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The effects of long term and short term adaptation on cone-mediated spatial vision

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City University of New York, 1987

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THE EFFECTS OF LONG TERM AND SHORT TERM ADAPTATION ON CONE-MEDIATED SPATIAL VISION

by

Franklin Naarendorp

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

1987

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.

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The City University of New York

Abstract

EFFECTS OF LONG TERM AND SHORT TERM ADAPTATION UPON CONE-MEDIATED SPATIAL VISION

by

Franklin Naarendorp

Advisor: Professor Thomas E. Frumkes

Part One of the present study concerns the influence of selective long term rod adaptation on cone-mediated spatial acuity. On-off squarewave gratings of 6° diameter and 600 ms duration were presented to the parafovea by means of a projection system. Threshold Grating Luminance (TGL) was the index of spatial acuity. TGL was determined as a function of background luminance. With fine gratings, TGL decreased (acuity increased) as background luminance increased up to -2 log cd/m^2. This effect was small for coarse gratings, but increased with spatial frequency up to one log unit for a 21 cycle per degree (cpd) grating. Action spectra established that enhancement of acuity was due to an influence by rods.

During the rod recovery stage of long term dark adaptation, TGL increased. This effect was small with coarse gratings but increased with spatial frequency. The results suggest that dark adapted rods tonically inhibit cone-mediated spatial acuity.

Part Two concerns the influence of short term adaptation of both rods and cones upon cone-mediated spatial acuity. A test stimulus of 54' diameter, 10 ms duration and a concentric adapting flash (AF) of 20° diameter, 500 ms duration, variable in illuminance were presented in Maxwellian view to either the fovea or parafovea. The test was either a homogeneous flash (TF) or an 18 cpd grating. TF threshold and Threshold Grating Illuminance (TGI) were determined as a function of Stimulus Onset Asynchrony (SOA). Results obtained with a homogeneous TF resembled Crawford's (1947) early light and dark adaptation data, but TGI results were much different. AFs too dim to influence cones decreased TGI. This effect gradually reached a maximum at an SOA of 250 ms and then remained steady. Following offset of bright AFs, TGI decreased below control values. TGI was minimal at an SOA of 900 ms, but returned to control level by an SOA of 5000 ms. Action spectra show that: 1. the influence of dim and bright AFs were attributable to rods and cones, respectively; 2. TGI is always cone-mediated; 3. enhancement of grating acuity involves an increase in sensitivity at the red end of the spectrum.

Acknowledgements

The work for this dissertation was carried out in the Doctoral Program in Neuropsychology at Queens College. Members of the Faculty and Staff and all my student colleagues were extremely helpful throughout my time in the Program. I thoroughly enjoyed the intellectual atmosphere present and feel proud to have made some memorable friends in the ranks of the Department. As far as I am concerned this dissertation is the result of the collective effort of the Faculty and Staff who prepared me academically to assume the final responsibility for this piece of work.

I am most indebted to my mentor Dr. Thomas E. Frumkes. He stirred my enthusiasm for visual processes with his superb knowledge of the Visual Sciences and creative insights in the conducting of experiments. Tom has supported me generously all the way, at every stage of my education and training in Queens. I am also indebted to the members of my dissertation committee, Drs. R. J. Bodnar and R. N. Lanson. The feedback which I received from Dr. Lanson during the writing of this dissertation was really exceptional. I am also very grateful to my outside readers, Drs. W. H. Seiple and J. F. Sturr. I was especially impressed with Dr. Sturr's critical reading of the manuscript.

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for some years, with a peaceful environment which has been a powerful force in helping me to reach this goal.

Finally, my greatest appreciation goes to my parents, Henny and Es, who have instilled, with patience and love, in all their children, a sense of determination. Ultimately, I relied on this quality in pursuing my goal.

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List of Abbreviations

AF -	Adapting Flash
cpd -	cycles per degree
SOA -	Stimulus Onset Asynchrony
SRCI -	Suppressive Rod Cone Interaction
TF -	Test Flash
TGI -	Threshold Grating Illuminance
TGL -	Threshold Grating Luminance

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PART ONE

Chapter 1: GENERAL INTRODUCTION

Based upon comparative anatomical studies of different vertebrate retinae, Schultz originally proposed the Duplicity Theory of Vision in the latter part of the 19th century. As it is most often stated, vertebrate vision is mediated by two different types of photoreceptors, the rods and the cones. In general, the rod system mediates vision under scotopic (low) levels of retinal illumination and the cone system mediates vision under photopic (high) levels of retinal illumination.

Probably the best known data pertaining to the duplicity theory are classical dark adaptation data provided by Hecht (1937; Hecht, Haig & Chase, 1937; Hecht, Peskin & Patt, 1938; Hecht & Smith, 1933). As dark adaptation is usually studied, the observer is presented with a bright bleaching light, and absolute threshold of a test flash is subsequently determined during the time course of recovery. According to typical results, the upper limb of the duplex curve is attributed to cone function, the lower limb to rod function. An alternate way of showing this difference in rod and cone function is to determine "a light adaptation" or "increment threshold" function. Accordingly, the threshold of the test stimulus is determined as a function of the luminance of a continuously presented background. Once again, the classical light adaptation function consists of a lower rod and an upper cone limb (e.g., Crawford, 1947).

As used today, the term "duplicity theory" is really a summary of empirical data related to differences in rod- versus cone-vision in vertebrates with heavy emphasis on the performance of the human psychophysical observer (for reviews see Hecht, 1937; Wyszecki & Stiles, 1967; Ripps & Weale, 1976). In general, it can be said that scotopic vision is mediated by rhodopsin in rods, has low spatial and temporal resolution, has a relatively high Weber ratio, gives no sense of color, is best a few degrees from the fovea, and has a spectral sensitivity curve that peaks at about 500 nm. Photopic vision is mediated by three types of cones that contain different photopigments. Photopic vision has a high spatial and temporal resolution, is best in the fovea, mediates color perception, has generally a lower Weber ratio, and its spectral sensitivity peaks at approximately 560 nm.

Mesopic Vision and Rod-Cone Interaction

Classical light adaptation studies usually emphasize the differences between rod and cone vision (e.g. see Stiles, 1959). In the dark-adapted state, the rod system is clearly more sensitive, and as retinal illumination is gradually increased the rods become desensitized until a transition from rod- to cone-mediation of visual function is evidenced. Under most common circumstances, this transition occurs with a background retinal illuminance of about 1 td. But although the cones are usually more sensitive at higher background illuminance levels, rods still function until background levels exceed 1000 tds (Aguilar & Stiles, 1954). Thus, there is a mesopic range of background illumination over which both rods and cones function simultaneously and quite possibly interact. This possibility is referred to throughout this thesis as rod-cone interaction. Although physiologically this could conceivably involve a direct interaction between photoreceptors (Nelson, 1977; Nelson, Kolb, Robinson & Marianni, 1981), in this thesis this term implies an interaction between neurons receiving photic information from the two different types of photoreceptors, not necessarily an interreceptor interaction.

There is an ever growing body of literature indicating rod-cone interaction. Studies involving color mixing and additivity have shown that rod activity contributes to hue and saturation judgments, particularly when extrafoveal retinal areas are stimulated (Stabell & Stabell, 1971, 1973, 1977, 1979; Trezona, 1970, 1976). Results of dark adaptation experiments suggest that the rod and cone systems interact during the recovery from photopigment bleaching (Drum, 1981; Spillmann & Conlon, 1972). For example, Wooten and Butler (1976) reported a transient elevation of the cone plateau (by a factor of 1.4) during the course of dark adaptation due to rod influence. Rod and cone signals can also engage in temporal summatory interactions (Frumkes, Sekular, Barris, Reiss & Chapula, 1973). Frumkes et al. reported that the difference in rod versus cone latency determines whether subliminal rod and cone signals will add together to produce a threshold sensation. Rod system responses are sluggish, cone system responses are faster. MacLeod (1972, 1974; see also van den Berg & Spekreijse, 1977) showed that for a constant latency difference, rod and cone related flicker signals would either enhance or cancel each other depending upon the response phase.

Suppressive Rod-Cone interaction

Several recent studies describe a novel type of rod-cone interaction (Goldberg, Frumkes & Nygaard, 1983; Alexander & Fishman, 1983; Coletta & Adams, 1984; Arden & Hogg, 1985) involving the suppression of cone-mediated responses to high frequency flicker by rod dark adaptation. Typically, cone sensitivity to rapid flicker measured during the course of dark adaptation is maximal at the time of the cone plateau but decreases progressively as the rod system gradually reaches absolute threshold. Goldberg et al. (1983) showed that selective rod light adaptation enhances cone-mediated responses to rapid flicker. A most typical result is obtained when a 2° parafoveal test stimulus is modulated at a frequency higher than 15 Hz in the presence of a background with an illuminance near rod-saturation: flicker illuminance thresholds decrease by about 1 log unit. Frumkes and Eysteinsson (1987) have designated this effect Suppressive Rod-Cone Interaction (SRCI) and attributed it to a tonic, probably inhibitory influence of dark adapted rods upon cone-related pathways: the enhancement of flicker produced by rod-light adaptation is, hence, due to a removal of this inhibition. SRCI can be demonstrated over almost the entire retina including the fovea (Coletta & Adams, 1984).

SRCI involves neural interaction in the distal retina as it is observed in amphibians (Frumkes & Eysteinsson, 1987) and cat (Pflug & Nelson, 1986) by intracellular recordings from many distal retinal neurons including the cones, and by means of electroretinogram procedures in a wide variety of species including humans (Arden & Frumkes, 1986; Goldberg & Frumkes, 1983; Hood, 1972; Loew & Arden, 1985). Psychophysical measurements on some human subjects with pathological conditions in the distal retina show characteristic abnormalities in this SRCI-effect (Alexander & Fishman, 1984; Arden & Hogg, 1985). Additionally, in individuals with protanopic deficiencies cone-flicker sensitivity is not suppressed by the dark adapted state of the rod system (Goldberg & Frumkes, 1983). Collectively, these studies strongly suggest a distal retinal mechanism for SRCI when flicker sensitivity is used as a measure.

SRCI and spatial acuity

In all of the foregoing references, SRCI was studied using flicker sensitivity as a measure of cone functioning. In the present thesis, I am concerned with the possibility that SRCI also involves a similar influence of rod-adaptation upon cone-mediated spatial acuity. This possibility is suggested by three different types of observations. First, SRCI cannot be observed with a flickering Ganzfeld as a stimulus (Arden & Hogg, 1985; Arden & Frumkes, 1986): as the size of the flickering test probe increases the influence of a rod-background field upon cone-mediated flicker decreases (Frumkes, Naarendorp, Eysteinsson, Denny & Goldberg, 1986; but for negative results see Alexander & Fishman, 1985). Secondly, such an influence of rod adaptation upon cone-mediated spatial acuity was indirectly suggested by Brown and Woodward (1957; but also see Brown, Metz and Yohman, 1969). Thirdly, Arden and Hogg (1985) reported a much larger than normal magnitude of SRCI in three individuals (>2.5 log units as opposed to 1 log unit in usual subjects) who were all clinically normal but they refused to drive at night. It seemed unlikely that the night driving difficulty is totally attributable to temporal vision problems. Therefore, there is a strong *a priori* reason for suspecting that rod adaptation has a facilitatory influence upon cone-mediated spatial acuity which is similar to its influence upon cone-mediated flicker.

Rationale for the present study

The present study examines the influence of rod-light and dark adaptation upon cone-mediated spatial acuity. In Part One of this thesis, the influence of long term dark adaptation (changes in cone-mediated spatial acuity following bleaching of rod-photopigment) and light adaptation (influence of continually exposed dim adapting fields upon cone-mediated spatial acuity) were explored. The luminance of squarewave test gratings (spatial frequency between 1.75 and 21 cycles per degree) whose bars could just be detected served as an index of spatial acuity. These results showed that the influence of rod adaptation upon cone-mediated spatial acuity is similar to its effect upon cone-mediated flicker.

In the course of Part One, I noticed that upon extinguishing a bright adapting field, cone-mediated spatial acuity was briefly enhanced rather than depressed. For this reason it seemed worthwhile to study the influence of short term rod- and cone-adaptation upon cone-mediated spatial acuity. Thus in Part Two, I examined the influence of 500 ms duration adapting fields of various illuminance levels upon cone-mediated spatial acuity. The illuminance of a 10 ms duration test grating of 18 cycles per degree whose bars could just be detected served as an index of spatial acuity.

Chapter 2: METHODS

Apparatus - Two Kodak carousel slide projectors were used to provide the test stimuli. Each projector was equipped with a ELH (300 watt, 120 volt) tungsten halogen source and a focussing lens. The projectors were placed in a light-tight box at a fixed distance from a white diffusing screen. A red light emitting diode attached to the screen served as fixation target. The projectors were so arranged that when all apertures were removed the projected fields superimposed on the screen. Observers viewed all projected stimuli through a 2.5 mm diameter artificial pupil.

Spatial features - The extent and shape of the stimuli were determined by gratings, apertures or annuli placed in the slide mounts of the projectors. Best possible focus was easily obtained by manipulating the focussing lens. All gratings were on-off squarewave gratings. The lower spatial frequency gratings (50 lines per inch or less on the slide) as well as the annuli were fabricated photographically using high contrast film. As determined with the aid of a United Detector Technology (UDT) radiometer (model 263), the projected luminance difference between dark and light bars or regions exceeded 2.5 log units. Higher spatial frequency gratings were 2 x 2 inch Ronchi gratings of between 50 and 300 lines per inch obtained from Edmund Scientific Corporation. Although no objective means were available to assess the projected grating contrast, both the quality of the optics and subjective impression suggested that contrast decreased with number of lines per inch for gratings finer than 100 lines per inch.

Spatial calibration - The distance between the viewing screen and the observer was always 2.5 meters. At this distance, trigonometry shows that a 2.5 cm spatial extent on the screen produced a retinal image of 1° of arc. The largest homogeneously illuminated field was accordingly determined to be 24° of arc. A grating of 50 lines per inch provided a spatial frequency of 3.5 cycles per degree (cpd) on the retina. Finer gratings of 100, 200 and 300 lines per inch provided spatial frequencies of 7, 14 and 21 cpd, respectively.

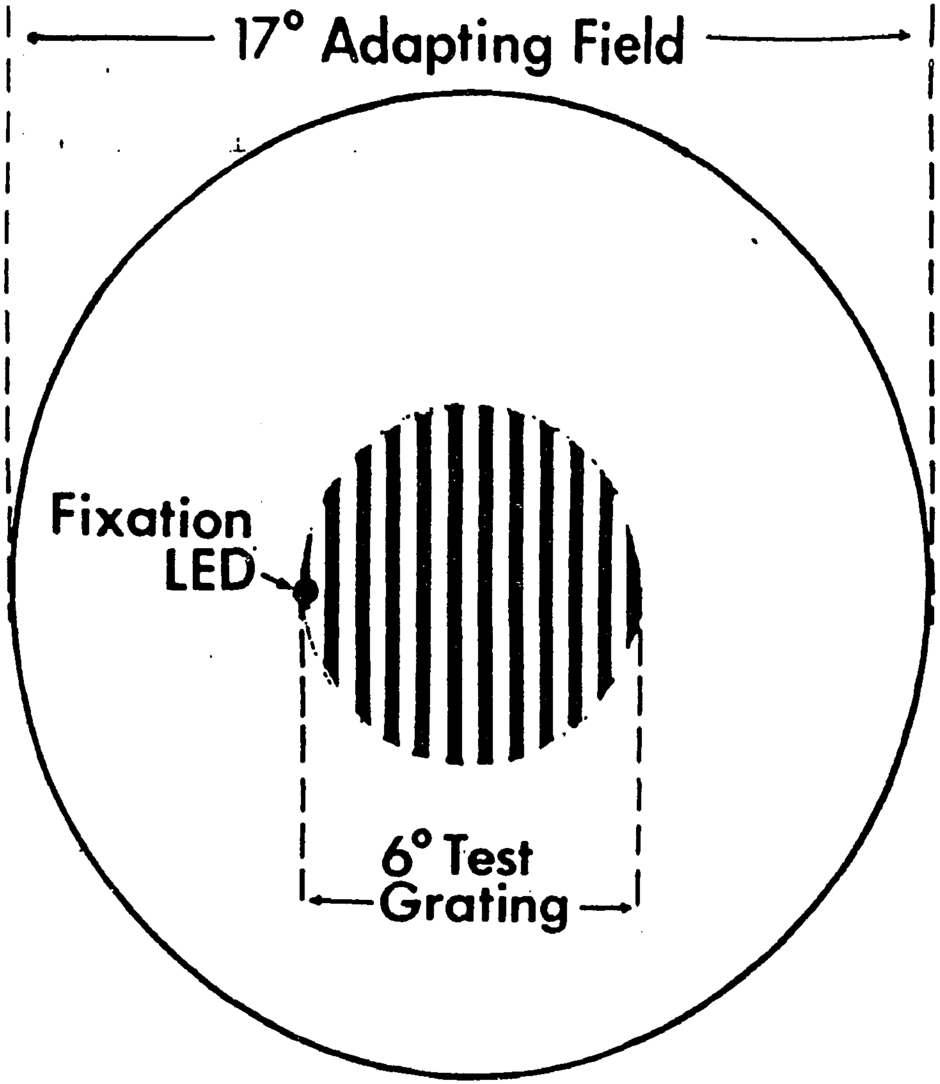
The present study used a 6° circular test stimulus of variable spatial frequency (1.75, 3.5, 7, 14, and 21 cpd) always presented 3° from fixation. If present, the background was always circular, concentric and steady. Background sizes were either 17° or 6° in diameter. The background was either shaped as a homogeneous disc or as an annulus with an outer diameter of 17° and an inner diameter of 6°.

The observer's view of the stimulus configuration is illustrated in Figure 1. The observer, whose head position was fixed by a full mouth bite bar, viewed the stimulus display through an artificial pupil of 2.5 mm in diameter at a distance of 2.5 meters.

Duration control - The temporal properties of all stimuli were controlled by a standard physiological dual channel stimulator (Grass Model S88). This triggered Uniblitz shutters which were 25 mm in diameter and placed at the output port of the focussing lens. The test stimulus was a squarewave flash 600 ms in duration presented once every five seconds. The background was either "on" or "off".

Figure 1

Stimulus display. The test stimulus was a 600 ms duration flash presented once every 5 seconds. It was a 6° diameter, vertically oriented squarewave grating centered 3 to the right of a red light emitting diode used for fixation. The background field used in the experiments represented by figures 2-6 and 9 was continually exposed and concentric to the test flash: for most experiments, it was 17° in diameter and 480 nm in wavelength.


17° Adapting Field
Fixation LED
6° Test Grating

Luminance control - The luminance of the test stimulus was controlled by balanced 4.0 log unit circular neutral density wedges placed just after the shutter. An indicator dial governed the position of the wedge such that each dial turn caused the wedge to make 1/40 of a wedge revolution. Thus a full turn of the dial indicator resulted in a luminance change of 0.1 log unit. Additional filtering could also be achieved by means of fixed neutral density filters. Placing any grating in the slide mount reduced the overall luminance of the display by 0.4 log units. This probably can be accounted for by the 0.3 log units (i.e., 50% of the total area) occupied by the dark bars of the grating, while the additional 0.1 log units probably is attributable to scatter and absorption.

Wavelength control - The spectral composition of the test stimulus was determined by either a 512 nm Baird- Atomic interference filter (with half bandwidth of 12 nm) or a Kodak Wratten 29 filter. These were placed just after the shutters. The spectral composition of the background was determined by similar narrow band interference filters (Baird Atomic or Ditric Optics). In most experiments, the background field was 480 nm but in other cases, was either 450, 512, 540, 580, or 655 nm.

Luminance calibration - A Pritchard photometer was used to measure the photopic luminance of all stimuli. The scotopic luminance of a 512 nm stimulus was calculated with the formula, $\log Ts = \log Tp + \log [2.567 (V'_\lambda / V_\lambda)]$ which is taken from Wyszecki and Stiles (1967, p. 226). Tp is the photopic luminance value of the stimulus; V'_λ and V_λ are the scotopic and photopic luminous efficiency coefficients at 512 nm, respectively. This formula is accurate for all monochromatic stimuli but is inappropriate for use with stimuli with extended spectral properties (e.g., white or Wratten 29 stimuli). Therefore, the scotopic luminances of all other stimuli were calibrated by equating their absolute threshold values with that of a 512 nm stimulus.

Since most spatial acuity literature calibrates stimuli in terms of luminance expressed in cd/m^2, most of the data in Part I are presented in such terms. Retinal illuminance could be readily obtained from the formula proposed by Wyszecki and Stiles (1967, p. 212): T = L x p, where T is the troland value of a field with photopic luminance L (cd/m^2) seen through a pupil; p is equal to pi x the pupil diameter raised to the power of 2 and is expressed in mm^2. Since the diameter of the artificial pupil was 2.5 mm, 1 cd/m^2 correspond to .6 tds.

For the dark adaptation experiments presented in Figures 7 through 9 below, a bleaching light source was achieved by placing a Nikon microscope illuminator directly behind the artificial pupil. I had no way to directly measure the illuminance provided by this source, but based upon comparison with the influence of a bleaching stimulus provided in Maxwellian view, this source provided a retinal illuminance of about 30.000 trolands.

<u>Irradiance calibration</u> - The relative irradiance of the narrow band chromatic stimuli was measured with a UDT radiometer (model 263). The log relative irradiance was converted into log relative quanta, Q, by the formula Q = E x L/1243, where E is the relative irradiance, L is the peak

wavelength of the filter, and 1243 is a constant.

EXPERIMENTAL METHOD

The general goal of the experiments in Part One was to examine the influence of the adapted state of rods upon cone mediated spatial acuity. Six experiments were undertaken to reach this general goal, generally following the procedures employed by Goldberg et al (1983). Experiments 1-4 were light adaptation experiments. The specific purpose of Experiment 1 was to establish whether or not a dim background exerted any influence on spatial acuity. Experiments 2, 3 and 4 attempted to elucidate and localize the photoreceptor mechanism(s) responsible for the background effect, e.g., that in fact rod light adaptation is influencing cone-mediated spatial acuity. Experiments 5 and 6 were performed to determine differential effects of rod dark adaptation on spatial acuity.

Observers - Three observers were used in this study. FN, the author, was 37 years old, is an experienced psychophysical observer and served in all aspects of this study. He is amblyopic in the right eye, but has uncorrected 20/20 vision in the left eye. ND and MV, both 24 years old females with corrected Snellen acuities of 20/20, served as additional observers in key portions of the study. ND was a well-practiced psychophysical observer, MV was inexperienced. For observers ND and MV stimuli were presented to the right eye temporal field, but for FN to the left eye nasal field.

General procedure for data collection - Prior to each experimental session, the observer aligned his eye with a steady projected bright grating and the fixation target. To obtain a focussed image of both targets, the observer could adjust the position of an artificial pupil attached to the bite bar in three different planes. Experiments 1-4 were light adaptation experiments. Data collection in these experiments followed an initial 25 minute period of dark adaptation. Except in Experiment 2, the observer adjusted the position of the neutral density wedge controlling grating luminance until the bars of the grating just became visible. This threshold is referred to throughout the text of Part One as the threshold grating luminance (TGL). It should be obvious that TGL is always higher than absolute threshold, considerably so for high spatial frequency stimuli. After each determination of TGL, the experimenter randomly turned the wedge to higher density levels. Thus, all thresholds are ascending. For the action spectra in Experiment 2, a grating of subliminal luminance was repetitively presented. The observer increased the radiance of the background until the bars of the grating became just visible. Experiments 5 and 6 were dark adaptation experiments. Following 10 minutes of dark adaptation the observer's eye was bleached for one minute with a white light of 30.000 trolands. The observer's task was to adjust for TGL with intervals of 30 seconds throughout the time course of dark adaptation. After each determination of TGL, the wedge was randomly turned to higher density levels.

In general, data collection proceeded according to a set of rules. First, no experimental session lasted more than 90 minutes after dark adaptation was completed. Second, except for data obtained in dark adaptation experiments, for each set of test gratings or background parameters, three threshold values were consecutively taken. If the range of threshold values exceeded 0.1 log unit, at least one additional threshold value was obtained. Third, except for data obtained in dark adaptation experiments, every data point plotted was based on observations in at least three experimental sessions, and consequently, involved a minimum of nine threshold determinations. Each plotted datum obtained in dark adaptation experiments is the median of three threshold determinations.

Chapter 3: LIGHT ADAPTATION EXPERIMENTS

Experiment 1

The goal of Experiment 1 was to determine the influence of the ambient level of illumination upon grating acuity. To this end, TGL was determined as a function of the luminance of a steady 480 nm background field using test gratings between 1.75 - 21 cpd. The test grating was either "green" (512 nm) or "red" (Wratten 29 filter).

Results and discussion

Figure 2 plots TGL as a function of background luminance for observer FN. Both coordinates are expressed in photopic units. A control value, i.e., the TGL in the absence of the background, is indicated on the abscissa at the point labeled "minus infinity". Since TGL is inversely proportional to spatial sensitivity a lowering on the ordinate indicates an increase of acuity. Figure 2 shows that for a 1.75 cpd grating, of 512 nm in wavelength (small open circles) TGL increases with background luminance as a two limbed function. This function resembles a classical increment threshold function (e.g., Crawford, 1947) displaying a rod limb (low background intensity) and a subsequent cone limb (high background intensity). This seems quite reasonable since previous literature (e.g., Brown & Woodward, 1957; Long, 1978) reported that spatial frequencies lower than 2.5 cpd are detected by rods at lower luminance levels, but by cones at higher luminance levels.

According to a variety of sources in the literature (e.g., Long, 1978;

Figure 2

Observer FN: Threshold grating luminance as a function of the luminance of a 480 nm background field. In Figures 2-9, luminance is expressed in log photopic cd/m^2. The shapes of the symbols represent the different spatial frequencies of the grating as indicated in cycles per degree. Open symbols represent data obtained with 512 nm gratings, the closed symbols with red (Wratten 29 filter) gratings.

