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**The effects of visual adaptation upon spatial and temporal  
resolution**

**Lange, Gudrun, Ph.D.**

**City University of New York, 1994**

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THE EFFECTS OF VISUAL ADAPTATION UPON  
SPATIAL AND TEMPORAL RESOLUTION

by

GUDRUN LANGE

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

1994

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## Abstract

THE EFFECTS OF VISUAL ADAPTATION UPON  
SPATIAL AND TEMPORAL RESOLUTION

by

Gudrun Lange

Adviser: Professor Thomas E. Frumkes

Light adapting rods increase cone-mediated visibility of either rapid flicker (Flicker effect) or fine spatial gratings (Grating effect). This study determined whether these effects reflect the action of one or several. Monocular and interocular contrast sensitivities of normal observers were measured using test gratings modulated sinusoidally in both temporal and spatial domains. In general, a  $1^\circ \times 1^\circ$  sided test display of  $10 \text{ cd/m}^2$  average luminance presented to the same eye as a  $20.8^\circ \times 15^\circ$ ,  $0.03 \text{ cd/m}^2$  adapting field. However, the influences of size, shape, luminance, and retinal position of both test and background field as well as monocular versus interocular viewing were examined.

Rod-stimulating adapting fields enhanced sensitivity to low spatial frequencies ( $< 2 \text{ cpd}$ ) flickered rapidly ( $> 12 \text{ hz}$ ) and to high spatial frequencies ( $> 12 \text{ cpd}$ ) flickered

slowly ( $< 2$  hz), but exerted negligible influence upon intermediate spatial and temporal frequency combinations (4-8 hz and 4-8 cpd). Although both effects can involve rod-cone interaction, the Grating effect can additionally reflect rod-rod interaction while the Flicker effect can involve cone-cone interaction. Both effects decreased as test display size increased and increased with parafoveal displacement; the gradient of these influences is much steeper for the Flicker than the Grating effect. Monocular and interocular adaptation produce near-identical influences upon grating visibility, while interocular backgrounds have an insignificant influence upon flicker visibility. Collectively, these findings indicate that Grating and Flicker effects are mediated by different mechanisms.

The influence of adaptation upon visibility of different sized gratings was more intensively studied to indicate practical significance. The present results show that the influence of display size upon visibility of high spatial frequency gratings reflects a "global" influence of light-adaptation rather than any effect of display size per se.

## Acknowledgements

This dissertation is dedicated to the memory of my father, Werner Ettwig, who died at the age of 49 years from a brain tumor.

I gratefully acknowledge the support and encouragement of my family, my husband Heinrich and my sons Christian and Andreas, which enabled me to start and finish this thesis. I thank Patty C. and particularly John Zhu, without whose help this project would have taken even longer. The members of my dissertation committee, Drs. Richard Bodnar, Robert Lanson, Joy Hirsch and Franklin Naarendorp, provided many valuable suggestions and I much appreciated their assistance. I especially express my gratitude to my mentor, Dr. Thomas E. Frumkes, for his advice, constructive criticism and the many hours spent revising this dissertation. Through years of collaboration, I gained a valued friend.

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## Chapter 1

### Introduction

Visual adaptation is the change in visual processing resulting from exposure to darkness (dark adaptation) or light (light adaptation). Traditionally, visual psychophysicists studied the influence of adaptation upon the threshold of a small, brief "test flash" of light which was presented intermittently to a specified region of the retina. The resulting test flash threshold was considered to be an index of the visual system's overall sensitivity.

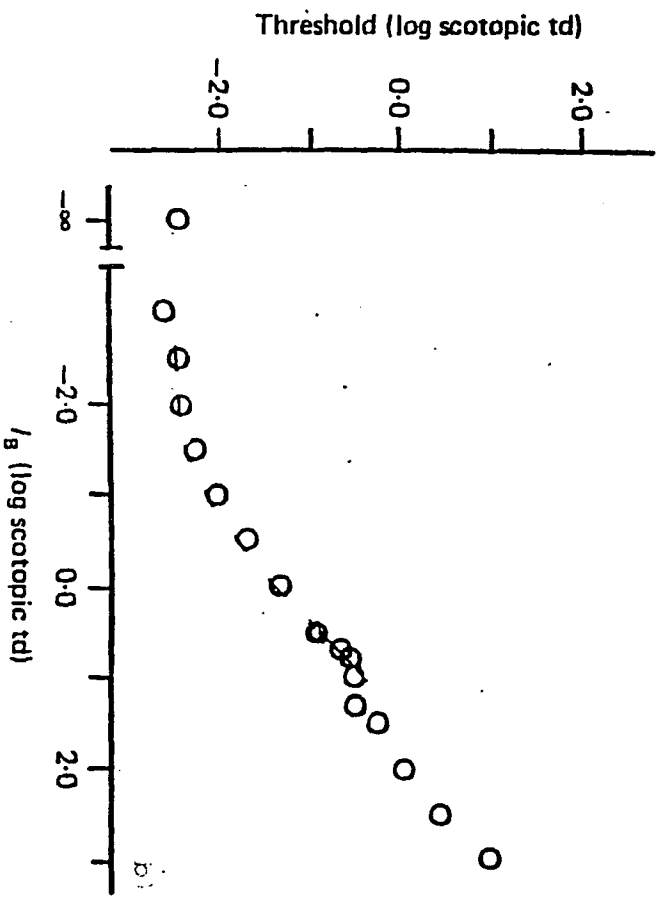
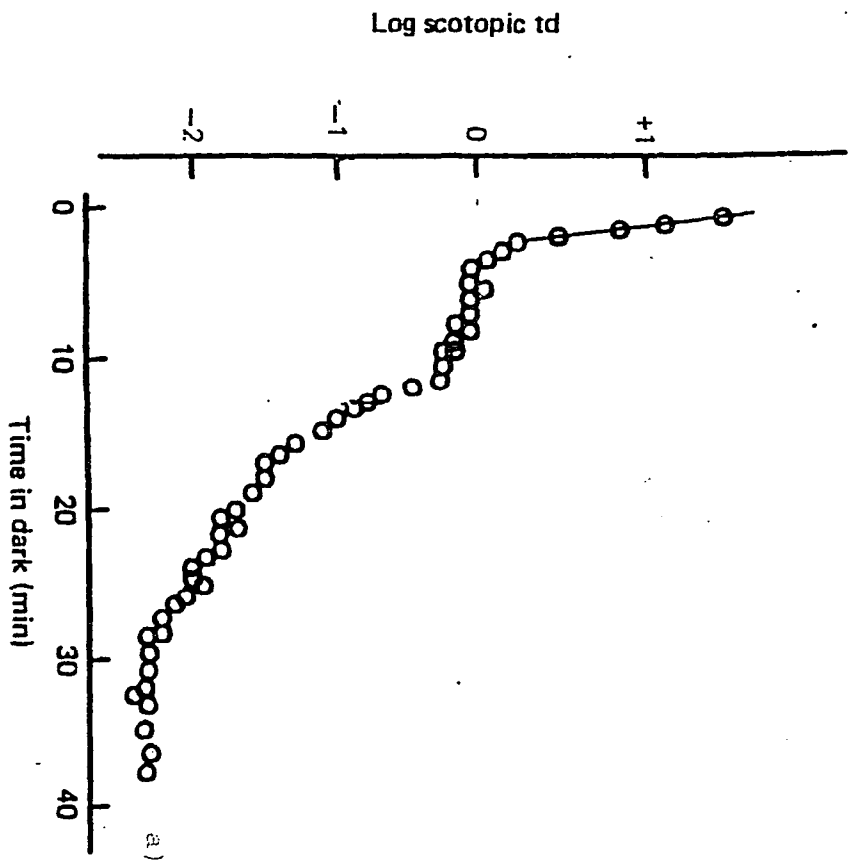
Using this detection threshold approach, psychophysicists were able to uncover a number of key features about visual adaptation. For example, in the late 19th and early 20th centuries, Aubert (1865), Piper (1911), and Kohlrausch (1922) studied dark-adaptation measuring the threshold of a test flash throughout the time course following exposure to a photopigment bleaching light source (e.g., see Hecht, 1937; Frumkes, 1990). As shown in figure 1a, threshold to a test flash presented to the periphery of the retina approaches asymptotic levels after about 30 minutes in the dark: the upper, more rapid limb of this curve was related to the function of cones, while the lower, slower limb represents rod function. More recent research showed that for either rods or cones, the logarithm of this threshold measure is directly proportional to the amount of bleached photopigment (Rushton, 1963).

Figure 1a

Classical dark adaptation curve derived from Bauer, Frumkes, and Holstein (1983). The threshold of a 500 ms duration, 512 nm wavelength, 40' diameter test flash was determined as a function of time in the dark following exposure to a photopigment bleaching light source. The stimulus was presented 7° from the fovea. The upper, more rapid limb of the curve is related to the function of cones, while the lower, slower portion represents rod function.

Figure 1b

Classical light adaptation curve derived from data by Bauer et al. (1983). The threshold of a 500 ms duration, 512 nm wavelength, 40' diameter test flash was determined as a function of background illuminance of 480 nm. The stimulus was presented 7° from the fovea. The lower limb of this function is attributable to rod activity, while the upper portion corresponds to the function of cones.



As an alternative to this dark-adaptation or "bleaching adaptation" procedure, psychophysicists also used "light-adaptation" or "field-adaptation" techniques in which test threshold is measured as a function of the luminance of a larger steady background field (e.g., Crawford, 1947). As shown in figure 1b, a typical plot of test threshold as a function of retinal illuminance also produces a two-limbed adaptation curve with the lower limb attributable to rod function and the upper limb to the function of cones. Modifications of these classical light- and dark-adaptation techniques led to a distinction between photochemical and neural processes underlying visual adaptation (Adelson, 1982; Barlow & Andrews, 1973; Crawford, 1947; Baker, 1963; Geisler, 1978; MacLeod, Williams, & Makous, 1985; Rushton & Westheimer, 1962). However, the neural processes involved in visual adaptation are more commonly studied by non-behavioral measures (for review, see Leibovic, 1990; Shapley & Enroth-Cugell, 1984; Walraven, Enroth-Cugell, Hood, MacLeod, & Schnapf, 1990).

In the "real world" visual adaptation is not restricted to changes in detection thresholds of a strictly controlled stimulus, but usually involves appreciation of color as well as spatial and temporal detail. Moreover, most modern views assume that the visual system is mediated by a number of channels working either cooperatively or in parallel. Hence, there is no reason for believing that color, space, and time perception relate in a unitary, orthogonal fashion to detection threshold. Nevertheless, the vast majority of psychophysical adaptation studies continues to exclusively examine the influence of visual adaptation upon detection threshold.

The present study investigates the influence of visual adaptation upon the visibility of fine temporal and spatial detail. In particular, it considers the influence of the adapted state of rods distributed over a large retinal area upon the sensitivity of cone-vision restricted to a small region of the retina. In these experiments, the cone-detected test stimulus is a display which is modulated concomitantly in both the spatial and temporal domains. The following overview first considers traditional and more recent measures of temporal and spatial sensitivity, and then reviews the literature concerning the influence of visual adaptation upon temporal and spatial resolution. The last portion of this chapter presents the rationale for the experimental research comprising this dissertation.

### Measurement of Temporal Sensitivity

Temporal resolution of the visual system was traditionally assessed by the critical flicker fusion or CFF paradigm. In CFF experiments, the observer increased the frequency of a flickering light source until flicker could no longer be detected, i.e., to achieve the critical flicker frequency. Many "laws" described the relationships between the influence of different stimulus parameters upon CFF including the influence of stimulus luminance (Ferry-Porter law), light/dark ratio in the flicker train (Ives law), and stimulus size (Granit-Harper law). Although more difficult to describe, CFF also relates to stimulus wavelength and retinal position (for references to the CFF literature, see Landis, 1954; Piéron, 1965). Although useful, CFF has two serious limitations as an

index of temporal sensitivity. First and of greatest importance to this thesis, it now seems likely that vision is mediated by a number of parallel information channels that respond preferentially to separate ranges of flicker frequencies, and that these separate channels are differentially influenced by varying a particular stimulus parameter (Nygaard & Frumkes, 1985; Livingston & Hubel, 1987; Smith, 1970; Tyler, 1975). However, CFF only provides information relating to the fastest flicker following capacity of the subject for a given stimulus condition, which is probably associated with the activity of the fastest channel.

A second limitation of the traditional CFF paradigm is that flicker was commonly modulated as rectangular or square waves. Since flicker frequency, duration of the light pulse, and the light-to-dark-time ratio of the waveform are interdependent variables, one variable cannot be varied without also altering one of the other two variables. If flicker frequency was varied and the light-to-dark-time ratio (the duty cycle) was fixed, the duration of the light being on per cycle would vary; if the duration of the light was fixed in each cycle, the duty cycle would vary. Changes in duration of the light pulse or duty cycle are accompanied by a change in the average luminance of the stimulus and an associated change in the level of adaptation of the eye. Moreover, discrepancies in results were reported when nonsquare waveforms were employed, such as triangular or sine waves (Lukiesh, 1914). To overcome these limitations, deLange (1954; 1958) suggested the use of the modulation threshold measure of flicker sensitivity. As first suggested by Ives (1922), the visual system has many characteristics which resemble a

linear system. For such a system, the amplitude, phase, and frequency of any regularly repeated temporal waveform can be described in terms of fundamental sinusoidal components which has been stated as Fourier's theorem. This analysis provides a technique by which results obtained with sinewave flicker can accurately predict results with any other stimulus waveform. Subsequently, Kelly (1961) established the use of this paradigm to assess flicker sensitivity with sinusoidally modulated stimuli at any temporal frequency.

In modulation threshold studies, a subject is presented with a stimulus of a fixed average illuminance which is usually sinusoidally modulated over time at a predetermined frequency. The observer is instructed to adjust the modulation amplitude until flicker can just be perceived. This procedure is repeated with many different flicker frequencies to obtain a characteristic function. In general, sensitivity (the reciprocal of threshold) is plotted as a function of flicker frequency on log-log coordinates so that data resemble the Bode plot used to characterize a linear system.

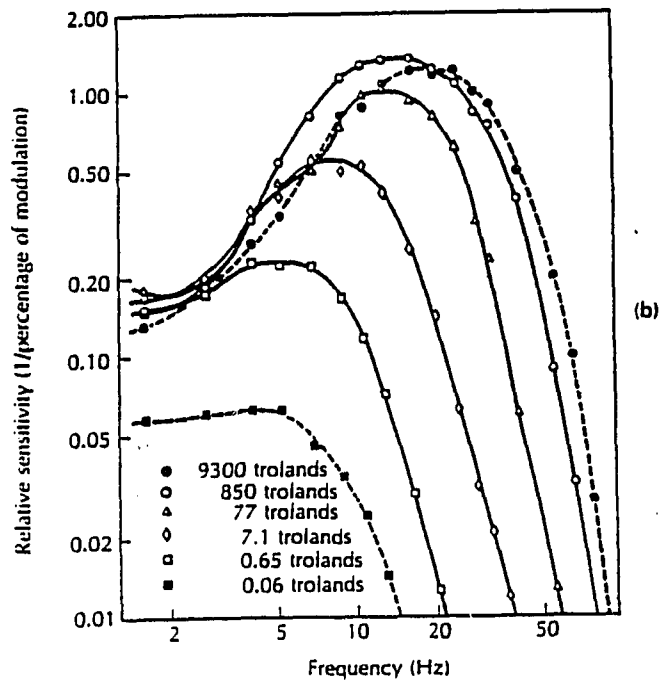
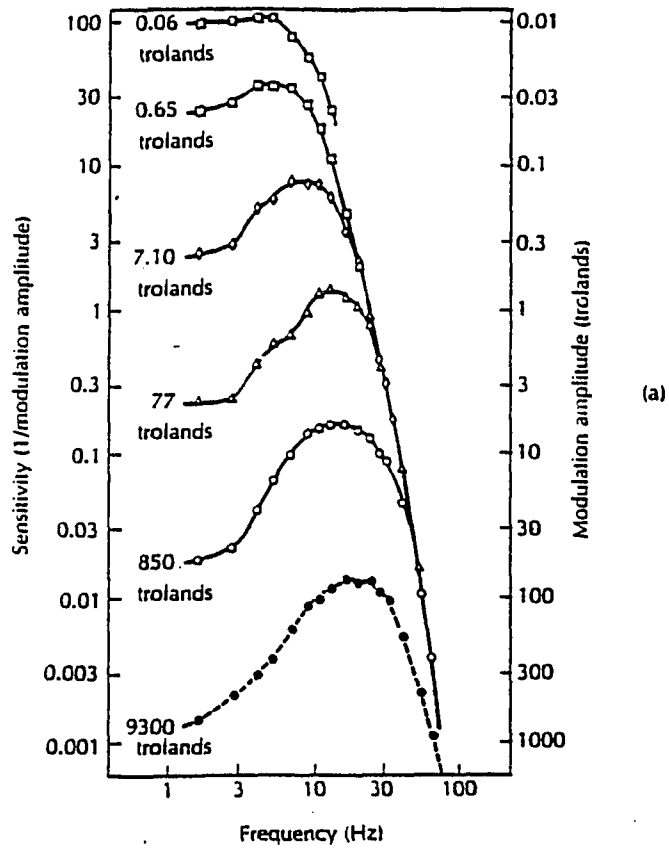
Figure 2 illustrates data of Kelly (1961) obtained using many different average luminance stimuli, and plotted in two different fashions. The upper coordinates plot the absolute sensitivity to the amplitude modulation of the stimulus as a function of temporal frequency. Data for the lowest luminance are at the top, representing highest absolute sensitivity, curves for successively higher luminance levels are displaced downward. Flicker sensitivity is maximal between about 10 and 30 hz and falls off at both higher

Figure 2a

Modulation threshold function derived from Kelly (1961). The absolute sensitivity to the amplitude modulation of a uniformly illuminated 60° disk was measured as a function of temporal frequency (hz) on log-log coordinates. The stimulus was presented to the fovea. The separate curves are for different average levels of intensity (log photopic trolands). Intensity was varied sinusoidally at some particular frequency. Throughout the measurement the average level of illuminance was held constant.

Figure 2b

Same data as above (Kelly, 1961) are plotted in a different fashion to illustrate the non-linear (Weber's law) and linear components of the modulation threshold functions. Here, relative sensitivity (the inverse of percent modulation threshold) is plotted as a function of temporal frequency on log-log coordinates.



and lower frequencies. Except for the only scotopic (0.06 td) illuminance level used, all curves fall on one downward line at the high temporal frequencies, so it seems that sensitivity for fast flicker is independent of the average luminance of the eye and depends solely on the modulation amplitude of the stimulus, a characteristic consistent with the operation of a linear system. However, the visual system acts non-linearly at lower frequencies, since functions obtained with the different average luminance stimuli do not correspond. In the lower set of coordinates in figure 2, relative sensitivity (the inverse of percent modulation threshold) is plotted as a function of temporal frequency. Here, save for the data obtained with the only scotopic (0.06 td) illuminance level used, the low frequency (1-4 hz) end of each curve describes a common function which is consistent with Weber's law.

Kelly used these data to describe a number of general properties of the visual system. In general, the photopic visual system acts according to Weber's law for low frequencies and as a linear system for higher frequencies. However, these data were also used to derive a number of above-mentioned square-wave/CFF laws of flicker, as well as to predict the influence of flicker frequency on apparent brightness (Bartley-Brücke enhancement effect) and the effects of stimulus duration on threshold (Bloch's law). Thus, sensitivity to flicker can be assessed separately as a function of virtually any independent variable. In addition, the modulation threshold paradigm has more recently been used to investigate the differential influence of neurological as well as ophthalmological disorders on high and low flicker frequencies (Alexander, Fishman, &

Derlacki, 1988; Arden & Hogg, 1985; Bodis-Wollner, Marx, Mitra, Bobak, Mylin, & Yahr, 1987; Lovegrove, Martin, & Slaghuis, 1986; Martin & Lovegrove, 1987; Smith, Early, & Grogan, 1986; Reeves, 1980), suggesting that temporal resolution may be mediated by more than one temporal frequency channel.

#### Measurement of spatial sensitivity

Traditionally, the spatial resolving power of the visual system has been characterized by the term "visual acuity," i.e., the finest spatial detail that can be resolved. Commonly used experimental measures of visual acuity include the Snellen chart (Snellen, 1862) or the Landolt ring (Landolt, 1889).

Visual acuity measures in the spatial domain are analogous to CFF in the temporal domain. Although visual acuity provides useful information about the visual system's capability to resolve fine detail (high spatial frequencies), no information about sensitivity to intermediate or low spatial frequencies is gained. If vision is processed by separate channels with different spatial resolving power, as is generally assumed by many modern visual scientists (Graham, 1980, 1989; Livingston & Hubel, 1987; Merigan & Maunsell, 1993; Sachs, Nachmias & Robson, 1971; Schiller, 1991; Tolhurst, 1973), such acuity measures only provide limited information. In fact, different neurological diseases have been shown to differentially influence sensitivity to high versus low spatial frequencies (Alexander, Derlacki, Fishman, & Peachey, 1991; Bodis-Wollner et al., 1987;

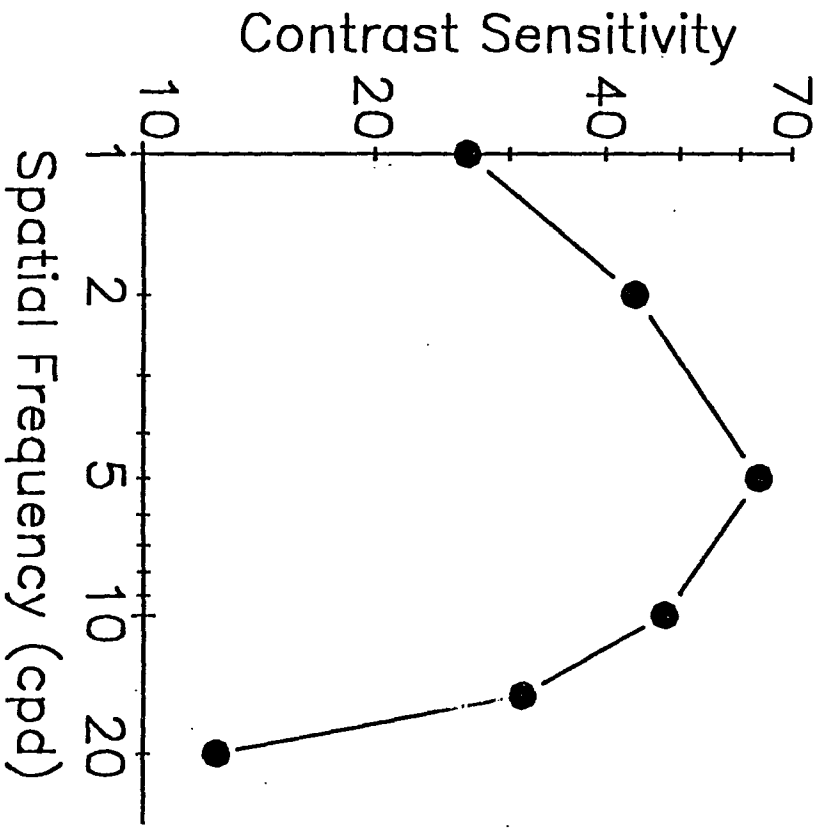
Lovegrove et al., 1986).

In a fashion comparable to that used by Ives (1922) and deLange (1954) to study temporal resolution, spatial resolution has more recently been studied using contrast sensitivity measures. Campbell and Robson (1968) were the first to measure spatial sensitivity of the human visual system using sine wave gratings to obtain a contrast sensitivity function (CSF). To measure CSF, the observer is presented with a grating of fixed average luminance modulated sinusoidally in one spatial dimension and asked to adjust contrast until the visibility threshold is reached. This procedure is repeated for a number of spatial frequencies. As shown in figure 3, contrast sensitivity (the inverse of percent modulation at threshold) is plotted as a function of spatial frequency on log-log coordinates. The illustrated inverted U-shaped function is typical of data obtained with a grating of fixed average luminance; the CSF shows peak sensitivity for some intermediate spatial frequency [typically between 3 - 6 cycles per degree (cpd)] and declines at both higher and lower frequencies.

Since the pioneering effort of Campbell and Robson (1968), many studies have established influences of a variety of stimulus variables upon CSF. In general, overall sensitivity increases as a function of stimulus luminance particularly at higher spatial frequencies (Banks, Geisler, & Bennett, 1987; Kelly, 1977; Van Nes & Bouman, 1967). Also, overall spatial sensitivity increases as the display size increases particularly for lower spatial frequencies (Pantle & Sekuler, 1968; Virsu & Rovamo, 1979). As was

Figure 3

Contrast sensitivity (the inverse of percent modulation at threshold) of a sinusoidally modulated  $3.2^\circ \times 2.4^\circ$  grating is plotted as a function of spatial frequency on log-log coordinates. The stimulus was presented to the fovea. This typical contrast sensitivity function shows peak sensitivity for intermediate spatial frequencies and declines at both higher and lower frequencies (Denny, Frumkes, Barris, & Eysteinnsson, 1991).



predictable from earlier acuity studies (Jones & Higgins, 1947), sensitivity to higher spatial frequencies decreases with the extent of parafoveal displacement (Perry & Cowey, 1985; Rovamo, Virsu & Naesaenen, 1978).

In the early 1960's, Kelly and other investigators (Kelly, 1960, Robson, 1966) began to modulate visual displays concomitantly in temporal and spatial domains. These stimuli consist of horizontally or vertically oriented sinewave gratings with alternating bright and dark bars modulated sinusoidally. More recently, psychophysicists (e.g., Livingston & Hubel, 1987) have utilized this method of investigation to correlate anatomical (e.g., Livingston & Hubel, 1987) and physiological findings (e.g., Derrington & Lennie, 1984) suggesting the existence of at least two distinct visual processing channels such as the magnocellular (transient) and parvocellular (sustained) pathways. These visual pathways not only differ in their response characteristics to stimuli modulated in time and space, but also to their color and contrast attributes (for review, see Lennie, Trevarthen, Van Essen, & Wässle, 1990).

#### The Influence of Visual Adaptation upon Resolution of Spatial and Temporal Detail

In typical spatial or temporal contrast sensitivity experiments, the test display is the only stimulus presented to the observer. The average luminance of this stimulus is fixed by the experimenter and defines the state of visual adaptation. But in "real life" viewing situations, exposure to many different sources of illumination, which vary over

time and space, determine the observer's state of adaptation. Indeed, these "uncontrolled" stimuli may have a much larger influence upon the state of adaptation than the average luminance of an experimentally controlled stimulus. In fact, even early CFF studies showed that surrounding annular fields (Fry & Bartley, 1936; Hecht, Shlaer, & Verrijp, 1933) influence sensitivity to a flickering test spot. In addition, more recent studies show that dim, surrounding annular fields (Naarendorp, Denny, and Frumkes, 1988) increase spatial sensitivity, particularly to higher spatial frequencies. Finally, recent studies show that the adapted state of one eye (as determined by either photopigment bleaching or by steady adapting fields) greatly influences sensitivity to sinewave gratings presented to the contralateral field (Denny et al., 1991; Eysteinson, Barris, Denny, & Frumkes, 1993).

The following section separately considers the concomitant influence of adaptation upon temporal and spatial resolution.

### 1. Temporal Resolution

Following the early work by Lythgow and Tansley (1929), the influence of visual adaptation upon flicker sensitivity was further studied parametrically in the early 1980's in three independent investigations in the fovea as well as parafovea (Goldberg, Frumkes, & Nygaard, 1983; Alexander & Fishman, 1984; Coletta & Adams, 1984). In all three studies, the observer adjusted the illuminance of an intermittent test probe until flicker

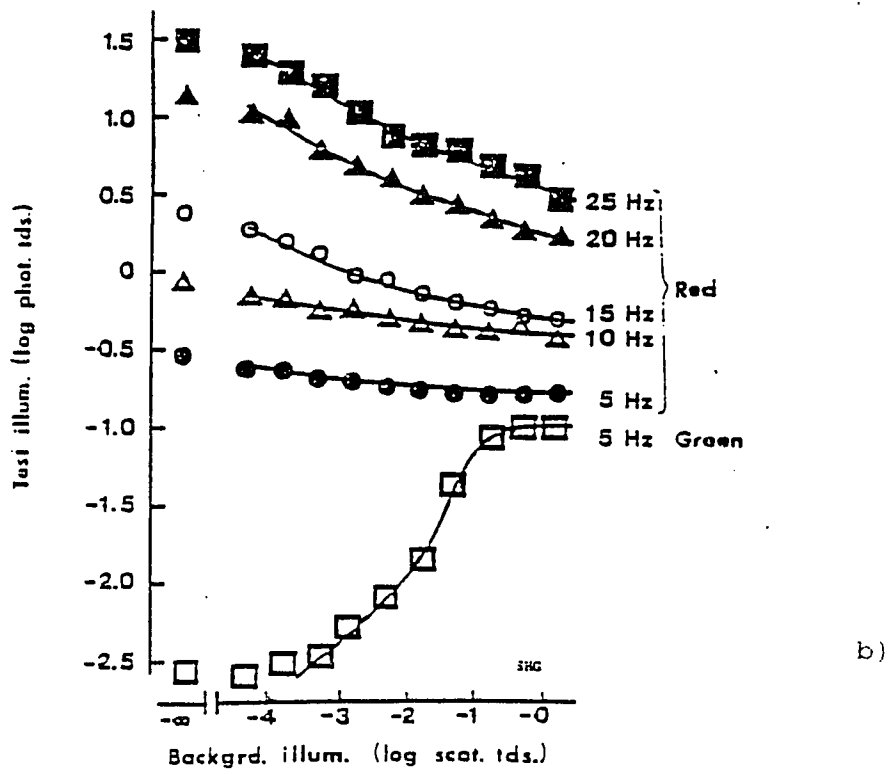
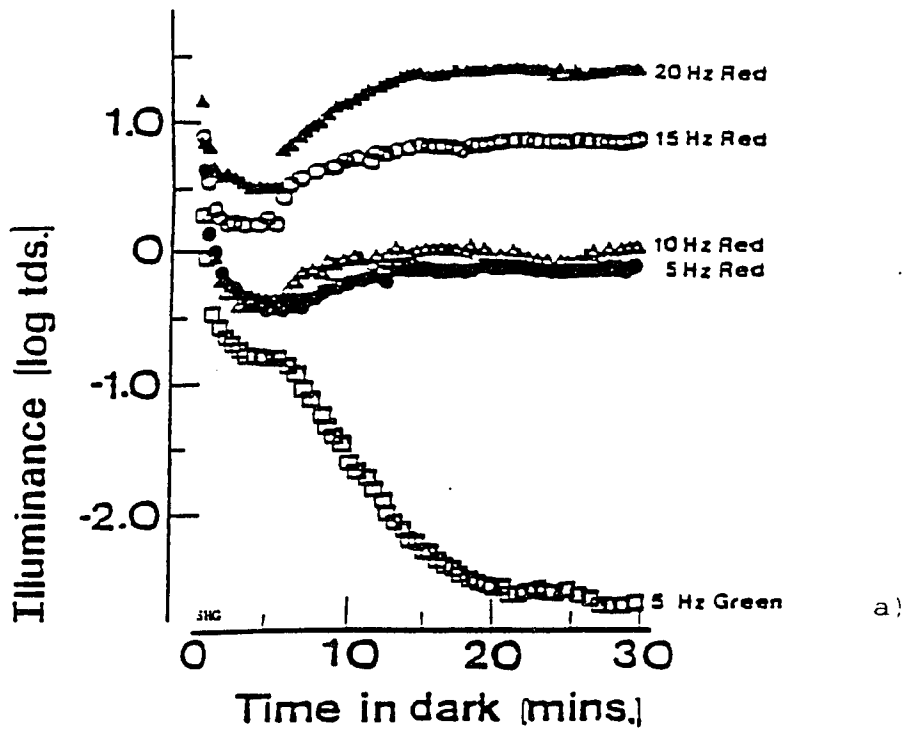
could just be detected, rather than using contrast sensitivity or CFF measures. Illustrative data are shown in figure 4, in which the illuminance threshold for flicker detection is plotted along the ordinate as a function of either time in the dark (part A) or the illuminance of a steady, large, dim, background field (part B). Since threshold (rather than sensitivity) is plotted, an upward shift along the ordinate indicates an increase in sensitivity. The open squares represent data obtained with a 560 nm, 5 hz flicker probe which, depending upon illuminance, could either be detected by rods or cones. As shown in part A, flicker sensitivity increases for this probe as a two-limbed curve which is very similar to the conventional dark-adaptation curve shown in figure 1A. Similarly, part B shows that sensitivity to this probe decreases as a dim background field increases in illuminance in a fashion similar to the light-adaptation function shown in figure 1b. An upper, "cone-limb" of this function would be observed if background illuminance had increased to higher levels than illustrated. The other curves in figure 4 were obtained with red-probes which had a greater influence upon cone- than rod-mediated flicker (for detailed discussion, see Frumkes, Naarendorp, & Goldberg, 1986; Denny, Frumkes, & Goldberg, 1990). During the rod-recovery stage of adaptation in figure 4a, as rods become dark-adapted, cone sensitivity to flicker decreases monotonically. The magnitude of the effect is small for a low frequency stimulus, but increases to almost a 1  $\log_{10}$  unit with the highest flicker frequency illustrated, 20 hz. In a similar fashion, Figure 4b shows that cone-mediated sensitivity to flicker increases as rods are selectively light adapted. Since analogous findings can be obtained with either CFF (Lythgoe & Tansley, 1929) or contrast sensitivity measures (Denny et. al.,

Figure 4a

This dark adaptation plot was derived from data by Goldberg et al. (1983) and shows the influence of rod adaptation on cone-mediated flicker sensitivity. The illuminance threshold for a 2° 20' diameter flickering test stimulus is plotted as a function of time in the dark. The stimulus was presented 7° from the fovea. Since threshold rather than sensitivity is plotted, an upward shift along the ordinate indicates an increase in sensitivity. The open squares represent data obtained with a 560 nm, 5 Hertz (hz) flicker probe, which depending upon level of adaptation can be detected by either cones or rods. The other curves in this figure were obtained with long wavelength stimuli, exclusively stimulating cone photoreceptors.

Figure 4b

Results are plotted in the same conventions as for figure 4a. However, here sensitivity to a flicker stimulus is plotted as a function of background illuminance. The stimulus was presented 7° from the fovea. The open squares represent data obtained with a 560 nm, 5 (hz) flicker probe, which depending upon level of adaptation can be detected by either cones or rods. The other curves in this figure were obtained with long wavelength stimuli, exclusively stimulating cone photoreceptors.



1990), these findings do not depend upon the specific index of flicker sensitivity used. Moreover, Goldberg et al. (1983) performed a large number of control experiments to ascertain that this phenomenon must be due to a tonic, suppressive influence of dark-adapted rods upon cones. More recently, an analogous influence of cone-adaptation upon rod flicker (Frumkes, Naarendorp, & Goldberg, 1986) and cone-adaptation upon cone-flicker (Coletta & Adams, 1984; Eisner, 1989) has been shown. Although possible, no analogous rod-rod effect has yet been observed.

A number of electrophysiological studies have intensively studied the influence of rod-adaptation upon cone-mediated flicker sensitivity involving ERG procedures in humans (Arden & Frumkes, 1986) and intracellular recordings in amphibians (Frumkes & Eysteinson, 1988) and cats (Pflug, Nelson, & Ahnelt, 1990). These studies clearly show that this phenomenon involves a tonic, suppressive influence of dark-adapted rods upon cones and hence, is referred to as suppressive rod-cone interaction (SRCI). SRCI can be detected in intracellular recordings of all types of distal retinal neurons including the cones themselves. Moreover, the spatial limitations of SRCI, as documented by intracellular recordings, resemble the spatial limitations of SRCI observed by psychophysical procedures, and quantitatively compare to the electrical coupling properties of horizontal cells (HC's). Finally, pharmacological treatments which eliminate the rod-mediated response of HC's eliminate SRCI in all distal retinal neurons, while drug treatments which eliminate the response of amacrine and ganglion cells fail to influence SRCI in distal retina (Eysteinson & Frumkes, 1989; Nelson, Frumkes,

Eysteinnsson, & Pflug, 1993; Eysteinnsson, Barris, Denny, & Frumkes, 1993). Collectively, these results indicate that SRCI reflects a distal retinal mechanism. Most probably, horizontal cells in the outer plexiform layer mediate an inhibitory influence of rods upon cone pathways.

