straight line function. Although not shown a similar log-linear relationship was obtained when data from two other observers were similarly plotted. However, the slope of these functions was much steeper. The meaning of this log-linear relationship is obscure at this point.

Conclusions:

The foregoing results indicate that during the time course of rod dark adaptation, the cone system becomes increasingly less sensitive to flicker. The effect seems to depend directly on the dark-adapted state of rods and cannot be attributed to any interference between rod- and cone-related flicker signals. One problem with this type of experiment, however, is that the flickering test stimulus by itself light adapts rods. This influence cannot be totally ignored since in the counterphase control experiments doubling this level of local light adaptation does, to some

Figure 20. Log magnitude of the decrease in flicker sensitivity, after the cone plateau, as a function of frequency (scaled linearly) for green (squares), red (circles), red-green (dots), and yellow (triangles) stimuli presented to SHG. Each point was derived by calculating the log difference between the thresholds at 5 minutes and the last time tested in the dark for the indicated stimulus.


Diff. Final Asymptote - Cone Plateau
(Log. Tds.)
0
0.2
0.4
0.6
0.8
1.0
SHG
5
10
15
20
Frequency (Hz.)
□ - Green
○ - Red
● - Red/Green
△ - Yellow

small extent, influence sensitivity to flicker. Moreover, it is difficult to concentrate on any particular stage of dark adaptation since recovery is continuous over time. For these reasons, the types of questions asked by these experiments were addressed by examining the influence of rod light adaptation on cone-mediated flicker sensitivity. These results are presented in the following chapter.

Chapter 4: The Influence of Light Adaptation on Flicker Sensitivity

The experimentation described in the present chapter examined the influence of rod light adaptation (as provided by a steadily exposed adapting field) on cone-mediated flicker sensitivity. It would be expected from the dark adaptation experiments of the previous chapter that the sensitivity of the cone system to flicker would be enhanced when rods are light adapted and that this effect should be greatest with higher flicker frequencies. The results, presented in this chapter, also describe the influence of some spatial parameters on this type of rod-cone interaction.

Prodcedure

Before data collection, the observer dark adapted for 25 minutes and was aligned with the optical system. At each level of adapting field illuminance, the observer viewed the fixation target and adapting field for one minute before a flickering stimulus was presented. This was to insure that light adaptation was complete before data collection. The sensitivity to red, green, or red-green counterphase flickering test stimuli was then assessed in the presence of steady adapting fields. The adapting fields were derived from the tungsten source channel with chromatic properties determined by means of interference filters. With two exceptions this was the full 28° diameter field of 512 nm in wavelength presented concentrically with the fixation target. In the case of an experiment aimed at verifying that rod adaptation was the underlying mechanism (page 89), these fields were varied in wavelength as indicated and were again 28° in diameter. In the case of an experiment on the spatial parameters of the adapting mechanism (page 95), this field was 512 nm in wavelength but was presented concentrically with the flickering test stimulus, and was either a disc (varying from 2°-7° 20' diameter) or an annulus with inner diameter contiguous with the test stimulus (2° 20') and an outer diameter of 7° 20'.

One of two dependent variables was used to assess flicker sensitivity. Most commonly as in the case of the data presented in the previous chapter, the flickering test stimulus was fixed in modulation depth at 87% and the observer varied its illuminance such that the flicker could just be perceived. An experimental session encompassed investigation of the effect of six different adapting field illuminance levels, including dark adapted, on sensitivity to two flicker frequencies. The frequencies were chosen prior to the experimental session according to a random schedule. The actual order of presentation was semi-random. That is, within an experimental session, the frequency was randomized at each level but the dark adapted condition was run first, subsequently, successively presented adapting field illuminances were never reduced more than 1.5 log units. All illustrated data points represent a minimum of six observations over at least two experimental sessions. In collecting the data of the, above mentioned, experiments on the rod nature and spatial parameters of the adapting mechanism the size, shape, and/or wavelength of the adapting field were randomly varied.

According to a second procedure, the observer was presented with a stimulus of constant mean illuminance and frequency while adjusting the modulation depth to just perceive flicker. In collecting such data, a flickering test stimulus of one mean illuminance (0.4, 2.5, or 12.5 photopic trolands) was used in an experimental session. Data were collected with all flicker frequencies appropriate for a particular test mean illuminance and with all adapting field illuminance levels in one experimental session. After choosing a particular adapting field level, for the first adjustment at each frequency, the frequencies were presented in a random order which was reversed for the second adjustment. After changing adapting field level, the procedure was repeated.

Results and Discussion

Influence of Adapting Field Illuminance on Flicker Sensitivity: Illuminance Dependent Variable

As in the last chapter all Figures are plotted so that increases in sensitivity are reflected by a lowereing of the ordinate position. Figure 21 exhibits typical data obtained (observer SHG) with a red flickering test stimulus. Illuminance necessary to perceive flicker is plotted as a function of the illuminance of a continuously exposed, 28° adapting field of 512 nm wavelength, with flicker frequency as a parameter. For comparison purposes, the data similarly obtained with a 5 Hz green flickering stimulus are plotted as open squares. It can be seen that as the adapting field illuminance increases from −4.3 to −0.3 log scotopic trolands, there is a marked decrease in green flicker sensitivity and a rod-cone break can be observed at higher illuminance levels. In contrast, as adapting field illuminance increases, sensitivity to red flicker increases. The increase in sensitivity, from the dark adapted condition, is only 0.2 log units with 5 Hz flicker but increases with frequency to the extent that it is about 1.0 log units with 25 Hz flicker.

There is little doubt that the red flicker data of Figure 21 represent a cone sensitivity function, without a rod flicker signal involved. To be more confident that this was the case, the experiments done with 10-25 Hz red flicker were repeated but with the previously described red-green counterphase stimulus which precluded a rod-flicker stimulus (Figure 22). Inspection of the results presented in Figures 21 and 22, indicate that the same tendencies occur whether

Figure 21. Red flicker sensitivity as a function of 28°, diameter, adapting field illuminance, for 5 (closed circles), 10 (open triangles), 15 (open circles), 20 (closed squares), and 25 Hz (closed squares) flicker. 5 Hz green (open squares) data is included for comparison of rod and cone-mediated flicker sensitivity changes as the adapting field is varied in the scotopic range of adapting field illuminance. The data collected in dark adapted conditions correspond to the "minus infinity" sign on the abscissa. (Observer SHG, for this observer ninety-five percent confidence intervals were always smaller than the representative symbols in this and all following plots).