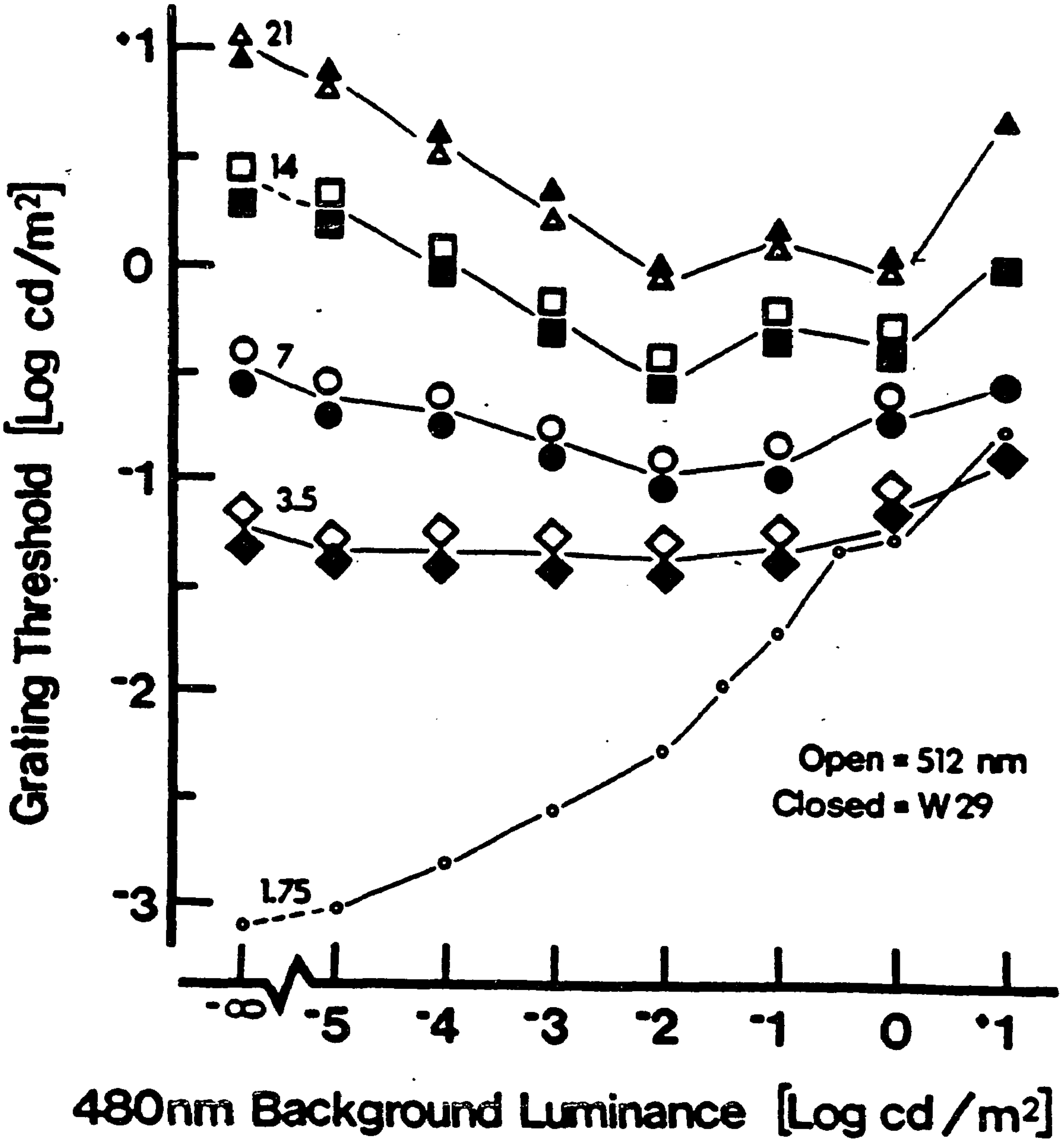
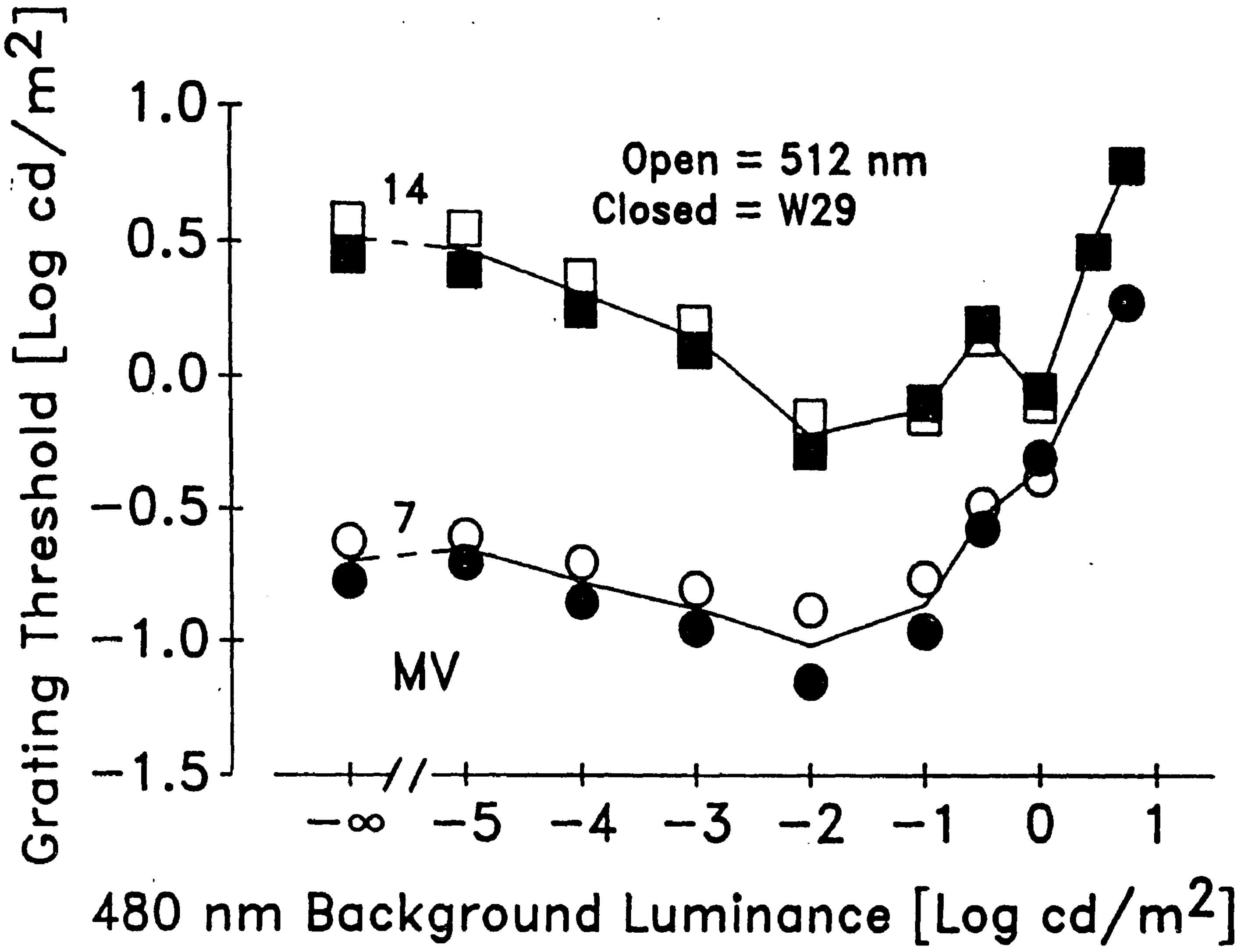

Grating Threshold [Log cd/m²]
+1
0
-1
-2
-3
21
14
7
3.5
1.75
Open = 512 nm
Closed = W29
-∞
-5
-4
-3
-2
-1
0
+1
480nm Background Luminance [Log cd/m²]

Figure 3

Observer MV: Threshold grating luminance as a function of the luminance of a 480 nm background field. The shapes of the symbols represent the different spatial frequencies of the grating as indicated in cycles per degree. Open symbols represent data obtained with 512 nm gratings, the closed symbols with red (Wratten 29 filter) gratings.


Grating Threshold [Log cd/m^2]
1.0
0.5
0.0
−0.5
−1.0
−1.5
Open = 512 nm
Closed = W29
14
7
MV
−∞
−5
−4
−3
−2
−1
0
1
480 nm Background Luminance [Log cd/m^2]

Hess, Nordby & Pointer, 1987) spatial frequencies higher than 2.5 cpd are invisible to the rod-related visual system and hence, are always detected by cones. In Figure 2, the results obtained with gratings of spatial frequencies equal to or higher than 3.5 cpd, are much different from those obtained with gratings of lower spatial frequencies. As background luminance increases to -2 log cd/m^2, TGL gradually <u>decreases</u>. This effect, which is observed with "red" as well as "green" gratings, is hardly noticeable in the case of a 3.5 cpd grating. But it increases in magnitude with grating frequency to more than a one log unit effect with the highest frequency used, 21 cpd. As background luminance increases from -2 to 0 log cd /m^2, no clear change in grating visibility occurs. But as background luminance increases beyond 0 log cd/m^2, TGL begins to increase again.

Figure 3 shows results of a similar experiment with a second observer, MV. Although not as much data were collected, the same essential trends are apparent.

Experiment 2

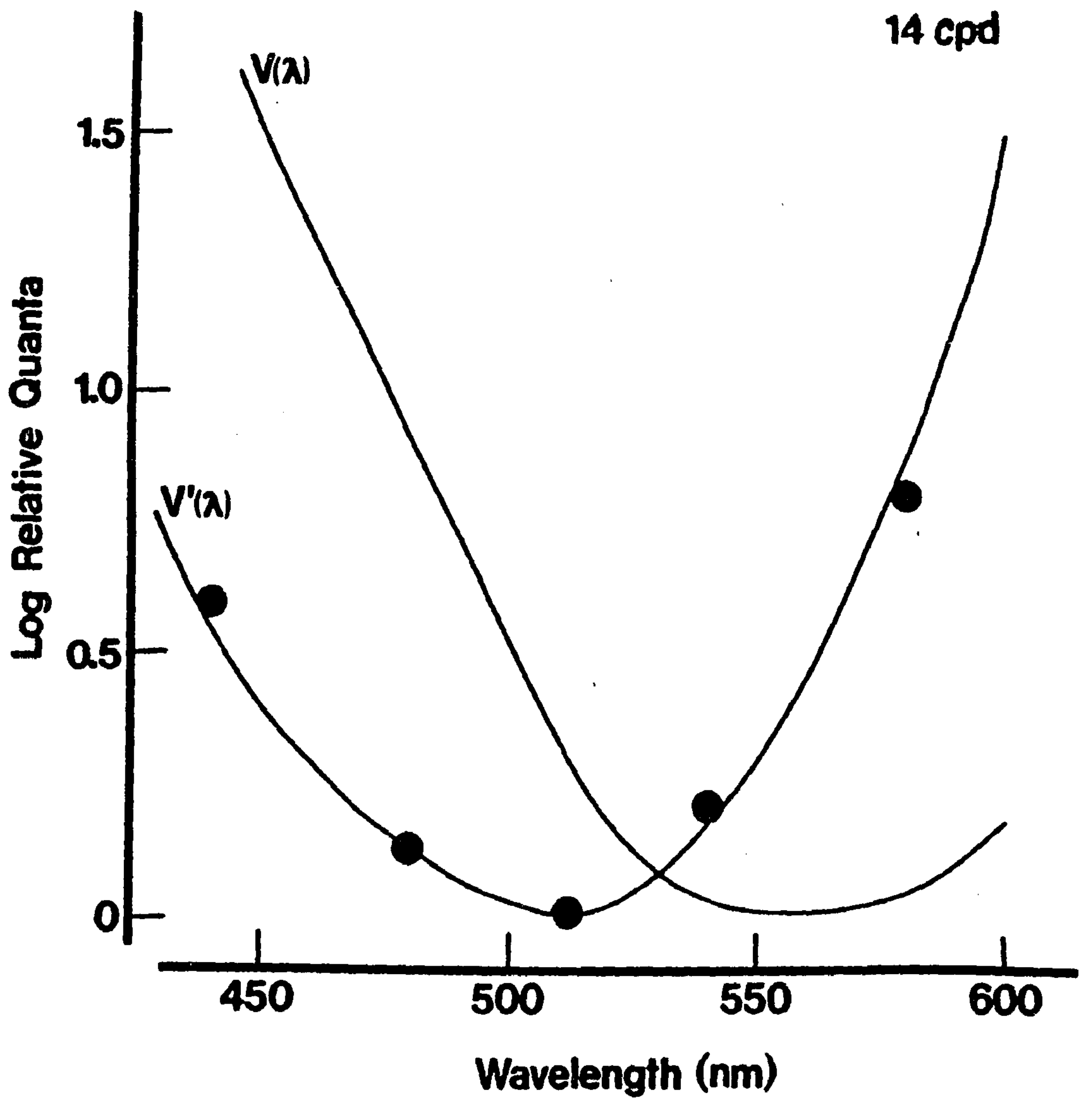
The results of Experiment 1 obtained with gratings higher than 3.5 cpd and background luminance levels <-2 log cd/m^2 probably involve rod-cone interaction. Specifically, in Figures 2 and 3, the data are plotted in photopic units which match different wavelengths for cone sensitivity. Notice that data obtained with these higher spatial frequencies are essentially independent of grating wavelength. Thus, a cone-match of these gratings produces essentially similar data. In contrast, a plot of these data in scotopic units (which match different wavelengths for rod sensitivity) would show that the "red" and "green" functions are vertically displaced by 1.6 log units with respect to each other. Thus, all the data in Figs. 2 and 3 obtained with higher spatial frequencies involve detection of TGL by cones.

The low luminance values themselves argue quite strongly that backgrounds dimmer than -2 log cd/m^2 are producing their effect by stimulating rods. In order to show this more clearly, an action spectrum for the adaptational influence of the background upon TGL was determined according to the following procedure. A 14 cpd grating was presented at a value 0.6 log units below the TGL obtained with no background present (i.e., -0.2 log cd/m^2). The observer adjusted the radiance of a variable wavelength background until the grating became just visible.

Figure 4 shows the resulting action spectrum for the only observer used, FN. Accordingly, the log relative quanta provided by the background are plotted as a function of background wavelength. The solid curves labeled V'_λ and V_λ indicate the CIE scotopic and photopic luminosity functions respectively (Wyszecki & Stiles, 1967). The relative ordinate values of the data points in Figure 4 as well as those of the CIE luminosity functions were shifted such that their minima correspond at the 0 log relative quanta ordinate position. This is the only curve fitting manipulation. The plotted data points show good agreement with the CIE scotopic luminosity function indicating that rods and only rods are mediating the effect of the background.

Figure 4

Observer FN: Action spectrum for the influence of a 17° diameter adapting field upon the visibility of a red (Wratten 29 filter) grating of 14 cycles per degree. For these experiments the test grating luminance was set at -0.2 log cd/m^2 and would be invisible if no background was present: the observer increased the radiance of the background field until the grating was just detected. These criterion values are plotted on the ordinate as a function of the background wavelength. The relative ordinate values of these data points as well as that of the CIE photopic and scotopic luminosity function were shifted such that their minima correspond at the 0 log relative quanta ordinate position, but no other curve fitting manipulation was used.


14 cpd
V(λ)
V'(λ)
1.5
1.0
0.5
0
Log Relative Quanta
450
500
550
600
Wavelength (nm)

Experiment 3

The action spectrum in Figure 4 only involves wavelengths shorter than 580 nm. It was impossible to extend this action spectrum to longer wavelengths, since such backgrounds either had no influence or impaired the visibility of high spatial frequency gratings. Classical literature (e.g., Wald, 1945) suggests an obvious explanation. That is, cone sensitivity for wavelengths longer than 610 nm is equal to or greater than that of rods. Thus, any background of these longer wavelengths that would adapt out rods would additionally directly adapt cones. Therefore, any change in grating acuity produced by a background would be likely to reflect conflicting tendencies of rod and cone adaptation.

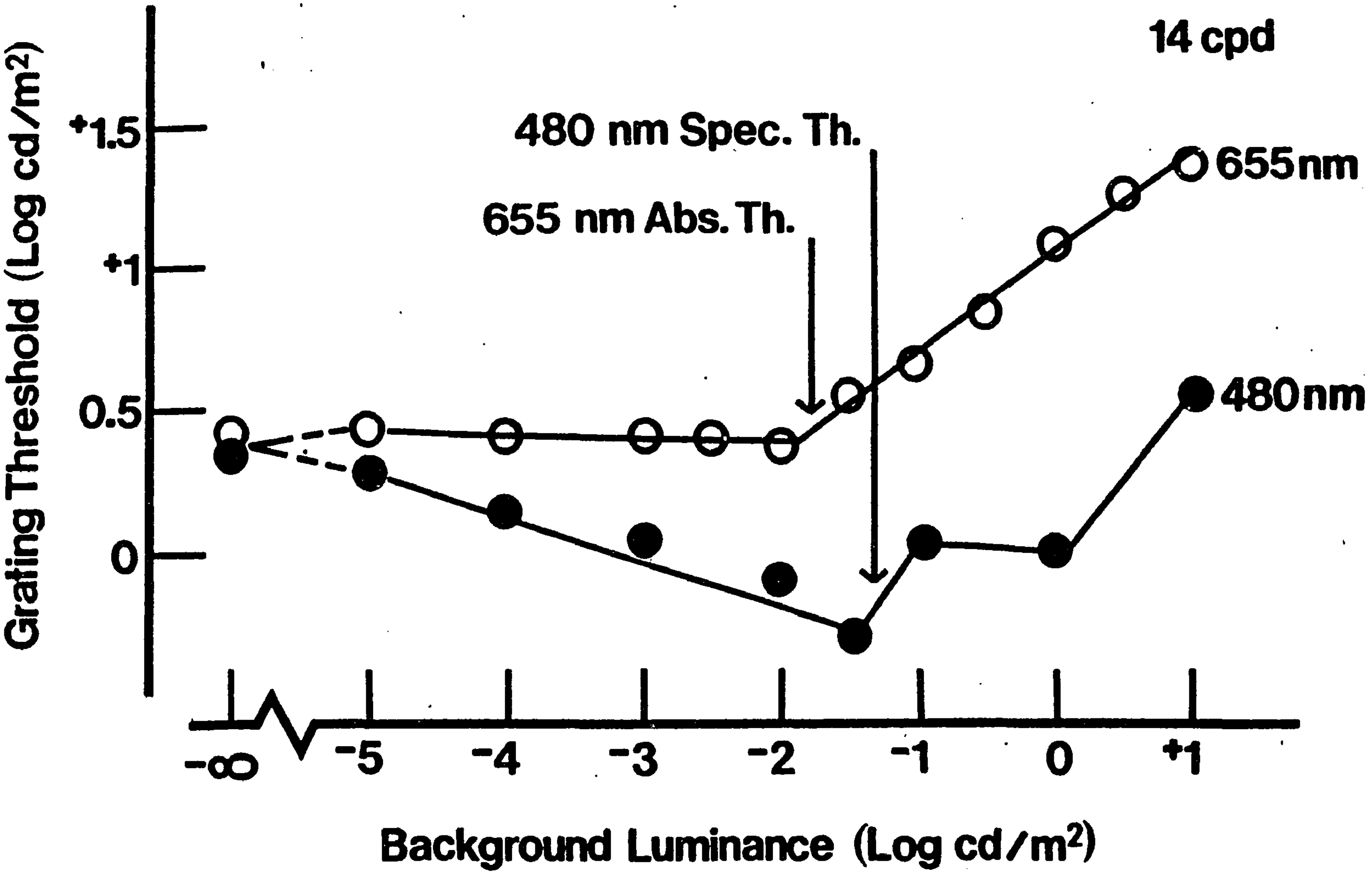
In order to more directly study the different influences of rod vs. cone stimulating background fields upon cone mediated spatial acuity, I compared in Experiment 3, the influence of a 480 nm (rod stimulating) background and a 655 nm (cone stimulating) background upon TGL.

Results and discussion

A "red" 14 cpd grating was used as test stimulus. In Figure 5, TGL is plotted as a function of background luminance, again in log photopic units. The function labeled 480 nm (closed symbols) is in fact a replication of the 14 cpd function displayed in Figures 2 and 3, and hence shows the same initial decrease of TGL as background luminance increases. This initial decrease is followed by a rise of TGL produced by background luminance levels high enough to have the observer appreciate the appearance of the

Figure 5

Observer FN: Threshold luminance for detecting a red (Wratten 29), 14 cycles per degree grating as a function of the luminance of a 480 nm (closed circles) or 655 nm (open circles) background field. The labeled arrows indicate the absolute threshold for the 655 nm background field and the specific (color identification) threshold for the 480 nm background.


14 cpd
480 nm Spec. Th.
655 nm Abs. Th.
655nm
480nm
Grating Threshold (Log cd/m²)
+1.5
+1
0.5
0
-∞
-5
-4
-3
-2
-1
0
+1
Background Luminance (Log cd/m²)

background as being blue in color (noted by the arrow labeled "480 nm spec. th"). To the extent that color appearance necessitates cone activity, this suggests that the increase in TGL at luminance levels exceeding specific thresholds is attributed to a background influence upon cones.

In Figure 5, the 655 nm function (open symbols) initially does not show any change in TGL as background luminance increases. As indicated by the arrow on the left of Figure 5, absolute threshold of the 655 nm field is only reached at an abscissa value of -1.8 cd/m^2, which explains the negligible influence of dimmer fields on TGL. Once visible, the field appears red in color to the observer, probably directly stimulating cones. Higher luminance levels of both wavelength backgrounds appear to elevate TGL. This elevation is in both cases most likely due to cone-mediated background influence. However, the data obtained with higher background luminance levels are inconsistent with the operation of only one cone mechanism. Despite the photopic match of background wavelength the two sets of data are displaced by more than 1 log unit with respect to each other when fit by straight lines with the same slope. Also, the "kink" occurring in the 480 nm function cannot be ignored. Similar "kinks" are also apparent in Figures 2 and 3. Possibly these irregularities indicate a shift in detection from one mechanism to another or the interaction between several differently tuned spectral mechanisms.

Experiment 4

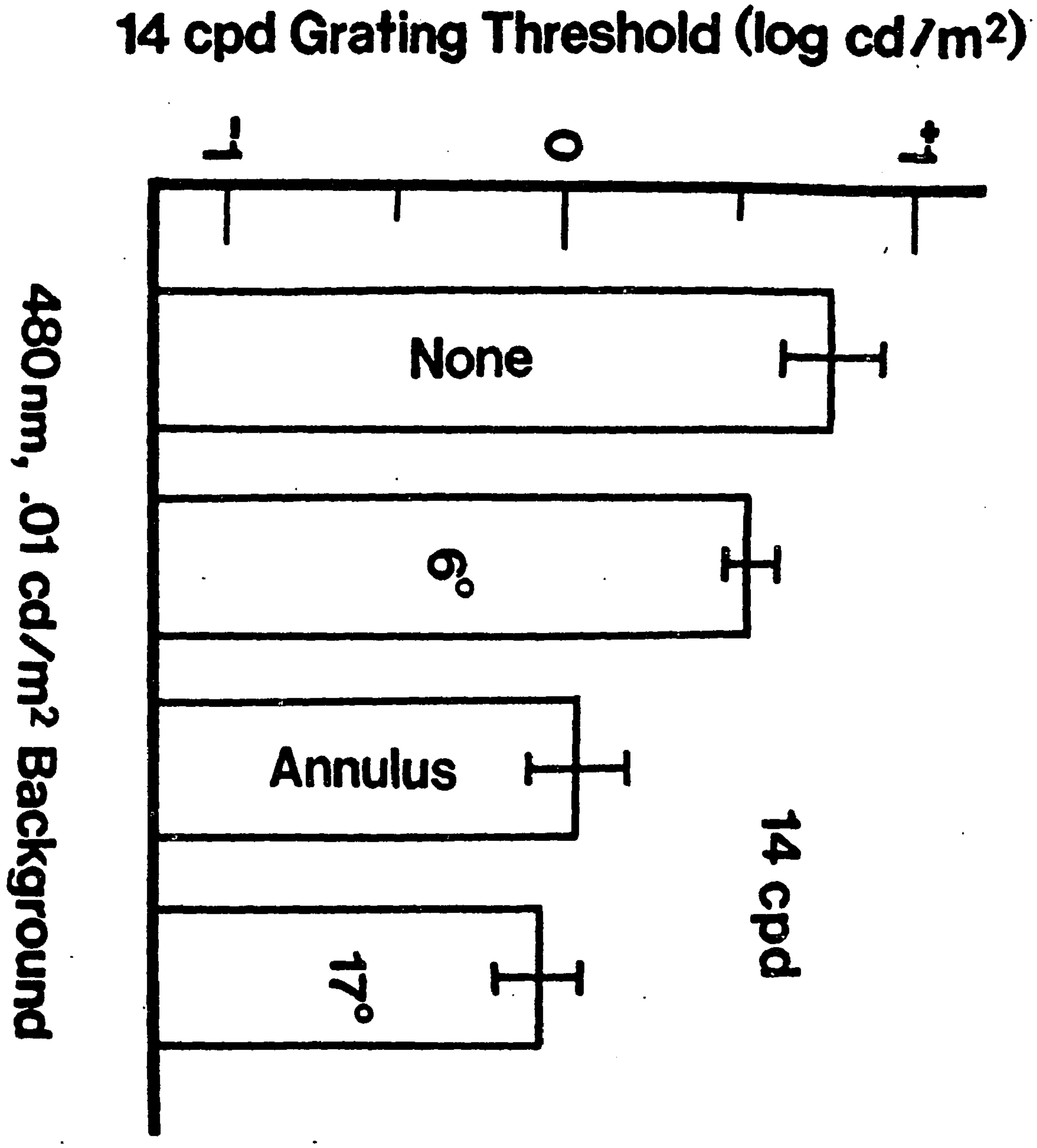
In studies of SRCI using flicker, the adapted state of rods influences cone sensitivity at a considerable distance from a test probe (e.g., Goldberg et al., 1983; Coletta and Adams, 1984; 1986). Experiments 1-3 clearly establish that rods stimulated by a large background influence cone-mediated spatial acuity. These rods could either be those in the general area of the test grating (e.g., those in the "dark bar" region of the grating) or those adjacent to the grating. Experiment 4 attempted to determine the population of rods involved. To that end, I determined the influence of different shaped backgrounds, all -2 log cd/m^2 in luminance and 480 nm in wavelength upon TGL. A "red" 14 cpd grating was used as a test stimulus. One of these backgrounds was again a homogeneous disc of 17° which stimulated rods within and adjacent to the grating area. A second was a 6° diameter background which could only influence rods in the same general area of the test grating. The last background was an annulus which only stimulated rods adjacent to the grating, i.e., had an inner diameter of 6° and an outer diameter of 17.°

Results and discussion

The results of Experiment 4 are plotted in Figure 6. TGL is plotted as a function of the shape and size of the various background fields. The TGL values shown are mean values. The indicated vertical line on top of each bar is the 95% confidence interval for each TGL value; hence, a lack of overlap indicates extremely high statistical signficance. The first bar represents TGL in the fully dark adapted eye, i.e., in the absence of a background. The second bar shows data obtained in the condition in which background diameter is equal to that of the test grating. Such a background appears to have a small influence on TGL. The third bar

Figure 6

Observer FN: Mean threshold luminance for detecting a red (Wratten 29), 14 cycles per degree grating as a function of the spatial parameters of a concentric continually exposed, 480 nm background field of -2 log cd/m^2 luminance. From left to right the four bars indicate conditions in which the background field was absent, was a 6° diameter disc, was an annulus with a 6° inner and 17° outer diameter, or was a disc of 17° diameter. The vertical hashmarks indicate 95% confidence intervals (+/- standard error).


14 cpd Grating Threshold (log cd/m²)
-1
0
+1
None
6°
Annulus
17°
14 cpd
480nm, .01 cd/m² Background

represents data obtained with an annular background. As illustrated, the annulus is almost as effective as the usual solid background (fourth bar), when they are of equal outer diameter. These experimental results strongly suggest that the adaptational influence of the background is largely mediated by rods adjacent to the test grating and not by rods beneath the test grating. However, the presence of a greater number of rods adjacent to the test grating might be primarily responsible for the observed effect. The present results are compatible with observations made by Coletta, Schefrin and Adams (1986) conducting similar experiments but used gratings restricted to the rod-free area of the fovea. They observed a similar laterally mediated rod-adaptational influence upon TGL.

DARK ADAPTATION EXPERIMENTS

Experiment 5

The previous experiments established that rod light adaptation increases the spatial sensitivity of the cone system. This is particularly obvious with higher spatial frequencies. To the extent that light and dark adaptation reflect opposite sides of the same coin, it logically follows that spatial acuity of the cone system should decrease during rod dark adaptation, and that this result should similarly depend on spatial frequency.

Experiment 5 examines the influence of dark adaptation upon spatial sensitivity. Following 10 minutes of dark adaptation, the observer's eye was bleached for one minute with a white light of 30,000 trolands. The observer continually obtained TGL throughout the time course of dark adaptation. The gratings used had spatial frequencies of 1.75, 7, 14 and 21 cpd and were either "red" (Wratten 29) or "green" (512 nm) in color.