## 2. Spatial Vision

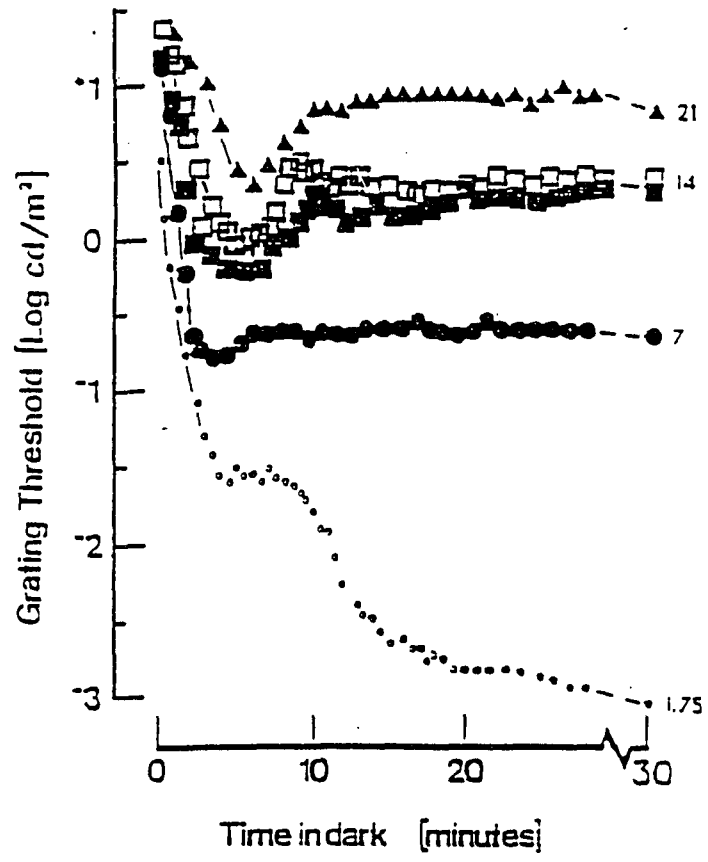
In a fashion analogous to that described above for flicker sensitivity, Naarendorp, Denny, and Frumkes (1988) studied the influence of long-term dark adaptation upon sensitivity to spatial frequency gratings. In figure 5, the luminance of a square-wave test grating whose orientation could just be detected is plotted as a function of time in the dark (part A) or as a function of the luminance of a large background field (part B). Once again, for a green, 1.75 cycle per degree (cpd) stimulus which could be detected by rods or cones, sensitivity increased throughout the entire period of dark adaptation or decreased as background luminance increased. However, for gratings  $\geq 3.5$  cpd, sensitivity decreased throughout the rod recovery stage of adaptation or increased as rods became increasingly more light adapted. Once again, this is a small effect with a 3.5 cpd grating but increases to a  $> 1 \log_{10}$  unit effect with the highest spatial frequency used (21 cpd). All findings seem to involve rod-cone interaction, since a large number of control experiments established that light-adapted rods adjacent to the stimulus area increased cone-mediated grating acuity. However, the possibility of a cone-cone or cone-rod effect has not been studied. More recently, the influence of rod-adaptation upon cone-mediated

### Figure 5a

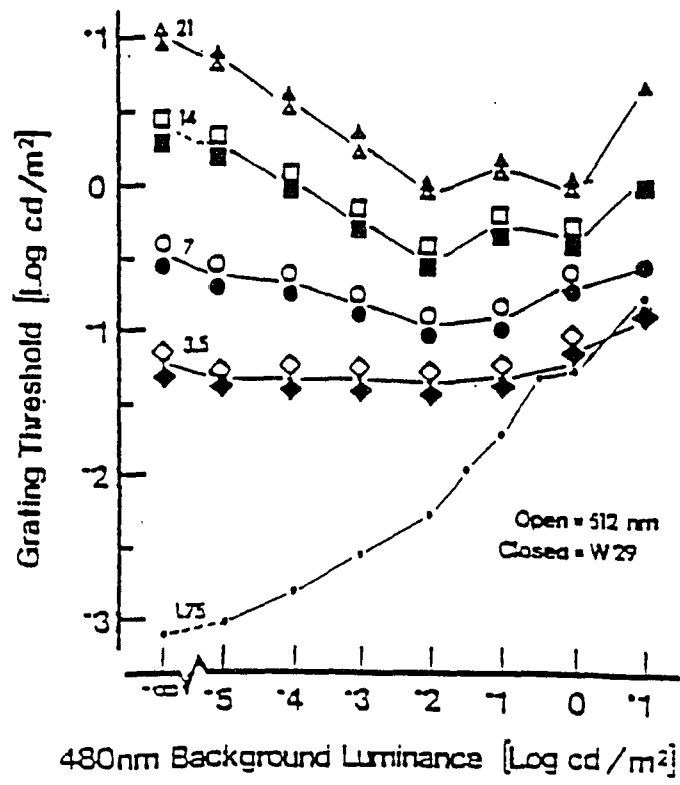
This dark adaptation plot was derived from data by Naarendorp et al. (1988) and shows the influence of rod adaptation on cone-mediated grating sensitivity. The luminance of a 6° diameter, 500 ms duration square-wave grating whose orientation could just be detected is plotted as a function of time in the dark. The stimulus was presented at 3° from the fovea. Since threshold rather than sensitivity is plotted, an upward shift along the ordinate indicates a decrease in sensitivity. The open circles represent data obtained with a 560 nm, 1.75 cycle per degree (cpd) grating, which depending upon the level of adaptation can be detected by either cones or rods. The other curves in this figure were obtained with long wavelength stimuli, exclusively stimulating cone photoreceptors.

### Figure 5b

Following the same conventions as in figure 5a. However, this time sensitivity to a grating stimulus is plotted as a function of the luminance of a 14° diameter continually exposed background field of 480 nm wavelength. The stimulus was presented 3° from the fovea. The dotted line represents data obtained with a 560 nm, 1.75 cpd grating probe, which depending upon level of adaptation can be detected by either cones or rods. The other curves in this figure were obtained with long wavelength stimuli, exclusively stimulating cone photoreceptors.



a)



b)

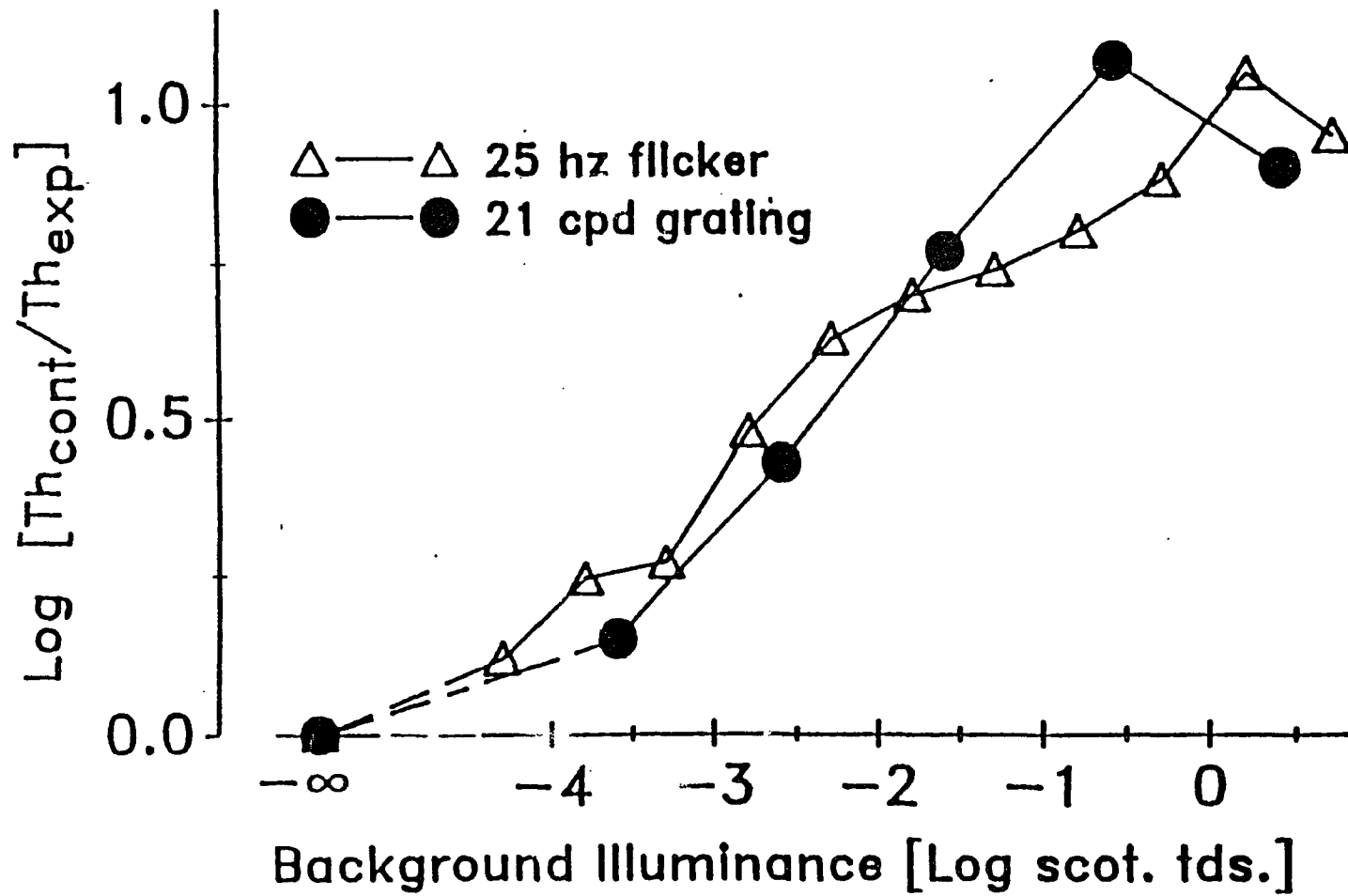
spatial sensitivity has been reliably replicated using contrast sensitivity measures (Denny, 1992), suggesting that results are independent of psychophysical method used. No published reports have examined whether there are analogous rod-rod, cone-cone, or cone-rod influences upon grating visibility.

3. Does the influence of rod-adaptation upon spatial and temporal vision involve the same or separate mechanisms?

There are a number of similarities between the influences of rod-adaptation upon temporal and spatial sensitivity, (e.g., data such as illustrated in figures 4 and 5). Both effects are dependent upon frequency; with an increase in spatial (up to 21 cpd) or temporal (up to 25 hz) frequency the effect increases to a circa 1  $\log_{10}$  unit effect. The dynamic range over which rod adaptation influences temporal as well as spatial sensitivity is also comparable, as shown in figure 6. The open triangles were derived from Goldberg et al. (1983), and the solid circles were derived from Naarendorp et al. (1988). Log change in threshold is plotted as a function of the illuminance of a large background field. Rod-light adaptation influences flicker as well as grating sensitivity over a 4  $\log_{10}$  unit range. Also, both functions produce maximal enhancement at the similar illuminance levels. In addition, several investigators (Coletta & Adams, 1985; Frumkes, 1990; Comerford, Thorn, & Malloy, 1993) compared SRCI in normal observers with that of protanopes, individuals missing the normal long-wavelength cone pigment. They reported that rod light adaptation effects on temporal as well as spatial cone-mediated

Figure 6

This derived plot compares rod adaptation on cone-mediated sensitivity to high frequency flicker (25 hz) as well as gratings (21 cpd). The open triangles are from Goldberg et al. (1983) and the solid circles from Naarendorp et al. (1988). Log change in threshold is plotted as a function of the illuminance of a large background field.



vision are absent.

The foregoing similarities suggest that the same underlying mechanism may account for the influence of rod adaptation upon temporal and spatial vision. However, no additional psychophysical or neurophysiological evidence has been provided to date to support this assumption. Therefore, the possibility remains that rod-adaptation upon cone-mediated temporal or spatial displays reflects separate mechanisms.

#### Rationale for the Present Study

The purpose of the present series of experiments was to discern whether long term visual adaptation influences temporal and spatial resolution by a common mechanism or separate mechanisms. In addition, so much as it is possible using behavioral procedures in normal human subjects, I wished to determine the type of mechanism likely to account for these adaptational influences.

The first series of experiments parametrically investigated the influence of rod-light adaptation upon visual displays modulated concurrently in both spatial and temporal domains. Since a number of similarities exists between these two experimental paradigms (Goldberg et al., Naarendorp et al., 1988), it has been previously suggested (Naarendorp et al., 1988; Naarendorp & Frumkes, 1991) that the same distal retinal mechanism may account for both effects. Results obtained show that rod-adaptation

influences the sensitivity of cone-vision to either high spatial frequency gratings flickered slowly or low spatial frequency gratings flickered rapidly, but little influence was exerted upon sensitivity to intermediate spatial-temporal frequency combinations.

Previous studies have established that specific stimulus manipulations can be used to investigate differences in neural visual pathways. The next set of experiments examined that stimulus variables such as retinal position, size, and shape of the test display and adapting field as well as variations in stimulus and background luminance differentially influenced spatial- and temporal-adaptation effects. However, this type of parametric manipulation provided few clues as to differences between the mechanism or mechanisms underlying spatial and temporal effects.

Denny and co-workers (Denny et al., 1991; Eysteinnsson et al., 1993) recently demonstrated that light-adapting one eye enhances grating visibility in the contralateral eye. However, much earlier studies showed that light adapting one eye slightly lowers CFF in the contralateral eye (Lipkin, 1962; Vernon, 1934). Therefore, in a third series of experiments, I presented flickering gratings monocularly and compared the influence of rod-light adaptation upon display visibility when adapting either the same or the contralateral eye. The results show that the effects of light adaptation upon grating visibility are quantitatively as well as qualitatively similar whether the viewing or non-viewing eye was adapted. In comparison, flicker sensitivity is only enhanced by monocular adaptation, and contralateral adaptation has a negligible influence upon

sensitivity to flicker. These findings strongly suggest that the influence of adaptation upon grating sensitivity must involve a neural mechanism which is proximal to the outer plexiform layer of the retina and at least in part, must involve post-retinal neural structures.

Finally, in the last set of experiments, I demonstrated the practical significance of rod-cone interaction in real-world situations, i.e., driving at night. I specifically investigated the influence of the interaction between the average luminance of a display (i.e., size per se) and the eye's long term state of visual adaptation upon the visibility of gratings. These results showed that adaptation exerts an influence upon cone mediated grating visibility which is independent of the mean luminance of the grating. They also showed that the increase in contrast sensitivity produced by increasing display size (i.e., increase in total luminous flux) is attributable to rod-adaptation. Therefore, sensitivity to spatial and temporal detail might be enhanced under nighttime driving conditions by light-adapting rods.

## Chapter 2

### Methods

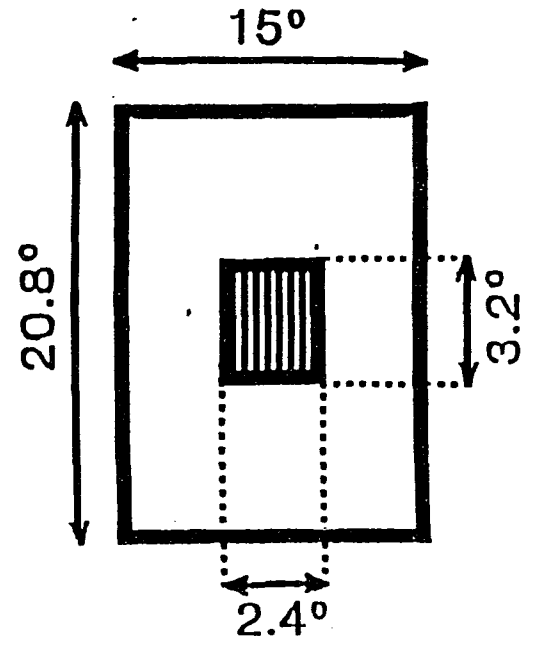
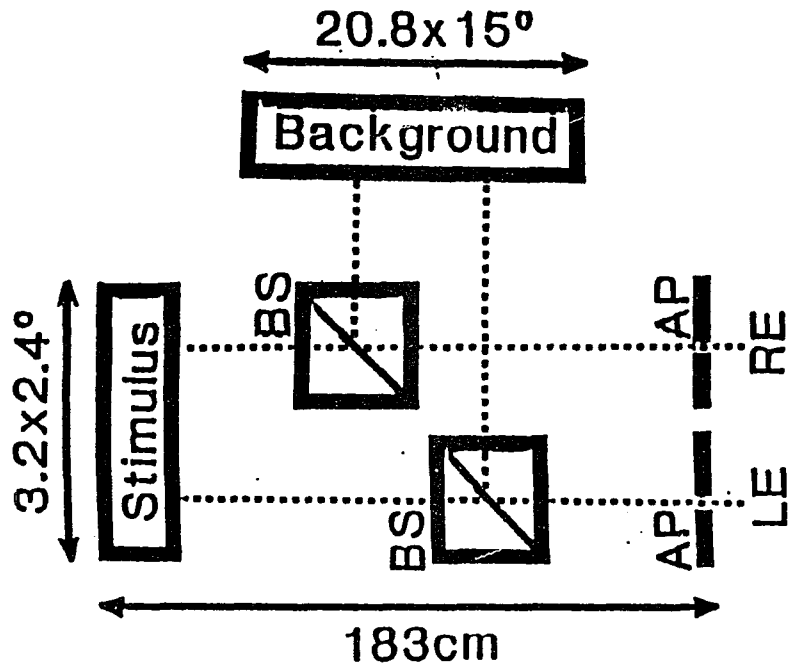
#### A. Apparatus

##### 1. General Description

All stimuli were presented by means of a two channel, binocular optical system which is schematically described in figure 7. The test stimulus, in most cases a flickering grating, was displayed on a "5 inch" (12.5 cm) Ikegami black and white monitor which presented a rectangular viewing surface that was 4 inches (10 cm) wide by 3 inches (7.5 cm) long, and was driven by a Vision-Metrics sine-wave grating generator described below. A fluorescent, photographic light box which was 26 x 18.75 inches (65 cm wide and 46.90 cm long) was used to produce an adapting stimulus. Both of these sources of illumination were placed in separate black, light-tight tunnels, each at an optical distance from the observer of 6 feet (1.87 meters). At this viewing distance, 1.25 inches is equivalent to  $1^\circ$  of arc, and the maximum stimulus size was  $3.2^\circ$  x  $2.4^\circ$  (for the test display) and  $20.8^\circ$  x  $15^\circ$  for the adapting field. This size test display is similar to that previously used in other contrast threshold experiments (i.e., Banks et al., 1987; Campbell & Green, 1965; Rovamo et al., 1978). The size of both stimuli could be reduced and their shape altered by placing opaque occluding material (black

Figure 7

Apparatus used to collect data in all experiments is seen at the top of the figure and has been described previously by Denny et al. (1991). Unless otherwise indicated, the test stimulus consisted mostly of a  $1^\circ \times 1^\circ$  square grating modulated concomitantly in the spatial and temporal domains. Gratings were oriented horizontally as shown in the bottom of the figure (gratings appear in diagram as square waves for representational purposes only). The background or adapting stimulus was a  $20.8^\circ \times 15^\circ$  diffuse field. Test and background stimuli were placed at an optical distance of 187 cm. The dotted lines in the top figure indicate the possible pathways along which the test and adapting stimuli could pass. Through the use of beamsplitters (BS) and appropriate placement of occluders, the stimulus could be presented to the left eye only. Stimuli were viewed through 2.5 mm artificial pupils (AP) unless otherwise indicated. The diagram does not indicate a large number of baffles and a septum placed to minimize stray light.



cardboard) in front of the illuminated surface of each source. When stimuli were presented parafoveally, a dim red light-emitting diode was positioned next to the monitor screen to serve as a fixation target.

Light from the two sources, monitor screen and photographic light box, was combined and superimposed through prism type beamsplitters. In the configuration illustrated in figure 7, the maximal average luminance provided by the grating generator was 10 cd/m<sup>2</sup>; the adapting field provided a maximal luminance of 100 cd/m<sup>2</sup>. The luminance of each stimulus was controlled by interposing neutral density filters between the stimulus and beamsplitter. Stray light was minimized with flat-black painted baffles constructed from wood and cardboard. Observers viewed the superimposed stimuli monocularly through a 2.5 mm artificial pupil for most experiments, unless otherwise indicated. These artificial pupils ruled out any role for pupillary dilatation in determining results and also minimized stray light. Retinal illuminance could be readily obtained from the formula proposed by Wyszecki & Stiles (1967, p. 212) in equation 1:

$$T = L \times p \quad (1)$$

,where T is the troland value of a field with photopic luminance L (cd/m<sup>2</sup>) seen through a pupil with an area p (mm<sup>2</sup>). Therefore, a test stimulus of 10 cd/m<sup>2</sup> viewed through a 2.5 mm artificial pupil is equivalent to 39 Tds.

The observer was seated in a variable height chair during experimentation. Head position was fixed by a full-mouth bite bar whose position was continuously adjustable in three planes by means of a modified milling machine head. The artificial pupil in front of each eye was also adjustable in three planes using modified Kopf Stereotaxic micromanipulators. In the case of monocular experiments, one of the artificial pupils was grossly displaced, hence serving as a mask occluding stimulation in the non-viewing eye.

The luminance provided by both stimuli was calibrated by placing a Minolta LS 100 luminance meter in the viewing position with no artificial pupil present.

## 2. Test Stimulus Grating Generator

The test display was obtained by means of a sinewave-grating generator designed and built by Y. Ozawa. In 1987, when the unit was purchased from Vision Metrics, then located in Berkeley, California, the company was entirely under the control of Dr. Ozawa. Vision Metrics has since been purchased by Neuroprobe Corporation, Farmingdale, Long Island, which now sells a considerably modified product.

The Vision Metrics grating generator was designed to provide horizontally oriented sinewave gratings by means of an XT-clone microprocessor equipped with a CGA graphics board. This package was used with minimal modification; all experiments

were achieved with a Fountain 8088 microprocessor and an Ikegami monochrome monitor. The software package provided by Vision Metrics includes a procedure for calibrating stimuli (the PGDEMO program) and for obtaining contrast sensitivity functions, such as illustrated in figure 4, using a staircase procedure (the PGCONSEN program). With this latter program, all data were automatically stored in Lotus format, and additionally, could be printed out in graphical and/or numerical form on a dot matrix printer.

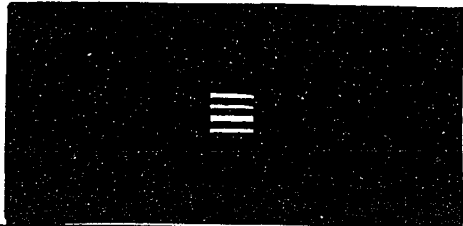
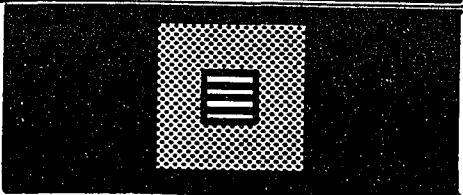
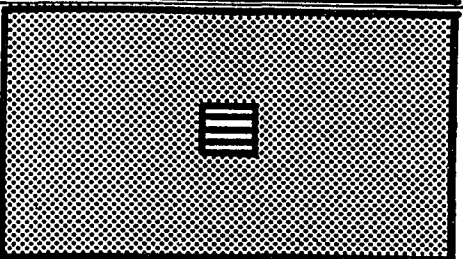
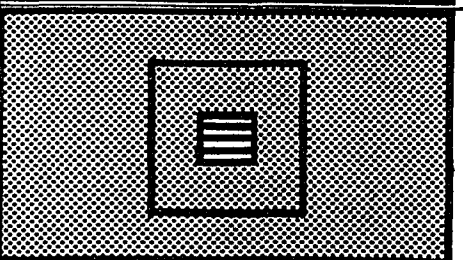
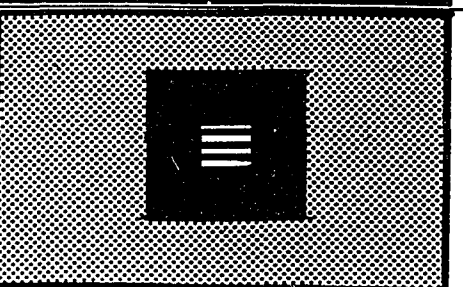
Although useful for demonstration purposes with naive subjects, the PGCONSEN program proved very time-consuming and introduced a number of problems (for details, see Denny, 1992). For this reason, most data were collected using modifications of the PGCONSEN program written by Mr. John Zhu and as described below. These alterations permitted automatic data collection with a forced-choice version of the method of adjustment.

### 3. Stimuli

In most experiments, the test stimulus was a  $1^\circ$  sided square and the adapting stimulus a  $20.8^\circ \times 15^\circ$  rectangle. However, other stimulus configurations were used as well, as shown in figure 8. With very few exceptions, which are noted below, all stimuli were concurrently modulated in both spatial and temporal domains as sinewaves. Hence, light and dark bars making up the grating were flickered in counterphase, with the spatial

Figure 8. Various stimulus configurations used in experiments.

List of Display Configurations

<u>Stimulus</u>	<u>Display Configuration</u>	<u>Display Description</u>
Dark Adapted		<u>Test Stimulus:</u> 1° square of 10cd/m <sup>2</sup> <u>Adapting Stimulus:</u> None
Ring		<u>Test Stimulus:</u> 1° square of 10cd/m <sup>2</sup> <u>Adapting Stimulus:</u> 1° wide, 10cd/m <sup>2</sup> ring around stimulus
Full Annulus		<u>Test Stimulus:</u> 1° square <u>Adapting Stimulus:</u> 10 or 0.03cd/m <sup>2</sup> annulus with outer dim. of 20.8° x 15° around stimulus
Combination: Ring and Full Annulus		<u>Test Stimulus:</u> 1° square <u>Adapting Stimulus:</u> 1° wide, 10cd/m <sup>2</sup> ring w. contiguous 0.03cd/m <sup>2</sup> full annulus
Dark Ring		<u>Test Stimulus:</u> 1° square <u>Adapting Stimulus:</u> 1° wide ring - no illumination w. contiguous 0.03cd/m <sup>2</sup> full annulus

component of the test stimulus oriented horizontally. To present a spatially homogeneous (non-grating) flicker stimulus, no spatial frequencies were specified to be produced by the computer. If a non-flickering grating was needed, flicker presentation was inactivated by the "off" option written into the computer program.

The contrast of the stimulus was calibrated according to the Michelson contrast definition ( $C_M$ )

$$\begin{aligned} C_M &= (L_{\max} - L_{\min}) / (L_{\max} + L_{\min}) \\ &= (L_{\max} - L_{\min}) / 2L_{\text{mean}} \end{aligned} \quad (2)$$

,where  $L_{\max}$  and  $L_{\min}$  are the maximum and minimum luminance provided by the stimulus, and peak-to-peak amplitude ( $L_{\max} - L_{\min}$ ) is relative in respect to the average background ( $L_{\text{mean}}$ ). The contrast was calibrated with a Minolta LS 100 Luminance meter. The test grating always had an initial contrast modulation of 20% for parafoveal presentation and 5% for foveal stimulus presentation. The Vision Metrics units worked well as long as contrast did not exceed 33%, spatial frequencies did not exceed 21 cycles per degree, and temporal frequencies did not exceed 20 hz. That is, within these limiting values, the average luminance provided by the grating generator remained constant, stimuli were sinusoidal in both spatial and temporal domains, and nominal frequency values set by the microprocessor were in fact produced on the monitor screen. At higher contrast levels or with higher spatial and temporal frequencies, however, the device no

longer provided useful stimuli. In some experiments, the background luminance was fixed at  $0.03 \text{ cd/m}^2$  but in others it was varied parametrically.

## B. Experimental Method

Previous results (i.e., Denny, 1992) showed that even the slightest amount of extraneous light adaptation grossly distorted results. For this reason, both eyes of the observer were dark adapted for at least 25 minutes prior to data collection, and every effort was made to minimize stray light. After full dark adaptation, the observer aligned him/herself with the apparatus. This was quite easy as the null situation involved viewing a screen of the same average luminance ( $10 \text{ cd/m}^2$ ) as when the flickering grating was presented. After placing him/herself in front of the apparatus properly, the observer began a session by depressing a pushbutton.

Unless otherwise indicated, all data collected in this study represent contrast threshold determinations for a stimulus with an average luminance of  $10 \text{ cd/m}^2$ . Each plotted datum is the sensitivity value (the reciprocal of the contrast threshold). In general, such sensitivity values were collected in experimental sittings lasting about 2 hours which consisted of between 5-20 viewing sessions as defined below.

All data were collected using a temporal forced choice version of the method of adjustment. After a series of pilot experiments with other psychophysical methods, the

temporal forced choice method of adjustment proved to be most reliable and efficient. A single presentation of the stimulus involved an 8 second time period consisting of an initial 3 second viewing period, a 2 second inter-viewing period interval, and another 3 second viewing period. The test display was presented in either the first or second viewing period. The observer did not have to report in which period he/she saw the stimulus. The presentation of the stimulus was detected in either viewing period, the observer was required to depress one pushbutton which would decrease the stimulus contrast by 1 dB to adjust contrast sensitivity. In order to double-check and fine-tune contrast sensitivity, the observer was able to depress a second pushbutton which would increase stimulus contrast by 3 dB. In case the subject could not determine the viewing period in which the stimulus was detected, a third pushbutton was available to repeat the stimulus presentation. Catch trials were not presented. Whether the first or second viewing period actually involved stimulus presentation was randomly sequenced by the computer, but the observer determined whether he/she could in fact detect the stimulus. The observer signaled a threshold setting by depressing a fourth pushbutton. After such a threshold had been achieved, either another stimulus presentation was generated (involving a change in either temporal and/or spatial frequency), or the computer terminated a viewing session by printing out contrast sensitivity values on a dot matrix printer.

Using the Vision Metrics grating generator as programmed, the spatial or temporal frequency of the test display could be varied within a viewing session, and the

desired stimuli entered were presented in random order. Because of apparatus limitations, variations of the luminance of the adapting field, the size and/or shape of the adapting or test stimulus, or retinal position were made between viewing sessions. A single experimental session involved a time period in which the size, shape, retinal position, and luminance of all stimuli was fixed. In addition, either the spatial or temporal frequency of the display was also fixed; hence, in a viewing session, contrast sensitivity values were determined as a function of the spatial OR temporal frequency of the stimulus. In general, five different frequency values were examined with two different determinations of contrast threshold for each value. Generally, the lowest spatial frequency examined was 1 cycle per degree (cpd), which, given the typical size of the test stimulus ( $1^\circ$ ), was the lowest value providing useful information; although temporal frequencies as low as 0.2 hz were used in some preliminary experiments, 1 hz was found to provide the lowest useful temporal frequency. Finally, under most experimental circumstances, the stimulus generator did not present a sufficient range of contrasts for the use of spatial frequencies  $> 16$  cpd or temporal frequency  $> 16$  hz.

The sequence of experimental sessions was randomized, and within sessions, the computer randomized the sequence of stimulus values used. Furthermore, when examining situations in which both spatial and temporal frequencies were varied, the same data were collected in at least three different experimental sessions in which either the spatial or the temporal frequency was varied. All data points presented below involve at least six determinations of each sensitivity value collected in at least three

different experimental sittings. When data are plotted as line graphs, the symbol size used for each datum was chosen to approximate  $\pm 1$  standard error of  $>90\%$  of the plotted data. Hence, failure of two sensitivity value data points to overlap for the same spatial or temporal frequency is generally an indication of statistical significance in lieu of more conventional quantitative methods. When necessary, this graphical procedure for indicating significance was supplemented with other procedures.

### C. Observers

Three observers were used in this study. GL, the author, was a 38 year old female and an experienced psychophysical observer. She wore contact lenses or glasses to correct for myopia in both eyes. TEF, a 50-year old male, had uncorrected normal vision except for presbyopia and mildly deuteranomalous color vision; neither of these problems were relevant for this achromatic study with the viewing distance employed. TEF is a well-practiced observer. PC, a 22-year old inexperienced female observer, wore her contact lenses throughout experimentation to correct for myopia. With the optical correction worn during experimentation, the visual acuity of all observers was at least 20/20. For all observers stimuli were presented to the left eye temporal field unless otherwise indicated. The right eye was patched throughout all monocular phases of experimentation.

Contrast sensitivity values were determined for the author, GL, in all

experimental situations. Key experimental findings were replicated using observer TEF and/or PC.

### Chapter 3

#### The effects of rod-light adaptation upon visibility of cone-mediated displays modulated concurrently in spatial and temporal domains

The goal of the experiments described in this chapter was to psychophysically differentiate the mechanisms underlying the enhancement effects of rod-light adaptation upon cone-mediated flicker (Goldberg et al., 1983) and grating (Naarendorp et al., 1988) sensitivity. As reviewed in chapter 1, there are a number of similarities between these two effects; Naarendorp and his colleagues (Naarendorp et al., 1988; Naarendorp & Frumkes, 1991) specifically suggested that the same distal retinal mechanism which accounts for the increase in sensitivity to cone-mediated flicker (for review, see Eysteinnsson & Frumkes, 1989) also accounts for the increase in sensitivity to cone-mediated grating visibility.

In the experiments described in this chapter, a visual display was sinusoidally modulated in both temporal and spatial domains. I examined the influence of a 0.03 cd/m<sup>2</sup> background field upon the visibility of displays whose spatial and temporal frequencies were parametrically varied. This fixed value background was chosen because preliminary studies indicated that this luminance most reliably influenced cone-detected stimulus sensitivity. The complete results of these experiments show that this rod-stimulating background field increased sensitivity to high spatial frequency stimuli that

flickered slowly as well as to low spatial frequency stimuli that flickered rapidly. However, comparatively little influence upon the sensitivity to stimuli involving intermediate combinations of temporal and spatial frequencies was observed. These findings suggested the possibility that spatial and temporal enhancement effects may involve partially distinct mechanisms.

### Methods

All experiments were conducted according to the procedures specified in chapter 2. In brief, after the initial dark adaptation period of at least 25 minutes, contrast sensitivity for the observer's left eye was determined. The test stimulus was a  $1^\circ$  square shaped display with an average luminance of  $10 \text{ cd/m}^2$ , presented  $5^\circ$  parafoveally with no background field presented. After finishing data collection in the otherwise dark-adapted eye and prior to obtaining corresponding data under "light-adapted conditions", the observer viewed the  $20.8^\circ \times 15^\circ$  sized adapting field of  $0.03 \text{ cd/m}^2$  luminance for two minutes. This procedure insured that the eye was completely light-adapted to the moderate scotopic luminance background and further ensured reliable data collection. Finally, the background field was extinguished again, the observer dark-adapted again for three minutes and "dark-adapted" sensitivity was assessed for a second time. A typical experimental sitting for this series of experiments consisted of four viewing sessions; two in which the spatial frequency was held constant and the temporal frequency was parametrically changed and two in which the temporal frequency was held

constant and the spatial frequency was parametrically changed.

### Results and Discussion

Figure 9 displays results for observer GL in which contrast sensitivity (the reciprocal of threshold) is respectively plotted as a function of temporal frequency for the indicated spatial frequency (left panel) and as a function of spatial frequency for a specified temporal frequency (right panel). The closed circles represent control data when no background field was present (i.e., the observer was totally dark adapted). The open triangles show data obtained in the presence of the large,  $0.03 \text{ cd/m}^2$  luminance background. When error bars are present they indicate  $\pm 1$  standard error; if no error bars are visible, the interval representing  $\pm 1$  standard error is smaller than the size of the plotted datum. Hence, lack of overlap between any pair of data points indicates statistically significant differences.