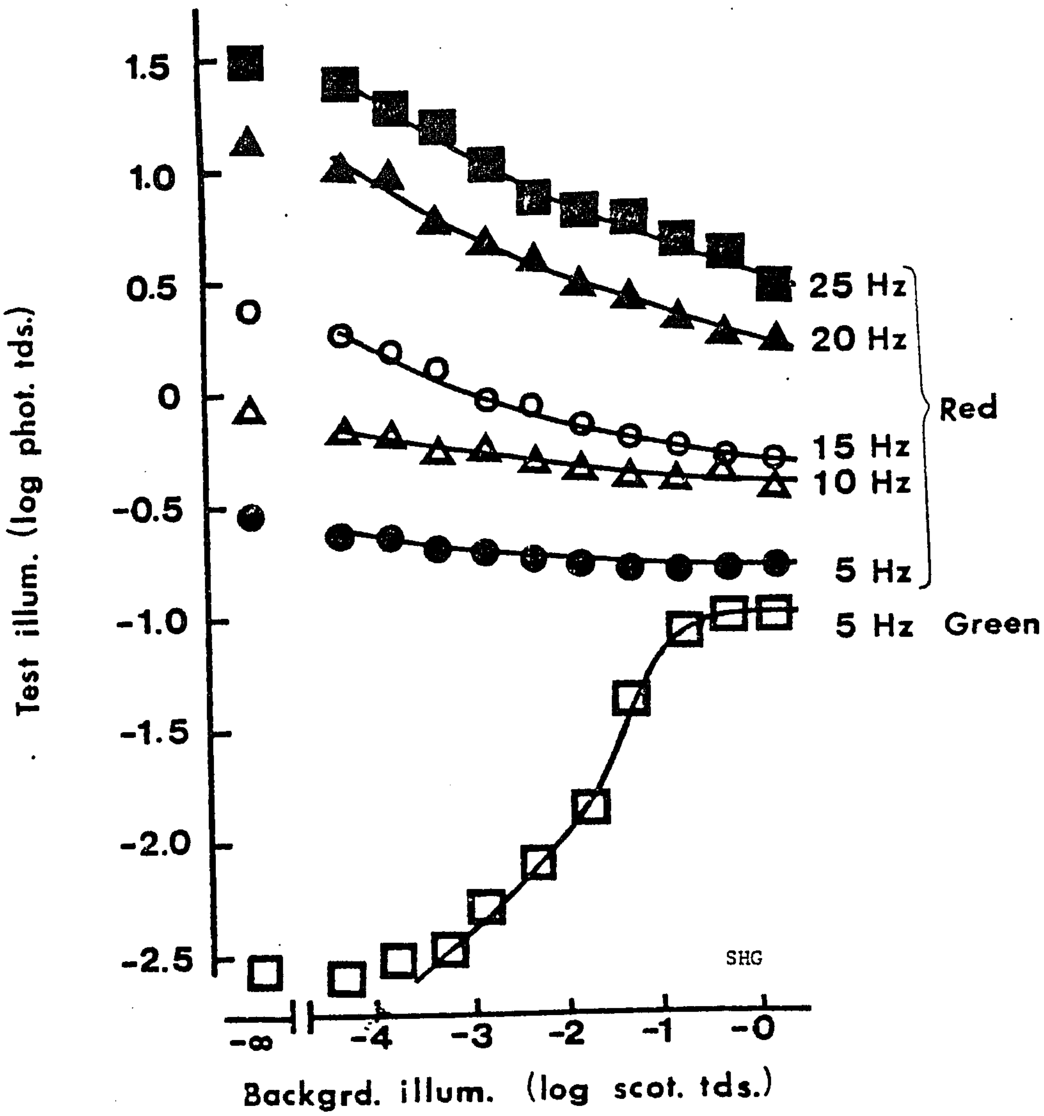
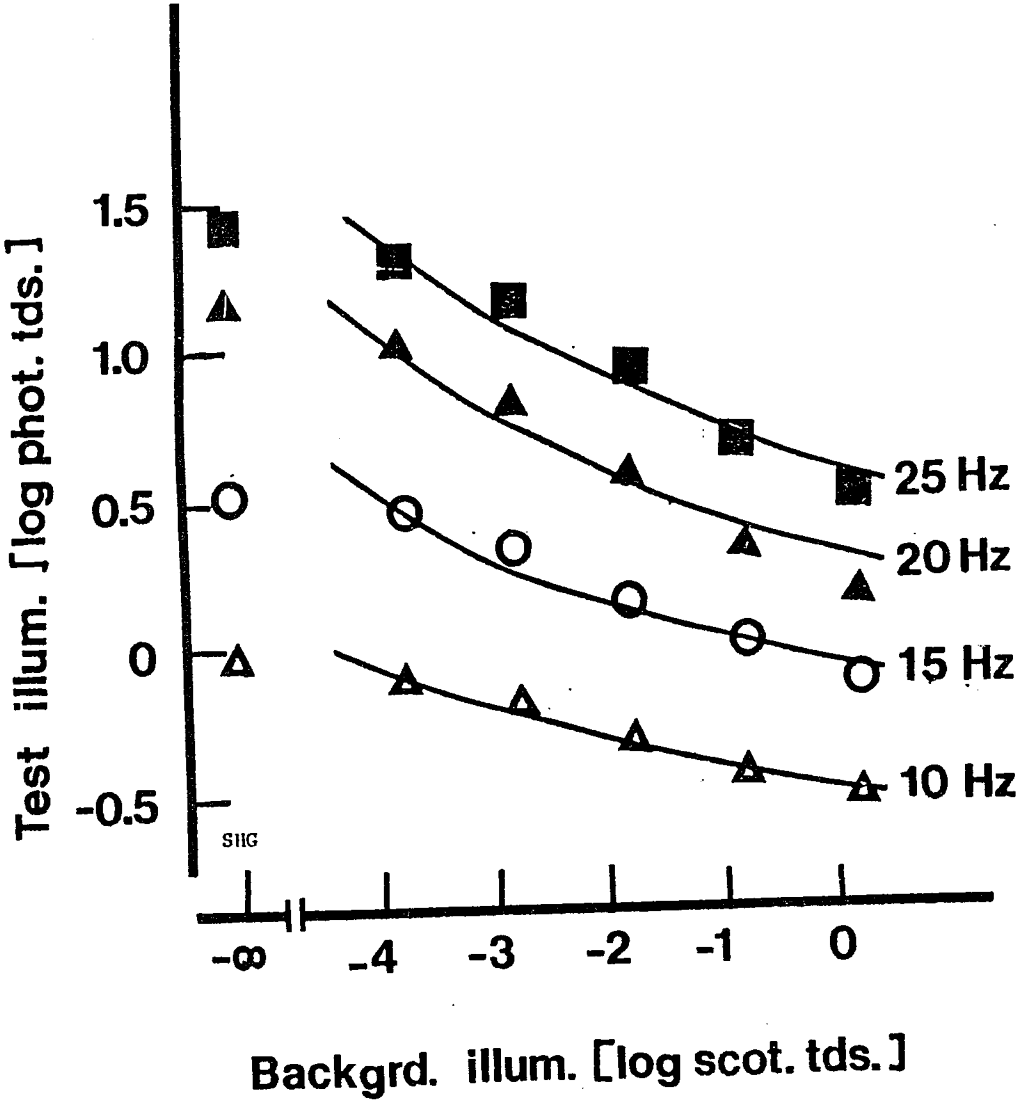

1.5
1.0
0.5
0
-0.5
-1.0
-1.5
-2.0
-2.5
Test illum. (log phot. tds.)
-∞
-4
-3
-2
-1
-0
Backgrd. illum. (log scot. tds.)
25 Hz
20 Hz
15 Hz
10 Hz
5 Hz
Red
5 Hz Green
SHG

Figure 22. Same as Figure 21, but only for the red-green counterphase condition and the indicated frequencies.


Test illum. [log phot. tds.]
1.5
1.0
0.5
0
-0.5
SIIG
-∞
-4
-3
-2
-1
0
Backgrd. illum. [log scot. tds.]
25 Hz
20 Hz
15 Hz
10 Hz

or not a rod-flicker stimulus is precluded, thus indicating that these data represent a direct influence of light adaptation on cone-mediated flicker sensitivity. Essentially the same tendencies are seen in the results from a second observer in Figure 23. Unfortunately, this observer became ill before all intended data were collected, thus precluding more thorough analysis.

Finally, in order to show that the influence of the adapting field on cone-mediated flicker sensitivity presented in Figures 21-23 is due to rods, similar data were obtained with a 20 Hz red stimulus in the presence of adapting fields of five different wavelengths, scotopically equated at three different illuminance levels. As illustrated in Figure 24, scotopically matched 472-580 nm fields have identical influence on cone-mediated flicker sensitivity, strongly suggesting that it is the adapted state of rods alone that is influencing cone-mediated flicker sensitivity. Data obtained with a 655 nm adapting field, which at all illuminance levels influences both rods and cones (Wald, 1945) differ from the others at the highest illuminance illustrated. Most probably, rods adapted by this field have the same influence on cone flicker as for other wavelengths, but in addition, cones stimulated by the background tend to depress cone flicker sensitivity. These two opposing tendiencies yield data which shows a less reliable influence of background illuminance on cone-mediated flicker sensitivity.

Figure 23. Same as Figures 21 and 22, but for 15 Hz red-green (circles), 20 Hz red-green (triangles), and 20 Hz red (squares) flicker and observer KJL. No line fit seemed appropriate for this observer's data, although the same trends as illustrated in SHG's data are evident. Ninety-five percent confidence intervals are approximately the size of a square symbol for this observer.