Results and discussion

For observer FN, Figure 7 shows TGL as a function of time in the dark following the offset of the bleaching light. The open symbols represent data obtained with a "green" grating. Data obtained with a "red" grating are represented by the closed symbols. The small open circles show that for the coarse gratings of short wavelength (1.75 cpd, 512 nm), TGL decreases throughout the course of dark adaptation. In essence, such data resemble

Figure 7

Observer FN: Threshold grating luminance (on the ordinate in log cd/m^2) as a function of time in the dark. The different shaped symbols represent different frequency gratings in cycles per degree as indicated. The open symbols represent data obtained with green (512 nm) gratings.

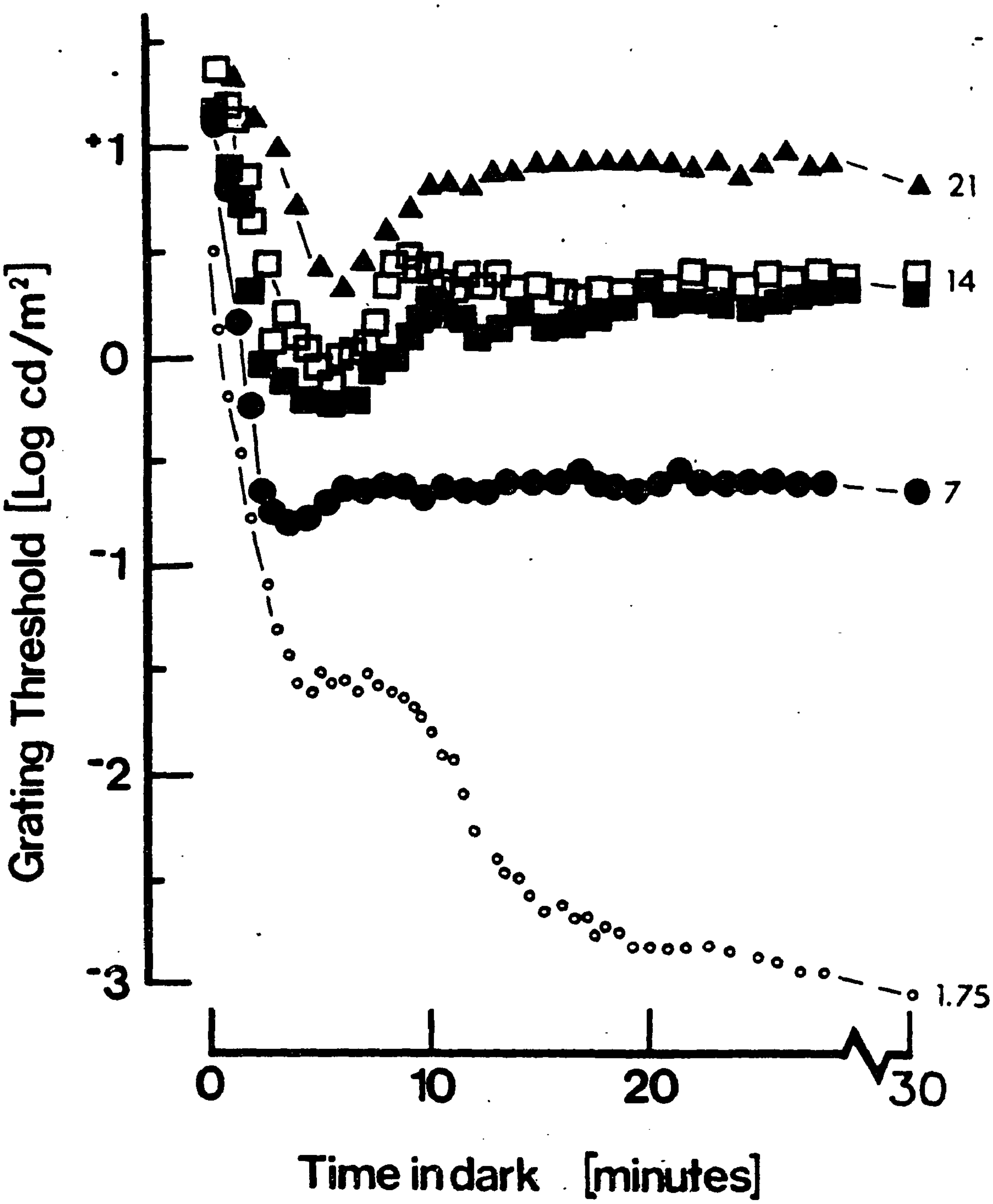
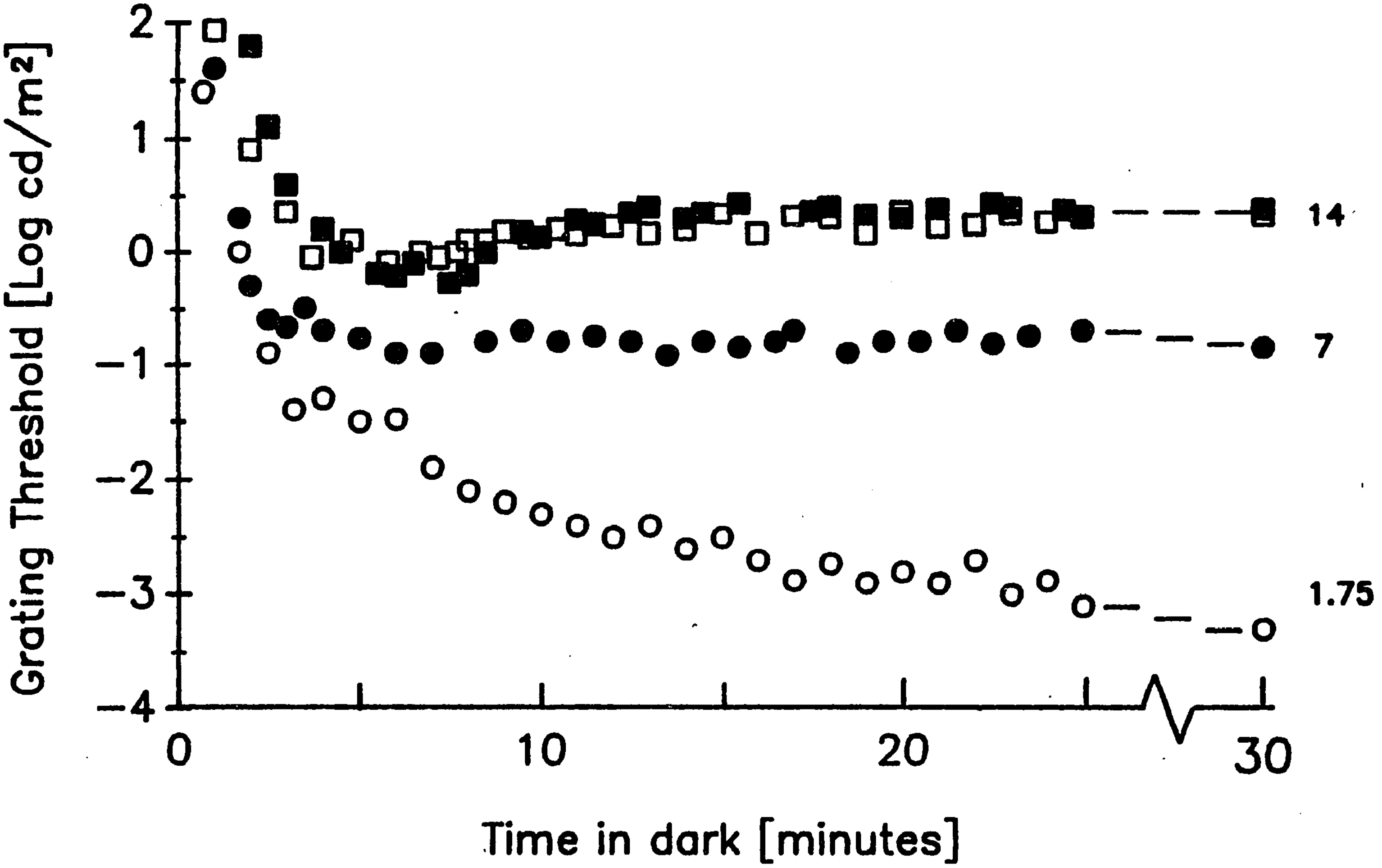

Grating Threshold [Log cd/m²]
+1
0
-1
-2
-3
0
10
20
30
Time in dark [minutes]
21
14
7
1.75

Figure 8

Observer ND: Threshold grating luminance (on the ordinate in log cd/m^2) as a function of time in the dark. The different shaped symbols represent different frequency gratings in cycles per degree as indicated. The open symbols represent data obtained with green (512 nm) gratings.


Grating Threshold [Log cd/m²]
2
1
0
−1
−2
−3
−4
0
10
20
30
Time in dark [minutes]
14
7
1.75

more conventional dark adaptation curves (e.g., Crawford, 1947) and display an initial cone and a subsequent rod limb. But with higher spatial frequencies, TGL increases during the rod recovery stage of dark adaptation. This tendency is relatively small with a 7 cpd grating, but increases with spatial frequency. With the highest frequency used, 21 cpd, the effect exceeds 0.8 log units. As was the case for the light adaptation data of Experiment 1, these thresholds are largely independent of grating wavelength when plotted in photopic units, and thus represent changes in cone mediated acuity concomitant with rod dark adaptation, as illustrated for the 14 cpd grating. Thus, the results of Experiment 5 show that cone mediated spatial acuity is increasingly suppressed during the rod recovery stage of dark adaptation. Similar results are shown for observer ND in Figure 8.

One highly significant, but unquantified observation was made by both observers while obtaining the data represented by Figures 7 and 8. Shortly after extinguishing the bleaching field, both observers reported a transient enhancement of visibility of the high spatial frequency gratings. Although the change in visibility was apparently large, the observers were asked to ignore them for the following reasons: 1) these changes did not interfere or coincide with critical observations to be made in this experiment: that is, the effect of slow rod recovery from a bleach on visual acuity; 2) these changes were too rapid to be quantified reliably with the experimental technique used (i.e. a quantifiable threshold could not be obtained until 30 seconds after bleach-offset). This subjective impression, however, provided the impetus for Part II of the present study.

Experiment 6

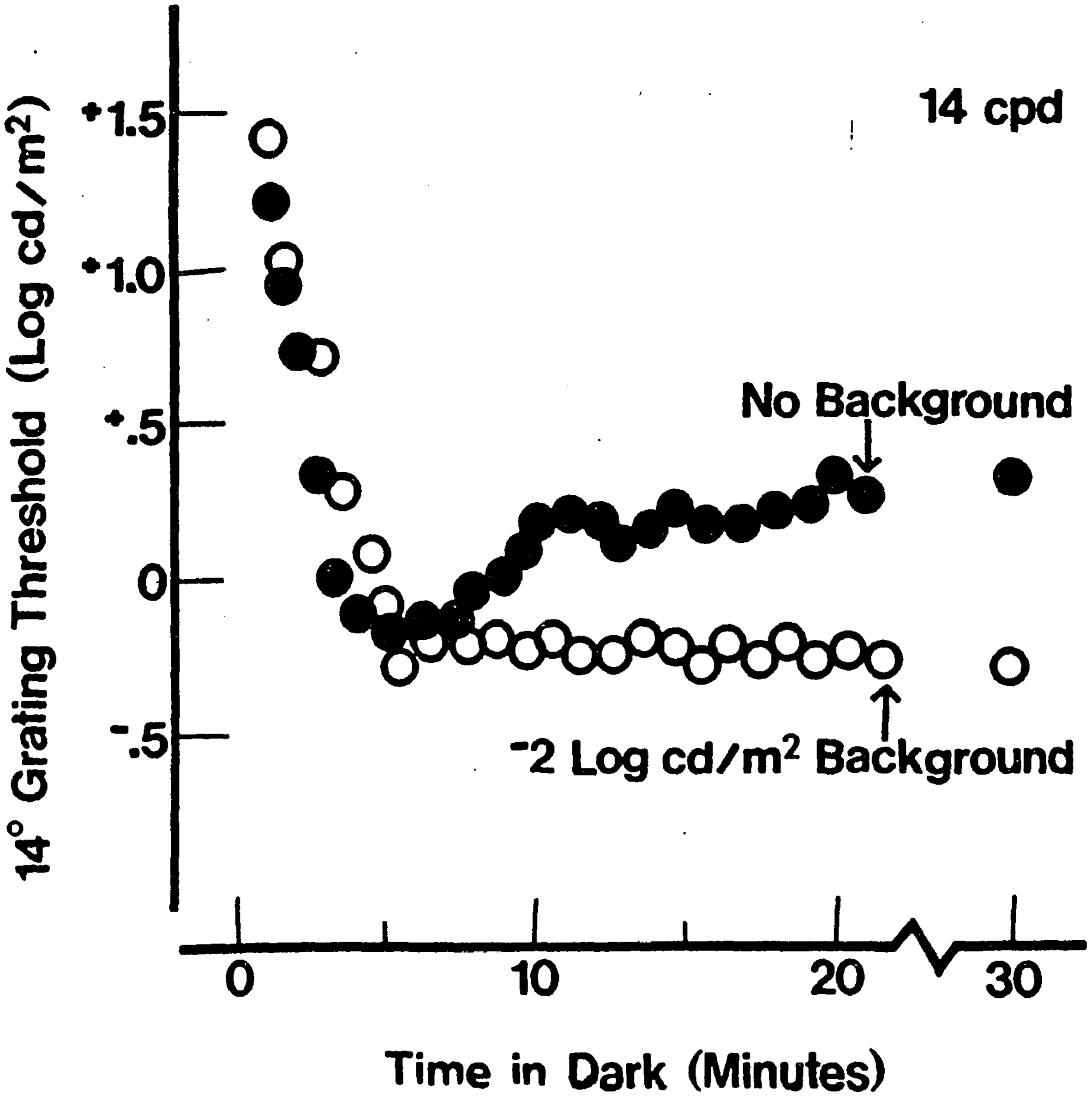
Experiment 6 was conducted to demonstrate that the data obtained during the "rod recovery stage" of dark adaptation in Figures 7 and 8, in fact, reflect dark adaptation. To this end, the dark adaptation experiment involving the use of a "red" 14 cpd grating in Figure 7 was repeated using two slightly different procedures. In one case, the data were merely a replication. In a second case, however, TGL was tracked following photopigment bleaching but in the presence of a continually exposed, 17° diameter background, 480 nm in wavelength and -2 log cd/ m^2 in illuminance. By preventing rods from dark adapting, this procedure should eliminate the rise in TGL associated with the "rod limb" of dark adaptation.

Results and discusssion

Figure 9 plots TGL as a function of time in the dark after bleach offset. The closed symbol function is a replication of the dark adaptation data obtained with a "red" grating illustrated in Figure 7. The open symbols delineate the function obtained with a "red" 14 cpd grating in the continuous presence of the rod-light adapting background during dark adaptation. The latter function shows that throughout the cone limb of adaptation, this dim field has little influence upon TGL. This is not surprising as this field was quite invisible to the observer during this time period. But after five minutes in the dark, the rods have sufficiently recovered to respond to this dim field. Thus the presence of

Figure 9

Observer FN: Thresholds for a red (Wratten 29 filter), 14 cycles per degree grating as a function of time in the dark. The closed circles were obtained with no adapting field present, and are a replot of some of the data presented in figure 8. The open circles were obtained in the presence of a concentric, 17° diameter, continually exposed adapting field of -2 log cd/m^2 luminance and 480 nm wavelength.


14 cpd
14° Grating Threshold (Log cd/m²)
+1.5
+1.0
+.5
0
-.5
No Background
-2 Log cd/m² Background
0
10
20
30
Time in Dark (Minutes)

this adapting field maintains the rods in a somewhat light adapted state and as such prevents any further change in cone-mediated grating acuity from occurring. The remarkable difference in shape between these two functions clearly indicates the influence of the dark adapted state of rods upon cone-mediated spatial acuity.

GENERAL DISCUSSION

The present study has shown that cone-mediated spatial acuity is suppressed by rod dark adaptation, and enhanced by selective rod light adaptation. This effect is barely apparent with low spatial frequencies (3.5 hz) but increases to a <u>nearly</u> 1 log unit effect with the highest spatial frequency used, 21 cpd. The results of the present study bear a striking resemblance to flicker studies cited earlier in the Introduction which were referred to as SRCI. In those flicker studies, the magnitude of the interaction between rod and cone activity has been shown to depend upon temporal frequency: as frequency increases, the greater the influence of rod-adaptation on cone-mediated rapid flicker (Goldberg et al., 1983; Alexander & Fishman, 1984; Coletta & Adams, 1984).

This similarity in the influence of spatial and temporal frequency upon the magnitude of rod-cone interaction is shown more clearly by placing comparable data on the same set of coordinates. Figure 10 plots log threshold change (i.e., log control threshold - log experimental threshold) as a function of the illuminance of a background field. The closed circles are derived from the 21 cpd/Wratten 29 function in Figure 2. The open triangles plot data obtained by Goldberg, Frumkes, and Nygaard (1983,

Figure 10

Change in threshold (expressed on the ordinate as log deviation from dark adapted threshold) as a function of the retinal illuminance provided by a large, steady background field. The closed symbols are derived from the 21 cycles per degree, Wratten 29 data shown in Figure 2. The open triangles are 25 Hz flicker data derived from Goldberg, Frumkes and Nygaard (1983; Figure 2).

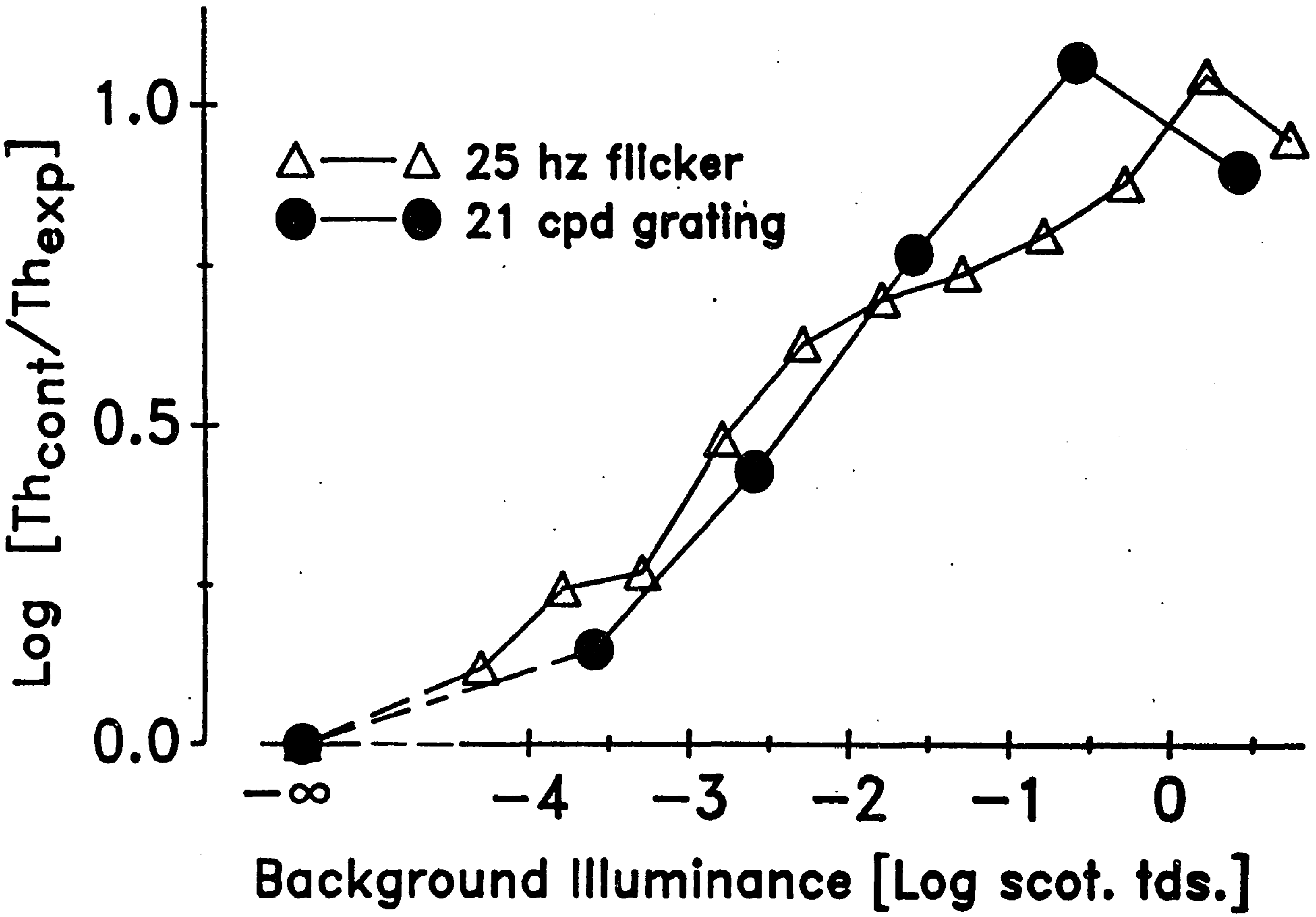

△—△ 25 hz flicker
●—● 21 cpd grating
Log [Th$_{cont}$/Th$_{exp}$]
1.0
0.5
0.0
−∞
−4
−3
−2
−1
0
Background Illuminance [Log scot. tds.]

fig. 2) using a 25 hz red flicker and a large, 512 nm background. These particular values, 21 cpd and 25 hz were chosen for comparison because both produced approximately the same maximal threshold change (i.e., 1.1 log unit). Ordinate and abscissa values are plotted in terms of retinal illuminance (tds.) in order to permit more direct comparison of visual influence as obtained by the Maxwellian view stimulator of Goldberg et. al. (1983), and by the free viewing system used in the present study. Finally, the ordinate is plotted in photopic units since both grating and flicker are detected by cones; the abscicca is plotted in terms of scotopic units, since the background influence is mediated by rods. Notice in Figure 10 that the range in rod background illuminance effecting cone spatial and temporal acuity is quite similar. Both temporal and spatial acuity become maximal at a very similar value (approximately 0 log scotopic tds.), a value which is more than 3 log units below rod saturation (Aguilar and Stiles, 1954) but considerably above absolute threshold.

The similarity in frequency-dependency and the correspondence in test threshold change with specific background luminance levels may suggest that both temporal and spatial effects reflect one common mechanism, SRCI. However, I am unaware of any additional evidence to support this assertion. At least one difference between the cited flicker studies and the present study should be pointed out. This difference relates to the stimulus used. In the flicker studies the test probe was sinusoidally modulated, while squarewave gratings were used in the present study. Apparatus limitations made it impossible to collect data with sinewave gratings and particularly the use of contrast thresholds.

The results obtained at higher spatial frequencies were unlikely to be affected by the use of squarewave gratings. Specifically, for frequencies higher than 10 cpd, squarewave and sinewave grating sensitivity are indistinguishable (Campbell, Carpenter, and Levinson, 1969). At lower spatial frequencies, however, a squarewave can be considered to be a sum of a number of sinewaves, its fourier components. These components consist of the fundamental frequency and its odd harmonics. For spatial frequencies higher than 10 cpd, these odd harmonics are probably invisibile, but for spatial frequencies lower than 10 cpd, these odd harmonics are quite visible (e.g., Kelly, 1969). Therefore, it is possible that, as was the case for comparable flicker studies, rod-influence upon cone-mediated spatial sensitivity would become negligible at low spatial frequencies by using sinewave gratings. With more appropriate equipment, this possibility could readily be put to the experimental test.

PART TWO

Chapter 4: THE INFLUENCE OF SHORT TERM VISUAL ADAPTATION ON CONE-MEDIATED GRATING ACUITY

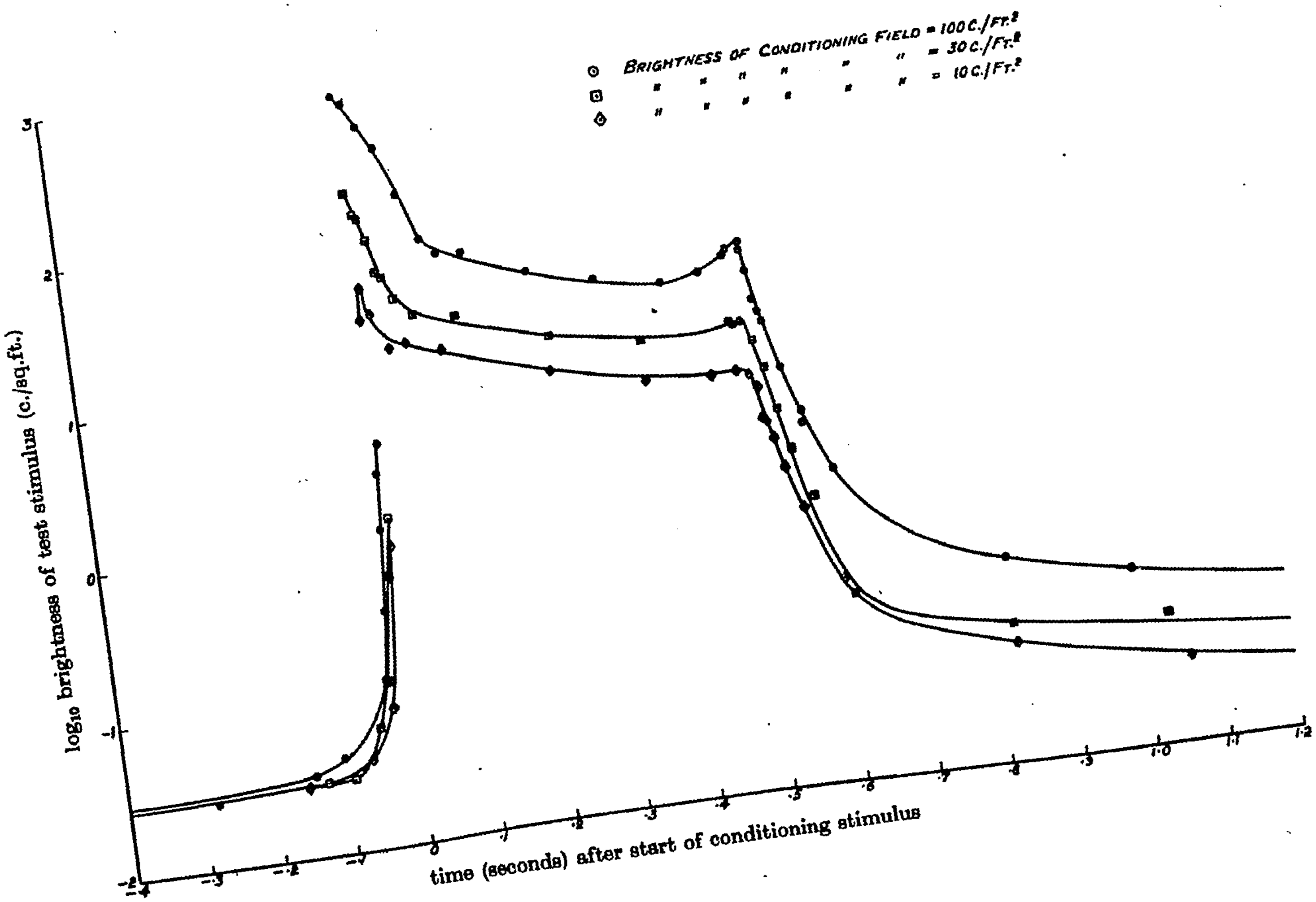
As indicated in the results of Part One, removal of a bleaching source transiently enhances the subjective visibility of high spatial frequency gratings. At the instant when grating visibility seems clearest, the grating appears colorless. These observations suggest that a number of critical changes in spatial vision accompany the earliest stages of visual adaptation.