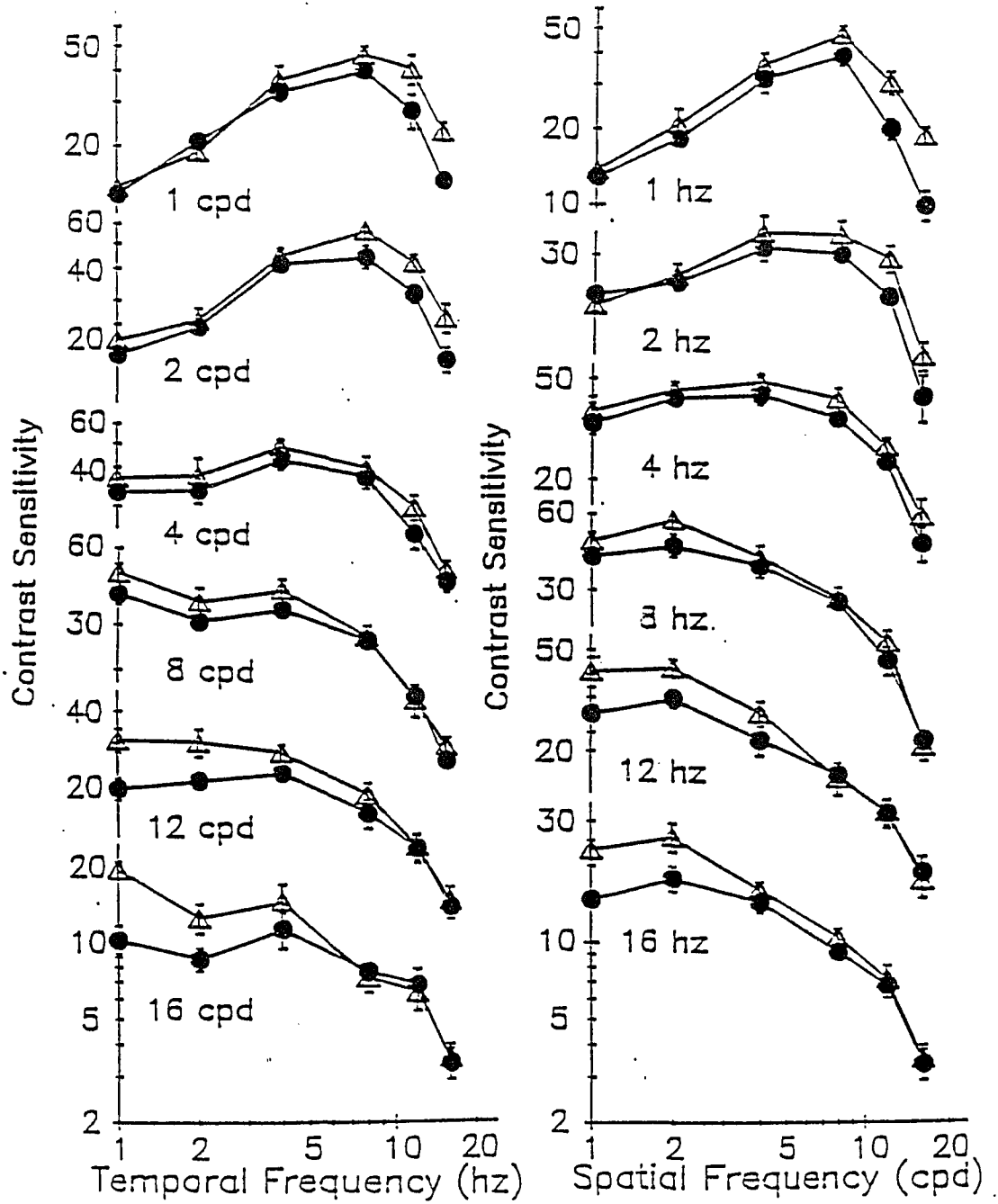
In general, the data in figure 9 replicate previous flicker (deLange, 1954) and spatial contrast sensitivity (Campbell & Robson, 1968) studies which did not specifically investigate the influence of adaptation on display visibility. When spatial frequency was fixed at 1 or 2 cpd (the upper two sets of coordinates on the left), the data resembled the classical flicker functions of deLange (1954), regardless of the addition of a rod light-adapting background field. Hence, flicker sensitivity was maximal for an intermediate flicker frequency of about 8 hz, and fell off at higher or lower flicker

Figure 9. Percent contrast sensitivity as a function of spatial and temporal frequency is plotted for observer GL. The data were collected according to the method of adjustment procedure. The stimulus was a  $1^\circ$  by  $1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating modulated concurrently in the spatial and temporal domains and presented to the left eye  $5^\circ$  in the TVF. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye at a luminance level of  $0.03 \text{ cd/m}^2$ . The closed circles represent control data obtained with no background while open triangular symbols represent the presence of a  $0.03 \text{ cd/m}^2$  monocular background field. The left set of coordinates shows contrast sensitivity as a function of temporal frequency for the indicated spatial frequencies, while the right set of coordinates shows contrast sensitivity as a function of spatial frequency for the indicated temporal frequencies.

$\Delta$  0.03 cd/m<sup>2</sup> monocular bkgmd.

● no background present

Obs.: GL



frequencies. However, if the spatial frequency was held at a value  $\geq 4$  cpd, the shape of the function appeared less regular. When temporal frequency was fixed at 1 or 2 Hz (the upper right two sets of coordinates), the data resembled the classical spatial tuning functions of Campbell and Robson (1968), regardless of the presence or absence of a rod light-adapting background field. Hence, spatial sensitivity was maximal for an intermediate flicker frequency of about 8 cpd, and fell off at higher or lower spatial frequencies. However, if the temporal frequency was held at a value  $\geq 4$  Hz, temporo-spatial sensitivity tended to decrease monotonically as spatial frequency increased. Overall, these findings are comparable with the temporo-spatial contours of Kelly (1972), although he used a much larger display size ( $16^\circ$  circular field), collected his data under photopic conditions of adaptation (0.72 to 720 tds) and presented the stimuli foveally.

The data in figure 9 established that the influence of a monocularly presented,  $0.03 \text{ cd/m}^2$  adapting field upon cone-mediated display visibility is highly dependent on both the spatial and temporal frequency of the stimulus. The dim background field reliably enhanced sensitivity to low spatial frequencies ( $\leq 2$  cpd) flickered rapidly ( $\geq 12$  Hz); these data are shown in either the upper left or lower right two panels. The dim background field also reliably enhanced sensitivity to high spatial frequencies ( $\geq 12$  cpd) flickered slowly ( $\leq 2$  Hz); these data are shown in either the upper right or lower left two panels. However, intermediate temporo-spatial frequency combinations were only sporadically enhanced by a rod-stimulating background presentation. This negative finding is most apparent with stimuli involving frequency combinations of 4 and 8 cpd

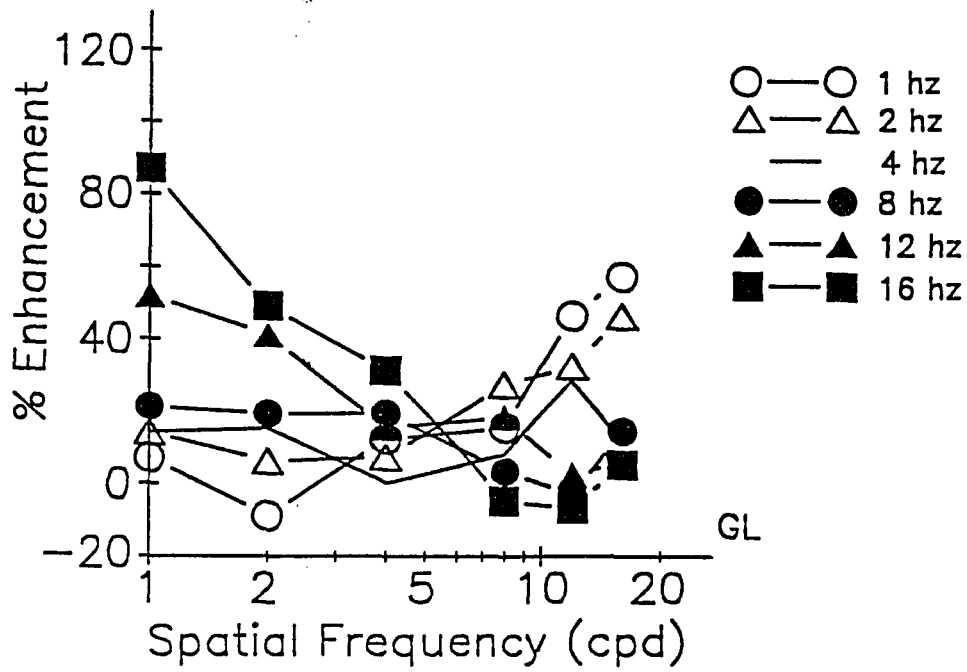
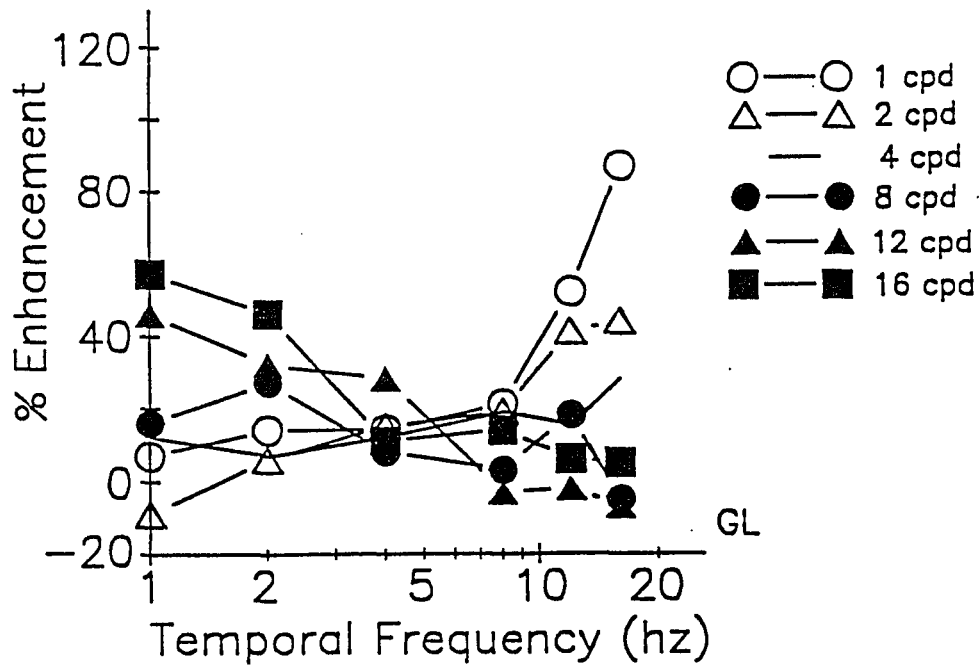
as well as 4 and 8 hz, indicated in the middle two sets of coordinates on both the left and right panels of figure 9.

In order to better display the magnitude of enhancement independent of temporal and spatial frequency, the background-induced enhancement effect for each set of data points was calculated according to the formula:

$$\text{Percent Enhancement} = [(\text{Experimental value}/\text{Control value})-1] \times 100 \quad (3)$$

,where "Percent Enhancement" is the change in contrast sensitivity, "Experimental value" is the sensitivity value obtained during experimental conditions with an adapting field present, and "Control value" is the sensitivity value obtained during control conditions without the presence of an adapting field. The upper panel of figure 10 shows this derived enhancement value plotted as a function of the temporal frequency of the display with spatial frequency as a parameter. In order to highlight the frequency-dependent nature of the enhancement effect, the low spatial frequencies (1 and 2 cpd) are represented with open symbols and the higher spatial frequencies (8-16 cpd) with closed symbols. In an analogous fashion, the lower plot in figure 10 shows enhancement as a function of the spatial frequency of the display with temporal frequency as a parameter. Once again, to highlight the frequency dependent nature of the enhancement effect, I graphed the low temporal frequencies (1 and 2 hz) with open symbols and the high temporal frequencies (8-16 hz) with closed symbols. These data clearly show that the

Figure 10. Percent enhancement as a function of temporal (upper plot) and spatial (lower plot) frequency is plotted for observer GL. These plots are derived from the same data presented in figure 9. The stimulus was a  $1^\circ$  by  $1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating modulated concurrently in the spatial and temporal domains and presented to the left eye  $5^\circ$  in the TVF. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye at a luminance level of  $0.03 \text{ cd/m}^2$ . In the upper plot, the low spatial frequencies (1 and 2 cpd) are represented with open symbols and the high spatial frequencies (8-16 cpd) with closed symbols. In an analogous fashion, the lower plot shows the low temporal frequencies (1 and 2 hz) with open symbols and the high temporal frequencies (8-16 hz) with closed symbols.

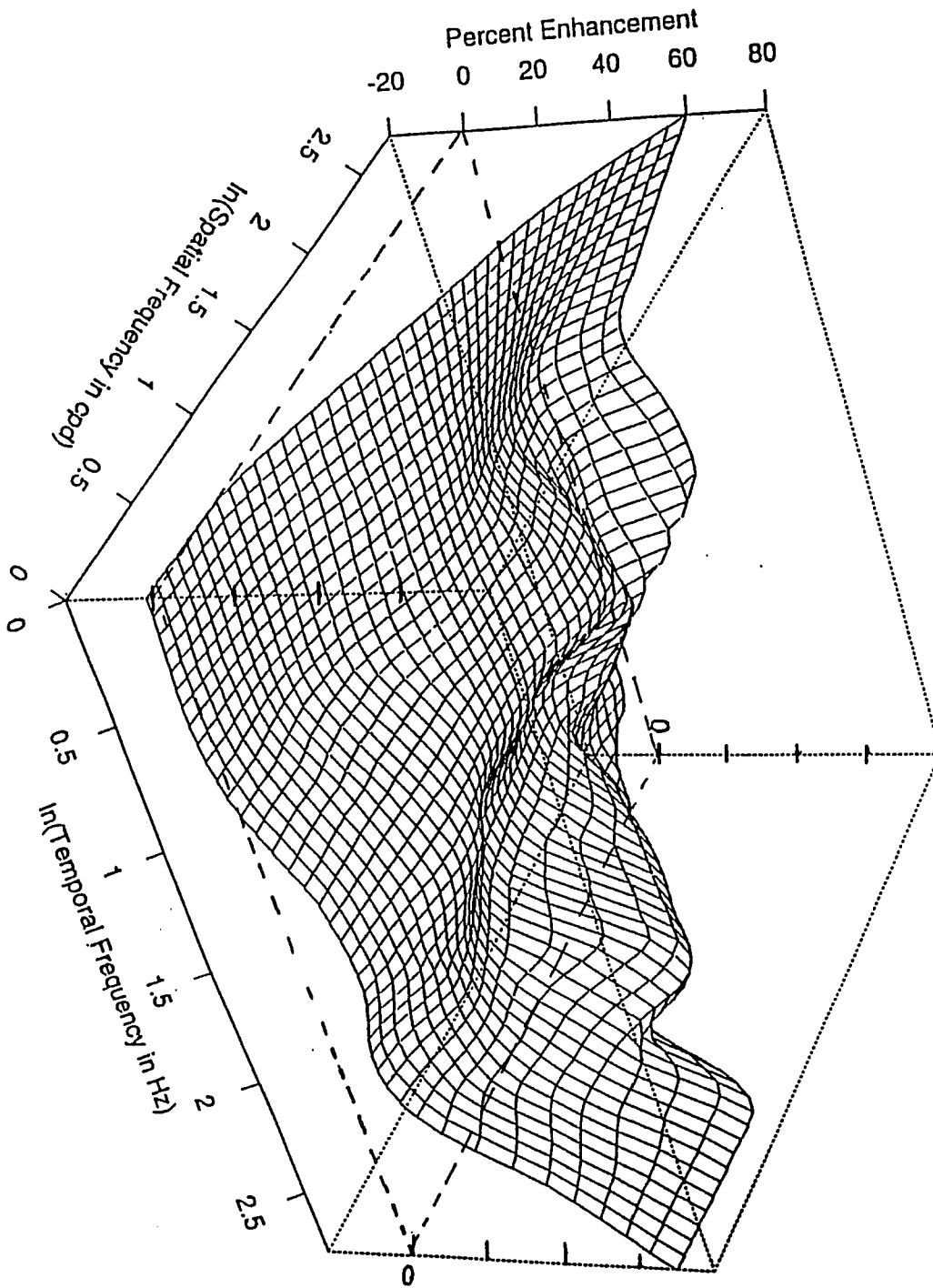


dim background field enhanced sensitivity to high spatial frequencies that flickered slowly (left upper panel and right lower panel) and low spatial frequencies that flickered rapidly (right upper panel and left lower panel). In comparison, enhancement was relatively small with 4 and 8 hz stimuli of any spatial frequency (middle of upper plot) or with 4 and 8 cpd stimuli of any temporal frequency (middle of lower plot). With combinations involving high spatial and high temporal frequencies, or low spatial and low temporal frequencies, background enhancement was even less effective. In fact, some data points indicated "negative enhancement" values suggesting that the dim background presentation actually decreased display visibility. Since negative enhancement was irregular, this finding was not investigated systematically.

Data involving three variables (spatial and temporal frequency and enhancement) can also be plotted as three dimensional graphs as is shown in figure 11. This figure shows a view of a three dimensional contour. Although this plot may be more aesthetically pleasing to a reader, it is considerably more difficult to obtain and does not reveal any findings not apparent in figures 9 and 10. For this reason, such 3-dimensional plots are not shown throughout the remainder of this thesis.

I was concerned if the data obtained in figures 9-10 were generalizable to other observers. Figures 12 and 13 show the results of a series of identical experiments collected from observer TEF. Although the results from observer TEF indicate greater enhancement effects with most displays than observer GL's and although his data were

Figure 11. Three-dimensional contour showing percent enhancement as a function of the  $\log_n$  of spatial and temporal frequency.



somewhat less regular, the same general tendencies were quite apparent from his data. This is more clearly shown in figure 14. In addition, data described in chapter 5 collected from observer GL and a third observer PC more than a year later, lend further support to the data presented in this section.

In summary, results from three observers showed that a large background field with a luminance insufficient to influence cones enhanced sensitivity to low spatial ( $\leq 2$  cpd) frequency gratings flickered rapidly ( $\geq 12$  Hz). These findings are very similar to previous studies which examined the influence of dim background fields upon the sensitivity to high frequency flicker (Denny et al., 1990; Frumkes et al., 1986; Frumkes & Eysteinnsson, 1988; Goldberg et al., 1983). Although this phenomenon has often been referred to in the literature as SRCI (suppressive rod-cone interaction, i.e., see Frumkes, 1990), it is referred to below as the "Flicker effect". In a similar fashion, the same dim background field enhanced sensitivity to high spatial frequency gratings ( $\geq 12$  cpd) flickered slowly ( $\leq 2$  Hz). This finding also replicates previous studies which examined the influence of dim background fields upon the sensitivity to high spatial frequency gratings (Naarendorp, 1988; 1991). This will be referred to below as the "Grating effect". However, dim background fields produced a much smaller enhancement effect on displays when combinations of intermediate spatial and intermediate temporal frequencies were used, and never enhanced combinations involving low spatial and low temporal or high spatial and high temporal frequencies. The implications of these findings are discussed more thoroughly in chapter 6.

Figure 12. Percent contrast sensitivity as a function of spatial and temporal frequency is plotted for observer TEF. The data were collected according to the method of adjustment procedure. The stimulus was a  $1^\circ \times 1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating modulated concurrently in the spatial and temporal domains and presented to the right eye  $5^\circ$  in the TVF. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye at a luminance level of  $0.01 \text{ cd/m}^2$ . The closed circles represent control data obtained with no background while open triangular symbols represent the presence of a  $0.01 \text{ cd/m}^2$  monocular background field. The left set of coordinates shows contrast sensitivity as a function of temporal frequency for the indicated spatial frequencies, the right set of coordinates shows contrast sensitivity as a function of spatial frequency for the indicated temporal frequencies.

$\triangle$  0.03 cd/m<sup>2</sup> monocular bkgmd.

● no background present

Obs.: TEF

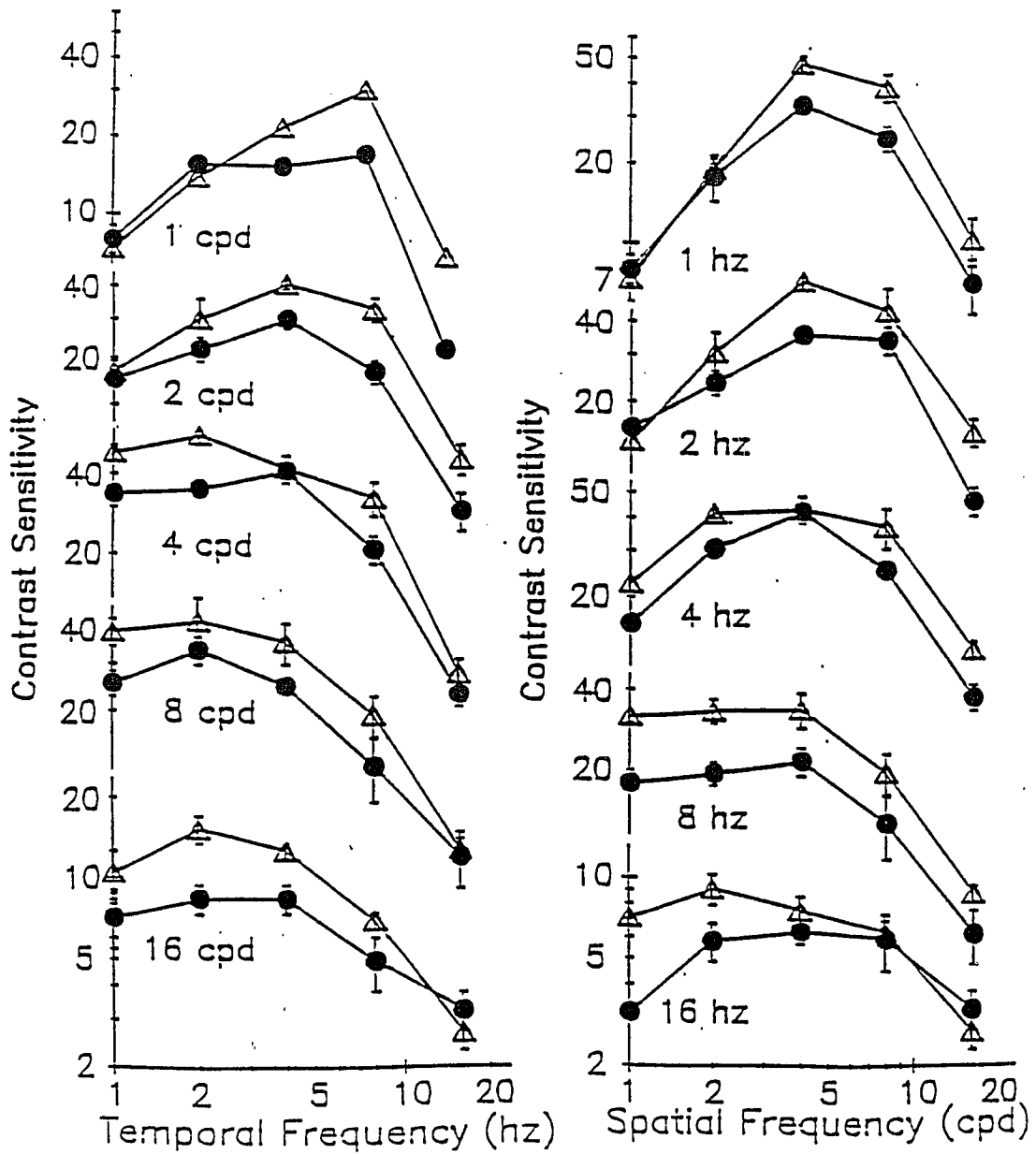


Figure 13. Percent enhancement as a function of temporal (upper plot) and spatial (lower plot) frequency is plotted for observer TEF. These plots are derived from the same data presented in figure 13. The stimulus was a  $1^\circ$  by  $1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating modulated concurrently in the spatial and temporal domains and presented to the left eye  $5^\circ$  in the TVF. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye at a luminance level of  $0.01 \text{ cd/m}^2$ . The low spatial frequencies (1 and 2 cpd) are represented with open symbols and the high spatial frequencies (8-16 cpd) with closed symbols. In an analogous fashion, the lower plot shows the low temporal frequencies (1 and 2 hz) with open symbols and the high temporal frequencies (8-16 hz) with closed symbols.

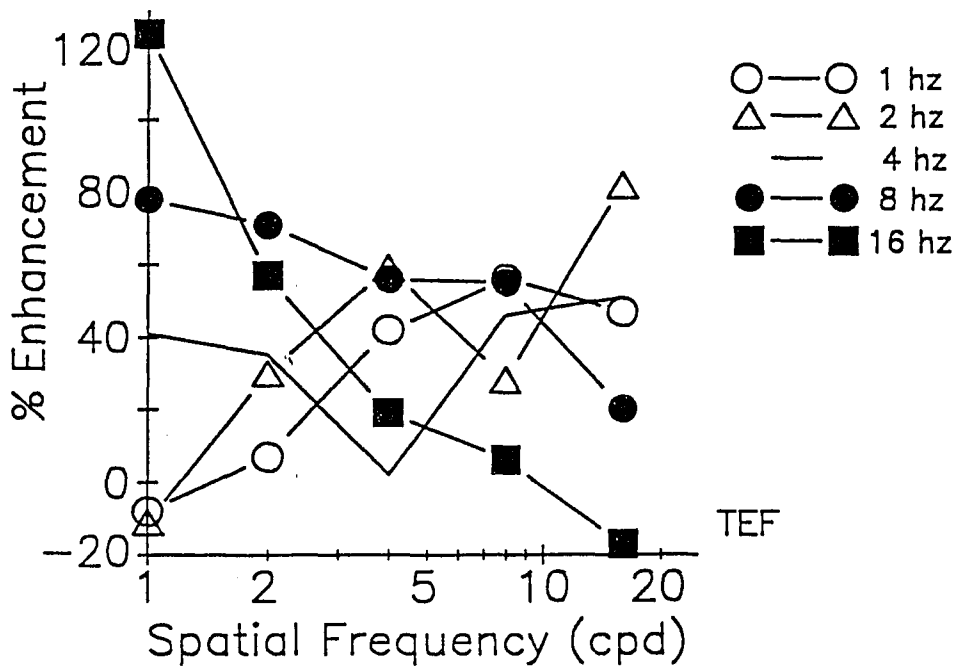
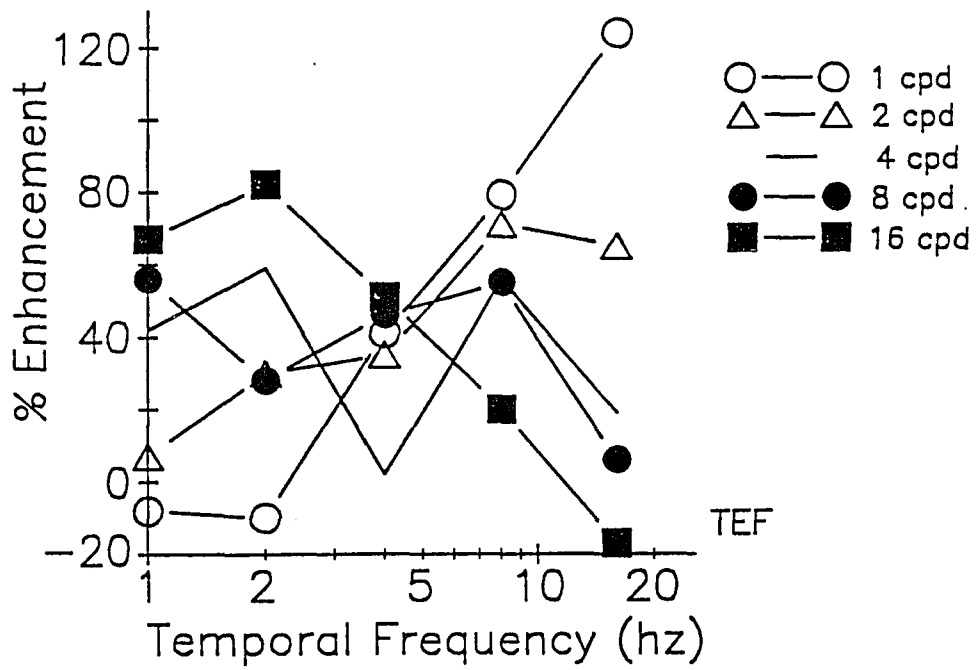
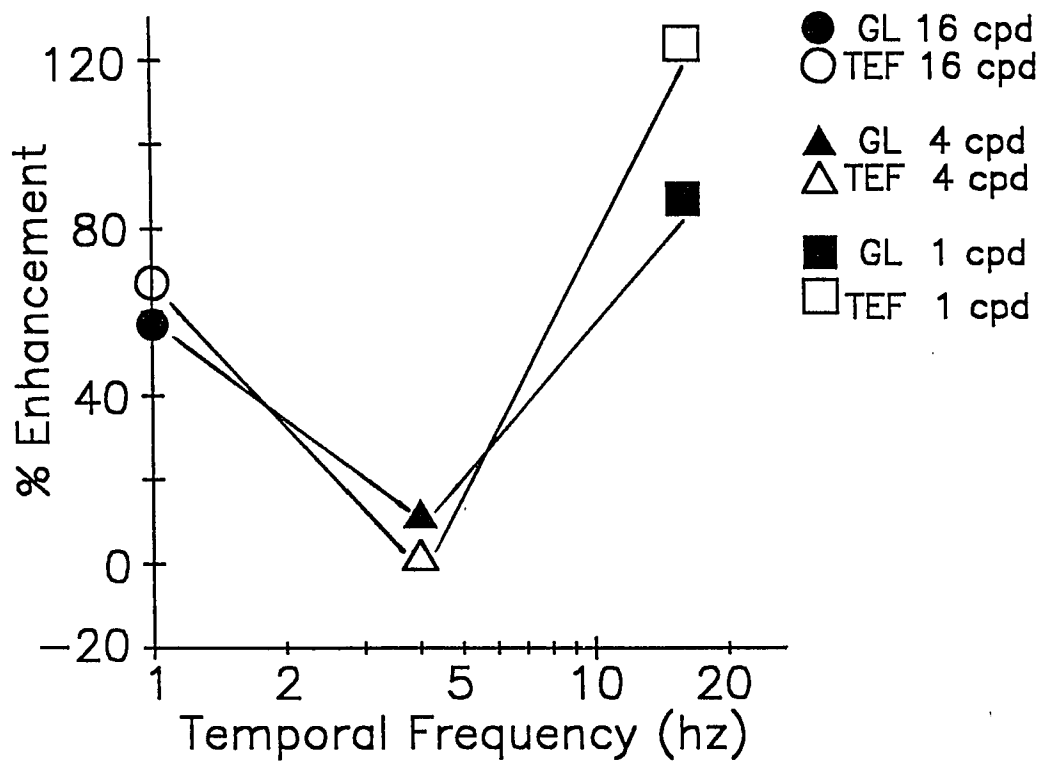


Figure 14. Comparison of percent enhancement as a function of temporal frequency is plotted for observers GL and TEF. These plots are derived from the same data presented in figures 10 and 13. The stimulus was a  $1^\circ \times 1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating modulated concurrently in the spatial and temporal domains and presented to the left eye  $4^\circ$  in the TVF for GL and  $5^\circ$  in the TVF for TEF. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye at a luminance level of  $0.03 \text{ cd/m}^2$  for GL and  $0.01 \text{ cd/m}^2$  for TEF. The filled symbols represent data from GL for the specified spatial frequencies (16, 4, and 1 cpd) and the open symbols show data from TEF for the specified spatial frequencies (16, 4, and 1 cpd).



## Chapter 4

The results summarized in the previous chapter indicated that dim background fields enhance sensitivity to visual displays in which high spatial frequencies are flickered slowly, or low spatial frequencies are flickered rapidly. However, rod-stimulating backgrounds have little effect upon the visibility of displays involving other tempo-spatial frequency combinations. Thus, at least operationally, a "Flicker effect" (influence of dim background upon the visibility of a low spatial frequency grating that is flickered rapidly) can be distinguished from a "Grating effect" (influence of dim background upon the visibility of a high spatial frequency grating that is flickered slowly). Given this operational distinction, it seems possible that these two effects may be mediated by distinct mechanisms involving a number of different functional characteristics which presumably reflect different neural pathways.

Several different stimulus manipulations can be used to investigate differences in the neural pathways underlying psychophysical effects obtained in normal human observers. The work of Schultze and Purkinje in the 19th century established that human vision is mediated by two different types of photoreceptors, the rods and the cones. Both types of photoreceptors (e.g., Oesterberg, 1935) as well as their post-synaptic connections within the retina (e.g., Polyak, 1941) and cerebral visual system (e.g., Talbot & Marshall, 1941) vary markedly as a function of retinal position. As a result, it is possible to stimulate specific types of photoreceptors directly by manipulating either

the luminance or the retinal position of the adapting field and/or the test stimulus. Therefore, if the Flicker and Grating enhancement effects reflect separate neural pathways, alteration of luminance or retinal position may produce differential influences upon these two effects.

Recent evidence (e.g., Frumkes & Eysteinnsson, 1988) suggests that the Flicker enhancement effect is mediated by a distal retinal mechanism. Although a number of interocular flicker effects have been demonstrated beginning with the work of Sherrington in 1906 (for review, see Cavonius, 1979), the state of light adaptation in one eye has generally remarkably little influence upon flicker perception mediated by the contralateral eye (Lipkin, 1962; Vernon, 1934). The lack of any interocular effect is certainly consistent with a distal retinal model for the "Flicker effect". In comparison, Denny and her coworkers (Denny et al., 1991; Eysteinnsson et al., 1993) documented the existence of an interocular "Grating effect". This interocular grating enhancement effect has many similarities to the monocular grating enhancement effect described by Naarendorp (Naarendorp et al., 1988; Naarendorp & Frumkes, 1991). Therefore, it may be possible that the Grating effect is mediated by a more proximal neural pathway which is likely to involve extra-retinal neural structures. Thus, a careful comparison of the influence of monocular versus interocular adaptation might further suggest differences between Flicker and Grating effects.

The experiments presented in this chapter all involve monocular viewing

conditions. I first investigated the influence of background luminance and the effects of stimulus retinal position upon the Flicker and Grating effects. In addition, the effects of the size and shape of both test and adapting stimuli were also examined. I also present data which were previously collected in our laboratory which examined the influence of the state of long term visual adaptation upon grating sensitivity. Collectively, these data suggest a number of fundamental differences between Flicker and Grating effects, although they do little to specify the neural pathways involved. The experiments presented in chapter 5 compare the effects of monocular and interocular adaptation and more directly explore the possibility that Flicker and Grating effects involve separate neural pathways.

### General Methodology

#### A. Determination of Prototypical Flicker and Grating Stimuli

Based upon the results presented in figure 9 of chapter 3, I initially intended to use a 1 cpd grating flickered at 16 hz as the "Flicker stimulus" and a 16 cpd grating flickered at 1 hz as the "Grating stimulus". However, pilot data indicated that the magnitude of the enhancement effect observed for a "Flicker stimulus" with a 1 cpd grating flickered at 12 hz was almost as great as the one obtained with a 16 hz stimulus; similarly, the magnitude of the effect observed with a "Grating stimulus" of a 12 cpd grating flickered at 1 hz was almost as great as the one obtained with a 12 cpd stimulus.

Moreover, use of these slightly lower frequencies considerably improved reliability of data as well as the speed at which data could be obtained. Therefore, I used a display modulated at 12 hz and 1 cpd as a prototypical "Flicker stimulus", and a display modulated at 12 cpd and 1 hz as a prototypical "Grating stimulus". Data illustrated in appendix show that these designations are quite appropriate. These appendix data show that results obtained with the "prototypical flicker stimulus" are essentially identical to those obtained with a "pure flicker stimulus" (a small diameter, spatially homogeneous stimulus). They additionally show that results obtained with the "prototypical grating stimulus" (cycled "on" for three seconds using a two second recycling rate) are essentially identical to those obtained with a "pure grating stimulus" (a grating which was cycled "on" for 1 second using a 500 ms recycling rate).

#### B. Light Adaptation Experiments

In the present experiments, I utilized the procedures described in chapter 2, except as noted. Every datum presented in figures 15,16 and 18-23 involves at least six determinations of each sensitivity value collected, in at least three experimental sittings. The light adaptation data presented are from two observers used in this series of experiments, GL and PC.

