INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313/761-4700 800/521-0600

Order Number 9218231

Tonic interocular suppression by a dark adapted eye upon spatial vision in the contralateral eye

Denny, Noreen M., Ph.D.

City University of New York, 1992

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

A

TONIC INTEROCULAR SUPPRESSION BY A DARK ADAPTED EYE UPON SPATIAL VISION IN THE CONTRALATERAL EYE

by

NOREEN M. DENNY

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.

1992

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

1/13/92
Date

Chair of Examining Committee

1/16/92
Date

Herbert D. Saltzstein
Executive Officer

Thomas E. Frumkes, Ph.D.
Robert Lanson, Ph.D.
Richard Bodnar, Ph.D.
William Seiple, Ph.D.
Ivan Bodis-Wollner, M.D.

Supervisory Committee

The City University of New York

Abstract

TONIC INTEROCULAR SUPPRESSION BY A DARK ADAPTED EYE UPON SPATIAL VISION IN THE CONTRALATERAL EYE

by

Noreen M. Denny

Advisor: Professor Thomas E. Frumkes

Monocular contrast sensitivity functions (contrast sensitivity to sinusoidal gratings as a function of their spatial frequency) were determined while the adapted state of the contralateral eye was systematically altered. Three observers were used.

1. In general, grating contrast sensitivity was least if the contralateral eye was totally dark adapted, and increased if it was light adapted. With gratings viewed foveally, this effect was observed for all spatial frequencies ≥2 cycles per degree (cpd), as long as the overall dimensions of the test grating were ≥1°. This effect increased with parafoveal displacement, but was absent when 0.5° foveal gratings were used. These interocular effects could not be mimicked by direct adaptation of the "test eye," or by binocular adaptation.

2. This interocular adaptation effect occurs over the entire range of grating luminance (0.01-10.0 cd/m^2) examined. This effect was obtained with 2-5 cpd gratings using any interocular background luminance >10x10^{-4} cd/m^2. For frequencies from 10-20 cpd,

this effect was obtained with interocular background luminance >0.1 cd/m^2. Dark adaptation experiments showed that grating sensitivity in the "test eye" decreased as the rods in the contralateral "adapting eye" progressively changed to being dark adapted. Both rod- and cone-mediated spatial sensitivity in the contralateral eye are influenced by the adapted state of rods.

3. Pressure blinding and light adapting one eye produce similar improvement in grating visibility in the contralateral eye. Therefore, dark adapted rods in one eye exert a tonic interocular suppression (TIS) upon spatial vision in the contralateral eye.

4. In the fovea, binocular presentation and interocular adaptation produce nearly identical grating sensitivity. In the periphery, binocular presentation produces greater sensitivity than interocular adaptation. However, both viewing conditions often improve grating visibility >0.3 $\log_{10}$, the maximum amount consistent with binocular summation. Therefore, the improvement in sensitivity resulting from binocular viewing may be due to a removal of TIS rather than to "binocular summation."

Acknowledgements

I would like to thank my mentor Dr. Thomas E. Frumkes for the encouragement and guidance he has given throughout my time at graduate school, and for the numerous hours he has spent serving as an observer in most of the experiments presented here. I would also like to thank the members of my dissertation committee, Drs. R. J. Bodnar and R. N. Lanson for their thorough readings of this manuscript and their helpful suggestions. I am grateful to my outside readers Drs. I. Bodis Wollner and W. H. Seiple.

I would like to thank Dr. Michael C. Barris for his assistance during the early stages of development of this thesis. I would like to express my thanks to Nan Min for the many hours she spent serving as an observer. I would also like to thank Gudrun Lange and Laura D for their assistance in collecting data for some experiments.

I am indebted to John Zhu for the modifications he made on the computer software. Without his skillful assistance, many of the experiments conducted for this dissertation would have been impossible to perform. I would also like to thank Mr. Sorrin Gottesman for his assistance in building the apparatus.

Finally, I would like to thank Roger Brown for his support and encouragement throughout the various stages involved in completing this thesis, and for his assistance in building the apparatus. I would especially like to thank my parents, Marie and Dale for their continued support and encouragement. This dissertation is dedicated to them.

Table of Contents

I. Title Page i

II. Approval Page iii

III. Abstract iv

IV. Acknowledgements vi

V. Table of Contents vii

VI. List of Tables xiv

VII. List of Illustrations xv

VIII. Chapter 1 1

Introduction and Overview 1

1. Total Independence 1

2. Summation 1

3. Comparative Mechanisms 2

4. Active Suppression 4

5. Tonic Suppression 5

Overview and Organization of this Dissertation 6

IX. Chapter 2 8

The Influence of Interocular Adapting Fields upon Monocular Spatial Vision 8

Introduction 8

A. Previous Psychophysical Evidence for Interocular Adapting Influences 8

1. Studies Involving Detection Threshold 8

a. The Paradigm of Wolf and Zigler 8

b. The Paradigm of Lansford and Baker 9

2. Studies not Involving Detection Threshold 15

B. Measurement of Spatial Sensitivity with Sine Wave Gratings 17

Methods 20

A. Observers 20

B. Apparatus 20

1. Overall Spatial Arrangement 20

2. Grating Generator 25

C. Procedure 26

1. General Psychophysical Methodology 26

2. General Experimental Procedure 29

Results and Discussion 31

A. Results Obtained with the Most Common Stimulus Values 31

B. Effects of Grating Luminance 45

C. Influence of Left versus Right Eye Stimulation 59

D. Influence of the Size and Shape of the Interocular Background. 60

E. Effects of Retinal Position 76

F. Subjective Changes in Brightness 79

X. Chapter 3 88

Interocular Adaptation Involves the Manipulation of a Purely Interocular Tonic Suppressive Influence 88

A. Stray Light Explanation 88

B. Interocular Neural Mechanisms and the Importance of Tonic Suppression 89

Methods 95

Results and Discussion 95

A. Interocular Adaptation Involves a Neural and Purely Interocular Mechanism: Comparison of Monocular,Interocular, and Binocular Adapting Influences. 95

1. Comparisons with Monocular Stimulus Presentation 95

a. Comparisons with Binocular Stimulus Presentation 98

B. Interocular Adaptation Involves a Tonic Interocular Suppression: Pressure Blindness Experiment 101

XI. Chapter 4 105

The Relationship of TIS to Binocular Summation 105

A. Overview of "Binocular Summation" 105

1.. Mechanistic Considerations 105

B. Summary of Published Data 109

1. Behavioral Studies of "Binocular Summation" 110

a. Absolute and Increment Threshold Studies 110

b. Studies of Apparent Brightness 112

2. Grating Sensitivity and Visual Acuity 112

3. Other Visual Tasks 114

Methods 116

Results 116

A. Foveal Comparison of Binocular Presentation with Interocular Adaptation 116

B. The Effects of Test Grating Size with Foveal Stimulus Presentation 121

C. The Effects of Retinal Position Using Large Test Gratings 131

D. Results Obtained with 1° Test Gratings in the Parafovea 140

E. Subjective Observations 145

Discussion 150

XII. Chapter 5 152

The Photoreceptors Pathways Involved in TIS 152

A. Rod-Cone Interaction and Interocular Adaptation Effects 153

- 1. Summation 154
- 2. Tonic Suppression 155
- 3. Active Suppression 156
- 4. Cerebral versus Retinal Mechanisms for Rod-Cone Interaction 156

Methods 159

A. Observers 159

B. Apparatus 159

C. Procedure 159

- 1. Psychophysical Methodology used for Dark Adaptation 159
- 2. General Experimental Procedure 160

Results, and Discussion 161

A. Is Rod and/or Cone Spatial Sensitivity Influenced by Contralateral Adaptation? 161

B. Is Rod and/or Cone Adaptation Involved with TIS Effects? 167

1. Low Spatial Frequencies 167

2. High Spatial Frequencies (10-20 cpd) 173

3. Direct Comparison of Monocular (SRCI) and Interocular(TIS) Adaptation Effects upon Grating Visibility 184

XIII. Chapter 6 190

General Discussion 190

A. Comparison of TIS Influences upon Grating Visibility with other Interocular Adaptation Effects 191

1. Detection Threshold Experiments 191

a. The Lansford-Baker Effect 191

b. Demonstrations of Interocular Visual Masking 193

2. Other Visual Tasks 194

B. Comparison of TIS with Other Contralateral Suppressive Effects 195

C. General Model for TIS 196

D. Related Phenomena 198

E. The Importance of TIS 199

F. Relationship to Existing Theories of Binocular Vision 200

XIV. Appendix A 203

XV. References 208

List of Tables

1. Studies of "binocular summation" which measure absolute and increment thresholds. 111

2. Studies of "binocular summation" which measure brightness. 113

3. Studies of "binocular summation" which measure acuity and contrast sensitivity. 115

List of Illustrations

1. Apparatus and spatial arrangement of stimuli. 10

2. Spatial arrangement of stimuli and data presented from Lansford and Baker (1969). 21

3. Percent threshold modulation as a function of spatial frequency for a 10 cd/m^2, 3.2° x 2.4° sized stimulus presented foveally and a variable luminance level background for ND. 32

4. Percent threshold modulation as a function of spatial frequency for a 10 cd/m^2, 3.2° x 2.4° sized stimulus presented foveally and a variable luminance level background for NM. 36

5. Percent threshold modulation as a function of spatial frequency for a 10 cd/m^2, 3.2° x 2.4° sized stimulus presented foveally and a 10 cd/m^2 luminance level background for TEF. 38

6. Percent change in contrast sensitivity as a function of log interocular background luminance for a 10 cd/m^2, 3.2° x 2.4° sized stimulus presented foveally for various frequencies for ND. 40

7. Percent change in contrast sensitivity as a function of log interocular background luminance for a 10 cd/m^2, 3.2° x 2.4° sized stimulus for NM. 42

8. Percent threshold modulation as a function of spatial frequency for a 1.0 cd/m^2 stimulus for ND. 46

9. Percent change in contrast sensitivity as a function of log interocular background luminance for a 1.0 cd/m^2 stimulus for ND. 48

10. Percent threshold modulation as a function of spatial frequency for a 0.1 cd/m^2 stimulus for ND. 51

11. Percent threshold modulation as a function of spatial frequency for a 0.1 cd/m^2 stimulus for TEF. 53

12. Percent change in contrast sensitivity as a function of log interocular background luminance for a 0.1 cd/m^2 stimulus for ND. 55

13. Percent change in contrast sensitivity as a function of log interocular backgroundluminance for a 0.1 cd/m^2 stimulus for TEF. 57

14. Percent threshold modulation as a function of spatial frequency for stimulus presentation in the left or right eye for ND. 61

15. Percent threshold modulation as a function of spatial frequency for different configurations of the interocular background for ND. 63

16. Percent threshold modulation as a function of spatial frequency for different configurations of the interocular background for NM. 65

17. Percent threshold modulation as a function of spatial frequency for different sizes of the test stimulus for ND. 68

18. Percent threshold modulation as a function of spatial frequency for different sizes of the test stimulus for TEF. 70

19. Percent change in contrast sensitivity as a function of spatial frequency for different sizes of the test stimulus for ND. 72

20. Percent change in contrast sensitivity as a function of spatial frequency for different sizes of the test stimulus for TEF. 74

21. Percent threshold modulation as a function of spatial frequency at differentretinal positions of the test stimulus for ND. 77

22. Percent threshold modulation as a function of spatial frequency at different retinal positions of the test stimulus for TEF. 80

23. Percent change in contrast sensitivity as a function of spatial frequency at different retinal positions of the test stimulus for ND. 82

24. Percent change in contrast sensitivity as a function of spatial frequency at different retinal positions of the test stimulus for TEF. 84

25. Percent threshold modulation as a function of spatial frequency for monocular and interocular background presentation for ND. 96

26. Percent threshold modulation as a function of spatial frequency for a binocularly presented test stimulus and monocular and binocular backgrounds for ND. 99

27. Percent threshold modulation for a 10 cpd grating when no background was present, when an interocular background was present, and when the eye contralateral to the test stimulus was pressure blinded for ND. 102

28. Percent threshold modulation as a function of spatial frequency for interocular adaptation and binocular test stimulus conditions for ND, TEF, and NM. 117

29. Percent change in contrast sensitivity as a function of spatial frequency for interocular adaptation and binocular test stimulus conditions for ND, TEF, and NM. 119

30. Percent threshold modulation as a function of spatial frequency for different sizes of the test stimulus for interocular adaptation and binocular test stimulus conditions for ND. 123

31. Percent threshold modulation as a function of spatial frequency for different sizes of the test stimulus for interocular adaptation and binocular test stimulus conditions for TEF. 125

32. Percent change in contrast sensitivity as a function of spatial frequency for different sizes of the test stimulus for interocular adaptation and binocular test stimulus conditions for ND. 127

33. Percent change in contrast sensitivity as a function of spatial frequency for different sizes of the test stimulus for interocular adaptation and binocular test stimulus conditions for TEF. 129

34. Percent threshold modulation as a function of spatial frequency for binocular stimulus presentation and interocular backgrounds of various configurations at two different retinal positions for ND. 132

35. Percent threshold modulation as a function of spatial frequency for binocular stimulus presentation and interocular backgrounds of various configurations at two different retinal positions for TEF. 134

36. Percent change in contrast sensitivity as a function of spatial frequency for binocular stimulus presentation and interocular backgrounds of various configurations at two different retinal positions for ND. 136

37. Percent change in contrast sensitivity as a function of spatial frequency for binocular stimulus presentation and interocular backgrounds of various configurations at two different retinal positions for TEF. 138

38. Percent threshold modulation as a function of spatial frequency for binocular stimulus presentation and interocular backgrounds of various configurations for a 1° sized grating presented 5° in the TVF for ND. 141

39. Percent threshold modulation as a function of spatial frequency for binocular stimulus presentation and interocular backgrounds of various configurations for a 1° sized grating presented 5° in the TVF for TEF. 143

40. Percent change in contrast sensitivity as a function of spatial frequency for binocular stimulus presentation and interocular backgrounds of various configurations for a 1° sized grating presented 5° in the TVF for ND. 146

41. Percent change in contrast sensitivity as a function of spatial frequency for binocular stimulus presentation and interocular backgrounds of various configurations for a 1° sized grating presented 5° in the TVF for TEF. 148

42. Percent threshold modulation as a function of spatial frequency for interocular presentation of a 0.01 cd/m^2 background with a monocularly or binocularly presented 0.01cd/m^2 test stimulus at low frequencies, 5° in the TVF for ND. 163

43. Percent threshold modulation as a function of spatial frequency for interocular presentation of a 0.01 cd/m^2 background with a monocularly or binocularly presented 0.01cd/m^2 test stimulus at low frequencies, 5° in the TVF for TEF. 165

44.	Dark adaptation curves for a 2 cpd stimulus after interocular adaptation for ND.	169
45.	Dark adaptation curves for a 2 cpd stimulus after interocular adaptation for TEF.	171
46.	Dark adaptation curves for an 11 cpd stimulus after interocular adaptation for ND.	176
47.	Dark adaptation curves for an 11 cpd stimulus after interocular adaptation for TEF.	178
48.	Derived plots of dark adaptation curves for an 11 cpd stimulus after interocular adaptation for ND.	180
49.	Derived plots of dark adaptation curves for an 11 cpd stimulus after interocular adaptation for TEF.	182
50.	Percent threshold modulation as a function of spatial frequency for various luminance levels of an interocular or monocular background for ND.	185
51.	Percent enhancement as a function of background luminance for an interocular and monocular background for ND.	187
52.	Percent threshold modulation as a function of spatial frequency for different psychophysical methods for ND.	204
53.	Percent change in contrast as a function of spatial frequency for different psychophysical methods for ND.	206

Chapter 1

Introduction and Overview

The two eyes of a human observer send independent signals to the brain where they combine to result in perception. From a conceptual standpoint, five different classes of mechanisms, which are not necessarily mutually exclusive, could explain how this information results in a visual percept.

1. Total Independence: The visual information from each eye sends totally independent signals to the perceptual apparatus, which do not interact with one another. Such a situation would result in two independent views of the world which could be quite disparate. This occurs, for example, under conditions of diplopia (double vision). However, the normal human percept involves a singleness of vision, so signals from the two eyes must be capable of interaction.

2. Summation: The signals from the two eyes could sum together to produce a larger binocular signal. The anatomical substrate for this could readily be provided by the convergence of geniculate input from the two eyes upon the same cortical neuron, (i.e., Polyak, 1957). In both the physiological and psychophysical literature, "binocular summation" is said to occur if

binocular stimulation proves more effective than stimulation of either eye alone. Many psychophysical demonstrations have been reported in the literature since the early part of this century (for a review, see Blake & Fox, 1973; Blake, Sloane & Fox, 1981). Pioneering physiological investigations begin with the work of Hubel and Wiesel (1962, 1965). They showed that the majority of cortical neurons studied in the cortex of cat receive excitatory input from each eye, and these binocular neurons respond in a similar fashion regardless of whether the dominant or non-dominant eye is stimulated. They also showed that binocular stimulation often results in a larger response than monocular stimulation.

The demonstration that binocular presentation results in a larger response and/or greater sensitivity is not sufficient for establishing the existence of "binocular summation." The evidence presented in chapter 3 suggests that many such demonstrations may be due to misinterpretation of results, or due to a removal of tonic interocular suppression.

3. Comparative Mechanisms: The signals from the two eyes are somehow compared, resulting in a unique binocular signal. An example of a comparative mechanism is that underlying stereopsis. Stereopsis refers to the perception of depth which occurs because each eye receives a slightly different view of the world, and only points lying on the elliptical horopter

in space can result in corresponding retinal images. As documented by Wheatstone (1838) with the stereoscope, perceptually-fused but disparate retinal images produce the most potent cue for depth perception. With respect to a binocularly-fused fixation point, stimuli producing crossed retinal images will appear to be closer, whereas stimuli producing uncrossed retinal images will appear further away. For stimuli resulting in singleness of vision rather that diplopia (i.e., are within Panum's fusional area, which is the area on one retina which results in fusion when a particular point on the other retina is being stimulated), the greater the disparity, the greater is the perceived difference in depth with respect to the fixation point.

In more recent studies, Julesz (1964) has shown that stereopsis is a "primary" cue for depth perception which does not depend upon monocular detection of a stimulus. Neurophysiological investigation into the mechanisms of stereopsis has revealed classes of depth-sensitive cells in monkey striate and prestriate cortex (Poggio & Fischer, 1977). In the striate cortex, tuned excitatory cells respond in an excitatory manner to monocular stimulation of either eye. In contrast, with binocular stimulation, an enhanced response is obtained at a certain depth at or near the plane of fixation. For tuned inhibitory cells, the monocular response is similar to the monocular response of tuned excitatory cells, but the response to binocular stimulation at a particular depth results in suppression. "Near" cells are excited by binocular stimulation in front of the fixation point and suppressed by stimulation behind it (i.e., they respond to uncrossed disparity); and "far" cells respond in the opposite fashion (to crossed disparity). These "near" and "far" cells respond over a wide range of depth values.

There are probably many other types of comparative mechanisms besides stereopsis. One often-cited example is "Fechner's Paradox" (after Fechner, 1860) which often occurs when each eye views different luminance stimuli. The apparent brightness of the fused perception is an "average" of that resulting from the monocular perception of brightness. The "paradox" is that neither summation (as described above) nor active suppression (as described below) occurs. The details of the mechanism underlying Fechner's paradox are far from clear. It may result from the comparative type of interaction underlying stereopsis as described by Poggio and Fischer (1977), or a tonic suppressive mechanism as described below.

4. Active Suppression: The signal provided by one eye is sent to the perceptual system and at the same time, suppresses the signal provided by the other eye. The clearest demonstrations for such active interocular suppressive mechanisms are either those involving dichoptic visual masking (e.g., Abadi, 1976; Battersby & Wagman, 1962; Boynton & Wisowaty, 1984; Werner, 1940), or those involving similar neurophysiological demonstrations (Henry, Bishop & Coombs, 1969; Ohzawa & Freeman, 1986 a, b), in which

a monocular response is suppressed when the contralateral eye is stimulated. Such active suppression has been suggested to be the predominant class of mechanism which results in the singleness of normal human binocular perception (Asher, 1953; Makous & Sanders, 1978; Wolfe, 1986).

5. Tonic Suppression: In the binocular vision literature, the term "suppression" is usually used in the manner described directly above as "active suppression," but another type of suppression is known to exist. Lansford and Baker (1969) presented, and then extinguished dichoptic adapting fields, which appeared to partially overlap in binocular view. Then dark adaptation was tracked for a monocular stimulus positioned just outside the area of overlap. Lansford and Baker reported that the interocular adapting stimulus shifted a typical dark adaptation curve to earlier time intervals. Makous, Teller and Boothe (1976) extended these results. They showed that pressure blinding the nonviewing "adapting" eye, which removes any influence upon the cerebrum, produces a similar influence as light adapting the "adapting eye." This suggests that a dark adapted eye exerts a tonic interocular suppression (TIS) upon visual sensitivity mediated by the other eye.

If the two eyes are normally tonically suppressing one another, TIS could readily explain demonstrations of Fechner's paradox. Other likely examples of TIS effects are presented in the introduction to chapter 3.

Overview and Organization of this Dissertation

This dissertation further explores the importance of TIS which was first established by the research of Lansford and Baker (1969) and Makous, Teller, and Boothe (1976). However, it does not concern detection threshold but rather, the influence of interocular light and dark adaptation upon the visibility of monocularly viewed gratings.

The following four chapters are essentially independent of each other. Each contains a detailed "introduction section" which presents the relevant literature, and a methods, results, and discussion section. The set of experiments presented in chapter 2 shows that interocular light adaptation has a potent influence upon grating visibility. These experiments include a parametric description of the importance of luminance, size, retinal position, and spatial frequency of both test and adapting stimuli upon this interocular effect. The experiments described in chapter 3 establish that this interocular adaptation effect involves a unique, interocular, neural effect which cannot be duplicated by either direct adaptation of the "test eye" or by binocular adaptation. These experiments also indicate that monocular light adaptation improves grating visibility by removing a tonic interocular suppression (TIS) which is most active when the "adapting eye" is in the dark.

While conducting the experiments contained in chapter 3, it was noted that binocular stimulus presentation produced an improvement in sensitivity nearly identical to that produced by contralateral light adaptation. The experiments described in chapter 4 directly compared the improvement in sensitivity (in comparison with monocular viewing) resulting from both of these stimulus manipulations. Results suggest that the improvement in sensitivity resulting from binocular viewing may be due to a removal of TIS rather than to binocular summation. Finally, the results presented in chapter 2-4 could represent an influence of either rod- and/or cone-pathways in the adapted eye upon either rod- and/or cone-mediated spatial vision in the contralateral eye. The experiments described in chapter 5 concerned the types of photoreceptor pathways involved in TIS. Chapter 6 is a general discussion of the results presented in the previous 4 chapters.

Chapter 2

The Influence of Interocular Adapting Fields upon Monocular Spatial Vision

Introduction

The work of Aubert, Fechner, Helmholtz, Sherrington, and other 19th century investigators indicated that visual adaptation reflects retinal rather than more central brain mechanisms (for review, see Frumkes, 1990). This conclusion was based in part on psychophysical evidence which showed that under usual experimental conditions, monocular visual sensitivity was negligibly altered by altering the adapted state of the contralateral eye. However, some psychophysical evidence has indicated interocular adaptation effects.

A. Previous Psychophysical Evidence for Interocular Adapting Influences

1. Studies Involving Detection Threshold

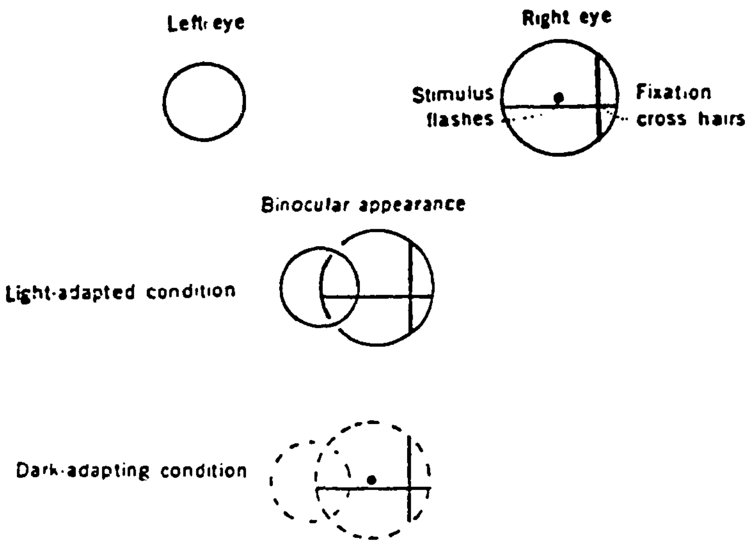
a. The Paradigm of Wolf and Zigler

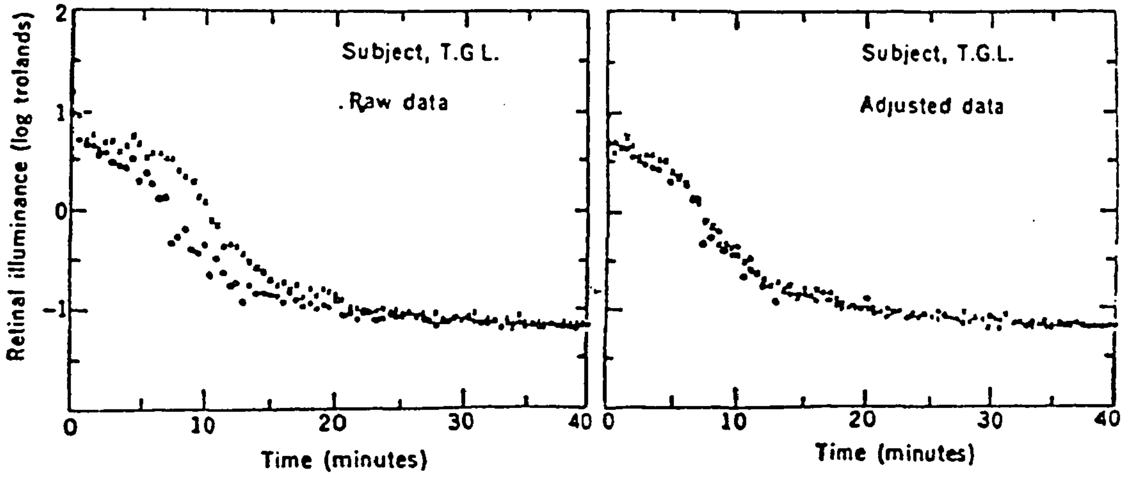
Wolf and Zigler (1955) studied the influence of monocular and interocular adapting fields on parafoveal detection thresholds. After unequal preadaptation of the two eyes, sensitivity was measured for each eye alternately. Under these conditions, the two dark adaptation curves obtained coincided or corresponded more closely than those obtained when dark adaptation to these preadapting luminance levels was measured separately. This outcome indicated an averaging of the adaptational states of the two eyes. This study suggests that under certain conditions, the adapting influence of the two eyes "average" in a manner reminiscent of Fechner's paradox. The Wolf and Zigler paradigm has apparently not been used in more modern investigations.

b. The Paradigm of Lansford and Baker

A large number of investigators have demonstrated "interocular masking" effects. For example, Battersby and colleagues (Battersby & Wagman, 1962, 1964; Battersby, Oesterreich & Sturr, 1964) have shown that interocular adapting fields ("masking stimuli") can depress contralateral sensitivity. However, using a specific spatial arrangement of test and adapting stimuli, illustrated on the top of figure 1, Lansford and Baker (1969) showed that interocular adaptation can increase monocular sensitivity. In fact, their data suggest that an interocular adapting field speeds up the time course of dark adaptation (i.e., shifts the dark adaptation function "to the left" by several minutes without altering its shape), as shown at the bottom of figure 1.

Figure 1. The upper part shows the test and adapting field configuration used in the Lansford and Baker (1969) experiment. A 12° adapting field was presented to the left eye and a 17°30' adapting field was presented to the right eye. In binocular view, these partially overlap. A 1° stimulus was presented to the right eye to the right of the area of overlap (5° in the nasal visual field). The bottom part shows data obtained with monocular and binocular preadaptation. The dark adaptation curve on the left shows data obtained with monocular preadaptation (control condition), as indicated by X's and binocular preadaptation (filled circles). The curve on the right shows the same data, but with the curve obtained with binocular preadaptation shifted to the left by 3 minutes.


Left eye
Right eye
Stimulus flashes
Fixation cross hairs
Binocular appearance
Light-adapted condition
Dark-adapting condition


Retinal illuminance (log trolands)
2
1
0
-1
Subject, T.G.L.
Raw data
0
10
20
30
40
Time (minutes)
Subject, T.G.L.
Adjusted data
0
10
20
30
40
Time (minutes)

It is necessary to consider carefully the importance of specific stimulus parameters which influence the Lansford-Baker effect. As shown in the upper part of figure 1, Lansford and Baker (1969) used adapting stimuli consisting of a 12° circle presented to the left eye, and a 17°30' circle presented to the right eye. In binocular view, this configuration appeared as a smaller circular patch of light on the left partially overlapping with a larger circular patch on the right. During dark adaptation, these stimuli were extinguished and a 1° stimulus was presented to the right eye, appearing in binocular view to be just to the right of the area of overlap of the adapting fields (5° in the nasal visual field of the right eye). The absolute threshold for detection of the stimulus was determined throughout 40 minutes of dark adaptation under conditions in which the adaptation stimuli were presented in both eyes, or just presented to the stimulus eye. Their data indicate that when the time of occurrence of the rod-cone break and the final threshold level are considered, the curve obtained when both eyes were preadapted reached these levels 3 minutes earlier compared to the curve obtained when only the test eye was adapted. This effect occurred in 3 observers but was absent in one with abnormal stereopsis, suggesting that normal binocular vision is necessary for showing this effect. When the adapting fields were made equal in luminance and size, the effect did not occur and it also did not occur if the left eye field was made much (1.2 $\log_{10}$ units) brighter. Furthermore, the effect did not occur if the adaptation stimulus in the left eye was presented for the entire period of dark adaptation. It did occur, however, if the left eye adapting field was made 0.3 $\log_{10}$ units dimmer. Lansford and Baker explained the importance of specific stimulus parameters in vague terms, i.e., the luminance requirements necessary for "local suppression effects." They state that under the condition in which the luminance the left eye is made much brighter, a condition of binocular rivalry is produced. When the adapting fields are similar in luminance and different in size, and also when one is made 0.3 $\log_{10}$ units dimmer, both fields are seen simultaneously, and are perceived as superimposed. With this stimulus arrangement, there is strong local suppression of one field upon the other. This local suppression dims the area where the test stimulus later appears, thereby accelerating the dark adaptation curve.

The results of Lansford and Baker (1969) have been replicated in several more recent studies (Makous, Teller & Boothe, 1976; Paris & Prestrude, 1975; Prestrude, 1976). Makous, Teller, and Boothe (1976) reported that the positions of the adapting fields relative to the test stimulus are critical for the occurrence of the effect. If the adapting field in the eye contralateral to the test is too far from, or overlaps with the area where the test stimulus appears, no effect occurs. Also critical is the relative luminance values for the two adapting fields: the luminance in the non-test eye must be between 0.1 and 0.5 $\log_{10}$ units less than the luminance of the test eye adapting field. Finally, Prestrude (1976) showed that the "Lansford-Baker" effect can be seen at almost any retinal position of the test stimulus, provided that the same relative positions of the adapting stimuli were maintained.

Makous, Teller and Boothe (1976) replicated and extended the study of

Lansford and Baker (1969) and attempted to determine the mechanism responsible for the interocular light adaptation effect. In this study, the adapting fields, which were 1 $\log_{10}$ unit dimmer than those used by Lansford and Baker (1969), were presented with a luminance difference of 0.2 $\log_{10}$ units, the same difference used by Lansford and Baker. They reasoned that three possible mechanisms might be involved, and the mechanism responsible for producing the effect could be determined by examining the effects of pressure blinding the eye contralateral to the test stimulus, thereby eliminating any light signals from that eye. One possibility is that light-adapting the contralateral eye sends a facilatatory signal to the brain. If the contralateral eye is first light-adapted and subsequently pressure-blinded, sensitivity should decrease: in fact, sensitivity increased, but did not decrease. A second possibility is that light adapting either eye causes decreased sensitivity which acts at some central locus in the brain which receives signals from both eyes. In this case, pressure-blinding the eye contralateral to the test eye should fail to alter sensitivity. However, sensitivity increases when the eye contralateral to the test stimulus is dark adapted and pressure blinded. This lends support to their third hypothesis, namely, that a dark-adapted eye sends signals to the brain which somehow interfere with the detection of the test stimulus.

More recently, Auerbach and Peachey (1984; also Reeves, Peachey & Auerbach, 1986) demonstrated the phenomenon of interocular sensitization, which may be a special case of the Lansford-Baker effect. In their experiment (Reeves, Peachey

& Auerbach, 1986), sensitivity was determined after the right eye was preexposed to a 16° red adapting field and the left eye to a 661 nm test stimulus which subtended an area of 1.02° on the retina. They state that their pilot results generally confirmed previous reports that threshold is not much affected by continuous contralateral light adaptation. This result was also found by Mitchell and Liaudansky (1955) who used test stimulus parameters virtually identical to those used by Wolf and Zigler (1955) but maintained the contralateral eye in a light adapted state. They concluded that there was no averaging effect since the slight increase in sensitivity for 3 of their observers, and no change for 1 observer, was not statistically significant for the group. However, when they used a red (632 nm) preadapting field, Reeves, Peachey and Auerbach (1986) found that an interocular sensitization effect did occur. They observed a sensitivity increase of approximately 0.15 $\log_{10}$ units approximately 12 minutes following adaptation for 10 to 15 minutes. This effect was abolished with a small, brief stimulus or when the stimulus was presented to the fovea or when a rod desensitizing adaptation light was presented in the test eye during threshold determination. It did occur, however, when a different stimulus, one which stimulated rods, was used.

2. Studies not Involving Detection Threshold

Several studies have examined interocular adapting influences upon color. Probably the most interesting involves an interocular version of the "Lie effect," in which specific (correct color identification) threshold is determined throughout the time course of dark adaptation. Lie (1963) found that the time course, magnitude, and polarity of threshold change during the cone-limb of dark adaptation were quite similar for specific and for detection threshold. During the rod-limb of adaptation, however, specific threshold rises while detection threshold decreases. Lie performed his experiments with monocular stimulation. If the adapting field was presented interocularly (Prestrude, Watkins & Watkins, 1978), the same effect occurred, again indicating that the state of adaptation of one eye can effect sensitivity of the other.

Various studies have considered the problem of perceived brightness during dichoptic stimulation with lights of with the same spectral composition (for a review see Blake & Fox 1973), but relatively little has been done with stimuli of different colors. deWeert & Levelt (1976) showed that the contribution each eye makes to perceived brightness depends upon wavelength, such that stimuli from the mid-portions of the spectrum make a larger contribution than low and high wavelengths. Yellott and Wandell (1976) contend that there may be two types of masking effects. One occurs at the retinal level and in some instances appears to be receptor (wavelength) specific but in other cases does not. Another type were dichoptic interactions that they observed in their study which were receptor specific. Steady interocular backgrounds have also been found not to affect brightness (Whittle & Challands, 1969). Some have found a summation effect for brightness (De Silva & Bartley, 1930; Fry & Bartley, 1933). Blake and Fox (1973) suggest brightness summation may occur only when both eyes receive identical stimulation, and averaging, as occurs in Fechner's paradox, is found with unequal luminances.

A few studies address flicker sensitivity by measuring critical flicker fusion (CFF) with contralateral light adaptation (Lipkin, 1962; Perrin, 1954; Vernon, 1934). These show that CFF decreases slightly when the contralateral eye is light adapted. In addition, it was found that the decrease in sensitivity was the greatest when the test and adapting field were the same hue, and there was actually an increase in CFF when they were composed of complementary hues (Allen, 1923).

B. Measurement of Spatial Sensitivity with Sine Wave Gratings

The effects of interocular adaptation on spatial sensitivity can also be studied. Historically, spatial sensitivity was usually measured by obtaining "visual acuity" values. In general, this involved the use of a forced-choice psychophysical procedure. This task was to identify the position of a gap using the Landolt C (Landolt, 1889), a "C" shaped stimulus with a gap of the same width as the width of the letter; or correctly identifying a letter using the Snellen Acuity chart (Snellen, 1862). Although such a measure provides useful information, it says little about the ability of an individual to see objects which do not require the resolution of fine spatial detail, for example,in a contrast detection task at various frequencies.

More recent studies have used sine wave gratings to study visual perception. These are alternating bright and dark areas which are spatially sinusoidally modulated and can be varied, for example in terms of spatial frequency and contrast. Gratings allow sensitivity measures for a variety of spatial frequencies, not just the maximum frequency which can be resolved. Aside from allowing the measuring of sensitivity to a variety of frequencies, the use of sine wave gratings has a further advantage. Fourier theorem states that any wave form or distribution can be completely described by a particular synthesis of sine waves with particular frequencies, amplitudes and phases in a linear system.