Changes in visibility accompanying the earliest stages of light and dark adaptation were first formally addressed by Crawford (1947). The threshold of a small, brief, Test Flash (TF) was determined as a function of the Stimulus Onset Asynchrony (SOA) in respect to the onset of a concentric, larger and longer duration Adapting Flash (AF). Results with three AF luminance levels are shown in Figure 11. TF threshold is plotted on the ordinate as a function of the SOA on the abscissa. With the convention used here, a negative abscissa value indicates that TF onset precedes AF onset, while positive values indicate that TF onset follows AF onset. In this particular figure, AF onset occurs at a value of 0 ms on the abscissa and its offset occurs at a value of 524 ms, i.e., the AF was 524 ms in duration.

The data plotted in Figure 11, as well as subsequent replications by many other investigators (Boynton & Kandel, 1957; Boynton, 1961; Battersby

Figure 11

Crawford's measurements of test flash (TF) threshold during brief light adapting flashes (1947). The threshold of a 10 ms duration, 30' diameter TF was determined as a function of time (seconds) after start of conditioning stimulus (CS). The CS was always 524 ms in duration and 12° in diameter. The whole cycle of operations - exposure of TF and of CS - was repeated every 7.2 sec. Three luminance levels of the CS are shown here: 100, 30 and 10 cd/ft^2. The CS was exposed at zero time and cut off 524 ms later. The data points indicate the times at which TF was exposed and the corresponding luminance at which it was just visible. Negative times indicate exposure of TF before exposure of the CS.



⊙ Brightness of Conditioning Field = 100 c./ft.²
⊡ " " " " " = 30 c./ft.²
◈ " " " " " = 10 c./ft.²
log₁₀ brightness of test stimulus (c./sq.ft.)
3
2
1
0
-1
-2
time (seconds) after start of conditioning stimulus
-.4
-.3
-.2
-.1
0
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
1.1
1.2

& Wagman, 1959; Sperling, 1965), show that TF threshold begins to rise approximately one hundred milliseconds before AF onset, is maximal when the two flashes are simultaneous in onset, and then gradually decreases again to a plateau value at an SOA of about 400 ms. I will refer to this portion of Crawford's data as _early light adaptation_. Figure 11 also shows that TF begins to rise shortly before AF offset and then rapidly decreases to a value approaching control levels. I will refer to this portion of Crawford's data as _early dark adaptation_.

Early light adaptation

Figure 11 shows an initial rise of TF threshold at -100 ms and a subsequent rapid threshold increase up till an SOA of 0 ms. This particular phase of early light adaptation has been referred to as "Backward Masking" or "The Crawford Effect" (e.g, Kahneman, 1968); "Forward Masking" refers to the change in TF threshold following AF onset. Following the onset of the AF (at an SOA of 0 ms), TF threshold falls.

Although there is no general agreement about all of the factors underlying early light adaptation, a number of relevant considerations should be stated. First, most of the changes occurring cannot be related to photochemical bleaching. That is, retinal densitometry data show that the amount of photopigment bleached by an AF is directly proportional to the I x T product of the AF: this verification of Bloch's Law holds true for AFs up to at least several seconds in duration (Rushton, 1965). Thus, if photopigment bleaching were to explain early light adaptation, TF threshold should rise throughout the time period an AF is presented. Since TF threshold rises prior to the presentation of the AF and then decreases during AF presentation, adaptation cannot merely reflect the amount of photopigment available for bleach. The fact that early light adaptation involves a variety of neural factors is stressed by several neurophysiological investigations including studies of the lateral eye of the horseshoe crab (Riggs and Graham, 1940), the B-wave of the human ERG (Boynton & Triedman, 1953), evoked potentials at many loci throughout the cat visual system (Sturr and Battersby, 1966), and intracellular study in most types of retinal neurons of the mudpuppy (Copenhagen, 1974).

A much wider variety of human psychophysical data also suggests that early light adaptation involves neural processing. The following review of this psychophysical literature is not meant to be all inclusive, but stresses findings of particular relevance to the present investigation of adaptational induced changes in visual acuity.

The importance of AF luminance and duration - In the typical increment threshold situation, TF threshold is determined as a function of a steady adapting background but variable in luminance. Under such circumstances, TF threshold is proportional to background luminance as predicted by Weber's law over a wide range of background luminance values (for review see Barlow, 1972; Geisler, 1978). In fact, using either electrophysiological (Dowling, 1963) or psychophysical (Rushton, 1965) procedures, it is also possible to relate TF threshold to the amount of bleached photopigment. Thus, the relationship between TF threshold and the luminance of a steady background can be explained by photochemical bleaching.

Although TF threshold tends to increase as the luminance of a flashed background increases (e.g., see Figure 11), significant deviations from Weber's law occur, particularly at an SOA of 0. There could be several reasons for this result. Brief adapting flashes produce much less bleaching and no photochemical equilibrium is likely to occur. But there is evidence that, depending upon the duration of an AF, the TF is detected by different neural mechanisms. When a bright AF is continuously exposed, the increment threshold is mediated by its initial image (Geisler, 1978). When the AF is brief, TF is detected either by the late afterimage (Brindley, 1959; Sakitt, 1976) or by a short term afterimage (Geisler, 1978).

Spatial Factors - A variety of experiments have manipulated the spatial properties of either the TF and/or the AF in early light adaptation experiments. These have shown that when the AF and TF stimulate different areas of the retina, TF threshold still increases (Rushton and Westheimer, 1962; Alpern, 1952) clearly indicating the importance of neural factors. The influence of AF size per se depends complexly upon its illuminance and retinal position as well as TF size. Under photopic conditions and using relatively large TF diameters, the overall influence of an AF was reported to increase as its diameter decreased (Battersby and Wagman, 1962; Frumkes & Sturr, 1968). But if the test stimulus is small in diameter, and/or if peripheral retinal loci are stimulated at scotopic luminance levels, the overall influence of the AF at first increases, then decreases again as AF diameter increases (Frumkes & Sturr, 1968; Teller, 1973; Teller, Matter, Phillips & Alexander, 1971). Without exploring temporal interval per se, such size effects were well known from prior studies (e.g., Crawford, 1940; Westheimer, 1965). Most probably, these relate to the receptive field properties of retinal ganglion cells as first suggested by Teller, Andrews, and Barlow (1966) and Frumkes and Sturr (1968). In fact, Teller et. al. (1966; Teller, 1971) emphasized that short term light adaptation produces a marked change in spatial neural organization, a finding which preceded counterpart intracellular study in mudpuppy retina (e.,g., Werblin, 1972, 1974; Copenhagen, 1974) by several years.

A number of psychophysical studies (e.g. Green, 1981; Tolhurst, 1975) have used gratings as adapting and test stimuli. The overall influence of the adapting grating was reported to increase with spatial frequency and its greatest effect to occur at longer SOA's (Rogowitz, 1977). The adapting influence, however, decreases with increased difference in spatial frequency between test- and adapting-grating (Watson & Nachmias, 1980), while the largest threshold change obtains when the TF and AF are uniform fields (Green, 1981). Several studies (e.g. Kulikowski & Tolhurst, 1973; Keesey, 1971) using short and long term adaptation to gratings have provided evidence for the existence of two visual sub-systems: a transient and a sustained system. The transient system has been shown to be most sensitive to low spatial frequencies (Tolhurst, 1975), the sustained system to high spatial frequencies (Keesey, 1971). In fact, these sub-systems operate over a broad range of spatial frequencies and may interact under conditions of short term adaptation (Schenkein, 1982).

Chromatic variables - Early examinations of the chromatic properties of early light adaptation suggested little influence upon the time course of TF, or upon the types of photoreceptors mediating TF threshold (Bush, 1955; Sperling, 1965, Frumkes & Sturr, 1968). However, later studies have demonstrated significant influence of chromatic variables. For example, Frumkes et al. (1973) have shown that the stimulation of one photoreceptor type by an AF can produce changes in TF threshold mediated by another type of photoreceptor. Work by Augenstein and Pugh (1977) showed that the time courses of adaptation of the blue sensitive cone mechanism to short wavelength and long wavelength adapting fields are very distinct: a large and relatively long-lasting transient threshold elevation occurs at the onset of the long wavelength, but not at the onset of the short wavelength, fields. The achromatic appearance near threshold of small, brief lights with spectral sensitivities resembling that of the CIE photopic observer, has led to a hypothesis which links TF detection to an independent class of non-opponent cells (King-Smith & Carden, 1976). However, more recent studies suggest that AFs change the type of neural mechanism mediating TF. For example, Finkelstein and Hood (1982) using a variation of the Stiles two-color threshold procedure reported that red/green opponent cells can substantially influence the detectability of small, brief lights.

A few studies (e.g. Frumkes & Holstein, 1979; Buck, Stefurak, Moss, and Regal, 1983) have specifically attempted to measure the time course of different types of rod-cone interactions using a "Crawford masking paradigm". Frumkes and Holstein (1979) measured rod thresholds at various times relative to the onset of scotopically equated 512 nm and 655 nm AFs: when so equated, only the 655 nm AF stimulus had an appreciable effect upon cones. Depending upon spatial factors, this cone influence caused more extensive "backward masking" and an overall greater elevation of TF threshold was observed. The desensitizing was found at negative SOA's and for most of the time of background presentation. Near offset of the 655 nm background cone stimulation depressed rod threshold. Buck et al. (1983) using a technique of rapidly exchanging scotopically matched, equal sized 490 nm and 630 nm background discs, found rod-cone interaction (as described by Frumkes et al., 1979) to rise and fall with various time courses depending upon the spatial dimensions of the test flash and adapting flash.

In summary, the foregoing review suggests that a number of profound changes in visual-neural organization occur during the earliest stages of light adaptation. Most investigations emphasize the change in TF absolute threshold produced by various AF parameters. However, these studies and those involving adaptation with gratings suggest that profound, complex changes occur in the overall spatial and perhaps chromatic organization of the visual system during early light adaptation. This suggests the possibility that changes in TF absolute threshold produced by an AF do <u>not</u> necessarily imply that a homogeneous AF will produce similar changes when visual acuity is used as a measure of sensitivity. The present study examines the influence of various AF illuminance levels upon grating acuity.

Early dark adaptation

Figure 11 shows that TF threshold rises slightly before AF-offset, and then rapidly declines. This rise near AF-offset has been sporadically reported throughout the literature, and is believed to reflect an inhibitory effect of the changing AF reacting upon the test stimulus (Ratliff, 1965; Rinalducci, 1968; Baker, 1963). However, this small elevation of threshold is not reliably obtained across laboratories, can only be obtained with the psychophysical method of adjustment, and is not observed with a forced choice psychophysical procedure (Teller & Lindsey, 1970). Throughout the rest of this thesis, the term 'early dark adaptation' will ignore this intial small increase in threshold and be used only to refer to the subsequent sudden drop of TF threshold immediately after AF-offset (Crawford, 1947; Baker, 1953; Battersby & Wagman, 1959).

The early drop is surprisingly large. In the top curve of Figure 11 the threshold falls 1.7 log units (a factor of 50) in 200 ms; the subsequent change in threshold over the next half second or so is much smaller. Because the changes in sensitivity are so rapid, a neural rather than a photochemical mechanism underlying early dark adaptation was postulated by early psychophysical studies (Baker 1953, 1963, 1975; Battersby & Wagman, 1959). Such a conclusion has been entirely verified by more modern neurophysiological studies (Pepperberg, Brown, Lurie & Dowling,

1978) which show the same phenomenon in retinal preparations in which photopigment regeneration following a bleach cannot take place, yet a similar recovery of sensitivity following the removal of an AF is observed.

As is the case for light adaptation, a variety of parametric studies examined the influence of AF illuminance (Baker, 1953), pre-adaptation (Baker, 1963; Battersby & Wagman, 1962) and the spatial configuration between TF and AF (Kitterle & Leguire, 1975; Baker, 1973). Photopic as well as scotopic luminance levels of the AF produce a sudden drop of test threshold for both cones and rods, respectively. The rate of the early fall seems to be specific to the receptor systems, with a fast rate for cones and a slower rate for rods. Baker (1963) using pre-adaptation techniques argued that the extent of the early fall is apparently within the receptor system: long early falls are associated with bright photopic pre-adaptation, but long falls are also associated with bright scotopic pre-adaptation. In addition, the early drop may overshoot the terminal level and rebound to it when a weak adapting level is dimmed to a lower level. It has been proposed that early dark adaptation reflects the decay of the receptor potential to the adapting light (Baker, 1963, 1982). However, Kitterle et. al. (1975; also Battersby & Wagman, 1962; Rinalducci, 1968) found that the shape of the early dark adaptation curve is influenced by the presence of contours and borders; they showed that conditions maximizing lateral effects increased the magnitude of the early threshold drop. Kitterle et al. (1975) using disc-shaped and contoured test stimuli equal in size, reported a facilitation of detection of contoured stimuli at high photopic levels of illumination. It has been suggested (Rinalducci, 1968; Kitterle et. al. 1975) that in addition to the decay of lateral effects, a functional reorganization of the visual system related to the spatial integration of light should be implicated to explain the changes in sensitivity during the course of early dark adaptation.

There is, in fact, substantial neurophysiological evidence for a change in spatial-retinal organization with dark adaptation. For example, the receptive field surround of retinal ganglion cells is known to decrease markedly in strength with dark adaptation (Barlow, Fitzhugh, and Kuffler, 1957; Enroth-Cugell and Shapley, 1973). This change in neural organization is apparent at all levels of the retina, from photoreceptors through ganglion cells (Dowling, 1967; Dowling & Werblin, 1969; Werblin & Dowling, 1969; Kleinschmidt & Dowling, 1975; Werblin, 1973, 1974; Dowling & Ripps, 1970). These neurophysiological data are supported by some psychophysical evidence for adaptational induced changes in neural organization (Barlow, 1964; Glezer, 1965; Kelly, 1974). Thus, for example, spatial summation increases dramatically with dark adaptation (Glezer, 1965) and grating acuity becomes considerably reduced (Kelly, 1974). In fact, there are several psychophysical studies which have claimed to show changes in human receptive field organization with dark adaptation (Glezer, 1965; Westheimer, 1967). Glezer, in particular, showed changes in spatial summation occurring during the first (cone) stage of dark adaptation.

Although early reports (e.g., Baker, 1963) stressed that early dark adaptation was specific to receptor class, more recent data suggest a possible change in chromatic organization. Mollen and Polden (1975, 1977) found that the termination of a high intensity (but not higher than 100,000 tds) yellow AF produced a large rise of the threshold of a short wavelength TF. However, when very high adapting levels were used (of the order of 1,000,000 tds or more), the anomalous rise did not occur. Their interpretation of the anomaly, which is referred to as transient tritanopia, is that the recovering green-sensitive mechanism exerts a strong inhibitory effect on the blue sensitive mechanism. Other studies (e.g., Augenstein & Pugh, 1977) demonstrated that the time courses of recovery of the blue-sensitive mechanism from short and long wavelength AFs are very distinct: a large and relatively long-lasting transient threshold elevation (transient tritanopia) occurs at the offset of the long wavelength, but not of the short wavelength AFs. Since adaptation transients are not observed in the green- and red-sensitive mechanisms, Augenstein et al. argue that the instantaneous signals stemming from these cones following AF termination, cannot be the cause of transient tritanopia. They propose that the cause lies either in the path by which red- and/or green-sensitive cones transmit their signals to the blue-sensitive mechanism, or in this mechanism itself.

To summarize, as is the case for early light adaptation, a considerable body of evidence suggests that the neural organization of the retina changes during the earliest stages of dark adaptation. However, most studies only examined the influence of early dark adaptation upon the absolute threshold of the TF. With the exception of the report on transient tritanopia, these studies did not further explore, at least psychophysically, the specific mechanisms mediating threshold during early dark adaptation.

Rationale for the present study

The foregoing review suggests that short term visual adaptation may induce profound changes in visual organization. These have never been directly measured since, with very few exceptions, previous studies used the absolute threshold of a TF as their sole index of visual function. Thus, changes in visual organization could only be inferred from one limited measure.

In the present study, I examine changes in both absolute threshold, and more importantly, the TGI of a high spatial frequency (cone-detected) grating throughout the time course of early light- and dark-adaptation. Since the results of Part One have suggested the possibility of rod-cone interaction, the retinal position of stimuli was varied as was the AF luminance level. Spectral controls indicated which type of spectrally tuned mechanism was directly influenced by the AF as well as the mechanism detecting the TF. The present results show that adaptation induced changes in grating acuity are often quite different from the changes in TF absolute threshold.

Chapter 5: METHODS

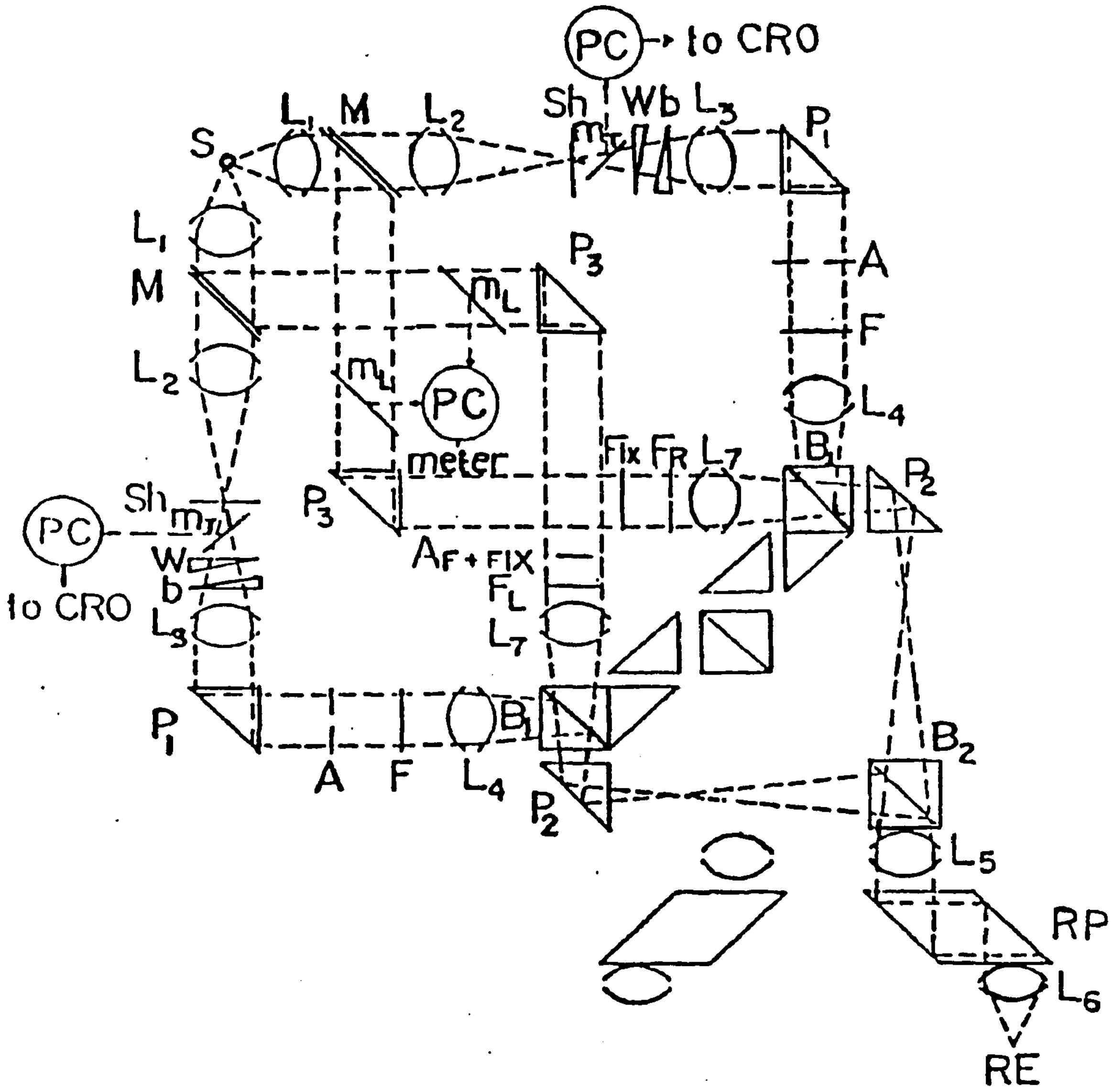
Optical system

A four-channel Maxwellian view optical system, modified slightly from that described by Frumkes and Sturr (1968), was used to present all stimuli. A schematic diagram of the optical system, designed to provide either binocular or monocular stimuli appears in Figure 12. Only the beams of light projected onto the right eye are indicated (dotted lines), since the present study was conducted monocularly.

Main beams - Two beams of light proceeded from source S. These beams were collimated by lenses L_1 into two beams forming symmetrical main channels. The main channel proceeding horizontally across Figure 12 provided the adapting stimuli, while the test stimuli were provided by the beam vertically proceeding from S. The beams were focused by lenses L_2 to form a filament image on the plane of the shutters Sh. Precise luminance control was obtained by means of two circular neutral density wedges, W, which were balanced by fixed wedges, b. L_3 recollimated these beams and the prisms, P_1, deflected the light beams 90°. Neutral density filters interposed at F provided gross luminance control of test and masking stimuli. The filter racks of F also accommodated chromatic filters that determined the wavelengths of the test and adapting stimuli. Apertures of various sizes could be placed at A controlling the spatial dimensions of the test and the adapting stimulus. The horizontal and vertical position of the apertures could be changed by means of a micromanipulator. The

Figure 12

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


PC
to CRO
Sh
m_I
Wb
L1
M
L2
L3
P1
S
L1
M
L2
P3
m_L
A
F
L4
m_u
PC
meter
Fix
F_R
L7
B1
P2
Sh
m_II
PC
to CRO
W
b
L3
P3
A_F+FIX
F_L
L7
P1
A
F
L4
B1
P2
B2
L5
RP
L6
RE

light beams were refocussed by lenses, L_4; they passed through beamsplitter B_1 and were deflected 90° by prisms, P_2. Beamsplitter, B_2, recombined the test beam with the adapting beam. The combined beams were recollimated by lenses, L_5, then passed through a rhomboid prism, RP, and focussed by L_6 to form filament images at the nodal point of the observer's eye, RE.

Background field and fixation target - Light beams collimated by lenses L_1 were deflected 90° by a partially reflecting mirror, M. Since relatively little light was needed for these subsidiary channels and as much light as possible was desirable for the main beams, this was a "mirror" which transmitted as much light as possible, a microscope cover glass. These collimated beams formed symmetrical channels and provided a background field and fixation target. Right angle prism P_3, deflected the collimated beams passing them through aperture Af + Fix or Fix which determined the spatial configuration of the background field and fixation target respectively. Neutral density and chromatic filters placed into filter racks Fr and Fl controlled the illuminance and wavelengths of these stimuli. Lenses L_7, refocussed the background field and fixation target beams passing them into beamsplitter B_2, where they were recombined with the adapting and test channel beams.

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

Spatial calibration: stimulus size, retinal position and spatial frequency - When all apertures were removed from the optical system, any of the four channels provided a 28°of arc field of view as determined by a projection technique. An aperture of 1 mm in diameter placed at A projected a retinal image of 1.2°. With this knowledge, the spatial dimensions of all stimuli were determined.

The fixation target consisted of four dots, each 15' in diameter and arranged as a 3° x 3° square. The fixation target was centered in the background field. By changing aperture size, test or adapting stimuli could be altered in size. The test stimulus was 54' in diameter, the adapting stimulus 20° and the background field 28°. By moving an aperture with a micromanipulator, field position of the stimuli could be changed with respect to the fixation target. The test stimulus was presented either to the fovea or to the nasal retina, 5°from the fovea along the horizontal meridian of the right eye. One observer using the left eye but the right eye piece of the optical system had the test stimulus presented to the temporal retina, 5°from the fovea along the horizontal meridian of the left eye.

The adapting stimulus was always concentric to the test stimulus. The

Figure 13a

Stimulus display. The test stimulus is either a 54' diameter homogeneous test flash (TF) or a flashed 54' diameter, 18 cpd squarewave grating located in the center of a fixation target. The adapting flash is a 20° diameter disc concentric with the test stimulus.

Figure 13b

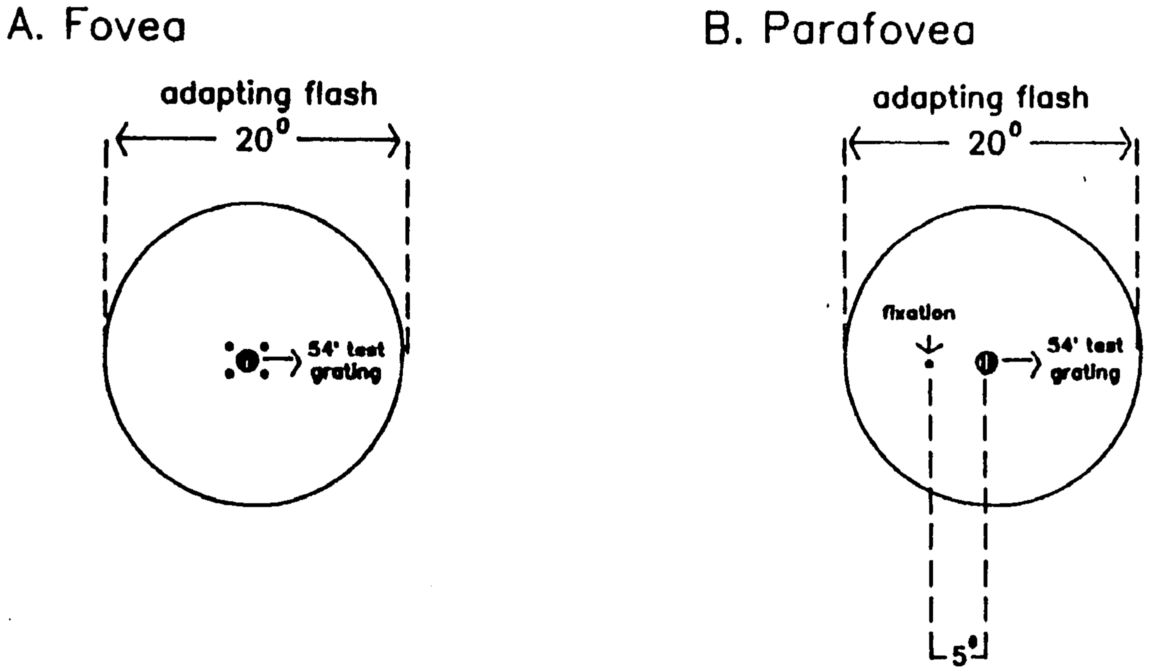
Stimulus display. The test stimulus is either a 54' diameter homogeneous test flash (TF) or a flashed 54' diameter, 18 cpd squarewave grating located 5° from the center of a fixation target along the horizontal meridian in the temporal field of the right eye.

The adapting flash is a 20° diameter disc concentric with the test stimulus.