### C. Dark Adaptation Experiments

This chapter also includes some unpublished data which were collected by Noreen Denny in our laboratory several years ago. She used the same apparatus as described in chapter 2 of this thesis. These dark adaptation data were also collected with the PGCONSEN program supplied by Vision Metrics, however, with a different modification also written by Mr. John Zhu. Prior to an experimental session the experimenter chose a single spatial frequency. The stimulus was initially presented at a predetermined contrast level. Throughout the time period of adaptation, the observer responded by pressing the appropriate pushbutton which increased or decreased grating contrast. The stimulus was presented for 500 ms with a minimum interstimulus interval of 1000 ms. Contrast was always increased or decreased by 1 dB. When the observer thought grating modulation was adjusted to threshold, he/she threw the lever and this value was recorded. The stimulus was again presented at the previously chosen contrast level and the observer continued to track threshold. Other than the use of spatial modulation thresholds, data were collected with the type of method of adjustment procedure used by most previous investigators who studied dark adaptation using detection thresholds.

#### 1. General Experimental Procedure

The general experimental procedure was as follows. The experimenter first set up a particular program and chose the parameters to be used in an experimental session.

The observer was properly aligned with the apparatus by adjusting the height of the chair and the bite bar and positioning the artificial pupil so that the stimuli could be appropriately viewed monocularly passing through the beamsplitters. After alignment, the room lights were extinguished and the viewing as well as the non-viewing eye of the observer was dark adapted for 20 minutes. Subsequently, the observer's viewing eye was exposed to a Nikon microscope illuminator placed approximately 2 inches from the eye. Light from this source first passed through diffusing material and heat absorbing glass. The luminance of the source was approximately  $800 \text{ cd/m}^2$  and was determined by matching the brightness of this source to the brightness of another known source. Some thresholds in the viewing eye were then obtained using the Maxwellian view stimulator described by Frumkes and Sturr (1968). Stimuli were  $1^\circ$  circular discs which were either red (655 nm) or green (512 nm), presented in the fovea or  $7^\circ$  in the temporal visual field (TVF) for a period of 500 ms. The observer adjusted the luminance of the stimulus to threshold by adjusting the position of a circular neutral density wedge. In general, however, the observer was quickly aligned with the free field optical system and proceeded to track sensitivity for 20 minutes to one spatial frequency of a test grating presented to the viewing eye. For observer ND, data presented in figure 17 below represent the median of 3 experimental runs.

#### Part I: Class or Classes of Photoreceptors involved

Recently, a growing number of psychophysical studies have examined the

interaction between different types of photoreceptors and their effects on flicker and grating visibility. Studies by Coletta and Adams (1984; 1986) and by Eisner (1993) together showed that laterally mediated cone-cone interactions enhance cone-mediated flicker sensitivity. This enhancement is brought about by light adapting parafoveal cones. However, it has not been established whether the improvement in foveal cone sensitivity results from a removal of a suppressive influence from dark-adapted cones, or is mediated by a facilitatory influence of light-adapted parafoveal cones.

Frumkes et al. (1986) have investigated the adaptational influence of light-adapted cones on rod-mediated flicker. This interaction is distinctly different from cone-cone interaction as it occurs at much dimmer illuminance levels. It has not yet been established whether cone-light adaptation removes a suppressive influence on rods or if it actively facilitates rods. These investigators also provide evidence that rod-stimulating backgrounds have no significant influence upon rod-detected stimuli of low ( $< 3$  Hz) temporal frequencies.

The influence of dark adapted, photically unstimulated rods upon cone-mediated flicker sensitivity has been the most thoroughly studied type of photoreceptor interaction (Alexander & Fishman, 1984; Coletta & Adams, 1984; Drum, 1981; Goldberg et al., 1983; Peachey, Alexander, & Derlacki, 1990). Goldberg et al. (1983) were the first to suggest that cone-mediated flicker sensitivity is suppressed when rods are dark-adapted, especially for flicker frequencies  $\geq 15$  Hz. As a consequence, flicker sensitivity is

greatly enhanced when rods are selectively light-adapted. This flicker enhancement effect has been referred to as SRCI or suppressive rod-cone interaction (Frumkes & Eysteinson, 1988). More recent neurophysiological data in lower species (Frumkes & Eysteinson, 1988; Eysteinson & Frumkes, 1989; Pflug, Nelson, & Ahnelt, 1990) show a strikingly similar effect which involves an inhibitory influence upon cones and cone-mediated second order neurons which is mediated by retinal horizontal cells. This similarity suggests that neurophysiological/SRCI data and psychophysical/Flicker enhancement effect findings reflect an identical mechanism. Hence, it has been proposed that the Flicker enhancement effect is mediated in the retinal outer plexiform layer. This conclusion is also consistent with recent psychophysical data from patients with distal retinal pathology (for review, see Frumkes, 1990).

More recently, the involvement of photoreceptor interactions has also been examined for grating visibility using psychophysical procedures. Although some evidence (Naarendorp & Frumkes, 1991) indicates that light adapting cones can enhance cone-mediated grating visibility, I am unaware of published evidence for cone-rod interaction or an influence of rod adaptation upon grating visibility mediated by rods. However, corresponding to the SRCI phenomenon for high frequency flicker described above, light-adapting rods enhances cone-mediated sensitivity to gratings, specifically to high spatial frequency gratings (Naarendorp et al., 1988; 1991). Although not as systematically investigated as the corresponding Flicker effect, enhancement of high spatial frequency grating sensitivity is dependent upon stimulus size and retinal location

(Naarendorp et al., 1988; 1991).

In the experiments presented in this chapter, I wished to consider which class or classes of photoreceptors may be involved in the Flicker or Grating effects. Traditionally, psychophysicists determine the type of photoreceptor involved in a particular experiment by obtaining action spectra according to modifications of the two-color threshold technique first used by Stiles (1939). Using this procedure, Coletta and her colleagues were able to show that either rod- or cone-adaptation influences the sensitivity of cone-mediated flicker (Coletta et al., 1984; 1985). This procedure requires the use of optical systems, such as a Maxwellian view stimulator, which efficiently stimulate an observer's eye with light coming from a very intense source. Thus, even if  $6 \log_{10}$  units of the total energy emitted by a stimulus is removed by narrow-band interference filters used to provide "monochromatic stimuli", the apparatus still provides a useable range of retinal illuminance over most of the range of the visible spectrum. However, with my apparatus, the maximal luminance provided by the spectrally unfiltered adapting stimulus (a photographic fluorescent light box) and test stimulus (a monochrome cathode ray display) were both about  $100 \text{ cd/m}^2$ , which is about  $3 \log_{10}$  units above rod threshold. When viewed through a 2.5 mm artificial pupil, interposition of narrow-band interference filters would reduce this luminance by a minimum of about  $2 \log_{10}$  units. Further reduction occurs due to the necessary interposition of beamsplitters used to combine test and adapting stimulus fields used throughout this study. Hence, the tactic used by Coletta et al. (1984; 1985) could not be adopted in the present study.

Another procedure commonly used to distinguish rod- versus cone-specificity, the Stiles-Crawford effect, also requires the use of a Maxwellian view or similar apparatus not available for this study.

Therefore, in the present study, I relied upon three less elegant criteria to determine the types of photoreceptors involved in Grating and Flicker effects. First, I used adapting field luminance as a parameter. Since rod threshold is much lower than cone threshold, an increase in grating or flicker sensitivity following the addition of the rod-stimulating background field, must be due to rod mediation. Second, rods are unable to resolve spatial frequencies greater than about 3.5 cpd (e.g., Hess & Nordsby, 1986; Naarendorp et al., 1988). Therefore, the detection of the high spatial frequency test stimuli must be due to cones. Third, the fovea is well-known to be rod-free (Polyak, 1941; Curcio et al., 1990). Hence, a centrally presented stimulus which is sufficiently small to be confined to the fovea will only influence cones. I also had available to me data collected with my apparatus by N.Denny, which examined the influence of long-term dark adaptation upon the sensitivity to high spatial frequency gratings. These data provided a fourth source of information regarding the type(s) of photoreceptors mediating Flicker and Grating enhancement effects, since I was able to relate the time-dependent change in grating sensitivity to the time-dependent changes in detection threshold which are clearly related to rod or cone-functioning.

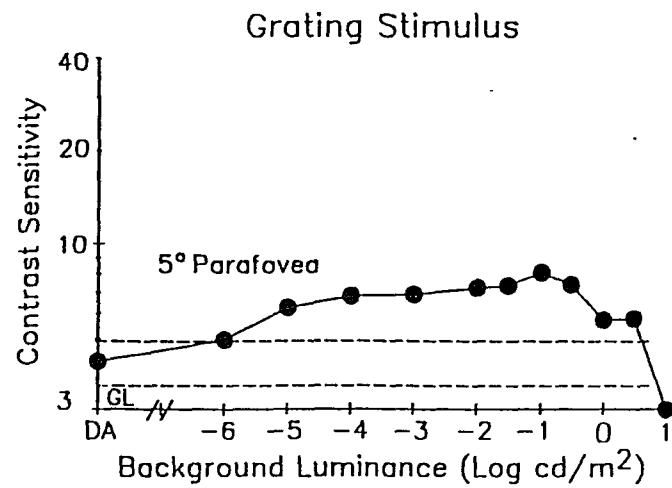
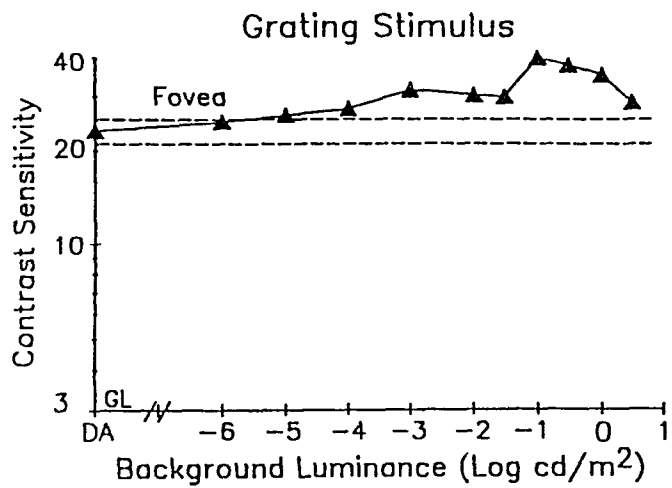
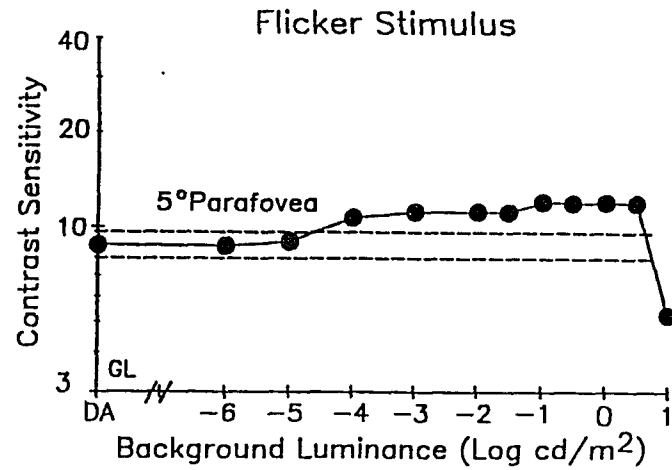
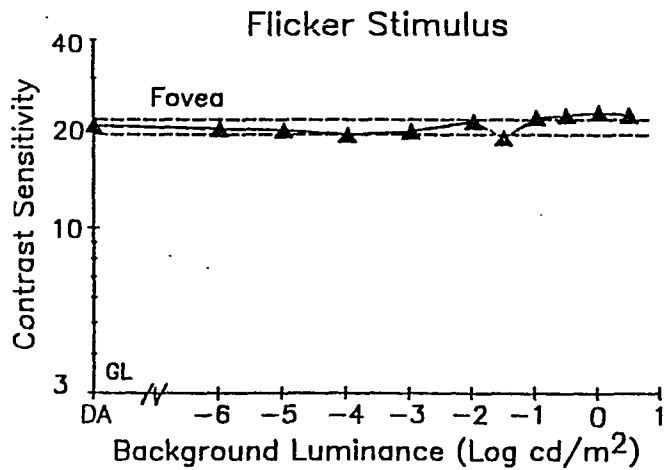
## Results and Discussion

### A. Background Enhancement in Foveal and Parafoveal Retina: Evidence for Rod-Cone Interaction

Figure 15 compares the influence of the luminance of a  $20.8^\circ \times 15^\circ$  background field upon the contrast sensitivity to a  $1^\circ$  sided square of  $10 \text{ cd/m}^2$  as a test probe. The upper sets of coordinates show results for the Flicker stimulus, the lower figure represents data for the Grating stimulus; the left coordinates show foveal data, the right coordinates present results for  $5^\circ$  parafoveal stimuli. For each set of coordinates, 95% confidence intervals for the sensitivity value obtained with no background present are indicated by the pair of dashed horizontal lines. Since the size of a plotted datum always exceeds  $\pm 1$  standard error, a departure of a data point from within this interval always indicates a statistically significant deviation from control sensitivity.

Consider first the parafoveal data on the right of figure 15. These results show that increasing background luminance from  $-6$  to about  $-1 \text{ log cd/m}^2$  gradually increased contrast sensitivity to both the Flicker and Grating stimuli. When viewed through a  $2.5 \text{ mm}$  diameter artificial pupil, this range of luminance values is below cone-threshold and hence, involves selective stimulation of rod photoreceptors. Further increases in background luminance from  $-1$  to  $0.5 \text{ log cd/m}^2$  produced different changes in grating and flicker visibility: while flicker visibility remained essentially stable, grating visibility

Figure 15. Percent contrast sensitivity as a function of log monocular background luminance is plotted for observer GL. The data were collected according to the method of adjustment procedure. The stimulus was a 1° by 1°, 10 cd/m<sup>2</sup> sine wave grating concurrently modulated at 12 hz and 1 cpd (upper set of coordinates) or 12 cpd and 1 hz (lower set of data). It was presented to the left eye either foveally (left set of coordinates) or at 5° in the TVF (right set of data). The background stimulus was a 20.8° x 15° diffuse adapting field presented to the same eye at various luminances. The closed triangles represent data obtained foveally while the closed circular symbols represent parafoveal data. A control value, i.e., the stimulus in the absence of the adapting field is indicated on the abscissa as DA (dark adapted). 95% confidence intervals for this control condition are indicated by the pair of dashed horizontal lines. Since the size of a plotted datum always exceeds  $\pm 1$  standard error, a departure of a data point from within this interval always indicates a statistically significant deviation from control sensitivity.



decreased, although sensitivity always remained above control value. However, for both Flicker and Grating stimuli, an increase in background luminance from 0.5 to 1 log cd/m<sup>2</sup> produced an abrupt drop in contrast sensitivity. This sharp decline is most likely attributable to the 50% reduction in physical contrast resulting from the superposition of the modulated test stimulus upon a non-flickering, spatially homogeneous background of the same average luminance.

Now consider the foveal data on the left of figure 15. The influence of the background upon grating visibility is similar to that observed in the parafovea. Although the magnitude of the effect is somewhat smaller, background fields between -5 and +0.5 log cd/m<sup>2</sup> luminance clearly enhanced sensitivity for foveal as well as parafoveally viewed gratings. This similarity between foveal and parafoveal Grating effects confirmed previous findings (Naarendorp & Frumkes, 1991). However, as shown in the upper left, the same range of background luminance produced no such influence upon flicker visibility in the fovea, a result which diverges sharply from parafoveal findings.

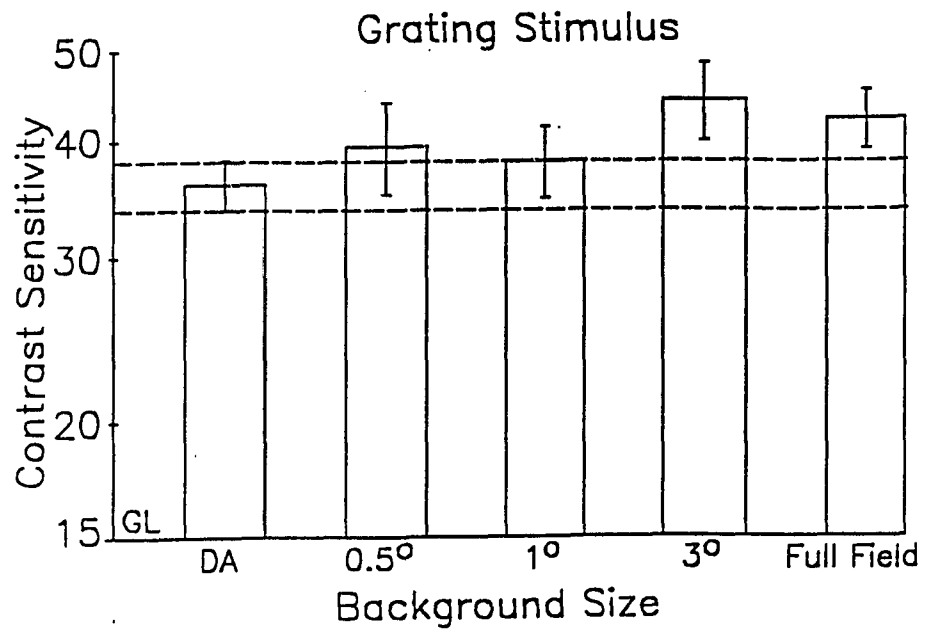
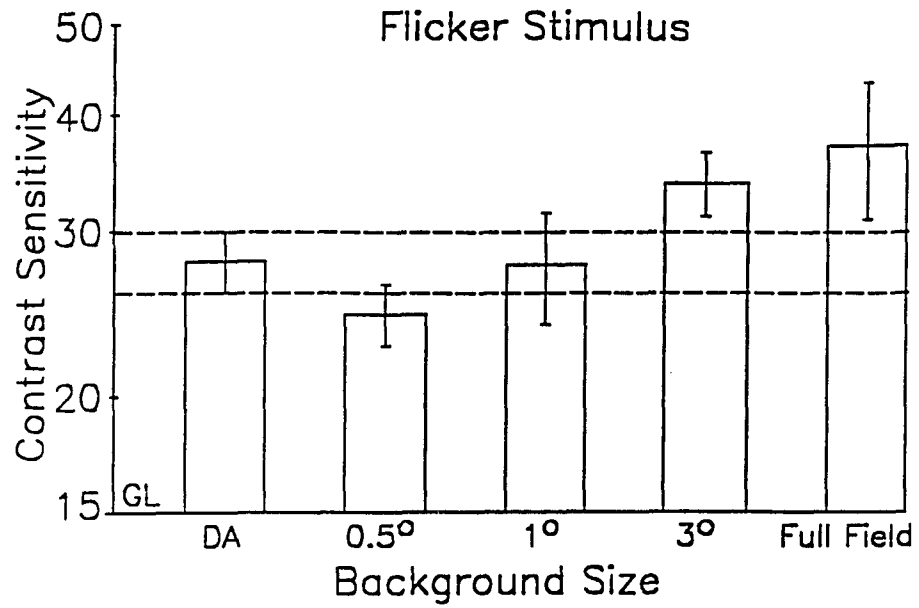
The difference between the foveal and parafoveal flicker data illustrated in figure 15 agrees with Alexander and Fishman (1984; 1985), who reported that the magnitude of background enhancement of flicker sensitivity was considerably reduced or absent in the fovea. In their studies, they used a test probe of 1.7°. More recently, however, other investigators (Denny, Frumkes, & Goldberg, 1990; Eisner, 1993) reported background enhancement of flicker in the fovea. However, these later investigators used

test probes which were smaller than  $1^\circ$  in diameter. Because of possible size effects, I proceeded to compare the magnitude of the Flicker and Grating effects in the fovea using a  $0.5^\circ$  stimulus. Assuming that the rod-free area of the fovea is  $1.25^\circ$  (Curcio et al., 1990), use of this size stimulus made certain that cones were the only photoreceptors stimulated by the test stimulus. I only used a fixed luminance background of  $0.03 \text{ cd/m}^2$ , as the parametric variation in background luminance demonstrated in figure 15 did not prove very conclusive. However, I additionally varied the size of the adapting field from  $0.5^\circ$  to a full size. If one assumes that a luminance of  $0.03 \text{ cd/m}^2$  was truly below cone threshold, the background field should only have an effect on flicker and grating visibility if it exceeded  $1^\circ$  and, hence, directly stimulated non-foveal retina.

Figure 16 shows contrast sensitivity of the  $0.5^\circ$  Flicker (upper coordinates) or Grating (lower coordinates) test stimulus presented to the fovea as a function of background field size. In this plot all error bars indicate  $\pm 1$  standard error. Notice that neither a  $0.5^\circ$  nor  $1^\circ$  background field improved the sensitivity of either the Flicker or Grating stimulus. This suggests that the background field, which had a luminance chosen to be below cone threshold, must in fact influence rods to enhance stimulus sensitivity. However, unlike the case observed with the  $1^\circ$  test stimulus as shown in figure 15, a large ("full field") background which clearly stimulated rods significantly improved the sensitivity of the Flicker as well as the Grating stimulus.

Collectively, the data in figures 15 and 16 lead to two conclusions. Firstly, rod

Figure 16. Percent contrast sensitivity as a function of background size is plotted for observer GL. The data were collected according to the method of adjustment procedure. The stimulus was a  $0.5^\circ$  by  $0.5^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating concurrently modulated at 12 hz and 1 cpd (upper set of coordinates) or 12 cpd and 1 hz (lower set of data). It was foveally presented to the left eye. The background stimulus was a diffuse adapting field of  $0.03 \text{ cd/m}^2$  whose size was either a  $0.5^\circ$ ,  $1^\circ$ , or  $3^\circ$  square or a full field rectangle of  $20.8^\circ \times 15^\circ$  presented to the same eye. For each data column, the error bar indicates  $\pm 1$  standard error. A control value, i.e., the stimulus in the absence of the adapting field is indicated on the abscissa as DA (dark adapted).  $\pm 1$  standard error for this control condition is indicated by the pair of dashed horizontal lines. A departure from within this interval always indicates a statistically significant deviation from control sensitivity.



light-adapting backgrounds enhance both cone-mediated flicker and grating visibility, and both effects can be obtained in foveal as well as non-foveal regions of the retina. Secondly, the magnitude of this background influence is dependent upon the size and retinal position of both test and adapting fields. At least one condition exists (i.e., use of a 1° test stimulus presented foveally), where a background enhances the visibility of a grating but which produces no influence upon sensitivity to flicker.

#### B. Dark Adaptation Studies: Further Evidence for Rod-Cone Interaction

In prior experiments, Frumkes and his colleagues also examined the influence of long-term visual adaptation upon the visibility of high temporal frequency flicker (Goldberg et al., 1983) and gratings (Naarendorp et al., 1988). These established that cone-mediated flicker and grating sensitivity decreased as rods became progressively more dark-adapted. Eisner (1989) similarly showed in the fovea that sensitivity to high frequency flicker increases as cones dark adapt. (I am unaware of any parallel findings involving gratings.) In these three investigations, the luminance of a constant contrast test stimulus determined flicker and grating sensitivity.

In unpublished portions of his doctoral dissertation, Goldberg (1983) reproduced his flicker findings using modulation thresholds for a 15 hz stimulus with constant time-averaged luminance. Collectively, the light-adaptation data presented in figure 15 and the dark-adaptation data of Goldberg establish that the Flicker effect often involves rod-

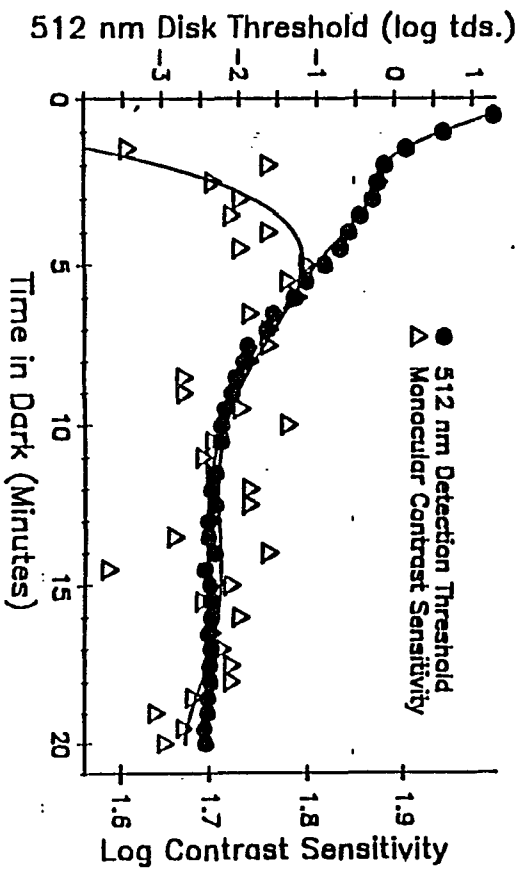
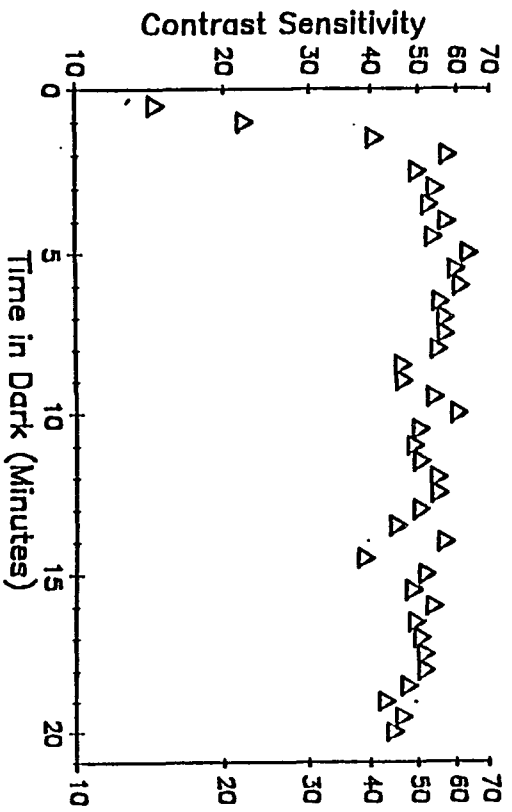
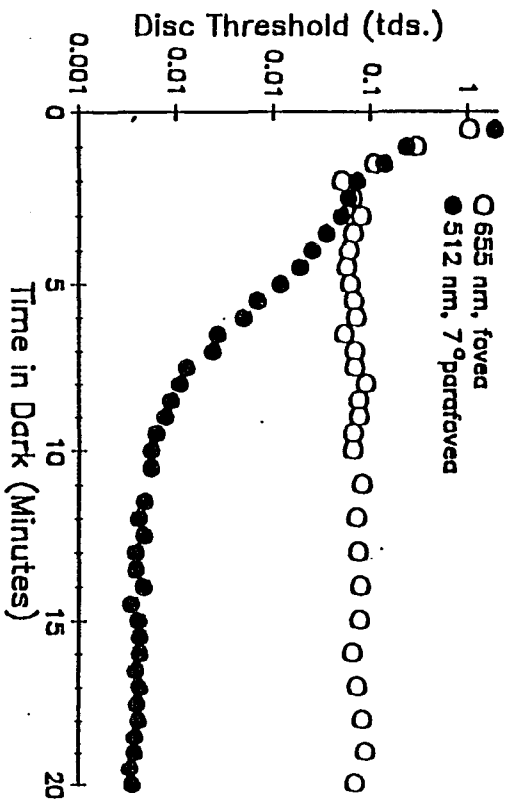
cone interaction. In a similar fashion, involving data that were not published or included in her dissertation, N. Denny (Personal Communication) also established that the Grating effect often involves rod-cone interaction. In her experiments, she tracked sensitivity changes in the viewing eye following exposure to a bleaching source of "white light" of approximately  $800 \text{ cd/m}^2$  for 60 seconds duration.

The upper portion of figure 17 shows the detection threshold for a 655 nm stimulus presented foveally reflecting cone function, and a 512 nm stimulus presented  $7^\circ$  parafoveally reflecting both cone and rod sensitivity. As is well known, detection threshold monotonically decreases during dark-adaptation. Probably, the relatively slight rod-cone break in the 512 nm function (at about 3 minutes in the dark) reflects the relatively low luminance of the "bleaching source".

The middle portion of figure 17 shows changes in contrast sensitivity (the reciprocal of threshold) of a  $3.2^\circ \times 2.4^\circ$  grating of 11 cpd and  $10 \text{ cd/m}^2$  average luminance presented  $7^\circ$  parafoveally. Although these data are somewhat variable, they show that modulation sensitivity at first increases, then decreases again during dark adaptation.

The lowest portion of figure 17 relates the change in threshold of the 512 nm stimulus (the filled circular symbols and left ordinate) to the change in sensitivity (the reciprocal of threshold) of the 11 cpd grating (the open triangular symbols and right

Figure 17. Changes in the sensitivity of observer ND as a function of time in the dark (along abscissa in minutes) following a bleach of one eye with an  $800 \text{ cd/m}^2$  source for one minute. All data points are the median values from three experimental runs. For the experiments illustrated in the top coordinates, the detection threshold for a 500 ms duration,  $1^\circ$  diameter test probe was determined in the observer's right eye following exposure to the bleaching field. The stimuli, which were presented via a Maxwellian view optical system, were of the indicated wavelength and retina position. Notice the logarithmic spacing along the ordinate. For the experiments illustrated in the middle coordinates, contrast sensitivity for an 11 cpd grating was determined in the left eye following a bleach to the observer's left eye. This stimulus was presented  $5^\circ$  in the temporal field, was  $10 \text{ cd/m}^2$  in luminance, and was shaped as a  $1^\circ$  sided square. Once again, notice the logarithmic scaling along the ordinate. The smooth function is a fourth order regression fit through the interocular data. The bottom sets of coordinates are derived from the upper two sets of data. Detection threshold for the 512 nm disk (the closed circles and left ordinate) and sensitivity to the 11 cpd grating (the open symbols and right ordinate) are plotted as a function of the time the dark. Notice that the spacing along the two ordinates differs by a factor of about 10.



ordinate). The data obtained for both sets after 3 minutes were fit by a fourth order regression to show the correspondence of time courses. The similarity between these two functions suggests that a common mechanism is likely to be responsible for both functions. In other words, as rods dark adapt, cone-mediated sensitivity to the high spatial frequency gratings decreases.

Collectively, the work of Goldberg et al. (1983) and Denny (Figure 17) using modulation thresholds, and Goldberg et al. (1983) and Naarendorp et al. (1988) using luminance thresholds establish that sensitivity to high temporal frequency flicker and high spatial frequency gratings decreases as rods progressively dark adapt.

C. Adaptation of Photoreceptors Adjacent to the Test Display Produce Background Enhancement: Further Evidence for Rod-Cone and Possibly Cone-Cone Interaction.

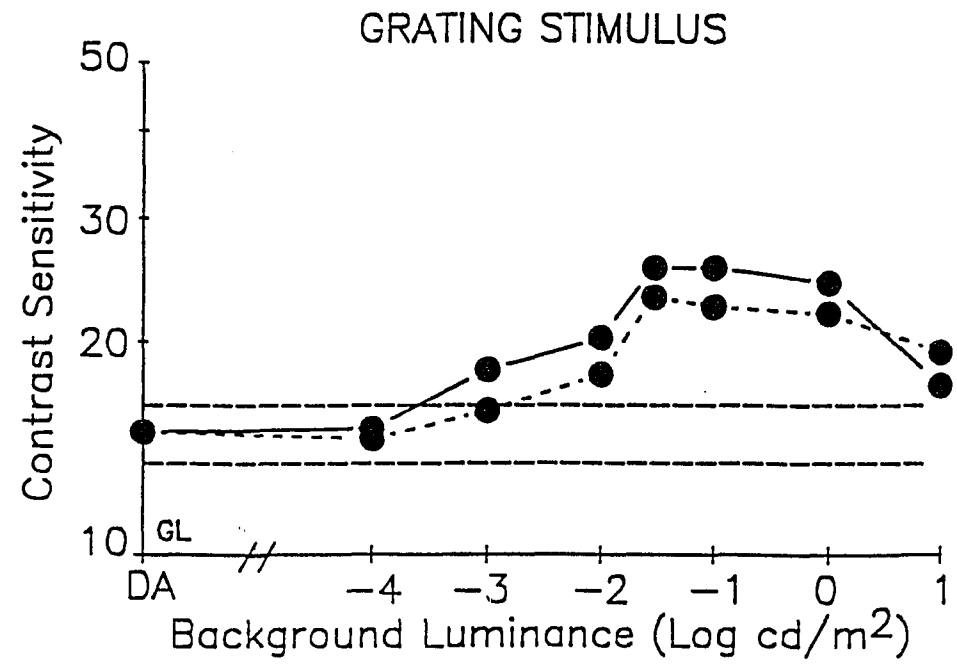
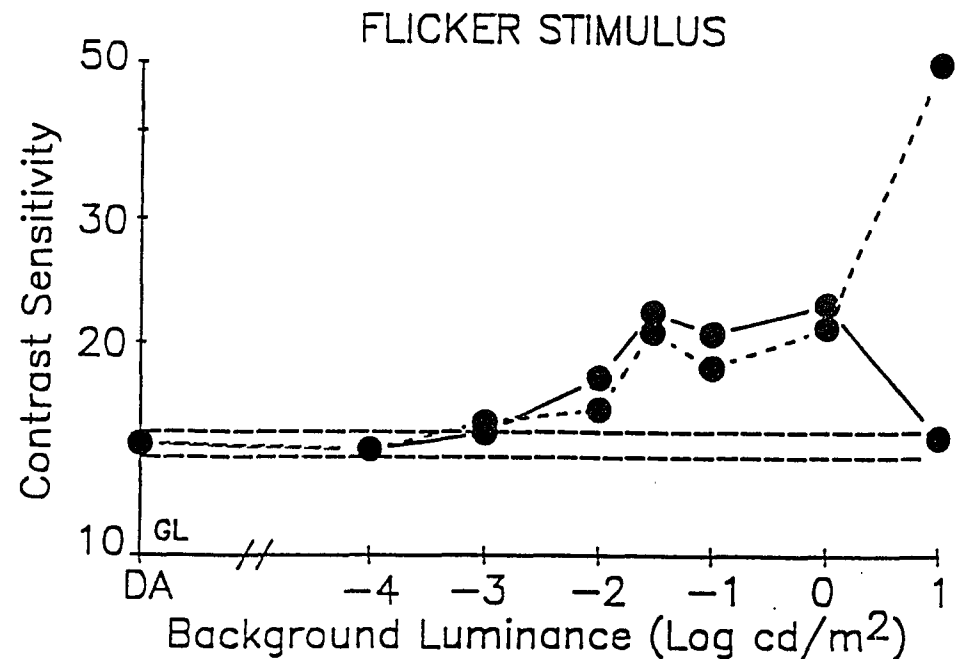
Previous investigations showed that the rods which enhance the visibility of cone-detected flicker (Coletta & Adams, 1984; 1986; Denny et al., 1990; Drum, 1981) and grating stimuli (Naarendorp et. al., 1988) are adjacent to the test display. In brief, an annular adapting background which stimulated retinal regions adjacent to the test display proved as effective as a background with the same outer dimensions, but additionally stimulating the test display. In comparison, a background field with the same dimensions as the test display exerted a negligible influence upon display visibility.

In the course of the present study, I replicated these findings in the parafoveal retina using a  $1^\circ$  stimulus. In the experiments summarized in figure 18, I examined the influence of a variable luminance background with the outer dimensions of  $20.8^\circ \times 15^\circ$  upon the visibility of a flicker and grating stimulus (respectively, the upper and lower sets of coordinates). However, one background was "solid" and additionally stimulated the retinal area underneath the test displays (solid lines). The second background configuration was an annulus neatly surrounding the test display, therefore just stimulating photoreceptors adjacent to the test stimulus.