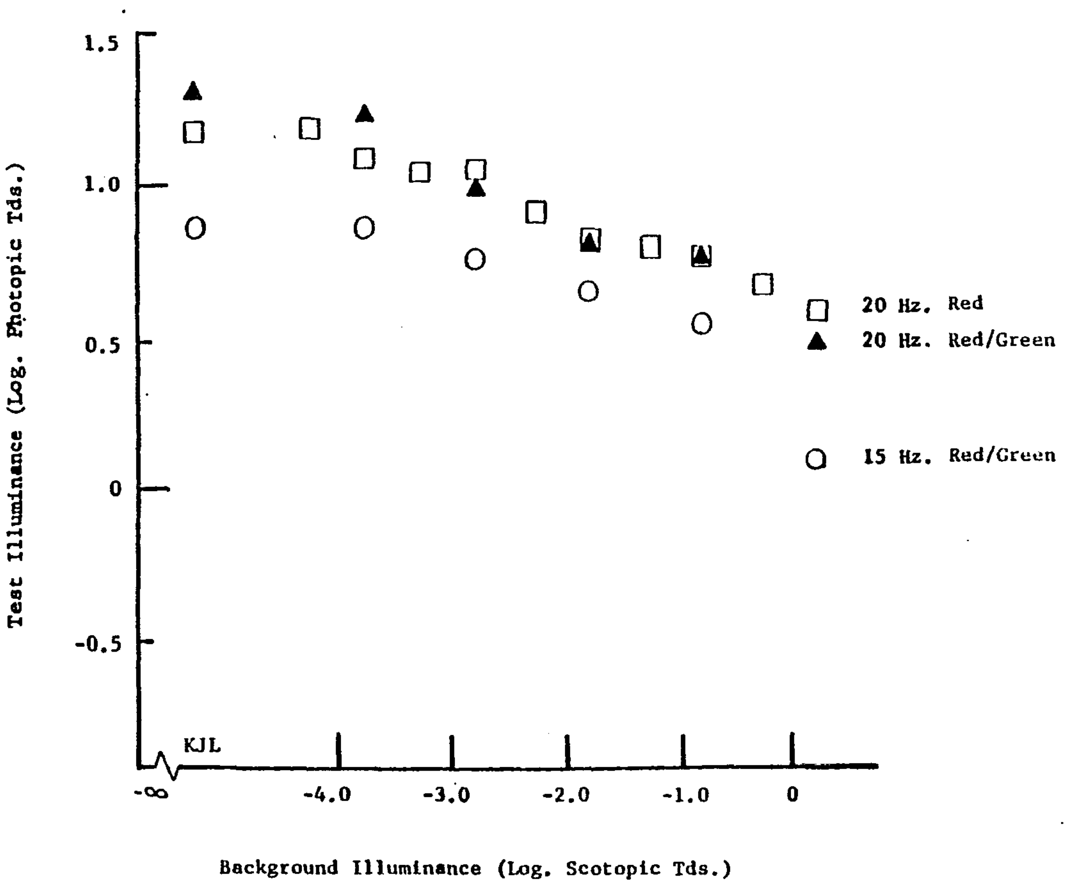
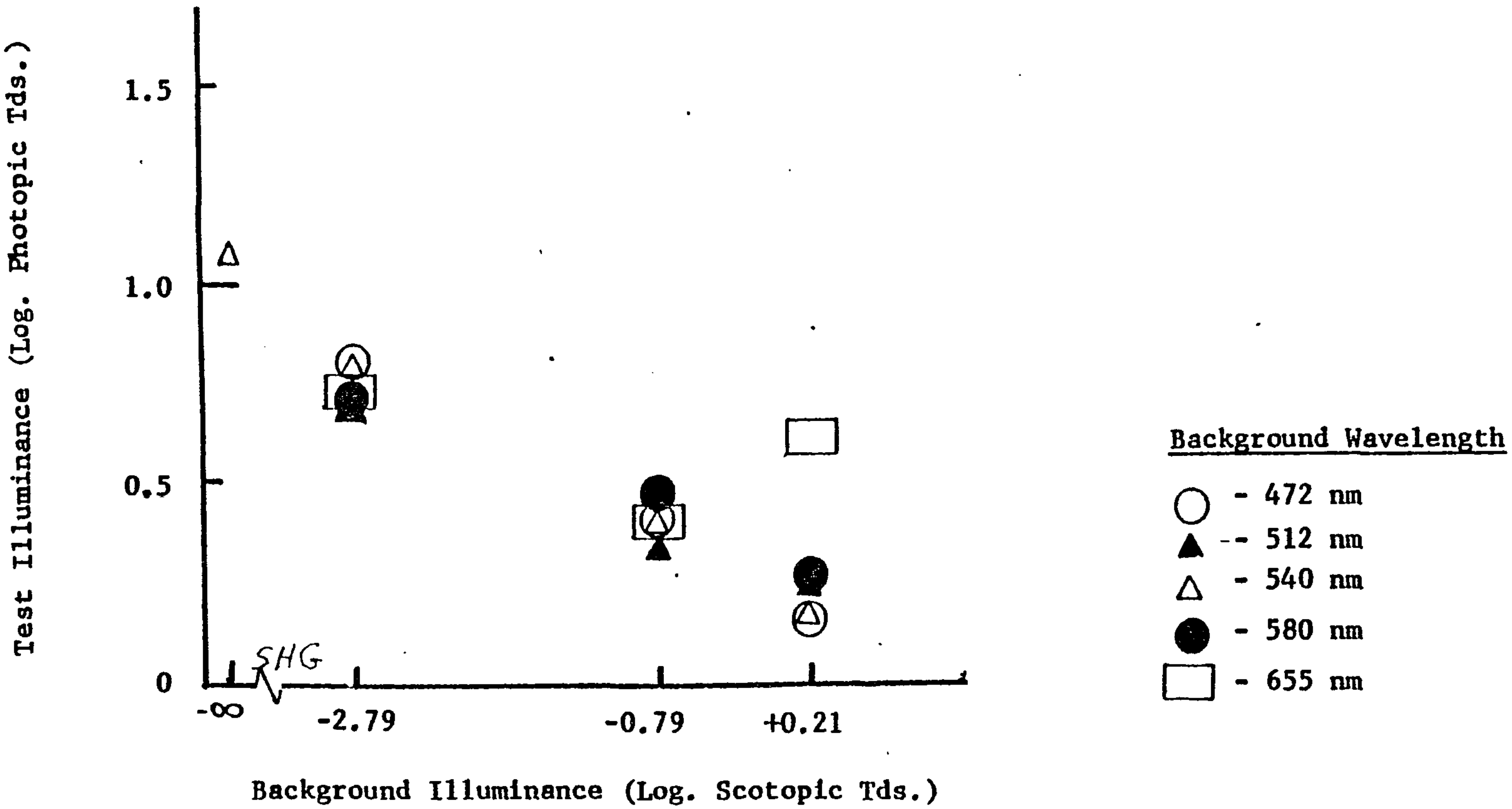

1.5
1.0
0.5
0
-0.5
Test Illuminance (Log. Photopic Tds.)
KJL
-∞
-4.0
-3.0
-2.0
-1.0
0
Background Illuminance (Log. Scotopic Tds.)
□ 20 Hz. Red
▲ 20 Hz. Red/Green
○ 15 Hz. Red/Green

Figure 24. Red, 20 Hz, flicker sensitivity as a function of five different wavelength adapting fields, presented at three different scotopically equal illuminances. (Observer SHG)


Test Illuminance (Log. Photopic Tds.)
1.5
1.0
0.5
0
-∞
SHG
-2.79
-0.79
+0.21
Background Illuminance (Log. Scotopic Tds.)
Background Wavelength
○ - 472 nm
▲ -- 512 nm
△ - 540 nm
● - 580 nm
□ - 655 nm

In summary, the results presented in Figures 21-24 suggest the same conclusion as the counterpart dark adaptation experiments of chapter 3. That is, the sensitivity of the cone system to flicker is increased by selectively light adapting rods. Although this tendency can be seen at many different flicker frequencies, it is most apparent at higher flicker frequencies.

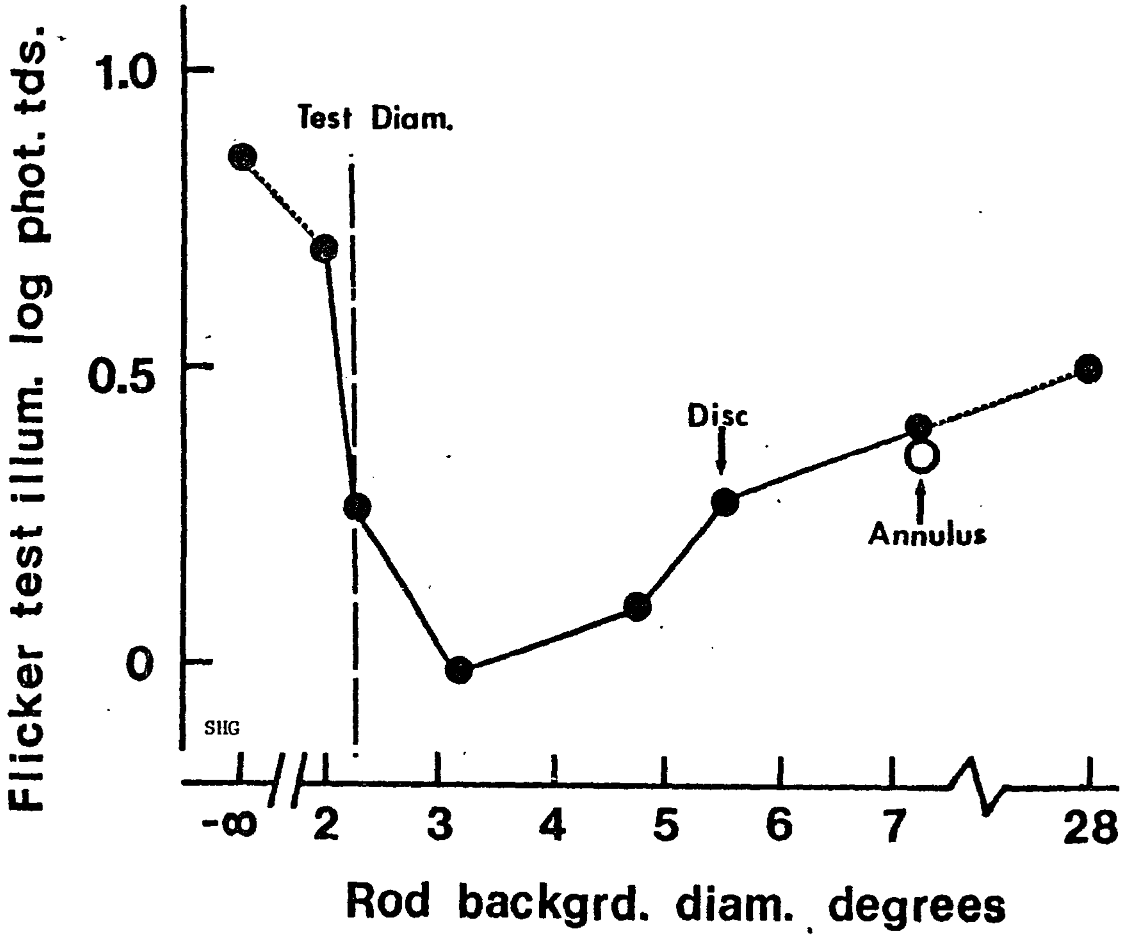
The Influence of Scotopic Adapting Field Shape and Size on Photopic Flicker Sensitivity

One surprising aspect of the present study is that an exceedingly dim adapting field can have such a striking influence on flicker sensitivity. For example, in Figure 21, the scotopic illuminance (i.e., if it were scaled in scotopic trolands) of the flickering test stimulus is 1.3 log units less than that indicated on the ordinate in photopic trolands. By comparing the values on the ordinate and the abscissa, it becomes clear that in scotopic units, adapting fields which clearly influence cone-mediated flicker sensitivity are often more than 1 log unit dimmer than the illuminance of the test stimulus which elicits a flicker perception. In addition, in the counterpart dark adaptation experiments described in the previous chapter (see pages 67-76), the counterphase red-green stimulus which doubles the scotopic illuminance of the red test stimulus had a negliglible influence on cone-mediated sensitivity to flicker.