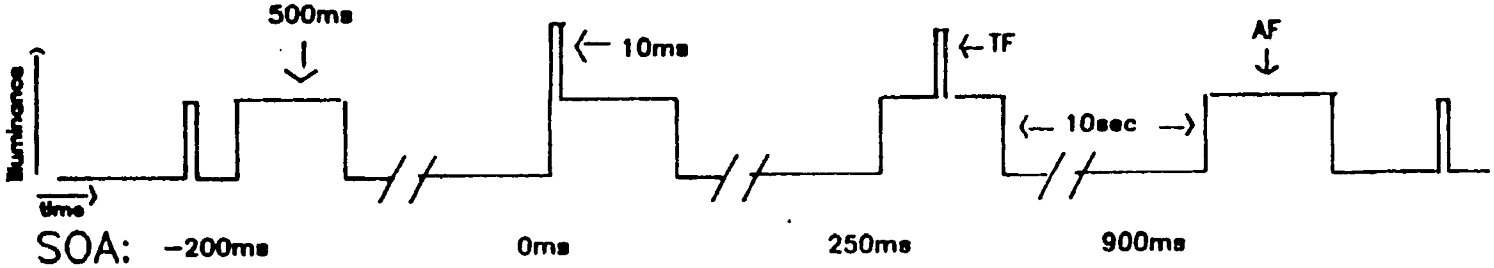
Figure 13c

The temporal arrangement of the test flash and adapting flash. The 10 ms duration test flash is presented either before, during or after presentation of the 500 ms duration adapting flash.

Spatial relationship test stimulus – adapting flash



C. Temporal relationship test stimulus – adapting flash



test and adapting stimulus were always circular in shape. The test stimulus was either a homogeneous disc or a grating. The spatial frequency of this 18 cycle per degree squarewave grating was determined by placing a 2 x 2 inch, 300 lines per inch Ronchi squarewave grating (Edmund Scientific Corporation) in the aperture holder at A. No means were available to assess grating contrast objectively, which were supposed to be completely "on-off." The observer's view of the spatial configuration of the stimuli is illustrated in Figure 13a.

Duration control - The fixation target was continuously exposed. The durations of the test and adapting stimuli were controlled by shutters, Sh, which were driven by electromagnets modified from a Grass polygraph. The shutter system and a Tektronix 5103N oscilloscope (CRO) were triggered by a standard dual channel physiological stimulator (Grass model S88). The adapting flash (AF) was a 500 ms duration flash, and the test flash (TF) was 10 ms. in duration. By varying the delay in onset of either the test flash or the adapting flash (AF), the test stimulus could be presented before, during or after presentation of the AF. The time difference between test flash-onset and AF-onset has been designated as Stimulus Onset Asynchrony (SOA). During all phases of the present study the recycling rate of the stimuli was once every ten seconds. The temporal relationship between the test flash and AF is illustrated in figure 13b.

Light passing through an open shutter was partially deflected by mirror Ml into photocell circuit PC whose output fed into the 5103 N oscilloscope. Thus, flashing stimuli duration, rise time and onset could be continuously monitored. The rise and fall times of the flashing stimuli were approximately 1.0 ms.

Light source - The light source was a tungsten filament incandescent General Electric Projector lamp which was designed to function at 6-volts, 18 amps (Electro Products Model H). The output of the power supply was regulated with a rheostat and the current was monitored by an ammeter. The lamp was intentionally underpowered at approximately 16.5 amperes in order to increase its lifetime. Luminous flux was continuously monitored by means of a photocell, PC (see figure 12), which received input from partially reflecting mirrors, M_L. The photocell output was fed into a milliammeter. Source intensity was adjusted as necessary to achieve a constant output on this meter.

Illuminance control - The illuminance of the test flash and AF were controlled by 4.0 log unit circular and balanced neutral density wedges. Additional illuminance control was obtained by placing fixed neutral density filters in the beams at F. When the 300 lines per inch Ronchi grating was placed in the aperture holder, an additional illuminance change of .4 log units in the test channel had to be taken into account. Control of fixation target illuminance was achieved by placing neutral density filters at Fr.

Wavelength control - The wavelength of the test flash and adapting stimuli were determined by Baird-Atomic or Ditric Optics interference filters inserted at F with half bandwidths between 6 and 12 nm and peak transmittance at 450, 480, 512, 540, 558, 580, 620, 655, 680 and 700 nm. The wavelength of the fixation target was determined by a Kodak Wratten 29 broadband filter which passes wavelengths greater than 630 nm.

Illuminance calibration - The photopic illuminance of spectrally filtered channels was determined by a procedure outlined by Nygaard and Frumkes (1982) using a UDT S351C equipped with a photometric filter (model 1157) and a diffuser (model 151). The detector head with attached photometric filter was placed normal to the optical axis of the final eye lens L_6 , at least 20 mm beyond the filament image and such that the total filter surface was illuminated. Measurements of spectrally unfiltered and filtered test, adapting and background beams were read out directly in cd/m^2. Thus, a direct measure of light in terms of photometric units, i.e. the influence of light on the human cone system, was obtained. Retinal illuminance expressed in photopic trolands, Er, was determined by the formula $Er = 10^6 E \times d^2$, where E is the illuminance on the photometric filter surface expressed in Lumen/mm^2, and d the distance between the filament image and the detector head expressed in mm. Throughout the remainder of this thesis, the term illuminance denotes retinal illuminance. The scotopic illuminance of a 512 nm stimulus was calculated with the formula $\log Ts = \log Tp + \log [2.567 (V'_\lambda / V_\lambda)$ for monochromatic stimuli (Wyszecki and Stiles, 1967). Tp is the photopic illuminance value of the stimulus, V'_λ and V_λ are the scotopic and photopic luminous efficiency coefficients at 512 nm, respectively. The scotopic illuminance of stimuli at each wavelength and that of a spectrally unfiltered stimulus were calibrated by equating their absolute threshold values with that of a 512 nm stimulus. All stimuli were 1.2° in diameter, 1 sec in duration and were successively presented at 5° from fixation along the horizontal meridian. Under dark adapted conditions, the observer adjusted the illuminance of the stimulus until it was just visible.

EXPERIMENTAL METHOD

The general goal of the experiments in Part Two was to compare the influence of short term adaptation upon test flash threshold and upon grating acuity. Four different experiments attempted to achieve this general goal. Experiment 7 measured changes in threshold throughout the entire time course of short term light and dark adaptation according to the method of Crawford (1947). Since there was good reason to obtain data under conditions in which rods or cones were adapted, this experiment was done both in the rod-free fovea as well as the parafovea, and done under conditions in which the AF was too dim to have an effect on cones (-0.5 log tds) or clearly bright enough to influence cones directly (2.5 log tds). All stimuli used in this experiment consisted of spectrally unfiltered "white light".

Experiment 8 was designed to elucidate the photoreceptor mechanism(s) responsible for the effects observed in the results of Experiment 7. To that end, action spectra for various AFs and test stimuli were determined, in the fovea and parafovea, using variable wavelength stimuli (as produced by interference filters).

Experiment 9 examined, in a manner very similar to that adopted in Experiment 7, the changes in visual acuity (as measured by threshold grating illuminance, TGI) throughout the entire time course of short term light and dark adaptation. The same retinal positions and AF luminance values were used. All stimuli, consisted of spectrally unfiltered "white light".

Experiment 10 was conducted to identify the photoreceptor mechanism(s) mediating the effects observed in the results of Experiment 9. Foveal action spectra data were collected for AFs and test stimuli using a technique similar to the one used in Experiment 8.

Observers - Three observers, all males were used in this study. FN, who served in all aspects of this study was 37 years old, was emmetropic and an experienced psychophysical observer. SL, who also served in all aspects of this study was 21 years old and emmetropic. RR was 22 years old, emmetropic and was used to replicate key findings. For observers SL and RR parafoveal stimuli were presented to the right eye temporal field, but for FN to the left eye nasal field.

General procedure - Prior to each experimental session, the observer aligned his eye with the full background field which was set at an illuminance of 2 log scotopic trolands. If necessary, he adjusted the position of the final eye lens until the fixation target was seen in sharp focus. When the test stimulus was a grating, special checks were made to insure that the bars as well as the fixation target were seen in sharp focus. The observer then dark adapted for 25 minutes after which an experiment was initiated. In all experiments to be reported, threshold illuminance values for the homogeneous test flash, the test grating or the adapting stimulus were measured. The observer adjusted the position of the neutral density wedge controlling test or adapting stimulus illuminance. After each threshold determination the experimenter quasi-randomly turned the wedge to higher density levels. Hence, the psychophysical method of adjustment was used throughout.

The general procedure followed in Experiments 7 and 9 was to present the test stimulus initially in the absence of the AF. In subsequent trials of a session the TF and AF were presented in a series of randomized SOA's. Thus, Experiment 7 determined the illuminance threshold of the TF as a function of the SOA; whereas Experiment 9 determined the TGI as a function of the SOA.

The general procedure followed to obtain an action spectrum for the influence of the AF upon the TF at a predetermined SOA, was to fix the illuminance of a "white" TF at a suprathreshold value. The observer's task was to adjust the irradiance of a variable wavelength AF until the visibility of the TF was just canceled (Experiment 8). Action spectra for the influence of AFs on TGI were determined with a slightly different procedure (Experiment 10). The illuminance of a "white" grating was fixed at a subthreshold value. The observer's task was to adjust the irradiance of a variable wavelength AF until the bars of the grating became just visible.

Action spectra for TF detection as well as TGI were obtained by determining the irradiance necessary to just detect a variable wavelength TF or grating presented at a fixed SOA in respect to a "white" AF which was preset in illuminance (Experiments 8 and 10, respectively).

Data collection proceeded according to a set of rules. First, no experimental session lasted more than 90 minutes after dark adaptation was completed. Second, for each set of test and/or adapting stimulus parameters, three threshold values were consecutively taken. If the range of threshold values exceeded 0.1 log unit, at least one additional threshold value was taken. Third, every data point plotted was based on observations in at least three experimental sessions and, consequently, involves a minimum of nine threshold determinations.

Chapter 6: SHORT TERM ADAPTATION EXPERIMENTS AND ACTION SPECTRA

Experiment 7

The overall aim of Experiment 7 was to examine the changes in the absolute sensitivity of both the cone and rod system during the early stages of light and dark adaptation.

Procedure - The threshold illuminance of a homogeneous test flash 54' in diameter and 10 ms in duration was determined as a function of the SOA in respect to a concentric AF of 20° diameter and 500 ms duration. The test and AF were either presented to the fovea or 5° to the right of fixation: the AF was set at -0.5 log tds (a value found to be below cone threshold) or at 2.5 log tds (a value clearly above cone threshold). In general, the test and AF were spectrally unfiltered and "white."

In each experimental session, one retinal position and one AF-illuminance value was used. Each session proceeded in the following manner. After 25 minutes of pre-experimental dark adaptation, the threshold of the test flash (TF) was determined in the absence of the AF. Then, the test threshold was determined in the presence of an AF at a given SOA value and three more thresholds were similarly determined. The SOA was then altered (according to a quasi-randomized sequence) and the same procedure was followed. Every 30 minutes a test flash-AF sequence at an SOA of 5000 ms was presented to insure that the AF-induced light adaptation was of a transient nature.

Results and discussion

Figure 14 shows the mean threshold illuminance of the homogeneous test flash as a function of the SOA in respect to the onset of the AF for observer FN. The upper coordinates represent foveal data, the lower coordinates parafoveal data. The symbol shape represents, as indicated, the illuminance of the AF. The threshold illuminance value of the test stimulus in the absence of the AF is indicated on the abscissa at the point labeled "minus infinity". The standard errors for these data points were usually about the size of a plotted datum. In general, the standard errors for other data points throughout this study are less than plus/min 0.1 log units. Figures 15 and 16 show similar data for observers SL and RR.

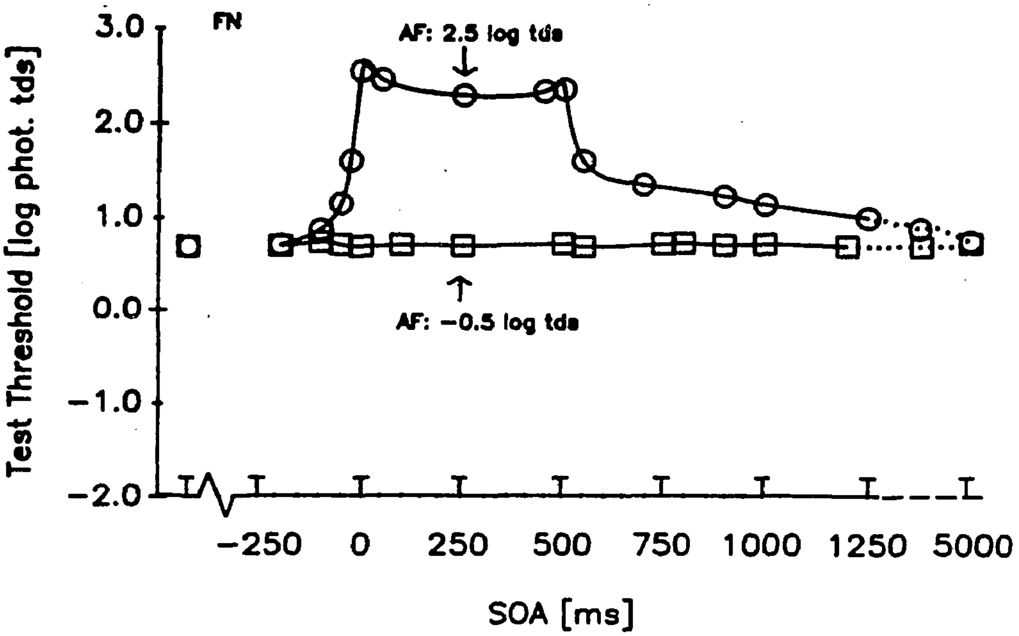
In Figures 14-16, the data obtained with the brighter AF in the fovea (i.e., the data indicated by the open circles in the upper coordinates) represent the condition most similar to that originally employed by Crawford (1947). For observer FN in Figure 14, test flash threshold begins to rise around 150 ms before AF onset, is maximal at an SOA of 0, and then decreases slightly. Prior to AF offset, TF threshold rises slightly and at offset, drops quite rapidly (more than 1 log unit in 100 ms). TF threshold then more slowly recovers clearly reaching control values by an SOA of 5000 ms. These results compare quite favorably with prior results (e.g., the data of Crawford, 1947, shown in Fig. 11). Data from observer SL (Figure 15) are quite similar, except that there is no "off"-response near AF offset. Observer RR's data (Figure 16) also lack this "off"-response, and show maximal TF threshold value at an SOA of 50

Figure 14

Observer FN, upper coordinates: Threshold illuminance of a TF as a function of SOA. AF illuminance value was either 2.5 log tds (open circles) or -0.5 log tds (open squares). The TF was "white", 54' in diameter and 10 ms in duration. The AF was "white", 20° in diameter and 500 ms in duration. The stimuli were presented to the fovea. Negative abscissa values indicate that the test flash preceded adapting flash onset; positive abscissa values indicate that the adapting flash occurred first; the "minus infinity" condition indicates test flash threshold when no adapting flash was present. Notice that the interval (250 ms) of the scale on the abscissa changes after 1250 ms. The broken line represents greater lapses of time.

Observer FN, lower coordinates: The threshold illuminance for the TF as a function of SOA. AF illuminance value was either 2.5 log tds (closed triangles) or -0.5 log tds (open diamonds). The TF was "white", 54' in diameter and 10 ms in duration. The AF was "white", 20° in diameter and 500 ms in duration. The stimuli were presented to the parafovea.

FOVEA



PARAFOVEA (5°)

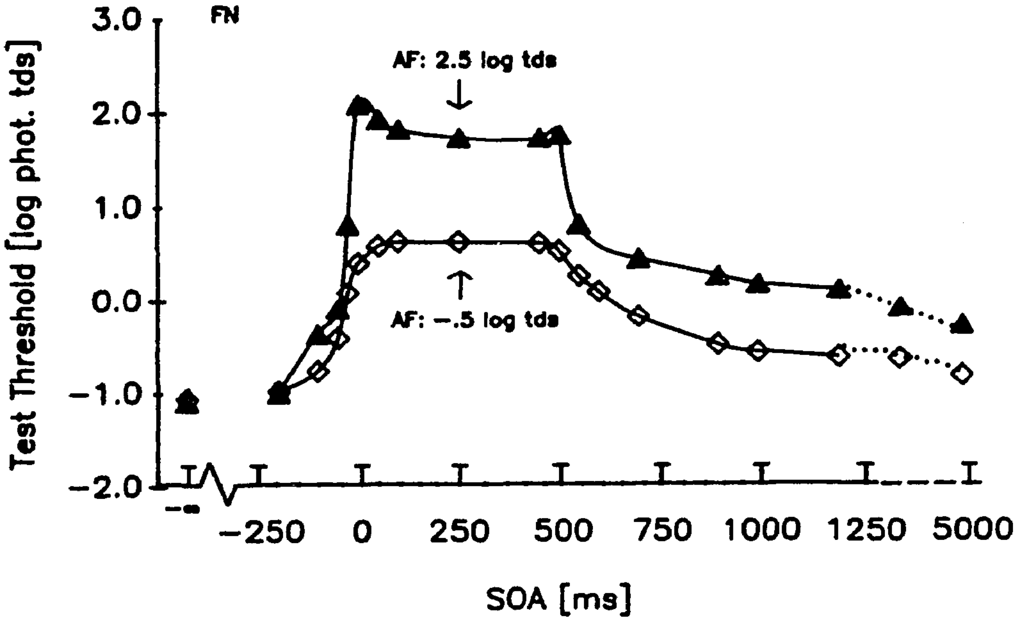
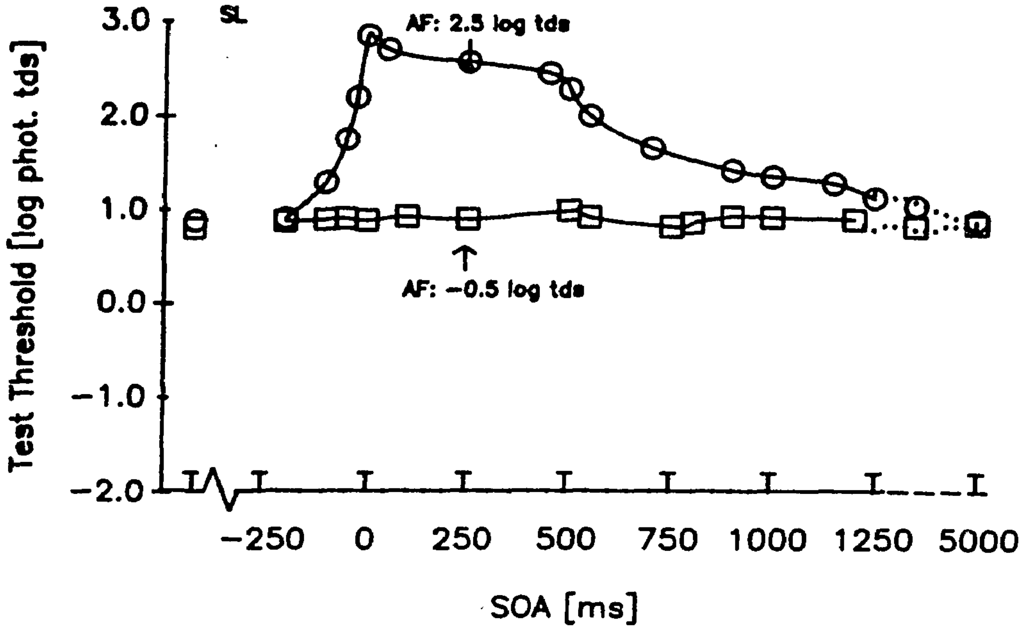


Figure 15

Observer SL, upper coordinates: Threshold illuminance for the TF as a function of SOA. The AF illuminance value was either 2.5 log tds (open circles) or -0.5 log tds (open squares). The TF was "white", 54' in diameter and 10 ms in duration. The AF was "white", 20° in diameter and 500 ms in duration. The stimuli were presented to the fovea. See legend of Figure 14 for an explanation of the abscissa values.

Observer SL, lower coordinates: Threshold illuminance for the TF as a function of SOA. The AF illuminance value was either 2.5 log tds (closed triangles) or -0.5 log tds (open diamonds). The TF was "white", 54' in diameter and 10 ms in duration. The AF was "white", 20° in diameter and 500 ms in duration. The stimuli were presented to the parafovea.


FOVEA

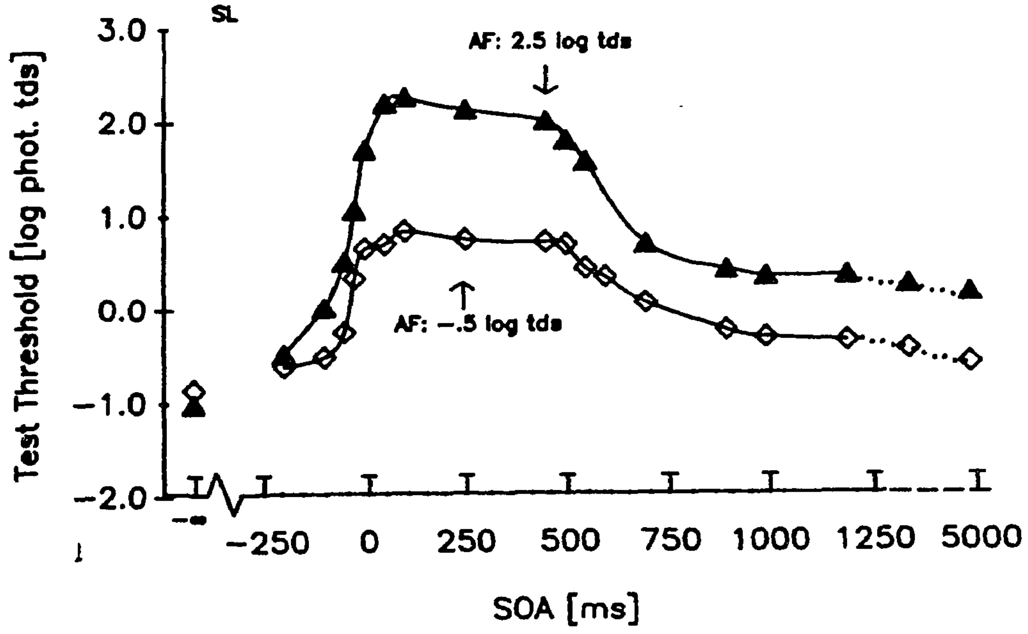
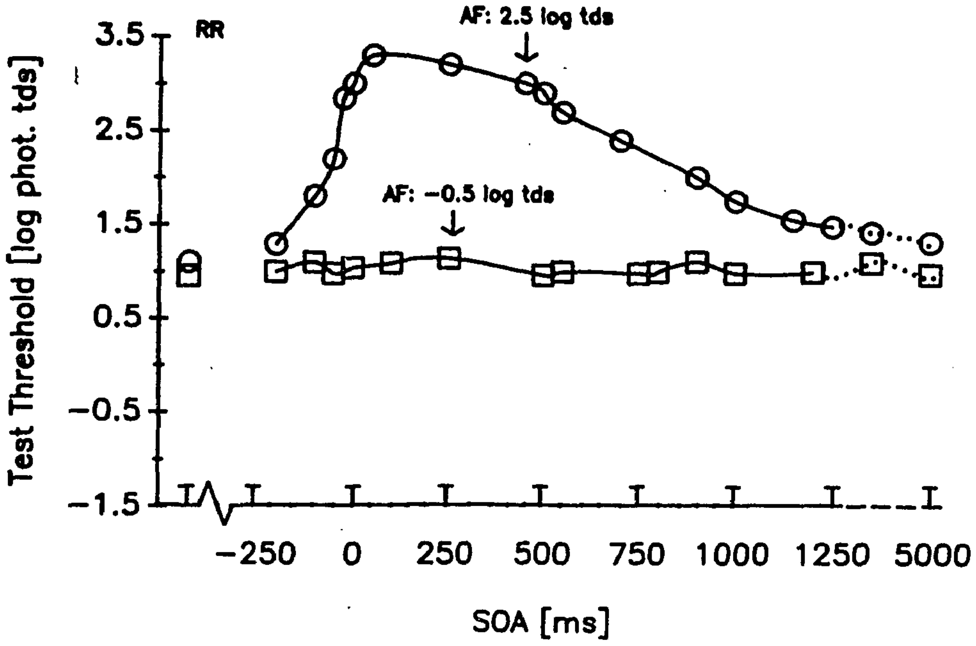

PARAFOVEA (5°)

Figure 16

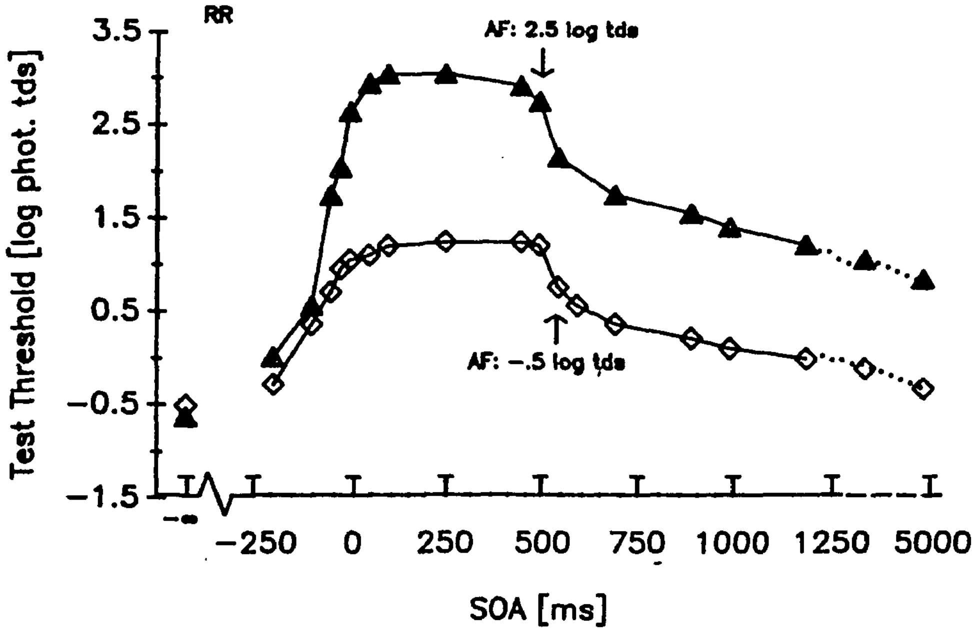
Observer RR, upper coordinates: Threshold illuminance for the TF as a function of SOA. The AF illuminance value was either 2.5 log tds (open circles) or -0.5 log tds (open squares). The TF was "white", 54' in diameter and 10 ms in duration. The AF was "white", 20° in diameter and 500 ms in duration. The stimuli were presented to the fovea. See legend of Figure 14 for an explanation of the abscissa values.

Observer RR, lower coordinates: The threshold illuminance value for the TF as a function of SOA. The AF illuminance value was either 2.5 log tds (closed triangles) or -0.5 log tds (open diamonds). The TF was "white", 54' in diameter and 10 ms in duration. The AF was "white", 20° in diameter and 500 ms in duration. The stimuli were presented to the parafovea.

FOVEA



PARAFOVEA (5°)



ms. Such individual differences, however, have been reported previously (e.g., Boynton and Kandel, 1957; Sperling, 1965; Frumkes & Sturr, 1968). In addition to these quantitative measurements, all observers reported that when the test flash was noticeably presented before AF-onset or after AF-offset, at threshold, it appeared clearly dimmer than the AF. During AF presentation, however, the TF always appeared at threshold brighter than the AF. These subjective impressions might possibly be attributed to detection upon the basis of a primary image vs. afterimage basis as suggested previously (Sakitt, 1976; Geisler, 1978).