Figure 18 shows that either shaped background with luminance levels of between -4 and 0  $\log \text{ cd/m}^2$  produced very similar influences upon both flicker and grating visibility: visibility of displays is enhanced with luminance values of between -2 and 0  $\log \text{ cd/m}^2$ . However, a further increase in background luminance from 0 to +1  $\log \text{ cd/m}^2$  clearly distinguishes the different test stimuli. For the grating stimulus, the increase in luminance produced a decrease in stimulus visibility which is much more pronounced with the solid than the annular background field. As previously postulated (see interpretation of figure 15 above), the solid background clearly reduces the physical contrast of the grating image in the retina. For the Flicker stimulus, the difference in findings between the solid and annular background fields is even more obvious. While the increase in luminance of the solid background decreased the visibility of the flicker stimulus (presumably reflecting a decrease in contrast), an increase in luminance of the annular background greatly increased the visibility of the stimulus.

Figure 18. Percent contrast sensitivity as a function of log monocular background luminance with a full field background or a full annular background is plotted for observer GL. These data were collected with the method of adjustment procedure. The stimulus was a  $10 \text{ cd/m}^2$ ,  $1^\circ \times 1^\circ$  sine wave grating modulated concurrently at 12 hz and 1 cpd (plot on the top) or at 12 cpd and 1 hz (lower set of coordinates). The stimulus was presented at  $4^\circ$  in the TVF of the left eye. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye, and was varied in luminance. The closed circles connected by a solid line represent data in the presence of a full background field while the closed circles connected by the dashed line show data presented with a full annular background. A control value, i.e., the stimulus in the absence of the adapting field is indicated on the abscissa as DA (dark adapted). 95% confidence intervals for this control condition are indicated by the pair of dashed horizontal lines. Since the size of a plotted datum always exceeds  $\pm 1$  standard error, a departure of a data point from within this interval always indicates a statistically significant deviation from control sensitivity.

- full field bkgrnd.
- - -● annular bkgrnd.



The precipitous increase in flicker sensitivity caused by increasing the background luminance of the annular adapting stimulus from 1 to 10 log cd/m<sup>2</sup> closely resembles previous results obtained in the fovea by Coletta and Adams (1984). In their study, they were able to show that the enhancing effect on cone-mediated high frequency flicker sensitivity was due to the influence of cone-adaptation upon flicker sensitivity. They postulated that the cone-cone effect has an influence similar to the one rod-adaptation has upon cone-detected flicker sensitivity. This phenomenon has since been studied in considerably greater detail (Coletta & Adams, 1986; Eisner, 1989; 1993). Unfortunately, due to the constraints of the apparatus, I was not able to determine whether the large annular background enhancement effect was indeed attributable to cones. However, it is noteworthy that the data in figure 18 fail to show an analogous effect with gratings.

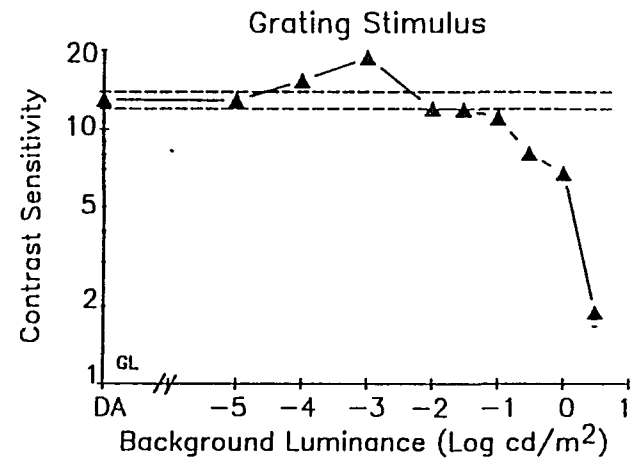
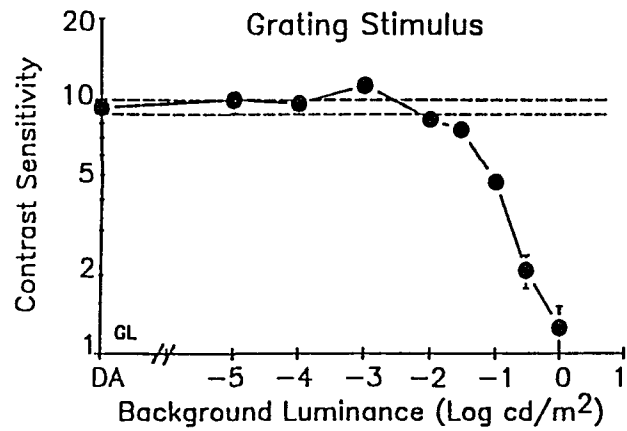
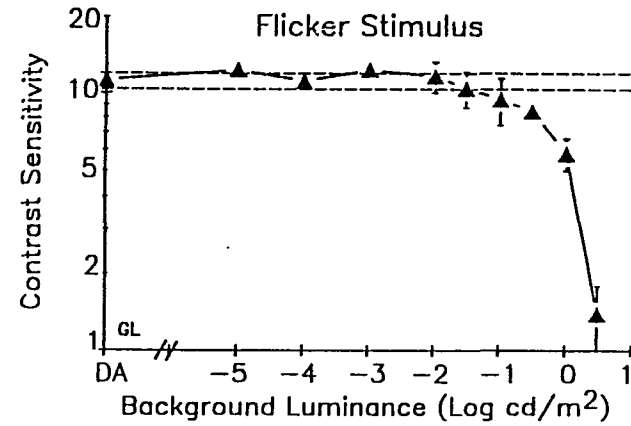
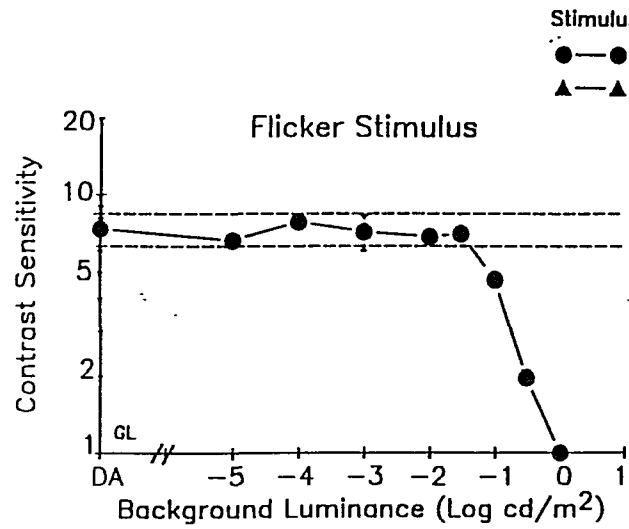
Collectively, the data in figure 18 and the results of Coletta and Adams (1984; 1985) suggest that background enhancement of flicker can involve either rod-cone or cone-cone interactions. To date, the only evidence for a cone-adaptation influence upon grating visibility is due to an "after-flash effect" (Naarendorp & Frumkes, 1991) involving stimulus sequences considerably different than employed in the present study. Although far from conclusive, these results suggest that the presence of cone-cone interaction distinguishes the Flicker from the Grating effect.

D. Rod-Backgrounds Enhance Sensitivity to Rod-Detected Gratings but not to Rod-Detected Flicker

The foregoing experiments examined the influence of rod-adaptation upon Flicker and Grating stimuli detected by cones. However, it is also possible that rod-adaptation influences the sensitivity to flicker and gratings detected by rods. To this end, I investigated the influence of dim background fields upon the sensitivity of rod-detected stimuli. I presented either a "Flicker stimulus" (a display modulated at a temporal frequency of 3 Hz and a spatial frequency of 0.3 cpd) or a "Grating stimulus" (only modulated at a spatial frequency of 2 cpd). Both stimuli were shaped as a  $3.2^\circ \times 2.4^\circ$  sided rectangle presented  $5^\circ$  parafoveally for 3000 ms at two different luminance levels, 0.01 log cd/m<sup>2</sup> and 0.1 log cd/m<sup>2</sup>. These spatial and temporal frequency combinations are well within the resolving power of rods (Campbell & Robson, 1968; Nygaard & Frumkes, 1985; Naarendorp et al., 1988) and involve luminance levels which are most likely below cone threshold.

Figure 19 shows contrast sensitivity for the presumed rod-detected Flicker (on top) and Grating (on bottom) stimuli, which had a luminance of either 0.01 log cd/m<sup>2</sup> (on the left) or 0.1 log cd/m<sup>2</sup> (on the right). As background luminance increased to -1.5 log cd/m<sup>2</sup>, flicker sensitivity remained quite stable; further increases in background luminance only served to decrease the sensitivity to the Flicker stimulus. These results confirmed prior findings (Frumkes et al., 1986) which fail to show any enhancement

Figure 19. Percent contrast sensitivity as a function of log monocular background luminance is plotted for observer GL. These data were collected with the method of adjustment procedure. The  $3.2^\circ \times 2.4^\circ$  stimulus had a luminance of either  $0.01 \text{ log cd/m}^2$  represented by filled circles (on the left) or  $0.1 \text{ log cd/m}^2$  shown as filled triangles (on the right). Stimuli were modulated at  $3 \text{ hz} \times 0.3 \text{ cpd}$  (plots on top) or at  $2 \text{ cpd}$  (lower set of coordinates), and presented to the left eye at  $5^\circ \text{ TVF}$ . The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye, and was varied in luminance. A control value, i.e. the stimulus in the absence of the adapting field, is indicated on the abscissa as DA (dark adapted). 95% confidence intervals for this control condition are indicated by the horizontal dashed lines. If error bars are not visible, the size of a plotted datum always exceeds  $\pm 1$  standard error. Therefore, a departure of a data point from the control interval indicates a difference which is statistically significant.



effect produced by rod-backgrounds upon rod-flicker. However, as background luminance increases beyond  $-2 \log \text{ cd/m}^2$  flicker sensitivity decreased. In comparison, background luminance values of  $-4$  and  $-3 \log \text{ cd/m}^2$  enhanced grating sensitivity, particularly sensitivity to the  $0.1 \log \text{ cd/m}^2$  test grating. Thus, unlike the corresponding Flicker effect, the Grating effect can involve rod-rod as well as rod-cone interactions. As is the case for flicker sensitivity, increases in background luminance beyond  $-2 \log \text{ cd/m}^2$  reduced sensitivity to rod-detected gratings.

#### E. Summary

The foregoing experiments establish the following similarities between Flicker and Grating effects.

1. Background fields too dim to directly stimulate cones enhance sensitivity to both the prototypical Flicker and Grating stimuli, suggesting that both effects may be mediated by rod-cone interaction. In addition, background enhancement of both flicker and grating visibility is attributable to light-adapting the rods adjacent to the area of the retina stimulated by the test stimulus.

2. When annular background fields are increased from 0 to  $1 \log \text{ cd/m}^2$ , flicker sensitivity sharply increases. Coletta and Adams (1984) suggested that this effect was due to a direct cone-adaptation influence upon cone-detected flicker sensitivity. In

comparison, an increase in annular background luminance from 0 to 10 cd/m<sup>2</sup> decreases grating sensitivity. These data suggest that while the flicker enhancement effect can involve cone-cone interaction, the grating enhancement effect does not involve cone-cone interaction.

3. Dim rod-stimulating backgrounds enhance sensitivity to gratings that are detected by rods, but produce no similar influence upon rod-detected flicker.

In conclusion, although both Flicker and Grating enhancement effects may often be mediated by rod-cone interaction, the Flicker effect may also involve cone-cone interaction but not rod-rod interaction. In comparison, the Grating effect can involve rod-rod interaction, but I am unaware of any evidence for cone-cone interaction.

## Part II. The Importance of Retinal Position and Stimulus Size for determining the Magnitude of Flicker and Grating Effects.

A growing body of data suggests that the characteristics of the visual system of higher primates, including man, change dramatically as a function of retinal position. These changes may be directly related to the anatomy, physiology, and function of photoreceptors. The fovea, the central 0.35 mm (1.25°) of the retina, only contains cones (Curcio et al., 1990; Oesterberg, 1935; Polyak, 1941). While cone density beyond this area decreases, rod density increases and is highest along an elliptical ring at the

eccentricity of the optic disk extending into nasal retina (Curcio et al., 1990). Among other procedures, the differing distribution of rods and cones was used in Part I above to determine rod versus cone-specificity of Flicker and Grating enhancement effects.

However, differences in visual processing due to changes in retinal position may also be postreceptoral and therefore only indirectly related to the types of photoreceptors involved (Waessle & Boycott, 1991). As mentioned above, photoreceptor density is dependent on retinal position. Since all visual information passes through at least two retinal synapses before leaving the brain, in the outer plexiform and inner plexiform layers, the ratio of connections between photoreceptors and second and third order neurons may change as a function of retinal position. In the outer plexiform layer of the primate retina, up to 45 rod terminals may be presynaptic to one rod bipolar cell before it connects to third order neurons in the inner plexiform layer (Dowling, 1987). Similarly, each cone is found to be presynaptic to above three bipolar cells (Waessle & Boycott, 1991). Two of these neurons are midget bipolar cells, a flat and an invaginating type. Since their axons end at different levels in the inner plexiform layer, information from these cells is processed by two different types of third order neurons; the flat midget bipolar cells by OFF-ganglion cells and the invaginating midget bipolars by the ON-ganglion cells. In addition, each cone is presynaptic to a variety of "parasol" bipolar cells (Waessle & Boycott, 1991) synapsing on yet another type of ganglion cell, again relaying different visual information. Therefore, the input to ganglion cells may differ in terms of the proportion of bipolar and third order neuron synapses. Although midget

bipolar and ganglion cells are found at most retinal eccentricities (Watanabe & Rodieck, 1989; Waessle & Boycott, 1991; Kolb, Linberg, & Fischer, 1992), their prevalence markedly decreases as a function of retinal position. In fact, a recent study in macaque monkey reports a decrease in ganglion cell to cone ratio from 3-4 ganglion cells for every foveal cone to one ganglion cell per cone at an eccentricity of 15-20 degrees (Waessle, Gruenert, Roehrenbeck, and Boycott, 1990). Although accurate descriptions of intrinsic neuronal connections near the fovea of the primate retina have not been reported yet, the large number of second and third order neuron subtypes, as well as their various types of synaptic connections leads to the conclusion that their interactions may vary markedly with changes in retinal position.

The postretinal visual system also varies as a function of retinal position. Talbot and Marshall (1941) were the first to describe a cortical retinotopic map in primates, whose most striking feature was a cortical magnification of the foveal area. Although this may merely reflect differences in the density of retinal ganglion cells as a function of retinal position (Waessle & Boycott, 1991), it also may involve an additional, factor producing "cortical magnification" (Perry & Cowey, 1985). As a consequence, the representation of 1° in the fovea extends over 15 mm in primate visual cortex, whereas by 10° of parafoveal displacement, 1° of retina is only represented by 1 mm in the cortex (Van Essen, Newsome, & Maunsell, 1984). Indeed it appears that over 40% of striate cortex is devoted to process information from the central 5° of the visual field (Connolly & Van Essen, 1984). This difference has been popularized by the term cortical

magnification factor,  $M^{\circ}$  (Daniel & Whitteridge, 1961), which is defined as millimeters of cortex per degree of visual angle and is thought to be inversely related to retinal ganglion-cell sampling density. Virsu and Rovamo (1979) expanded on this concept by adding the F-factor, where the average stimulus luminance is reduced in inverse proportion to Ricco's area (luminous flux).

In light of the change in neural substrate with retinal position, it is not surprising that the functional characteristics of the visual system also change. These characteristics include spatial acuity (Polyak, 1957) and CFF (Hylkema, 1942), as well as changes in the receptive fields of ganglion cells and cerebral neurons. Given this background, it seems possible that variation of retinal position may produce different influences upon flicker and grating enhancement effects.

### Methods

In these experiments, I initially intended to study the influence of a  $0.03 \text{ cd/m}^2$  background field upon the prototypical Flicker and Grating stimuli which were parametrically varied in both retinal position and stimulus size. However, preliminary data in the peripheral retina indicated that the rod-adapting background influences upon both types of stimuli decreased as display size increased from a  $0.5^{\circ}$  square to a  $3^{\circ}$  square. Specifically, a  $3^{\circ}$  test stimulus showed relatively little adapting field enhancement. Moreover, contrast sensitivity to a  $0.5^{\circ}$  display at any retinal position

except in the fovea was insufficient to perform a meaningful experiment. Given these limitations, the results of this "parametric" study were largely restricted to the data shown in figures 20 and 21 below.

An alternative way to determine the importance of retinal locus involves variation of the shape of a foveally positioned test stimulus in which increasing portions of the center of the stimulus are removed. To this end, I again compared the influence of a large,  $0.03 \text{ cd.m}^2$  rod-stimulating background upon a prototypical Flicker and Grating stimulus of  $10 \text{ cd/m}^2$  luminance centered in the fovea. This time, however, the test stimulus was the full "3° test stimulus", which in fact had an outer dimension of  $3.2^\circ \times 2.4^\circ$ . The annular stimulus had the same outer dimensions but a center square of  $0.5^\circ$ ,  $1^\circ$ , or  $2^\circ$  cut out. Since usual estimates of the fovea are far less than  $2^\circ$  in diameter (Curcio et al., 1990; Polyak, 1941) such a manipulation stimulates the fovea itself progressively less.

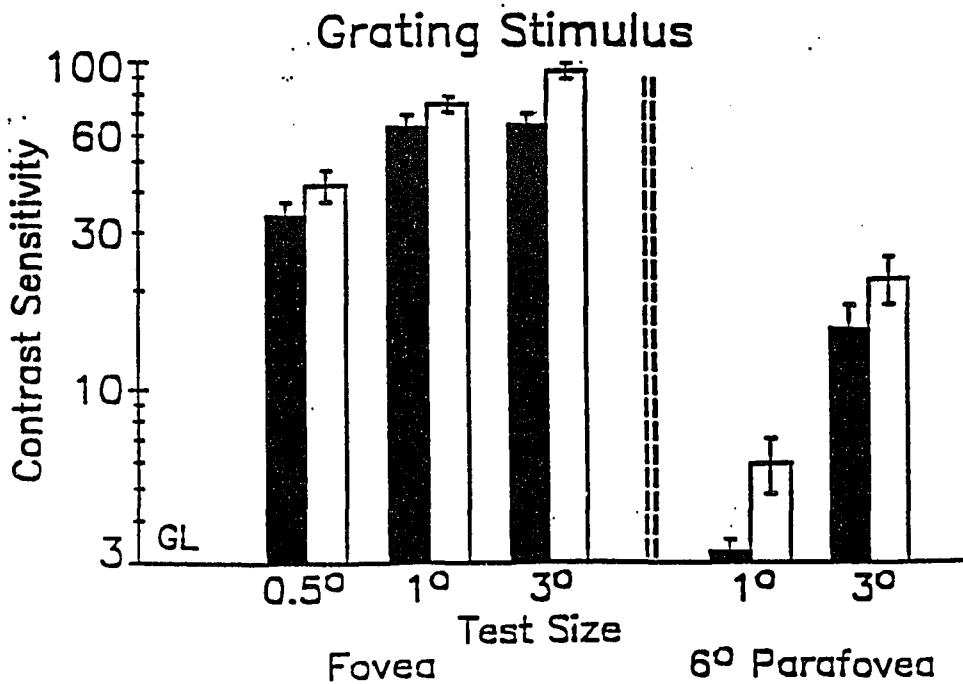
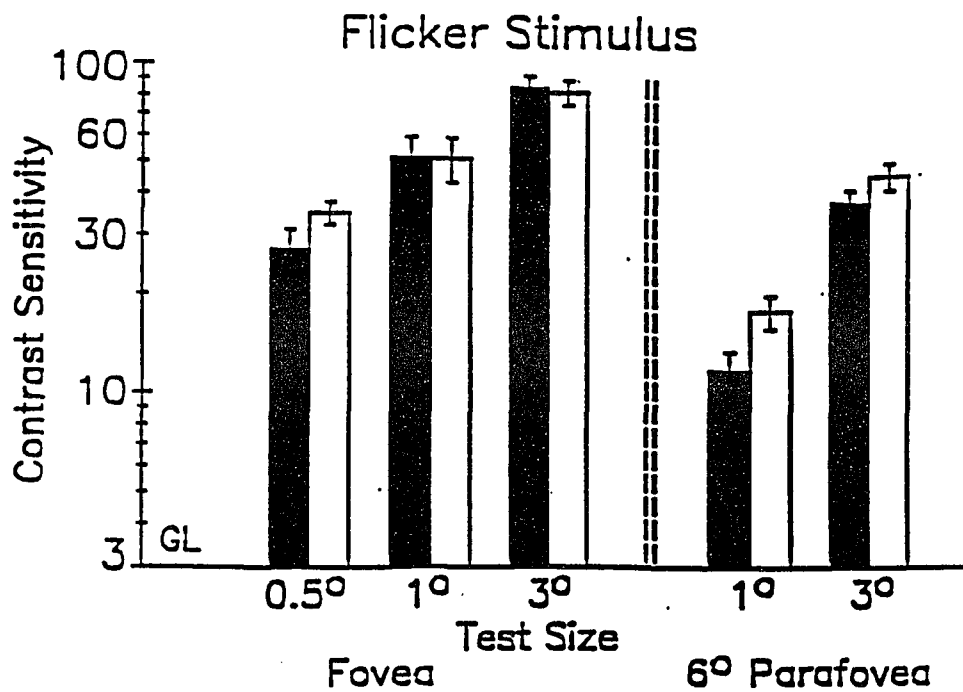
## Results and Discussion

### A. Importance indicated by direct manipulation of stimulus size and retinal position.

Figure 20 shows the influence of stimulus size upon the visibility of a Flicker (upper coordinates) and Grating stimulus (lower coordinates) in the fovea (on the left) and  $6^\circ$  parafoveally (on the right). In all cases, dark bars indicate data when no adapting

Figure 20. Comparison of percent contrast sensitivity as a function of test stimulus size and retinal position is plotted for observer GL. The data were collected according to the method of adjustment procedure. The stimulus was a 10 cd/m<sup>2</sup> sine wave grating of various sizes concurrently modulated at 12 hz and 1 cpd (upper set of coordinates) or 12 cpd and 1 hz (lower set of data). It was presented to the left eye either foveally (left sets of coordinates) or at 6° in the TVF (right sets of data). The background stimulus was a 0.03 cd/m<sup>2</sup>, 20.8° x 15° diffuse adapting field presented to the same eye. The error bars indicate  $\pm 1$  standard error. No overlap of error bars always indicates a statistically significant deviation from control sensitivity.

No background  
 0.03 cd/m<sup>2</sup> bkgmd.



field was present, while the open bars show data obtained in the presence of the 0.03 cd/m<sup>2</sup> rod-light adapting background. The error bars indicate  $\pm 1$  standard error, so that statistical significance is easy to discern. As would be expected from the CFF literature (Granit & Harper, 1930; Hecht, Schlaer, & Verrijp, 1933; Hylkema, 1942), sensitivity to the Flicker stimulus is higher in the fovea than parafovea, and increases monotonically with stimulus size. However, of greater interest to this thesis is the influence of retinal position and stimulus size upon the magnitude of background enhancement. For the Flicker stimulus, background enhancement is marginally evident in the fovea with the smallest (0.5°) stimulus used (also see figure 16), and is not apparent with larger stimuli. In comparison, background enhancement for the 3° and particularly the 1° Flicker stimulus is evident at 6° parafoveally. Unfortunately, absolute sensitivity to the 0.5° test stimulus was not sufficient to obtain data at parafoveal eccentricities greater than 3°. Generally then, these Flicker data suggest that background enhancement increases with the amount of parafoveal displacement (also see figure 21 below) and is inversely related to the size of the test display.

The bottom portion of figure 20 shows comparable data examining the influence of rod-light adapting backgrounds upon contrast sensitivity to the Grating stimulus. For all illustrated conditions, there is some evidence for background enhancement of grating sensitivity. The influence of stimulus size for foveal presentation is hard to interpret since grating enhancement is greatest with a 3° stimulus which due to the small size of the fovea (<2°), must excite regions of the non-foveal retina. However, unlike the

comparable Flicker data, the extent of enhancement seen with a Grating stimulus centered in the fovea is greatest with the largest stimulus used. Therefore, the effect of test display size upon the magnitude of background enhancement is different for Flicker and Grating effects.

The influence of retinal position is better discerned in figure 21, which shows the influence of retinal position on a  $1^\circ$  square Flicker (upper coordinates) and Grating (lower coordinates) stimulus in the presence and absence of a  $0.03 \text{ cd/m}^2$  adapting field. The error bars indicate  $\pm 1$  standard error. Under either adapted state, absolute sensitivity decreases with parafoveal displacement as would be expected by classical psychophysical data. However, the magnitude of the background enhancement of both Flicker and Grating visibility also increases with the degree of parafoveal displacement. In order to better compare the influence of retinal position upon flicker and grating enhancement, I calculated, from the data presented in figure 21, background enhancement according to formula 3. Figure 22 plots these background enhancement values as a function of the degree of parafoveal displacement for the Flicker (filled circles) and Grating (filled triangles) stimulus. This plot clearly shows that background enhancement of both Flicker and Grating visibility tends to increase with parafoveal displacement, but that the gradient is much steeper for the Flicker stimulus.

Figure 21. Percent contrast sensitivity as a function of retinal position is plotted for observer GL. The data were collected according to the method of adjustment procedure. The stimulus was a  $1^\circ \times 1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating concurrently modulated at 12 hz and 1 cpd (upper set of coordinates) or 12 cpd and 1 hz (lower set of data). It was presented to the left eye either foveally at  $3^\circ$ ,  $6^\circ$ , or  $9^\circ$  in the TVF. The background stimulus was a  $0.03 \text{ cd/m}^2$ ,  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye. The error bars indicate  $\pm 1$  standard error. No overlap of error bars always indicates a statistically significant deviation from control sensitivity.

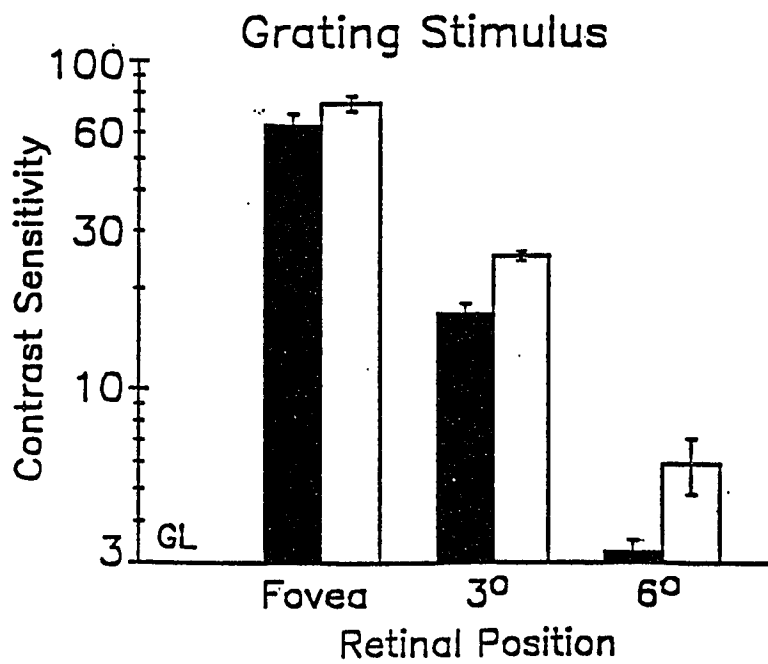
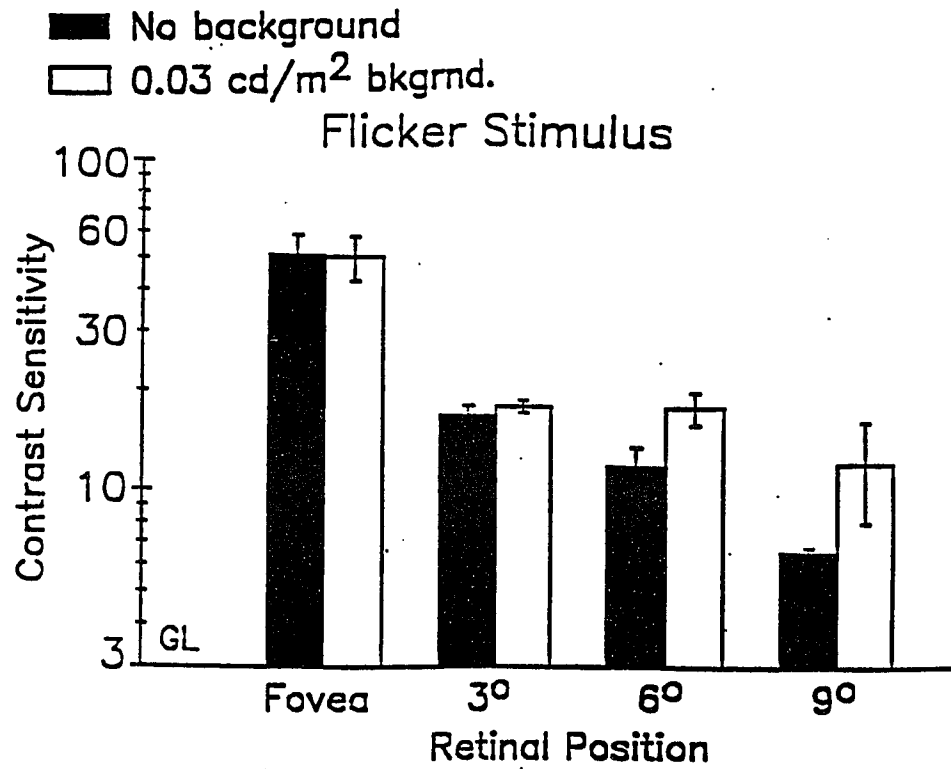
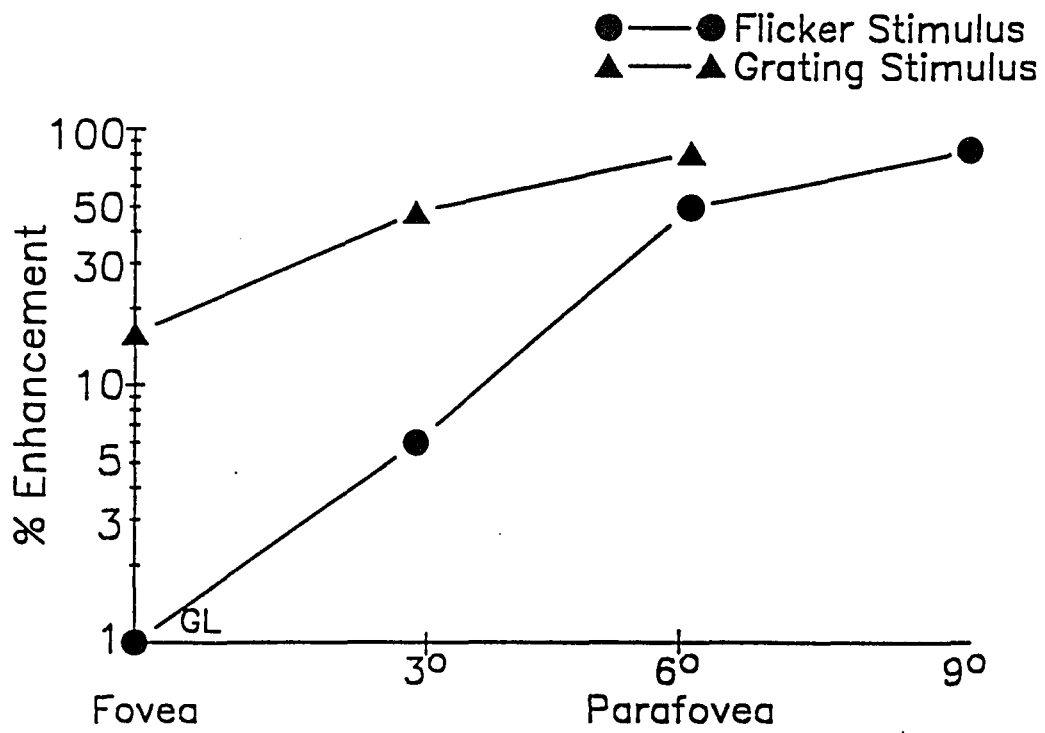


Figure 22. Percent enhancement as a function of retinal position for the Flicker and Grating stimulus is plotted for observer GL. These data were collected with the method of adjustment procedure and derived from data plotted in figure 21. The stimulus was a 10 cd/m<sup>2</sup>, 1° x 1° sine wave grating modulated concurrently at 12 hz and 1 cpd (closed circles) or at 12 cpd and 1 hz (closed triangles). The stimulus was presented foveally and at 3°, 6° , and 9° in the TVF of the left eye. The background stimulus was a 0.03 cd/m<sup>2</sup>, 20.8° x 15° diffuse adapting field presented to the same eye. Since the size of a plotted datum always exceeds  $\pm 1$  standard error, no overlap of data points always indicates a statistical significance.



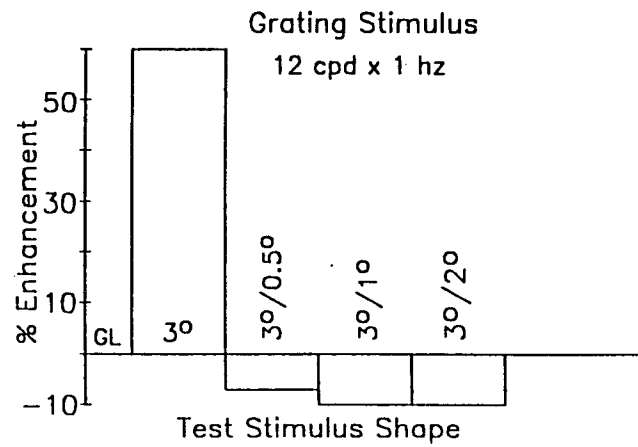
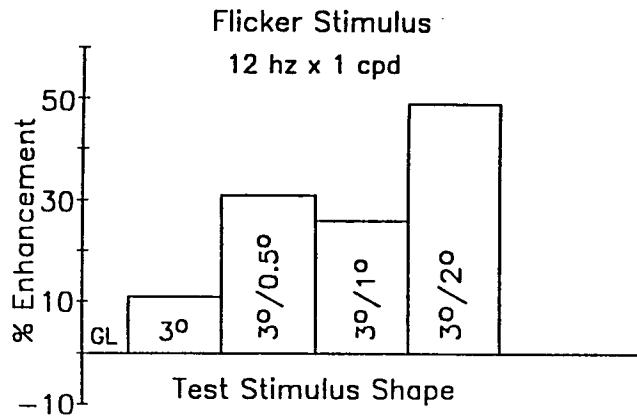
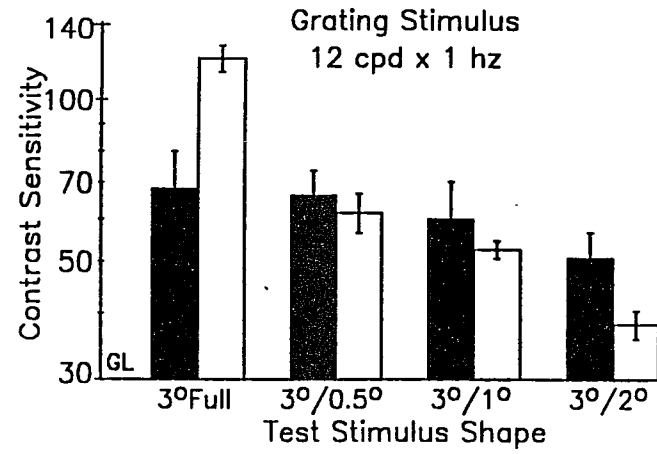
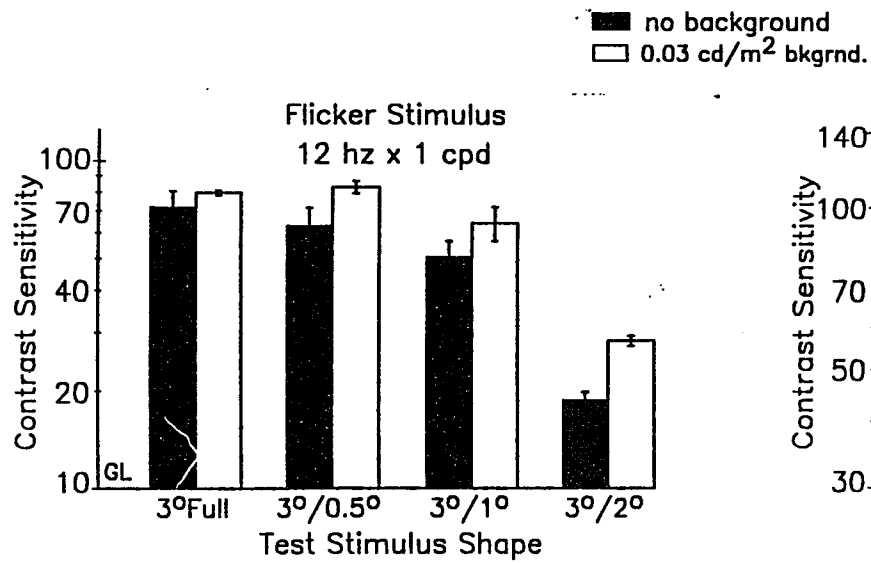
### B. Importance indicated by manipulation of stimulus shape

Figure 23 shows the influence of the shape of a foveally centered test probe upon the sensitivity to the prototypical Flicker (12 hz x 1 cpd stimulus, on the left) and Grating (12 cpd x 1 hz stimulus, on the right) stimulus with and without the presence of a 0.03 cd/m<sup>2</sup> rod-stimulating background. On both sets of coordinates, the four sets of bars show from left to right results obtained with the full size ("3°") test stimulus, and annuli with inner central 0.5°, 1°, and 2° removed.