The foregoing observations suggest that in addition to the influence of the adapted state of rods underlying the test stimulus on cone-mediated flicker sensitivity, it is the influence of rods over a larger area that influence cone-mediated sensitivity to flicker. In order to examine this possibility, the influence of the size and shape of the adapting field on 20 Hz red flicker sensitivity was studied. The resulting data are shown in Figure 25. Here, the illuminance of the red flickering stimulus which just elicits a flicker perception is plotted as a function of the diameter of a concentric, 512 nm adapting field of −0.3 log scotopic tds. On this plot there is also a comparison of the influence of a 7°20’ disc and a 7°20’ outer diameter annulus (open circle), whose inner diameter is contiguous with the flickering test. As adapting field diameter increases up to 3° 20’, flicker sensitivity increases, suggesting a summating area for this rod influence which is much larger than the flickering test stimulus. Along these same lines, the 7°20’ annulus and disc have essentially the same influence on flicker sensitivity.

On the other hand, as the adapting field increases, in diameter, beyond 3°20’, sensitivity to cone flicker begins to decrease again. At the present time, the reason for this decrease is unknown. Such a result, however, is not entirely unexpected since in increment thresholds studies involving cone vision, rod vision, and also rod-cone interaction, adapting fields produce a similar nonmonotonic

Figure 25. Influence of size (2°-7° 20') and shape (full field or annulus) of a -0.3 log scotopic troland adapting field on 20 Hz, red flicker sensitivity. (Observer SHG)


Flicker test illum. log phot. tds.
1.0
0.5
0
Test Diam.
Disc
Annulus
SHG
-∞
2
3
4
5
6
7
28
Rod backgrd. diam. degrees

influence on threshold (Bauer, Frumkes, & Nygaard, 1983; Hayhoe, 1979; Westheimer, 1965, 1967).

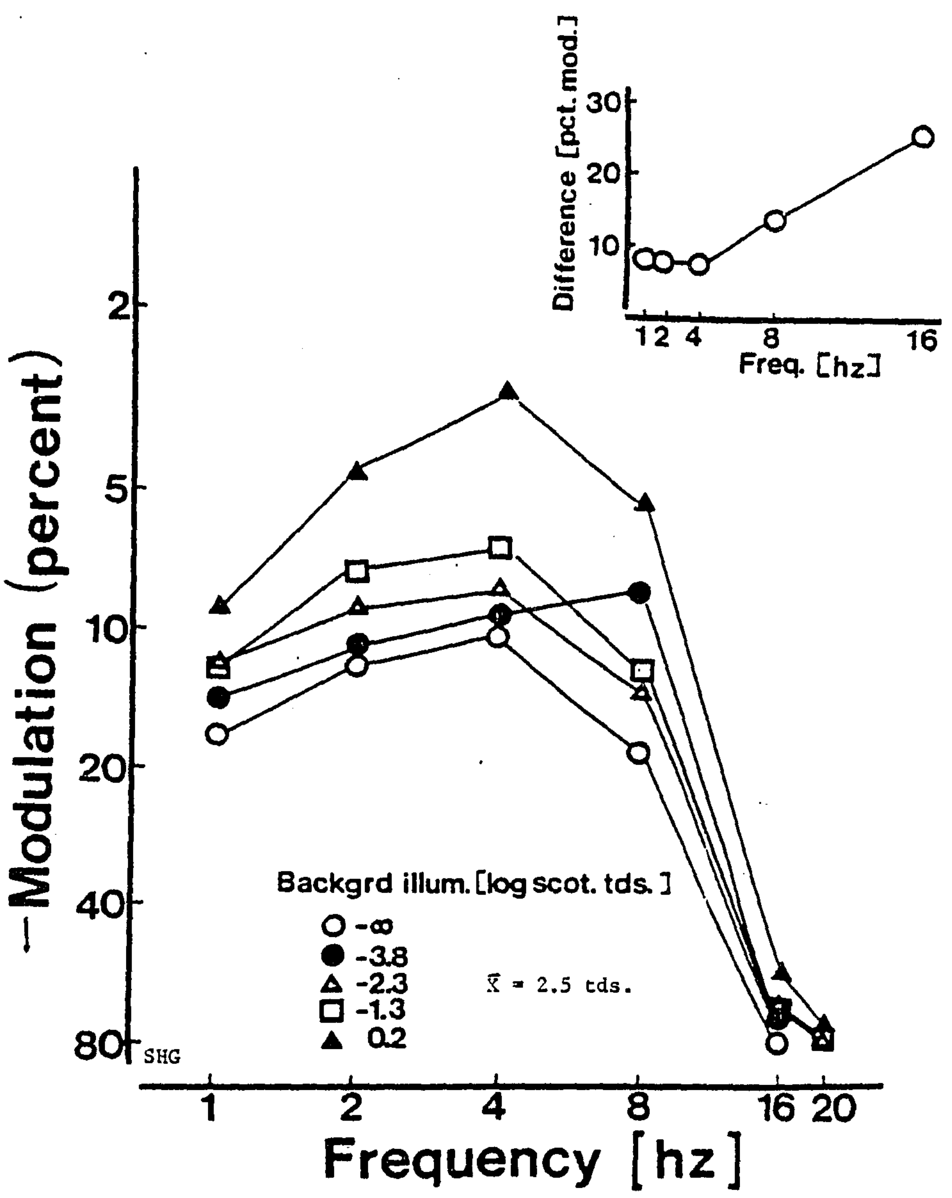
Modulation Dependent Variable

The foregoing results show that cone system sensitivity to flicker is related to the adapted state of rods. However, the dependent variable employed, the illuminance necessary to detect flicker, is infrequently used. As indicated on page 6, two other dependent variables, both much more frequently used, could have been used to obtain the same results. Alexander and Fishman (personal communication) have similarly shown that when rods are light adapted, cone-mediated CFF increases.

But most modern flicker data are obtained in experiments where the depth of modulation is used as the dependent variable. This measure was not used in the main experiments, here, since it introduces a parametric variable, mean illuminance of the flickering test stimulus that limits the range over which flicker sensitivity can be influenced. One advantage that use of this modulation approach has, in the present situation, is the separating out of the effects of rod light adaptation on modulation depth or amplitude sensitivity as a function of frequency at a constant mean illuminance level. Modulation depth and amplitude change together at a constant mean illuminance level. The illuminance threshold procedure changes both amplitude and mean illuminance simultaneously. To provide comparability with much of the modern literature and examine the effects of rod adapting fields on cone modulation sensitivity data were also obtained in the present study with modulation depth adjustments. For observer SHG, the data obtained for a flickering stimulus, with a mean illuminance of 2.5 photopic trolands, and in the presence of five different adapting field illuminances are illustrated in the main plot of Figure 26. Following the convention of Ives (1922), deLange (1958) and Kelly (1961), the sensitivity is plotted as a function of flicker frequency on logarithmically spaced coordinates (as it also is in Figures 27-29). To achieve this, modulation depth is plotted on the ordiante such that higher modulation thresholds are indicated by lower ordinate positions. Also note that as opposed to the plots of, for example Kelly (1961, Figure 2b) here the mean flicker illuminances are constant for all curves of a single plot. The parameter is adapting field illuminance.

In Figure 26, the data obtained with no background present (the open circles) illustrate the usual interrelationship between sensitivity and flicker frequency. Hence, sensitivity is maximal at an intermediate frequency (in this case, 4 Hz) and falls of at lower and higher frequencies. Notice that as the adapting field illuminance increases, sensitivity to cone flicker increases at virtually all flicker frequencies.

Figure 26. Effect of adapting field illuminance on cone-mediated (red-green counterphase flicker) modulation sensitivity as a function of frequency. The axes are logarithmically scaled in the main plot. The insert (upper right) plots the sensitivity difference, in percent modulation, between the 0.2 log scotopic troland (closed triangles) and dark adapted (open circles) conditions on linear coordinates. The flickering sinusoid had a mean illuminance of 2.5 photopic trolands. (Observer SHG)


Difference [pct. mod.]
30
20
10
1 2 4 8 16
Freq. [hz]
—Modulation (percent)
2
5
10
20
40
80
SHG
Backgrd illum. [log scot. tds.]
○ -∞
● -3.8
△ -2.3
□ -1.3
▲ 0.2
$\bar{X}$ = 2.5 tds.
1
2
4
8
16 20
Frequency [hz]

The preceding experiments (e.g., Figure 21) using illuminance thresholds demonstrated that the influence of background illuminance is most prevalent with higher frequencies. This tendency is difficult to discern on logarithmic coordinates but is more readily discerned on linearly spaced coordinates, as in the inserted derived plot on the upper right of Figure 26. In this plot, the difference between the modulation threshold obtained with no background field and in the presence of the 0.2 log scotopic troland adapting field is plotted as a function of flicker frequency. In agreement with the results of this and the previous chapter, this plot illustrates that the influence of rod adaptation is greatest on higher flicker frequencies. Similar data obtained from observer SHG with two other mean illuminance levels of the flickering test stimulus (Figures 27 and 28) as well as similar data from a second observer (Figure 29) are also presented. Although all the cone-mediated flicker sensitivities represented by these functions, are not influenced by the adapting field illuminance in an orderly fashion, these results reflect the same tendencies. Therefore, it can be concluded that the influence of rod adaptation on cone-mediated flicker sensitivity is not related to the use of an unusual dependent variable. Furthermore, rod adaptation appears to have similar influence on amplitude sensitivity, measured separately from changes in mean illuminance. It is interesting, though, that the effect of frequency seems to

Figure 27. Same as Figure 26, but for a red-green sinusoid of higher mean illuminance (12.5 photopic trolands).