During the past 25 years, contrast sensitivity functions (CSFs) have been obtained by presenting many different spatial frequency sine waves to the observer, who always adjusts the contrast of the grating to threshold. The usual CSF function is a plot of contrast sensitivity (the inverse of contrast threshold) as a function of spatial frequency on double logarithmic coordinates. Under moderate photopic levels of illumination, the CSF shows maximal sensitivity at about 5-6 cycles per degree (cpd), but peak sensitivity falls to lower spatial frequencies if the grating luminance is reduced to dimmer photopic or scotopic levels (Campbell & Green, 1965a; Patel, 1966; Kelly, 1977).

It is generally believed that several different mechanisms or channels account for contrast sensitivity (Graham, 1989). Electrophysiological literature suggests that the magnocellular pathways are more sensitive to lower spatial frequencies since they have larger receptive fields. The parvocellular pathways have smaller receptive fields and respond to higher spatial frequencies (i.e., see Purpura, Kaplan & Shapley, 1988). Since these two subdivisions of the geniculate seem to project to different areas of the cortex (e.g., see Livingston & Hubel, 1987), it would seem that psychophysical data would likely reflect processing of at least two different sets of spatial frequency channels. In fact, most current psychophysical models suggest the existence of at least three separate spatial frequency channels (see Graham, 1989).

In the following experiments, a systematic examination of the influence of various levels of interocular adaptation upon a wide spectrum of different spatial frequencies was performed.

Methods

A. Observers

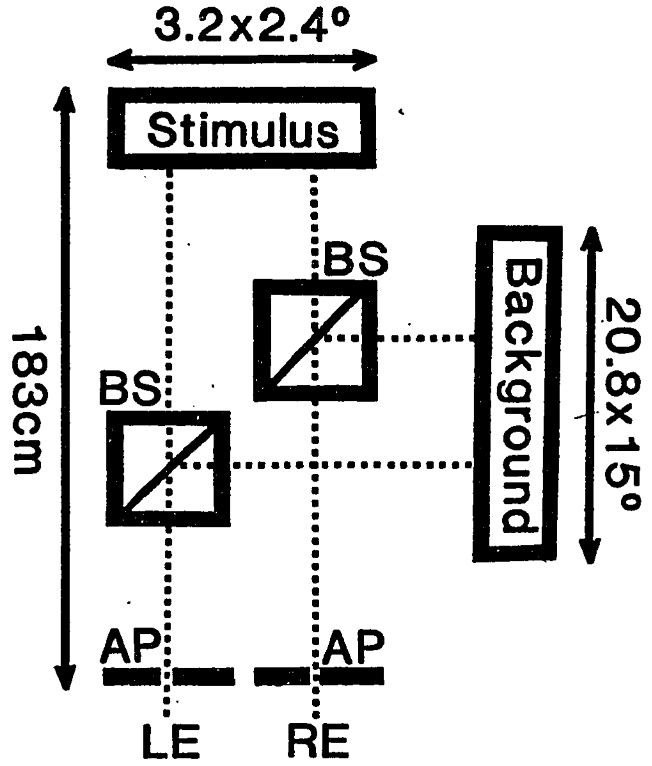
Three observers were used. The author, a 27 year-old female, was used in all experiments and wore contact lenses to correct for myopia. The second most commonly-used observer, TEF, was a 48 year-old male who, except for presbyopia and mildly deuteranomalous color vision, had uncorrected normal vision. NM, a 24 year-old female, was used as an observer and wore her glasses throughout experimentation to correct for myopia. With the optical correction worn during experimentation, the visual acuity of all observers was at least 20/20.

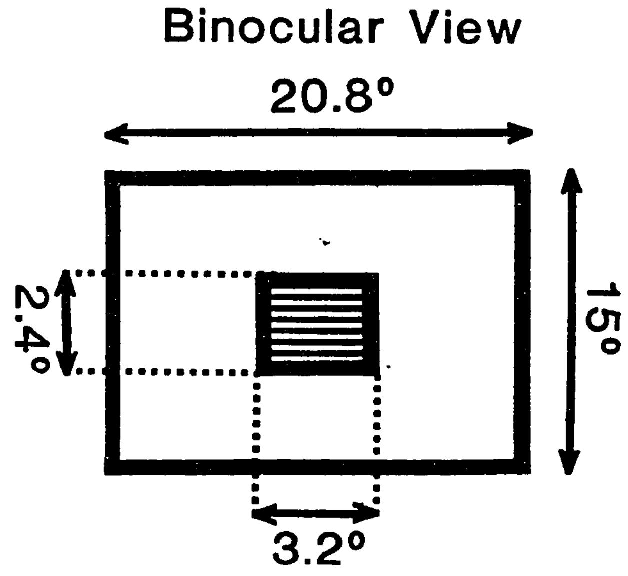
B. Apparatus

1. Overall Spatial Arrangement

A Maxwellian view system, which has been described elsewhere (Frumkes & Sturr, 1968), was used to collect some ancillary detection thresholds during dark adaptation. Most experiments, however, were conducted using a free field binocular system (figure 2). During experimentation, the observer was seated in a height-adjustable chair. The head was maintained in a fixed position by a full-mouth bite bar, which could be adjusted to move in three planes. The observer viewed stimuli through

Figure 2. Apparatus used to collect data in the majority of experiments is seen at the top of the figure. The test stimulus was a 3.2° x 2.4° sine wave grating. 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° x 15° diffuse field. Test and background stimuli were placed at an optical distance of 183 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 stimuli could be presented to the left (LE), right (RE), or both eyes. Stimuli were viewed through 2.5 mm artificial pupils (AP), which were placed before each eye. The diagram does not indicate a large number of baffles and a septum placed to minimize stray light.


3.2x2.4°
Stimulus
183cm
BS
BS
Background
20.8x15°
AP
AP
LE
RE


Binocular View
20.8°
2.4°
15°
3.2°

2.5 mm artificial pupils which were placed before each eye to rule out consensual pupillary dilation. The artificial pupils could also be individually adjusted in three planes (using modified Kopf Stereotaxic micromanipulators) to obtain an appropriate view of the stimulus.

The test stimulus consisted of sine wave gratings positioned so that the alternating bright and dark bars were oriented horizontally, and appeared on a 12.5 cm Ikegami black and white monitor. A background or adapting field stimulus consisted of a fluorescent photographic light box. Both stimuli were placed at an optical distance of 6 feet (1.83 m) from the artificial pupils in order to obtain the range of spatial frequencies used. The images from test and adapting stimuli were combined through prism type beamsplitters. Stray light was minimized with flat-black painted baffles constructed from wood and cardboard. Also, a septum placed between the two beamsplitters insured that each eye received totally separate stimulation. In figure 2 the dotted lines indicate the pathways along which the test and background stimuli could pass. Through appropriate placement or absence of occluders near the beamsplitters, either the test and/or adapting stimulus could be delivered to the left, right, or both eyes. This diagram does not indicate the large number of baffles and septum used to minimize stray light.

The maximum size retinal image produced by the test stimulus was 3.2° x 2.4° (dimensions reported refer first to width, followed by height); and 20.8° x 15° for the adapting stimulus. The size of the stimulus was limited by the stimulus monitor size. However, this size is similar to that used in many contrast threshold experiments (i.e.; Campbell & Green, 1965b; Lema & Blake, 1977; Anderson & Movshon, 1989). In initial pilot studies, fixation targets (dim red light-emitting diodes) were always used to aid in fixation. However, these proved of little value when stimuli were viewed foveally and were omitted, except in cases when gratings were presented at a stated peripheral retinal locus.

The size and shape of the test and adapting stimulus could be reduced or changed by placing apertures constructed from flat black paper directly on the stimulus surface. The luminance of the test and the adapting stimulus could be attenuated separately by appropriate placement of neutral density filters. Luminance was carefully calibrated with a Minolta LS 100 luminance meter while all baffles and beamsplitters were in place. Measurements were made with the meter placed at the spatial location usually occupied by the artificial pupil. Under these conditions, the maximal luminance provided by the test and adapting stimulus in either eye was 10 and 100 cd/m^2 respectively. With the use of neutral density filters to decrease luminance, it was possible to present luminance values to stimulate rods or cones (Wysecki & Stiles, 1967)

2. Grating Generator

The test stimulus monitor was driven by a Sine-Wave Grating Generator which was purchased from Vision Metrics, Inc. in the summer of 1987. The Vision Metrics Grating Generator was built by Y. Ozawa in Berkeley, California. The rights for this device were since sold to Neuroprove Corporation of Farmingdale, Long Island and the grating generator since sold under the same name has been modified several times. This "generator" consisted of a hardware/software package which was run by an XT clone (Fountain) microprocessor. The software package included a program for data collection, calibrating spatial frequency and contrast (PGCONSEN), and calibrating contrast (PGDEMO). The latter program allowed any contrast value to be measured whereas the calibrating program allowed the measuring of only one contrast value. With the PGCONSEN program, all data are automatically stored in Lotus format on the hard-drive of the microprocessor, and if desired, plotted out in both tabular and graphic form on a dot matrix printer. Most data were collected using several modifications, described below, of PGCONSEN written by Mr. John Zhu.

C. Procedure

1. General Psychophysical Methodology

The majority of data collected in this study were contrast sensitivity functions (CSFs). A contrast sensitivity function is obtained by determining sensitivity to a one dimensional sinewave grating as a function of the spatial frequency of the grating. To obtain a CSF, several different spatial frequency sine wave gratings are presented in a random order. For each frequency, the observer varies the contrast for threshold.

Several different procedures were utilized to collect such thresholds. The first procedure involved use of the PGCONSEN program supplied by Vision Metrics, which automatically collected data according to a two-alternative forced-choice staircase procedure. Prior to a testing session, the experimenter selected the spatial frequencies to be used, in most cases, 2, 5, 10, and 15 cycles per degree (cpd). The observer indicated his/her readiness to begin the session by depressing a pushbutton, at which time stimuli were automatically presented. The observer was allowed to rest between trials, that is, after presentation of a single spatial frequency, by not responding, or by flipping a toggle switch before responding. Testing would resume when the observer placed the toggle switch in its original position. The test stimulus was a horizontally-oriented sine wave grating presented for 500 msec which, on the first trial, was presented at a contrast level above threshold. Presentation of the grating involved no change in average luminance level from that occurring during the intervals between stimulus presentation. The interstimulus interval, between the offset of one stimulus and the onset of the next, was 1000 msec. Since the interstimulus interval also depends on how quickly the observer makes a response to the stimulus, 1000 msec represents the minimum interstimulus interval. Various spatial frequencies, which were previously specified by the experimenter, were presented randomly. The observer responded by pressing the key located on the left to signal that the stimulus was detected during the first temporal alternative, or the key on the right for the second. Each temporal alternative was indicated by the presence of a tone. If the observer was unsure of the alternative, they were instructed to guess. If the observer responded correctly, the contrast of the stimulus was decreased; when an incorrect response was made, grating contrast increased. A change from an increase in contrast to a decrease or vice versa, comprised a reversal. Contrast steps were in three dB units for the first two reversals, and one dB steps thereafter. The number of reversals in one session was six for each frequency, plus the two initial three dB reversals which were not computed in the threshold value. A different randomly-chosen frequency was presented on each trial until six reversals had been obtained at each frequency. After the reversals for all of the chosen frequencies had been obtained, the mean of all the midpoints between each reversal for a particular frequency was computed as the threshold by the program.

Although usable, the PGCONSEN program had two difficulties: 1) data collection was time-consuming and 2) it often produced spuriously low threshold values. Specifically, after presentation of a subthreshold grating, there was a 50% chance that grating contrast would be still further reduced, and after the session had ended, in some instances, the observer never believed that a specific grating frequency was detected after initially reaching threshold. Although difficult to specify, the chance of a spuriously low threshold was probably at least 20%.

Mr. John Zhu, the computer technician in the Queens College Psychology Department, wrote two modifications of this program in order to speed up data collection and to overcome the spuriously low threshold values which occurred in the staircase procedure. The first of these procedures involved a yes/no method of adjustment procedure. After the observer signaled the beginning of a session, a randomly-chosen grating was presented at a preset value. Whereas depressing one push button would automatically increase grating contrast by three dB on the next trial, depressing the other would decrease contrast by three dB. Again, after the first two reversals in contrast, the contrast step was decreased from three dB to one dB. When the observer thought the grating was at threshold, a third button would be pushed which would signal that the grating was at threshold. Then a different frequency grating was presented and the sequence was repeated. In order to make the criterion threshold value less subjective, a second program was introduced which involved the use of a forced-choice method of adjustment procedure. Stimuli were again presented in one of two given time blocks as in the staircase procedure described above. If the observer thought he/she could detect the interval during which the grating was presented, he/she pressed the button which decreased contrast on the next programmed stimulus presentation; if it was not detected, depressing the other button increased contrast.

Results obtained with all three procedures described above provided comparable data (see Appendix A), and for this reason no further reference is made to them throughout the main body of this thesis. However, all figure legends indicate the specific psychophysical procedure used.

After the data were collected, they were entered onto a spreadsheet (Lotus-123), and means were calculated for all sessions for each experiment.

2. General Experimental Procedure

The general procedure used in most experimental sessions 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, adjusting the position of the bite bar and positioning the two artificial pupils so that the stimuli could be appropriately viewed passing through the beamsplitters. After the observer was aligned, the room lights were extinguished and both eyes of the observer were dark adapted for 20 minutes. The observer then viewed the test stimulus with the left eye and a contrast sensitivity function was obtained monocularly as the control condition. Then the procedure was repeated in the presence of interocular adapting stimuli of differing luminance levels, sizes, and/or shapes; or stimuli were presented to different eye combinations. Only one luminance test grating was used in any experimental session. In a session, every contrast sensitivity function was obtained twice. Since each function was obtained in at least three different experimental sessions, data presented below represent means of at least six threshold determinations. In figures 3-13, one standard error is usually about the size of the plotted datum, and mean 95% confidence intervals (±2 standard errors) for control values are shown.

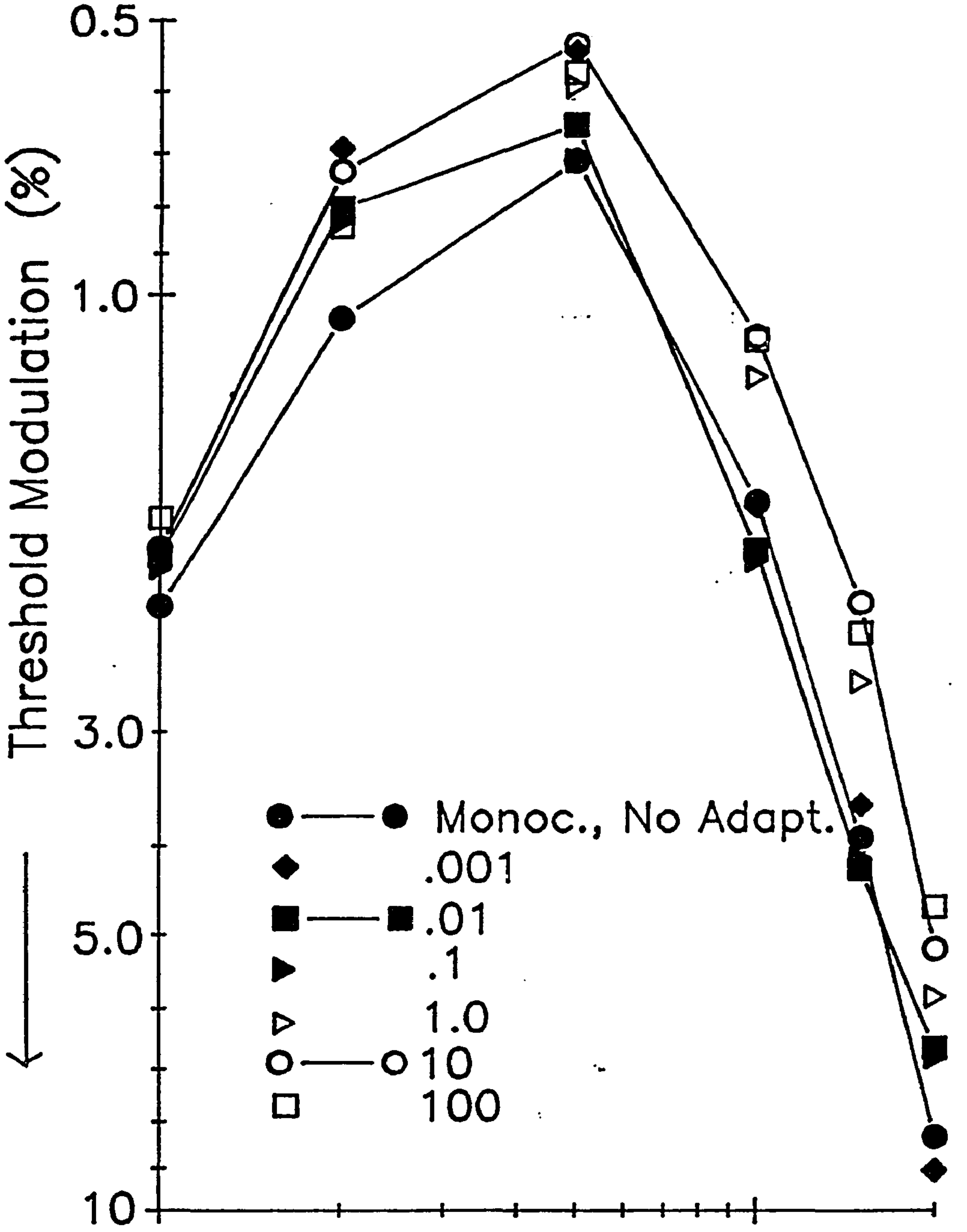
Results and Discussion

A. Results Obtained with the Most Common Stimulus Values

Figure 3 displays results for observer ND with the conditions most typically used in this study. The figure follows the convention established by Campbell and Robson (1968) to portray spatial modulation sensitivity data for sine wave gratings. Percent threshold modulation (increasing logarithmically downward along the ordinate) is examined as a function of the logrithm of the spatial frequency of the grating; this is most commonly known as a contrast sensitivity function (CSF). With this convention, an increase in sensitivity is thus indicated by an upward shift along the ordinate.

For the data shown in figure 3, the grating was 3.2° x 2.4° in overall spatial extent, had an average luminance of 10 cd/m^2 and was presented foveally to the left eye. The closed circles show data obtained when this test grating was presented monocularly and no other illumination was presented to either eye (i.e., the other eye of the observer was totally dark adapted). As is typical in the contrast sensitivity literature (i.e., Kelly, 1977), sensitivity is greatest for an intermediate spatial frequency of about 5 cycles per degree (cpd) and falls off for lower or higher spatial frequencies. The other data in figure 3 were obtained when the contralateral eye was continuously exposed to an adapting field which was 20.8° x 15° in spatial extent with luminance

Figure 3. Percent threshold modulation as a function of spatial frequency is plotted for observer ND. These data were collected according to a two-alternative forced-choice staircase procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° sine wave grating (between 1 and 20 cpd) presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye, and was varied in luminance as indicated in the key. Note that the closed circles represent control data obtained with a monocular stimulus and no background. Other closed symbols represent the presence of dimmer interocular background luminance values while open symbols represent brighter interocular background levels.


0.5
1.0
3.0
5.0
10
Threshold Modulation (%)
1
2
5
10
20
Spatial Frequency (cycles per degree)
● Monoc., No Adapt.
◆ .001
■ .01
▶ .1
▷ 1.0
○ 10
□ 100

(in cd/m^2) systematically varied. The following aspects of these data are general properties of interocular light adaptation.

1. The overall shape of the CSF is not grossly changed by presentation of any luminance of the contralateral adapting field. In general, an interocular adapting field had either no effect, or increased spatial sensitivity.

2. Interocular backgrounds have a very small influence upon sensitivity to 1 cpd gratings. For the specific data presented in Figure 3, all interocular background fields slightly increased sensitivity to this low frequency grating. As shown in figure 8 below, however, interocular adaptation sometimes had no influence upon sensitivity to 1 cpd gratings.

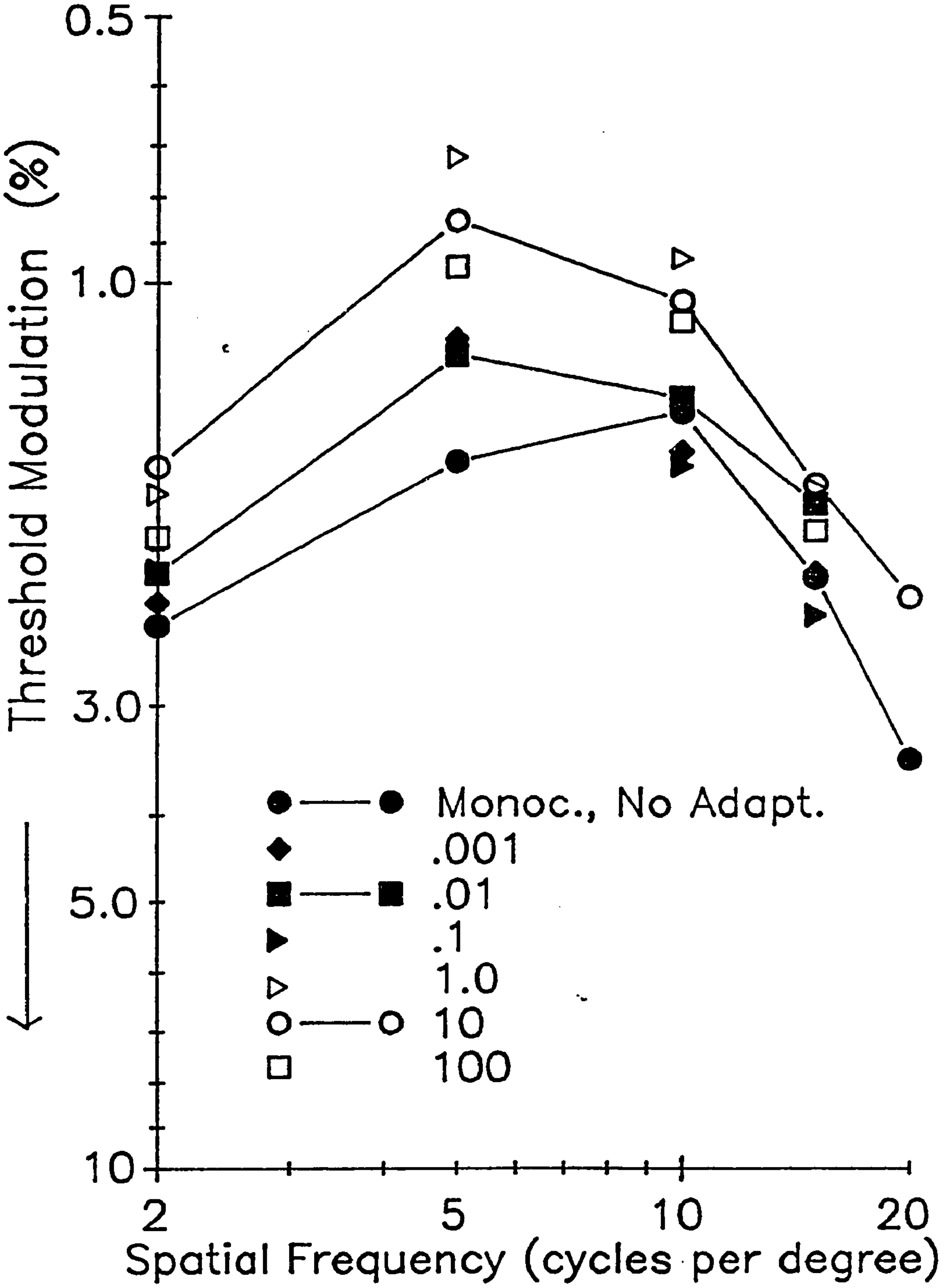
3. Background fields with luminance levels between 0.001 and 0.1 cd/m^2 (figure 3, filled diamonds, squares and triangles) increased sensitivity to 2 and 5 cpd gratings, but had no reliable influence upon sensitivity to spatial frequencies of 10-20 cpd.

4. Background fields with luminance levels between 1.0-100 cd/m^2 (figure 3, open symbols) increased sensitivity to 2-20 cpd gratings.

Although the CSF has a somewhat anomalous shape (sensitivity is quite high to the high spatial frequency), the same general influences of interocular backgrounds are observed for observer, NM (figure 4). Dim interocular backgrounds tend to be more effective in increasing sensitivity for lower spatial frequencies, (sensitivity is increased for a 5 cpd grating). Brighter interocular backgrounds increase sensitivity to all spatial frequencies presented (2-20 cpd). The data for a third observer, TEF (figure 5) show that for the one background luminance level presented, an interocular background produces an increase in sensitivity for all frequencies examined (2-15 cpd). These results are consistent with those obtained from observers ND and NM (figures 3 and 4).

The data in figure 3 are replotted in figure 6 for observer ND and the data in figure 4 are replotted in figure 7 for observer NM to further illustrate several tendencies. Percent change in contrast sensitivity is plotted as a function of interocular background luminance. Since threshold measurements of contrast represent ratio measurements, percent change rather than differences between experimental and control values were plotted. To determine the percent change in contrast sensitivity the ratio of the sensitivity obtained with interocular adaption to sensitivity with no interocular adapting field present was calculated for every spatial frequency. The formula (equation (1)) was as follows:

Figure 4. Percent threshold modulation as a function of spatial frequency is plotted for observer NM. These data were collected according to a two-alternative forced-choice staircase procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye, and was varied in luminance as indicated in the key. Note that the closed circles represent control data obtained with a monocular stimulus and no background. Other closed symbols represent the presence of dim interocular background luminance values while open symbols represent brighter interocular background levels.



0.5
1.0
3.0
5.0
10
Threshold Modulation (%)
2
5
10
20
Spatial Frequency (cycles per degree)
●——● Monoc., No Adapt.
◆ .001
■——■ .01
▶ .1
▷ 1.0
○——○ 10
□ 100

Figure 5. Percent threshold modulation as a function of spatial frequency is plotted for observer TEF. These data were collected according to a two-alternative forced-choice staircase procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea. The background stimulus was a 10 cd/m^2, 20.8° x 15° diffuse field presented to the right eye. The closed circles represent control data obtained with a monocular stimulus and no background.

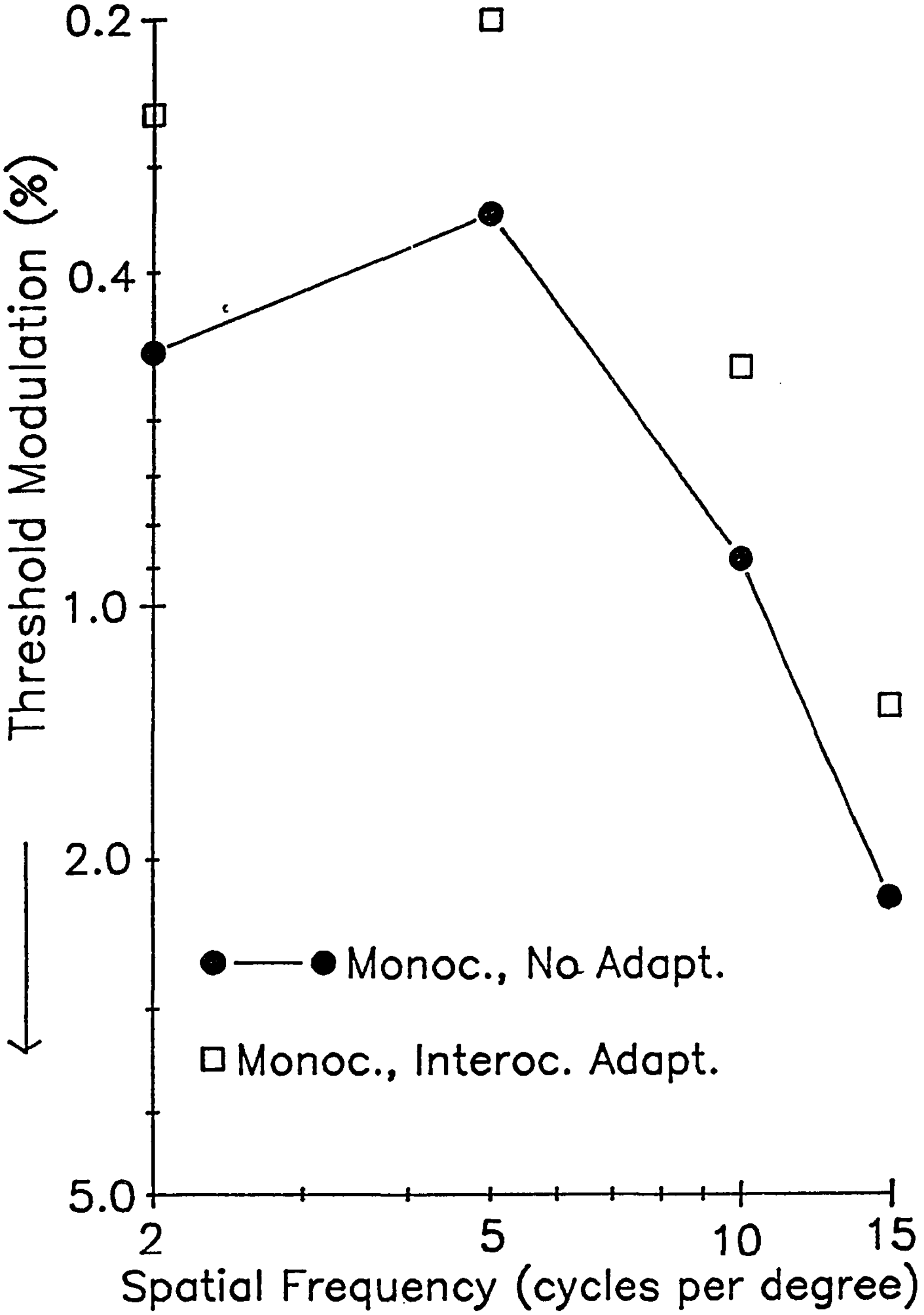
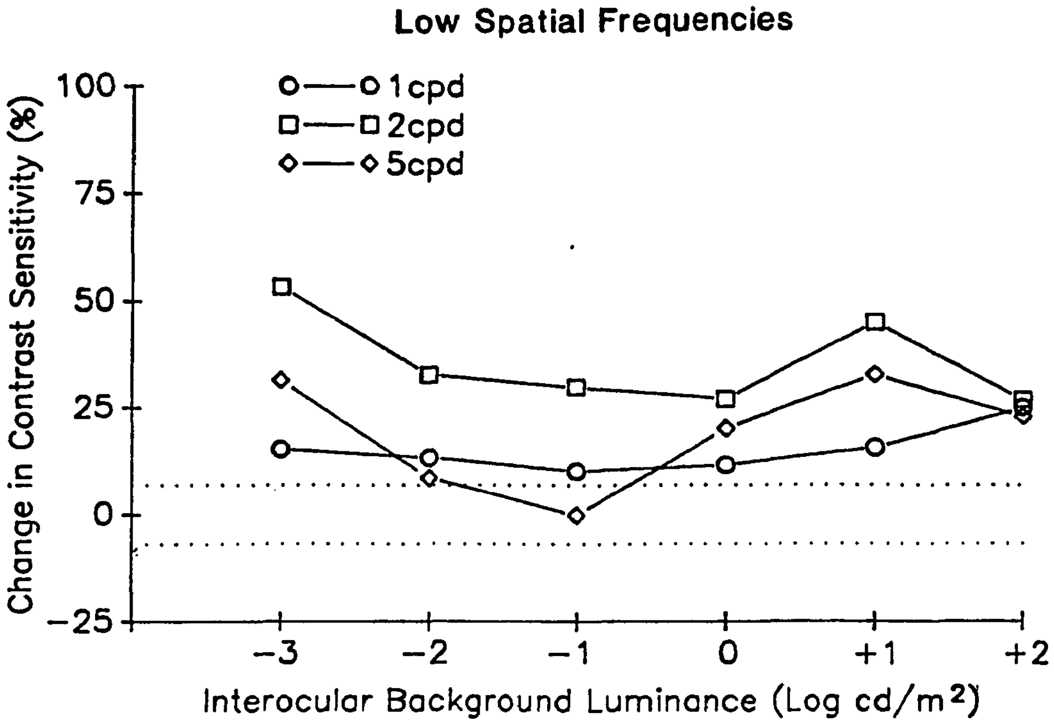

0.2
0.4
1.0
2.0
5.0
Threshold Modulation (%)
2
5
10
15
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
□ Monoc., Interoc. Adapt.

Figure 6. This figure represents a replot of the data shown in figure 3 and shows percent change in contrast sensitivity as a function of log interocular background luminance with spatial frequency as a parameter for observer ND. These data were collected according to a two-alternative forced-choice staircase procedure. The stimulus was a 3.2° x 2.4°, 10 cd/m^2 sine wave grating presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye and varied in luminance. The upper plot shows contrast sensitivity for lower spatial frequencies (as indicated in the key) and the lower plot shows contrast sensitivity for higher spatial frequencies. The dotted horizontal lines indicate mean 95% confidence intervals (±2 standard errors) for control data.


Low Spatial Frequencies
1cpd
2cpd
5cpd
Change in Contrast Sensitivity (%)
100
75
50
25
0
−25
−3
−2
−1
0
+1
+2
Interocular Background Luminance (Log cd/m²)

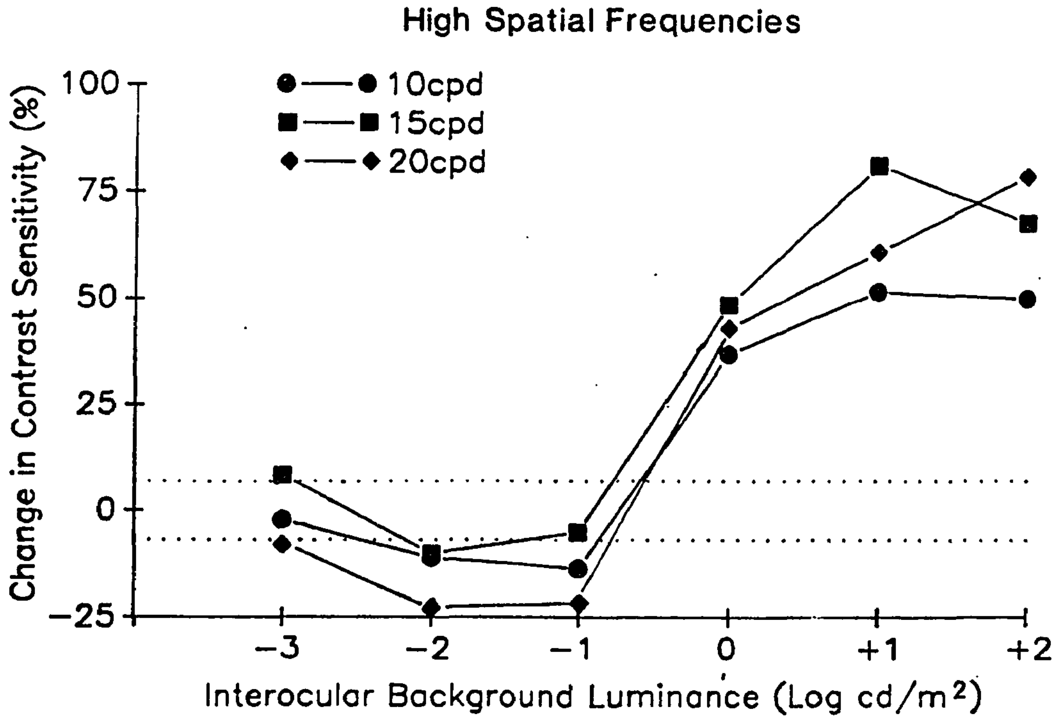
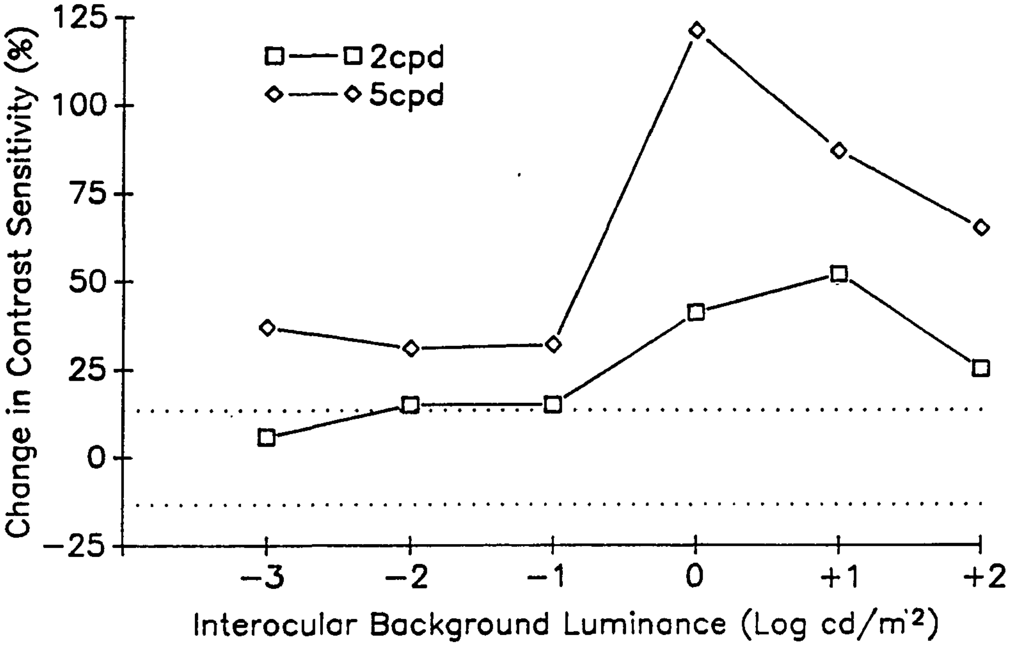
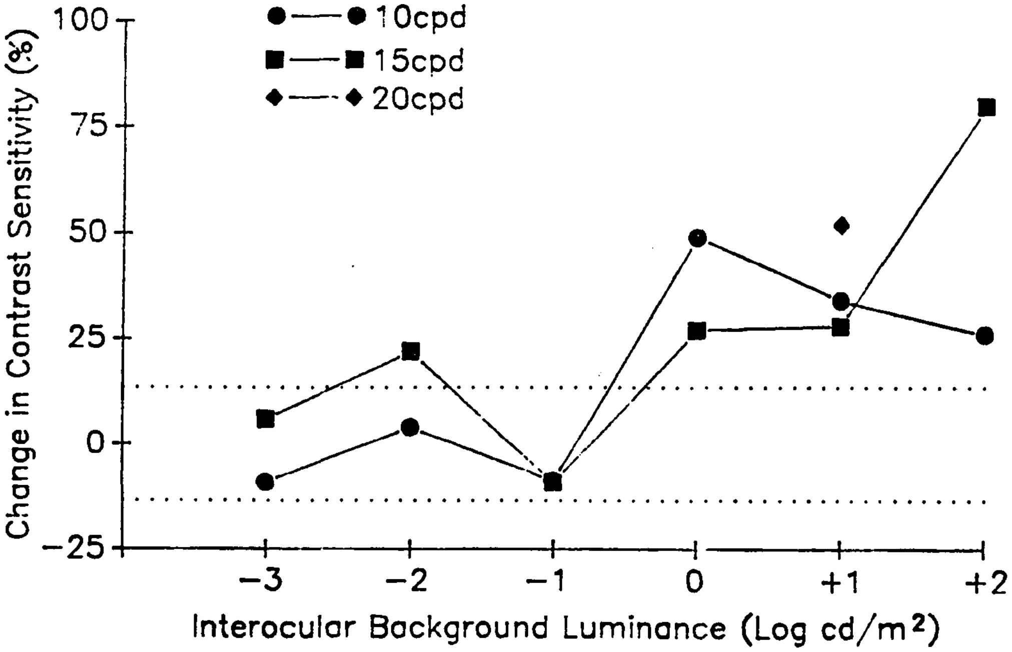

High Spatial Frequencies
10cpd
15cpd
20cpd
Change in Contrast Sensitivity (%)
100
75
50
25
0
−25
−3
−2
−1
0
+1
+2
Interocular Background Luminance (Log cd/m²)

Figure 7. This figure represents a replot of the data shown in figure 4 and shows percent change in contrast sensitivity as a function of log interocular background luminance with spatial frequency as a parameter for observer NM. These data were collected according to a two-alternative forced-choice staircase procedure. The stimulus was a 10 cd/m^2 3.2° x 2.4° sine wave grating presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye and varied in luminance. The upper plot shows contrast sensitivity for lower spatial frequencies (as indicated in the key) and the lower plot shows contrast sensitivity for higher spatial frequencies. The dotted horizontal lines indicate mean 95% confidence intervals (±2 standard errors) for control data.