First consider the influence of removing the center of the stimulus upon overall sensitivity. Whether or not the background was present, sensitivity of the Flicker stimulus was not significantly impaired by removing the central 0.5° or 1° of the stimulus. This finding might seem surprising, since the central retinal area might be expected to be most sensitive to both higher temporal and spatial frequencies. However, this finding is in line with results of Roehrig (1959), who found that removal of the central 20% of a foveally centered stimulus of any size would have no effect upon CFF. The data in figure 23 show that removal of the central 2° of the test stimulus did reduce flicker sensitivity.

In comparison, under dark adapted conditions, sensitivity to the grating stimulus was also hardly impaired by removing the central 0.5° or 1° of the test stimulus. However, in the presence of the dim adapting field, sensitivity is grossly reduced by

Figure 23. Percent contrast sensitivity as a function of test stimulus shape is plotted for observer GL (upper set of coordinates). The data were collected according to the method of adjustment procedure. The stimulus was a  $3.2^\circ \times 2.4^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating which was either presented fully or as annuli with the inner central  $0.5^\circ$ ,  $1^\circ$ , and  $2^\circ$  removed. The grating was concurrently modulated at 12 hz and 1 cpd (left set of coordinates) or 12 cpd and 1 hz (right set of data). It was presented foveally to the left eye. The background stimulus was a  $0.03 \text{ cd/m}^2$ ,  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye. The error bars indicate  $\pm 1$  standard error. No overlap of error bars always indicates a statistically significant deviation from control sensitivity. The lower set of graphs is derived from the same data as the upper set of coordinates and shows percent enhancement as a function of test stimulus shape also for observer GL.



removing the central portion of the test stimulus. Kelly (1978) found, under much more light adapted conditions but with no "extra" adapting field (i.e., he used an achromatic 300 td stimulus of 7.5°), that failure to stimulate the central fovea decreased grating sensitivity.

In order to better appreciate the influence of the background upon sensitivity independent of the absolute sensitivity changes discussed above, the magnitude of enhancement was obtained for the various stimulus conditions according to formula 3 and is plotted on the bottom of figure 23. For the Flicker stimulus (on the left), the background produces no significant enhancement of the solid test stimulus as already discussed above (see figure 20). However, the background enhances the sensitivity to all of the annuli, particularly the stimulus with the central 2° removed. Without stabilizing retinal images, eye movements are inevitable; for this reason, this stimulus probably influenced the fovea to some extent, but certainly much less than the other annuli. The fact that enhancement is seen with this shape stimulus alone suggests that under the conditions of the present study (i.e., using a large stimulus) the Flicker effect is minimal or absent in the fovea.

In comparison, the data on the bottom right side of figure 23 shows that the rod-stimulating background only enhances sensitivity to the solid grating stimulus, and does not enhance sensitivity to annular grating stimuli. In fact, the visibility of all annuli is decreased by background presentation. Clearly, the influence of background presentation

upon grating visibility is much different than the corresponding influence upon flicker visibility. This finding at first seemed perplexing since, like the Flicker effect, the Grating effect also was observed to increase with the extent of parafoveal displacement (see figures 20 and 21 above). However, results presented in part III of this chapter suggest an explanation.

In conclusion, the foregoing experiments established that in parafoveal retina, the Flicker as well as the Grating effect increased in magnitude with a decrease in stimulus size, and that the magnitude of both Flicker and Grating effect increased with the degree of parafoveal displacement. However, the magnitude of this retinal position effect is much greater for the Flicker than the Grating effect. Although the Grating effect can be obtained with foveal stimulation, the Flicker effect is absent.

### Part III. Importance of Background Field Size and Shape upon the Magnitude of the Flicker and Grating Effect.

In the course of performing the experiments described in parts I and II above, I additionally examined the influence of the shape and size of adapting stimuli upon the visibility of the prototypical Flicker and Grating stimuli. None of these manipulations produced any additional distinctions between the Flicker and Grating effects which have not already been described above. However, they seem to illustrate a number of important points characteristic of enhancement due to adapting field influences. These

characteristics led to meaningful practical implications which will be discussed in chapter 7.

### Methods

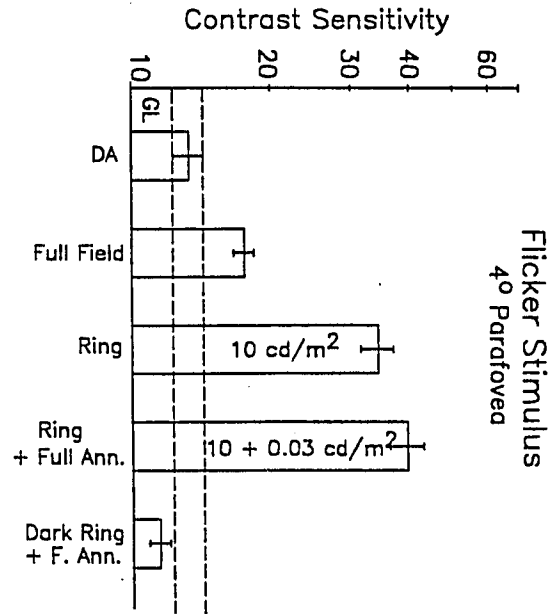
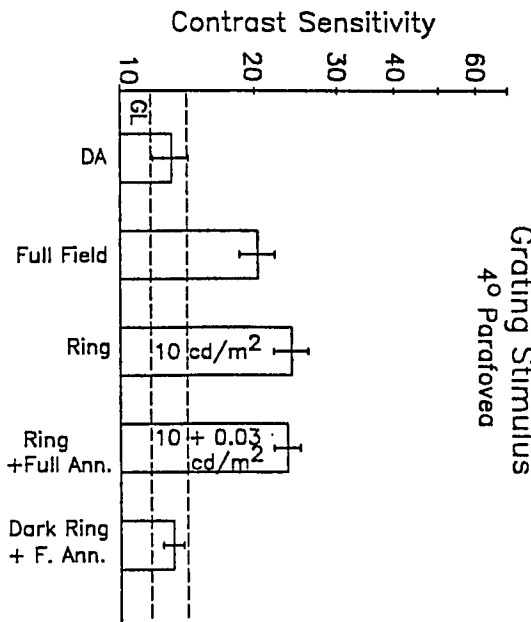
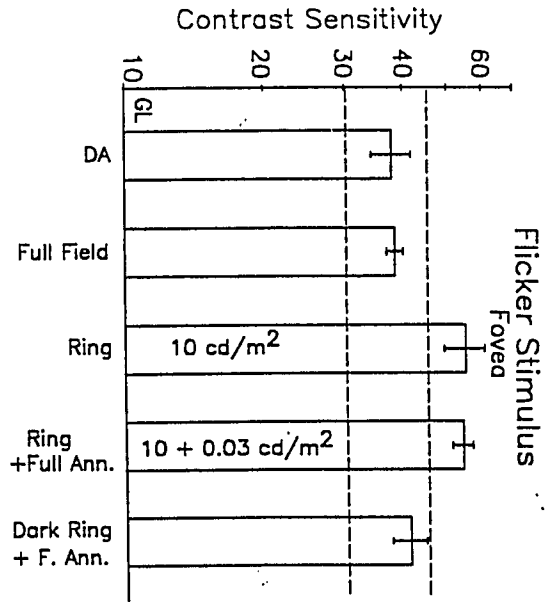
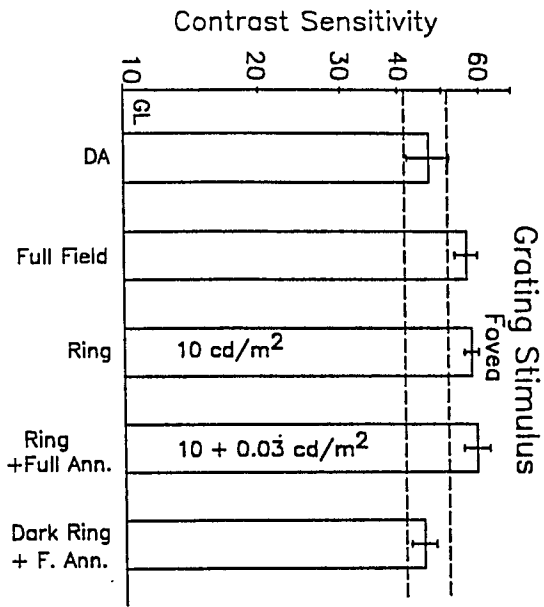
All procedures used are as described in parts I and II above.

### Results and Discussion

Results from observer GL are shown in figure 24. All four coordinates show contrast sensitivity for a  $10 \text{ cd/m}^2$  stimulus which was a  $1^\circ$  sided square. The four sets of coordinates represent data obtained in the fovea (on the left) or  $4^\circ$  parafoveally (on the right) in which the test stimulus was the prototypical flicker stimulus (12 hz x 1 cpd, on top) or grating stimulus (12 cpd x 1 hz, on the bottom). The sequence of stimulus conditions represented by the five vertical bars is the same for all sets of coordinates, test and adapting stimulus configurations are fully illustrated and described in figure 8 of chapter 2. The error bars indicate  $\pm 1$  standard error, the dashed line represents a 95% confidence interval. A departure of an error bar from the control interval indicates a difference which is statistically significant.

First consider the parafoveal flicker data (upper right coordinates). The left most bar shows the sensitivity to the  $1^\circ$  flicker stimulus in the otherwise dark-adapted eye.

Figure 24. Percent contrast sensitivity as a function of background size and luminance is plotted for observer GL. These data were collected with the method of adjustment procedure. The  $1^\circ \times 1^\circ$ ,  $10 \text{ cd/m}^2$  stimulus was presented without a rod-adapting background field (DA), in the presence of a full  $0.03 \text{ cd/m}^2$  adapting stimulus (Full Field), in the presence of  $1^\circ$ ,  $10 \text{ cd/m}^2$  contiguous ring (Ring), in the presence of a  $1^\circ$ ,  $10 \text{ cd/m}^2$  contiguous ring in addition to a full,  $0.03 \text{ cd/m}^2$  contiguous annulus (Ring and Full Annulus), or in the presence of a  $1^\circ$ , unilluminated contiguous ring plus a full,  $0.03 \text{ cd/m}^2$  contiguous annulus (Dark Ring and Full Annulus). Stimuli were modulated at  $12 \text{ hz} \times 1 \text{ cpd}$  (plots on top) or at  $12 \text{ cpd} \times 1 \text{ hz}$  (lower set of coordinates), and presented to the left eye foveally (plots on left) or at  $4^\circ$  TVF (right set of coordinates). A control value, i.e. the stimulus in the absence of the adapting field, is indicated on the abscissa as DA (dark adapted). 95% confidence intervals for this control condition are indicated by the horizontal dashed lines. Error bars always represent  $\pm 1$  standard error. Therefore, a departure of an error bar from the control interval indicates a difference which is statistically significant.



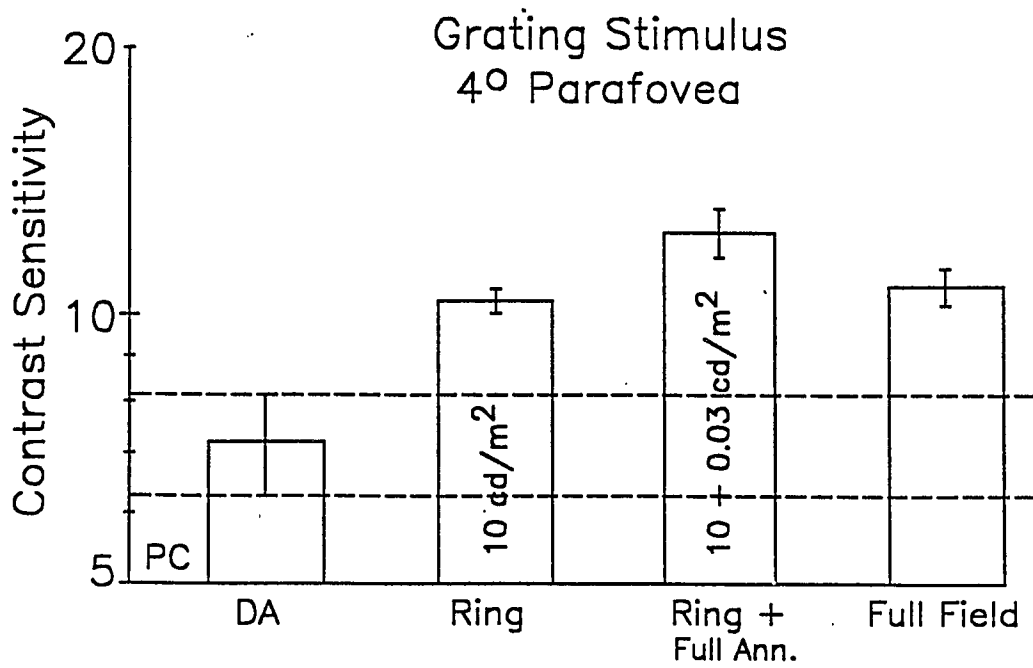
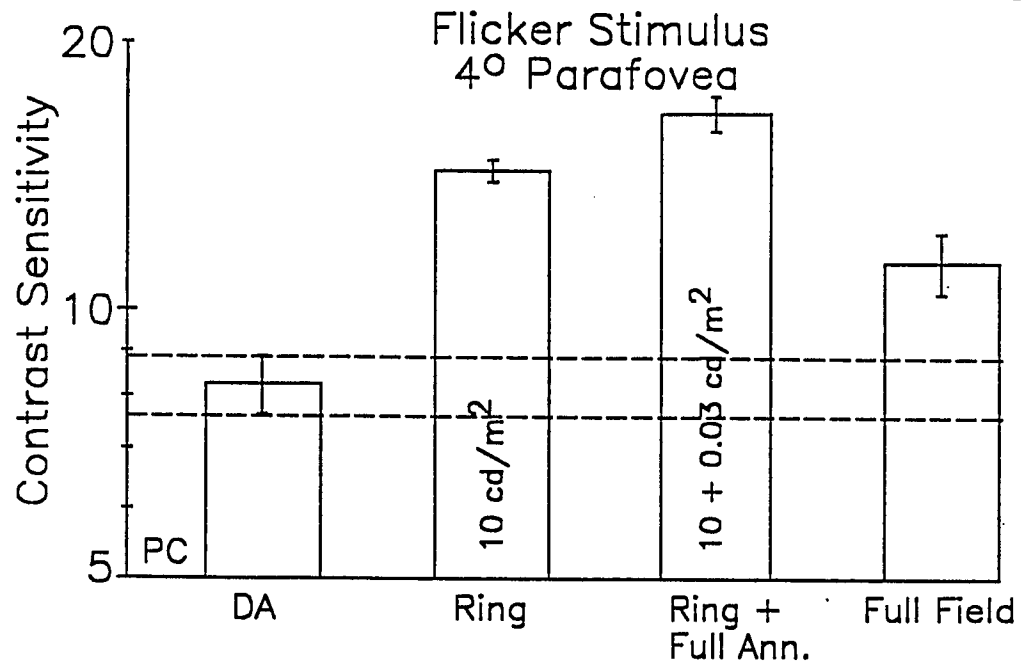
Presentation of a  $0.03 \text{ cd/m}^2$  solid background of  $20.8^\circ \times 15^\circ$  (second bar from the left) enhances flicker visibility as would be expected on the basis of results reported previously in this thesis. However, a much greater increase in sensitivity is produced by introducing a much smaller annular background field (third bar from the left) with a luminance equal to that of the test stimulus,  $10 \text{ cd/m}^2$ . This annulus has an inner border which is contiguous with the test stimulus (i.e., is shaped as a  $1^\circ$  sided square) and with an outer dimension equalling that of the "full-sized" test stimulus of  $3.2^\circ \times 2.4^\circ$ . The importance of this observation is considered further in chapter 6. In the presence of this smaller annulus, further introduction of the full, large, dim background field no longer significantly enhanced flicker sensitivity significantly (fourth bar from the left). This observation probably reflects the same mechanistic limitation which accounts for the decrease in background field enhancement with larger sized test stimuli (i.e., see figure 20 and 21 above). The fifth bar from the left shows that if a "black annulus" (inner dimension shaped as a  $1^\circ$  sided square, a  $3.2^\circ \times 2.4^\circ$  outer dimension) surrounds the test stimulus, introduction of the  $0.03 \text{ cd/m}^2$  background (i.e., an annulus with  $3.2^\circ \times 2.4^\circ$  inner dimension,  $20.8^\circ \times 15^\circ$  outer dimension) no longer improves the visibility of the test stimulus.

The other three quadrants in figure 24 show similar influences of background field shape, regardless of whether flicker or grating visibility is examined in both foveal and parafoveal retina. In the parafoveal retina, background field shape exerts a remarkably similar influence upon flicker visibility (upper right coordinates) and grating visibility

(lower right coordinates). In the fovea, similar results are observed save that the dim, full sized background field failed to enhance visibility of the flicker stimulus (upper left coordinates). This "exception" is, in fact, consistent with results reported in figures 20 and 21 above.

Data in figure 25 display results for observer PC. Data are shown either without a background field present (DA) or in the presence of backgrounds with sizes and intensities as indicated. Data are similar to those of observer GL. For both flicker and grating stimuli, contrast sensitivity increases significantly when a  $1^\circ$ ,  $10 \text{ cd/m}^2$  ring is added. A further slight increase is achieved, when a  $0.03 \text{ cd/m}^2$  rod-stimulating annulus is added. The presence of a full field, rod-stimulating background is not as effective in enhancing either flicker or grating visibility as the  $1^\circ$  ring of luminance equal to that of the stimulus.

Figure 25. Percent contrast sensitivity as a function of background size and luminance is plotted for observer PC. These data were collected with the method of adjustment procedure. The  $1^\circ \times 1^\circ$ ,  $10 \text{ cd/m}^2$  stimulus was presented without a rod-adapting background field (DA), in the presence of a full  $0.03 \text{ cd/m}^2$  adapting stimulus (Full Field), in the presence of  $1^\circ$ ,  $10 \text{ cd/m}^2$  contiguous ring (Ring), in the presence of a  $1^\circ$ ,  $10 \text{ cd/m}^2$  contiguous ring in addition to a full,  $0.03 \text{ cd/m}^2$  contiguous annulus (Ring and Full Annulus), or in the presence of a  $1^\circ$ , unilluminated contiguous ring plus a full,  $0.03 \text{ cd/m}^2$  contiguous annulus (Dark Ring and Full Annulus). Stimuli were modulated at  $12 \text{ hz} \times 1 \text{ cpd}$  (plot on top) or at  $12 \text{ cpd} \times 1 \text{ hz}$  (lower set of coordinates), and presented at  $4^\circ$  TVF. A control value, i.e. the stimulus in the absence of the adapting field, is indicated on the abscissa as DA (dark adapted). 95% confidence intervals for this control condition are indicated by the horizontal dashed lines. Error bars always represent  $\pm 1$  standard error. Therefore, a departure of an error bar from the control interval indicates a difference which is statistically significant.



## Chapter 5

As reviewed in previous chapters, dim monocular adapting fields enhance sensitivity to high frequency flicker and high spatial frequency gratings (e.g., Goldberg et. al., 1983; Naarendorp et. al., 1988). The results in chapter 3 established that rod-light adaptation enhances the visibility of monocular displays modulated concurrently at high temporal and low spatial frequencies, as well as to displays modulated at high spatial and low temporal frequencies. However, these background fields have remarkably little influence upon other spatio-temporal frequencies. Hence, a Flicker and Grating enhancement effect can be distinguished operationally. The results in chapter 4 established that various manipulations, including the retinal position, size and shape of both test and adapting stimulus, and the types of photoreceptors stimulated by test and adapting stimuli differentially influence Flicker and Grating effects. This suggests the possibility that distinct neural mechanisms mediate these separable effects.

Physiological research suggests that the Flicker enhancement effect (SRCI) is likely to reflect a mechanism which is at least partially within the distal-most retina (Frumkes & Eysteinson, 1988; Nelson, Pflug, & Baer, 1990). Moreover, several older psychophysical studies (Vernon, 1934; Lipkin, 1962) have shown that light-adapting one eye has only little influence upon flicker sensitivity in the contralateral eye, a result which is certainly consistent with a distal retinal locus of interaction.

To date, no published evidence provides a clue regarding the site of interaction

for the Grating effect. However, recent psychophysical and evoked potential evidence shows that light-adapting one eye significantly improves grating sensitivity in the contralateral eye (Denny et. al., 1991; Eysteinson et. al., 1993). Moreover, there are a large number of similarities between Denny's interocular adapting-effect which have been documented by Denny (1992) and the Grating effect as documented both in previous studies (Naarendorp et. al., 1988; 1991) as well as by results reported in chapter 4 of this thesis. Collectively, these findings suggest that the interocular adapting influence reported by Denny may involve the same mechanism as the grating enhancement effect.

The experiments in the present chapter examine and compare the influence of monocular versus interocular light and dark adaptation upon sensitivity to visual displays which were concomitantly modulated in both spatial and temporal domains. Interocular adaptation proves to be as effective as monocular adaptation in influencing the visibility of high spatial frequency gratings flickered slowly but has no influence upon low spatial frequency gratings flickered rapidly. These findings are the most clear-cut evidence that I have obtained indicating that distinct neural mechanisms mediate Flicker and Grating enhancement effects.

### Methods

All monocular experiments reported below were conducted according to the procedures specified in chapter 2. Chronologically speaking, the first set of data which

were collected are these summarized by figures 26-28 in which the author was the observer. These experiments were conducted in as identical a fashion as possible to the experiments summarized in figures 9, 10, 12, and 13 described in chapter 3. Hence, a  $1^\circ$  square display of  $10 \text{ cd/m}^2$  average luminance was presented  $4^\circ$  parafoveally to the left eye. This time, however, two adapting conditions were used. Specifically, the  $0.03 \text{ cd/m}^2$  adapting field shaped as a  $20.8^\circ \times 15^\circ$  rectangle was presented either to the left eye (which directly viewed the test display) or to the contralateral right eye. Although these data were collected about 14 months after obtaining results presented in figures 9 and 10 of chapter 3 from the same observer, the results obtained with the same (monocular) stimulus conditions are remarkably consistent. I then replicated some of these findings in a second observer, PC, to assure their generality (figure 29).

The dark adaptation experiments reported in figure 31 involve data collected by N.Denny according to the procedure specified in chapter 4. In these experiments, however, the following sequence of events was used prior to obtaining the indicated data. Both eyes of the observer were first dark-adapted for 20 minutes. Then either the "test eye" was exposed to the  $800 \text{ cd/m}^2$  bleaching stimulus or the eye contralateral to the "test eye" was so exposed. Following this bleach, contrast sensitivity for the 11 cpd grating was tracked throughout the ensuing period of dark adaptation.

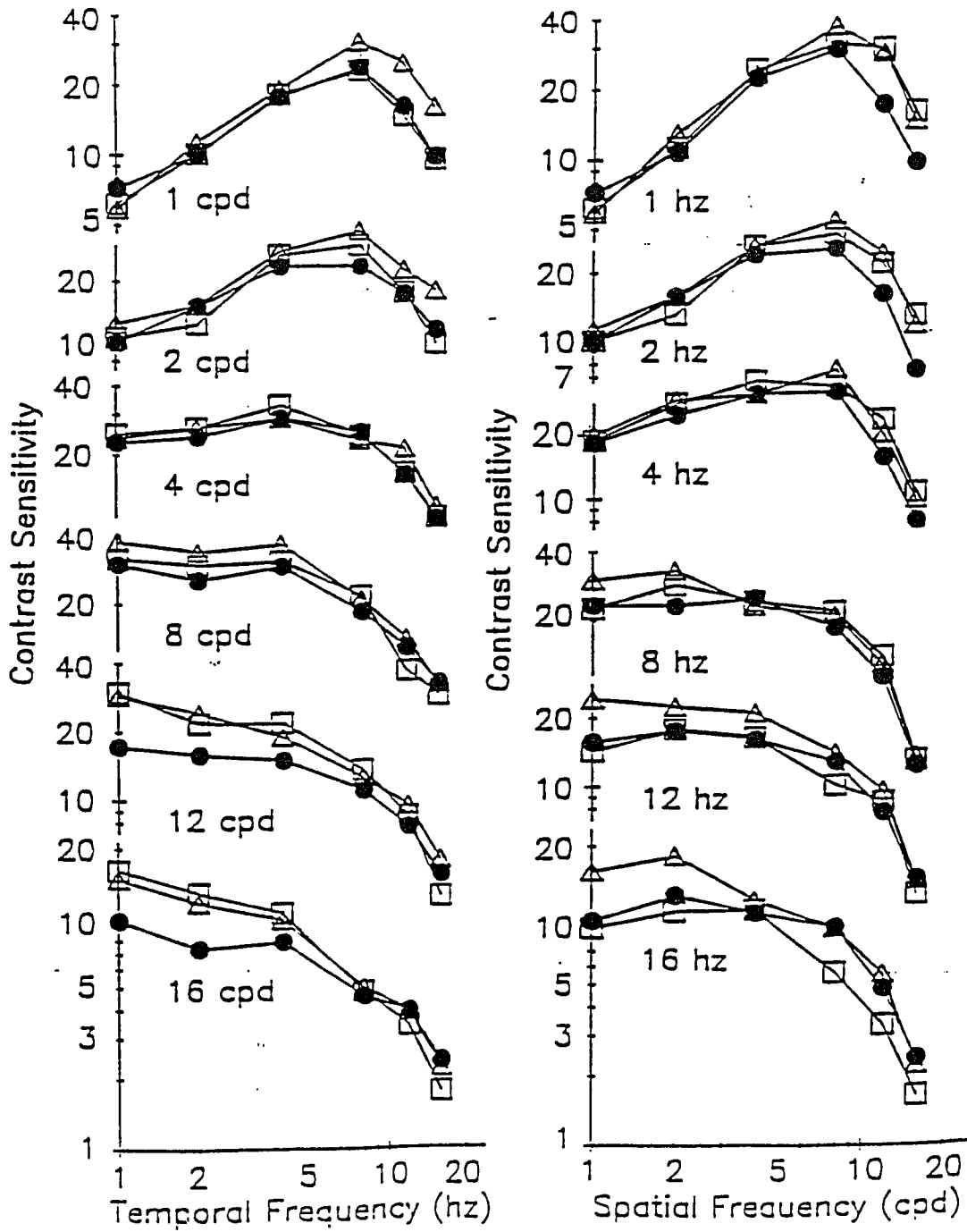
## Results

Figure 26 displays results for observer GL on log-log coordinates in a fashion which is identical to that used to present figure 9 in chapter 3. Figure 26 shows monocular contrast sensitivity when no background field was present (filled circles), in the presence of a dim background field presented to the same eye as the test stimulus (open triangles), and additionally when a dim background field is presented to the contralateral eye (open squares). On the left, contrast sensitivity is plotted as a function of temporal frequency for the indicated spatial frequency. On the right, the same data is replotted so that contrast sensitivity is shown as a function of spatial frequency for a specified temporal frequency.

As reported in chapter 3, dim, monocular background fields enhance sensitivity to low spatial frequencies flickered rapidly which is best observed in the upper left or lower right sets of coordinates. In comparison, interocular backgrounds have a negligible influence upon low spatial frequencies flickered rapidly. Also as reported in chapter 3, dim, monocular background fields enhance sensitivity to high spatial frequencies flickered slowly best observed in the upper right or lower left sets of coordinates. However, interocular backgrounds have essentially the same influence upon high spatial frequencies flickered slowly. Hence, the "Flicker" and "Grating" effects can be distinguished on the basis of monocular versus interocular presentation. Figure 26 also shows that neither monocular nor interocular backgrounds influence sensitivity to combinations of

Figure 26. Percent contrast sensitivity as a function of spatial and temporal frequency is plotted for observer GL. The data were collected according to the method of adjustment procedure. The stimulus was a  $1^\circ \times 1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating modulated concurrently in the spatial and temporal domains and presented to the left eye at  $4^\circ$  in the TVF. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field either presented monocularly or interocularly at a luminance level of  $0.03 \text{ cd/m}^2$ . The closed circles represent control data obtained with no background, the open triangular symbols indicate the presence of a  $0.03 \text{ cd/m}^2$  monocular background field while the open squares symbolize the addition of a  $0.03 \text{ cd/m}^2$  interocular adapting field. The left set of coordinates shows contrast sensitivity as a function of temporal frequency for the indicated spatial frequencies, the right set of coordinates shows contrast sensitivity as a function of spatial frequency for the indicated temporal frequencies.

□ 0.03 cd/m<sup>2</sup> interocular bkgmd.  
 △ 0.03 cd/m<sup>2</sup> monocular bkgmd.  
 ● no background present  
 Obs.: GL



intermediate spatial (4-8 cpd) and temporal (4-8 hz) frequencies.

In order to better display the magnitude of the enhancement independent of the absolute sensitivity to a specific spatial or temporal frequency, I calculated the background-induced enhancement effect for each set of data points according to formula 3. Figure 27 shows this derived enhancement value plotted as a function of the temporal frequency of the display with spatial frequency as a parameter. In order to emphasize the frequency dependent nature of the enhancement effect, the low spatial frequencies (1 and 2 cpd) are represented with open symbols and the higher spatial frequencies (8-16 cpd) with closed symbols. The upper plot of figure 27 displays the enhancement effect of monocular adaptation, whereas the lower plot shows the enhancement effect of a contralaterally presented background field. The upper coordinates present clear evidence for both a Grating effect indicated by dark symbols on the left (the 12 and 16 cpd grating data at low temporal frequencies) and a Flicker effect indicated by open symbols on the right (the 1 and 2 cpd grating data at high temporal frequencies). In comparison, the lower coordinates also clearly show evidence for a Grating effect but a complete absence of a Flicker effect.

In a similar fashion figure 28 plots enhancement as a function of the spatial frequency of the display with temporal frequency as a parameter for either monocular (upper coordinate) or interocular backgrounds (lower coordinates). Again, to highlight the frequency dependent nature of the enhancement effect, I plotted the low temporal

Figure 27. Percent enhancement as a function of temporal frequency is plotted for observer GL. These plots are derived from the same data presented in figure 26. The stimulus was a  $1^\circ \times 1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating modulated concurrently in the spatial and temporal domains and presented to the left eye  $4^\circ$  in the TVF. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye (upper plot) or to the contralateral eye (lower set of coordinates) at a luminance level of  $0.03 \text{ cd/m}^2$ . The low spatial frequencies (1 and 2 cpd) are represented with open symbols and the high spatial frequencies (8-16 cpd) with closed symbols.