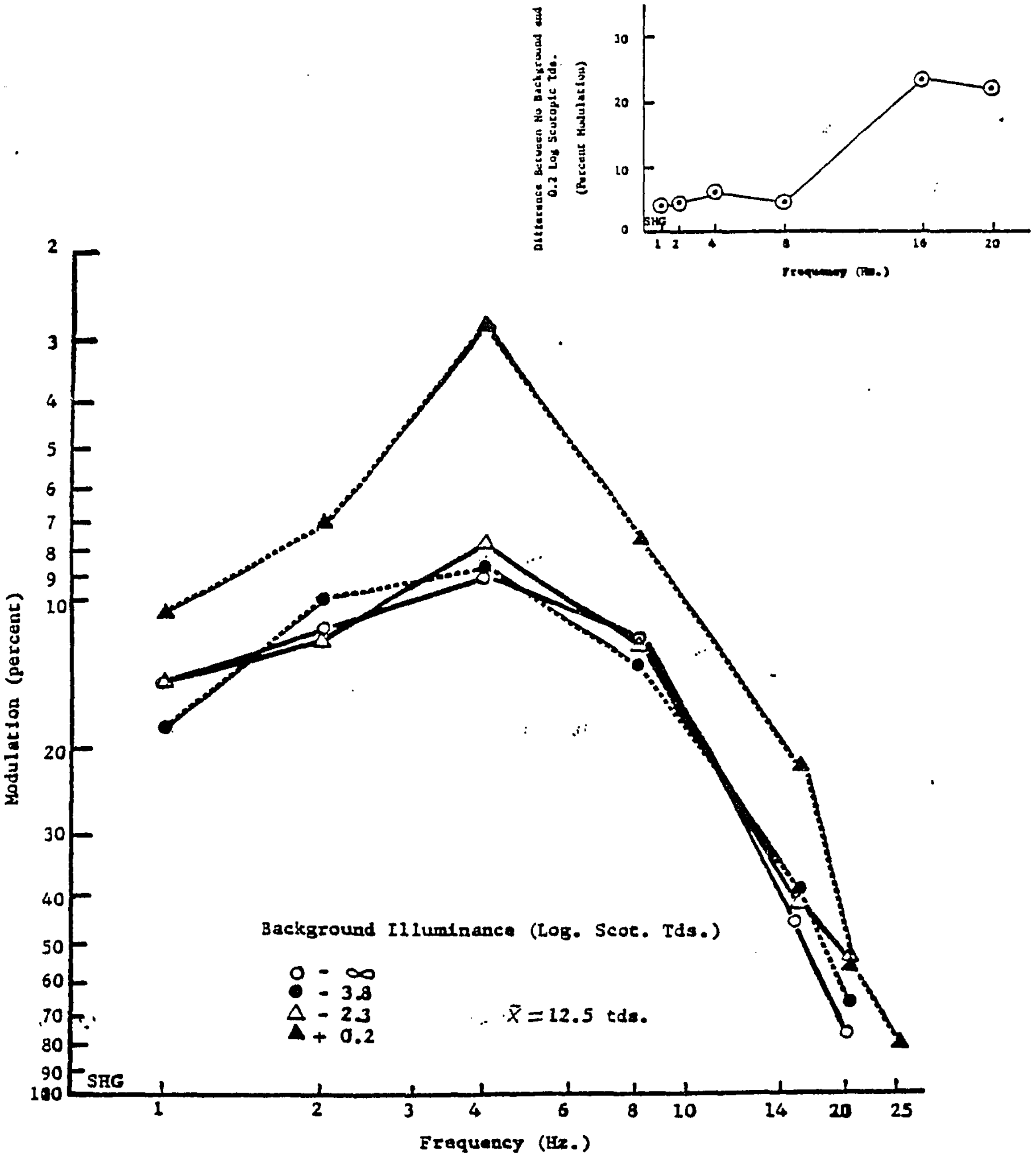

Difference Between No Background and
0.2 Log Scotopic Tds.
(Percent Modulation)
30
20
10
0
SHG
1
2
4
8
16
20
Frequency (Hz.)
Modulation (percent)
2
3
4
5
6
7
8
9
10
20
30
40
50
60
70
80
90
100
SHG
1
2
3
4
6
8
10
14
20
25
Frequency (Hz.)
Background Illuminance (Log. Scot. Tds.)
○ - ∞
● - 3.8
△ - 2.3
▲ + 0.2
$\bar{X} = 12.5$ tds.

Figure 28. Same as Figure 26, but for a red-green sinusoid of lower mean illuminance (0.40 photopic trolands).