Low Spatial Frequencies



High Spatial Frequencies



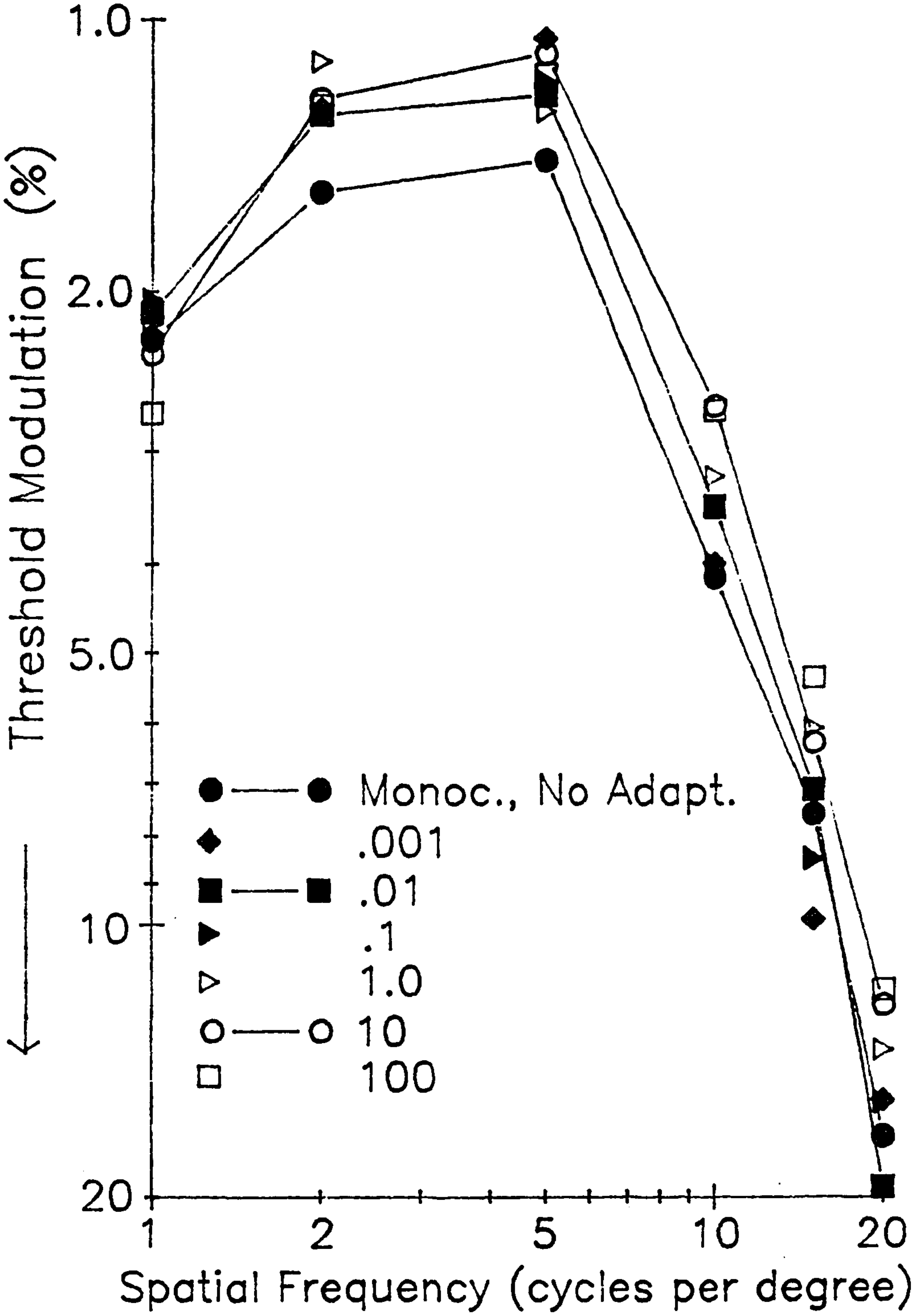
$$\text{Sensitivity Change} = \left(\frac{\text{Experimental Threshold}}{\text{Control Threshold}} - 1\right) \times 100\% \qquad (1)$$

Where "Sensitivity Change" is the % change in contrast sensitivity, "Experimental Threshold" is the sensitivity value obtained during experimental conditions with an interocular background present, and "Control Threshold" is the sensitivity value obtained during control conditions when no interocular background was present. In these figures, percent change in sensitivity is plotted linearly on the ordinate as a function of the log of the background luminance. The horizontal dotted lines represent mean 95% confidence intervals (±2 standard errors) for control sensitivity. The upper panel of figures 6 and 7 indicates results obtained with low spatial frequencies for observers ND (1-5 cpd) and NM (2-5 cpd) respectively. Increases in interocular background luminance from -3 to -1 $\log_{10}$ cd/m^2 fail to produce a systematic change in sensitivity. There is perhaps some tendency for sensitivity to increase slightly (by approximately 20%) if background luminance increases to higher values. In contrast, the results obtained with higher spatial frequencies (figures 6 and 7, lower panels) show clear influences of the luminance level of the interocular backgrounds upon sensitivity. Background luminance levels between -3 and -1 log cd/m^2 generally failed to influence sensitivity. However, as the background luminance increases to still higher levels (>-1 log cd/m^2), sensitivity increases (by approximately 75%). This effect is most clear in observer ND with the highest spatial frequency employed, 20 cpd.

B. Effects of Grating Luminance

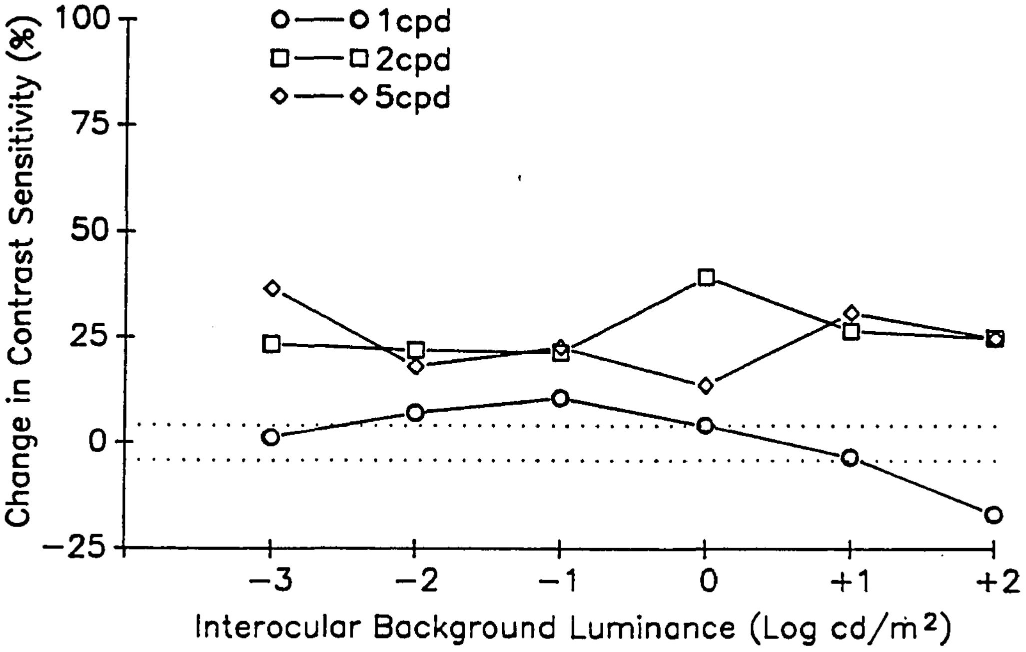
The effects of interocular adaptation upon grating visibility reported above (figures 3-7) were robust, and did not depend upon the use of specific stimulus parameters. For example, figure 8 shows data collected when a 3.2° x 2.4° size test stimulus was presented to the left eye with an average luminance of 1.0 cd/m^2, while interocular backgrounds of various luminance levels and 20.8° x 15° in spatial extent were presented to the contralateral eye. As has been shown previously, (Patel, 1966), such a reduction in luminance decreases sensitivity, particularly for higher spatial frequencies. The same overall conclusions enumerated above apply as well to these data. In particular, sensitivity to a 1 cpd grating is negligibly influenced by any background. Dimmer backgrounds (0.001-0.1 cd/m^2) increase the sensitivity to 2 and 5 cpd gratings (by approximately 25%), while brighter backgrounds (1.0-100 cd/m^2) increase sensitivity to gratings with frequencies of 2-20 cpd (up to approximately 50%). Figure 9 replots these data showing percent change in contrast sensitivity as a function of the log interocular background luminance. The top panels shows results for spatial frequencies from 1 to 5 cpd and the bottom for frequencies from 10-20 cpd. The percent changes in sensitivity reported above are more easily seen in these figures. The same general tendencies observed with a brighter grating (i.e., figures 6 and 7 above) are again observed.

Figure 8. Percent threshold modulation as a function of spatial frequency is plotted for observer ND. These data were collected according to a two-alternative forced-choice staircase procedure. The stimulus was a 1.0 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye, and was varied in luminance as indicated in the key. Note that the closed circles represent control data obtained with a monocular stimulus and no background. Other closed symbols represent the presence of dim interocular background luminance values while open symbols represent brighter interocular background levels.

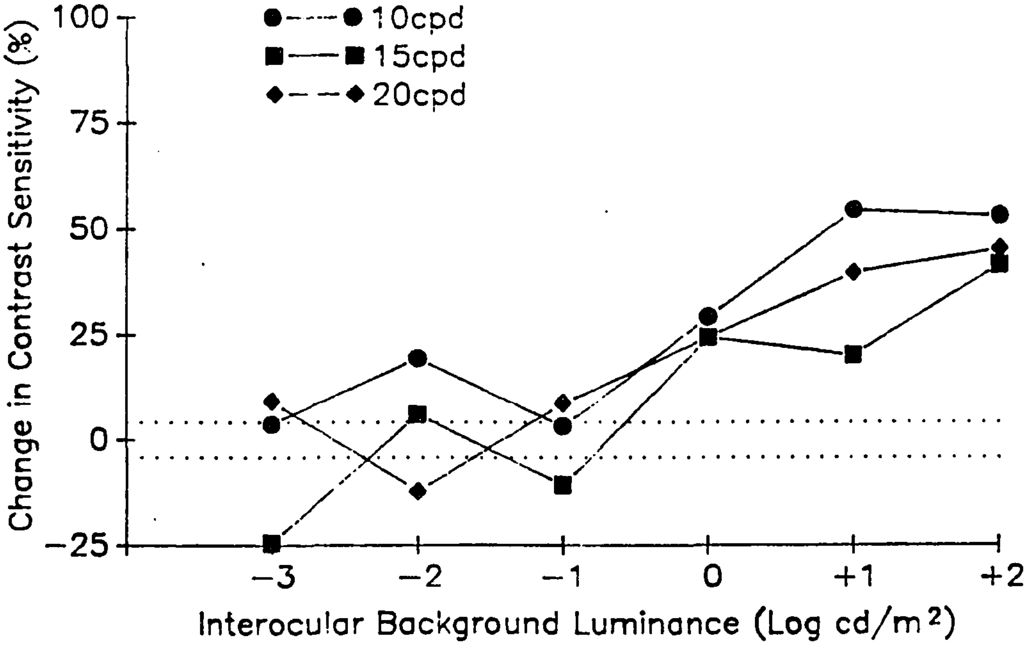


Threshold Modulation (%)
1.0
2.0
5.0
10
20
1
2
5
10
20
Spatial Frequency (cycles per degree)
● —— ● Monoc., No Adapt.
◆ .001
■ —— ■ .01
▶ .1
▷ 1.0
○ —— ○ 10
□ 100

Figure 9. This figure represents a replot of the data shown in figure 8 and shows percent change in contrast sensitivity as a function of log interocular background luminance with spatial frequency as a parameter for observer ND. These data were collected according to a two-alternative forced-choice staircase procedure. The stimulus was a 1.0 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye and varied in luminance. The upper plot shows contrast sensitivity for lower spatial frequencies (as indicated in the key) and the lower plot shows contrast sensitivity for higher spatial frequencies. The dotted horizontal lines indicate mean 95% confidence intervals (±2 standard errors) for control data.



Low Spatial Frequencies



High Spatial Frequencies

Figure 10 shows for observer ND CSFs obtained with a 0.1 cd/m^2 test grating but stimulus parameters otherwise identical to those used above. Use of this dim test grating further reduced sensitivity to higher spatial frequencies and the peak of the CSF is now observed with gratings of 2 rather than 5 cpd. However, in other respects these data are similar to those shown for observer ND in figure 3 and 8 above. That is, backgrounds of 0.01 and 0.1 cd/m^2 improve the sensitivity to 2 and 5 cpd stimuli, higher luminance backgrounds improve sensitivity to spatial frequencies between 2-15 cpd. One difference between the data obtained with this dim test stimulus compared to the brighter stimulus is that sensitivity to a 1 cpd grating is increased with both dim and brighter interocular backgrounds. The increase in sensitivity can reach approximately 50% with the presentation of the brightest interocular background. A 20 cpd grating was not presented since sensitivity to this dim stimulus was too low for this high spatial frequency. Essentially similar results are shown for another observer (TEF) in figure 11. These data additionally show that a background of 10 x 10^{-4} c/m^2, 1 log unit dimmer than any used with observer ND, influences sensitivity in the contralateral eye, by as much as 30%. Dimmer backgrounds could not be presented due to the ambient level of stray light. Again, the data for observer ND and TEF are replotted in figures 12 and 13, respectively, for this luminance level stimulus in order to more clearly represent the magnitude of the interocular effect. The interocular effect here seems to depend more upon background luminance for all frequencies for observer ND but not for observer TEF.

Figure 10. Percent threshold modulation as a function of spatial frequency is plotted for observer ND. These data were collected according to a two-alternative forced-choice staircase procedure. The stimulus was a 0.1 cd/m², 3.2° x 2.4° sine wave grating presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye, and was varied in luminance as indicated in the key. Note that the closed circles represent control data obtained with a monocular stimulus and no background. Other closed symbols represent the presence of dimmer interocular background luminance values while open symbols represent brighter interocular background levels.

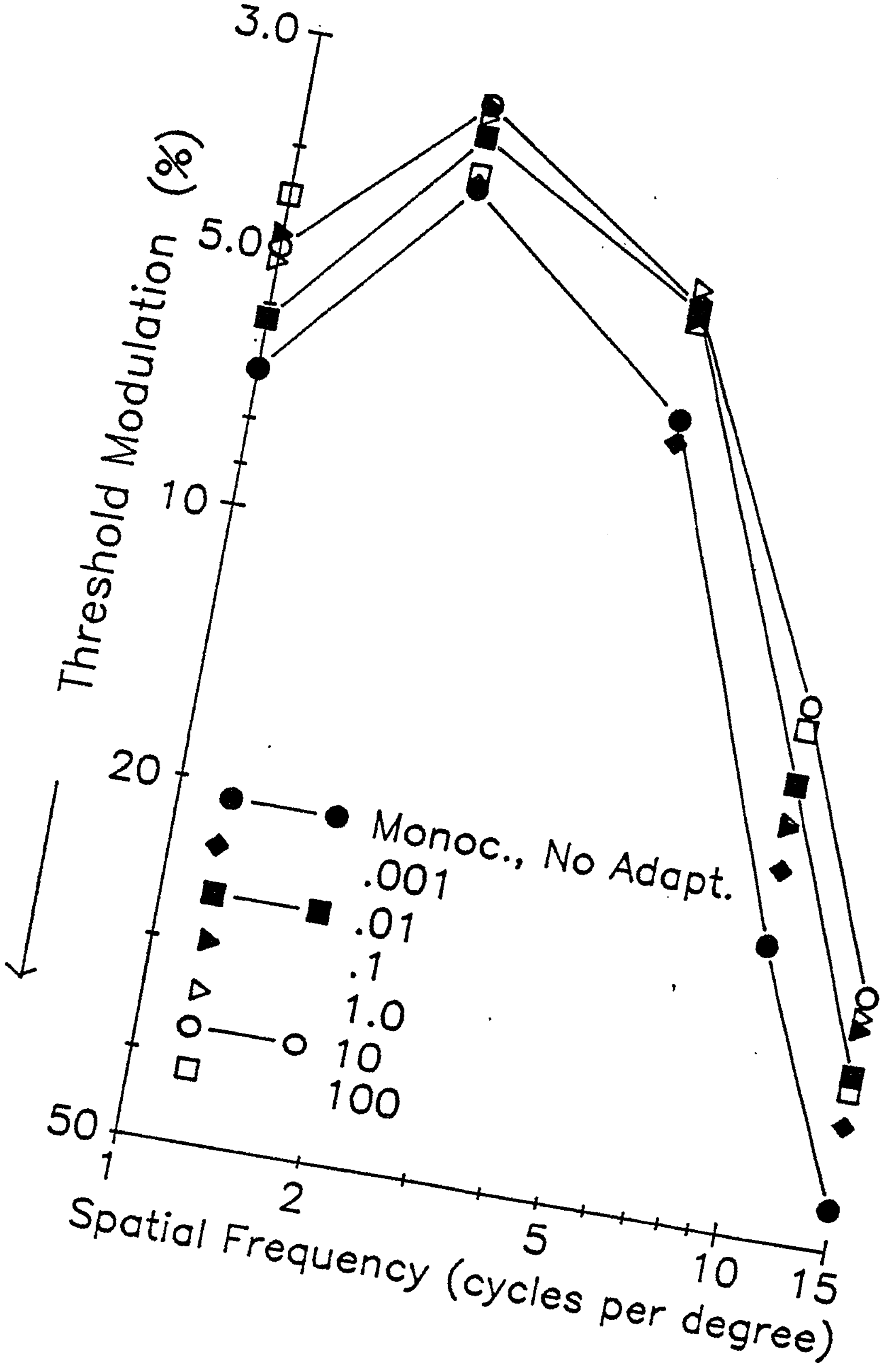

Threshold Modulation (%)
3.0
5.0
10
20
50
Spatial Frequency (cycles per degree)
1
2
5
10
15
Monoc., No Adapt.
.001
.01
.1
1.0
10
100

Figure 11. Percent threshold modulation as a function of spatial frequency is plotted for observer TEF. These data were collected according to a two-alternative forced-choice staircase procedure. The stimulus was a 0.1 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye, and was varied in luminance as indicated in the key. Note that the closed circles represent control data obtained with a monocular stimulus and no background. Other closed symbols represent the presence of dimmer interocular background luminance values while open symbols represent brighter interocular background levels. The closed circle connected by dotted lines-function show data collected with a .0001 cd/m^2 background.

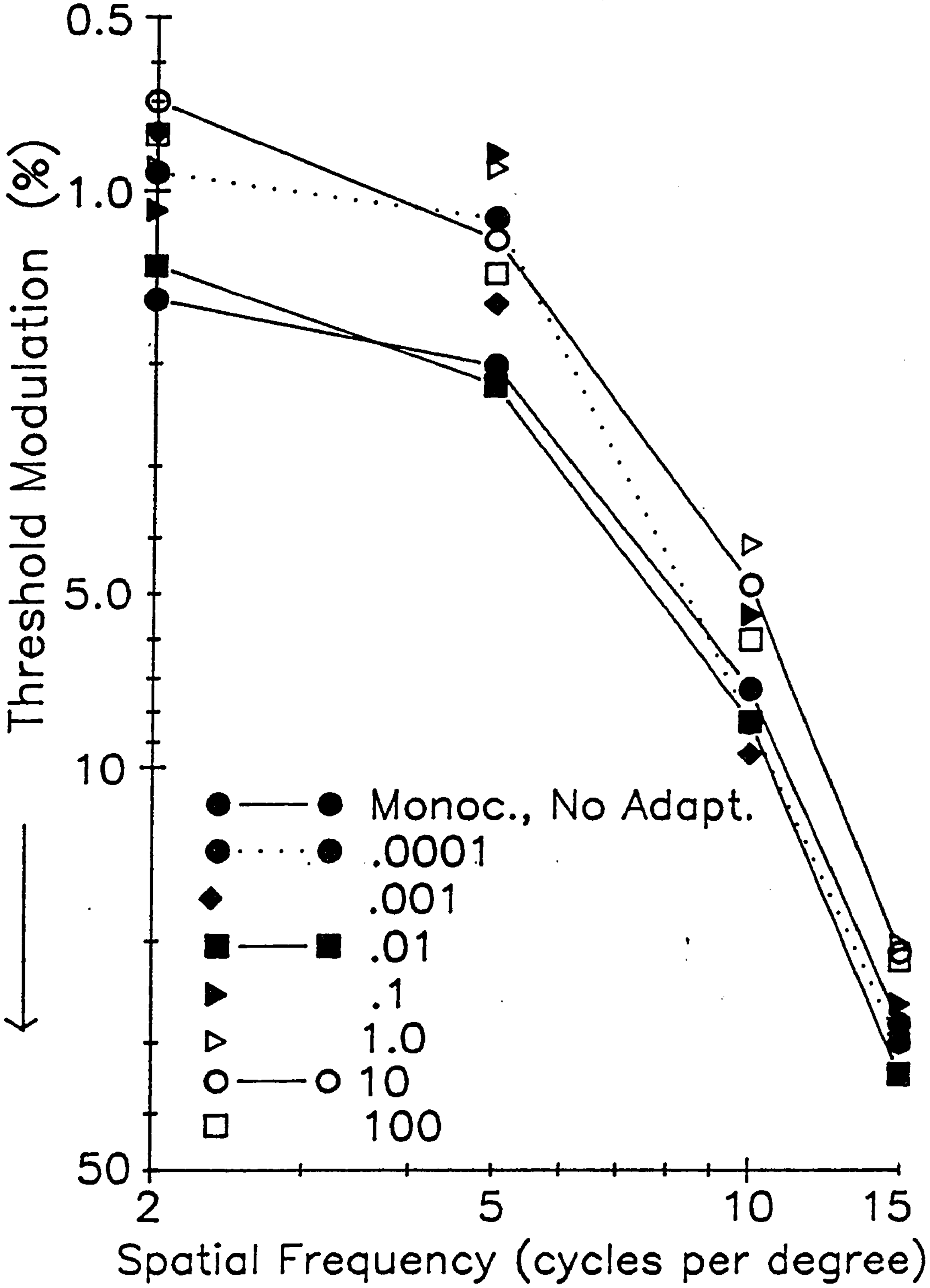
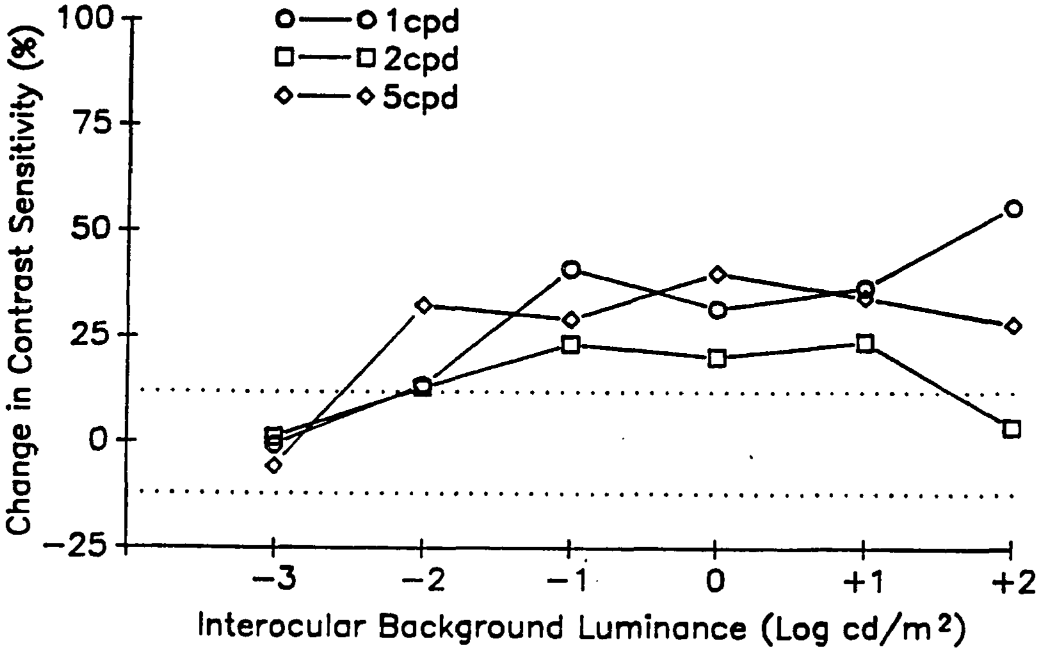

0.5
1.0
5.0
10
50
Threshold Modulation (%)
2
5
10
15
Spatial Frequency (cycles per degree)
●——● Monoc., No Adapt.
●·····● .0001
◆ .001
■——■ .01
▶ .1
▷ 1.0
○——○ 10
□ 100

Figure 12. This figure represents a replot of the data shown in figure 10 and shows percent change in contrast sensitivity as a function of interocular background luminance with spatial frequency as a parameter for observer ND. These data were collected according to a lternative forced-choice staircase procedure. The stimulus was a 0.1 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye and varied in luminance. The upper plot shows contrast sensitivity for lower spatial frequencies (as indicated in the key) and the lower plot shows contrast sensitivity for higher spatial frequencies. The dotted horizontal lines indicate mean 95% confidence intervals (±2 standard errors) for control data.

Low Spatial Frequencies



High Spatial Frequencies

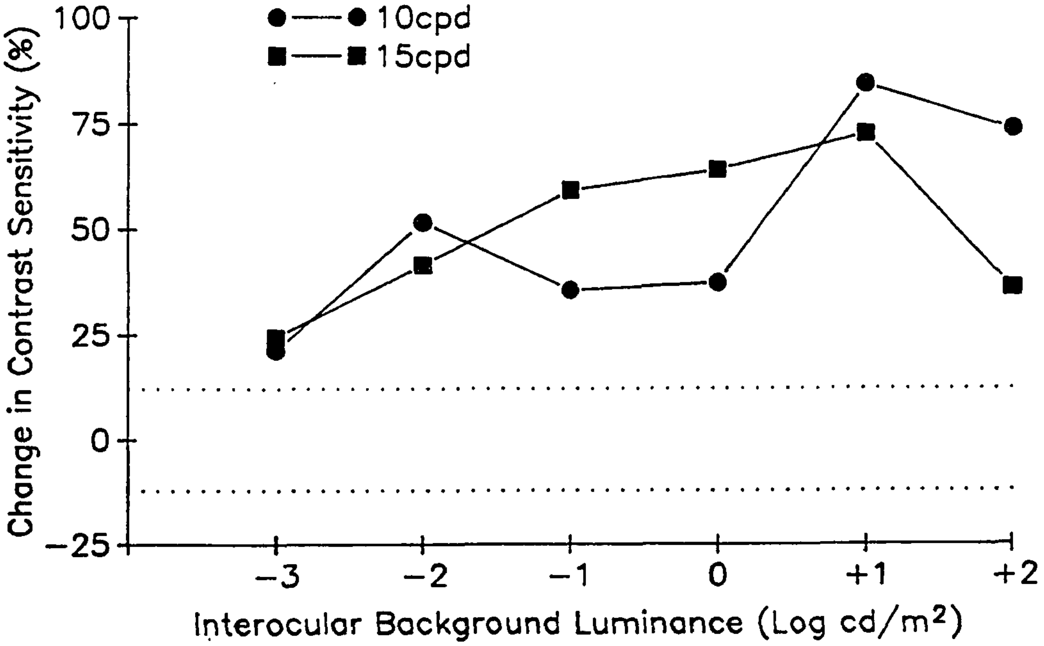
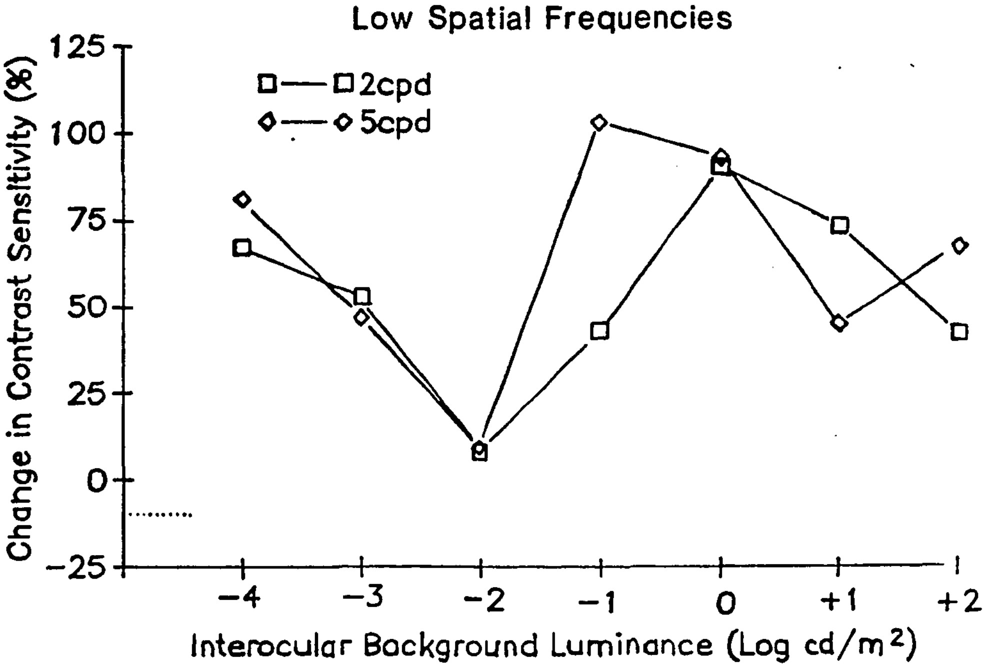
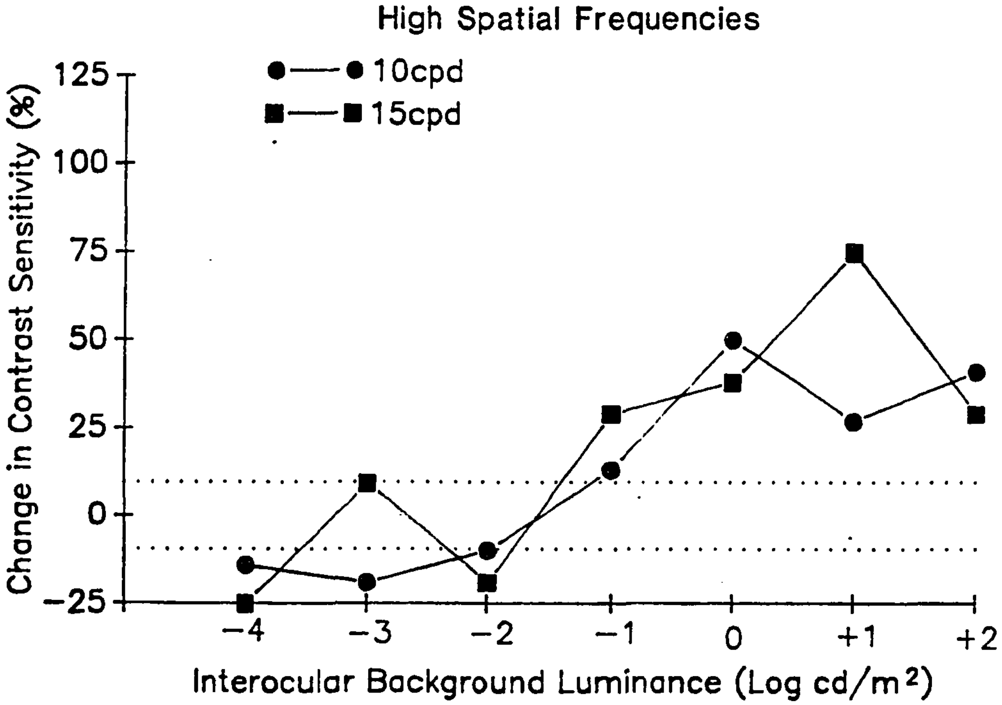


Figure 13. This figure represents a replot of the data shown in figure 11 and shows percent change in contrast sensitivity as a function of interocular background luminance with spatial frequency as a parameter for observer TEF. These data were collected according to a lternative forced-choice staircase procedure. The stimulus was a 0.1 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea. The background stimulus was 20.8° x 15° and presented to the right eye and varied in luminance. The upper plot shows contrast sensitivity for lower spatial frequencies (as indicated in the key) and the lower plot shows contrast sensitivity for higher spatial frequencies. The dotted horizontal lines indicate mean 95% confidence intervals (±2 standard errors) for control data.


Low Spatial Frequencies
□—□ 2cpd
◇—◇ 5cpd
Change in Contrast Sensitivity (%)
125
100
75
50
25
0
−25
−4
−3
−2
−1
0
+1
+2
Interocular Background Luminance (Log cd/m²)


High Spatial Frequencies
●—● 10cpd
■—■ 15cpd
Change in Contrast Sensitivity (%)
125
100
75
50
25
0
−25
−4
−3
−2
−1
0
+1
+2
Interocular Background Luminance (Log cd/m²)

To summarize, light adapting the contralateral eye improves sensitivity to a monocularly viewed test grating. In general, this sensitivity increase of up to approximately 50% appears at low spatial frequencies when dim interocular test stimuli are presented interocularly. Brighter interocular backgrounds increase sensitivity to all frequencies above 1 cpd, for the two higher stimulus luminance levels and for all frequencies for the dimmest stimulus level. The increase in sensitivity produced by the brighter interocular backgrounds can be greater than 100%. It is of interest that Purpura, Kaplan, and Shapley (1988) showed that the magnocellular geniculate pathway, which responds to lower spatial frequencies, is considerably more sensitive to dim lights than the parvocellular geniculate pathways which respond best to higher spatial frequencies. Thus, the differing luminance dependencies of this interocular adaptation effect for higher versus lower spatial frequencies may reflect differences between magno- and parvo-cellular pathways.