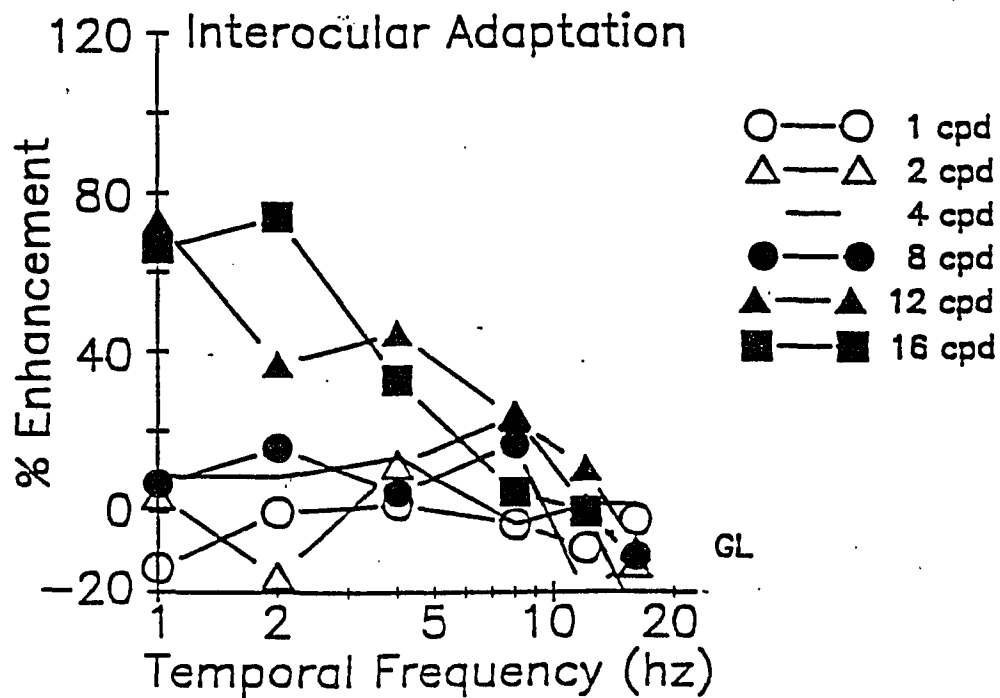
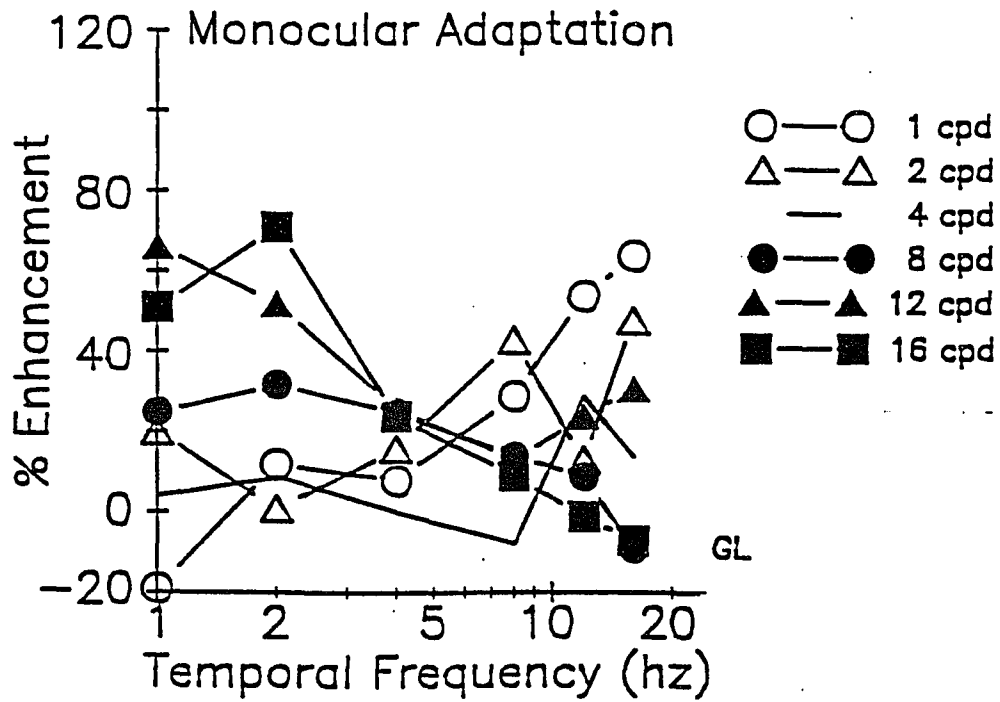
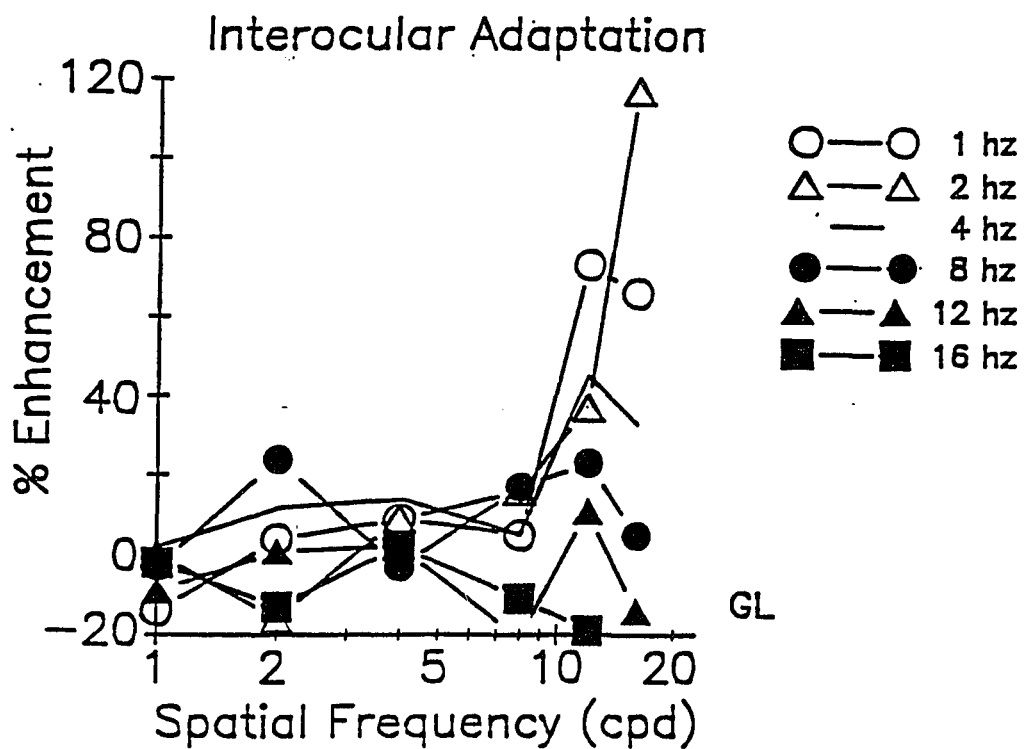
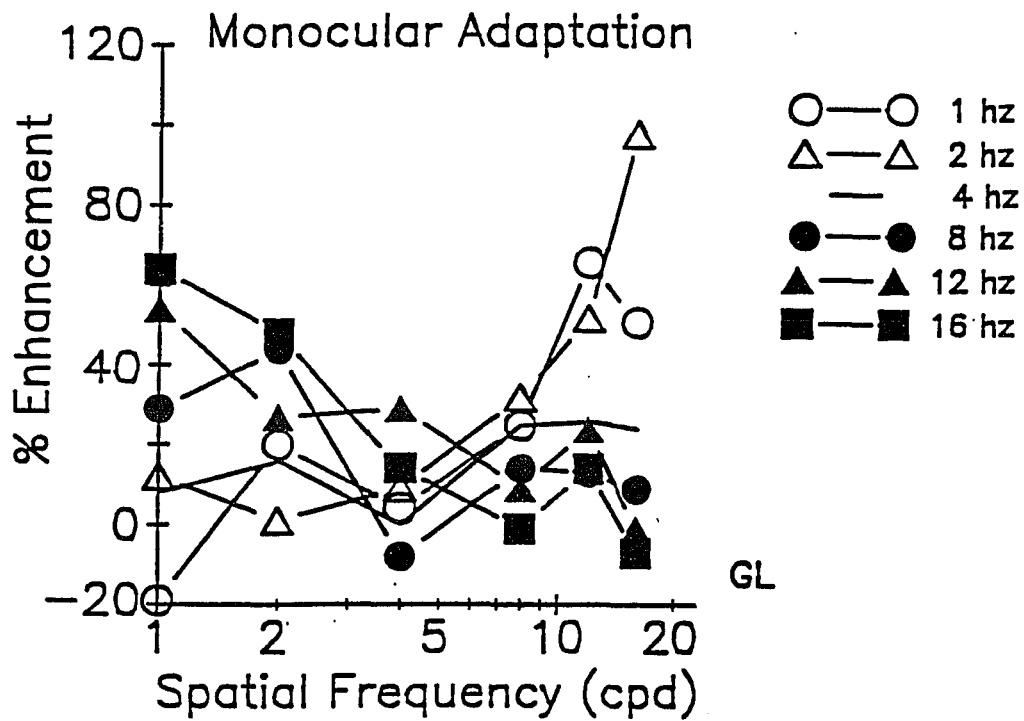


Figure 28. Percent enhancement as a function of spatial frequency is plotted for observer GL. These plots are derived from the same data presented in figure 26. The stimulus was a  $1^\circ$  by  $1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating modulated concurrently in the spatial and temporal domains and presented to the left eye  $4^\circ$  in the TVF. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye (upper plot) or to the contralateral eye (lower set of coordinates) at a luminance level of  $0.03 \text{ cd/m}^2$ . The low temporal frequencies (1 and 2 hz) are represented with open symbols and the high temporal frequencies (8-16 hz) with closed symbols.



frequencies (1 and 2 Hz) with open symbols and the higher temporal frequencies (8-16 Hz) with closed symbols. The upper coordinates again present clear evidence for both a Grating effect indicated by the open symbols on the right (the 1 and 2 Hz data) and a Flicker effect by the closed symbols on the left (the 8, 12, and 16 Hz data). In comparison, the lower coordinates clearly show evidence for a Grating effect but an absence of any Flicker effect.

Similar results for a second observer, PC, are shown in figure 29. Contrast sensitivity is plotted as a function of temporal frequency for a display modulated at 1 cpd (upper display) or as a function of spatial frequency for a display flickered at 1 Hz (bottom coordinates). Notice that monocular adaptation enhances sensitivity to a low spatial frequency display flickered rapidly (upper coordinates) and to a high spatial frequency display flickered slowly (lower coordinate): evidence for both a Flicker and Grating effect. However, interocular backgrounds produce a grating enhancement effect but no corresponding flicker enhancement effect. These results from observer PC are entirely consistent with the monocular data from observers GL and TEF presented in chapter 3 and with the monocular and interocular data from observer GL presented in figures 26-28.

Figure 30 compares the influence of the luminance of a  $20.8^\circ \times 15^\circ$  background field upon the contrast sensitivity to a  $1^\circ$  sided square of  $10 \text{ cd/m}^2$  as a test probe. The upper sets of coordinates show results for the Flicker stimulus presented foveally as well

Figure 29. Percent contrast sensitivity as a function of spatial and temporal frequency is plotted for observer PC. The data were collected according to the method of adjustment procedure. The stimulus was a  $1^\circ \times 1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating presented to the left eye  $4^\circ$  in the TVF and concurrently modulated at 1 cpd and various temporal frequencies (plot on the top), or at 1 hz and various spatial frequencies (lower set of coordinates). The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field either presented monocularly or interocularly at a luminance level of  $0.03 \text{ cd/m}^2$ . The closed circles represent control data obtained with no background, the open triangular symbols indicate the presence of a  $0.03 \text{ cd/m}^2$  monocular background field while the open squares symbolize the addition of a  $0.03 \text{ cd/m}^2$  interocular adapting field.

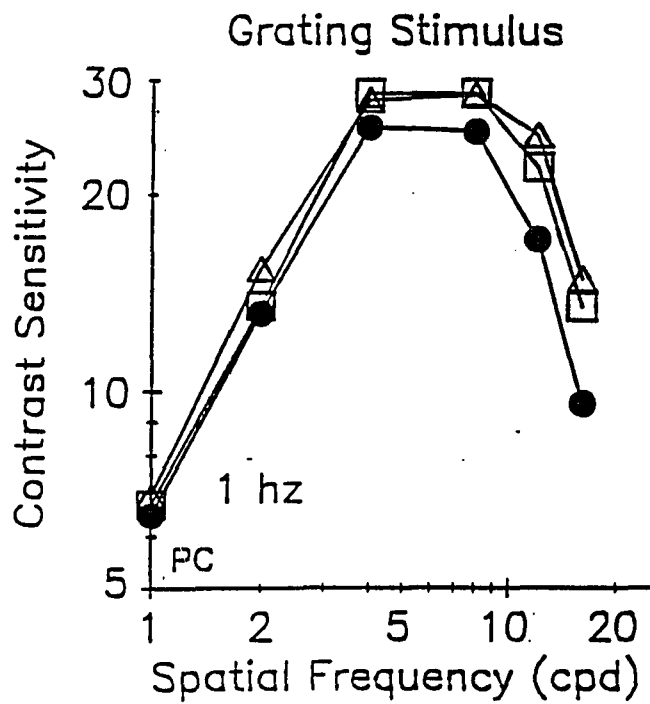
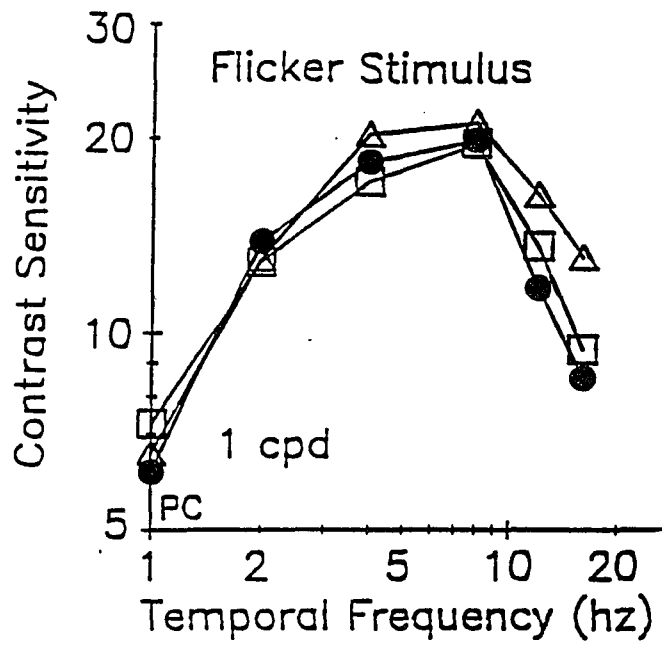
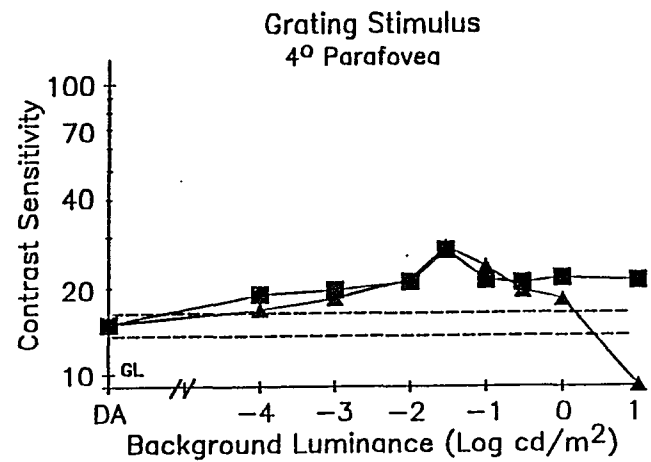
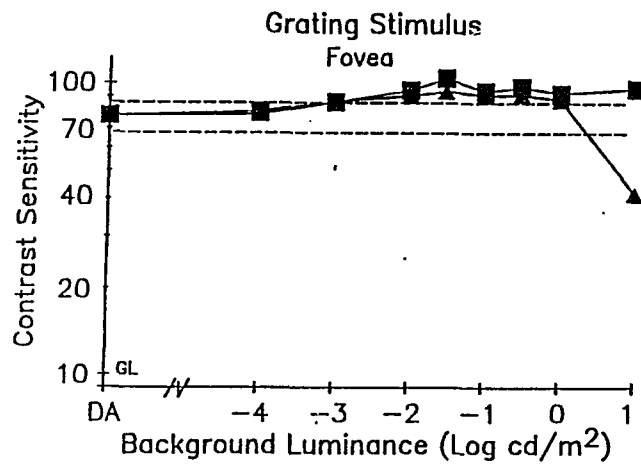
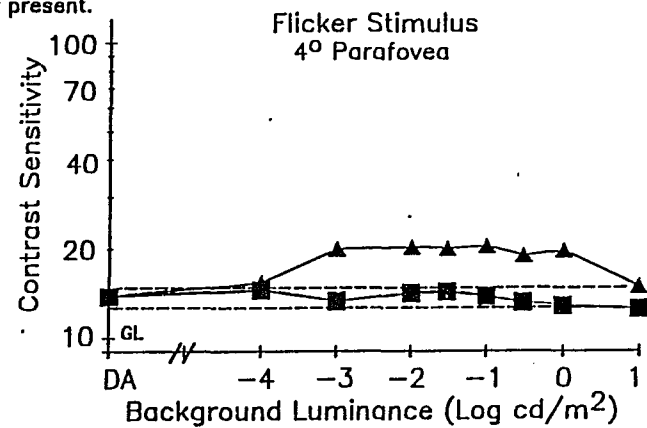
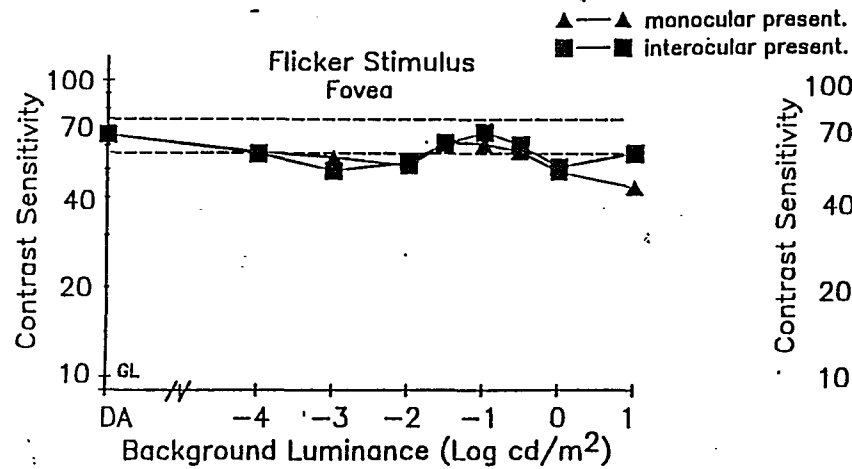


Figure 30. Percent contrast sensitivity as a function of log monocular and interocular background luminance is plotted for observer GL. These data were collected with the method of adjustment procedure. The stimulus was a  $10 \text{ cd/m}^2$ ,  $1^\circ \times 1^\circ$  sine wave grating and was concurrently modulated at 12 hz and 1 cpd (plots on the top), or at 12 cpd and 1 hz (lower set of coordinates). The stimulus was presented to the fovea (left sets of data) or  $4^\circ$  in the TVF (right sets of coordinates) of the left eye. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye or the contralateral eye, and was varied in luminance. The closed triangles represent monocular data and the closed squares show interocular data in either the fovea or the parafovea. 95% confidence intervals for this control condition are indicated by the pair of dashed horizontal lines. Since the size of a plotted datum always exceeds  $\pm 1$  standard error, a departure of a data point from within this interval always indicates a statistically significant deviation from control sensitivity.



as 4° parafoveally, the lower figure represents data for the Grating stimulus also presented foveally as well as 4° parafoveally. For each set of coordinates, 95% confidence intervals for the sensitivity value obtained with no background present is indicated by the pair of dashed horizontal lines. Since the size of a plotted datum always exceeds  $\pm 1$  standard error, a departure of a data point from within this interval always indicates a statistically significant deviation from control sensitivity.

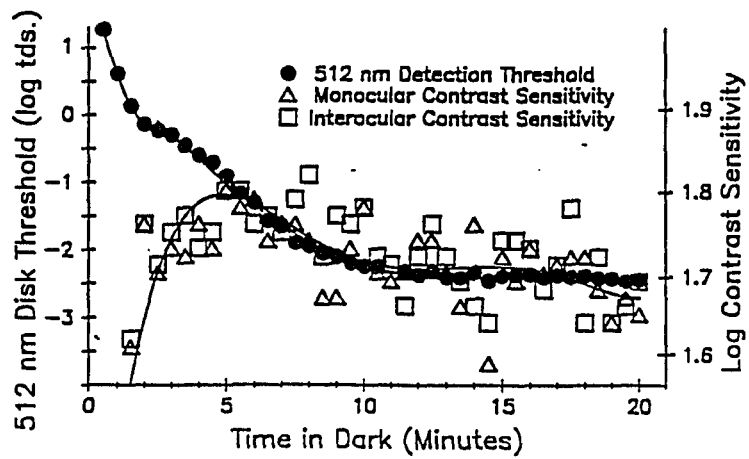
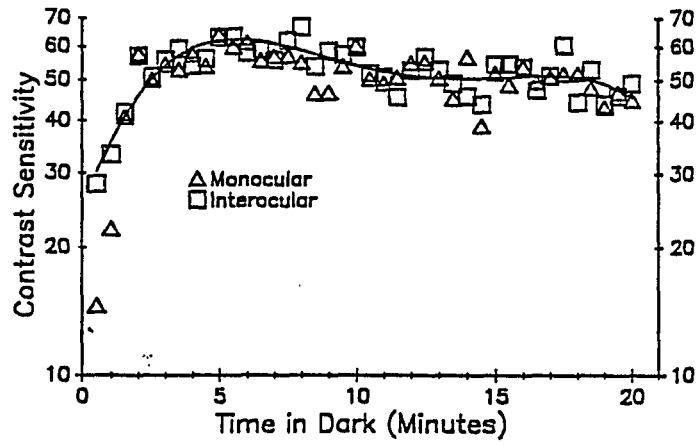
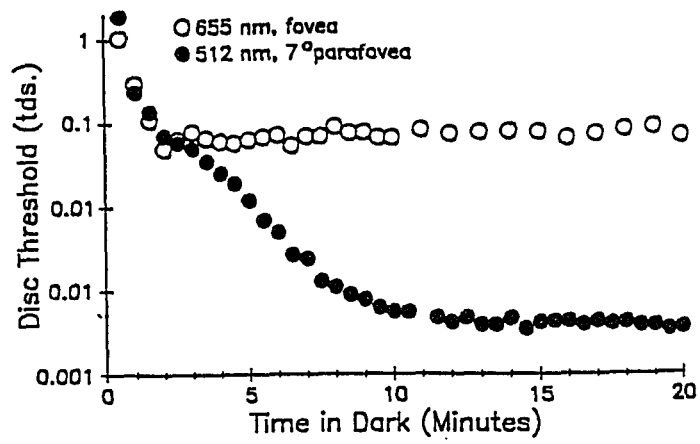
First consider the Flicker data in the plot on top of figure 30. Neither a monocular nor interocular background enhanced flicker visibility in the fovea. In the parafovea, a monocular enhancement effect is observed but interocularly, no background luminance level affects flicker visibility. These results show that the absence of an interocular Flicker effect reported on the basis of figures 26-29 was not dependent upon the use of one fixed luminance interocular background.

Now consider the grating data in the plots on the bottom of figure 30. Both monocular and interocular backgrounds with luminance values between -3 and 0 log cd/m<sup>2</sup> enhanced grating sensitivity. In fact, with exception of data collected with the highest luminance background used (10 cd/m<sup>2</sup>), monocular and interocular backgrounds have remarkably similar influences upon grating visibility. The exception is attributable to the reduction in the physical contrast of the retinal image as a result of the addition of a homogeneous field of equal luminance with monocular stimulation. Of course, this does not occur with interocular background presentation. Save for the exception, the

interocular Grating effect data presented in figures 26-30 are remarkably similar to the monocular Grating effect data suggesting the involvement of a common mechanism.

In the course of other investigations in our laboratory over the past 12 years, a variety of comparisons have been made between the influence of monocular and interocular dark-adaptation upon the sensitivity to high frequency flicker or high spatial frequency gratings. Hence, following exposure to a monocular bleaching source and throughout the time course of monocular dark adaptation, sensitivity in one eye was continually tracked in either the same or contralateral eye. Although dark-adaptation of one eye greatly reduces sensitivity to rapid flicker in the same eye (e.g., Goldberg et al., 1983), negligible influence is exerted upon flicker contrast sensitivity in the contralateral eye (Goldberg & Frumkes, unpublished findings 1983). In comparison, the effects of monocular and interocular dark adaptation have remarkably similar influences upon the sensitivity to high spatial frequency gratings. Figure 31 presents unpublished findings collected by N. Denny (1992) and shows sensitivity to an 11 cpd grating of 10 cd/m<sup>2</sup> luminance during the dark-adaptation period following a bleach of photopigment in either the viewing "test eye" or the contralateral eye. The monocular data (filled circular symbols) are those same shown in figure 17 of chapter 4 and show that sensitivity to the grating at first increases, then decreases again during dark-adaptation. Notice that with the exception of a few data points collected during the first two minutes of dark-adaptation, essentially the same data is obtained following bleaching of the contralateral eye. The similarity of these two sets of data strongly suggests that monocular and

Figure 31. Changes in the sensitivity of observer ND as a function of time in the dark (along abscissa in minutes) following a bleach of one eye with an  $800 \text{ cd/m}^2$  source for one minute. All data points are the median values from three experimental runs. For the experiments illustrated in the top coordinates, the detection threshold for a 500 ms duration,  $1^\circ$  diameter test probe was determined in the observer's right eye following exposure to the bleaching field. The stimuli, which were presented via a Maxwellian view optical system, were of the indicated wavelength and retina position. Notice the logarithmic spacing along the ordinate. For the experiments illustrated in the middle coordinates, contrast sensitivity for an 11 cpd grating was determined in the left eye following a bleach to the observer's left (triangles) or right (squares) eye. This stimulus was presented  $5^\circ$  in the temporal field, was  $10 \text{ cd/m}^2$  in luminance, and was shaped as a  $1^\circ$  sided square. Once again, notice the logarithmic scaling along the ordinate. The smooth function is a fourth order regression fit through the interocular data. The bottom sets of coordinates are derived from the upper two sets of data. Detection threshold for the 512 nm disk (the closed circles and left ordinate) and sensitivity to the 11 cpd grating (the open symbols and right ordinate) are plotted as a function of the time the dark. Notice that the spacing along the two ordinates differs by a factor of about 10.



interocular Grating effects reflect a common mechanism.

The data in figure 31 also indicate that at least in a qualitative sense, the influence of light and dark adaptation upon flicker sensitivity is equivalent. The monocular light adaptation experiment illustrated in chapter 4 (see figure 17 and related text) indicated that the decrease in sensitivity during dark adaptation follows the increase in rod-related detection sensitivity in the same eye. The results in figure 31 now extend these findings to bleaching of the contralateral eye. Since a grating  $>5$  cpd is detected only by cones and a background  $< 0.1$  cd/m<sup>2</sup> is detected by rods, both the Flicker and Grating effects in figure 26 represent rod-cone interaction.

To summarize, the results presented above indicate that the influence of monocular adaptation upon flicker sensitivity cannot be mimicked by interocular adapting stimuli. Considering the variety of interocular Flicker effects that have been reported (Sherrington, 1906; Cavonius, 1979), the complete absence of any effect of interocular adaptation might seem surprising. In comparison, Grating visibility is enhanced by monocular as well as interocular adaptation. Therefore, the Flicker and Grating effects may be distinguished by monocular versus interocular adaptation suggesting mediation of the enhancement effect by separate neural mechanisms.

## Chapter 6

### General Discussion

The results of the present study can be summarized as follows:

1. Dim background fields enhance sensitivity to high spatial frequencies flickered slowly and low spatial frequencies flickered rapidly. However, they have very little influence upon other spatial and temporal frequency combinations. Hence, there are operationally distinct Flicker and Grating enhancement effects;
2. Under the usual experimental circumstances examined in this study, dark-adapted rods tonically suppress cone sensitivity to rapid flicker as well as to high spatial frequency gratings, i.e., both Flicker and Grating effects involve rod-cone interaction. However, although the Grating effect can involve rod-rod interaction, no equivalent findings have been observed for the Flicker effect. In comparison, Coletta and Adams (1984) have obtained a Flicker effect involving cone-cone interaction, and some of the present flicker data obtained with background luminance values  $\geq 1 \text{ cd/m}^2$  are likely to similarly involve cone-cone interaction. I am unaware of any evidence for the Grating effect to involve cone-cone interaction;
3. Both Flicker and Grating enhancement effects decrease as the size of the stimulus increases, and increase with the extent of parafoveal displacement. However, the

gradient of the increase is much steeper for the Flicker stimulus than the Grating stimulus. Hence, with foveal stimulation, a Grating effect is often evident while a Flicker effect is difficult to discern;

4. Interocular adaptation has very little influence upon the sensitivity to rapid flicker. In comparison, interocular and monocular adaptation have a remarkably similar influence upon the visibility of a high spatial frequency gratings;

Although not part of this thesis, several different ERG and evoked potential studies have examined the effects of background enhancement upon both rapid flicker and high spatial frequency gratings. Using standard ERG procedures (Arden & Frumkes, 1986), these studies have demonstrated the flicker enhancement effect (SRCI). Under conditions involving interocular light- and dark-adaptation (Eysteinnsson et. al., 1993) a grating enhancement effect was observed. Moreover, an interocular grating enhancement effect was evoked with the pattern ERG (T. Eysteinnsson, personal communication). Based upon the results of the present dissertation and these electrophysiological studies, Table 1 summarizes many of the similarities and differences between the Flicker and Grating effects.

#### Theoretical Explanations

At this juncture, I consider the relevance of existing models for the results

summarized in Table 1.

A. Single Channel Models: Models for Suppressive Rod-Cone Interaction

Frumkes and Eysteinnsson (1988) and Pflug and Nelson (Pflug et al., 1990; Nelson et al. 1990) proposed a suppressive rod-cone interaction model (SRCI) which presumably accounts for both neurophysiological and psychophysical data. This model should be able to predict the Flicker enhancement effect of the present study. Although they never applied this model to grating visibility, their model does make some specific predictions regarding spatial factors. I am unaware of other models for rod-cone interaction, or other single channel models relevant to SRCI.

Frumkes and Eysteinnsson (1988) based their model upon their experiments in amphibian retina. Both rods and cones of the amphibian retina converge upon HCs; however, only the cones (but not the rods) receive HC input. In the dark, both photoreceptor types release their excitatory neurotransmitter maximally and as a consequence, HCs produce a maximal inhibitory influence upon cones. For unknown reasons, this inhibitory influence specifically affects transient but not sustained cone signals. Moreover, under their experimental conditions, only cones convey a meaningful signal to bipolar cells (and hence, to the rest of the visual system) in response to rapid flicker, since the sluggish rods cannot follow flicker  $> 3\text{hz}$ . Therefore, if the rods are selectively light adapted, the HCs will be less excited, which therefore will inhibit cones

Table 1.

Summary of Adaptation Influences upon the Flicker and Grating Effects

<u>Basic Property</u>	<u>Flicker Effect</u>	<u>Grating Effect</u>
1. Dark-adapted rods tonically suppress cone sensitivity	yes	yes
2. Dark-adapted cones tonically suppress cone sensitivity	yes	no
3. Dark-adapted rods tonically suppress rod sensitivity	no	yes
4. Effect is evident in foveal retina	no*	yes
5. Effect is evident in parafoveal retina	yes	yes
6. Effect <u>decreases</u> as size of display <u>increases</u>	yes	yes
7. Effect <u>increases</u> as extent of parafoveal displacement <u>increases</u>	yes	yes
8. Enhancement gradient is steep	yes	no
9. Enhancement gradient is shallow	no	yes
10. Effect can be obtained with <u>monocular</u> rod-light adaptation	yes	yes
11. Effect can be obtained with <u>interocular</u> rod-light adaptation	no	yes
12. Effect can be observed with standard ERG procedures which presumably reflect distal retinal activity	yes	no**
13. Effect can be observed with pattern ERG procedures which presumably reflect ganglion cell activity	no***	yes
14. Effect can be observed with Visual Cortical Evoked Potential	??****	yes
15. Timecourse of maximal background enhancement effect	<50 ms	250ms

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\* Flicker effect can be obtained in fovea, but only with very small stimuli. Corresponding Grating effect can be obtained in fovea with any size stimulus.

\*\* Standard ERG recordings show no spatially specific response.

\*\*\* Pattern ERG cannot be evoked by a flickering stimulus with no changing spatial component.

\*\*\*\* Visual Cortical Evoked Potentials were never investigated for flickering stimuli.

less. In essence, rods determine the bias of the negative feedback of HCs upon cones. In summary, when no background field is present (dark-adapted), HCs provide a steady, inhibitory influence upon cone signals which is reduced when rods are selectively light adapted. The horizontal cell model of Nelson (Nelson et. al., 1990; Pflug et. al., 1990) for cat retina is quite similar, save that there is no anatomical evidence in mammalian retina for rods and cones to converge upon the same HC process. Even though this is the case, physiological data show that by unspecified means, rods as well as cones provide a functional input to "cone-driven" HC processes (e.g., see Nelson, 1977).

To explain the influence of stimulus size and shape, Frumkes and Eysteinnsson (1988) and Nelson et. al. (1990) emphasize a role for electrical coupling properties of HCs. Because of coupling, a signal generated in an individual HC leaks into neighboring HCs of the same anatomical type. The space constant for HCs (the distance over which an electrical signal will degenerate to 37% of its initial amplitude) is typically about 200  $\mu\text{m}$  (Lamb, 1976; Nelson, 1977) which corresponds to about 40' of arc on the human retina. Thus, over a considerable distance, HCs will "pool" or "average" the signal of a whole network of individual HCs. For this reason, given a constant amount of illumination, the signal of a HC will be determined by the area of illumination well beyond the dendritic field of the individual neuron. If the voltage response of a HC to light is a hyperpolarization and if this is considered its signal, it follows that the larger the area of stimulation, the larger the signal. However, since the synaptic influence of any neuron increases as the cell depolarizes, it should be realized that the larger the area

of stimulation, the smaller the inhibitory influence of a HC upon cones.

In most neurophysiological and psychophysical experiments of flicker-SRCI, the background is a constant very large size and the size of the flicker-test probe is varied. In these experiments, the flicker-test probe is generally at least 100 fold more intense than the adapting field (i.e., in the present study, the luminance of the test display was usually 10 cd/m<sup>2</sup>, the background 0.03 cd/m<sup>2</sup> or a factor of 333 dimmer). For this reason, the adapting field directly under the flicker test probe has a negligible influence upon cone-flicker sensitivity; only the adapted state of retinal areas adjacent to the flicker-test probe appreciably influence sensitivity. Therefore, it logically follows that the larger the area of the test stimulus, the smaller the adapting influence upon flicker sensitivity. This finding has been directly verified by a large number of neurophysiological and psychophysical observations including many of the flicker results in chapter 4 (e.g., see figures 20 and 21). However, the main difficulty of the SRCI models is that they treat spatial factors as an artefact of horizontal cell electrical coupling: it predicts that the same temporal factors should limit visibility for any spatial parameter. If their single-mechanism model could account for the influence of adaptation on both flicker and gratings, an enhancement effect would have been expected at high temporal frequencies regardless of spatial parameters. Clearly, this is not the case.

It is of parenthetical interest that Nelson et. al. (1990) specifically ruled out an alternate model to account for their flicker data in which rod-adaptation would alter the

electrical coupling properties of horizontal cells. If expanded, such a model might account for the present spatial enhancement effect. However, even if this were the case, there is no obvious means to make a horizontal cell electrical coupling model compatible with the present interocular findings.

In conclusion, the SRCI models of Frumkes and Eysteinnsson and Nelson and co-workers cannot account for the present Grating data. Given the large number of distinctions between the Grating and Flicker effects that are listed in Table 1, I rule out single channel models as an explanation.

B. A Dual Process Model: The Excitatory and Inhibitory Channel Model of Burbeck and Kelly (1980)

In the 1970s, D. H. Kelly performed many different studies examining sensitivity of the human observer to displays modulated sinusoidally in both spatial and temporal domains. Burbeck and Kelly (1980) tried to account for the spatio-temporal threshold response surface with a model involving one excitatory and one inhibitory mechanism. In both the spatial and temporal domain, they postulated that a single "excitatory" mechanism accounts for contrast sensitivity at higher frequencies. The sensitivity of a single inhibitory mechanism had a similar shape in both temporal and spatial domains but was tuned to somewhat lower frequencies. Although parsimonious, this model is untenable since modern neurophysiological data clearly indicate that a number of parallel

channels are processing information at almost all levels of the visual system (see below). Of greater importance, this model predicts that if data is plotted on two dimensional log-log coordinates, the shape of a temporal tuning curve should not depend upon the spatial frequency of a stimulus; similarly, the shape of a spatial tuning curve should not depend upon the temporal frequency of the stimulus. The results in this thesis (figures 9 and 12 in chapter 3 and figure 26 in chapter 5) are not consistent with this type of prediction.

### C. Models Involving Parallel Processing

#### 1. Parvocellular versus Magnocellular Pathways

In recent years, a variety of physiological and neurophysiological data have described the functioning of the primate visual system in terms of two parallel information channels (see Livingston & Hubel, 1987; Merigan & Maunsell, 1993; Purpura, Kaplan, & Shapley, 1982). The dichotomy between these two pathways reflects in part the distinction made by Polyak (1941) between midget and flat cone bipolar cell pathways. However, they are usually traced from the ganglion cells, since the distinction also involves the influence of rod bipolar and amacrine cell input to the ganglion cell layers (see Waessle & Boycott, 1991). Presumably, the larger or  $P_{\alpha}$  cells of the retina project to the magnocellular layers of the lateral geniculate body, while the smaller or  $P_{\beta}$  cells converge onto the parvocellular layers of the lateral geniculate body. These information pathways remain segregated in function within known cerebral visual

pathways. The parvocellular pathway has relatively little input from rods, is not sensitive to low spatial contrast, has chromatic input, responds to higher spatial frequencies and lower temporal frequencies. In comparison, the magnocellular pathway has input from both rods and cones, is sensitive to low spatial contrast, does not process chromatic information from cones, and responds to lower spatial frequencies and higher temporal frequencies.

According to this viewpoint, one might attribute the findings in the present study to separate influences upon the magnocellular pathway to account for the Flicker effect and upon the parvocellular pathway to account for the Grating effect. Because these effects are distinct, these interactions must occur at a level in the visual system where these pathways are separable, i.e., proximal to the level that accounts for SRCI as suggested by Frumkes and Eysteinnsson (1988) and Nelson et. al. (1990). However, distinct anatomical pathways are not readily evident for two reasons. First, since rod-cone interaction is the most basic underpinning of the Flicker and Grating effects, the interaction might involve separate influences of the magno-pathway (rod-input) onto the magno pathway (to account for rapid flicker enhancement) and parvo pathway (to account for high spatial frequency enhancement). To be sure, this type of explanation is consistent with data showing that the Flicker effect involves an influence of rods or cones upon cone-mediated flicker. However, the Grating effect can involve an influence of rods upon rod or cone-mediated grating sensitivity. Therefore, the type of photoreceptor specificity summarized in table 1 seems to be inconsistent with this type of model.

Moreover, sensitivity to intermediate combinations of spatial and temporal frequencies (i.e., displays involving 4-8 cpd displays flickered at 4-8 Hz) would be mediated by both pathways. Therefore, an enhancement of these intermediate spatio-temporal frequency combinations similar in magnitude to the prototypical Flicker or Grating stimuli would be expected. In fact, the visibility of intermediate frequency displays is not enhanced by rod-stimulating backgrounds.