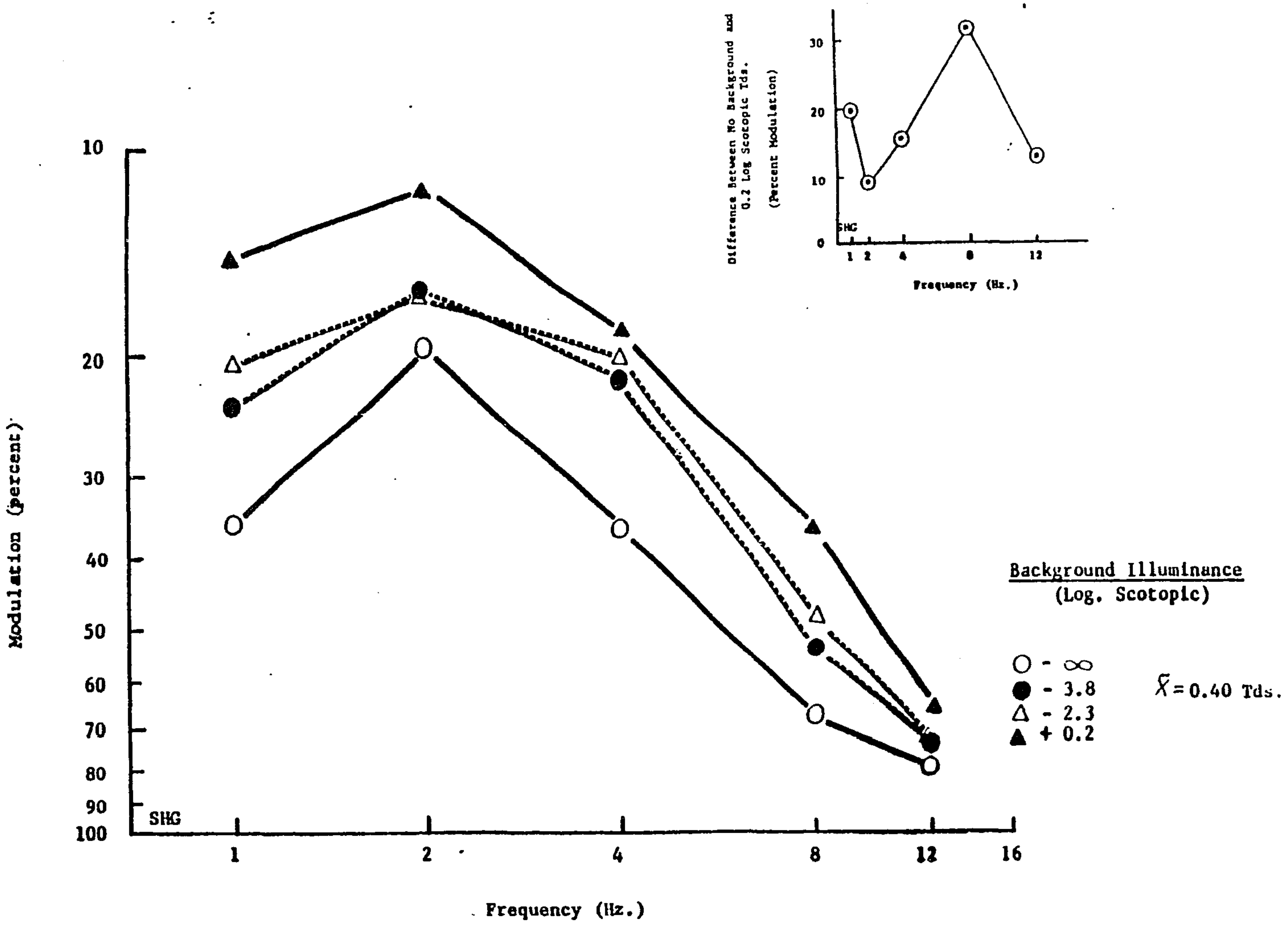
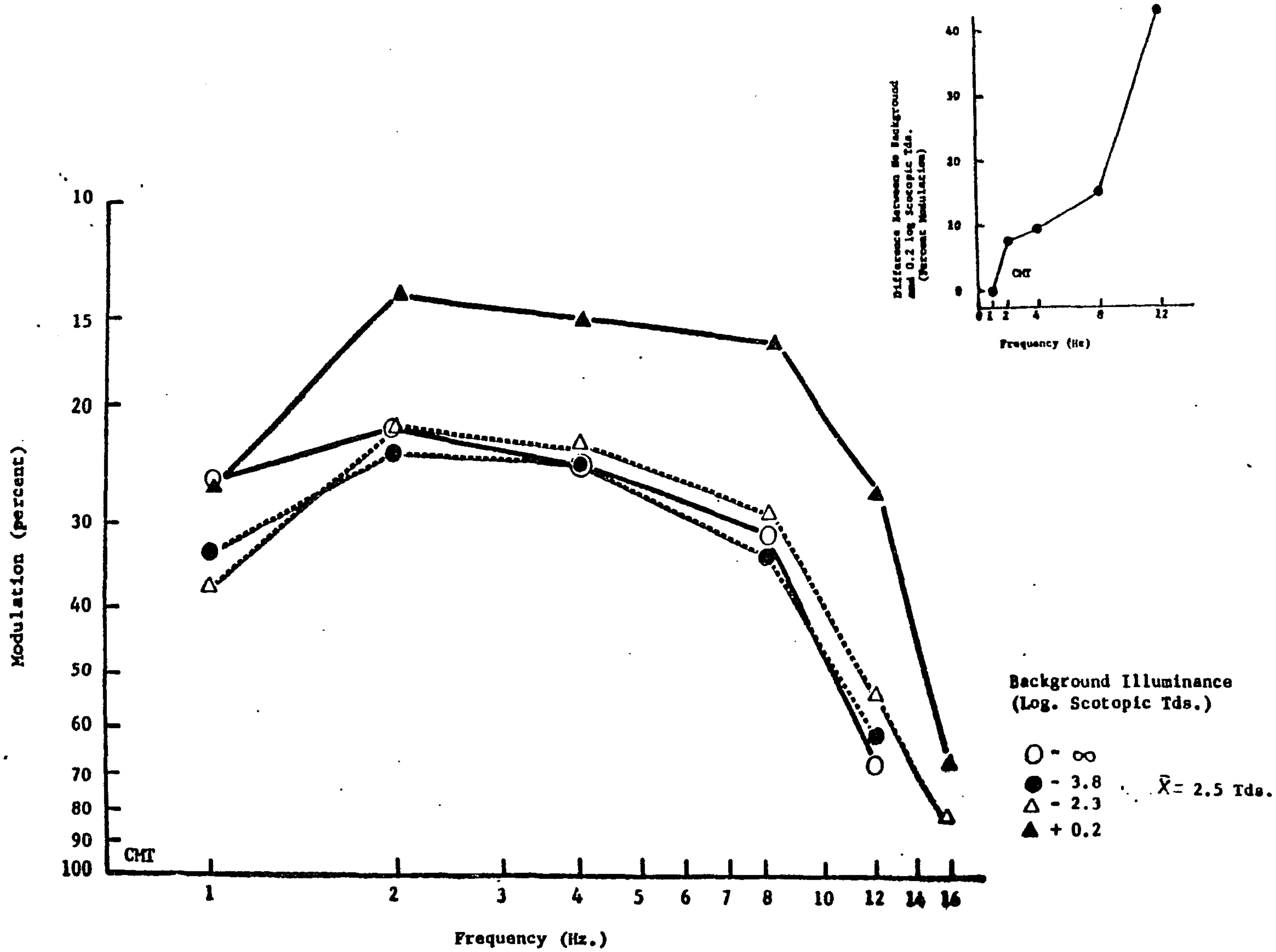

Difference Between No Background and
0.2 Log Scotopic Tds.
(Percent Modulation)
30
20
10
0
SHG
1
2
4
8
12
Frequency (Hz.)
Modulation (percent)
10
20
30
40
50
60
70
80
90
100
SHG
1
2
4
8
12
16
Frequency (Hz.)
Background Illuminance
(Log. Scotopic)
○ - ∞
● - 3.8
△ - 2.3
▲ + 0.2
X̄ = 0.40 Tds.

Figure 29. Same as Figure 26, but for a different observer (CMT). The ninety-five percent confidence intervals for this observer were approximately the size of the symbols.


Difference Between No Background and 0.2 log Scotopic Tds. (Percent Modulation)
40
30
20
10
0
CMT
0
1
2
4
8
12
Frequency (Hz)
Modulation (percent)
10
15
20
30
40
50
60
70
80
90
100
CMT
1
2
3
4
5
6
7
8
10
12
14
16
Frequency (Hz.)
Background Illuminance
(Log. Scotopic Tds.)
○ - ∞
● - 3.8
△ - 2.3
▲ + 0.2
X̄ = 2.5 Tds.

be linearly related to modulation sensitivity here (inserts to Figures 26-29), whereas threshold illuminance sensitivity changed logarithmically as frequency changed linearly in Figure 20 (dark adaptation experiments). At present I have no immediate explanation for this difference.

Chapter 5: General Discussion

The results of the present study confirm prior observations by Lythgoe and Tansley (1929) and Nygaard (1981) which show that under specified circumstances, sensitivity to flicker in the parafoveal retina decreases during the rod recovery stage of dark adaptation, or conversely, increases as rods become selectively light adapted. A large number of control experiments established that this alteration in flicker sensitivity has the following features.

1. This phenomenon is greatest for rapid (more than 10 Hz) flicker. In fact, using a different dependent variable (CFF), this influence of adaptation has been demonstrated for frequencies of more than 40 Hz (Goldberg, Frumkes, Nygaard, & Alexander, 1982).

2. It only applies to conditions under which cones are mediating the flicker sensations. Three types of control established this property. First, when rods are solely responsible for flicker detection, sensitivity to flicker is greatest when rods are dark adapted. This was evidenced by the 5 Hz flicker data obtained after 5 minutes in the dark in Figure 11, and with a background illuminance of less than -0.3 log scotopic trolands in Figure 21. Second, with 15 Hz or 20 Hz flicker, the photopic illuminance which is necessary to detect flicker is independent of test stimulus wavelength (Figure 15). Third, when a rod flicker stimulus

is precluded by means of the red-green counterphase stimulus, the same influence on flicker is found.

3. The influence of adaptation is not dependent on the particular dependent variable which is used to assess sensitivity to flicker i.e., CFF, modulation depth, or as generally employed in the present experiments, the illuminance necessary to perceive flicker. Separate experiments employing each of the three demonstrated the same effects.

4. Cone-mediated flicker sensitivity is dependent on the state of rod adaptation. This is implied by a good deal of data, but demonstrated most clearly by experiments in which the influence of the wavelength of the preadapting field (Figure 16) or adapting field (figure 24) were varied. By recalling point 2 above, it is therefore clear that this phenomenon must involve an influence of rods on cone-mediated flicker sensations.

5. The rod mediated influence on photopic flicker is not due to a rod flicker signal which adds to or cancels that of the cone signal. This is established by three types of considerations. First, the present phenomena has been demonstrated at flicker frequencies of more than 40 Hz (Goldberg et. al., 1982), beyond even the fastest estimate of human rod flicker-following capability (Conner, 1982). Second, a cancellation mechanism would require that the frequency of the flickering stimulus determined the relative

phases of the hypothetical rod and cone signals which would either add together or cancel out. Thus, the present phenomena would only occur at specific frequencies. In fact, Nygaard (1981, and personal communication) obtained the same result for flicker frequencies between 8-15 Hz, in 1 Hz steps. Third, and most convincingly, the elimination of any conceivable rod flicker signal, by means of the counterphase control, has only negligible influence on this type of rod-cone interaction.

6. This phenomenon involves an influence of the adapted state of a large number of rods next to as well as perhaps underlying the flickering stimulus, on cone-mediated flicker sensitivity. In the present study, this was best established by experiments which examined the influence of the size and the shape of a rod-effective adapting field on cone flicker sensitivity (Figure 25). Additionally, two other considerations make this point. Alexander and Fishman (personal communication) and Goldberg et. al., (1982) examined the same basic effect at many different retinal positions, up to 50° in the periphery. They both found the influence of rod adaptation on cone-mediated flicker is greater at retinal positions with the largest ratio of rods to cones (more than 15° from the fovea). Finally, the light adaptation experiments of the present study were largely replicated by Adams and Colletta (1983) using a 10' diameter flickering test stimulus placed in the fovea. They obtained results similar to those in Figure 21. Since they were

stimulating a rod-free region of the retina, this type of rod-cone interaction must involve the activity of rods covering a large retinal area. The results represented in Figure 25, suggest that for the conditions of the present study, adapting fields of 3°20' are most effective; an area which corresponds to about 1 mm, in diameter, on the retina.