C. Influence of Left versus Right Eye Stimulation

For arbitrary reasons, all of the data collected above involved presentation of the test grating to the left eye, and the adapting field to the right eye for each of the three observers. To insure that the interocular influence does not depend upon which eye is stimulated, the influence of a left eye background upon right eye grating sensitivity was compared with the influence of a right eye background upon left eye grating sensitivity in one set of experiments. In these control experiments, the background field was always 10 cd/m². The stimulus was 10 cd/m² in average luminance and 3.2° x 2.4° in size. The results presented in figure 14 show for observer ND that results do not depend upon which eye was chosen for test stimulation. Thus, with a normal observer, it does not matter whether the dominant eye (for observer ND, the right eye) or the nondominant eye is used for test grating or adapting field stimulation.

D. Influence of the Size and Shape of the Interocular Background

The influence of the size and shape of a 10 cd/m² interocular background was investigated in two observers using a 3.2° x 2.4° size test stimulus which was 10 cd/m² in average luminance presented in the contralateral eye. Background sizes included the large sized 20.8° x 15° background, a 3.2° x 2.4° sized background and an annulus with an outer diameter of 20.8° x 15°. Results for observer ND are presented in figure 15. The large background and background of equal dimensions to the test stimulus produced nearly identical improvements in grating sensitivity (differing by less than 10%), while the annular background had no influence upon grating sensitivity. Although more variable, the data from observer NM, as shown in figure 16, lead to similar conclusions, that large size backgrounds and backgrounds equal in size to the test stimulus yield increases in sensitivity but annular backgrounds do not. For this second observer the same sized background is consistently more effective than the large sized background.

Figure 14. Percent threshold modulation is plotted as a function of spatial frequency for observer ND. These data were collected according to the method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left (circles) or right (squares) eye. The background was either not present (closed symbols) or 20.8° x 15°, 10 cd/m^2 in average luminance and presented to the eye contralateral to the stimulus (open symbols).

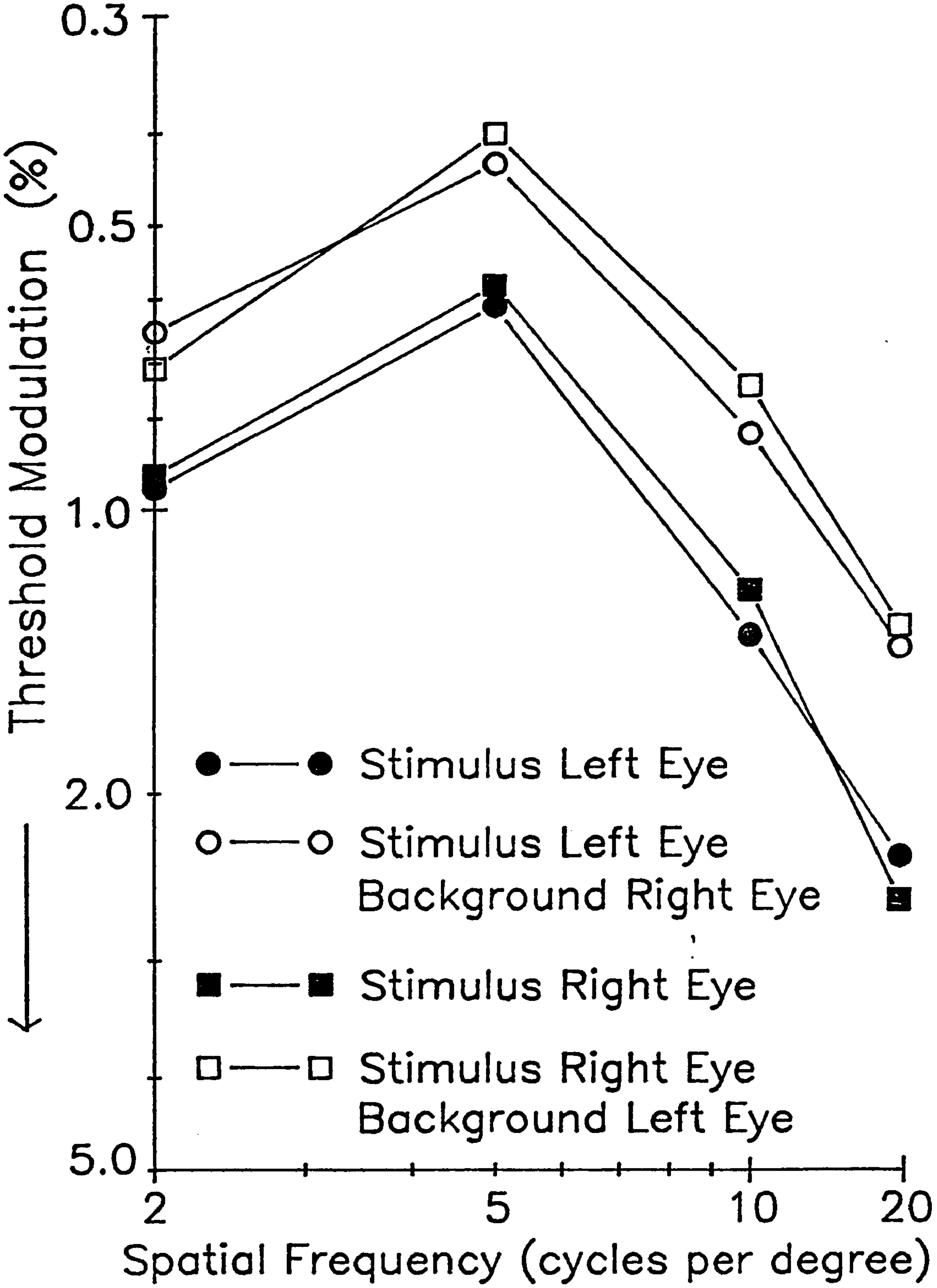

0.3
0.5
1.0
2.0
5.0
Threshold Modulation (%)
2
5
10
20
Spatial Frequency (cycles per degree)
●—● Stimulus Left Eye
○—○ Stimulus Left Eye Background Right Eye
■—■ Stimulus Right Eye
□—□ Stimulus Right Eye Background Left Eye

Figure 15. Percent threshold modulation is plotted as a function of spatial frequency for observer ND. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.4° x 2.4° sine wave grating presented to the left fovea. The background stimulus was a 10 cd/m^2 diffuse field presented to the right eye and was either not presented (closed circles), was the usual sized 20.8° x 15° full field (open circles), an interocular annulus (closed diamonds) presented to a nonhomotopic area in the contralateral eye, or the same size as the stimulus (open squares) presented at a homotopic position in the contralateral eye.

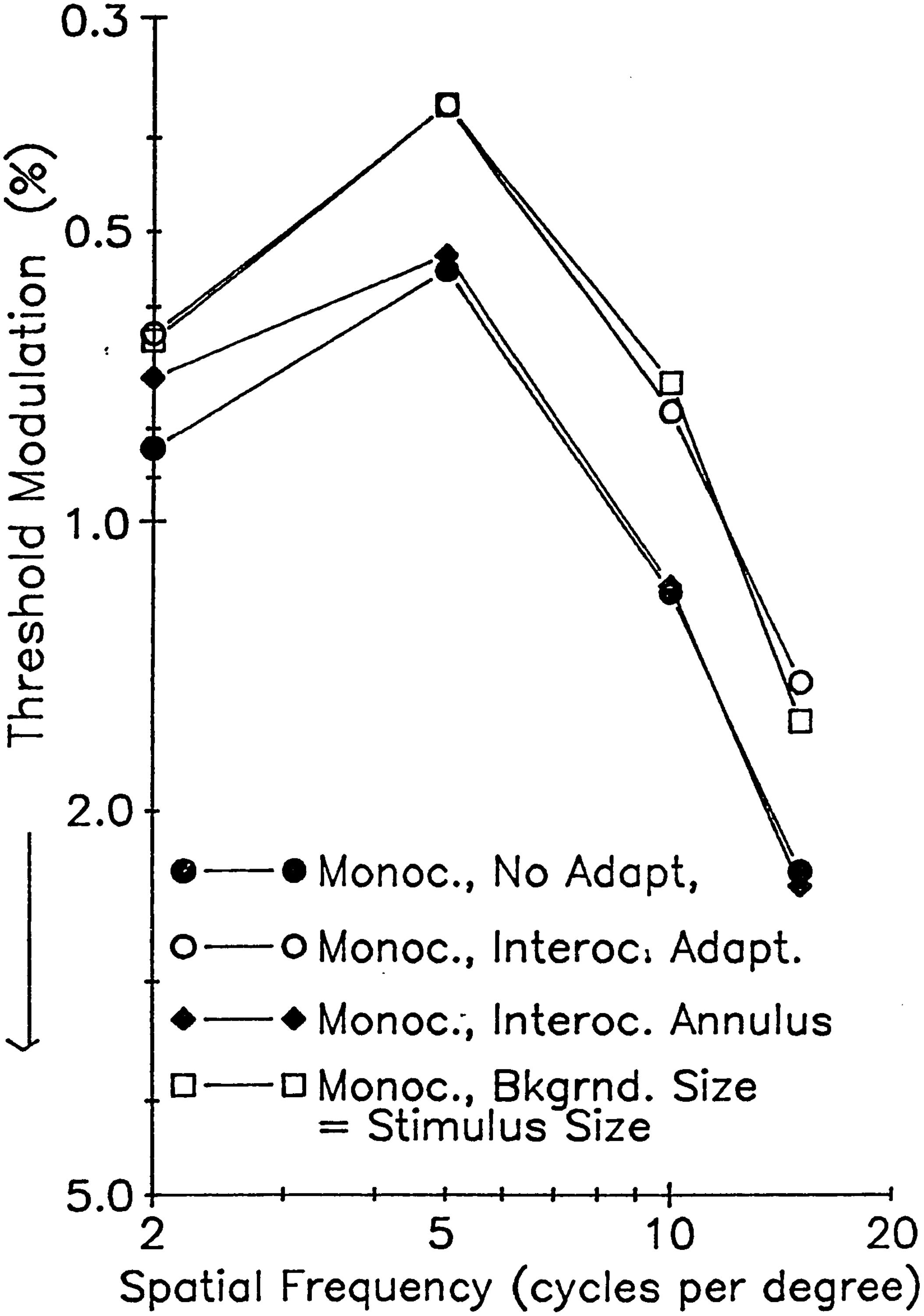
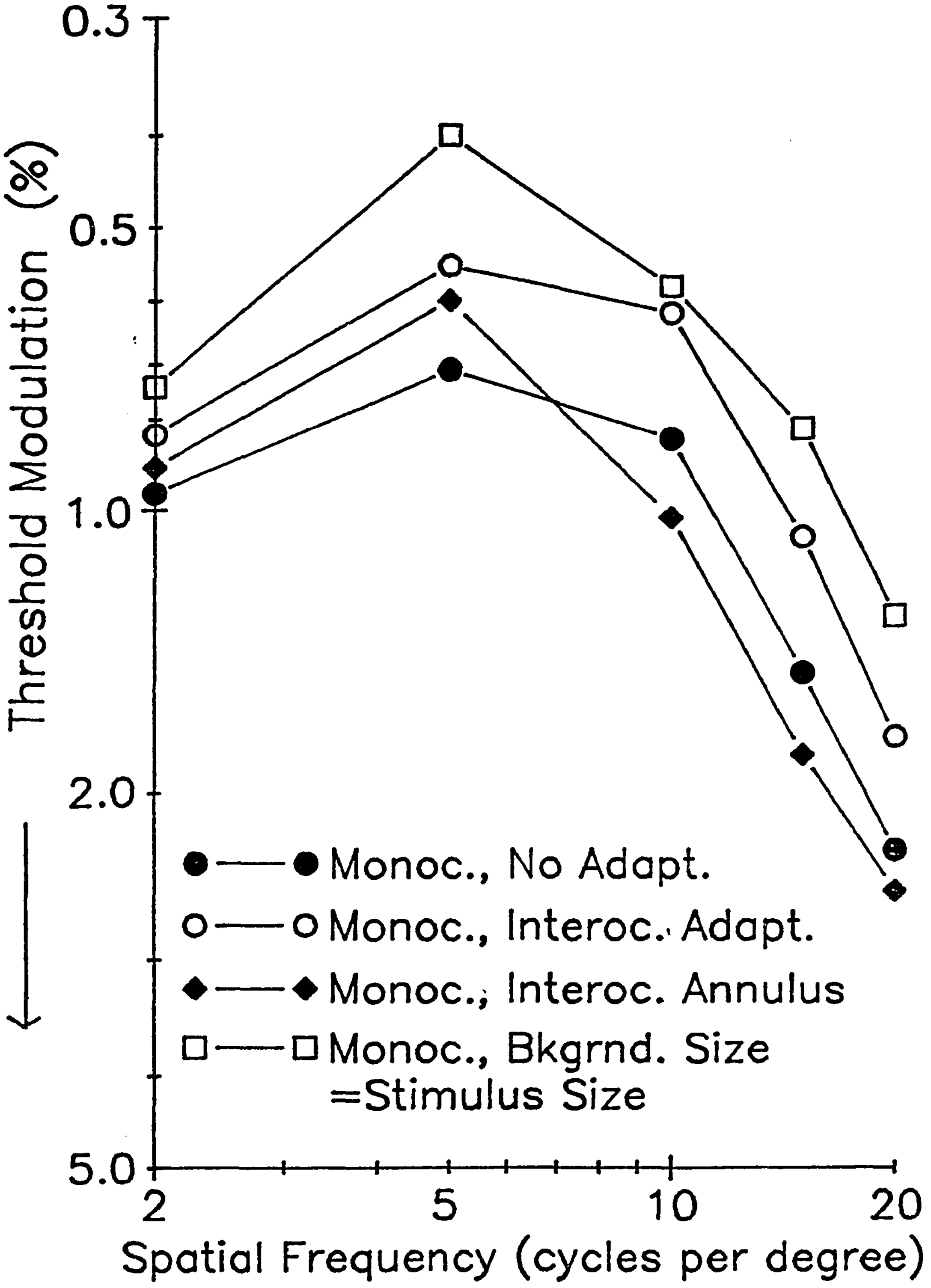

0.3
0.5
1.0
2.0
5.0
Threshold Modulation (%)
2
5
10
20
Spatial Frequency (cycles per degree)
● Monoc., No Adapt,
○ Monoc., Interoc. Adapt.
◆ Monoc., Interoc. Annulus
□ Monoc., Bkgrnd. Size = Stimulus Size

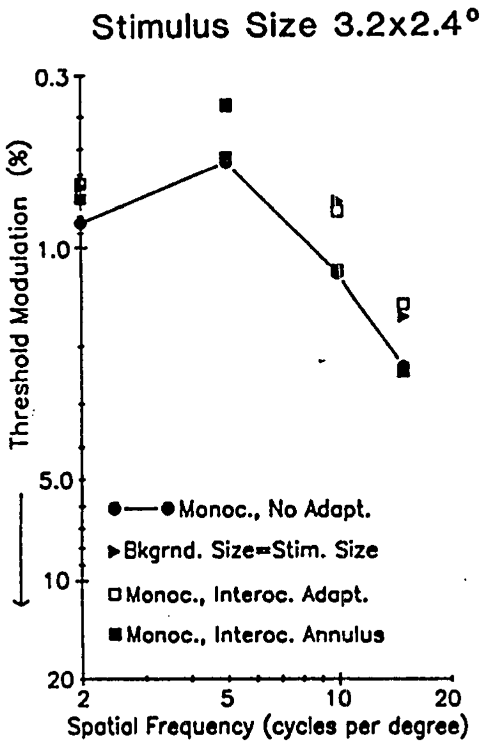
Figure 16. Percent threshold modulation is plotted as a function of spatial frequency for observer NM. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.4° x 2.4° sine wave grating presented to the left fovea. The background stimulus was a 10 cd/m^2 diffuse field presented to the right eye and was either not presented (closed circles), the usual sized 20.8° x 15° full field (open circles), an interocular annulus (closed diamonds) presented to a nonhomotopic area in the contralateral eye, or the same size as the stimulus (open squares) presented at a homotopic position in the contralateral eye.

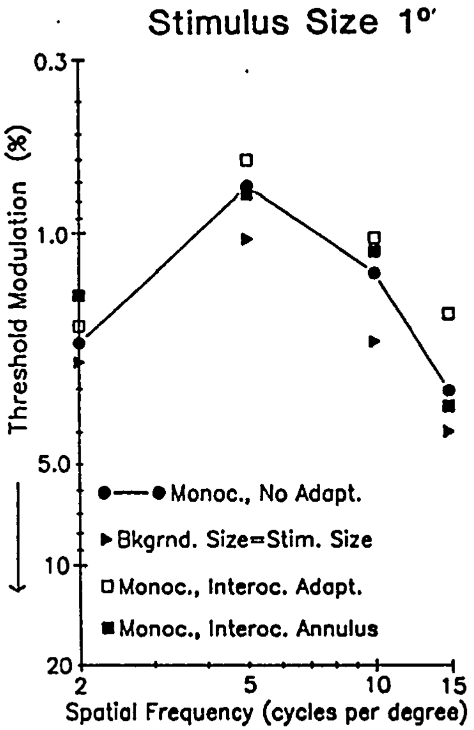

0.3
0.5
1.0
2.0
5.0
Threshold Modulation (%)
2
5
10
20
Spatial Frequency (cycles per degree)
●——● Monoc., No Adapt.
○——○ Monoc., Interoc. Adapt.
◆——◆ Monoc., Interoc. Annulus
□——□ Monoc., Bkgrnd. Size =Stimulus Size

The experiment presented in figures 15 and 16 was systematically replicated with different sized test stimuli in the fovea. Figures 17 (observer ND) and 18 (observer TEF) show results using 3 different sized test gratings. The data shown on the left were obtained with a 3.4° x 2.4° test grating and are replotted for ease of direct comparison of the data in figures 15 and 16. If the test grating was reduced to a 1° square (middle plots), the full sized background field still increased grating visibility but the annular background did not. The interocular background of the same size as the 1° test stimulus produced decreases in sensitivity for both observers. It should be noted that the backgrounds of the same size as the test stimulus and the annular backgrounds produced marked binocular rivalry. When the background field was further reduced to a 0.5° square, in both observers all interocular backgrounds produced decreases in sensitivity. The largest decreases occurred when the background was the same size as the test stimulus and the decrease was approximately 25%.

The data plotted in figures 17 and 18 are replotted in figures 19 and 20 respectively, in order to more easily compare the magnitude of the interocular effects. Percent change in contrast sensitivity is plotted as a function of spatial frequency for the three different sized gratings. Notice for both observers the change in sensitivity resulting from interocular adaptation changes from a large increase in sensitivity with a large background (approximately 65%) to a large decrease in sensitivity with the 0.5° grating (approximately 40%); results obtained with the 1° grating are intermediate.

Figure 17. Percent threshold modulation is plotted as a function of spatial frequency for observer ND. The data were collected according to the method of adjustment procedure. The stimulus was a 10 cd/m^2 sine wave grating and was 3.2° x 2.4° (plot on the left), 1° (middle set of coordinates), or .5° (plot on the right). The background was a 20.8° x 15°, 10 cd/m^2 diffuse field presented to the right eye.


Stimulus Size 3.2x2.4°
Threshold Modulation (%)
0.3
1.0
5.0
10
20
2
5
10
20
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▶ Bkgrnd. Size=Stim. Size
□ Monoc., Interoc. Adapt.
■ Monoc., Interoc. Annulus


Stimulus Size 1°
Threshold Modulation (%)
0.3
1.0
5.0
10
20
2
5
10
15
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▶ Bkgrnd. Size=Stim. Size
□ Monoc., Interoc. Adapt.
■ Monoc., Interoc. Annulus

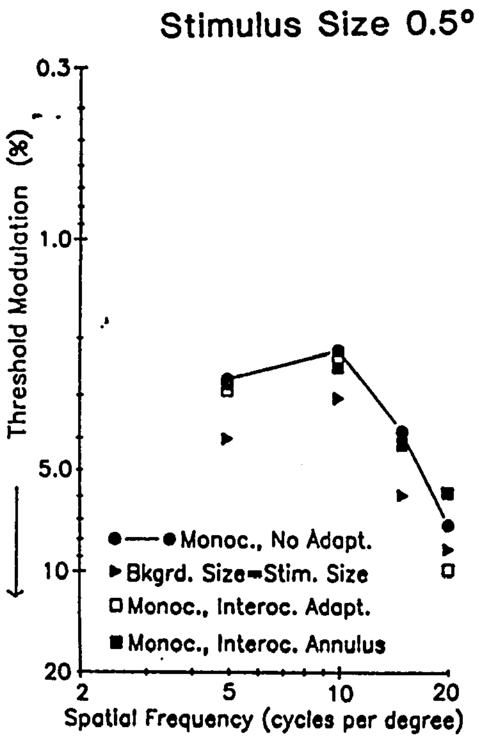
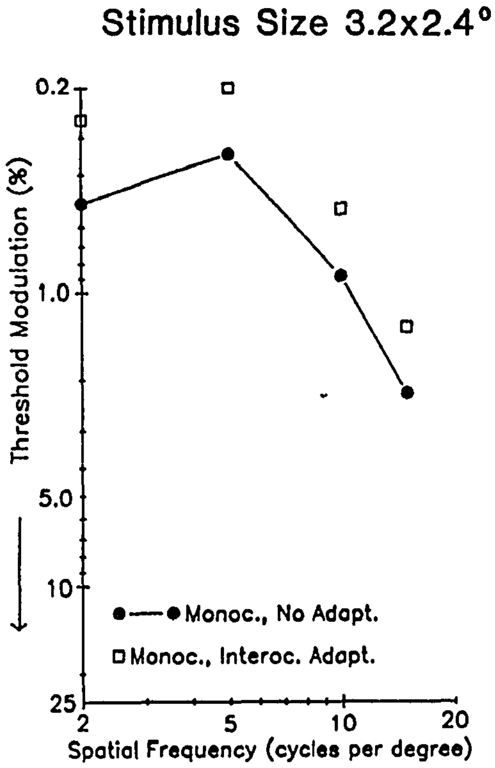
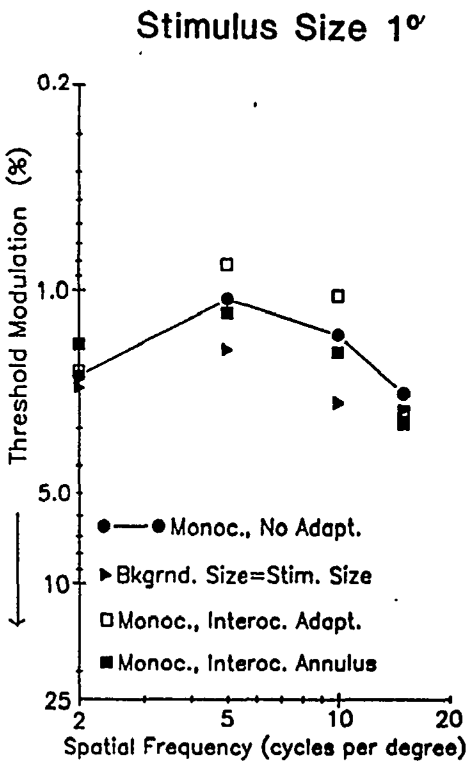

Stimulus Size 0.5°
Threshold Modulation (%)
0.3
1.0
5.0
10
20
2
5
10
20
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▶ Bkgrd. Size=Stim. Size
□ Monoc., Interoc. Adapt.
■ Monoc., Interoc. Annulus

Figure 18. Percent threshold modulation is plotted as a function of spatial frequency for observer TEF. The data were collected according to the yes/no method of adjustment procedure. The stimulus was a 10 cd/m² sine wave grating and was 3.2° x 2.4° (plot on the left), 1° (middle set of coordinates), or .5° (plot on the right). The background was a 20.8° x 15°, 10 cd/m² diffuse field presented to the right eye.


Stimulus Size 3.2x2.4°
Threshold Modulation (%)
0.2
1.0
5.0
10
25
2
5
10
20
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
□ Monoc., Interoc. Adapt.


Stimulus Size 1°
Threshold Modulation (%)
0.2
1.0
5.0
10
25
2
5
10
20
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▶ Bkgrnd. Size=Stim. Size
□ Monoc., Interoc. Adapt.
■ Monoc., Interoc. Annulus

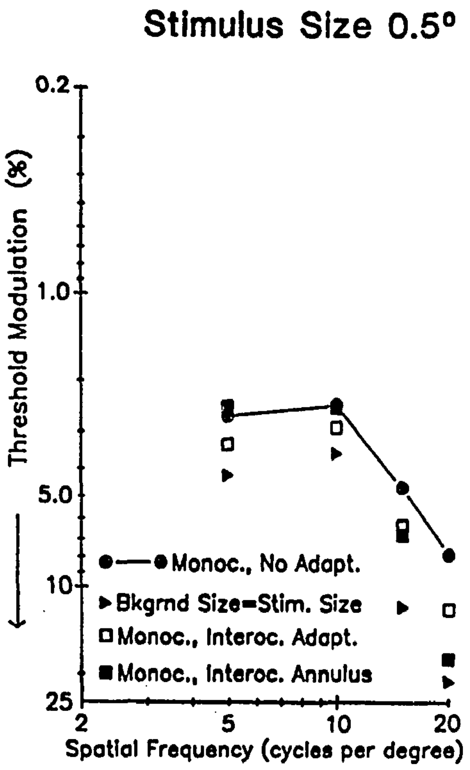
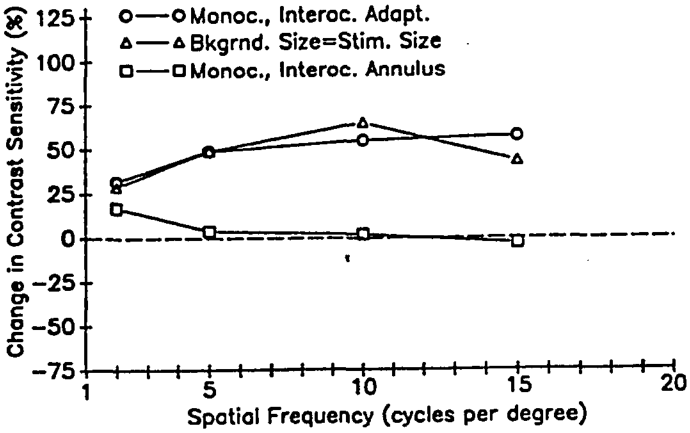
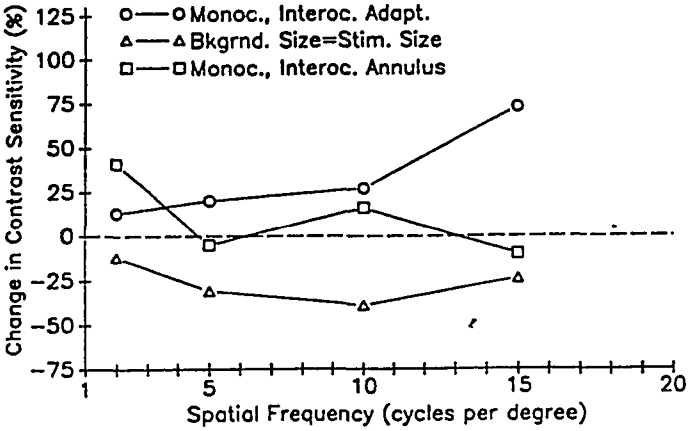

Stimulus Size 0.5°
Threshold Modulation (%)
0.2
1.0
5.0
10
25
2
5
10
20
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▶ Bkgrnd Size=Stim. Size
□ Monoc., Interoc. Adapt.
■ Monoc., Interoc. Annulus

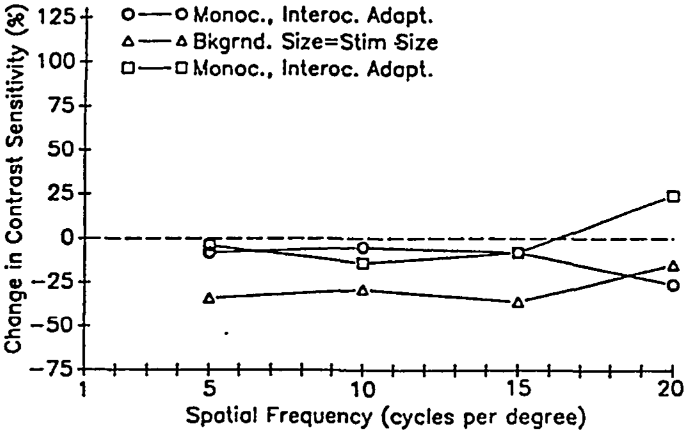
Figure 19. Percent change in contrast sensitivity is plotted as a function of spatial frequency for observer ND. The data were collected according to the method of adjustment procedure. The stimulus was a 10 cd/m^2 sine wave grating and was 3.2° x 2.4° (plot on the top), 1° (middle set of coordinates), or .5° (plot on the bottom). The background was a 20.8° x 15°, 10 cd/m^2 diffuse field presented to the right eye. Mean 95% confidence intervals (±2 standard errors) for control data are 15.7% for the large sized stimulus, 12.5% for the 1° size stimulus and 10.0% for the 0.5° size stimulus.



Stimulus Size 3.2x2.4°



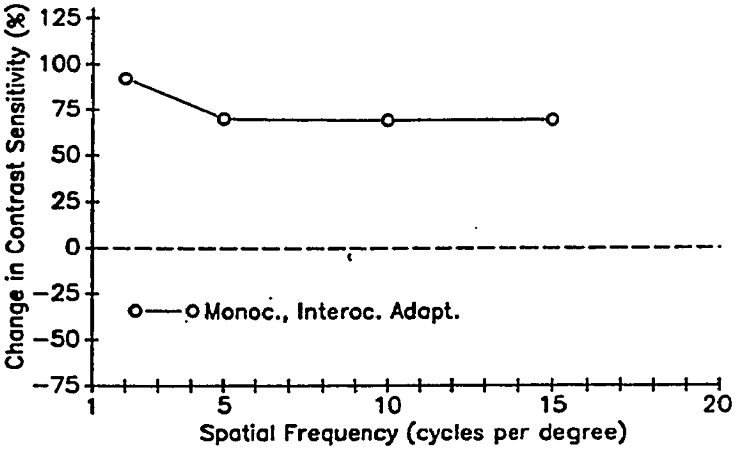
Stimulus Size 1°



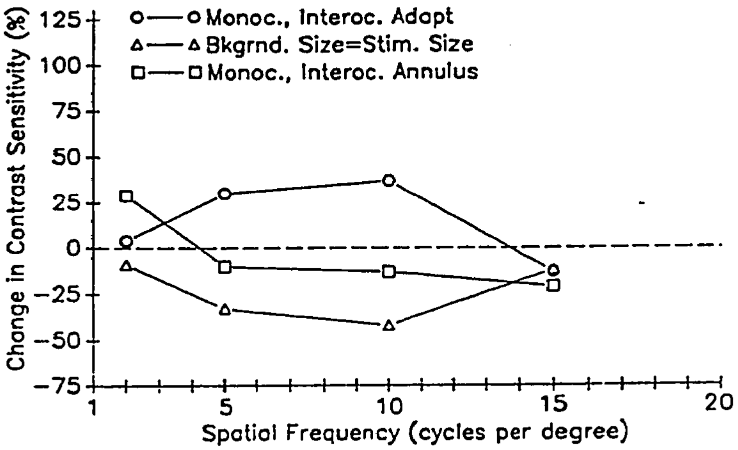
Stimulus Size 0.5°

Figure 20. Percent change in contrast sensitivity is plotted as a function of spatial frequency for observer TEF. The data were collected according to the yes/no method of adjustment procedure. The stimulus was a 10 cd/m^2 sine wave grating and was 3.2° x 2.4° (plot on the top), 1° (middle set of coordinates), or .5° (plot on the bottom). The background was a 20.8° x 15°, 10 cd/m^2 diffuse field presented to the right eye. Mean 95% confidence intervals (±2 standard errors) for control data are 14.6% for the 1° size stimulus and 6.75% for the 0.5° size stimulus.

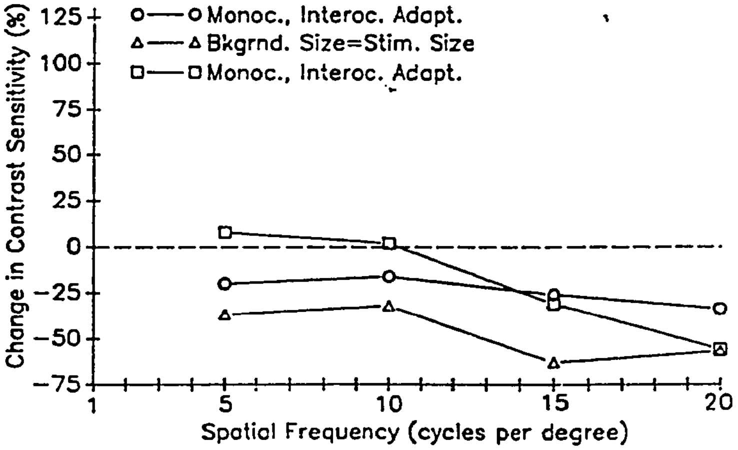
Stimulus Size 3.2x2.4°



Stimulus Size 1°



Stimulus Size 0.5°

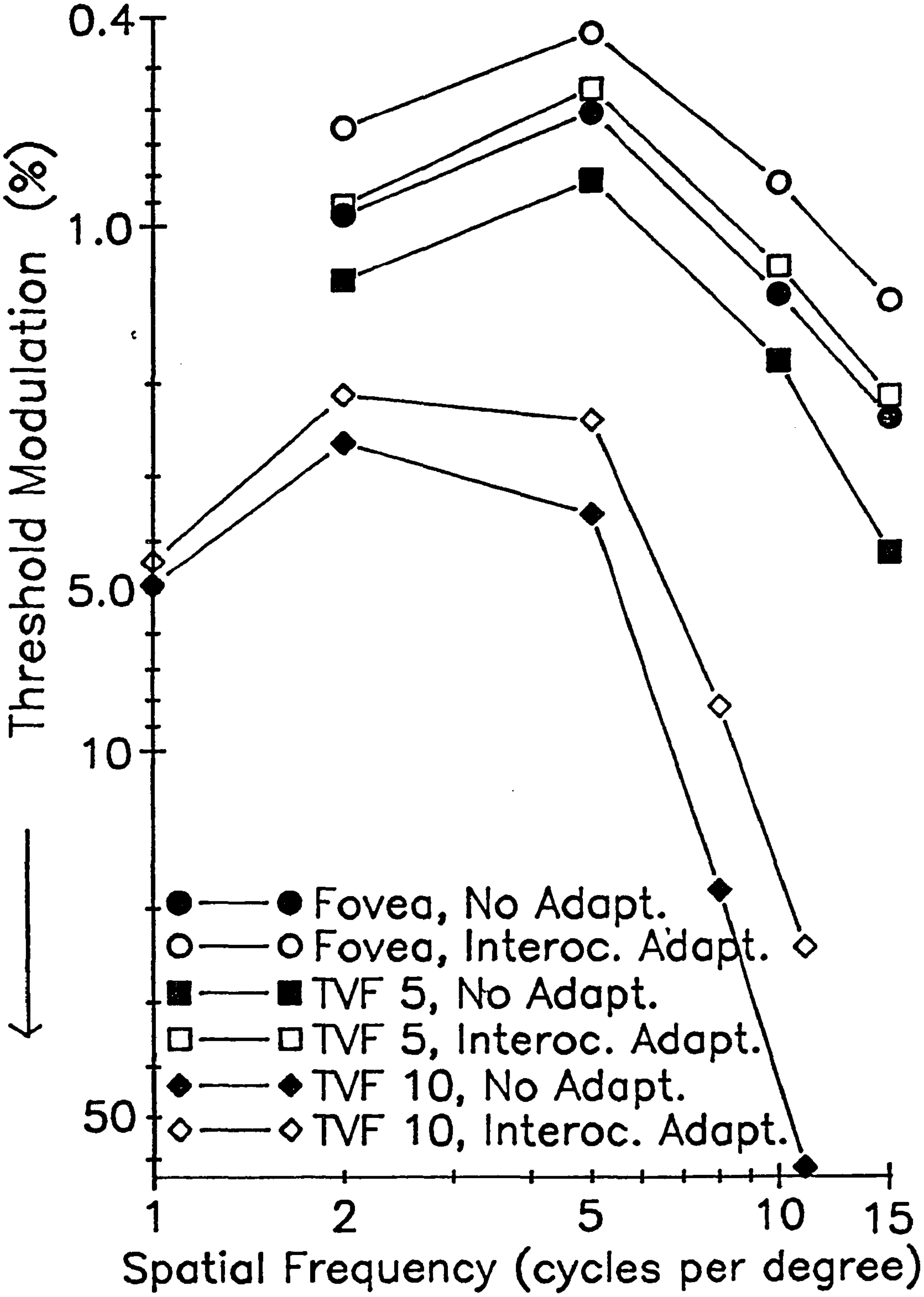


In summary, the data in figures 17-20 show that interocular backgrounds can either improve or impair grating visibility. In this respect, the present data bear some comparison with previous studies which demonstrated either visual masking or the "Lansford-Baker effect" summarized in the introduction to this chapter. In particular, some of the stimulus parameters used in these experiments resemble the interocular masking studies of Battersby and colleagues (Battersby & Wagman, 1962, 1964; Battersby, Oesterreich & Sturr, 1964). In these detection threshold experiments, Battersby used a circular test stimulus of about 1° diameter and obtained maximal masking when the adapting stimulus size was about the same size and shape. When a 1° test grating was used in the present study, presentation of the same sized adapting field impaired grating visibility while a large adapting field improved grating visibility. This outcome might suggest that the data in figures 3-20 reflect two interocular adapting tendencies: one which improves grating visibility and one which masks grating visibility.