Results in Figures 14-16 obtained in the fovea with the dimmer AF (i.e., the data indicated by the open squares in the upper coordinates), are strikingly different. Regardless of the SOA, TF threshold is uninfluenced by AF presentation. This is not too surprising since the test flash was presented to a rod-free retinal area and the AF illuminance was selected to be one which was distinctly below cone threshold. These foveal data suggest that cone threshold is influenced by the adapted state of cones and not of rods.

The lower coordinates in Figs. 14-16 show corresponding parafoveal data. The open diamonds and closed triangles represent data points obtained with a "white" test flash and a "white" AF with an illuminance value of -0.5 log tds and 2.5 log tds, respectively. The 2.5 log tds AF data appear very similar to the corresponding foveal function. Probably the quantitative differences in the parafoveal data represent a change from rod to cone mediation of vision. Thus, the initial rise in TF threshold is somewhat earlier (at an SOA of -200 ms), is much greater, and the recovery of sensitivity after AF offset is not complete by an SOA value of 5000 ms.

In contrast to the situation in the fovea, however, the dim AF presented to the parafoveal retina greatly influences test threshold. As shown by previous investigators under these circumstances (Baker, 1953; Frumkes and Sturr, 1968), a dim, parafoveal AF influencing only rods has a similar influence as that observed under conditions where just cone adaptation (bright AF in the fovea) or mixed rod-cone adaptation (bright AF in the parafovea) is studied. Threshold changes as a function of time at both light onset and offset are similar to those observed for cone adaptation, save that they return slower to control threshold.

In summary, the results of Experiment 7 confirm previous reports (Crawford, 1947; Baker, 1953, 1963; Frumkes & Sturr, 1968; Boynton & Kandel, 1957) and show that the influence of early light and dark adaptation depend upon retinal position and AF luminance.

In order to place the TGI experiments reported below in Experiment 9 in the best perspective, it was necessary to show that one of these functions represent early light and dark adaptation of cones and cones alone, and that another function described adaptation in rods and rods only. Therefore, in Experiment 8 below, I obtained action spectra for the two most likely candidates for pure cone and pure rod conditions, these are the foveal high illuminance and parafoveal low illuminance functions, respectively.

Experiment 8

Rationale

The purpose of these experiments was to identify the photoreceptors detecting the test flash in Experiment 7, as well as those photoreceptors mediating the influence of the AF upon TF threshold. To obtain an action spectrum for the mechanism detecting the test flash, the threshold irradiance for many different wavelength TFs is determined in the continual presence of some criterion value AF (e.g, of fixed illuminance and at a fixed SOA value). In a similar vein, an AF action spectrum should be determined by holding the illuminance level of the TF at some fixed value representing some important criterion. For a large number of AF wavelengths, the AF illuminance which then just cancels the visibility of this TF should be determined.

Ideally, these procedures should be repeated with all the SOA values, and at both retinal positions and AF illuminance values used in collecting the data in Experiment 7 above. Given real life constraints, this procedure must be curtailed. It was, therefore, decided to study representative conditions involving thresholds obtained with the bright AF in the fovea which as indicated above, were believed a priori to be indicative of cone function. To this end, TF action spectra were obtained in the dark adapted fovea and subsequently in the presence of a bright AF at an SOA value of 900 ms. This particular SOA (900 ms) was chosen for purpose of comparison with the grating experiments reported below. At this same SOA value, the TF was held 0.6 log units above absolute threshold and I determined an AF action spectrum.

It was additionally decided to study representative conditions involving thresholds obtained with the dim AF in the parafovea which as indicated above, were believed to be indicative of rod function. To this end, TF action spectra were obtained in the dark adapted parafoveal retina and in the presence of a dim AF at an SOA value of 250 ms. At this same SOA value, the TF was then fixed at an illuminance 1.2 log units above absolute threshold and determined an AF action spectrum.

Results

Figures 17 (observer FN) and 18 (observer SL) show action spectra involving data obtained in the fovea using a brighter AF. The upper and lower coordinates represent, AF and TF action spectra obtained at an SOA of 900 ms. In the upper coordinates, the log relative quanta necessary to just mask a TF fixed at an illuminance of 0.6 log units above absolute threshold is plotted as a function of AF wavelength. Similarly, the lower coordinates plot show the log relative quanta necessary to just detect a TF determined when no AF was present, or in the presence of a 2.5 log tds AF at an SOA of 900 ms. In these and all other action spectra shown below (in Figures 24-27), the relative ordinate position of the individual sets of data points and relevant spectra functions was shifted such that their minima correspond at an ordinate value of 0.0. No other curve fitting

Figure 17

Observer FN, upper coordinates: Action spectrum for the influence of a 20° diameter AF upon the visibility of a fovealy detected 54' diameter TF at an SOA of 900 ms. The illuminance of the "white" TF was set at a value 0.6 log units above its absolute threshold. The observer increased the radiance of the variable wavelength AF until the visibility of the TF was canceled. These criterion values are plotted on the ordinate as a function of AF wavelength.* The CIE V_λ function is shown.

Observer FN, lower coordinates: Action spectra for a fovealy detected TF obtained, respectively, without AF (open triangles) and with an AF, 2.5 log tds in illuminance at an SOA of 900 ms (open squares). With no AF present, the observer increased the radiance of the variable wavelength TF, until the TF was just detected; he similarly increased TF-radiance in the presence of the "white" AF. All criterion values are plotted on the ordinate as a function of the TF wavelength. Also shown are the CIE V_λ and V'_λ function and, Stiles' pi-4 and pi-5 mechanisms.

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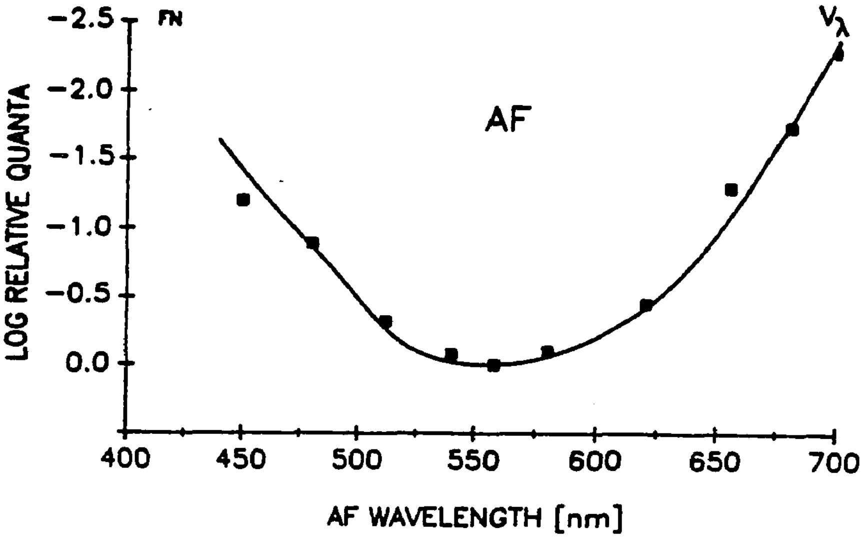
* The relative ordinate values of all action spectra data points reported in this thesis as well as those of the CIE luminosity functions and Stiles' pi-4 and pi-5 mechanisms are shifted such that their minima correspond at the 0.0 log relative quanta position. No other curve fitting manipulation was used.

FOVEA, SOA 900 ms



FOVEA, SOA 900 ms

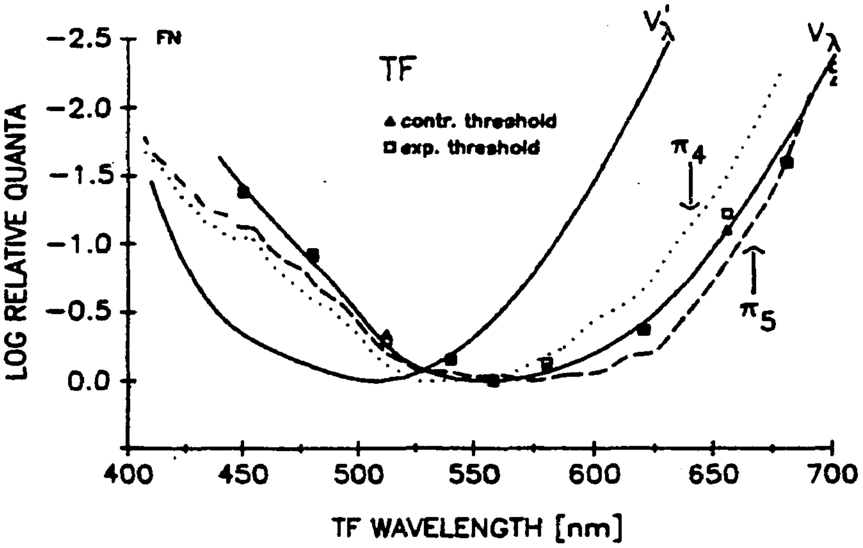
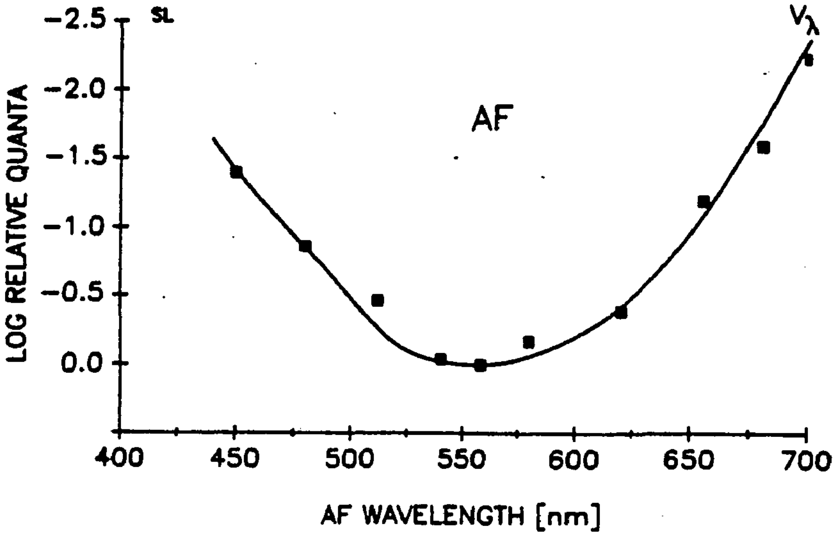


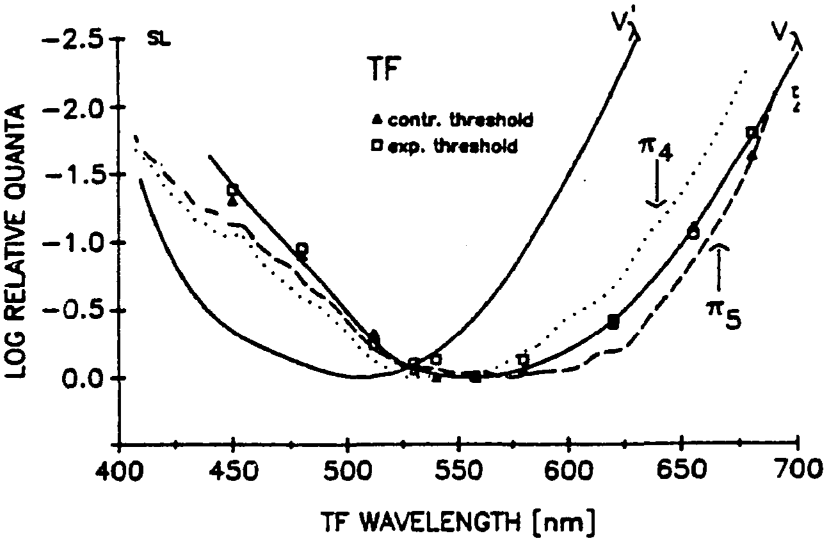
Figure 18

Observer SL, upper coordinates: Action spectrum for the influence of a 20° diameter AF upon the visibility of a fovealy detected 54' diameter TF at an SOA of 900 ms. The illuminance of the "white" TF was set at a value 0.6 log units above its absolute threshold. The observer increased the radiance of the variable wavelength AF until the visibility of the TF was canceled. These criterion values are plotted on the ordinate as a function of AF wavelength. The CIE V_λ function is shown.

Observer SL, lower coordinates: Action spectra for a fovealy detected TF obtained, respectively, without AF (open triangles) and with an AF, 2.5 log tds in illuminance, at an SOA of 900 ms (open squares). With no AF present, the observer increased the radiance of the variable wavelength TF until it was just detected; he similarly increased TF-radiance in the presence of the "white" AF. All criterion values are plotted on the ordinate as a function of TF wavelength. Also shown are the CIE V_λ and V'_λ function and, Stiles' pi-4 and pi-5 mechanisms.



FOVEA, SOA 900 ms



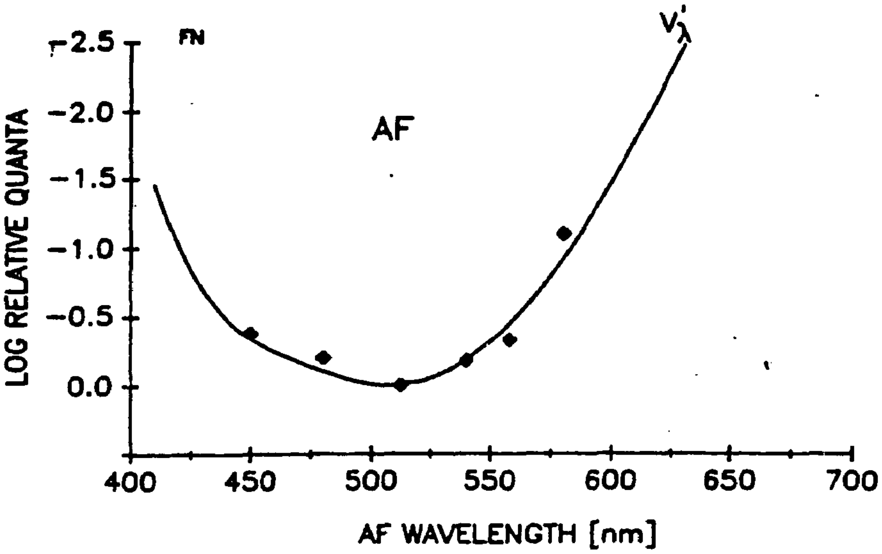
FOVEA, SOA 900 ms

Figure 19

Observer FN, upper coordinates: Action spectrum for the influence of a 20° diameter AF upon the visibility of a parafovealy detected 54' diameter TF at an SOA of 250 ms. The illuminance of the "white" TF was set at a value 1.2 log units above its absolute threshold. The observer increased the radiance of the variable wavelength AF until the visibility of the TF was canceled. The criterion values are plotted on the ordinate as a function of AF wavelength. The CIE V'_{λ} function is shown.

Observer FN, lower coordinates: Action spectra for the detection of a parafovealy detected 54' diameter TF obtained, respectively, without AF and with an AF, -0.5 log tds in illuminance, at an SOA of 250 ms. With no AF present, the observer increased the radiance of the variable wavelength AF until the TF was just visible; he similarly increased TF-radiance in the presence of the "white" AF. The criterion values are plotted on the ordinate as a function of TF wavelength. The CIE V'_{λ} function is shown.

PARAFOVEA, SOA 250 ms



PARAFOVEA, SOA 250 ms

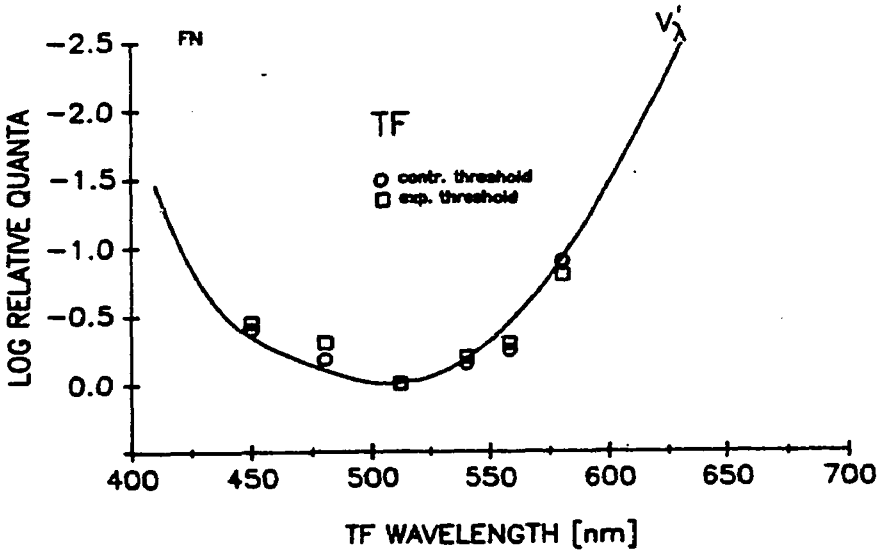
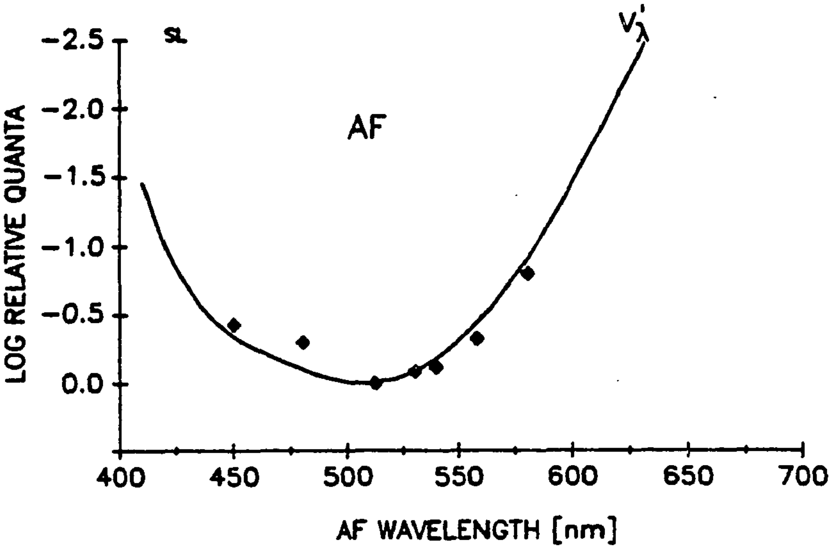


Figure 20

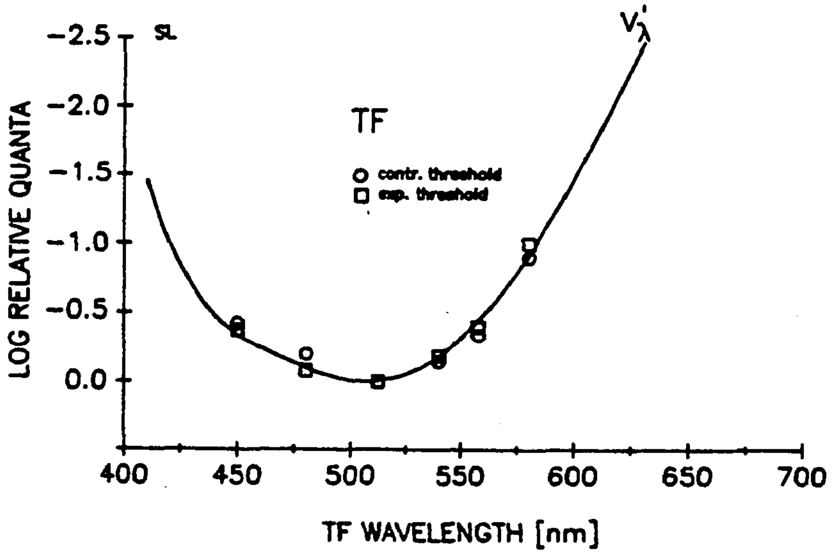
Observer SL, upper coordinates: Action spectrum for the influence of a 20° diameter AF upon the visibility of a parafovealy detected 54' diameter TF at an SOA of 250 ms. The illuminance of the "white" TF was set at a value 1.2 log units above its absolute threshold. The observer increased the radiance of the variable wavelength AF until the visibility of the TF was canceled. The criterion values are plotted on the ordinate as a function of AF wavelength. The CIE V'_λ function is shown.

Observer SL, lower coordinates: Action spectra for the visibility of a parafovealy detected 54' diameter TF obtained, respectively, without an AF and with an AF, -0.5 log tds in illuminance, at an SOA of 250 ms. With no AF present the observer increased the radiance of the variable wavelength TF until the TF was just detected; he similarly increased the TF-radiance in the presence of a "white" AF. The criterion values are plotted on the ordinate as a function of TF wavelength. The CIE V'_λ function is shown.

PARAFOVEA, SOA 250 ms



PARAFOVEA, SOA 250 ms



manipulation was used.

The results in Figures 17 and 18 are quite clear. All action spectra adhere quite closely to the V_λ function, the spectral sensitivity of the CIE photopic observer. Notice, these data adhere more closely to this function than to the presumed "red" and "green" cone functions (the indicated Pi-5 and Pi-4 functions of Stiles in the lower coordinates) and differ drastically from the human scotopic sensitivity function, the V'_λ function. These data suggest quite strongly that cones and cones alone mediate TF threshold and the influence of AF in the early light and dark adaptation function plotted in Figures 14-16 involving foveal presentation of a high illuminance AF.

In a similar vein, the upper and lower coordinates of Figures 19 and 20 represent corresponding data obtained with the dimmer AF at an S0A of 250 ms. The upper coordinates show AF action spectra, the lower coordinates TF action spectra. Notice that all these data points adhere quite closely to the spectral sensitivity of V'_λ, the spectral sensitivity of the human scotopic observer. These data again indicate that in the parafovea using dimmer AFs, the early light and dark adaptation functions in Figures 14-16 involve rods and rods alone.

In summary, the results of Experiments 7 and 8 clearly indicate that early light and dark adaptation follow the types of time courses suggested by previous investigators (Crawford, 1947; Baker, 1953, 1963; Battersby &

Wagman, 1959). Although the time course is faster under conditions where cones alone are involved (see Figures 14-16, open circles), and somewhat slower when just rods are involved (see Figures 14-16 open diamonds), the overall changes in visual sensitivity produced are quite similar. This is also true for conditions under which it is likely that both rod and cone adaptation are studied (see Figures 14-16, closed triangles). This is not surprising since similar functions have been obtained using a rod-cone interaction paradigm (Frumkes, Sekular, Barris, Reiss & Chalupa, 1973).

Collectively, Experiments 7 and 8 establish two baseline conditions describing the time course of early rod- and early cone-adaptation: the low illuminance parafoveal condition and the high illuminance foveal condition as delineated by the respective functions of Figures 14-16.

Experiment 9

The goal of Experiment 9 was to examine the changes in spatial acuity occurring during the early stages of light and dark adaptation. To that end, TGI for a 54' diameter, 10 ms duration, 18 cpd test flash were determined as a function of the SOA in respect to the onset of an AF. Based on studies reviewed above, and on the results of Part I of the present thesis, as well as on the action spectra described below, there is good reason to believe that this TGI measure does represent a spatial acuity measure which is mediated by cones and cones alone.

The conditions of Experiment 9 were in all other aspects the same as described for Experiment 7 above.

Results

Figures 21-23 plot TGI (threshold grating illuminance, i.e., the minimal TF illuminance value at which the grating lines could be detected) as a function of the SOA in respect to the onset of the "white" AF for observers FN, SL, and RR, respectively. The upper set of coordinates represent data obtained in the fovea, while the lower data were obtained in the parafovea. The different symbols represent the differing AF illuminance values as indicated.

For all observers, the results obtained are largely independent of retinal location but depend quite heavily upon AF illuminance. With the bright AF, TGI begins to rise 150-200 ms before AF onset and is maximal at an SOA of either 0 or 50 ms, and then declines slightly throughout the remaining presentation of the AF. In this respect, results are similar to the changes in absolute sensitivity occurring during rapid light adaptation using a cone-stimulating AF reported in Experiment 7 above (see Figures 14-16). However, the influence of rapid dark adaptation upon spatial acuity is much different than upon absolute sensitivity. First, notice that TGI returns to control value at an SOA of about 700 ms. (200 ms after AF offset). Then TGI continues to fall below control level representing an enhancement of visual acuity. TGI reaches a nadir at 900 ms. This maximal enhancement of visual acuity is about 0.5 log in the fovea, about 0.7 log units in the parafovea. TGI only then gradually increases again to

Figure 21

Observer FN, upper coordinates: TGI as a function of SOA. The illuminance of the "white" AF was either 2.5 log tds (closed circles) or -0.5 log tds (open squares). AF diameter was 20° and its duration 500 ms. TF was "white", had a spatial frequency of 18 cpd, a duration of 10 ms and a diameter of 54'. All stimuli were presented to the fovea. See legend of Figure 14 for an explanation of the abscissa values.

Observer FN, lower coordinates: TGI as a function of SOA. AF-illuminance was either 2.5 log tds (closed inverted triangles) or -0.5 log tds (open circles). AF was "white", 20° in diameter and 500 ms in duration. TF was "white", had a spatial frequency of 18 cpd, a duration of 10 ms and a diameter of 54'. All stimuli were presented to the parafovea.