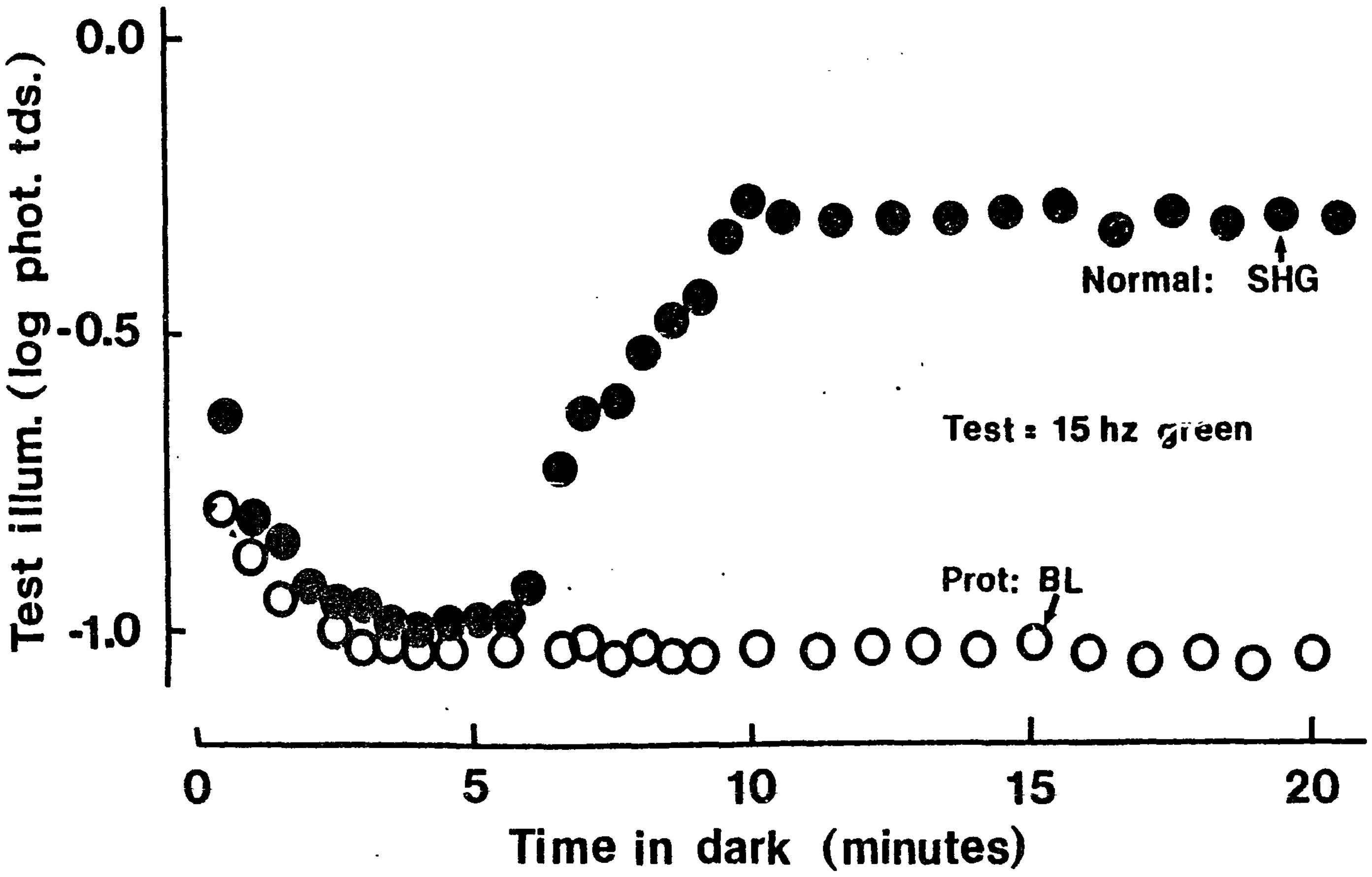
General Class of Mechanism

There are two possible classes of mechanism which would cause a cone signal to be largest when rods are light adapted. Photic stimulation of rods with a steady stimulus fascilitates the cone system, or dark adapted, unstimulated rods inhibit the cone system. The present results do not distinguish between these possibilities, but other data support the latter argument. That is, a wide variety of ophthalmological conditions are characterized by loss of rod vision but spared cone functioning, including flicker (for review see Ripps, 1982). Therefore, it would seem unlikely that cone-mediated flicker responses depend on the facilitatory influence of rods.

To better substantiate this inference, it would be ideal to study opthalmological patients with selective rod deficits which are popularly known as "night blindness." It would be particularly interesting to study patients with night blindness of the type described by Carr, Ripps, Siegal, and Weale (1966). These individuals show normal photopigment but no signs of rod neural activity (see Ripps, 1982). It would be expected that these individuals would have normal cone flicker sensitivity in the light and the same, i.e., superior to normal sensitivity under dark adapted conditions. To date, I know of no investigation of the present type involving such patients. However, there is data which indicates that rods are inhibiting cones in the present experiments. Goldberg and Frumkes (1983) and Alexander and Fishman (personal communication) have studied a number of colorblind individuals including both protanopes and deuteranopes in experiments very much like those presently reported. The general finding is that protanopes do not show this particular effect, even when they possess very keen vision. For example, Figure 30 illustrates the sensitivity to 15 Hz green (LED) flicker, during dark adaptation, of one protanope and one normal individual. Although not illustrated, the protanope had lower rod detection thresholds than the "normal" subject. But note that throughout the rod recovery stage of dark adaptation, the protanope's flicker sensitivity remains constant and only the normal subject's sensitivity decreases. The absence of this type of rod-cone interaction in an individual with superior sensitivity suggests that it is an inhibitory phenomenon.

One other type of indirect evidence also suggests that this effect is inhibitory. That is, recent experiments have examined the influence of selective rod adaptation on the flicker evoked electroretinogram in the leopard frog

Figure 30. Green, 15 Hz, flicker sensitivity as a function of time in the dark for a normal (SHG) observer and a protanope (BL). The data points represent medians as was the case for all dark adaptation data in chapter 3.


Test illum. (log phot. tds.)
0.0
-0.5
-1.0
Normal: SHG
Test = 15 hz green
Prot: BL
0
5
10
15
20
Time in dark (minutes)

(Goldberg & Frumkes, 1983; Frumkes & Eysteinsson, personal communication). Although from a vastly different species, these electrophysiological results show many similarities to the present behavioral results. That is, the influence of rod adaptation on the amplitude of cone responses is minimal for single flashes, is small for flicker signals of about 3 Hz, but increases as flicker frequency increases. Of particular relevance to the present argument, is that low concentrations of the selective GABA(gamma amino butyric acid) antagonist, picrotoxin, abolish this effect (and hence, enhance dark adapted cone flicker responses), while they found no other type of neurotransmitter antagonist that blocks this effect. Since GABA is only known to be an inhibitory neurotransmitter, this suggests that at least in frog this effect is due to inhibition.

Clearly, the best known types of rod-cone interaction, including those pertaining to brightness sensations (MacLeod, 1974), increment thresholds (Blick & MacLeod, 1978; Frumkes & Temme, 1977; Makous & Boothe, 1974), and color vision (Trezona, 1970; 1976) are thought to involve summation. However, the idea of inhibitory mechanisms (Hough & Ruddock, 1969; Spillman & Conlon, 1972) or for that matter, concomitant excitatory and inhibitory mechanisms (Barris & Frumkes, 1978) are not unknown. What is perhaps a more interesting question is the reason for this type of rod-cone interaction to be most prevalent with rapid flicker. A large number of recent papers have proposed that either rod and/or cone mediated flicker signals are mediated by different channels with different temporal tuning properties (Tyler, 1975; Smith, 1970; Nygaard, 1981; Conner, 1983). A more recent finding related to dark adaptation indicates, that following long (150 second) cone photopigment bleaching, the recovery of cone sensitivity to rapid flicker takes much longer than it does to slow flicker (Hayhoe and Chen Bing, 1983). Whether or not this latter observation bears any direct relation to the present phenomenon remains a moot point. What is pertinent is that there are several channels within the visual system and that they show differential sensitivity to adaptive influence.

Underlying Mechanism

Another, perhaps more important question is what is the neural substrate for this type of rod-cone interaction? Although there is the possibility that cortical factors play some role (i.e., Foster and Mason, 1977; Latch & Lennie, 1977 have advanced such arguments for threshold data showing rod-cone interaction) they are considered no further here for three reasons. First, flicker perception is generally thought to be limited by retinal factors (see Van de Grind, Grusser, & Lukenheimer, 1972). Second, and as summarized in the introduction, there are a number of known retinal mechanisms that could account for this type of rod-cone interaction while no cerebral mechaniam has been indicated, Third, a very similar type of rod-cone interaction has been shown in the retina with ERG techniques (Hood, 1972b;

Gordon, 1967; Frumkes & Eysteinsson, personal communication). In the following, I make the assumption that this frog ERG data and the present behavioral data are in fact, manifestations of the same underlying process and rely heavily on unpublished data from my own and other laboratories.