E. Effects of Retinal Position

The effect of the retinal position of the test stimulus on the present interocular effect was studied. Figure 21 (for observer ND) shows the amplitude of the interocular effect at three different retinal positions for a 10 cd/m^2, 3.2° x 2.4° grating and a 10 cd/m^2 interocular background for various spatial frequencies. The test stimulus was presented either in the fovea or at 5° of 10° in the temporal visual field

Figure 21. Percent threshold modulation is plotted as a function of spatial frequency for observer ND. The data were collected according to the method of adjustment procedure. The stimulus was a 3.2° x 2.4°, 10 cd/m² sine wave grating presented to the left fovea and the background was a 20.8° x 15°, 10 cd/m² diffuse field presented to the right eye. Circular symbols represent control and interocular background data for a foveally presented stimulus, squares represent data when the stimulus was presented 5° in the TVF, and diamonds represent data when the stimulus was presented 10° in the TVF.


0.4
1.0
5.0
10
50
Threshold Modulation (%)
1
2
5
10
15
Spatial Frequency (cycles per degree)
●——● Fovea, No Adapt.
○——○ Fovea, Interoc. Adapt.
■——■ TVF 5, No Adapt.
□——□ TVF 5, Interoc. Adapt.
◆——◆ TVF 10, No Adapt.
◇——◇ TVF 10, Interoc. Adapt.

(TVF). Figure 22 shows results at two different retinal positions (for observer TEF). These plots show that interocular backgrounds increase grating visibility in the periphery as well as in the fovea. To facilitate comparison at different retinal positions, figures 23 and 24 replot these data and show enhancement as a function of spatial frequency with retinal position as a parameter. There are considerable differences in the results obtained from the two observers used. Foveal data are, in general, similar for the two observers; but with the stimulus 5° in the periphery, observer ND shows larger effects with higher spatial frequencies and observer TEF shows larger effects with lower spatial frequencies. However, for both observers, the magnitude of the enhancement produced by interocular adaptation is generally larger in the peripheral retina, increasing from values of about 50% (for ND) or 90% (for TEF) in the fovea to values sometimes approaching 200% in the periphery. The influence of retinal position and adapting field size and shape are further investigated in experiments presented in chapters 3 and 4.

F. Subjective Changes in Brightness

In the course of producing the experimental data reported above, all three observers noted that the adapting field markedly changed the subjective brightness of the monitor used to display the gratings. Observers ND and TEF informally noted the following similarities in their subjective experiences.

Figure 22. Percent threshold modulation is plotted as a function of spatial frequency for observer TEF. The data were collected according to the yes/no method of adjustment procedure. The stimulus was a 3.2° x 2.4°, 10 cd/m^2 sine wave grating presented to the left fovea and the background was a 20.8° x 15°, 10 cd/m^2 diffuse field presented to the right eye. Circular symbols represent control and interocular background data for a foveally presented stimulus, and squares represent data when the stimulus was presented 5° in the TVF.

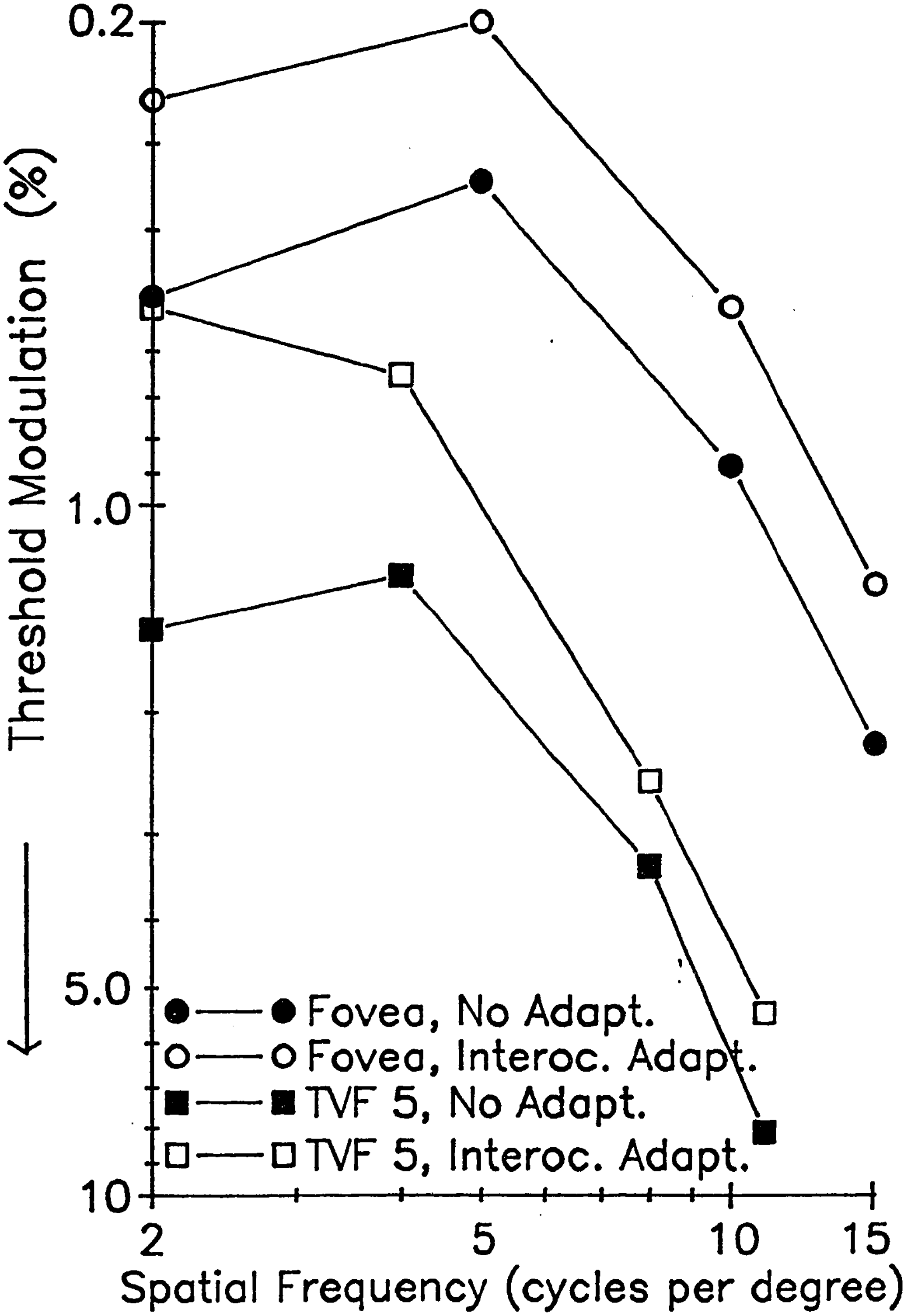

0.2
1.0
5.0
10
Threshold Modulation (%)
2
5
10
15
Spatial Frequency (cycles per degree)
●——● Fovea, No Adapt.
○——○ Fovea, Interoc. Adapt.
■——■ TVF 5, No Adapt.
□——□ TVF 5, Interoc. Adapt.

Figure 23. Percent change in contrast sensitivity is plotted as a function of spatial frequency for observer ND. The data were collected according to the method of adjustment procedure. The stimulus was a 3.2° x 2.4°, 10 cd/m^2 sine wave grating presented to the left fovea and the background was a 20.8° x 15°, 10 cd/m^2 diffuse field presented to the right eye. Circular symbols represent interocular background data for a foveally presented stimulus, squares represent data when the stimulus was presented 5° in the TVF, and diamonds represent data when the stimulus was presented 10° in the TVF. Mean 95% confidence intervals (±2 standard errors) for control data are 15.7% for the stimulus positioned in the fovea, 9.4% for the stimulus positioned 5° in the TVF, and 6.75% for the stimulus positioned 10° in the TVF.

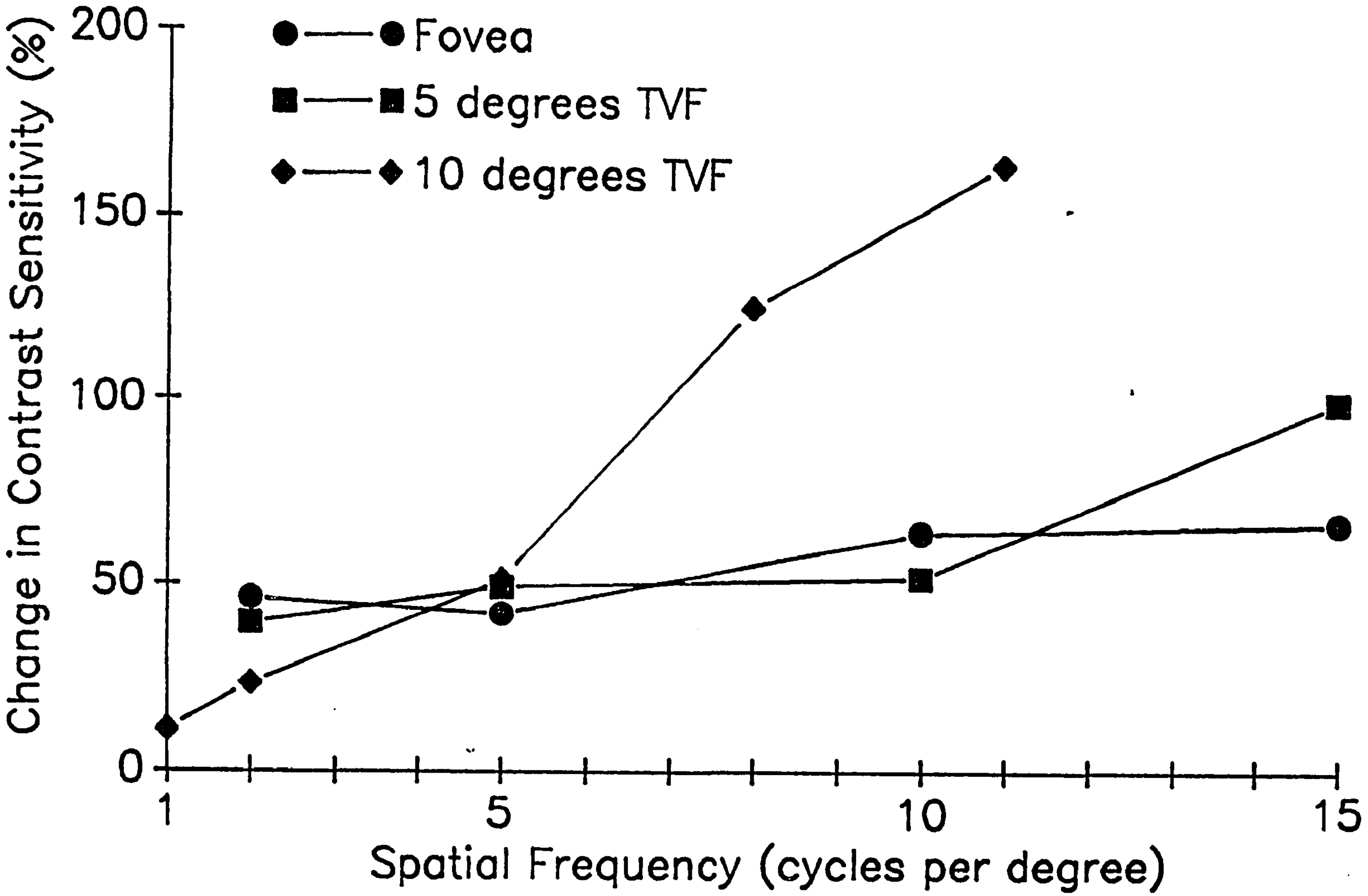
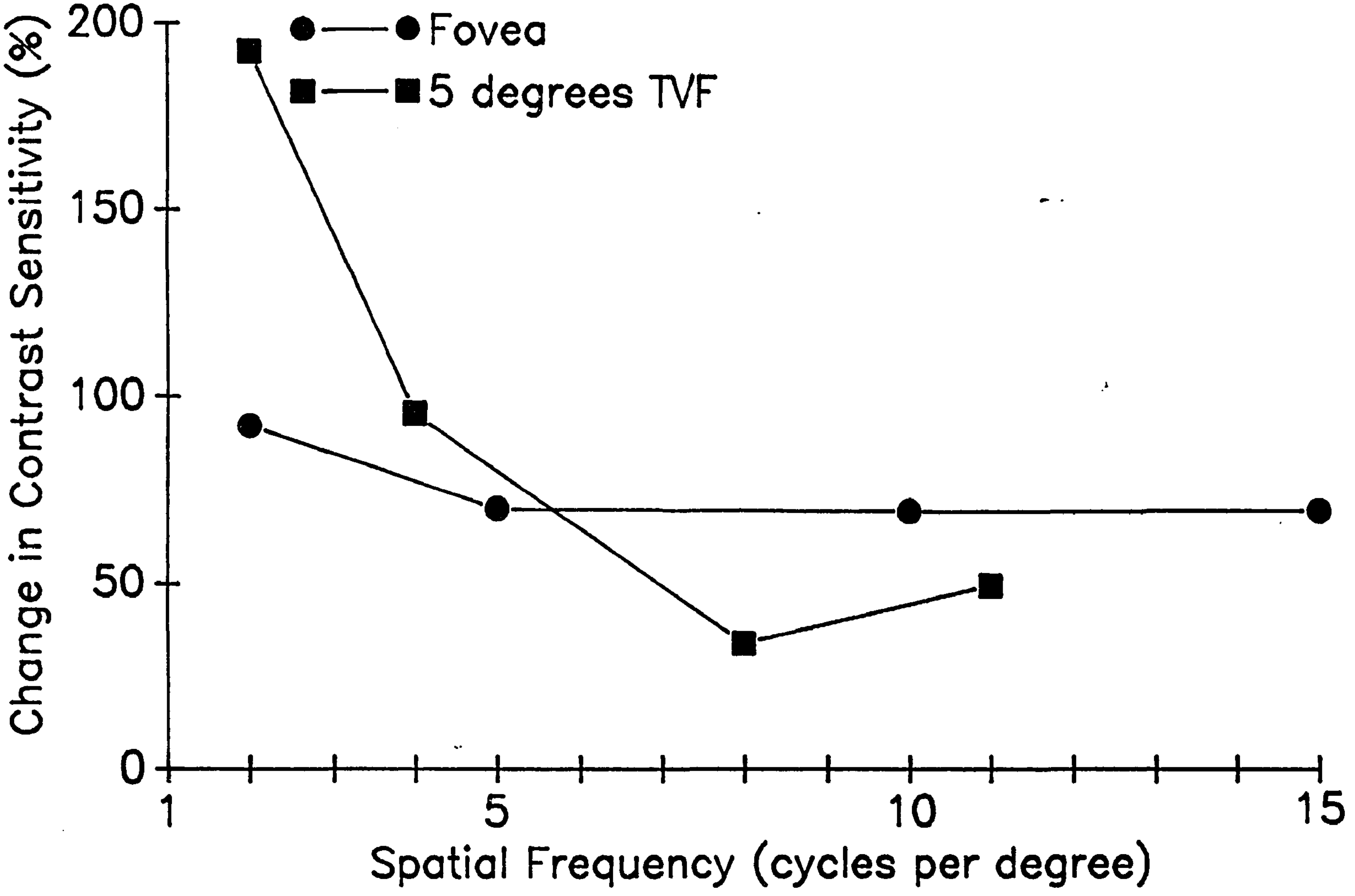

Change in Contrast Sensitivity (%)
200
150
100
50
0
1
5
10
15
Spatial Frequency (cycles per degree)
●——● Fovea
■——■ 5 degrees TVF
◆——◆ 10 degrees TVF

Figure 24. Percent change in contrast sensitivity is plotted as a function of spatial frequency for observer TEF. The data were collected according to the yes/no method of adjustment procedure. The stimulus was a 3.2° x 2.4°, 10 cd/m^2 sine wave grating presented to the left fovea and the background was a 20.8° x 15°, 10 cd/m^2 diffuse field presented to the right eye. Circular symbols represent interocular background data for a foveally presented stimulus, and squares represent data when the stimulus was presented 5° in the TVF. Mean 95% confidence intervals (±2 standard errors) for control data are 8.5% for the stimulus positioned 5° in the TVF.


Change in Contrast Sensitivity (%)
200
150
100
50
0
● Fovea
■ 5 degrees TVF
1
5
10
15
Spatial Frequency (cycles per degree)

1. With the full size or 1° test stimulus and regardless of retinal position or luminance, presentation of the full sized interocular adapting stimulus <u>always</u> increased the apparent brightness of the test stimulus. This occurred, regardless of whether the adapting stimulus luminance was dimmer (sometimes by as much as 5 $\log_{10}$ units) or brighter (sometimes by as much as 3 $\log_{10}$ units) than the test stimulus. These results suggest a similar interocular adapting influence upon apparent brightness and grating visibility, and contradicts demonstrations of Fechner's paradox.

2. With a full sized or 1° test grating, presentation of the same sized interocular background produced a subjective binocular brightness level intermediate between that produced by separate monocular viewing of the test or the full sized adapting stimulus. These results amount to a demonstration of Fechner's paradox. For observer ND, they are inconsistent with the influence of same sized backgrounds upon grating visibility. This perhaps suggests that independent interocular mechanisms influence brightness and grating visibility.

3. Presentation of the large interocular background produced no change in the apparent brightness of the 0.5° test stimulus. This is of interest since such backgrounds had little influence upon the visibility of the 0.5° test gratings.

4. Presentation of annular adapting fields had highly variable influences upon test stimulus brightness and generally produced marked binocular rivalry.

Chapter 3

Interocular Adaptation Involves the Manipulation of a Purely Interocular Tonic Suppressive Influence

The results presented in the previous chapter showed that interocular background fields can improve monocular grating visibility. Two broad classes of mechanisms could be responsible for producing this interocular effect.

A. Stray Light Explanation

The present results may not be due to an interocular influence but could instead be attributed to stray light. That is, light from the adapting source, intended to influence exclusively the interocular adapting eye, could stray directly into the test eye. This is an important consideration since Naarendorp, Denny and Frumkes (1988) established that sensitivity to monocularly presented gratings is enhanced by the presentation of a dim adapting field to the same eye. This effect, called suppressive rod-cone interaction (SRCI), is considered more thoroughly in chapter 5.

A priori, there are three reasons for discounting this stray light explanation. 1) For SRCI, grating visibility monotonically increases as background luminance increases up to about 0.2 cd/m^2. However, the interocular effect shown in figures 3-5 and 6-7 tends to be "all-or-none" and in many cases, reaches a maximal level at a much dimmer luminance level. 2) The magnitude of the SRCI effect is very small for low spatial frequencies (<3 cpd) and monotonically increases with grating frequency. In contrast, the interocular adapting effect is obvious for all grating frequencies examined greater than 1 cpd. 3) A great deal of care was taken to prevent light intended to stimulate one eye from directly impinging upon the other. One experiment in this chapter directly compares the effects of monocular, interocular, and binocular adaptation upon monocular grating visibility.

B. Interocular Neural Mechanisms and the Importance of Tonic Interocular Suppression

The artificial pupils used in the experiments described in chapter 2 rule out any role for a consensual pupillary response in the present interocular adaptation effect. If stray light adaptation influences can also be ruled out, then a role for an interocular neural mechanism is suggested. Two types of neural mechanisms could be involved. It is possible that a light adapted eye somehow facilitates contrast sensitivity in the contralateral eye. Under such conditions, monocular sensitivity values would be unaffected by the contralateral eye when it is dark adapted, but when that eye is stimulated with diffuse light, contrast sensitivity would be enhanced. There is no widely known evidence for the existence of such a facilitatory mechanism for these experimental paradigms. A second possibility is that a dark adapted eye exerts a tonic suppressive influence upon the contralateral eye, decreasing its contrast sensitivity; light adapting that eye removes the suppressive influence thereby increasing sensitivity.

The idea of a role for tonic suppressive influences in vision first became popular in the 1960s and 1970s as an outgrowth of physiological studies of the visual cortex and the role of visual deprivation. In a normally reared cat of any age, the vast majority of neurons in striate cortex are driven by visual stimulation of either eye. However, when a kitten is deprived of monocular vision during a critical period which has been found to occur between eye opening and 4 months of age, the deprived eye, when tested, can drive only approximately 5% of the cells recorded from in the striate cortex (Hubel & Wiesel, 1965; Hubel & Wiesel, 1970; Kratz, Spear & Smith, 1976).

Most explanations for the effects of monocular visual deprivation proposed a role for "binocular competition" during the critical period of visual development which, in the cat, is during the first four months of life. Some early experiments tried to establish this mechanism using "reverse suturing procedures" (Hubel & Wiesel, 1970). These showed that cortical cells could be driven by stimulation of the previously deprived eye if the reverse suturing occurred during the critical period. This phenomenon was also investigated by recording from different areas of cortex representing different areas of the visual field, including areas of binocular overlap and the monocular temporal crescent. Kratz, Spear and Smith (1976) compared the effects of monocular deprivation on cells recorded from the monocular far periphery as opposed to the larger binocular areas of cortex. They found that the effects of monocular deprivation were far less severe in monocular visual cortical areas, which supports the "binocular competition" hypothesis.

However, the most direct evidence for the "binocular competition" hypothesis comes from experiments performed by Kratz, Spear and Smith (1976) in which the non-deprived eye was removed. They reasoned that if the effects of deprivation are due to binocular competition, and if binocular competition continues to occur after the critical period has ended, removal of the non-deprived eye should result in a restoration of visual responses to stimulation of the previously deprived eye. They and other investigators (Crewther, Crewther & Pettigrew, 1978; Hoffmann & Cynader, 1977; Smith, Spear & Kratz, 1978) found an increased responsivity from stimulation of the previously deprived eye after the normal eye had been removed. In addition, they found that there was no increase in the relative numbers of cells which could be recorded from as a function of time since enucleation. Although these data do not pinpoint an exact mechanism, they certainly establish a role for tonic interocular suppression (TIS) in visual development. In combination with the findings of Makous, Teller and Boothe (1976) which showed that pressure blinding the eye contralateral to the test stimulus resulted in the same increase in sensitivity as interocular light adaptation, these results clearly suggest that TIS could play an important role in the interocular adapting effect described in this thesis.

Kratz, Spear and Smith (1976) suggested that the TIS mechanism they discerned was due to a tonic inhibitory influence from the normal eye upon vision in the deprived eye. This idea is analogous to data previously obtained by Taub and Berman (1968) who found that monkeys unilaterally deprived of sensory innervation of the arm did not make use of their arm but did so with bilateral severing of the dorsal root. To test the possibility of TIS in vision, Duffy, Snodgrass, Burchfiel and Conway (1976) reduced the overall amount of synaptic inhibition in visual cortex by applying the $GABA_A$ antagonist bicuculline to the visual cortex of cats which had been monocularly deprived during the critical period. In the presence of bicuculline, there was an increase in responsiveness to stimulation of the deprived eye. Similar claims have been made more recently by other investigators (Burchfiel & Duffy, 1981; Sillito, Kemp & Blakemore, 1986). In addition, in 60% of the cells recorded from, the receptive field location, size, shape, orientation specificity and directional specificity appeared to be the same as in the nondeprived eye. Using a considerably different type of experiment, Maffei and Fiorentini (1976) and Singer, Gruenau and Rauschecker (1979) also provide evidence for the importance of an interocular suppressive influence in visual development. They found that unilateral immobilization of one eye, even when both eyes are deprived of visual input, also leads to decreases in binocularity in the cat, suggesting that normal binocular visual and proprioceptive input are necessary for the development of binocularity.

Although tonic suppression may involve inhibition as suggested by Kratz, Spear and Smith (1976), other possible mechanisms may be involved. For more than 30 years, the auditory literature has described a suppressive phenomenon which is due to changes in signal-to-noise relationships, referred to as "masking level difference" or the "cocktail party effect" (Jeffress, 1972). As it is usually demonstrated, the monaural threshold is determined when a pure tone is presented in the presence of white noise also applied to the same ear. But if the white noise is additionally presented in phase to the other ear, test threshold decreases by as much as 12 dB. This is always explained as a change in the signal-to-noise relationship within the central nervous system and does not involve an active inhibitory mechanism which decreases the size of the signal. Such a mechanism is also quite capable of explaining the interocular adapting effects described above.

The question of a facilitatory versus a tonic suppressive mechanism can be addressed by observing the results obtained while measuring contrast sensitivity when the contralateral eye is pressure blinded. Fox, Blake and Bourne (1973) measured visually evoked cortical potentials before, during, and after pressure blinding. Cortical potentials could not be recorded when observers reported subjective blindness, indicating that signals from the retina were not being transmitted to the cortex. Evoked potentials returned to normal within 90 seconds after pressure blinding had been terminated. If this interocular effect is due to a facilitatory influence of diffuse light stimulation upon the contralateral eye, then pressure blinding the eye receiving diffuse stimulation should lead to sensitivity values which are the same as with monocular stimulus presentation while the contralateral eye is dark adapted. In contrast, if the increase in sensitivity occurs because a tonic inhibitory influence of a contralateral dark adapted eye is removed by light adapting that eye, than pressure blinding should lead to an increase in contrast sensitivity of that contralateral eye; and this increase in sensitivity should appear similar to that seen when the contralateral eye is light adapted. Following the procedure used by Makous, Teller and Boothe (1976), a pressure blinding experiment was performed to determine if a "light-facilitatory" or a "tonic-suppressive" mechanism provides a better explanation for the present effect.

Methods

All experiments which did not involve pressure blindness were conducted according to the procedures specified in chapter 2. The methods used in the pressure blindness experiments are summarized along with the results below.

Results and Discussion

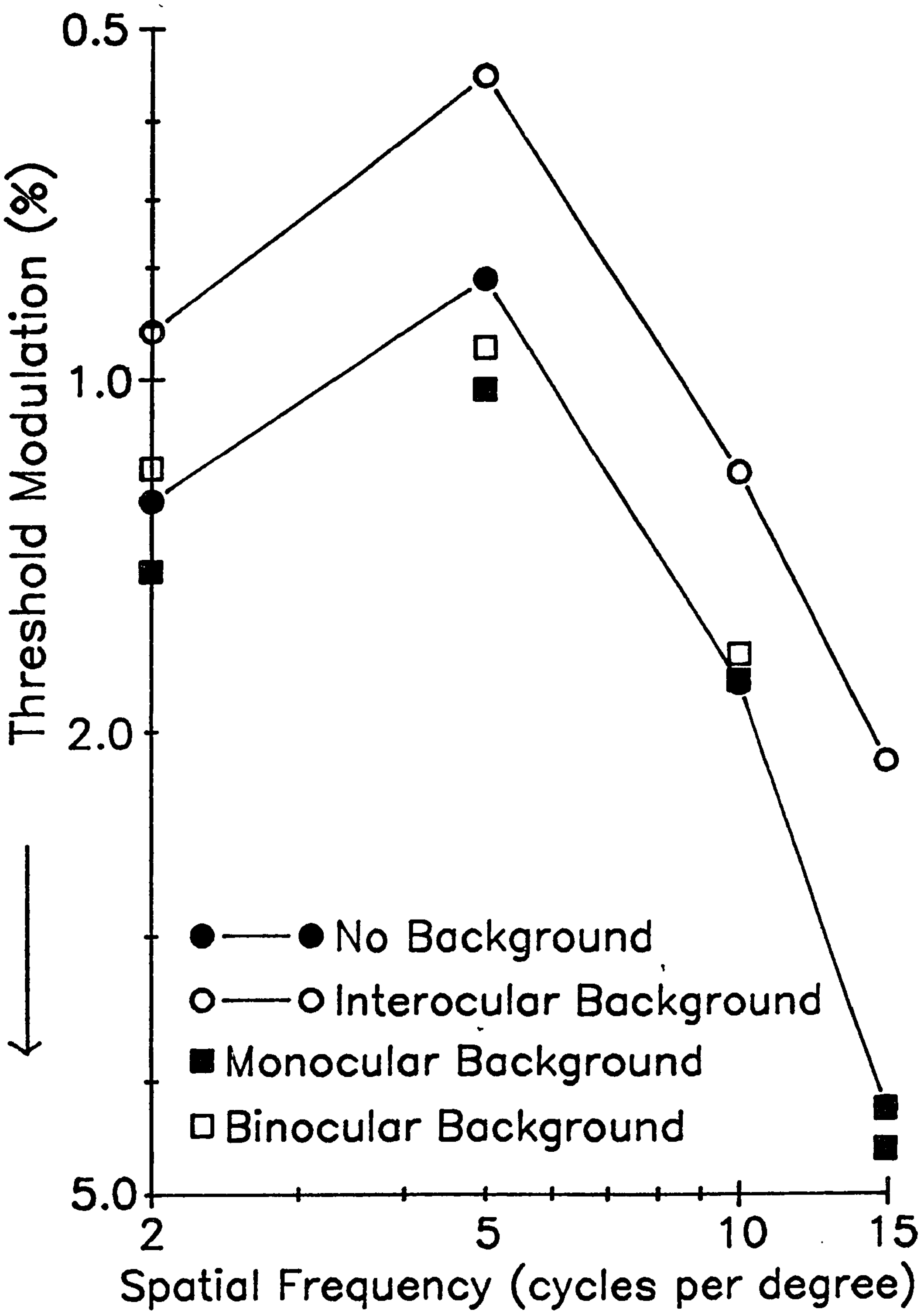
A. Interocular Adaptation Involves a Neural and Purely Interocular Mechanism: Comparison of Monocular, Interocular, and Binocular Adapting Influences.

1. Comparisons with Monocular Stimulus Presentation

In several experiments the effects of monocular, interocular, and binocular adaptation upon monocular test grating sensitivity were compared. Full sized monocular, interocular, or binocular backgrounds with luminance levels of 10 cd/m^2 were presented to the test eye and their influence upon the visibility of a 3.2° x 2.4° sized grating of 10 cd/m^2 average luminance was determined. Figure 25 shows that the 10 cd/m^2 interocular background increased monocular sensitivity, comparable to that reported in chapter 2. However, there was no increase in sensitivity with presentation of the background to the same eye as the test stimulus (monocular presentation of the background); instead, a slight decrease in sensitivity was seen. This

Figure 25. Percent threshold modulation is plotted as a function of spatial frequency for subject ND. The data were collected according to the method of adjustment procedure. The stimulus was a 3.2° x 2.4°, 10 cd/m^2 sine wave grating presented to the left eye fovea. The background was a 10 cd/m^2 diffuse field presented to the eye contralateral to the stimulus (open circles), to the same eye as the stimulus (filled squares), binocularly (open squares); or was not present (closed circles).

It should be further noted that the threshold values obtained separately with a monocularly presented test stimulus and a binocularly presented background cannot be predicted from the data obtained with the background superimposed on the test stimulus and a background presented interocularly (i.e., a binocular background), as seen here. The threshold values predicted by calculating the threshold increase which occurs with the decrease in contrast resulting from a background superimposed on the test stimulus and the threshold decrease which occurs with interocular adaptation are considerably higher than those obtained with a binocular background. These two effects must therefore interact with one another in a more complex fashion.


0.5
1.0
2.0
5.0
Threshold Modulation (%)
2
5
10
15
Spatial Frequency (cycles per degree)
●——● No Background
○——○ Interocular Background
■ Monocular Background
□ Binocular Background

is expected since monocular backgrounds of this intensity physically reduce the contrast of the grating stimulus. A binocular 10 cd/m^2 background produced no systematic effect upon grating sensitivity (see figure legend).

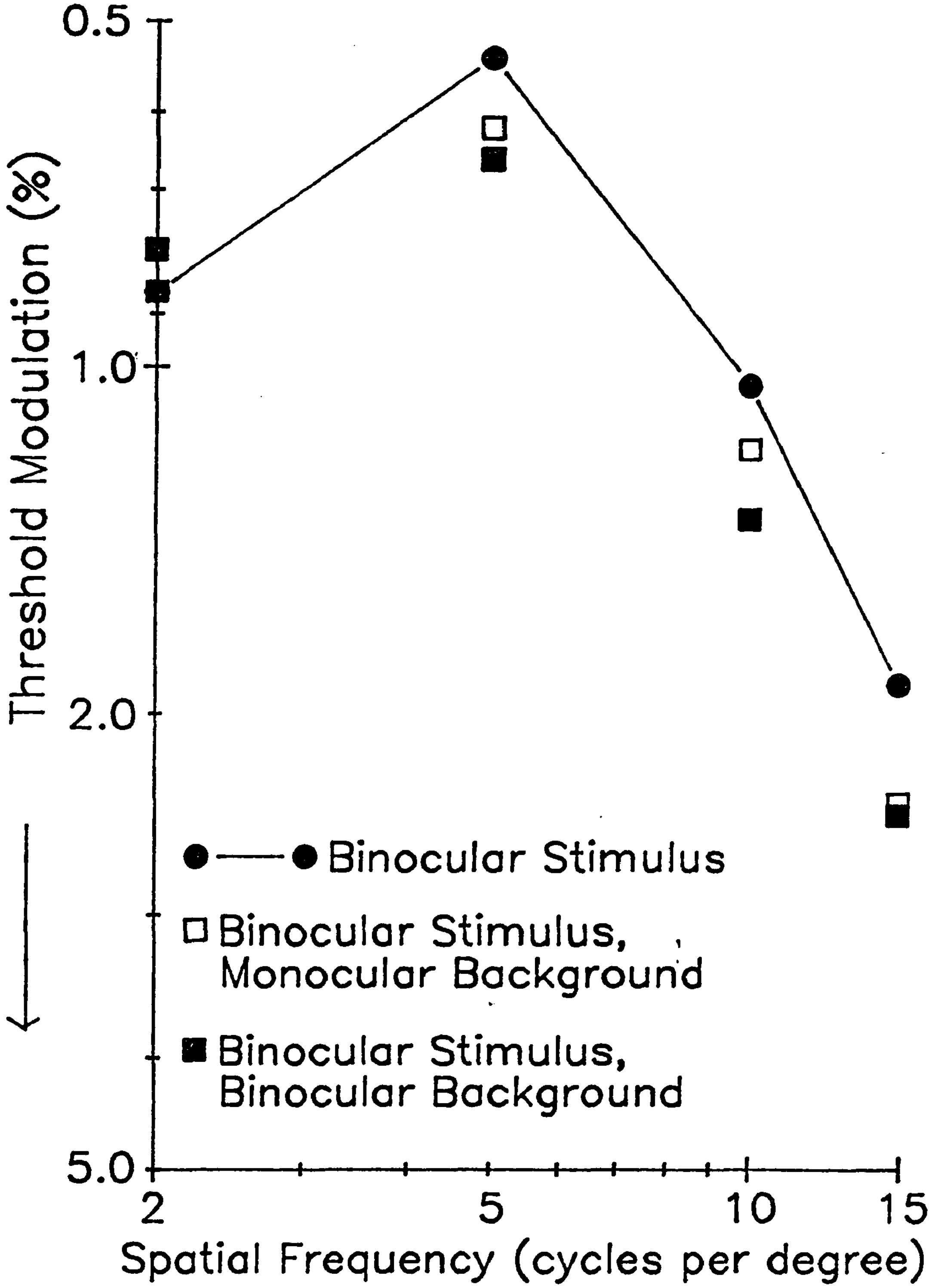
Although the types of comparisons reported in figure 25 were only made directly with observer ND, there is little reason to doubt that they would extend to other observers. Naarendorp, Denny and Frumkes (1988) showed similar influences of high luminance monocular backgrounds upon grating visibility, while interocular data similar to that in figure 25 for observers TEF and NM reported in chapter 2 above conform to these findings.

The above data show that the present effect is clearly due to an interocularly mediated mechanism and does not occur with presentation of the background to the same eye as the test stimulus or to both eyes.

2. Comparisons with Binocular Stimulus Presentation

Figure 26 presents data obtained when a binocular stimulus is viewed and monocular or binocular backgrounds of 10 cd/m^2 are presented. Under these conditions, background presentation produced slight but consistent decreases in sensitivity. This is likely to be due to the decrease in physical contrast which occurs when a uniform field is superimposed on the grating.