## 2. Psychophysical Models involving Parallel Pathways

Some psychophysical models are defined in a fashion similar to that just outlined. That is, physiological mechanisms originating in the retina may subserve psychophysically established pathways. Some investigators hypothesize (Grosser & Spafford, 1992) that the functioning of the rods and cones is directly linked to transient and sustained system functioning. They argue that the parvocellular/sustained system is almost entirely fed by cones, while the magnocellular/transient system is driven by rods and cones. Rods are supposed to be the receptors initiating the rapid response characteristic to the transient pathway. In addition, numerous psychophysical findings point to the existence of a channel preferring high temporal/low spatial frequency stimuli, a transient channel, and a channel thought to process high spatial/low temporal frequency information, a sustained channel (Breitmeyer & Ganz, 1976; Keese, 1971; Tolhurst, 1975; for review see, Maguire, Weisstein, & Klymenko, 1990). Since many of these models preceded the current surge of anatomical and physiological interest in primate

retina, the two channels were likened originally to the distinction between X and Y ganglion cells in cat retina (Enroth-Cugell & Robson, 1966). More recently, the psychophysical transient channel has often been related to the functioning of the magnocellular pathway of the primate visual system, the sustained channel to the parvocellular pathway (e.g., Kaplan & Shapley, 1982; Livingston & Hubel, 1987). Unfortunately, these psychophysical models are no more relevant to the present data than the physiological distinction between parvo- and magno-pathways. In particular, they cannot explain the lack of enhancement for intermediate frequency combinations, but only account for the "peak" interactions, i.e., high spatial frequencies flickered slowly (presumably processed by the parvocellular-sustained channels) and low spatial frequencies flickered rapidly (presumably processed by the magnocellular-transient channels).

#### D. Framework for a New Model

Since none of the above mentioned single-mechanism or multiple-pathway models can fully account for the findings summarized in table 1 above, I suggest a dual mechanism model which allows for the effect of visual adaptation upon temporal as well as spatial resolution.

1. Flicker Effect: Although not spelled out quantitatively, the distal retinal horizontal cell model proposed by Frumkes and Eysteinnsson (1988) and Nelson et al.

(1990) can account for the spatial data using the "prototypical flicker stimulus" (the 1 cpd x 12 hz stimulus) presented in chapter 4 of this thesis. However, this model can be criticized on at least two counts. Firstly, there is no clear mechanism which accounts for the high-pass filtering of the feedback from horizontal cells to cones, although Nelson et. al. (1990) suggest the involvement of a transient  $Ca^{++}$  channel, no one has provided supporting evidence. Secondly, there is still no clear-cut reason for expecting the spatial frequency of a  $1^\circ$  probe to influence the magnitude of the Flicker effect. That is, regardless of its detailed spatial structure, the visibility of a high temporal frequency stimulus should be improved by a rod-stimulating background field. A prediction which runs counter to the present findings. However, in most other respects, this model is thoroughly supported by a wide variety of physiological data from amphibian and cat retina, including most recently, intracellular recordings from cat retinal neurons other than horizontal cells (Nelson et. al., 1993).

2. Grating Effect: Contrary to previous postulations by Naarendorp et. al. (1988), the present interocular findings suggest that the Grating effect must involve some mechanism which is at least in part proximal to the retinal outer plexiform layer. The mechanism mediating the Grating effect might operate along a number of different pathways. Firstly, a post-retinal interaction may take place: a variety of neuronal types in the cat lateral geniculate body and striate cortex have receptive fields with monocular excitatory characteristics but with a "silent" inhibitory input from the contralateral eye (e.g., Freeman & Ohzawa, 1988). Secondly, the Grating effect may also involve a

centrifugal input into the eye. Although the evidence is not overwhelming, sporadic reports have described retinofugal input into the mammalian eye (Repperant & Gallego, 1976; Schuette & Frumkes, 1993). Whereas conventional recording procedures have failed to find physiological evidence for a centrifugal input into the mammalian eye, Eysteinnsson (personal communication) has recently found that the dark-adapted state of one eye alters the pattern ERG (pERG) response from the contralateral eye, a response which presumably reflects ganglion cell activity. Since the pERG can only be evoked by a pattern stimulus, it is suggested that the spatial effect may well involve a retinofugal mechanism instead of, or in addition to, a cerebral pathway. Other psychophysical studies (Auerbach, Doerrenhaus, & Cavonius, 1992; Denny et al., 1990; Krauskopf & Riggs, 1959; Makous, Teller, & Boothe, 1976) suggest that if two retinas are adapted to two different patterns of light, they send different signals to the brain, which may tend to dominate and/or suppress one another at some locus in the visual system.

Collectively, the foregoing review suggests that rod-light adaptation may influence Flicker and Grating effects at different sites in the visual system. Unfortunately, neither the anatomical, physiological, or psychophysical studies just cited provide any clue regarding the mechanism mediating the Grating effect, other than it must be distinct from the Flicker effect. Although the Flicker effect may be mediated by a distal retinal mechanism, the Grating effect is likely to be mediated more proximally in the visual system and may involve some extraretinal structures.

### E. Future Direction

The present experiments establish that Flicker and Grating effects may be mediated by separate mechanisms at different loci in the visual system. However, the nature of the Flicker and Grating effects has to be investigated further to establish the accuracy of the dual mechanism model proposed in this thesis.

A variety of experimental methods could clarify the physiological and anatomical bases for these effects. An understanding of the retinal synaptic mechanisms responsible for the biochemical mediation of the Flicker and Grating effects is important. Some studies have implicated a number of neurotransmitters/neuromodulators. Specifically, pharmacological studies in amphibians have shown that SRCI is partially GABAergic and is mediated by a GABA A mechanism (Nelson et al., 1993). Schuette and Frumkes (1993) found evidence for a centrifugal serotonergic input to the retina. Although there is no related physiology in mammals, in lower vertebrates such centrifugal input is well known to radically change center-surround antagonism of ganglion cell receptive fields (Uchiyama, 1989). This suggests the possibility of a serotonergic mechanism. Finally, Witkovsky (1992) has implicated a role for dopamine in rod-cone interaction in distal retina. Along these lines, Bodis-Wollner and co-workers (1987) found that Parkinson's patients, who are well known to have a deficiency of dopamine, show reduced spatial contrast sensitivity (Bodis-Wollner & Yahr, 1978). More directly, Comerford, Thorn, and Malloy (1993) found a decrease in flicker sensitivity in the elderly, which they

attribute to a decrease in age related modulation of dopamine. They attribute an increase in flicker sensitivity to an increase in the dopamine level secondary to light adapting the eye.

Electrophysiological studies would be useful to further pinpoint the loci and also the relationship to binocular vision of the Flicker versus the Grating effect, i.e. is the location of interaction pre-or-postchiasmatic. A study of optic nerve lesions secondary to multiple sclerosis (MS) (Auerbach, Dörrenhaus, & Cavonius, 1992) suggests that the increase in ERG amplitude with a concomitant increase of VEP latency and a decrease of VEP amplitude following an MS attack is due to suppressed neural activity in the optic nerve. The authors suggest that the increase in ERG amplitude could be due to a release from efferent inhibition, normally carried by centrifugal fibers. A return to normal ERG and VEP levels and a shortening of the VEP latency was interpreted as a result of the restoration of efferent inhibition. It would be interesting to investigate the influence of fiber demyelination secondary to MS on the Flicker and Grating effect. Based on these previous findings, a loss of the Grating effect would be expected, but not of the Flicker effect. In addition, advances in technology, in conjunction with standard ERG or pERG procedures, also allow us to look at brain anatomy and brain function in vivo (fMRI) in normal and diseased human brains and might further distinguish the Flicker and Grating effects. Comparisons of psychophysical findings of normal observers with results in humans with abnormal vision, i.e., protanopes, may give important clues as to the types of photoreceptors involved in the Flicker versus the Grating effect. For instance, one

protanope (Naarendorp & Frumkes, personal communication) lacks the Flicker as well as the Grating effect. In comparison, Alexander and coworkers (1988) have studied rod-cone interaction in patients who have stationary night blindness who lack usual behavioral signs of rod-vision and lack a rod-related B-wave in their ERG. These patients all demonstrate the Flicker effect, but do not exhibit the Lie-effect, an influence of rod-adaptation upon color vision. It would be of interest to determine whether these individuals also show a Grating effect.

In conclusion, numerous pharmacological, electrophysiological, anatomical, and behavioral techniques can be used in animal preparations and human patients to further identify characteristics specific to the Flicker and Grating effects. The final chapter of this thesis considers the practical significance of rod-cone interaction.

## Chapter 7

Practical Implications and Simple Demonstration of "Global" Adaptation: The Influence of Display Size versus Light Adaptation upon Sensitivity to Higher Spatial Frequencies.

Beginning with the work of Campbell and Robson (1968), an evergrowing body of literature has measured spatial sensitivity of the human visual system by means of contrast sensitivity functions (for reviews see Cornsweet, 1970; Graham, 1989; Kelly, 1977). In a typical experimental or clinical situation, a grating modulated sinusoidally in one spatial dimension is presented to the observer who adjusts the contrast of the grating for threshold. In general, sensitivity, the inverse of threshold, is usually plotted as a function of grating frequency. As is illustrated in figure 3 of chapter 1, typical data obtained at one fixed luminance level describes an inverted U-shaped function: sensitivity is greatest for some intermediate spatial frequency (typically between 3-6 cycles per degree [cpd]) and falls off as spatial frequency either increases or decreases.

A number of parameters typically influence both the quantitative and qualitative properties of the spatial contrast sensitivity functions, including average luminance, retinal position, and size of the grating.

Average Luminance: Contrast sensitivity increases and peak sensitivity shifts to higher spatial frequencies as the average luminance of the grating increases (Banks,

Geisler, & Bennett, 1987; Van Nes and Bouman, 1967; Denny, 1992). Presumably, this reflects a variety of changes in receptive field properties that are related to visual adaptation (e.g., Dowlings's [1987] concept of "Network Adaptation").

Until recently, it was assumed that the average luminance of a cone-detected test display fixes the level of light-adaptation of the visual system (e.g., Kelly, 1972). Such an interpretation seems reasonable in light of more recent arguments (Shapley & Enroth-Cugell, 1984) emphasizing a role for "local adaptation", i.e., adaptation only involving the specific area of retina to which the test stimulus is presented. In comparison, the term "global adaptation" as used by Shapley and Enroth-Cugell (1984) involves post-receptor changes, i.e., the mean involvement of the entire receptive field of a recorded ganglion cell, even if these regions have not been stimulated by light directly. Many psychophysical studies have clearly shown that there are many adaptation sites for steady illuminance levels, each predominating in a different luminance range (Adelson, 1982; Makous et al., 1976). The results in chapters 3-5 of this thesis certainly concur with these findings suggesting the existence of a global adaptation factor which must involve retinal areas beyond the receptive field of a ganglion cell, i.e., an interaction between different retinal areas. Moreover, as indicated by the importance of the adapted state of the contralateral eye, this global factor extends beyond the retina to the cyclopean (binocular) visual field.

Retinal Position: The peak of the contrast sensitivity function shifts toward lower

spatial frequencies if the stimulus is displaced from the fovea into the periphery (Campbell & Green, 1965; Merigan & Katz, 1990; Denny, 1992; Mustonen, Rovamo, & Nasanen, 1993). The shift in sensitivity involves a large decrease in sensitivity to higher spatial frequencies, and a slight increase in sensitivity to lower spatial frequencies. Most probably, this reflects the increase in size of receptive field organization of the retina and cerebral visual system which have been specifically related to retinal position (Shapley & Perry, 1986; Westheimer, 1990).

Size of the Grating: Overall sensitivity increases with the size of the grating stimulus (Virsu & Rovamo, 1979, Denny, 1992). For low spatial frequencies ( $< 10$  cpd), the influence of display size on sensitivity, which can be of a 2-3  $\log_{10}$  magnitude (Kelly, 1977), is likely to reflect two factors. For foveally centered stimuli, the increase in sensitivity may involve an increase in receptor fields with parafoveal displacement (Shapley & Perry, 1986). Hence, an increase in grating size will cause stimulation of pathways which are better tuned to low spatial frequency stimuli than those encountered in the fovea. Furthermore, at any retinal position, simply more channels are stimulated by a larger grating, causing the activity of more units to be able to sum together, and consequently improving sensitivity. However, even at spatial frequencies exceeding 10 cpd, an increase in the overall spatial dimensions of a grating can increase appreciably. The remainder of this chapter addresses the influence of display size upon contrast sensitivity for spatial frequencies  $\geq 10$  cpd.

When measuring contrast sensitivity under usual experimental conditions, the sinusoidally modulated grating is usually the only visual stimulus presented to the observer. Therefore, the only variable affecting the subjects' state of long term visual adaptation is the average luminance of the grating. In comparison, under "everyday life" viewing conditions, the state of visual adaptation is usually influenced by many factors including additional objects in the field of view and/or previous exposure to different luminance stimuli. Since the fovea is the area of the retina most sensitive to higher spatial frequencies, the contribution provided by non-foveal areas should be insignificant. Therefore, it seems that the increase in contrast sensitivity with grating size is more likely to be attributed to a change in the state of adaptation over a wide ranging area of the retina rather than to display size per se.

In the present set of experiments, I examined contrast sensitivity under conditions in which the steady state of adaptation of the eye viewing the grating stimulus remains stable. The test stimulus is fixed at 10 cd/m<sup>2</sup> average luminance and presented at one of two fixed retinal locations. The state of monocular adaptation will be altered by the introduction of background fields of various sizes and luminance levels. In addition, I refer to data presented in chapter 5, in which the state of visual adaptation is influenced by the addition of monocular or interocular adaptation fields. The following experiments have two practical implications. First, they show that the state of adaptation over a large retinal area exerts an influence upon visual sensitivity which is independent of the luminance of the test stimulus. Hence, archival data (e.g., Kelly, 1961) obtained at

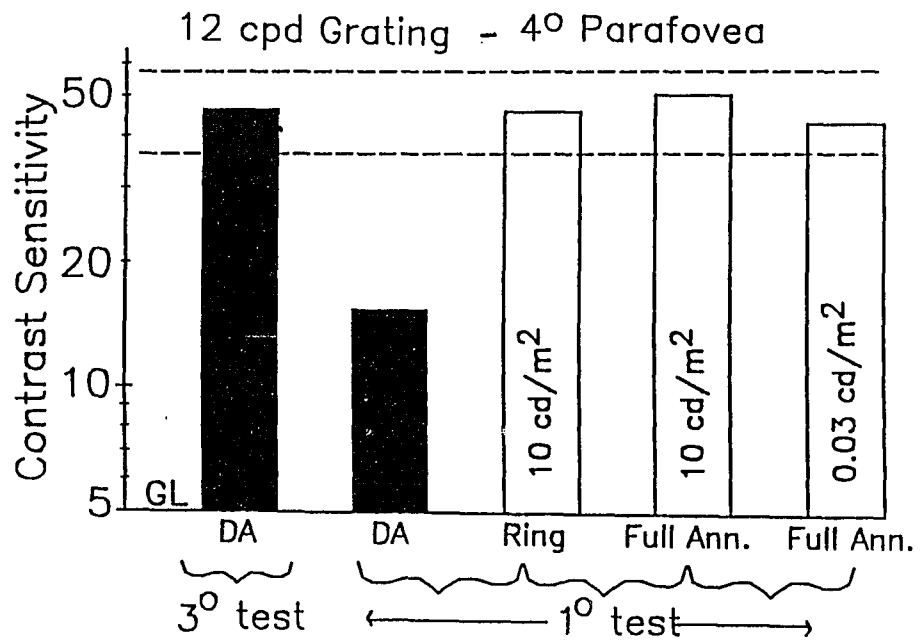
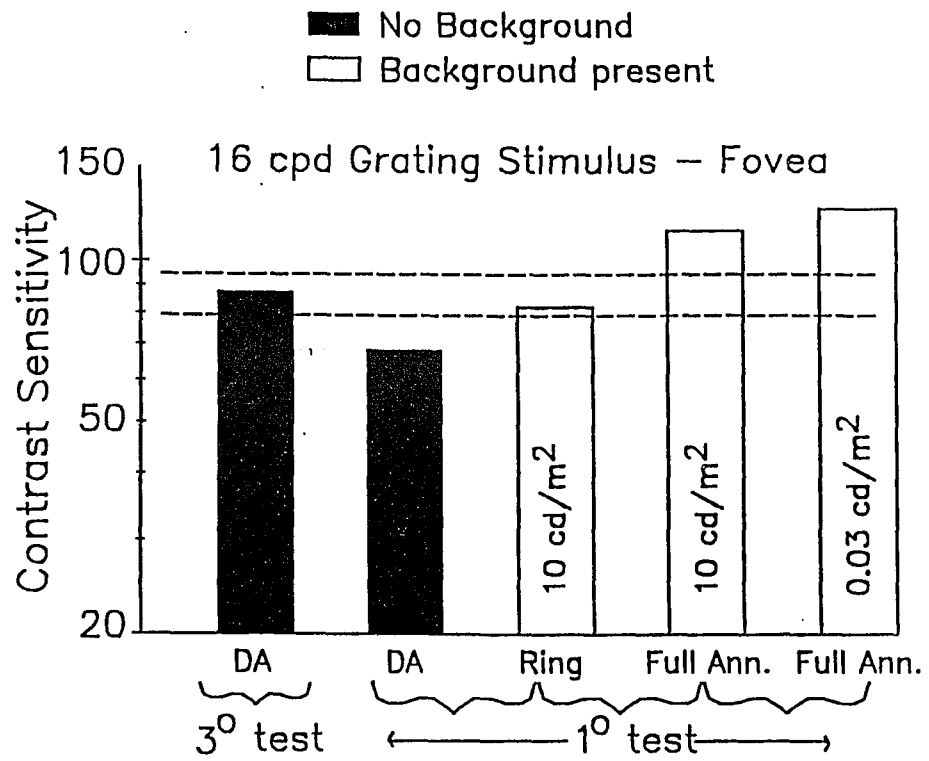
many average luminance levels cannot be used to characterize the influence of adaptation. Secondly, they show that the increase in sensitivity to larger sized high spatial frequency stimuli is attributable to an increase in the light adapted state of a larger retinal area rather than to the grating size.

### Methods

Many of the results included in this chapter are near replications of data collected in a variety of previous investigations in our laboratory (Denny et. al., 1991; Denny, 1992; Frumkes, Lange, Naarendorp, & Eysteinson, 1994; Lange & Frumkes, 1992; 1993; Naarendorp et. al., 1988). The experiments reported in figure 32 below were all designed to demonstrate: 1. the reason that display size influences sensitivity to high spatial frequencies; 2. the practical importance of global light adaptation.

Specific methodology has been described chapters 2-5. In brief, the size of the non-flickering test display was  $3^\circ \times 3^\circ$  or  $1^\circ \times 1^\circ$  presented for 500 ms. The adapting stimulus was as  $15^\circ \times 15^\circ$  square. Although GL was the only observer specifically examined under these test situations, similar conclusions can be obtained by analyzing the data from observer TEF, PC, as well as GL illustrated in chapters 3-5 of this thesis.

Figure 32. Comparison of contrast sensitivity for different stimulus sizes and background configurations under various conditions of background luminance for observer GL. The data were collected according to the method of adjustment procedure. The upper coordinates show contrast sensitivity for a 16 cpd grating presented foveally. The left most bar shows sensitivity to a  $3^\circ$ ,  $10 \text{ cd/m}^2$  square grating when no background field was present; the horizontal dashed lines show 95% confidence intervals for this sensitivity value. The second bar to the left shows contrast sensitivity to a  $1^\circ$ ,  $10 \text{ cd/m}^2$  square grating, also when no adapting field was present. The right three bars indicate sensitivity to a  $1^\circ$ ,  $10 \text{ cd/m}^2$  sided test grating when surrounded by annular adapting fields presented to the same eye as the test stimulus. For the third bar from the left, the outer dimension of the  $10 \text{ cd/m}^2$  background annulus was a  $3^\circ$  sided square. The fourth bar from the left shows a  $1^\circ$  sided square when the outer dimension of the adapting field annulus was a  $15^\circ$  sided square with a luminance of  $10 \text{ cd/m}^2$  (fourth bar from left) or a luminance level of  $0.03 \text{ cd/m}^2$  (right most bar). The lower plot shows corresponding data. However, here a 12 cpd grating is presented at  $4^\circ$  in the TVF of the left eye.



## Results

Figure 32 compares contrast sensitivity to a non-flickering, sinusoidally modulated grating of  $10 \text{ cd/m}^2$  average luminance, shaped as either a  $1^\circ$  or  $3^\circ$  sided square. The lower coordinates show contrast sensitivity for a 12 cpd grating presented  $4^\circ$  parafoveally. The left most bar shows sensitivity to a  $3^\circ$  square grating when no background field was present; the horizontal dashed lines show 95% confidence intervals for this sensitivity value. The second bar to the left shows contrast sensitivity to a  $1^\circ$  square grating, also when no adapting field was present. In agreement with reports in the literature (e.g., Kelly, 1977), the sensitivity is less to the smaller sized grating. The right three bars also indicate sensitivity to a  $1^\circ$  sided test grating when surrounded by annular adapting fields presented to the same eye as the test stimulus. For the third bar from the left, the outer dimension of the  $10 \text{ cd/m}^2$  background annulus was a  $3^\circ$  sided square. Hence, the total luminance flux presented to the viewing eye was the same as provided by the  $3^\circ$  test stimulus (first bar from left). Notice that sensitivity to this test-and-adapting-stimulus combination was nearly the same as that to the  $3^\circ$  test stimulus by itself. Essentially the same level of sensitivity is achieved when the outer dimension of the adapting field annulus was a  $15^\circ$  sided square, regardless of whether its luminance was  $10 \text{ cd/m}^2$  (fourth bar from left) or when it was reduced to a sub-cone luminance level of  $0.03 \text{ cd/m}^2$  (right most bar). These results suggest that the increase in contrast sensitivity produced by increasing display size is attributable to light adapting the surrounding retinal region rather than to display size per se.

The upper set of coordinates in figure 32 show results of a comparable experiment with foveally centered gratings of 16 cpd. The layout of the upper coordinates is identical to that described below for the parafovea. The results in the fovea are even more striking than the parafoveal data just described. In the fovea, the difference in sensitivity between 1° and the 3° gratings in the dark-adapted eye is still significant; presentation of the 3° sided background annulus increased the sensitivity to the 1° grating to a level approaching that of the 3° grating presented with no background. However, a rod-stimulating 15° sided annulus of either 0.03 or 10 cd/m<sup>2</sup> caused the sensitivity to the 1° grating to exceed the sensitivity to the 3° stimulus in the dark-adapted eye. Although I could not examine grating sensitivity with a 15° test stimulus without grossly changing the properties of the apparatus used throughout this thesis, I suggest that it would be no greater than that obtained with a 1° grating in the presence of a dim background field.

### Discussion

The results presented in figure 32 above have three implications. First and as emphasized in prior portions of this dissertation, some aspects of adaptation are quite global and exert an influence independent of test stimulus luminance. Second, the importance of display size upon sensitivity to fine spatial detail is more likely to be attributed to global adaptation rather than display size per se. Finally, global adaptation has an important practical significance.

#### A. Global Adaptation Acts Independent of Target Luminance

Shapley and Enroth-Cugell (1984) distinguish two aspects of light and dark adaptation which they generally consider from the perspective of neurophysiological study of the receptive field properties of a cat or primate retinal ganglion cell. From their perspective, local adaptation involves an adaptation induced change in sensitivity attributable to that patch of retina directly influenced by a stimulus; global adaptation is an adaptation induced change which extends to portions of the receptive field of the specific neuron studied which are not directly influenced by light. They suggest that adaptation is largely a local phenomenon.

As illustrated in figure 32 above and throughout this entire thesis, sensitivity to gratings has been altered by the presentation of adapting fields which predominantly influence retinal areas adjacent to the test stimulus. Two sorts of observations make it highly unlikely that this adapting influence is spatially restricted to the conventional dimensions of the receptive field of any known retinal neuron. First, Naarendorp et. al. (1988) obtained results very similar to the present findings using a 6° diameter grating surrounded by a contiguous annulus with spatial frequency as high as 21 cpd. At the studied retinal location (3° parafoveally), this certainly exceeds the diameter of the receptive field center of any recorded neuron within the retina or geniculocortical pathway (Westheimer, 1990). Secondly, and as reported in chapter 5, similar adaptation effects can be observed regardless of whether the adapted state of the test eye or the

contralateral eye is manipulated, or whether light adaptation (background fields) or dark adaptation (bleaching) procedures are employed. It appears that aspects of light and dark adaptation act quite independently of target luminance. Therefore, some features of adaptation are far more "global" than considered by Shapley and Enroth-Cugell (1984). However, this conclusion is neither new nor unique. For example, in his description of the receptive field properties of cat retinal ganglion cells, Kuffler (1953) reported that receptive field size increased as his test probe increased in luminance, but decreased with progressive light adaptation. Unfortunately, this aspect of Kuffler's well-cited paper seems to have largely been forgotten.

To summarize, adaptation can act in a fashion which is independent of target luminance, and is far more global than conventionally defined.

B. The Influence of Stimulus Size upon Sensitivity to High Spatial Frequencies Pertains to Global Adaptation:

Along with prior communications (e.g., Virsu & Rovamo, 1979; also see chapter 4) the results presented in figure 32 show that sensitivity to higher spatial frequencies increases with display size. The present results strongly suggest that these findings do not depend upon display size per se but upon the adapted state of the retinal regions surrounding the test display. Specifically, the right sets of data in figure 32 show that the sensitivity to a 1° high spatial frequency grating is increased by an equiluminant

surround. No further improvement results by extending the grating into this surround field.

This finding may not be surprising. The Nyquist limit (the physical limitation from unambiguous spatial acuity based upon the packing density of photoreceptors) is about 50-60 cpd for foveal cones (Hirsch & Hylton, 1984; Williams, 1988). This limit falls off sufficiently with the amount of parafoveal displacement (e.g., Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987) so that a retinal area several degrees from the center of the stimulus is unlikely to play a direct role in the perception of the 16 cpd grating used in the present experiments. In comparison, results presented in prior chapters in this thesis clearly establish that the adapted state of photoreceptors in these regions does influence spatial sensitivity. Thus, it is not surprising that the increase in sensitivity to a 16 cpd grating relates more to the adapted state of adjacent non-foveal retina than its capacity of spatial resolution of high frequency gratings.

It might be argued that the results in figure 32 are specific to observer GL. However, although not presented in this content, essentially similar findings from two other observers in addition to GL were presented in earlier parts of this thesis. It also might be argued that the results in figure 32 depend upon very specific details of the stimulus used as well as the dependent variable used. This is also not the case. Naarendorp et. al. (1988; 1991) obtained essentially similar findings. In his studies, Naarendorp measured spatial sensitivity by having the observer vary the luminance of a

grating fixed in contrast; in the present study, the observer varied the contrast of a grating with fixed luminance. It also might be argued that the results presented in figure 32 only relate to the specific dimensions of the stimuli used. Once again, Naarendorp obtained the same sorts of findings as reported here using different size stimuli at several different retinal positions. Unfortunately, given the 2 meter viewing distance used in this study, I could not study gratings with a spatial dimension much greater than  $3^\circ$ .

### C. The Practical Importance of Global Adaptation

A wide variety of older literature suggested that visibility was considerably improved by surrounding a visual display with an illuminated surround field (e.g., Craik, 1939; Marshall & Day, 1951). This older literature was likely to have affected the manufacturers of american television sets in the 1940s, 50s, and 60s. At that time, an almost invariant feature of every television set was some type of annulus (either reflective material which would presumably be "lit" by ambient light in the viewers field of vision other than the cathode ray screen) or in some cases, an annular illuminated field. The reasons for abandoning this feature have not been documented, but might relate to the increase in the size of the viewing area of most commercial television screens. Based upon the results presented in figure 32, the manipulations mentioned above probably had an enhancing influence upon the viewers' sensitivity to fine spatial detail. Although discontinued in the area of TV screens, illuminated annular surrounds could still have practical applications. For example, it would seem that when viewed at night, any object

such as highways signs would become more clearly visible if surrounded by a reflecting or illuminated surface.

I believe that the global adaptation factor, as presented above, may have an important implication for night-time vision. Let me consider two specific examples. Three different investigations (Arden & Hogg, 1985; Arden & Frumkes, 1986; Lange & Frumkes, 1993) have documented the existence of an "exaggerated-SRCI syndrome." As summarized in chapter 4, SRCI (suppressive rod-cone interaction) is the term used by Frumkes and Arden and their colleagues for the "Flicker effect" as defined in chapter 3. Using their usual experimental situation, SRCI produces a change in flicker sensitivity in the parafoveal retina of about  $0.7 \log_{10}$  units in normal subjects. In these subjects ( $N > 30$ ), the SRCI influence is  $\geq 2$  log units. This "syndrome" has only been documented in well-educated people including one ophthalmologist and several opticians who have normal rod-vision but who still claim to have a great deal of difficulty seeing at night. In fact, failure of visual impairment after intensive ophthalmological examination can be listed as a usual characteristic of the syndrome. However, the most commonly reported feature is significant difficulty driving an automobile at night. Several of these individuals have described the only way they confidently drive an automobile at night: to keep one of the interior cabin lights on. I suggest a more carefully designed source of illumination than an interior cabin light would be even more effective to alleviate night driving difficulties.

In normal aging adults, rod-sensitivity barely degrades over the first 80 years of life (Eisner, 1989) nor does cone-mediated spatial visual acuity providing the luminance of the tested object remains at high photopic levels (Bailey, 1987). However, as the luminance of the test target decreases, the visual acuity of the elderly decreases radically in respect to that of younger subjects (Owsley, 1987). Although this finding has been reported in a number of studies, no satisfactory explanations have been advanced in terms of retinal or other neural pathology. Unfortunately, the procedures used in these studies do not permit a distinction between the effects of average luminance level and level of adaptation. However, findings of younger exaggerated-SRCI patients and older individuals with low visual acuity, are sufficiently similar to suggest that the same factors or group of factors may be responsible. Therefore, the global adaptation factor referred to throughout this chapter may be one of the more general factors affecting the aging process in normal humans.

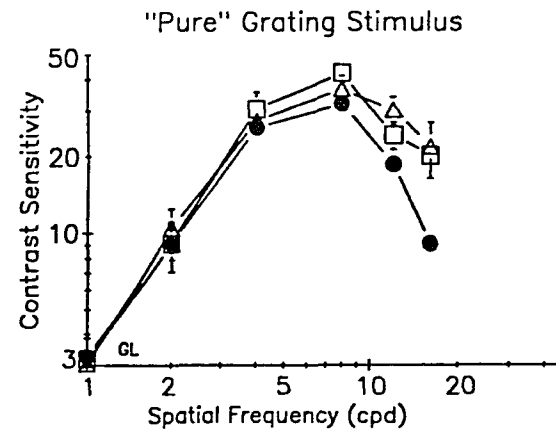
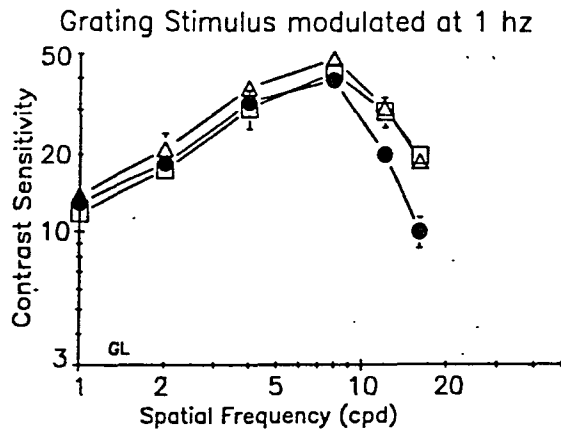
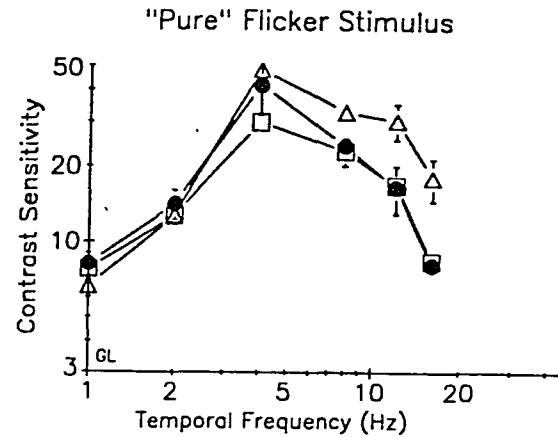
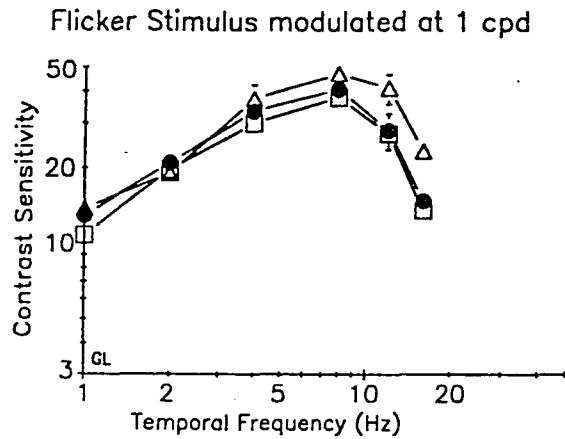
## Appendix

Throughout the foregoing thesis, I assumed that results obtained with a 1 cpd display flickered at 12-16 hz and a 12-16 cpd display flickered at 1 hz would be analogous to data obtained with a spatially unmodulated flicker stimulus and a non-flickering grating. This assumption seemed warranted based upon a comparison of the present results with data obtained in studies in which flicker sensitivity was studied alone using a small diameter, spatially homogeneous test probe (e.g., Goldberg et al., 1983) or grating sensitivity was studied using a 500ms duration grating (Naarendorp & Frumkes, 1991; Denny et al., 1990).

Figure 33 shows the effect of a  $0.03 \text{ cd/m}^2$  adapting field presented monocularly as well as interocularly upon both flicker and grating visibility to displays of  $10 \text{ cd/m}^2$ . The upper sets of coordinates show results for the Flicker stimulus, the lower figure represents data for the Grating stimulus. The upper left coordinates show data for the "prototypical Flicker stimulus" (12 hz x 1 cpd), and the lower left graph shows results for the "prototypical Grating stimulus" (12 cpd x 1 hz). The upper right side of figure 33 shows data for a spatially unmodulated ("pure") flicker stimulus, and the lower right coordinates show data for a non-flickering ("pure") grating. All stimuli were presented at  $4^\circ$  parafoveally. For each set of coordinates, the size of a plotted datum always exceeds  $\pm 1$  standard error, a departure of a data point from within this interval always indicates a statistically significant deviation from control sensitivity. First consider the

Figure 33. Percent contrast sensitivity as a function of temporal and spatial frequency is plotted for observer GL. The data were collected according to the method of adjustment procedure. The stimulus was a  $1^\circ$  by  $1^\circ$ ,  $10 \text{ cd/m}^2$  sine wave grating presented to the left eye  $4^\circ$  in the TVF. The background stimulus was a  $20.8^\circ \times 15^\circ$  diffuse adapting field presented to the same eye at a luminance level of  $0.03 \text{ cd/m}^2$ . The closed circles represent control data obtained with no background while open triangular symbols represent the presence of a  $0.03 \text{ cd/m}^2$  monocular background field. The upper right set of coordinates shows contrast sensitivity as a function of temporal frequency, while the left upper plot shows contrast sensitivity as a function of temporal frequency for a stimulus modulated concurrently at 1 cpd. The lower right set of coordinates shows contrast sensitivity as a function of spatial frequency, while the lower left plot shows contrast sensitivity as a function of spatial frequency for a stimulus concurrently modulated at 1 hz. Since the size of a plotted datum always exceeds  $\pm 1$  standard error, a departure of a data point from within this interval always indicates a statistically significant deviation from control sensitivity.

- No Background
- △—△ 0.03 cd/m<sup>2</sup> monocular bkgnd.
- 0.03 cd/m<sup>2</sup> interocular bkgnd.



Flicker data on top, for both the prototypical Flicker stimulus as well as the "pure" Flicker stimulus, rod-light adaptation only exerts an influence on monocular high frequency flicker sensitivity. In comparison, for the Grating data in the lower part of figure 33, dim backgrounds influences both monocular as well as interocular sensitivity to high spatial frequencies. Although the enhancement effect is smaller when displays are modulated in two domains, they are clearly similar to that of "pure" flicker and grating stimuli.

In conclusion, data presented in figure 33 suggest that the effect of rod-light adaptation upon the "prototypical" flicker and grating stimuli is comparable to that of the "pure" flicker and grating stimuli. It appears that in both cases, a Flicker effect is only achieved with monocular rod-light adaptation, whereas a Grating effect can be obtained with monocular as well as interocular rod adaptation.

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