Frumkes and Eysteinsson (personal communication) have established that the influence of adaptation on the flicker evoked ERG in the frog involves either an influence on the b-wave, or on both the a and b-wave. Although the genesis of ERG components is open to dispute, it is generally agreed that the a-wave represents the activity of the photoreceptors and the b-wave represents either directly or indirectly , excitatory activity related to the on-bipolar cells (Brown, 1980, Dick & Miller,1978). Furthermore in mammal there is no evidence for a second order neuron receiving direct input from both rods and cones, and in no species is there evidence for an inhibitory chemical or electrical synapse between rods and cones (for consideration of this possibility see Lasansky, 1973). Therefore, two possible types of pathways could be involved: a horizontal cell mechanism (involving feedback onto the photoreceptors or feedfoward onto the bipolars) or a mechanism involving feedback from amacrine cells onto the bipolars.

Let us first consider the possibility of a horizontal cell pathway, or the more distal mechanism, for which there are several different types of evidence. First, the collective results of Goldberg and Frumkes (1983; Figure 30) and Alexander and Fishman (personal communication) have shown that this type of rod-cone interaction is absent in 8 of 9 protanopes and extreme protans. To the extent that this color vision anomaly is usually attributed to a difference at a very distal retinal locus (Hurvich, 1972), this implies the more distal locus. Secondly, Alexander and Fishman (personal communication) have obtained this phenomenon in a patient with stationary night blindness of a type described by Schubert and Bornschein (in Ripps, 1982). These patients show a rod generated a-wave but no rod generated b-wave. They also lack any direct behavioral signs of rod vision. Since a b-wave (by a modulation of the bipolar cells which limit input to amacrine cells) is necessary for this type of rod-cone interaction, this strongly argues against amacrine cell involvement. Thirdly, Nelson (personal communication) has observed a similar rod adaptation influence on intracellular, flash responses of cone-driven horizontal and bipolar cells of the cat. Unfortunately, he has yet to examine flicker. Fourthly, Frumkes (personal communication) has attempted to try to study this phenomenon electrophysiologically in a number of different species. This effect is absent in the mudpuppy, an organism for which there is no evidence for horizontal cell feedback onto photoreceptors.

However, some evidence would argue for either a horizontal cell or amacrine cell pathway. First, the apparent spatial summating properties of this effect (according to Figure 25 it is around 1 mm) is very large. This could involve either horizontal or amacrine cells, both of which are known to be well electrically coupled and have large receptive fields (Naka & Rushton, 1967). Also, Figure 25 illustrates that increasing the size of a rod adapting field at first increases, then decreases sensitivity to cone-mediated flicker. This suggests a retinal mechanism with center-surround antagonism which has been shown in virtually all classes of retinal neurons from the cones through ganglion cells.

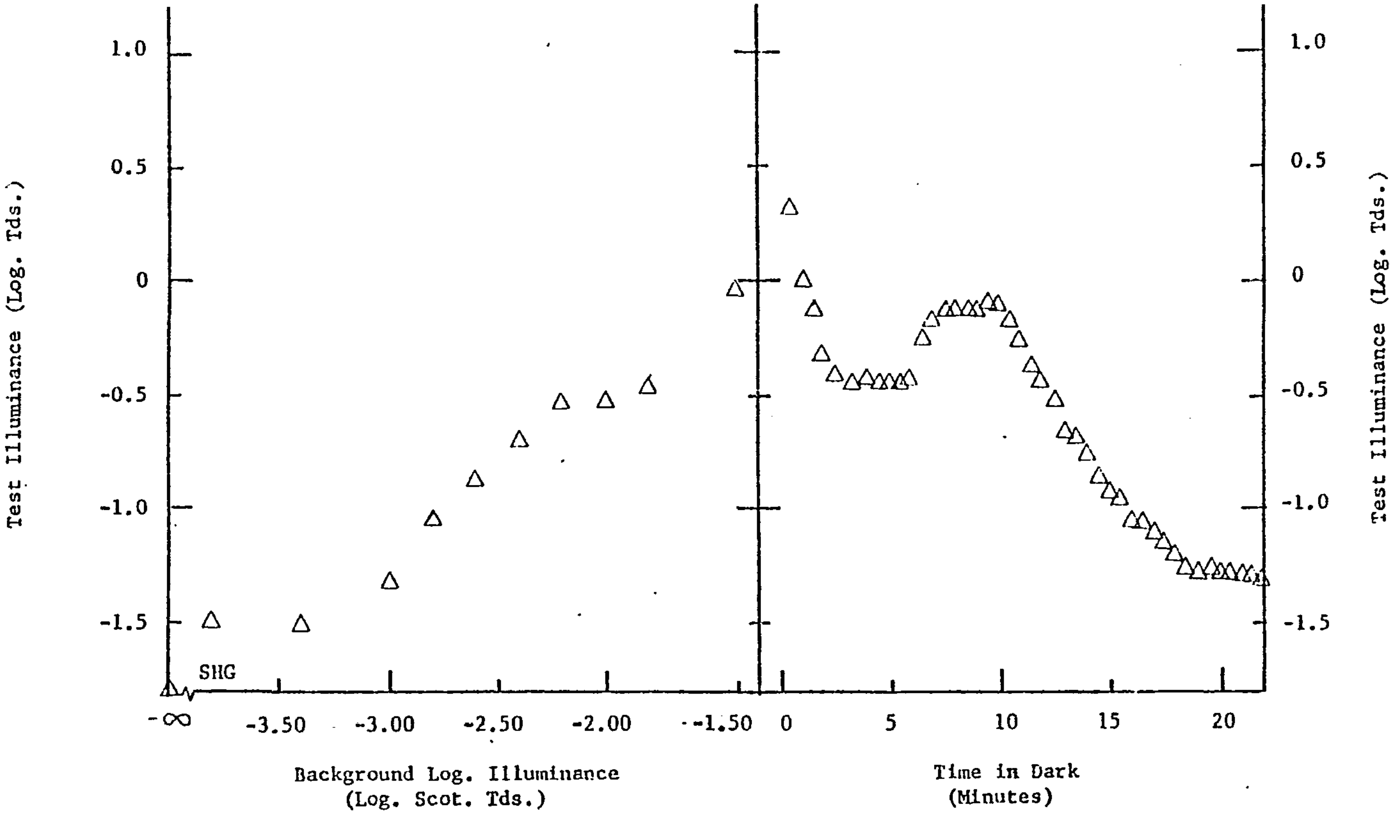
On the other hand, two different types of evidence would suggest that the present type of rod-cone interaction more probably involves a more proximal locus. First, although the interrelation of mammalian photoreceptors and horizontal cells has been extremely well studied, no pathway has been demonstrated which involves an input from rods and an output to cones or cone-bipolar cells. Secondly, flicker is generally thought to involve the action of amacrine cells which on the basis of both electrophysiological (Thibos & Werblin, 1978) and psychophysical (Enoch, 1977) data are known to be particularly sensitive to transient illumination.

On the basis of the available evidence, it is impossible to indicate which of these two different types of pathways, distal or proximal, is involved with the present type of rod-cone interaction. However, the similarity between the ERG data in the frog and the present behavioral data is sufficiently great to suggest that in this case the electrophysiologist and psychophysicist are studying manifestations of the same mechanism. The use of three different types of research could perhaps conclusively identify the underlying neural mechanism. First, the combined results from the laboratories of Alexander, Adams, and the present writer have shown that this is an easy phenomenon to study in almost any individual including ophthalmological patients. Therefore, it should be easy to obtain the desired data from individuals with known neuro-retinal deficits which relate to this phenomenon. Second, if the ERG data in frog and behavioral data in humans are manifestations of the same phenomenon, it should be possible to study this effect by means of the ERG in the same human subject investigated behaviorally. Finally, intracellular investigation in lower animals, particularly if combined with pharmacological procedures, should conclusively identify the neurons that are involved in this circumscribed type of rod-cone interaction.

Appendix: The Complex Time Course of Recovery of Green Flicker Sensitivity

The apparent complexity in the 10 Hz green data of Figure 11 (chapter 3) probably reflects the differences between the time courses of rod and cone recovery after bleaching. While the rods ultimately become sufficiently sensitive to detect 10 Hz (as was the case in Figure 3 for 7-9 Hz, Nygaard, 1981) they are not sufficiently recovered to follow 10 Hz until 10-12 minutes in the dark (Figure 11). Before this time cones are more sensitive and the desensitizing effect has time to manifest itself before rods are sufficiently sensitive to detect 10 Hz flicker. This explanation is substantiated by the data of Figure 31, which shows the illuminance necessary to detect 10 Hz green flicker as a function of the illuminance of a 28°, 512 nm adapting field (see chapter 4; procedures section). In these steady state measurements there's no reversal in sensitivity as was the case in the dark adaptation experiments of Figures 3 and 11, where sensitivity is changing over time. Thus, the reversal in sensitivity is not directly related to the state of adaptation. An incidental observation which is in line with this explanation is that at about 10-12 minutes in the dark, around the point that the 10 Hz green function begins to show increased sensitivity, the flickering test takes on a desaturated appearance.

Figure 31. The illuminance necessary to detect 10 Hz green flicker as a function of the illuminance of a 28°, 512 nm adapting field (left) and as a function of dark adaptation (right). (Observer SHG)


Test Illuminance (Log. Tds.)
1.0
0.5
0
-0.5
-1.0
-1.5
SHG
-∞
-3.50
-3.00
-2.50
-2.00
-1.50
Background Log. Illuminance
(Log. Scot. Tds.)
0
5
10
15
20
Time in Dark
(Minutes)
1.0
0.5
0
-0.5
-1.0
-1.5
Test Illuminance (Log. Tds.)

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