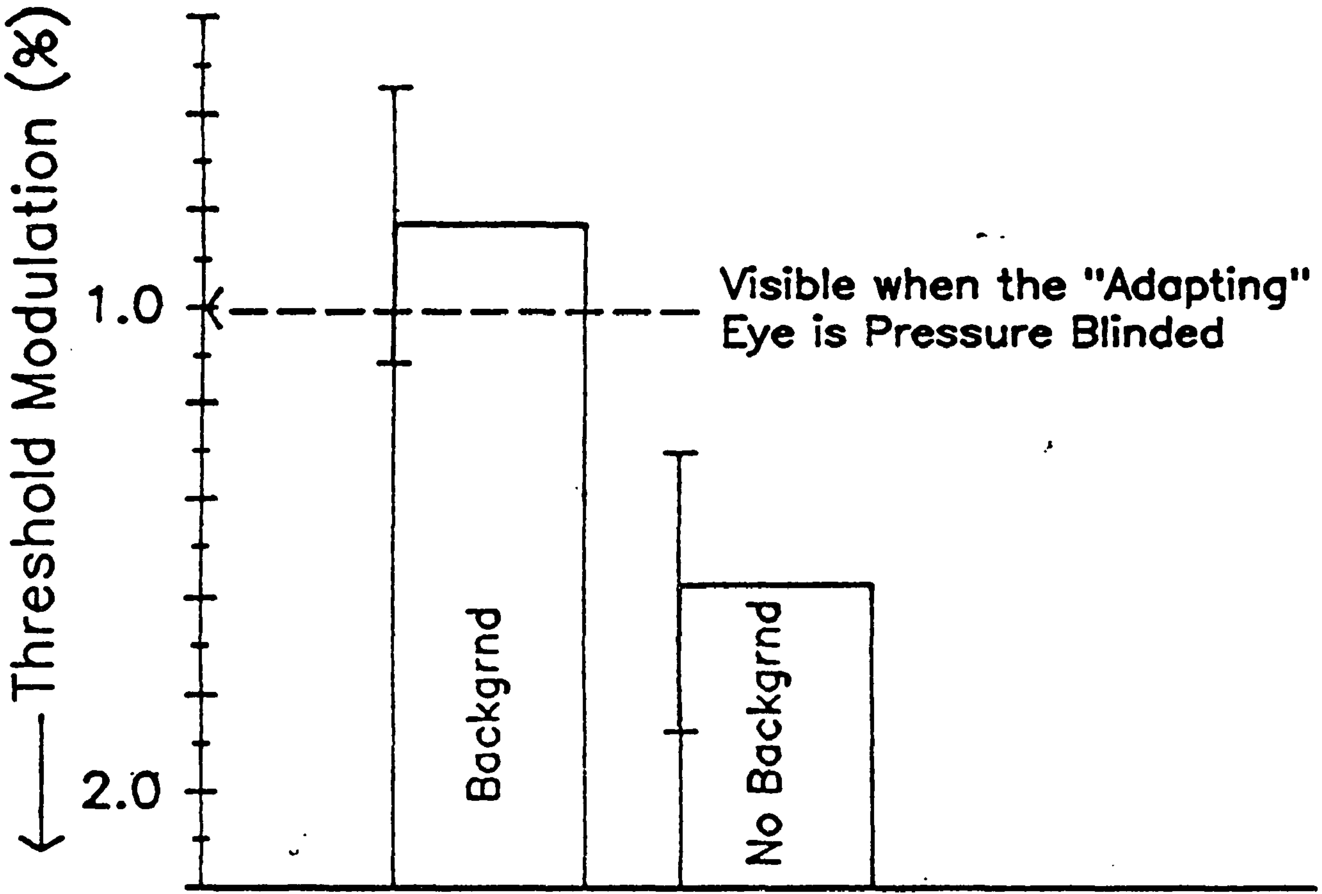
Figure 26. Percent threshold modulation is plotted as a function of spatial frequency for subject ND. The data were collected according to the method of adjustment procedure. The stimulus was a 3.2° x 2.4°, 10 cd/m^2 sine wave grating presented to both eyes. The background was a 10 cd/m^2 diffuse field presented to the right eye (open squares), or to the both eyes (closed squares); or was not present (closed circles).


0.5
1.0
2.0
5.0
Threshold Modulation (%)
2
5
10
15
Spatial Frequency (cycles per degree)
●—● Binocular Stimulus
□ Binocular Stimulus, Monocular Background
■ Binocular Stimulus, Binocular Background

B. Interocular Adaptation Involves a Tonic Interocular Suppression: Pressure Blindness Experiment

As summarized in the introduction to this chapter, there are two general classes of neural mechanisms which could account for the interocular adaptation effect. One possibility is that light adapting one eye somehow facilitates vision mediated by the other eye. A second possibility is that a dark-adapted eye somehow suppresses vision mediated by the other eye, and that light adaption removes this suppression. In order to choose between these two possibilities the following data were collected in one experimental session. Sensitivity was determined when a 3.2° x 2.4°, 10 cpd grating was presented to the test eye while the contralateral eye was either dark adapted or adapted to a 10 cd/m^2 background. These threshold values, with 95% confidence intervals (±2 standard errors) are shown in figure 27. Next, the test stimulus was presented at 1% contrast when the adapting eye was again fully dark adapted. Under these conditions, the test grating was not visible. The adapting eye was then pressure blinded for about 30 seconds. Blindness is produced when the pressure applied to the eye globe removes the blood supply to the retinal ganglion cells thereby preventing their signals from reaching the brain (for evidence in humans, see Fox, Blake & Bourne 1973; Makous, Teller & Boothe, 1976). Shortly after pressure blindness was initiated, the test grating became clearly visible, but was no longer visible within a few seconds after removing the pressure blinding. These observations

Figure 27. Percent threshold modulation for a 3.2° x 2.4°, 10 cd/m^2 sine wave grating of 10 cpd presented to the left eye obtained when either no background was present or in the presence of a 10 cd/m^2 background presented to the right eye. These data were collected according to the yes/no method of adjustment procedure for observer ND. The error bars indicate 95% confidence intervals. These data show that with monocular test stimulus presentation and a contralateral dark adapted eye, a test grating of 1% contrast modulation is invisible but becomes visible when the contralateral eye is pressure blinded.


← Threshold Modulation (%)
1.0
2.0
Backgrnd
No Backgrnd
Visible when the "Adapting" Eye is Pressure Blinded

suggest that when a stimulus is viewed monocularly, the contralateral dark adapted eye exerts a tonic suppressive influence upon the test eye.

To summarize, monocular spatial vision is apparently subject to a suppressive influence if the contralateral eye is dark adapted. Throughout the remainder of this thesis, this influence will be referred to as Tonic Interocular Suppression (TIS). This TIS influence can be removed by light adapting or pressure blinding the contralateral eye.

Chapter 4

The Relationship of TIS to Binocular Summation

While conducting the monocular, interocular, and binocular control experiments presented above (e.g., portrayed in figures 25 and 26), it was noted that the improvement in sensitivity resulting from interocular light adaptation was often similar to that resulting from binocular stimulus presentation (as seen when comparing these two functions in these figures). The present chapter reports results of experiments which directly compared the improvement in sensitivity resulting from these two different types of stimulus manipulations.

A. Overview of "Binocular Summation"

1. Mechanistic Considerations

An important question in the realm of binocular vision concerns whether visual sensitivity with two eyes is better than with one. The answer to this question has been investigated extensively, usually under the heading of "binocular summation" (for reviews, see Blake & Fox, 1973; Blake, Sloane & Fox, 1981). In the majority of these studies, sensitivity during a particular visual task (e.g., determining absolute threshold) is compared under conditions in which the left eye, right eye, and both eyes view a stimulus. For normal observers, the sensitivity for each eye alone is either equivalent or is made equivalent by appropriate experimental manipulation, usually through simple optical correction. Then, sensitivity for monocular vision (with either eye) is compared with binocular sensitivity.

When these experiments are performed, three different types of results can occur. It is possible that no physiological interaction occurs between the left and right visual pathways. Because viewing a stimulus with two eyes offers two independent opportunities to detect a stimulus, sensitivity with two eyes is expected to be somewhat superior to monocular sensitivity. This outcome would result in probability summation. For example, if a stimulus is presented at value producing 50% detection in either eye alone, detection with two independently operating eyes would be 75%. For a completely linear system, this is equivalent to an improvement in sensitivity of about 0.125 $\log_{10}$ units. Binocular probability summation was demonstrated by Pirenne (1943).

A second possible outcome is that sensitivity with two eyes is actually less than with one eye, so that binocular sensitivity falls below probability summation. Many of the references cited by Blake and Fox (1973) and Blake, Sloane and Fox (1981) fail to consider probability summation in evaluating their results (e.g., Bartlett & Gagné, 1939; Graham, 1930, 1931). For this reason, some of these authors have made erroneous claims from the results of their studies. Since they do not find probability summation, some older studies which showed no difference in binocular and monocular sensitivity claim "no summation" but in actuality some type of suppressive interaction between the two eyes must have taken place (e.g., Bartlett & Gagné, 1939; Graham, 1930, 1931). Also, some studies may claim "partial summation" when, in fact, only "probability summation" has occurred. These erroneous interpretations probably are more frequent in studies published prior to the report by Pirenne (1943).

Finally, some studies demonstrate an improvement in binocular sensitivity greater than that which could be attributed to probability summation (e.g., Anderson & Movshon, 1989; Campbell & Green, 1965b; Matin, 1962; Wolfe & Zigler, 1955, 1963). Such results clearly indicate an interaction between the signals from the two eyes, but the underlying mechanism responsible for this interaction is far from clear. It is generally accepted that if identical signals from the two eyes linearly sum together, "perfect summation" would be indicated by a doubling of sensitivity under binocular stimulus conditions. This is what would occur in a completely linear system. With a fixed criterion threshold such as a 50% detection threshold, such a result would be indicated by a 50% (0.3 $\log_{10}$ units) reduction in threshold. Although this interpretation may certainly be correct, an improvement in sensitivity could be due to factors other than summation. Specifically, removal of tonic suppression could as easily account for such an improvement in sensitivity.

Remarkably few studies have observed "perfect summation" (as did Bolanowski, 1987, for example). However, many have observed "partial summation," an improvement in sensitivity exceeding 33.5% as predicted by probability summation, but less than 100% improvement expected for perfect summation. Many studies showing "partial summation" (Campbell & Green, 1965b; Legge, 1984a; Legge, 1984b) suggest a "vector summation" or a "$\sqrt{2}$" type of summation, rarely specifying the underlying mechanism. In addition, few such studies present data that compellingly distinguish between outcomes consonant with probability summation (an increase for binocular, compared to monocular sensitivity of 33.5%, or 0.123 $\log_{10}$ units), or $\sqrt{2}$ summation (an increase in sensitivity of 41%, or 0.15 $\log_{10}$ units). Finally, results of evoked potential studies (Apkarian, Nakayama & Tyler, 1981) suggest a binocular improvement in sensitivity which is considerably greater than the 100% (0.3 $\log_{10}$ units) consistent with arguments for "perfect binocular summation" and facilitation. However, these data are not presented in any theoretical frame of reference nor are they compatible with any physiological or psychological model proposed by other investigators.

In summary, various studies have claimed "binocular summation" based on results showing sensitivity values under binocular conditions compared to monocular viewing conditions which exceed the amount consistent with probability summation.

B. Summary of Published Data

The anatomy of the visual system provides ample opportunity for the signals from the two eyes to interact at a variety of different sites. Studies which claim to demonstrate "binocular summation" can be considered according to three categories. The first category are behavioral studies which are usually psychophysical studies in human observers and are summarized in the subsection directly below. The second category are studies involving single unit recordings from neurons receiving binocular input in subhuman species. Included here are the classic cortical studies of Hubel and Wiesel (1962) and Ohzawa and Freeman (1986a, b) in cat. These studies have demonstrated a variety of different outcomes resulting from binocular stimulation (i.e., improvement in sensitivity reported by Hubel and Wiesel, the existence of units showing lower sensitivity reported by Ohzawa and Freeman). Finally, many evoked potential studies in humans (Apkarian, Nakayama & Tyler, 1981; Baitch & Levi, 1988; Harter, Seiple & Salmon, 1973; Katsumi, Tanino & Hirose, 1986; Trick, Dawson & Compton, 1982; White & Bonelli, 1970) indicate that binocular stimulation results in a larger evoked potential than does monocular stimulation. However, few distinguished between physical summation of non-interacting currents and true physiological summation. Others, using Fourier analyses (Apkarian, Nakayama & Tyler, 1981), present results in a non-theoretical context. Because of these limitations, the next section only considers psychophysical studies.

1. Behavioral Studies of "Binocular Summation"

Several different types of behavioral studies have examined the topic of "binocular summation."

a. Absolute and Increment Threshold Studies

Probably the most commonly used measure in studies of "binocular summation" is threshold. Studies conducted prior to 1950 that are cited by Blake and Fox (1973) indicate one clear tendency. Binocular summation was never observed when small stimuli were presented in the fovea under light adapted conditions, but was sometimes observed under dark adapted conditions in the periphery. Unfortunately, more recent studies have rarely directly studied the importance of stimulus size, retinal position, and state of dark adaptation. The results of threshold studies are seen in table 1. Although not easy to interpret, one tendency can be observed. No study has demonstrated "binocular summation" using stimuli <30' of arc presented foveally. Since this arrangement most likely stimulates only foveal cones, this suggests that receptors other than foveal cones are responsible for claims of "binocular summation". Although not directly obvious from table 1, the most compelling demonstrations of binocular summation at threshold occur in the peripheral retina. As described in the results below, retinal position and stimulus size exerted a large influence upon results in the present study of grating visibility.

Table 1. A list of studies of "binocular summation" which measure absolute thresholds or increment thresholds .

STUDY	SUMMATION	DEPENDENT VARIABLE	STIMULUS SIZE	RETINAL POSITION
Graham, 1930	No	Threshold during dark adaptation.	24'	Fovea
Cook, 1934	Yes, for some subjects.	Threshold during short dark adaptation times.	55'	Fovea
Bartlett & Gangé, 1939	No	Threshold for 115 sec. during dark adaptation.	30'	Fovea
Pirenne, 1943	No	Frequency of detection of flashes.	10'	20° below fovea
Collier, 1954	Yes	Frequency of detection of flashes.	10'	20° below fovea
Collier & Kubzansky, 1958	Yes	Frequency of detection of flashes	3°	7° below fovea
Wolfe & Zigler, 1958	Yes, except vertical meridian	Scotopic threshold.	0.3°	Various-along horizontal meridian.
Matin, 1962	Yes	Probability of detection of flashes.	35'	7° horizontally from fovea
Wolfe & Zigler, 1963	Yes, except vertical meridian	Photopic threshold.	1°	24 positions in 10° radius from fovea
Westendorf, Blake & Fox, 1972	Yes	Temporal forced choice for flashes.	1°	Fovea

b. Studies of Apparent Brightness

The question of binocular summation has also been addressed through comparisons of monocularly and binocularly presented suprathreshold luminance levels. Some studies have demonstrated Fechner's paradox, in which binocular presentation of two different luminance levels to each eye leads to brightness averaging (Fechner, 1860). Fechner discovered that when the view to one eye passes through a neutral density filter while the other eye is unattenuated, blocking the eye viewing through the filter results in a paradoxical increase in perceived brightness. The observer does not perceive the brightness level of the eye viewing the brighter luminance level. Instead, it appears as if the luminance levels in each eye are averaged. Other studies, as seen in table 2, have claimed to find "binocular summation: or have found neither brightness averaging nor "summation". Once again although there is a great deal of variability in these studies, no claim for "binocular summation" was based upon small (<30') stimuli presented foveally.

2. Grating Sensitivity and Visual Acuity

Various studies have found evidence of binocular summation using gratings or other acuity measures. It is difficult with these studies to make the same types of generalizations as above concerning stimulus size and retinal position, since most used stimulus sizes much greater than 30'. Although presentation is usually foveal, these

Table 2. A list of studies of "binocular summation" which measure brightness estimates to determine sensitivity

STUDY	SUMMATION	DEPENDENT VARIABLE	STIMULUS SIZE	RETINAL POSITION
Graham, 1931	No	Brightness estimation to comparison stimulus.	10°	Fovea
Leibowitz & Walker, 1956	Yes*	Brightness estimation to comparison stimulus.	15-60'	Near edge of stimulus 30' from fovea
Bolanowski, 1987	Yes No	Magnitude estimation.	Ganzfeld 2°	Fovea Fovea

* These authors claim greater summation with larger sized stimuli. However, maximum increases occurred with a 60' stimulus and was only approximately 15%.

larger stimuli additionally stimulate parafoveal loci. Table 3 summarizes some of these studies.

Campbell and Green (1965b) claimed a √2 superiority of binocular over monocular visual acuity. Although all studies do not conform to this prediction, several do find a √2 increase in sensitivity during binocular, compared to monocular viewing (Braccini, Gambardella & Suetta, 1980; Legge, 1984a; Legge, 1984b). This relationship indicates an increase in sensitivity which barely exceeds probability summation.

3. Other Visual Tasks

Monocular and binocular flicker sensitivity have been compared by a number of investigators beginning with Sherrington (1904; a review of these studies is given by Cavonious, 1979). In general, binocular sensitivity to high frequency flicker exceeds that of monocular sensitivity, but the improvement depends upon specific experimental parameters. Other studies have directly investigated the effect of binocular stimulation upon response latency. Consistent with the idea of "binocular summation," binocular presentation has been shown to result in shorter reaction times (Westendorf & Blake, 1988).

Table 3. A list of studies of "binocular summation" which measure acuity or contrast sensitivity.

STUDY	SUMMATION	DEPENDENT VARIABLE	STIMULUS SIZE	RETINAL POSITION
Horowitz, 1949	Yes	Acuity for Ives grating and Landolt C		Fovea
Campbell & Green, 1965b	Yes	Contrast sensitivity function	2° x 1.3°	Fovea
Williams, 1974	Yes	Identification of letters presented tachistoscopically		Fovea
Lema & Blake, 1977	Yes	Contrast sensitivity function	4°	Fovea
Braccini, Gambardella & Suetta, 1980	Yes	Contrast sensitivity function	2°	Fovea
Legge, 1984b	Yes	Contrast discrimination	11° x 6°	Fovea
Anderson & Movshon, 1989	Yes	Contrast sensitivity function	5° x 6°	Fovea

Methods

All methods are described in chapter 2.

Results

A. Foveal Comparison of Binocular Presentation with Interocular Adaptation

In the course of collecting the data presented in chapter 3 above, it was noted that monocular CSFs obtained in the presence of an interocular background were very similar to binocular CSFs obtained with no background field present. Here, binocular stimulus presentation with no background present is compared with monocular stimulus presentation with an interocular background present. Figure 28 shows data collected from three different observers with a 10 cd/m^2, 3.2° x 2.4° test grating presented foveally. As can be seen for all observers, both binocular stimulation and interocular adaptation similarly improve contrast sensitivity. However, for all three observers (as also seen in the replotted figure 29), binocular sensitivity is generally slightly greater than sensitivity for the interocular adaptation condition, which may represent the influence of probability summation.

These same data are replotted for all three observers in figure 29 to indicate the magnitudes of these effects and to show the change in sensitivity expected on the

Figure 28. Percent threshold modulation is plotted as a function of spatial frequency for subjects ND (left plot), TEF (middle plot), and NM (right plot). The data were collected according to the method of adjustment procedure for subject ND and the yes/no method of adjustment procedure for subjects TEF and NM. The stimulus was a 3.2° x 2.4°, 10 cd/m^2 sine wave grating presented to foveal regions in the left eye or both eyes. The background was a 20.8° x 15°, 10 cd/m^2 diffuse field presented to the eye contralateral to the monocular stimulus.

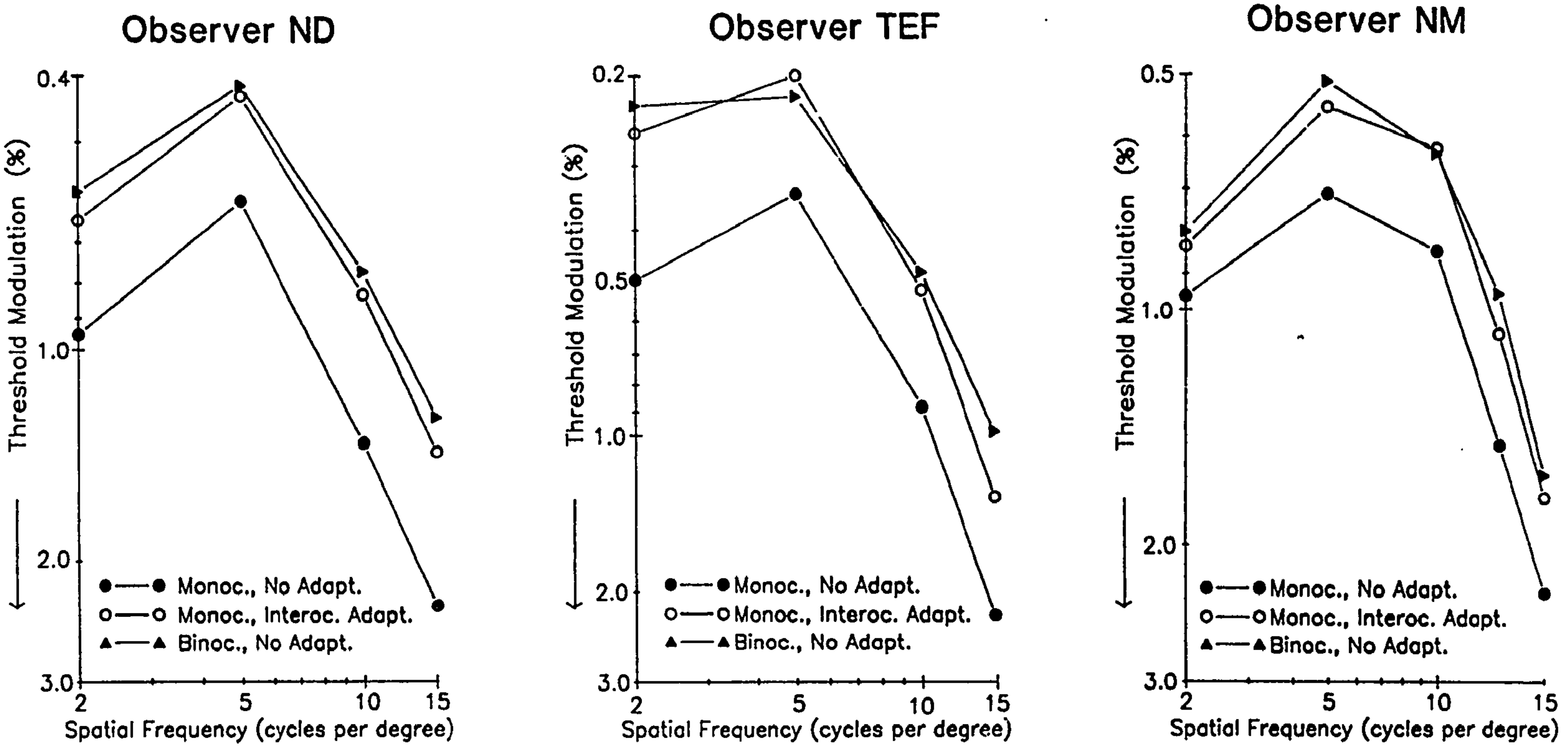
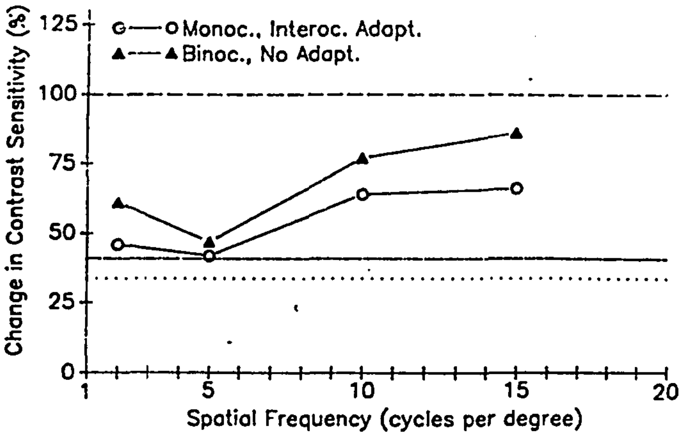
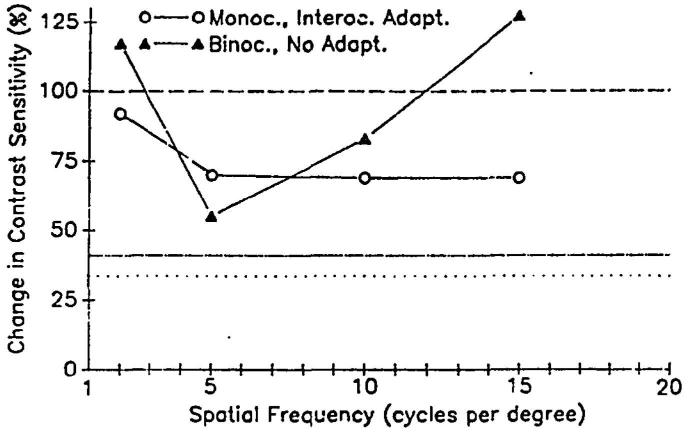

Observer ND
Observer TEF
Observer NM
Threshold Modulation (%)
0.4
1.0
2.0
3.0
0.2
0.5
1.0
2.0
3.0
0.5
1.0
2.0
3.0
2
5
10
15
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
○—○ Monoc., Interoc. Adapt.
▲—▲ Binoc., No Adapt.

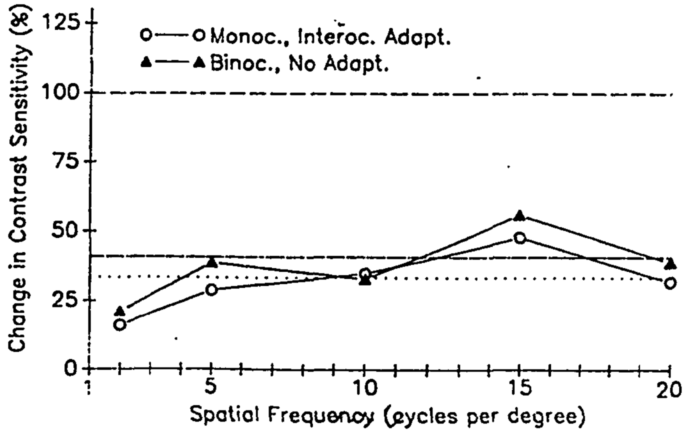
Figure 29. Change in contrast sensitivity is plotted as a function of spatial frequency for subjects ND (top), TEF (middle), and NM (bottom). The data were collected according to the method of adjustment procedure for subject ND and the yes/no method of adjustment procedure for subjects TEF and NM. The stimulus was a 3.2° x 2.4°, 10 cd/m^2 sine wave grating presented to foveal regions in the left eye or both eyes. The background was a 10 cd/m^2 diffuse field presented to the eye contralateral to the monocular stimulus. The dashed horizontal line represents perfect summation, the dotted horizontal line represents probability summation, and the dashed and dotted horizontal line represents $\sqrt{2}$ summation. Mean 95% confidence intervals (±2 standard errors) for control data are 19.2% for observer ND and 16.0% for observer NM.



Observer ND



Observer TEF



Observer NM

basis of probability summation (dotted horizontal line) and the $\sqrt{2}$ summation rule of Campbell and Green, (1965b) (dashed and dotted horizontal line). As can be seen from figure 29, increases in sensitivity are in all cases above probability summation and $\sqrt{2}$ summation except for observer NM, where both monocular and binocular effects are smaller. In fact, variability in the magnitude of "binocular summation" has been reported in the literature (Blake & Fox, 1973; Blake, Sloane & Fox, 1981).

B. The Effects of Test Grating Size with Foveal Stimulus Presentation

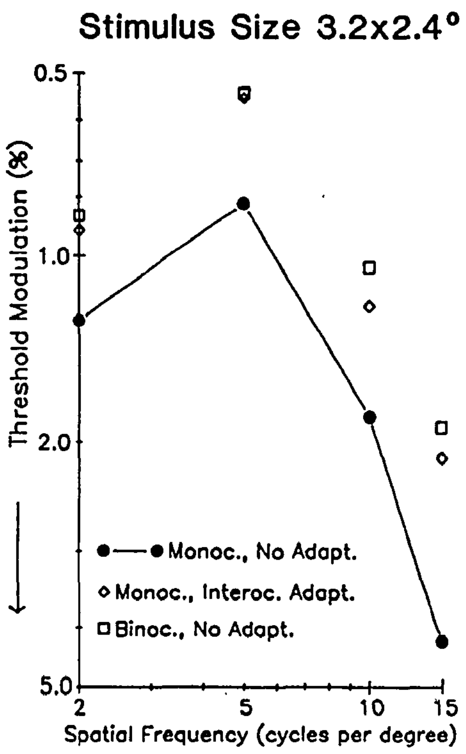
On the basis of these data, Denny, Frumkes, Barris and Eysteinsson (1991) postulated that the increase in sensitivity produced by binocular stimulation may not be due to physiological summation but to a removal of TIS. In order to achieve optimal sensitivity, TIS from a dark-adapted eye must be removed, either by presenting the same stimulus pattern binocularly, by pressure blinding the "non-stimulated" eye, or by light adapting the eye contralateral to the test stimulus. If this hypothesis has general validity, it would be expected that stimulus parameters which alter the effectiveness of interocular backgrounds would be equally effective in altering the effectiveness of binocular stimulus presentation. As indicated in chapter 2, both size and retinal position of the test grating alter the effectiveness of interocular backgrounds. Therefore, the influence of binocular stimulus presentation and interocular adaptation were compared at various retinal positions using different sized test gratings.

The effects of interocular adaptation and binocular stimulus presentation were studied when a foveal test grating was varied in size. For observers ND and TEF respectively, figures 30 and 31 show data obtained with 10 cd/m^2 foveal test gratings which were either 3.2° x 2.4°, a 1° square, or a 0.5° square in size. (Some of the data on the left from observer ND and TEF are replotted from earlier figures for ease of comparison.) As indicated previously with the large grating, binocular presentation and interocular adaptation produce similar increases in sensitivity (left coordinate-approximately 50% for ND and 75% for TEF). Qualitatively similar results are obtained with the 1° test grating (middle coordinates-approximately 25%). However, with the smallest sized test grating (right coordinates), neither binocular presentation nor interocular adaptation improve grating visibility.

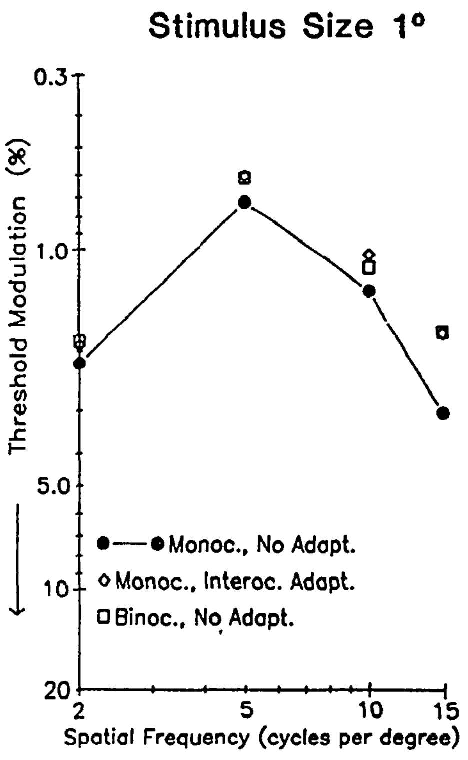
The data in figures 30 and 31 are replotted with percent change in contrast sensitivity from the monocular control condition as a function of spatial frequency for each test grating size in figures 32 and 33 (ND and TEF respectively). These plots clearly show that the improvements in contrast sensitivity resulting from either interocular adaptation or binocular stimulation are always quite similar. The enhancement obtained is greatest for the largest test stimulus and is absent with the 0.5° test stimulus.

In sum, results obtained with foveally centered test gratings suggest that the improvement in sensitivity resulting from binocular stimulus presentation and

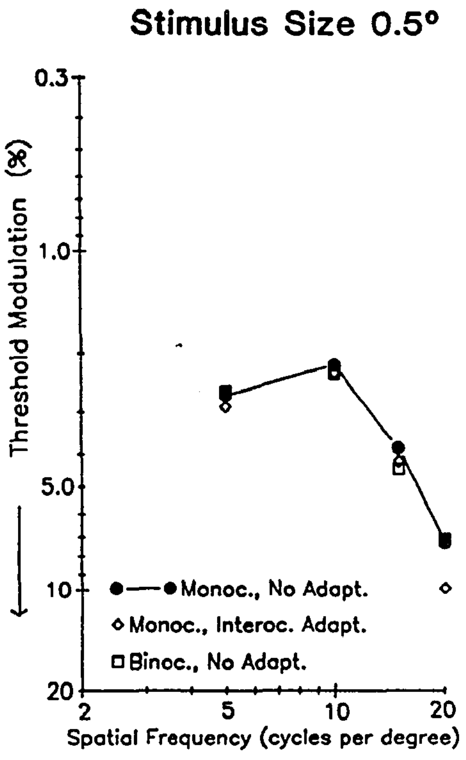
Figure 30. Percent threshold modulation as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° (left plot), 1° square (middle plot) or 0.5° square (right plot) sine wave grating. The stimulus was presented monocularly, monocularly with and interocular background, and binocularly, to the fovea. The background stimulus was 20.8° x 15° and presented to the right eye, and was 10 cd/m^2 diffuse field.



Stimulus Size 3.2x2.4°

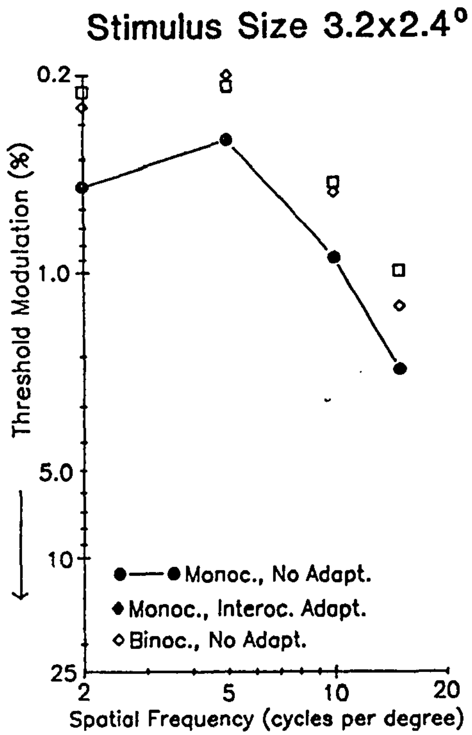


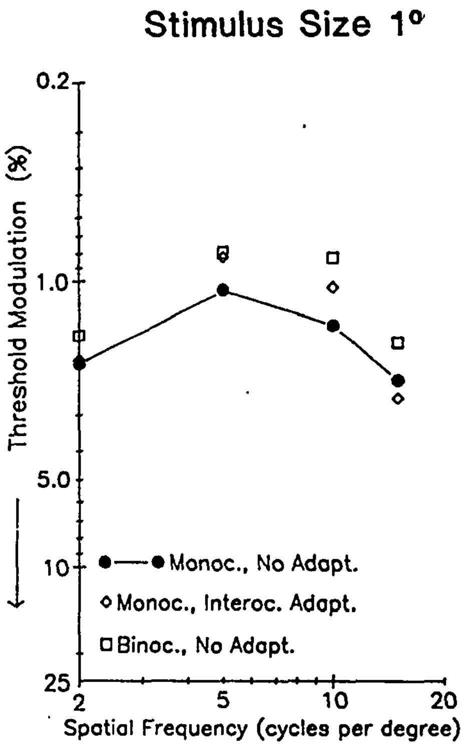
Stimulus Size 1°



Stimulus Size 0.5°

Figure 31. Percent threshold modulation as a function of spatial frequency is plotted for observer TEF. These data were collected according to a yes/no method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° (left plot), 1° (middle plot) or 0.5° (right plot) sine wave grating. The stimulus was presented monocularly, monocularly with and interocular background, and binocularly, to the fovea. The background stimulus was 20.8° x 15° and presented to the right eye, and was 10 cd/m^2 diffuse field.