GRATING

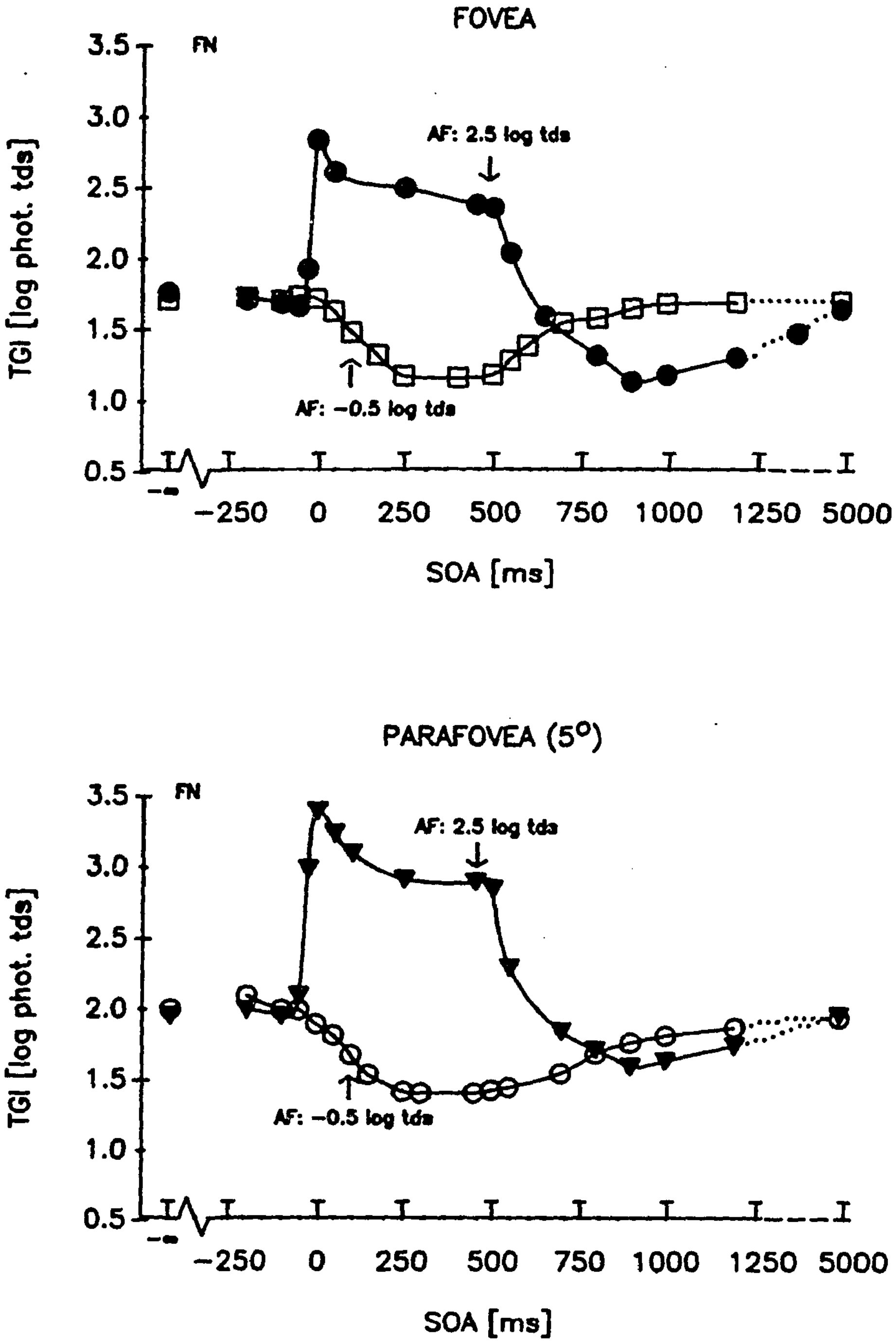
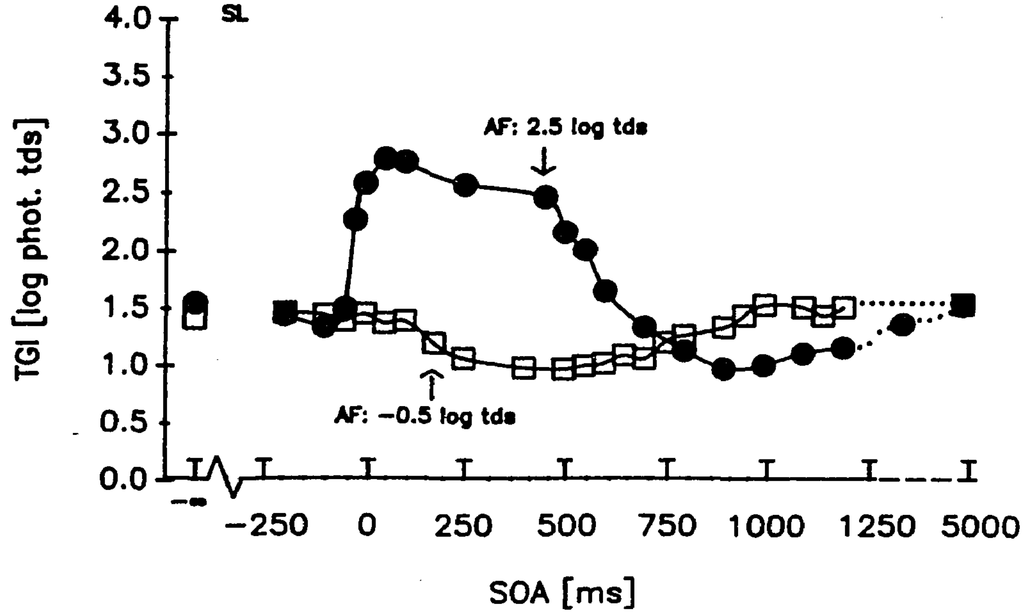

FOVEA
3.5
3.0
2.5
2.0
1.5
1.0
0.5
FN
TGI [log phot. tds]
AF: 2.5 log tds
AF: −0.5 log tds
−250
0
250
500
750
1000
1250
5000
SOA [ms]
PARAFOVEA (5°)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
FN
TGI [log phot. tds]
AF: 2.5 log tds
AF: −0.5 log tds
−250
0
250
500
750
1000
1250
5000
SOA [ms]

Figure 22

Observer SL, upper coordinates: TGI as a function of SOA. The illuminance of the AF was either 2.5 log tds (closed circles) or -0.5 log tds (open squares). AF was "white", 20° in diameter and 500 ms in duration. TF had a spatial frequency of 18 cpd, a duration of 10 ms and a diameter of 54'. All stimuli were presented to the fovea. See legend of Figure 14 for an explanation of the abscissa values.

Observer SL, lower coordinates: TGI as a function of SOA. AF-illuminance was either 2.5 log tds (closed inverted triangles) or -0.5 log tds (open circles). AF was "white", its diameter 20° and its duration 500 ms. TF was "white, had a spatial frequency of 18 cpd, a duration of 10 ms and a diameter of 54'. All stimuli were presented to the parafovea.

GRATING


FOVEA

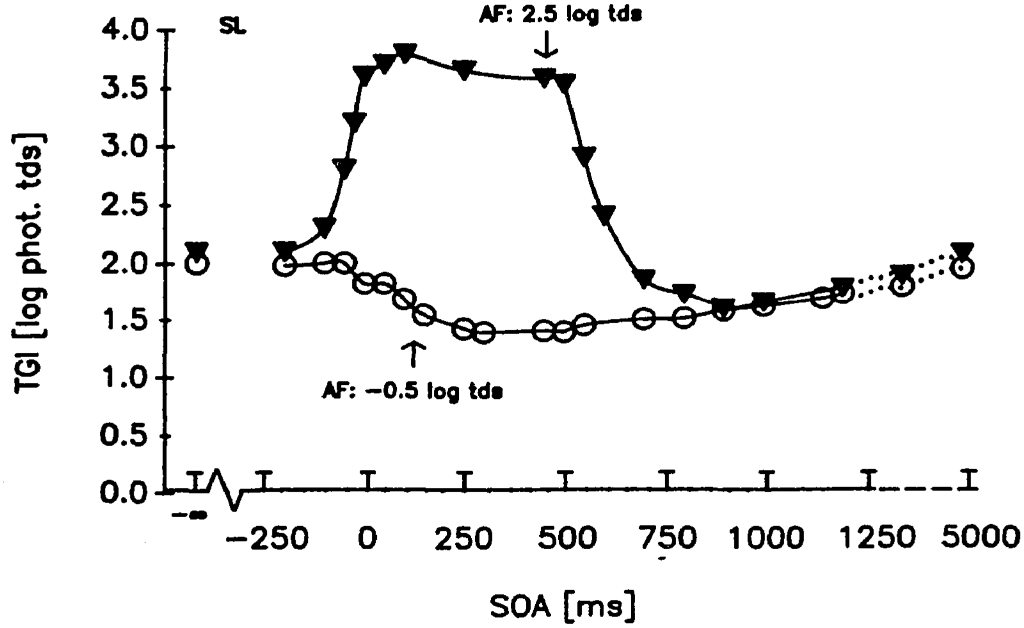
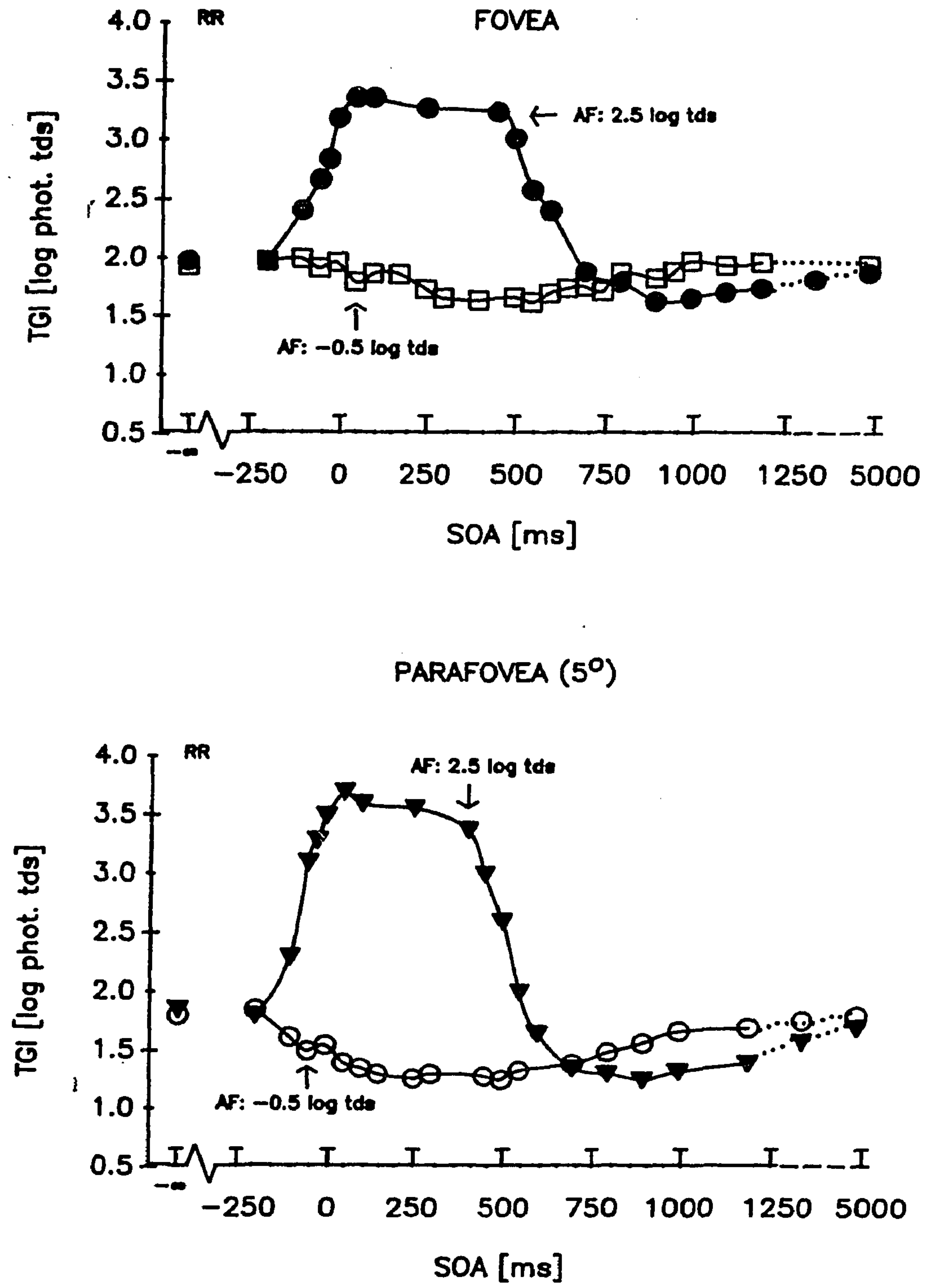

PARAFOVEA (5°)

Figure 23

Observer RR, upper coordinates: TGI as a function of SOA. The illuminance of the AF was either 2.5 log tds (closed circles) or -0.5 log tds (open squares). AF was "white", 20° in diameter and 500 ms in duration. TF was "white", had a spatial frequency of 18 cpd, a duration of 10 ms and a diameter of 54'. All stimuli were presented to the fovea. See legend of Figure 14 for an explanation of the abscissa values.

Observer SL, lower coordinates: TGI as a function of SOA. AF-illuminance was either 2.5 log tds (closed inverted triangles) or -0.5 log tds (open circles). AF was "white", its diameter was 20° and its duration 500 ms. TF was "white", had a spatial frequency of 18 cpd, a duration of 10 ms and a diameter of 54'. All stimuli were presented to the parafovea.

GRATING


FOVEA
RR
TGI [log phot. tds]
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
← AF: 2.5 log tds
AF: −0.5 log tds
−∞
−250
0
250
500
750
1000
1250
5000
SOA [ms]
PARAFOVEA (5°)
RR
TGI [log phot. tds]
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
AF: 2.5 log tds
AF: −0.5 log tds
−∞
−250
0
250
500
750
1000
1250
5000
SOA [ms]

its control value. At an SOA of 2000 ms the effect is almost negligible; at an SOA of 5000 ms TGI always appeared to be fully recovered.

The influence of the dim AF upon TGI was also much different than observed upon absolute sensitivity. For all observers and at both retinal positions, TGI values remained unaffected until an SOA of 50 ms. Then TGI gradually decreased (visual acuity became enhanced). This enhancement in acuity became maximal at an SOA of about 250 ms, and remained enhanced throughout the remaining presentation of the AF. Following AF offset, TGI determined in the fovea, gradually increased again reaching control values approximately 550-750 ms after AF offset (SOA value of between 1000-1250 ms.). In the parafovea the situation was slightly different. Full recovery was only reached at an SOA of about 4000 ms. For observer FN and SL one incidental observation should be noted. The minimal TGI illuminance value observed either in the fovea or parafovea was approximately the same in the presence of either luminance AF. Thus, whether enhanced during the presentation of the dim AF or following the presentation of the bright AF, the maximal enhancement obtained was the same, suggesting that both types of enhancement of visual acuity were mediated by the same underlying mechanism or very similar underlying mechanisms.

To summarize, a dim AF so chosen to only influence rods enhances spatial acuity (lowers TGI) with a time course much different than the depression in absolute rod sensitivity induced by the same AF. In contrast, an AF clearly bright enough to influence cones as well as rods raises TGI prior to and during AF onset, but enhances spatial acuity following AF offset. In order to place these results of Experiment 9 in the best possible perspective, I determined relevant action spectra to define as clearly as possible: 1) the mechanisms which detect the grating in the presence of a dim AF; 2) the mechanisms detecting the grating following the offset of a bright AF; and 3) the mechanisms directly influenced by the dim AF or bright AF.

Experiment 10

Rationale and Methods

The overall rationale for these experiments is identical to that outlined for Experiment 8 above, save that TGI and not TF threshold was involved and that all data were obtained with foveal stimulus presentation.

In one set of experiments, the test grating was set 0.4 log units below absolute threshold. The irradiance of a variable wavelength AF which just made this grating visible were determined. Alternatively, for many different wavelength gratings, the irradiance which just made the bars of the grating visible were determined. Such an action spectrum was obtained with no AF present, and with a -0.5 log tds AF present at an SOA of 450 ms.

In the second set of experiments, data were collected at an SOA of 900 ms, that time interval providing maximal facilitation of grating acuity in Figures 21-23. The procedures are as outlined in the previous paragraph, save that test action spectra were determined in the presence of a "white" AF fixed at 2.5 log tds.

Results

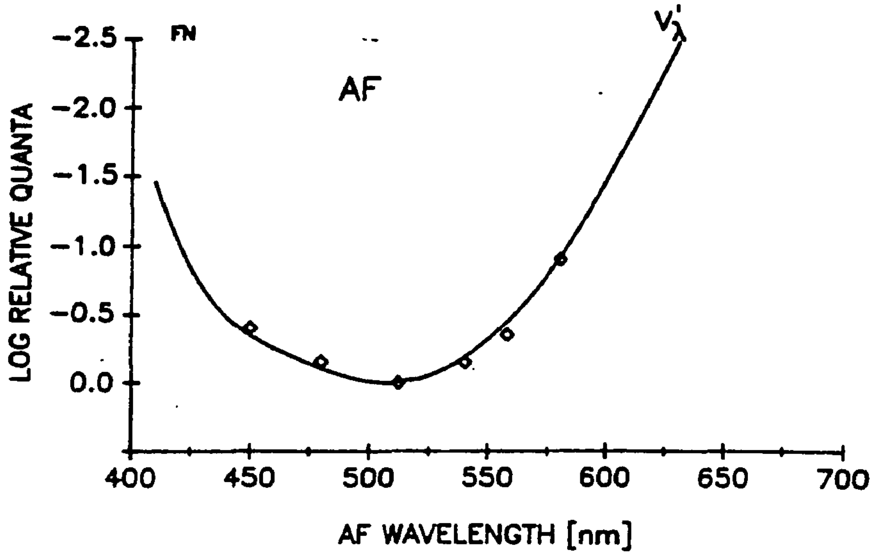
The enhancement of TGI by rod light adaptation - Figures 24 and 25 show action spectra involving data obtained with foveal presentation of stimuli for observers FN and SL, respectively. The upper and lower coordinates represent, AF and test action spectra, respectively, obtained at an SOA of 450 ms. The AF action spectrum on top shows the log relative quanta necessary to make visible, a grating set 0.4 log units below control threshold. This action spectrum adheres to the CIE V'_λ function, indicating that rods and rods alone are enhancing TGI at this and probably all other SOA intervals between +50 and +500 ms. As indicated in the lower coordinates, TGI with no AF present as well as at an SOA of 450 ms adheres to a cone-like action spectrum. Neither of these sets of data adhere precisely to any of the three cone functions indicated, the luminosity function of the CIE photopic observer, the Pi-4 or Pi-5 function of Stiles (respectively, the V_λ function, the 'green' or 'red' cone mechanism of Stiles). It is interesting, however, that when enhanced by the AF, the TGI shows, for both observers, greater sensitivity in the red end of the spectrum.

To summarize, the dim AF data presented in Figures 24 and 25 represent the influence of rod adaptation upon cone mediated spatial acuity. This enhancement of spatial acuity, evident while the AF is present, involves some selective increase in sensitivity at the red end of the visual

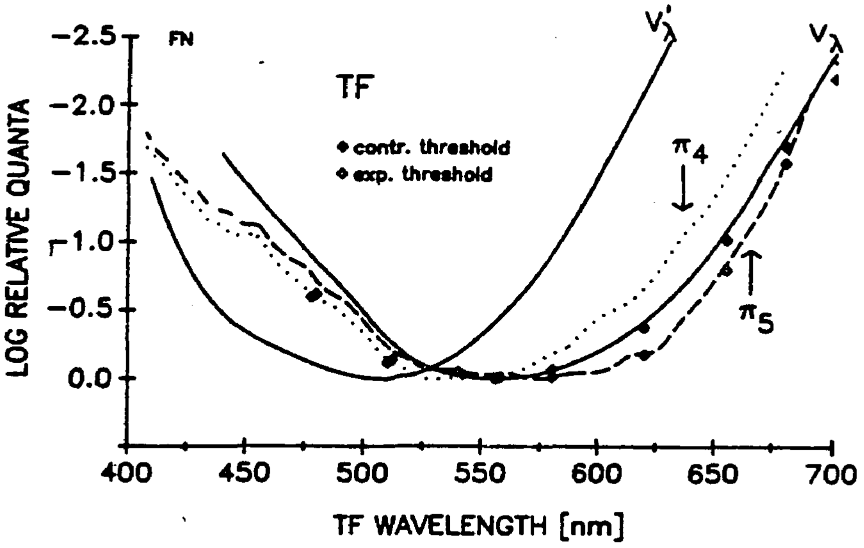
Figure 24

Observer FN, upper coordinates: Action spectrum for the influence of the 20° diameter AF upon the visibility of a fovealy detected 18 cpd grating at an SOA of 450 ms. The illuminance of the "white" test grating was set at a value 0.4 log units below the TGI value obtained at the point labeled "minus infinity" on the abscissa of the upper coordinates in Figure 21. The observer increased the radiance of the variable wavelength AF until the bars of the grating became just visible. The criterion values are plotted on the ordinate as a function of AF wavelength.

Observer FN, lower coordinates: Action spectra for the visibility of a fovealy detected 18 cpd grating obtained, respectively, without AF and with an AF, -0.5 log tds in illuminance, at an SOA of 450 ms. With no AF present, the observer increased the radiance of the variable wavelength TF until the bars of the grating were just visible; he similarly increased test grating-radiance in the presence of the "white" AF. All criterion values are plotted on the ordinate as a function of test grating wavelength.



FOVEA, SOA 450 ms – GRATING



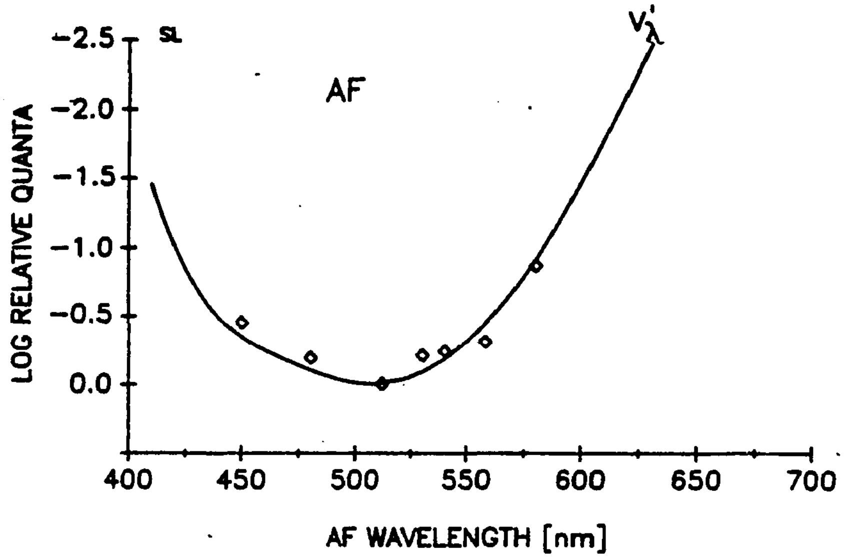
FOVEA, SOA 450 ms – GRATING

Figure 25

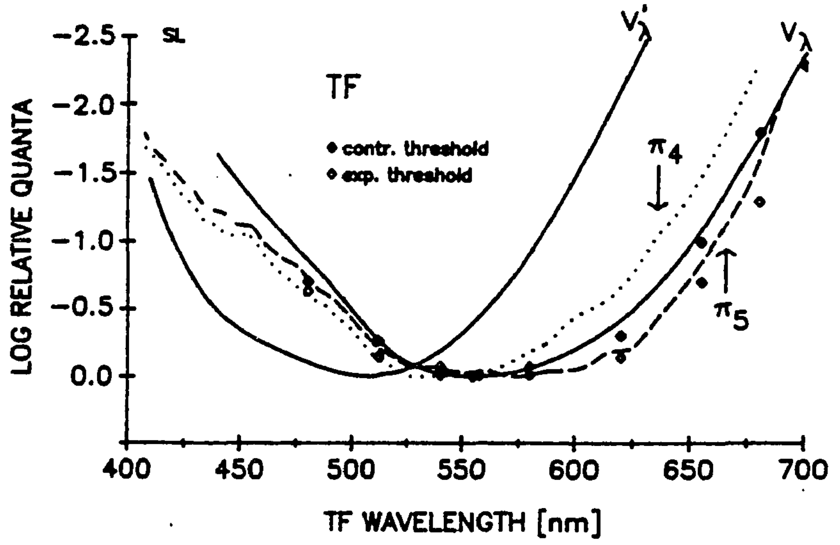
Observer SL, upper coordinates: Action spectrum for the influence of a 20° diameter AF upon the visibility of a fovealy detected 18 cpd grating at an SOA of 450 ms. The illuminance of the "white" test grating was set at a value 0.4 log units below the TGI value obtained at the point labeled "minus infinity" on the abscissa of the upper coordinates in Figure 22. The observer increased the radiance of the variable wavelength AF until the bars of the grating became just visible. The criterion values are plotted on the ordinate as a function of AF wavelength.

Observer SL, lower coordinates: Action spectra for the visibility of a fovealy detected 18 cpd grating obtained, respectively, without an AF and with an AF, -0.5 log tds in illuminance, at an SOA of 450 ms. With no AF present, the observer increased the radiance of the variable wavelength TF until the bars of the grating were just visible. All criterion values are plotted on the ordinate as a function of test grating wavelength.

FOVEA, SOA 450 ms – GRATING



FOVEA, SOA 450 ms – GRATING



spectrum.

The enhancement of TGI by cone light adaptation- Figures 26 and 27 represent action spectra obtained with foveal presentation of stimuli at an SOA of 900 ms for observers FN and SL, respectively. The upper and lower coordinates represent, respectively, AF and test action spectra. The upper coordinates show that it is a cone-like mechanism at this SOA which enhances spatial acuity. Clearly, this action spectrum adheres more closely to the luminosity function of the CIE photopic observer (V_λ) than to the other cone-functions plotted. The test action spectra below indicate the log relative quanta necessary to detect the grating with no AF present (closed circles) or in the presence of a 2.5 log tds AF at an SOA of 900 ms. Notice that TGI is mediated by a cone-like mechanism, whether or not the AF is present. Neither control or experimental data adhere too closely to any of the cone mechanisms plotted. But when enhanced by the AF, the action spectrum shifts to longer wavelengths.

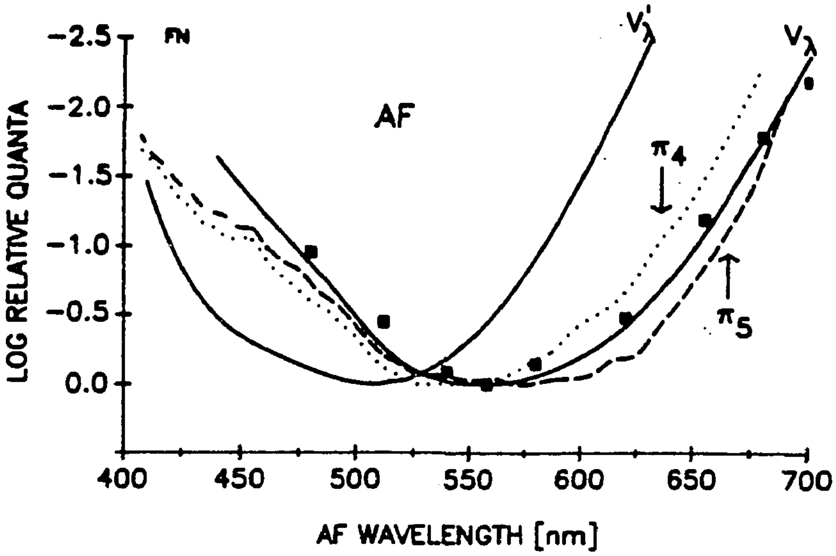
To summarize, the enhancement of grating acuity following the termination of a bright AF represents the influence of cone-dark adaptation upon cone mediated acuity. The enhancement of acuity involves some increase in sensitivity which is somewhat selective to the red end of the visual spectrum.

Figure 26

Observer FN, upper coordinates: Action spectrum for the influence of a 20° diameter AF upon the visibility of a fovealy detected 18 cpd grating at an SOA of 900 ms. The illuminance of the "white" test grating was set at a value 0.4 log units below the TGI value obtained at the point labeled "minus infinity" on the abscissa of the upper coordinates in Figure 21. The observer increased the radiance of the variable wavelength AF until the bars of the grating became just visible. The criterion values are plotted on the ordinate as a function of AF wavelength.

Observer FN, lower coordinates: Action spectra for the visibility of a fovealy detected 18 cpd grating obtained, respectively, without an AF and with an AF, 2.5 log tds in illuminance, at an SOA of 900 ms. With no AF present, the observer increased the radiance of the variable wavelength test grating until the bars were just visible; he similarly increased test grating-radiance in the presence of the "white" AF. All criterion values are plotted on the ordinate as a function of test grating wavelength.