Stimulus Size 3.2x2.4°


Stimulus Size 1°

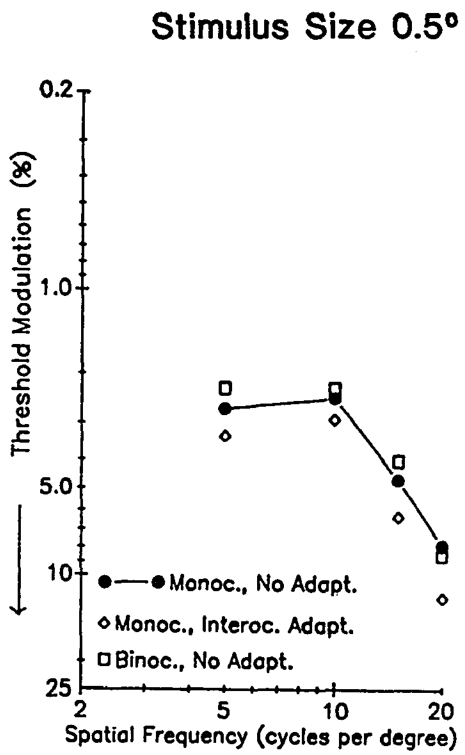
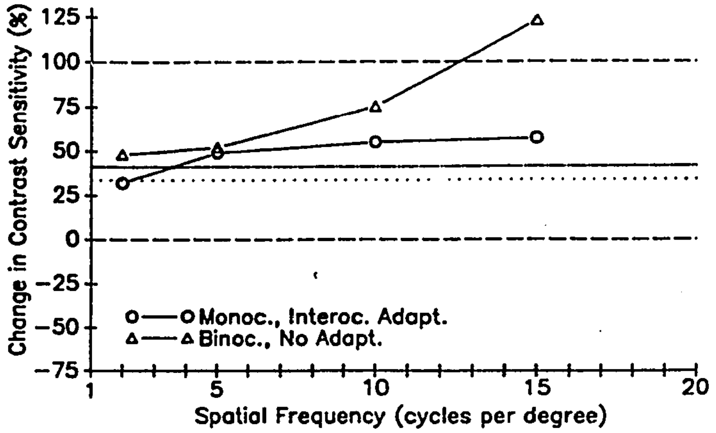
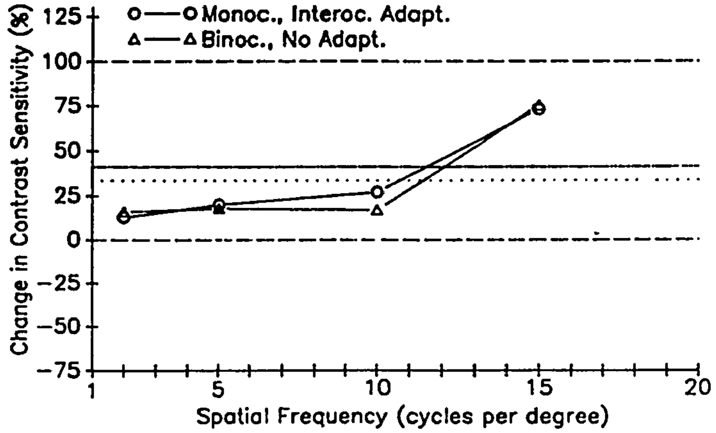

Stimulus Size 0.5°

Figure 32. Percent change in contrast sensitivity as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° (upper plot), 1° (middle plot) or 0.5° (lower plot) sine wave grating. The stimulus was presented monocularly, monocularly with and interocular background, and binocularly, to the fovea. The background stimulus was 20.8° x 15° and presented to the right eye, and was 10 cd/m^2 diffuse field. The horizontal dashed line represents perfect or zero summation, the horizontal dotted line represents probability summation and the horizontal dashed and dotted line represents $\sqrt{2}$ summation. Mean 95% confidence intervals (±2 standard errors) for control data are 12.3% for the large sized stimulus, 12.5% for the 1° size stimulus and 10.0% for the 0.5° size stimulus.


Stimulus Size 3.2x2.4°


Stimulus Size 1°

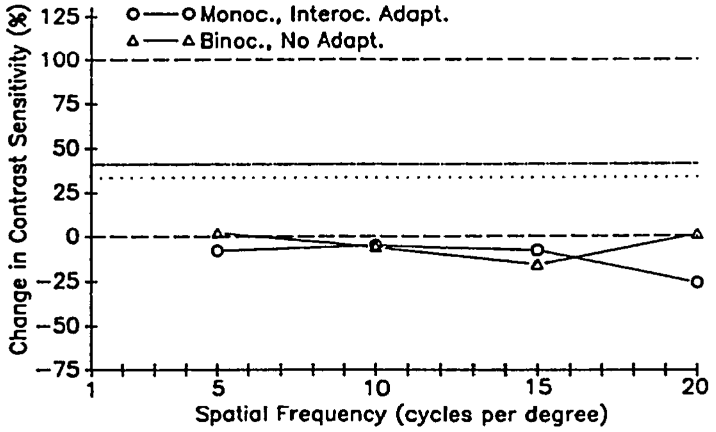
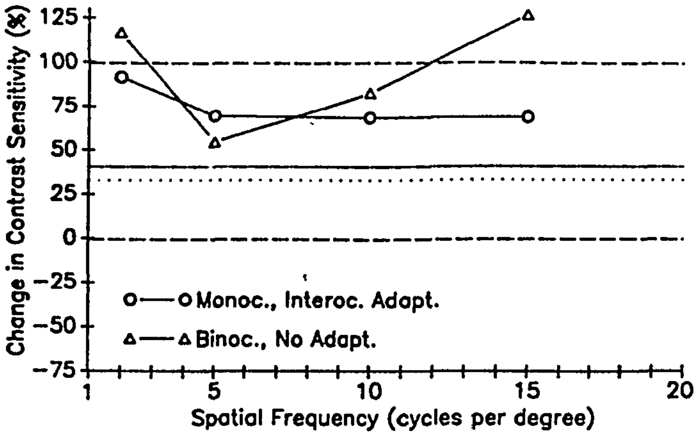
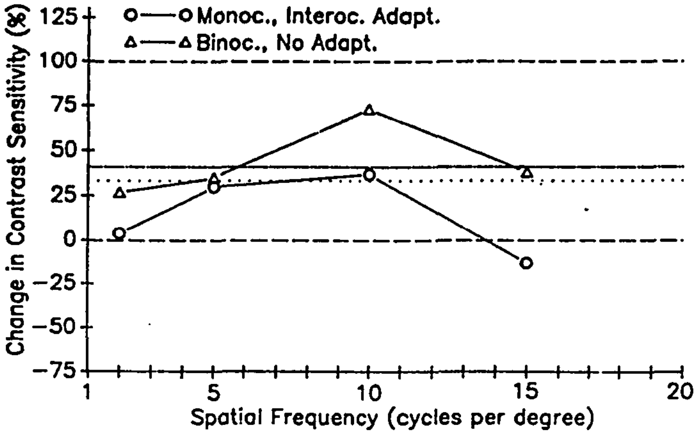

Stimulus Size 0.5°

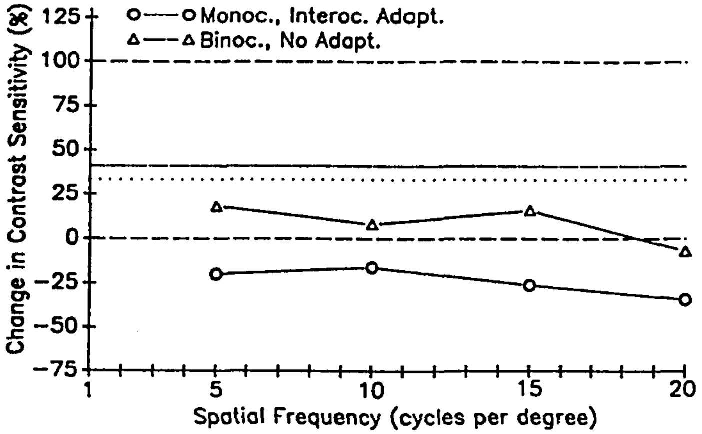
Figure 33. Percent change in contrast sensitivity as a function of spatial frequency is plotted for observer TEF. These data were collected according to a yes/no method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° (upper plot), 1° (middle plot) or 0.5° (lower plot) sine wave grating. The stimulus was presented monocularly, monocularly with and interocular background, and binocularly, to the fovea. The background stimulus was 20.8° x 15° and presented to the right eye, and was 10 cd/m^2 diffuse field. Mean 95% confidence intervals (±2 standard errors) for control data are 14.6% for the 1° size stimulus and 6.75% for the 0.5° size stimulus.



Stimulus Size 3.2x2.4°



Stimulus Size 1°



Stimulus Size 0.5°

interocular adaptation are similarly influenced by manipulation of test grating size. Neither manipulation improves the visibility of 0.5° test gratings. To the extent that these small gratings exclusively influence the fovea, these results suggest that TIS is small or minimal in the fovea and increases in nonfoveal retinal regions. This possibility is more directly tested in sections C and D immediately below.

C. The Effects of Retinal Position Using Large Test Gratings

The effects of different interocular background sizes and shapes (large background, background the same size as the stimulus and an annulus background) and binocular stimulus presentation were compared at different retinal positions. For observers ND and TEF, figures 34 and 35 compare results obtained with a 10 cd/m^2, 3.2° x 2.4° test grating presented in the fovea and 5° parafoveally (respectively, the left and right panels). The 5 functions indicate results obtained with binocular stimulation, monocular stimulation with no background present, and three different shaped adapting fields. Some of these data are replots of functions shown in figures 15, 18, 21, and 22. Since the parafoveal retina is less sensitive to higher spatial frequencies, data were collected there for spatial frequencies ≤ 11 cpd. In other respects, the stimulus was the same at both retinal positions. These data are also represented with percent change in sensitivity plotted as a function of retinal position in figures 36 and 37 (Note the difference in ordinate values for the two different observers). At both retinal positions, both interocular adaptation and binocular

Figure 34. Percent threshold modulation as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m², 3.2° x 2.4° sine wave grating presented to the left fovea (left plot) or 5° in the TVF (right plot). The stimulus was presented monocularly, binocularly, and along with different configurations of the interocular background, which was 10 cd/m² in luminance. Background sizes were 20.8° x 15°, 3.2° x 2.4°, and an annulus with an inside diameter of approximately 3.2° x 2.4°.

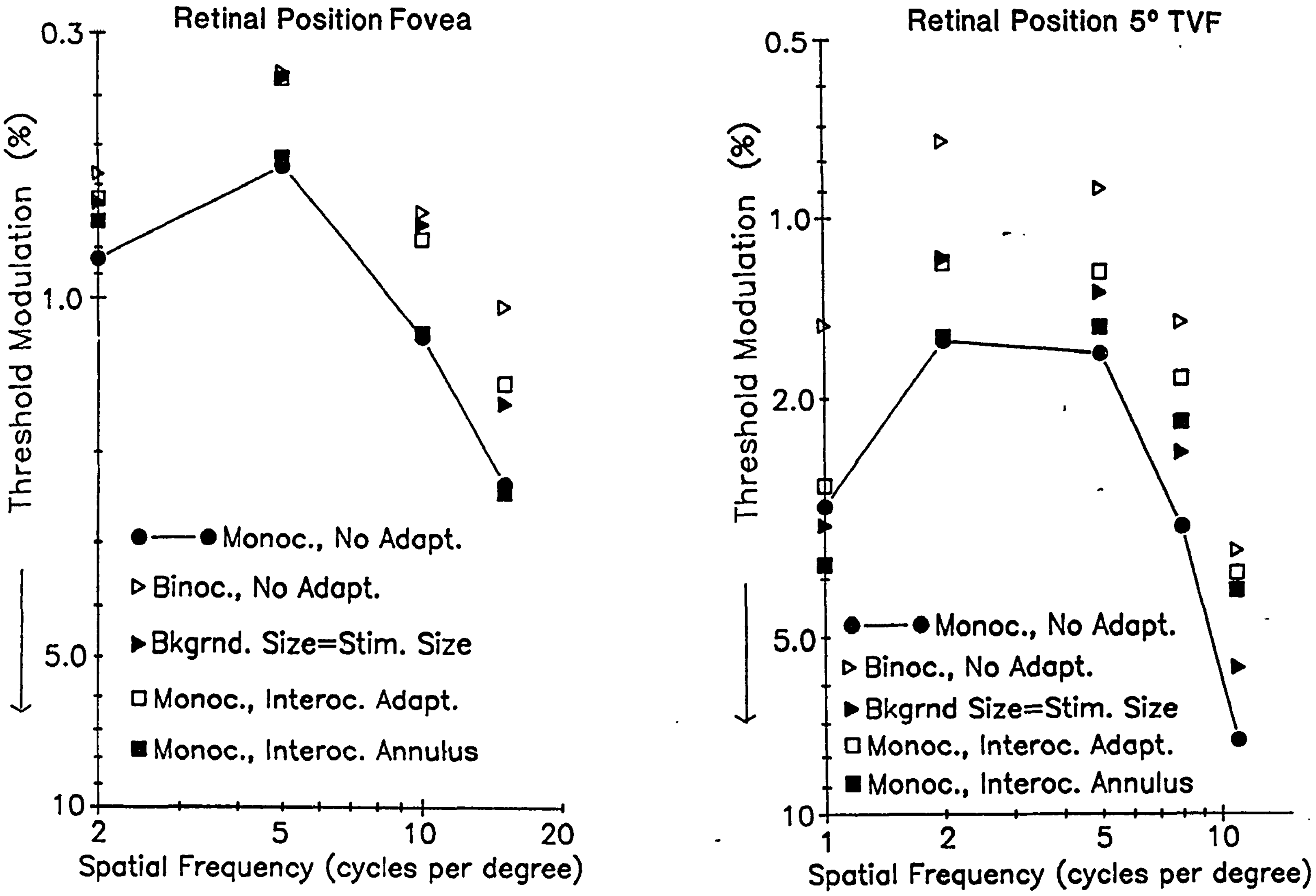
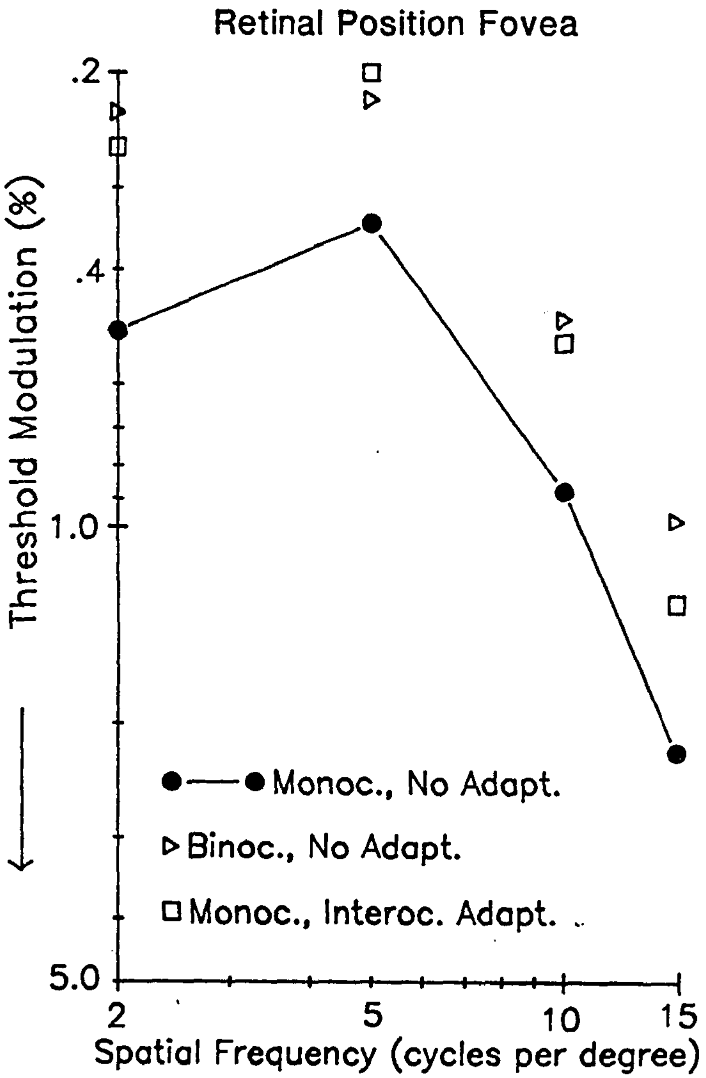

Retinal Position Fovea
Threshold Modulation (%)
0.3
1.0
5.0
10
2
5
10
20
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▷ Binoc., No Adapt.
▶ Bkgrnd. Size=Stim. Size
□ Monoc., Interoc. Adapt.
■ Monoc., Interoc. Annulus
Retinal Position 5° TVF
Threshold Modulation (%)
0.5
1.0
2.0
5.0
10
1
2
5
10
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▷ Binoc., No Adapt.
▶ Bkgrnd Size=Stim. Size
□ Monoc., Interoc. Adapt.
■ Monoc., Interoc. Annulus

Figure 35. Percent threshold modulation as a function of spatial frequency is plotted for observer TEF. These data were collected according to a yes/no method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea (left plot) or 5° in the TVF (right plot). The stimulus was presented monocularly, binocularly, and along with different configurations of the interocular background, which was 10 cd/m^2 in luminance.


Retinal Position Fovea
Threshold Modulation (%)
.2
.4
1.0
5.0
2
5
10
15
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▷ Binoc., No Adapt.
□ Monoc., Interoc. Adapt.

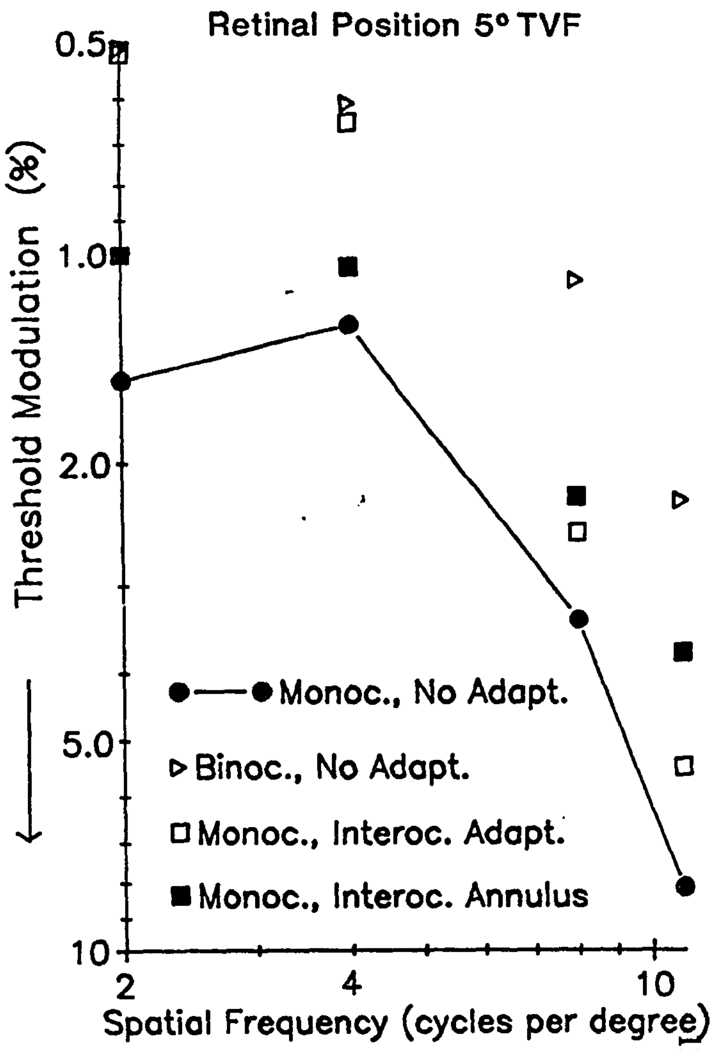
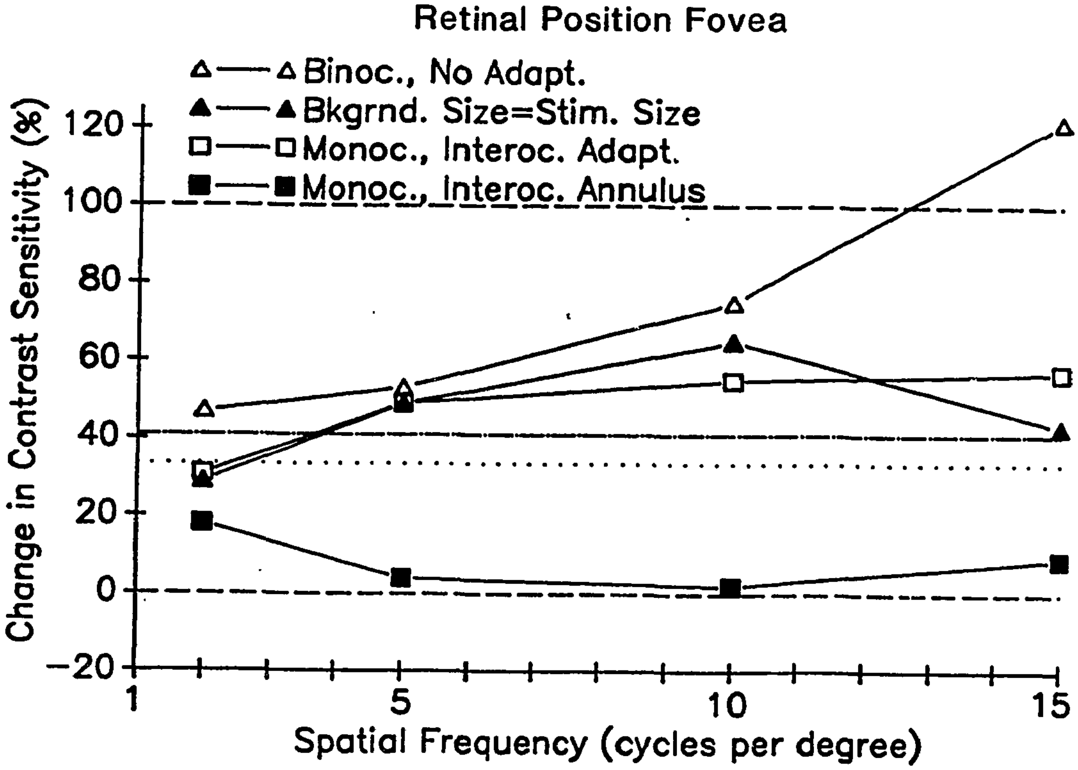

Retinal Position 5° TVF
Threshold Modulation (%)
0.5
1.0
2.0
5.0
10
2
4
10
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▷ Binoc., No Adapt.
□ Monoc., Interoc. Adapt.
■ Monoc., Interoc. Annulus

Figure 36. Percent change in contrast sensitivity as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea (top plot) or 5° in the TVF (bottom plot). The stimulus was presented monocularly, binocularly, and along with different configurations of the interocular background, which was 10 cd/m^2 in luminance. Background sizes were 20.8° x 15°, 3.2° x 2.4°, and an annulus with an inside diameter of approximately 3.2° x 2.4°. The horizontal dashed line represents perfect and zero summation, the horizontal dotted line represents probability summation and the horizontal dashed and dotted line represents $\sqrt{2}$ summation. Mean 95% confidence intervals (±2 standard errors) for control data are 15.7% for the stimulus positioned in the fovea, 9.4% for the stimulus positioned 5° in the TVF. Mean 95% confidence intervals (±2 standard errors) for control data are 8.5% for the stimulus positioned 5° in the TVF.


Retinal Position Fovea
△—△ Binoc., No Adapt.
▲—▲ Bkgrnd. Size=Stim. Size
□—□ Monoc., Interoc. Adapt.
■—■ Monoc., Interoc. Annulus
Change in Contrast Sensitivity (%)
120
100
80
60
40
20
0
−20
1
5
10
15
Spatial Frequency (cycles per degree)

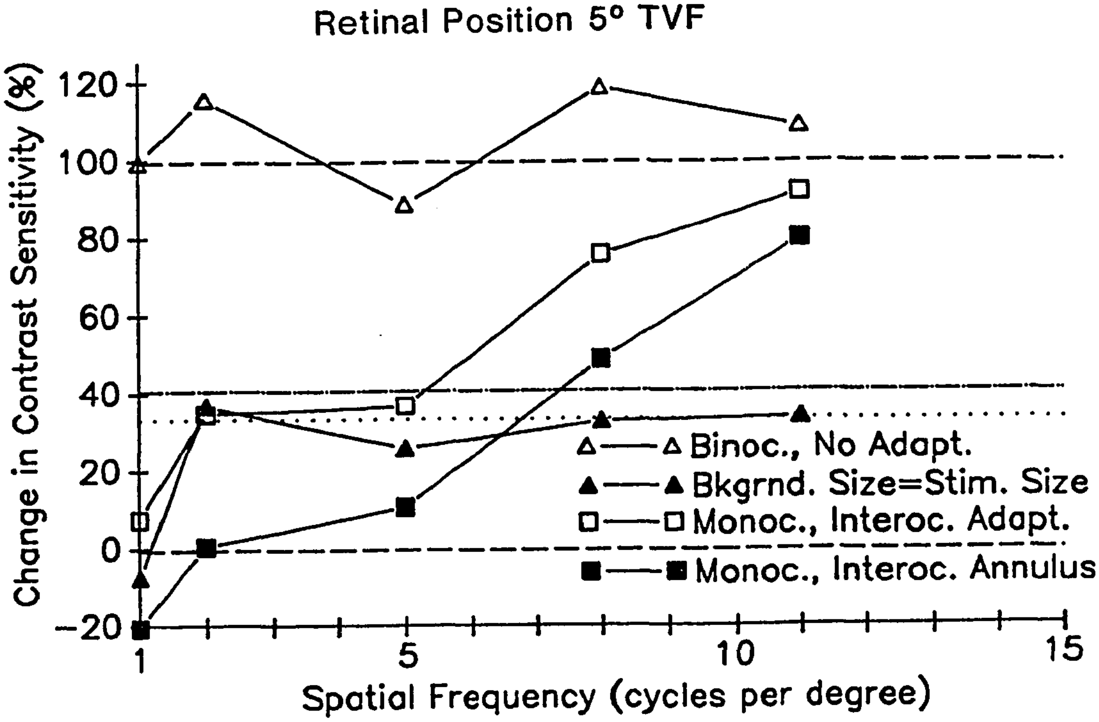
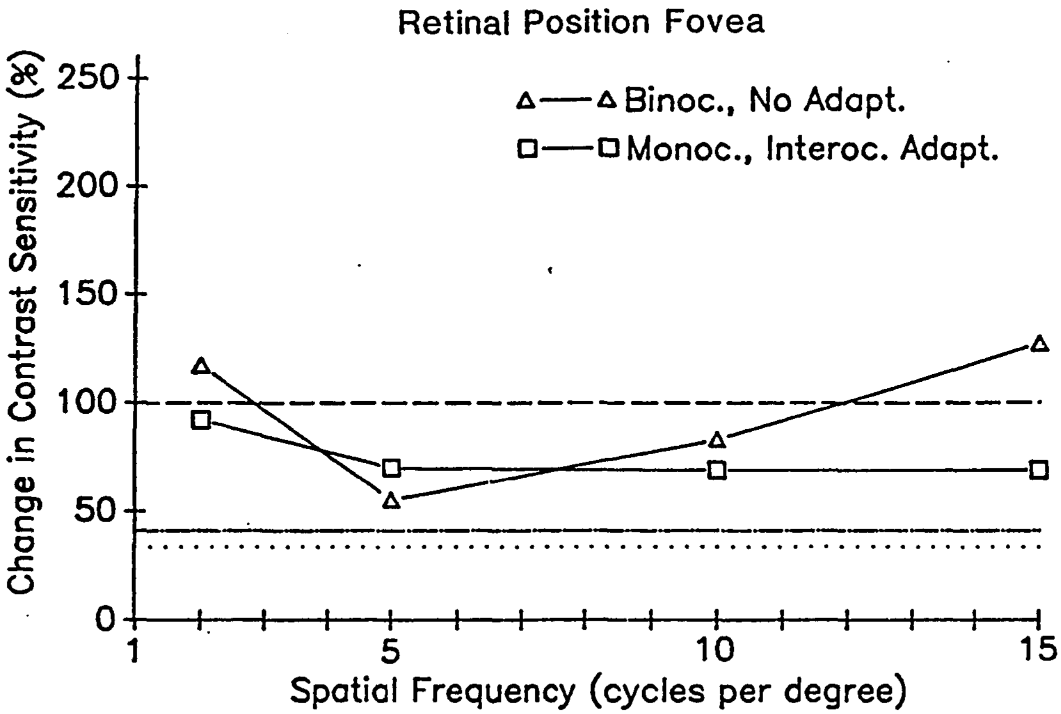
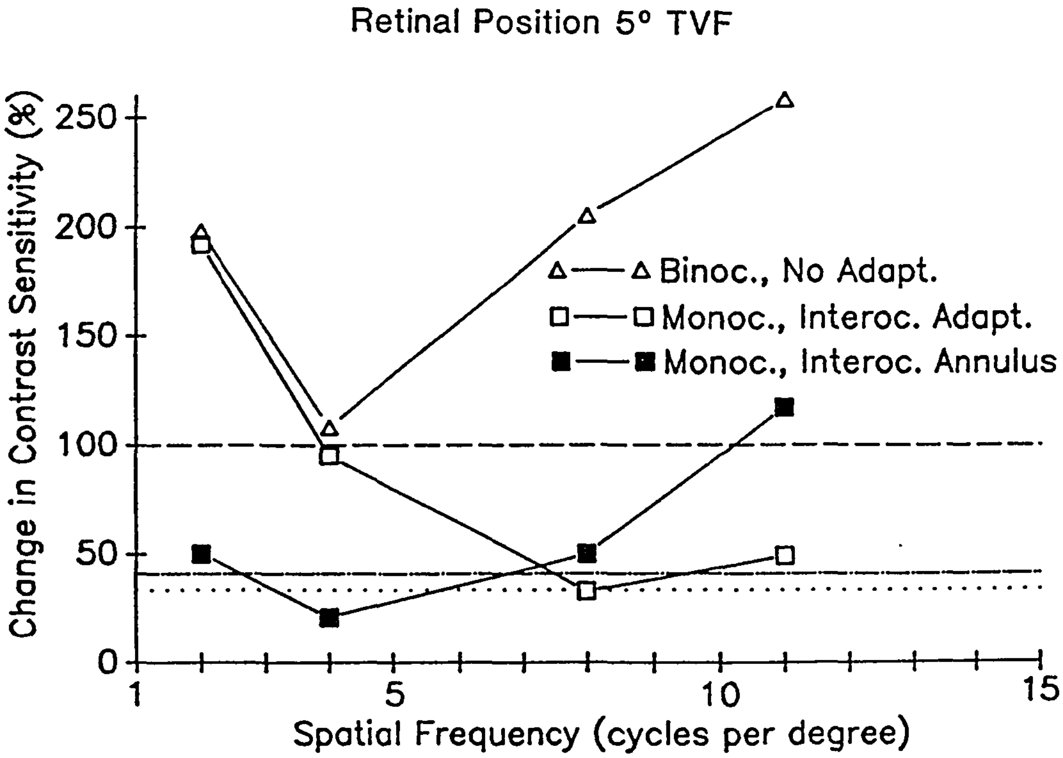

Retinal Position 5° TVF
Change in Contrast Sensitivity (%)
120
100
80
60
40
20
0
−20
△—△ Binoc., No Adapt.
▲—▲ Bkgrnd. Size=Stim. Size
□—□ Monoc., Interoc. Adapt.
■—■ Monoc., Interoc. Annulus
1
5
10
15
Spatial Frequency (cycles per degree)

Figure 37. Percent change in contrast sensitivity as a function of spatial frequency is plotted for observer TEF. These data were collected according to a yes/no method of adjustment procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea (left plot) or 5° in the TVF (right plot). The stimulus was presented monocularly, binocularly, and along with different configurations of the interocular background, which was 10 cd/m^2 in luminance.


Retinal Position Fovea
Binoc., No Adapt.
Monoc., Interoc. Adapt.
Change in Contrast Sensitivity (%)
250
200
150
100
50
0
1
5
10
15
Spatial Frequency (cycles per degree)


Retinal Position 5° TVF
Binoc., No Adapt.
Monoc., Interoc. Adapt.
Monoc., Interoc. Annulus
Change in Contrast Sensitivity (%)
250
200
150
100
50
0
1
5
10
15
Spatial Frequency (cycles per degree)

stimulus presentation results in sensitivity which is superior to that obtained with monocular stimulation. In this limited respect, results obtained parafoveally resemble those obtained with foveal stimulus presentation. However, there are important differences obtained at the two retinal positions. Firstly, as can be seem more clearly in the figures 36 and 37, binocular stimulus presentation in the parafovea often produces an improvement in sensitivity exceeding 100% or that expected from "perfect summation." Secondly, the improvement in sensitivity produced by interocular backgrounds is considerably less than produced by binocular stimulus presentation (up to 100% in observer ND). Thirdly, interocular annuli are considerably more effective in the periphery than in the fovea at high spatial frequencies. In the periphery, such annuli are either almost as effective (for observer ND-up to approximately 75%), or actually more effective (at the highest frequency for observer TEF-greater than 100%) in improving visual sensitivity than large, homogeneous backgrounds. Fourth, for observer ND, interocular adapting fields of the same size as the test grating are clearly less effective than either an annulus or large homogeneous backgrounds in improving grating visibility (up to approximately 35%). Similar results were also obtained at 10° in the peripheral retina for observer ND (data not shown).

D. Results Obtained with 1° Test Gratings in the Parafovea

The effects of stimulus size were further investigated in the parafovea. Figures 38 and 39 show data collected with a 1° square grating at 5° in the TVF for

Figure 38. Percent threshold modulation as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m^2, 1° square sine wave grating presented 5° in the TVF of the left eye. The stimulus was presented monocularly, binocularly, and along with different configurations of the interocular background, which was 10 cd/m^2 in luminance.