FOVEA, SOA 900 ms – GRATING



FOVEA, SOA 900 – GRATING

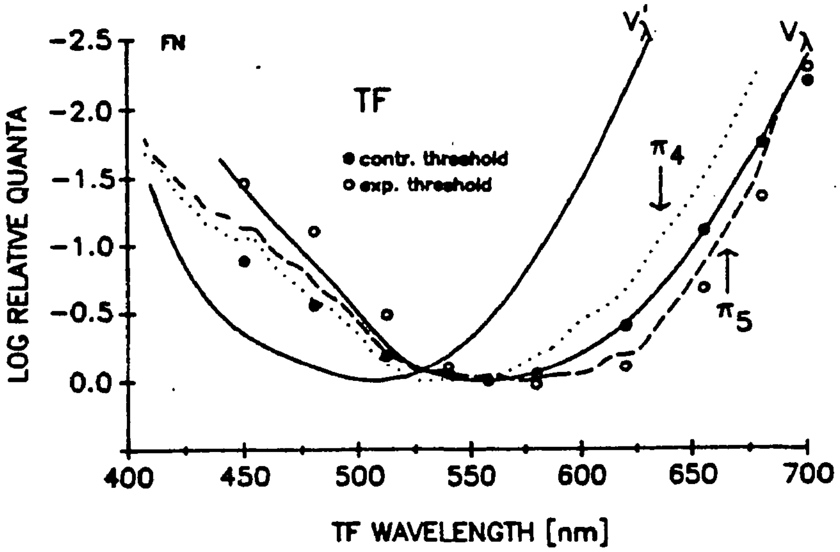
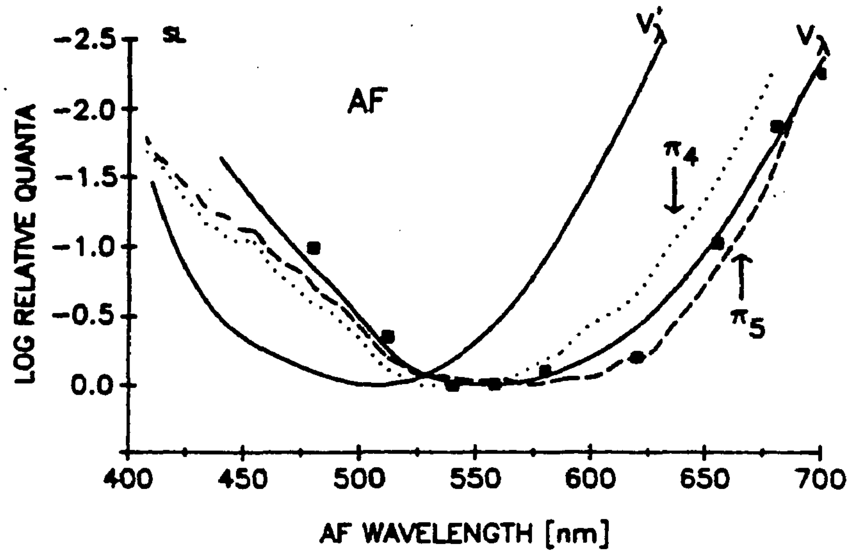


Figure 27

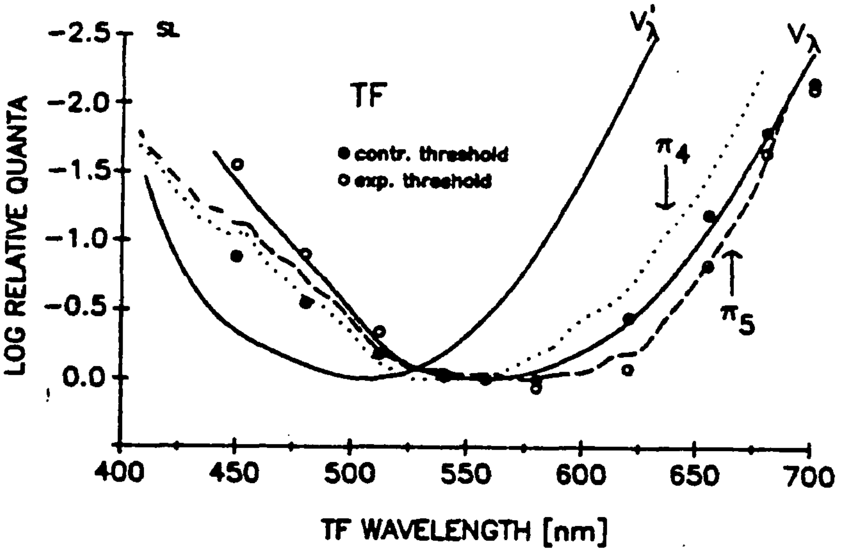
Observer SL, upper coordinates: Action spectrum for the influence of a 20° diameter AF upon the visibility of a fovealy detected 18 cpd grating at an SOA of 900 ms. The illuminance of the "white" test grating was set at a value 0.4 log units below the TGI value obtained at the point labeled "minus infinity" on the abscissa of the upper coordinates in Figure 22. The observer increased the radiance of the variable wavelength AF until the bars of the grating became just visible. The criterion values are plotted on the ordinate as a function of AF wavelength.

Observer SL, lower coordinates: Action spectra for the visibility of a fovealy detected 18 cpd grating obtained, respectively, without an AF and with an AF, 2.5 log tds in illuminance, at an SOA of 900 ms. With no AF prsent, the observer increased the radiance of the variable wavelength test grating until the bars were just visible; he similarly increased test grating-radiance in the presence of the "white" AF. All criterion values are plotted on the ordinate as a function of test grating wavelength.

FOVEA, SOA 900 ms – GRATING



FOVEA, SOA 900 – GRATING



DISCUSSION

The results of Part II of the present study show that the influence of early light and dark adaptation upon absolute visual sensitivity depends upon TF retinal position and AF luminance level. The influence of a dim parafoveal AF upon absolute threshold was shown to have a time course similar to that of either a bright foveal or parafoveal AF. However, much different results were obtained when grating acuity was measured during the early stages of light and dark adaptation. Dim AFs adapting rods only enhance spatial acuity with a time course much slower than the depression in absolute rod sensitivity induced by the same AF. The observed enhancement of spatial acuity when rods are selectively light adapted is most apparent for gratings with a wavelength content derived from the red end of the spectrum. Bright AFs following their termination also enhance spatial acuity with a time course much different from the changes in cone absolute threshold during early dark adaptation. This enhancement of acuity as cones rapidly dark adapt also involves an increased sensitivity to the red end of the visible spectrum.

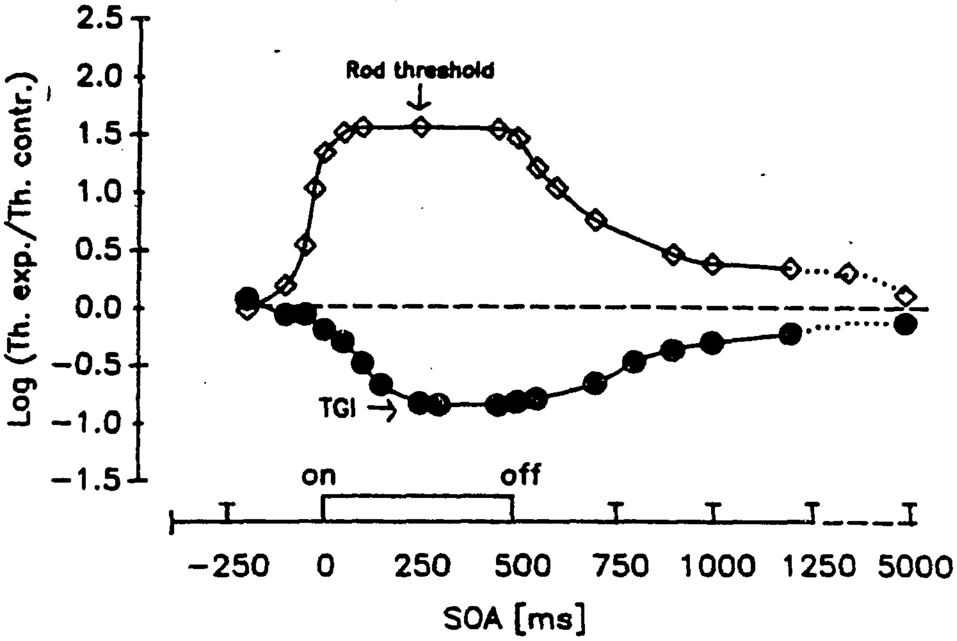
The differing influence of short term light and dark adaptation upon visual absolute sensitivity and TGI is probably best demonstrated by several derived plots. In Figure 28 some of the data in Figures 14 and 21 for observer FN are replotted. Log change in threshold (Log experimental threshold - Log control threshold) is plotted on the ordinate as a function of SOA. The upper plot shows data obtained with the dim AF in the parafovea. This derived plot clearly shows that the decrease in rod

Figure 28

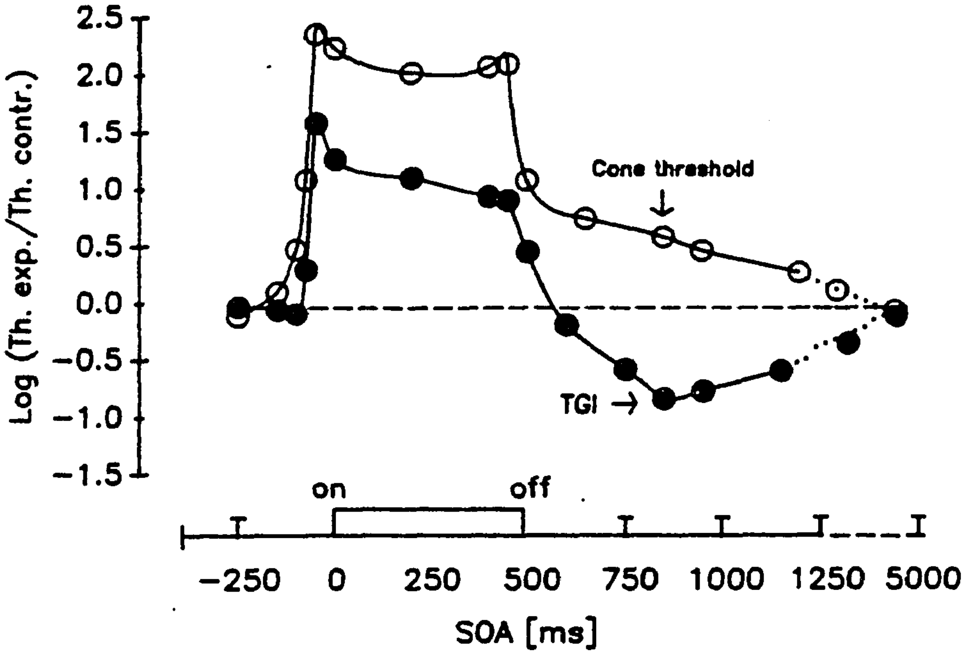
Upper coordinates, parafovea : Change in threshold (expressed on the ordinate as log deviation from dark adapted threshold) as a function of SOA. The open diamonds and closed circles are derived from the -0.5 log tds data plotted in the lower coordinates of Figures 14 and 21, respectively. The labeled arrows indicate rod threshold and TGI at an SOA of 250 ms. Notice that rod light adaptation produces a direction of change in rod threshold opposite to that produced in TGI. Also, maximal change is faster produced in rod threshold than in TGI. The duration of the AF is indicated by the rectangle on the abcissa.

Lower coordinates, fovea: Change in threshold (expressed on the ordinate as log deviation from dark adapted threshold) as a function of SOA. The open and closed circles are derived from the 2.5 log tds data plotted in the upper coordinates of Figures 14 and 21, respectively. The labeled arrows indicate cone threshold and TGI at an SOA of 900 ms. Notice that cone adaptation elevates cone threshold with at least 0.6 log units above absolute threshold, but produces a deviation of TGI from its dark adapted value of at least 0.5 log units.

PARAFOVEA (5°)



FOVEA



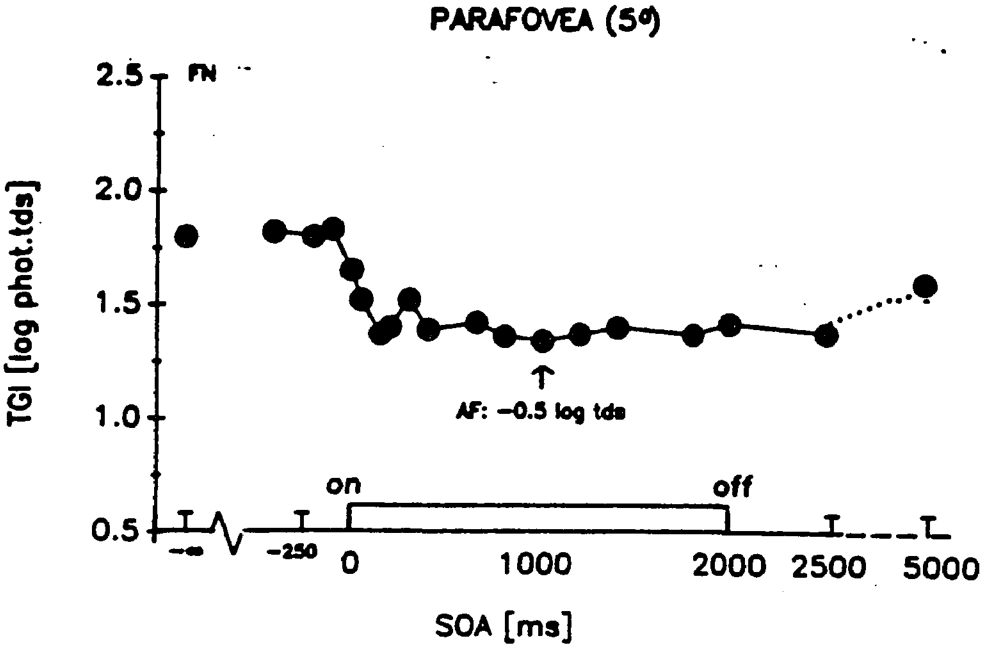
sensitivity produced by short term light adaptation largely precedes any change in cone spatial acuity, and that the change in threshold is much more rapid then the change in TGI. Clearly, then, the influence of rod-adaptation upon rod-threshold is not at all indicative of its influence upon cone-mediated acuity. However, the time course of changes in absolute sensitivity and visual acuity following AF offset are quite similar.

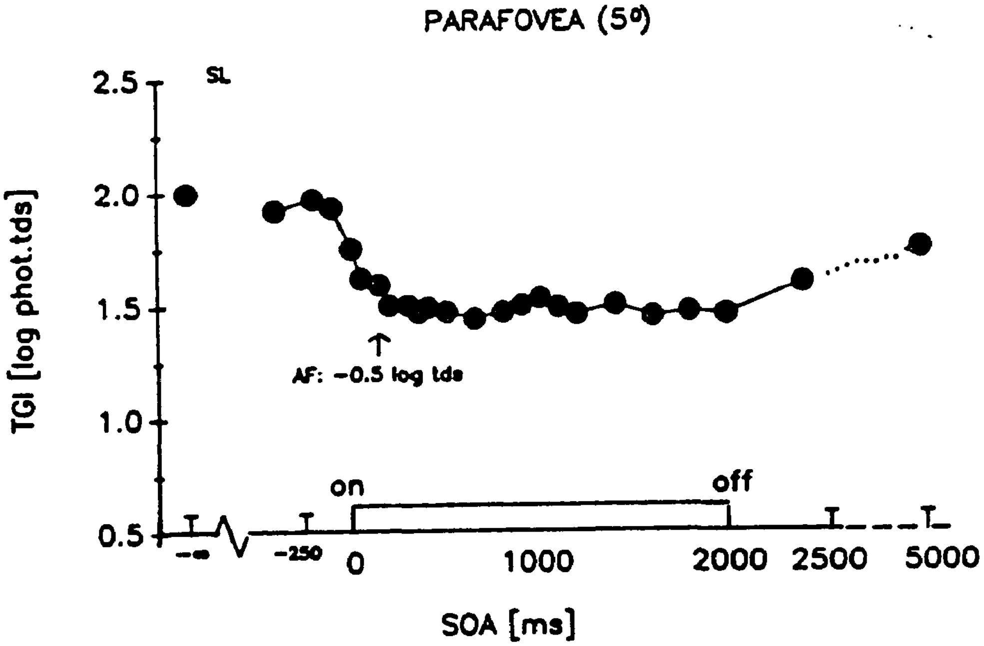
The lower plot in Figure 28 show data obtained with the brighter AF in the fovea. Notice that changes in TF threshold and TGI at light onset are quite similar, but changes at light offset are quite different. Thus, during rapid dark adaptation, absolute sensitivity recovers monotonically, while TGI at first decreases, then increases again.

As shown in Part One of the present thesis, steady backgrounds influencing rods only produce a sustained enhancement of cone-mediated spatial acuity. To determine whether the enhancement produced by a dim foveal or parafoveal AF was similar to the effect reported in Part One, I extended the duration of the AF from 500 ms up to 2000 ms but left all other aspects of Experiment 8 unchanged. Figure 29 plots TGI as a function of SOA in respect to the onset and offset of a "white" -0.5 log tds AF for observers FN (upper coordinates) and SL (lower coordinates). All data points were obtained at 5°to the right of fixation. Notice that, for both observers, TGI values remain unaffected until an SOA of about 250 ms and is maintained at that level for the remainder of the time of AF presentation. The data suggest that the enhancement of visual acuity will be sustained during the presence of the AF for any AF-duration longer than 250 ms.

Figure 29

Observers FN and SL, upper and lower coordinates, respectively: TGI as a function of SOA. The illuminance of the "white" AF was -0.5 log tds, its diameter 20° and its duration 2000 ms. The TF was "white", 54' in diameter and 10 ms in duration. All stimuli were presented to the parafovea. Notice that the interval (500 ms) on the scale on the abcissa changes after 2500 ms. The duration of the AF is shown by the rectangle on the abcissa.


PARAFOVEA (5°)
FN
TGI [log phot.tds]
2.5
2.0
1.5
1.0
0.5
AF: −0.5 log tds
on
off
−∞
−250
0
1000
2000
2500
5000
SOA [ms]


PARAFOVEA (5°)
SL
TGI [log phot.tds]
2.5
2.0
1.5
1.0
0.5
AF: −0.5 log tds
on
off
−∞
−250
0
1000
2000
2500
5000
SOA [ms]

Therefore, the effect of short term rod-adaptation upon cone-mediated spatial acuity is, beyond 250 ms, no different from the enhancement observed under conditions of steady state rod-adaptation. Hence, the time course for the onset of the influence of steady state rod-light adaptation upon cone-mediated spatial acuity, as described in Part One, is about 250 ms.

As discussed in Part One, the influence of rod adaptation upon cone-mediated spatial acuity bears a striking resemblance to SRCI. Specifically, similarity in influence of background luminance levels upon cone-mediated spatial and temporal effects have been mentioned. The technique used in the present study has made it possible to measure fairly accurate the onset of rod-cone interaction as determined with gratings. Most recently, Frumkes and Eysteinsson (1987) published intracellular records of Xenopus horizontal cell (see their figure 4) showing a time course of about 200 ms for the onset of SRCI as determined with flicker. Although, such measurements for the onset of SRCI have never been made in humans, the close correspondence of the Frumkes and Eysteinsson data (1987) with the present spatial data clearly provides another interesting parallel between the spatial and temporal effects.

A result of the present study which also appears to be akin to those obtained in flicker studies involves the mechanism mediating the enhancement. The present data suggest that when rods become light adapted, cone mediated enhancement of acuity may be specific for a mechanism sensitive to the red end of the visible spectrum. Similarly, Coletta and Adams (1984) reported high frequency flicker to be mediated by the long wavelength-sensitive cone type under conditions which favor rod-cone interaction. As was noted with flicker (Alexander & Fishman, 1983; Goldberg & Frumkes, 1983), protanopes who usually show a low luminous efficiency in the red end of the spectrum, do not exhibit the flicker threshold rise during dark adaptation which is evident for normals and deuteranopes. On the basis of the present spatial data it may then be expected that protanopes would show superior spatial acuity to normals and deuteranopes while dark adapting. Such a finding would undoubtedly reinforce the idea of a special physiological relationship between rods and long wavelength-sensitive mechanisms.

The similarities in frequency dependency, in test threshold change with specific background luminance levels, in the mechanism mediating enhancement and perhaps also correspondence in time course for the onset of the enhancement strongly suggest that both temporal and spatial effects may reflect one common mechanism, SRCI.

Since, it has been argued (Frumkes & Eysteinsson, 1987) that SRCI involves primarily retinal factors the suggestion made above presupposes at least that grating detection is also primarily limited by retinal factors. There is indeed evidence, obtained under conditions using incoherent light (Campbell & Gubisch, 1967), which showed spatial acuity to be limited primarily by the size of cones, the cone mosaic, and to a certain extent by light scatter. Williams (1985) using coherent light suggested that the upper limit for the perception of higher spatial frequencies is imposed primarily by spatial summation resulting from photoreceptor coupling or neural convergence at some higher stage. Strong indications for a retinal site of grating detection also comes from studies involving pattern-ERG's and single-unit recording from ganglion cells in cat (Enroth-Cugell, Robson, Schweitzer-Tong & Watson, 1983). Thus, both grating and flicker perception (van de Grind, Grusser & Lukenheimer, 1972) are thought to be largely limited by retinal factors.

Evidence that SRCI involves specifically interaction of distal retinal neurons comes from a variety of flicker-studies. First, some human subjects with distal retinal pathology (Alexander & Fishman, 1985; Arden & Hogg, 1985) and with common hereditary forms of color deficiency (Alexander & Fishman, 1983; Goldberg, Frumkes & Nygaard, 1983) do not show the effect. Second, analyses of ERG components reflecting distal retinal function have established the presence of SRCI in different species including man (Arden & Frumkes, 1986), cat and dog (Loew & Arden, 1985) and frog (Fatechand, 1979; Goldberg & Frumkes, 1983; Hood, 1972). Third and most recently, Frumkes and Eysteinsson (1987), showed that rod light adaptation enhances cone-driven responses to spatially discrete and relatively high frequency flicker in cones and other distal retinal neurons, most notably horizontal cells and bipolar cells lacking color opponency. They demonstrated like polarity responses to the flickering test probe and background in horizontal cells; while other cell types, including cones, showed opposite polarity responses to these stimuli reflecting center-surround antagonism in their receptive field. Thus, only horizontal cells seem to have the requisite spatial properties to mediate SRCI. The authors suggest that SRCI is likely to involve rod modulation of horizontal cell influence onto distal retinal neurons. Accordingly, the ambient level of rod adaptation determines the influence of these photoreceptors upon horizontal cells and hence, the horizontal cell influence upon cells to which they are presynaptic. Since horizontal cells feedback onto cones but not onto rods (Lasater, 1982; Pasino & Marchiafava, 1976) it is not surprising that SRCI is observed only in cones and not in rods. The feedforward influence of horizontal cells onto bipolar cells is reflected in the recorded presence of SRCI in bipolar cells and indirectly in ganglion cells.

It is impossible to state with any certainty, given the lack of intracellular data involving SRCI obtained with gratings, whether or not the spatial and temporal effects are mediated by the same retinal pathway. However, the temptation to speculate even more that they share a common pathway is instigated by the physiological determination that horizontal cell modulation of the influence of rod-adapting backgrounds onto cones depends upon background size. A similar dependency has been observed psychophysically for the spatial effect. Thus, the horizontal cell might also be the key element mediating the influence of rods upon cone-mediated spatial acuity.

At least three types of studies will be necessary in order to identify conclusively the underlying neural mechanism of the spatial effect. First, as with the flicker studies, it should be possible to obtain psychophysical data from ophthalmological patients with known distal retinal pathology. Second, the effect should be studied electrophysiologically in normal human retina's and subsequently in well defined clinical populations. Third, again as with the flicker studies, investigations by means of intracellular recordings in lower species combined with pharmacological procedures are necessary to identify the retinal neurons and their respective roles in this effect.

Cone-mediated spatial acuity is not only enhanced during early rod-light adaptation but also during early dark adaptation of the cone system. Both enhancements are of approximately the same magnitude and mediated by the same type of mechanism. There are however striking differences between these two effects. There is the difference regarding the spectral nature of the backgrounds responsible for inducing the effects. Another difference between these enhancements regards the response characteristic shown by the mediating red sensitive-mechanism. When enhanced by a rod-adapting background the mediating mechanism tends to show a sustained response. When enhanced after the termination of a cone-adapting background the mediating mechanism shows a transient response. A possible explanation for this difference in response characteristic is that the two effects are mediated by different retinal pathways.

It has been argued above that in SRCI rods are thought to modulate horizontal cell influence onto cone-mediated flicker or spatial acuity for that matter. That is, dark adapted rods induce inhibition of cones by horizontal cells by way of a feedback mechanism. Conversely, rod light adaptation removes horizontal cell inhibition. The mechanism by which horizontal cells exert their influence onto cones is largely unknown. A center-surround mechanism for the relationship between cones and horizontal cells cannot explain the enhancement, since the influence of rod light adaptation is removal of horizontal cell inhibition of cones. Hence, a more specific examination of the membrane properties of the neurons involved in SRCI is indicated.

There is, to my knowledge, no parallel of the enhancement of visual acuity during rapid cone dark adaptation reported in the neurophysiological literature. Although recently, Pflug and Nelson (1987) demonstrated a similar temporal effect, but found a rhodopsin action spectrum for the background influence.

On the basis of a variety of psychophysical and neurophysiological sources mentioned in the Introduction, I suspect that the enhancement of visual acuity during early dark adaptation is governed by a mechanism involving rapid changes in retinal receptive fields.

It has been suggested that short term light (Teller et. al., 1966) and dark adaptation (Rinalducci, 1968) produce marked changes in the spatial neural organization of the retina. Several neurophysiological studies (Burkhardt, 1974; Enroth-Cugell & Shapley, 1973; Barlow, Fitzhugh & Kuffler, 1957) have demonstrated such changes to occur in the center-surround mechanisms of retinal neurons, from photoreceptors to ganglion cells, with light and dark adaptation. In a study of short term light adaptation, Copenhagen (1974) reported that only on-off ganglion cells showed a transient elevation of threshold when adapted with decentered flashed backgrounds. It has been suggested (Copenhagen, 1974) that primarily amacrine cells, conducting signals laterally across the retina, contribute to the transient threshold elevation in the on-off ganglion cells.

I suspect that the changes in the on-off ganglion cell receptive field during early dark adaptation may be of particular relevance to the results of the present study. At least two events are possible. First, the enhancement of visual acuity may be due to increased sensitivity of on-off ganglion cells with small excitatory centers (X cells) at high photopic levels of illumination; while, at lower illuminance levels the sensitivity of these cells may be equal to that of cells with larger receptive field centers (Q cells). Recent evidence seems to support this interpretation (Enroth-Cugell & Shapley, 1973). Second, the surround signal concerning the photic stimulation produced by the adapting flash may be delayed relative to the central signal by a few hundred milliseconds. As such, the surround may signal for a brief moment a higher state of light adaptation, i.e., a condition for improved visual acuity.

The difference in time course for TGI and TF threshold during early dark adaptation is not self explanatory on the basis of the present data. Although, TF threshold has been found to be a photoreceptor property (Kleinschmidt & Dowling, 1975), TF threshold during rapid dark adaptation is widely believed to be determined by post-receptor factors (Baker, 1953, 1963; Graham, 1963; Geisler, 1983). Clearly, both TGI and TF threshold represent under these condition post- receptor activity, e.g., rapid changes in receptive field organization at the level of horizontal, bipolar, amacrine and ganglion cells. The source for the observed difference in time course may lay in the differing way in which light is distributed within the borders of the stimuli and therefore the types of cells mediating these stimuli. TGI may represent the activity of ganglion cells with small receptive fields and, hence, reduced spatial summation; whereas TF threshold may represent more sluggish responding ganglion cells with larger receptive field centers.

Clearly, it is impossible to identify the underlying mechanism of the transient acuity enhancement during rapid dark adaptation on the basis of the data collected in the present study. The use of different types of research in the future may elucidate the mechanism(s) governing this effect. First, more parametrical data involving luminance, wavelength and spatial frequency need to be collected with psychophysical means in the normal eye. Second, if indeed this effect pertains to the inner retina, it should be possible to study this phenomenon by means of ERG in the same human subject investigated behaviorally and in ophthalmological patients. Finally, ERG-studies and intracellular investigations in lower animals may conclusively identify the locus and role, respectively, of the retinal neurons involved in the transient enhancement of spatial acuity during early dark adaptation.

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