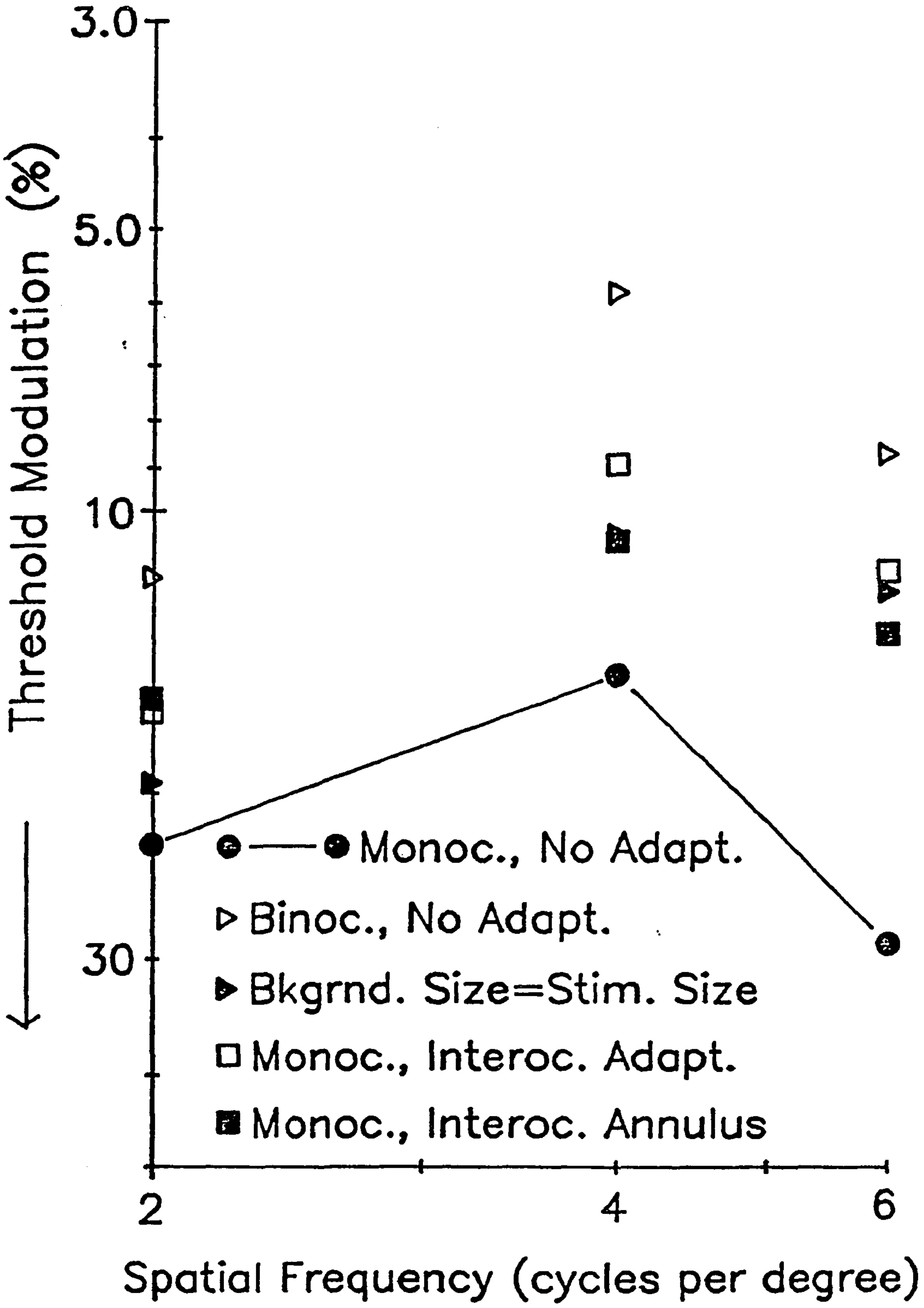
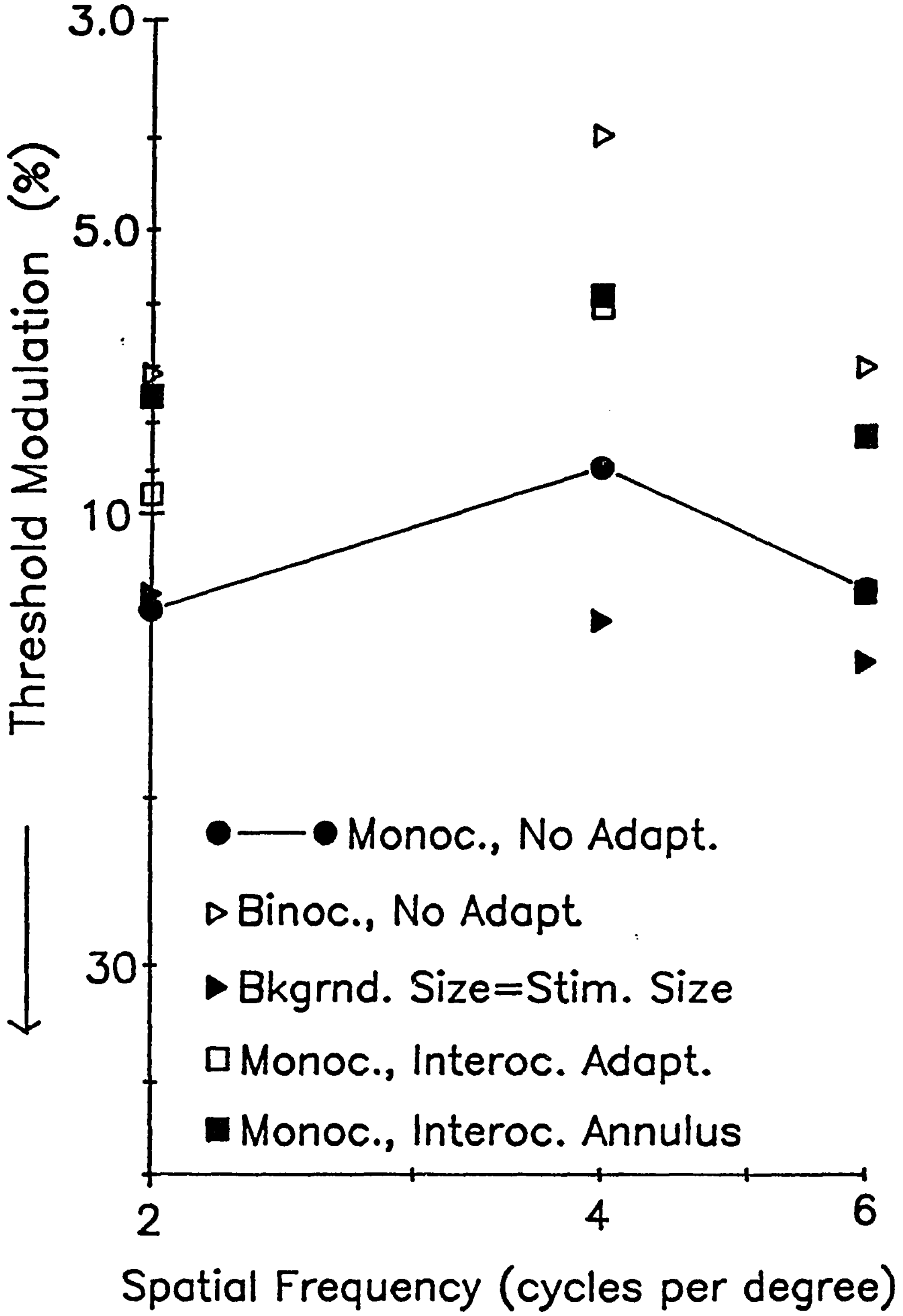

3.0
5.0
10
30
Threshold Modulation (%)
2
4
6
Spatial Frequency (cycles per degree)
Monoc., No Adapt.
Binoc., No Adapt.
Bkgrnd. Size=Stim. Size
Monoc., Interoc. Adapt.
Monoc., Interoc. Annulus

Figure 39. Percent threshold modulation as a function of spatial frequency is plotted for observer TEF. These data were collected according to a yes/no method of adjustment procedure. The stimulus was a 10 cd/m^2, 1° square sine wave grating presented 5° in the TVF of the left eye. The stimulus was presented monocularly, binocularly, and along with different configurations of the interocular background, which was 10 cd/m^2 in luminance.

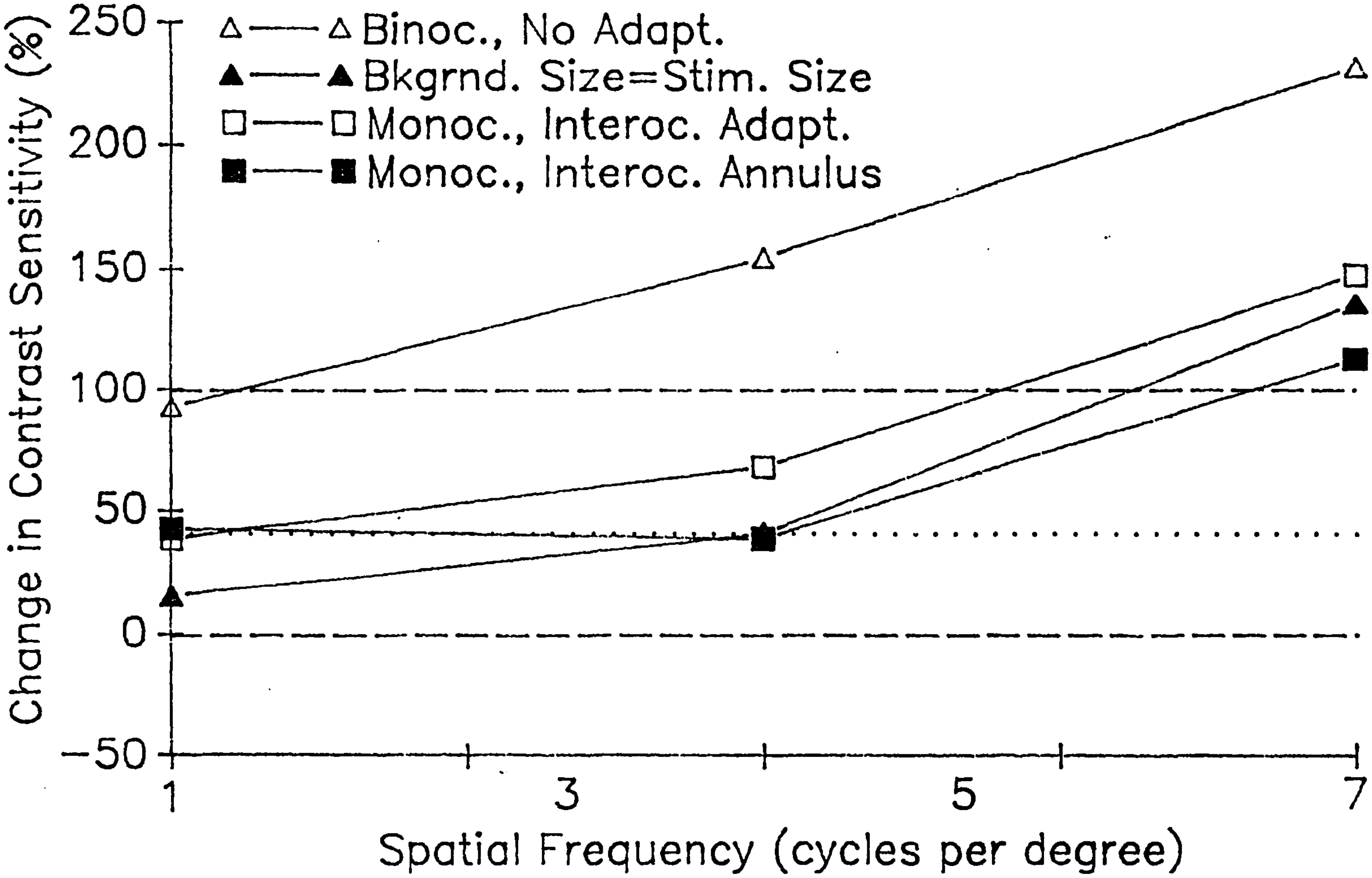

3.0
5.0
10
30
Threshold Modulation (%)
2
4
6
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▷ Binoc., No Adapt.
▶ Bkgrnd. Size=Stim. Size
□ Monoc., Interoc. Adapt.
■ Monoc., Interoc. Annulus

observer ND and TEF respectively. These data are also replotted as change in sensitivity as a function of retinal position in derived figures 40 and 41. In many respects, these data obtained with small sized test gratings are similar to those plotted on the left of figure 32 and 33. That is, binocular stimulus presentation and interocular adaptation increase sensitivity, but binocular stimulation is always considerably more effective. An interocular annulus is also effective in increasing sensitivity. Binocular stimulus presentation results in enhanced grating visibility greater than 100% for observer TEF and for observer ND, exceeds 200%. These results strongly suggest that the improvement in visibility resulting from binocular stimulus presentation is due in part to some factor other than "summation."

E. Subjective Observations

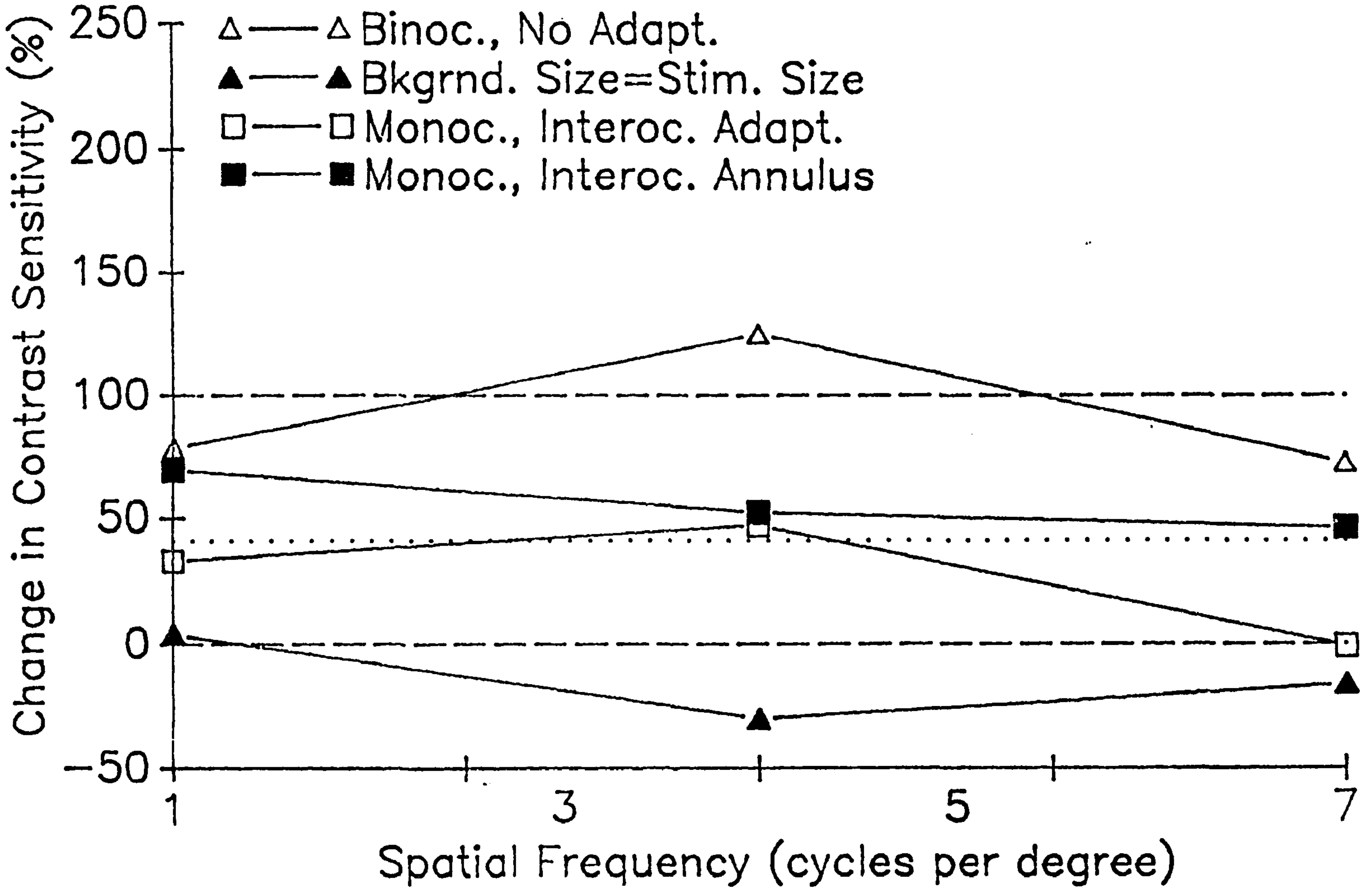
When no interocular background was present, a monocularly presented test grating appeared 2-dimensional and flat to observers ND and TEF. In contrast, binocular stimulus presentation caused the grating to have depth and have a 3-dimensional appearance resembling an old fashioned wash board. A similar, although slightly less striking dimensional appearance resulted from monocular stimulus presentation when coupled with an interocular adapting field.

Figure 40. Percent change in contrast sensitivity as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m^2, 1° square sine wave grating presented 5° in the TVF of the left eye. The stimulus was presented monocularly, binocularly, and along with different configurations of the interocular background, which was 10 cd/m^2 in luminance. The horizontal dashed line represents perfect and zero summation, and the horizontal dotted line represents $\sqrt{2}$ summation. Mean 95% confidence intervals (±2 standard errors) for control data are 1.6%.



△——△ Binoc., No Adapt.
▲——▲ Bkgrnd. Size=Stim. Size
□——□ Monoc., Interoc. Adapt.
■——■ Monoc., Interoc. Annulus
Change in Contrast Sensitivity (%)
250
200
150
100
50
0
−50
1
3
5
7
Spatial Frequency (cycles per degree)

Figure 41. Percent change in contrast sensitivity as a function of spatial frequency is plotted for observer TEF. These data were collected according to a yes/no method of adjustment procedure. The stimulus was a 10 cd/m², 1° square sine wave grating presented 5° in the TVF of the left eye. The stimulus was presented monocularly, binocularly, and along with different configurations of the interocular background, which was 10 cd/m² in luminance. The horizontal dashed line represents perfect and zero summation, and the horizontal dotted line represents √2 summation. Mean 95% confidence intervals (±2 standard errors) for control data are 2.6%.



△——△ Binoc., No Adapt.
▲——▲ Bkgrnd. Size=Stim. Size
□——□ Monoc., Interoc. Adapt.
■——■ Monoc., Interoc. Annulus
Change in Contrast Sensitivity (%)
250
200
150
100
50
0
−50
1
3
5
7
Spatial Frequency (cycles per degree)

Discussion

The results presented above show that binocular stimulus presentation and interocular adaptation produce somewhat similar influences upon grating visibility. In particular, neither improves the visibility of centrally presented 0.5° test gratings which are likely to exclusively stimulate the foveal retina. In this respect, these results compare favorably with those of detection threshold and brightness studies summarized in tables 1 and 2 indicating an absence of "binocular summation" in the fovea. Along similar lines, the improvement in grating visibility resulting from either presentation of large interocular adapting fields or from binocular stimulation increases as test grating size increases or if retinal position is shifted out of the fovea. However, presentation of large interocular backgrounds is not as effective as binocular stimulus presentation in improving grating visibility in the parafovea. Along these lines, it is of interest that the influence of the shape and size of an interocular background is also different in the periphery than in the fovea. Collectively this suggests that there may be two (or possibly more) interocular mechanisms effecting sensitivity. Recently Auerbach, Dörrenhaus and Cavonious (1991) showed that the effects of interocular backgrounds upon detection threshold depend heavily upon retinal position. They show a visual masking type effect for a .5° sized stimulus presented to the fovea (which is consistent with the present results), no influence at approximately 5° parafoveally, and results comparable to the Lansford-Baker effect further in the periphery for a 1° sized stimulus. Their results and those of the present study suggest that interocular adaptation involves both a TIS and masking mechanism. As the extent of parafoveal displacement increases, the TIS mechanism becomes potent while the masking mechanism decreases in potency.

Regardless of the correctness of this type of conjecture, the present results severely question most prior claims that the improvement in visual sensitivity resulting from binocular stimulus presentation is attributable to "binocular summation." In particular, results obtained with small stimuli in the parafovea (figures 38-41) show that binocular stimulus presentation often produces enhancement in sensitivity much greater than 100%. In this respect these results are comparable to similar claims for "binocular facilitation" resulting from evoked potential studies (Apkarian, Nakayama & Tyler, 1981).

The present results do not positively disprove the possible existence of binocular summation for grating visibility. It is also unclear how these results relate to claims for binocular summation resulting from studies of brightness, detection threshold, latency, and flicker as summarized in the introduction to this chapter. However, the present results clearly place TIS ahead of summation as a candidate mechanism which accounts for the superiority of binocular grating visibility.

Chapter 5

The Photoreceptors Involved in TIS

The results presented in chapters 2 and 3 above establish that a dark adapted eye exerts a tonic interocular suppression (TIS) upon spatial sensitivity in the contralateral eye. The experiments presented in this chapter were designed to determine the types of photoreceptor pathways involved in both the test and adapting eye which mediate TIS effects.

Some of the data presented in chapter 2 provide clues regarding which receptor pathways are involved in this interocular effect. Specifically, previous studies of grating visibility established that the upper limit of rod-spatial sensitivity is between 3 and 5 cpd (Nordby & Sharpe, 1988). Therefore, the TIS influences for spatial frequencies >5 cpd must indicate an influence upon cone-mediated sensitivity. However, both rods and cones are sensitive to spatial frequencies somewhere less than 3.5 cpd at the grating luminance value used, 0.1 - 10 cd/m^2 (Kelly, 1978; Naarendorp, Denny & Frumkes, 1988; Nordby & Sharpe 1988). Therefore, TIS may additionally influence rod-mediated spatial sensitivity. The experimental data described in the first part of the results section of this chapter were collected using gratings presented to the peripheral retina at luminance levels too dim to be detected by cones to examine the possibility that interocular adaptation influences rod-mediated vision.

In a similar fashion, the adapted state of either rods and/or cones could influence spatial sensitivity contralaterally. Since the absolute threshold for cones is about 0.1 cd/m^2 and since dimmer interocular backgrounds improve sensitivity to spatial frequencies of 2-5 cpd, the adapted state of rods must be involved with TIS. On the other hand, both rods and cones respond over the range of background luminance (1.0-100 cd/m^2) which influences contralateral sensitivity to spatial frequencies between 10-20 cpd. Therefore, it is possible that cone adaptation can additionally contribute to TIS effects. The experimental data summarized in the second part of the results section were collected in an attempt to relate TIS effects upon spatial sensitivity to the dark-adapted state of rod and/or cone photoreceptors.

In addition to the results presented in chapters 2 to 4 above, there have been a number of prior studies which have suggested that interocular adaptation effects involve rod-cone interaction. These are described below.

A. Rod-Cone Interaction and Interocular Adaptation Effects

As implied by the term "duplicity theory," it is well established that rods and cones produce separate influences upon the subsequent visual system. Just as it possible to conceive of several different mechanisms for binocular interaction (as presented in chapter 1 and the introduction to chapter 4), it is possible to conceptualize several different classes of mechanisms for interaction between rod- and cone-related signals.

1. Summation

Using single unit physiological procedures, a summation of rod and cone signals has been observed at every major level of neural organization in the mammalian visual system including observations within the photoreceptors themselves (Nelson, 1977); second order retinal neurons (Nelson, 1977; Steinberg, 1969); third order retinal neurons including the ganglion cells (Gouras & Link, 1966; Rodieck & Rushton, 1976); the lateral geniculate body (Purpura, Kaplan & Shapley, 1988); and visual cortex (Livingston & Hubel, 1987). Psychophysical studies have established that rod- and cone-related signals can summate to determine detection threshold (Frumkes, Sekuler, Barris, Reiss & Chalupa, 1973), flicker sensitivity (Denny, Frumkes & Goldberg, 1990; MacLeod, 1972), and brightness (MacLeod, 1974). It is unknown whether the summation of rod and cone signals as demonstrated through physiological techniques (in second and higher order visual neurons) or the summation shown through psychophysical procedures, merely 1) reflects the mixing of rod-cone signals known to occur within the photoreceptors, and/or 2) reflects some post-receptor neuronal processing. The latter possibility is also quite likely based upon anatomical evidence (for a review see Daw, Jensen & Breinhun, 1990).

2. Tonic Suppression

Dark adapted rods of the vertebrate retina exert a tonic inhibitory influence upon cone pathways in the distal retina (for a review, see Frumkes, 1991; Frumkes & Eysteinsson, 1988; Frumkes & Wu, 1990; Pflug, Nelson & Ahnelt, 1990). This phenomenon is referred to as suppressive rod-cone interaction, or SRCI. Selective light adaptation of rods enhances cone-mediated responses to rapid flicker by removing this inhibition (Alexander & Fishman, 1984; Coletta & Adams, 1984; Goldberg, Frumkes & Nygaard, 1983) and also enhances sensitivity to high spatial frequency gratings (Naarendorp, Denny & Frumkes, 1988; Naarendorp & Frumkes, 1991). Both ERG (Arden & Frumkes, 1986) recordings in human, and intracellular recordings in amphibians (Frumkes & Eysteinsson, 1988) and cat (Pflug, Nelson & Ahnelt, 1990) show that SRCI is at least in part a distal retinal phenomenon. It reflects rod modulation of horizontal cell influence upon cones and possibly bipolar cells as well. However, for a psychophysical observer, SRCI could additionally reflect the functioning of proximal retinal circuitry (Witkovsky, Stone, & Trencina, 1989) and perhaps even cerebral mechanisms. As described in the last part of the results section below, comparisons of the influence of monocular (SRCI) and interocular (TIS) backgrounds upon grating visibility were made.

3. Active Suppression

It is also conceivable that photic stimulation of rods directly suppresses the visibility of stimuli which are detected by cones. Gouras and Link (1966) first demonstrated this physiologically while recording from retinal ganglion cells in rhesus monkey. A number of investigators have suggested that rod-cone interaction studies using either "masking" or "increment threshold" stimulus paradigms involve such suppression (i.e., Foster, 1976; Barris & Frumkes, 1978), which is different from the tonic suppressive influences seen in the SRCI effects discussed above. However, almost all of these studies show that an adapting stimulus which influences both rods and cones is more effective than one which principally stimulates cones in altering cone-detection threshold. This masking could either involve a summation of rod and cone masking effects, or a more direct suppressive influence of rod-stimulation upon cone detection threshold. Indeed, the most theoretically rigorous study of rod-cone interaction using increment thresholds suggests a summation explanation (Bauer, Frumkes & Nygaard, 1983).

4. Cerebral versus Retinal Mechanisms for Rod-Cone Interaction

Regardless of which of the foregoing classes of mechanisms are involved in a particular psychophysical demonstration of rod-cone interaction, the site of interaction could either be within the retina or within the cerebrum. In general, most psychophysical researchers who consider the neural substrate for rod-cone interaction favor a retinal locus, primarily because a wealth of anatomical data indicate the likelihood of retinal rod-cone interaction (e.g. Frumkes & Denny, 1989, but for a different viewpoint, see Latch & Lennie, 1977).

Three different classes of psychophysical studies have demonstrated interocular rod-cone interactions. Since in higher mammals there is no evidence for centrifugal input from the brain to the retina, these interocular studies strongly suggest the existence of cerebral rod-cone interaction mechanisms. First, rod-cone interaction was demonstrated using a metacontrast stimulation paradigm (Barris & Frumkes, 1978; Foster, 1977). Foster and Mason (1977) obtained such interaction with interocular as well as monocular stimulation, suggesting a cerebral locus for rod-cone interaction.

Secondly, Lie (1963) showed that during the rod-limb of dark adaptation, specific (correct color identification) threshold gradually increases. Although Lie demonstrated this effect using monocular stimulation, Prestrude, Watkins and Watkins (1978) demonstrated the Lie effect through dichoptic presentation under stimulus conditions similar to those of Lansford and Baker (1969). Thus, the "Lie effect" seems to involve an interocular influence which in certain respects is similar to the present TIS influence upon grating visibility.

Thirdly, Paris and Prestrude (1975) provide evidence that the effect shown by Lansford and Baker (1969) involves rod-cone interaction. They reasoned that it should be possible to determine rod and cone contributions to the interocular light adaptation effect by preadapting the contralateral eye with longer wavelengths to more selectively preadapt cones and with shorter wavelengths to more selectively preadapt rods. Their results show that with contralateral preadapting lights of different wavelengths the interocular adaptation effect occurs in the rod and cone segments of the dark adaptation curve, but the effect is 2 to 3 times greater in the rod segment. However, with their procedure they could not exclusively measure either the rod or cone system. They also stress that this effect can only occur when stimuli are presented at retinal positions where both rods and cone are plentiful (the near parafoveal retina). Finally, Reeves, Peachey and Auerbach (1986) show that their interocular sensitization effect is seen only when long wavelength cones are strongly adapted relative to other cones while contralaterally a rod detected stimulus serves as the test stimulus. The experiments described in the second part of the results section adopt a procedure similar to that used by Prestrude, Watkins and Watkins (1978) in an attempt to determine the photoreceptors involved in the present effect.

Methods

A. Observers

Observers were two participants from the previous studies, ND and TEF.

B. Apparatus

The apparatus used was the same as described in chapter 2.

C. Procedure

1. Psychophysical Methodology used for Data Collection During Dark Adaptation

A modification of the Vision Metrics PGCONSEN program was used in dark adaptation experiments. 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 msec with a minimum interstimulus interval of 1000 msec. Contrast was always increased or decreased by 1 dB. When the observer thought the 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.

2. 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, adjusting the position of the bite bar and positioning the two artificial pupils so that the stimuli could be appropriately viewed passing through the beamsplitters. After alignment, the room lights were extinguished and both eyes of the observer were dark adapted for 20 minutes. Then the observer's "adapting 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 cd/m^2 and was determined by matching the brightness of this source to the brightness of another known source. Some thresholds in both the "adapting" eye and the "test" eye were then obtained using the Maxwellian view stimulator described by Frumkes and Sturr

(1968). Stimuli were 1° circular discs which were either red (655 nm) or green (512 nm), presented in the fovea or 5° in the temporal visual field (TVF) for a period of 500 msec. Observers 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 "test eye". For observer ND, data presented in figures 40, and 42 below represent the median of three experimental runs; for observer TEF, data presented in figures 41 and 43 below represent the median of 2 experimental runs.

Results and Discussion

A. Is Rod and/or Cone Spatial Sensitivity Influenced by Contralateral Adaptation?

In general, the spatial resolving power for rods is limited to frequencies under 4 cpd (Long, 1978), although under some circumstances where cones cannot mediate sensitivity, rod sensitivity may extend up to 5-6 cpd (Nordby, 1990). The results summarized in chapter 2 (e.g., figures 3, 4, and 5) show that interocular adaptation clearly influences higher spatial frequencies. Therefore, TIS must influence cone-mediated spatial sensitivity.

Both rods and cones respond to spatial frequencies <3cpd. Figures 42 and 43 show for observers ND and TEF respectively, CSFs obtained for rod vision using parafoveally (5° TVF) presented gratings too dim (0.01 cd/m^2) to be detected by cones with spatial frequencies between 1 and 4 cpd, and 3.2° x 2.4° in size. This range of spatial frequencies was limited by the size of the display monitor (precluding study of still lower spatial frequencies) and the lack of sensitivity of rods to higher spatial frequencies. For both observers, these data show that presentation of an interocular background of 0.01 cd/m^2 increases rod mediated spatial vision to all examined spatial frequencies by about 50%. The influence of binocular stimulus presentation upon grating visibility was also examined. For both observers, binocular stimulus presentation had a reliably greater influence upon grating sensitivity than interocular adaptation (between approximately 45 to 100% for observer ND and 100 to 130% for TEF).

To summarize, the foregoing results establish that TIS influences rod-mediated sensitivity to spatial frequencies <4cpd and cone-mediated sensitivity to spatial frequencies >5cpd. The possibility of a TIS influence upon cone-mediated sensitivity to lower spatial frequencies was not examined.

Figure 42. Percent threshold modulation as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure. The stimulus consisted of low spatial frequencies of 1-4 cpd, was a .01 cd/m^2, 3.2° x 2.4°, and presented 5° in the TVF of the left eye. The stimulus was presented monocularly, binocularly, and along with an interocular background 20.8° x 15° in size and .01 cd/m^2 in luminance.

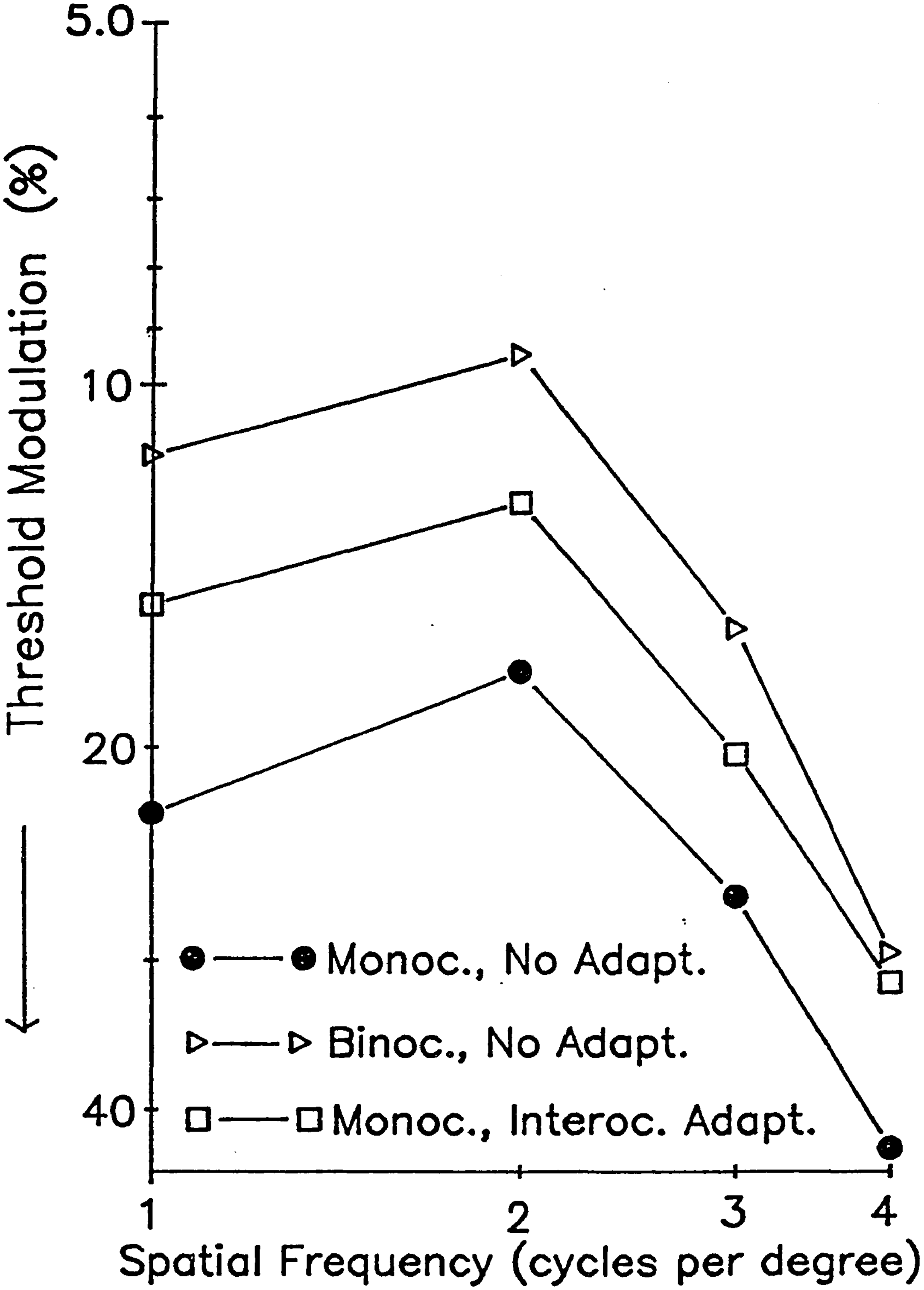
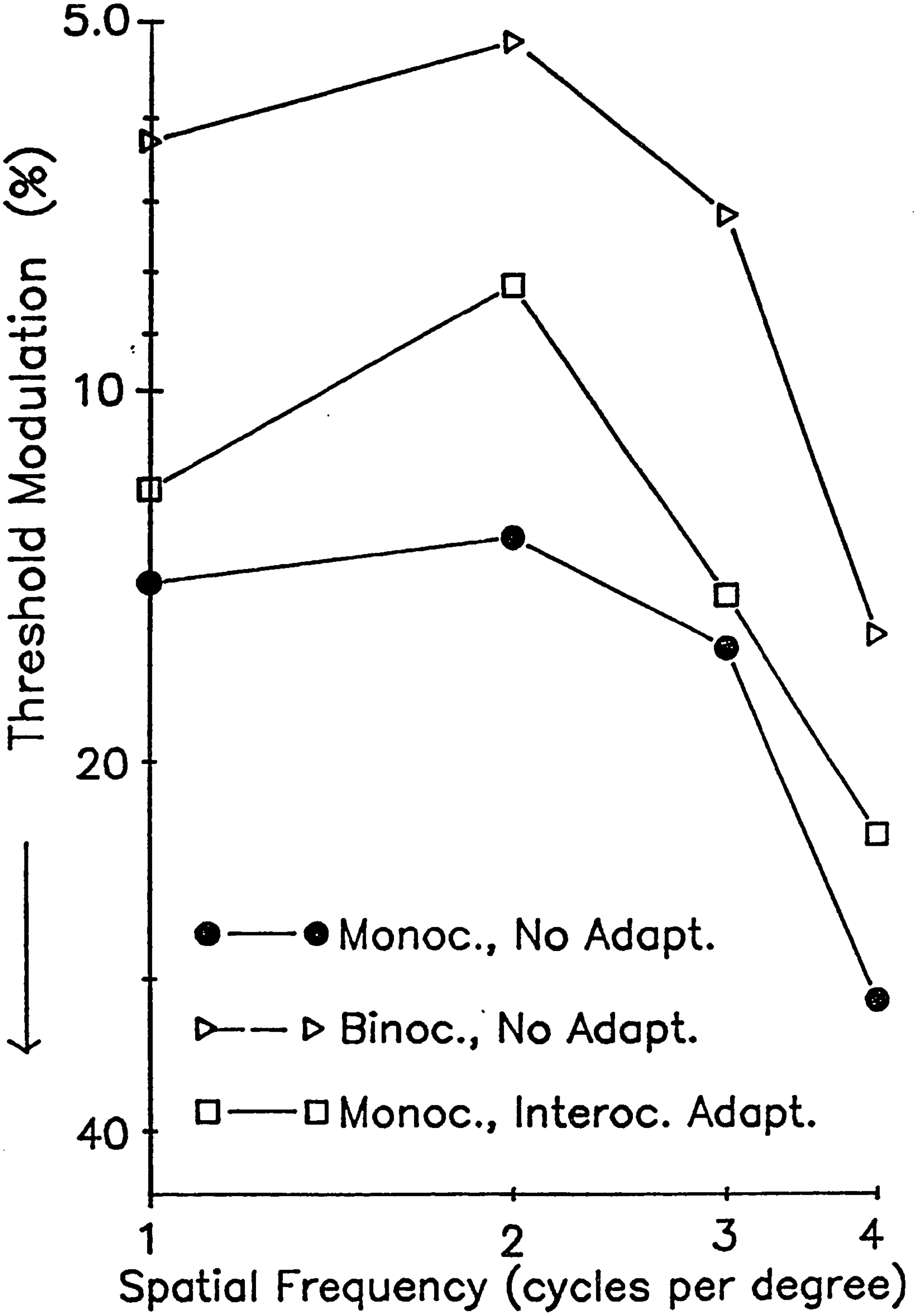

5.0
10
20
40
Threshold Modulation (%)
1
2
3
4
Spatial Frequency (cycles per degree)
●—● Monoc., No Adapt.
▷—▷ Binoc., No Adapt.
□—□ Monoc., Interoc. Adapt.

Figure 43. Percent threshold modulation as a function of spatial frequency is plotted for observer TEF. These data were collected according to a yes/no method of adjustment procedure. The stimulus consisted of low spatial frequencies of 1-4 cpd, was a .01 cd/m^2, 3.2° x 2.4°, and presented 5° in the TVF of the left eye. The stimulus was presented monocularly, binocularly, and along with an interocular background 20.8° x 15° in size and .01 cd/m^2 in luminance.


5.0
10
20
40
Threshold Modulation (%)
1
2
3
4
Spatial Frequency (cycles per degree)
● Monoc., No Adapt.
▷ Binoc., No Adapt.
□ Monoc., Interoc. Adapt.

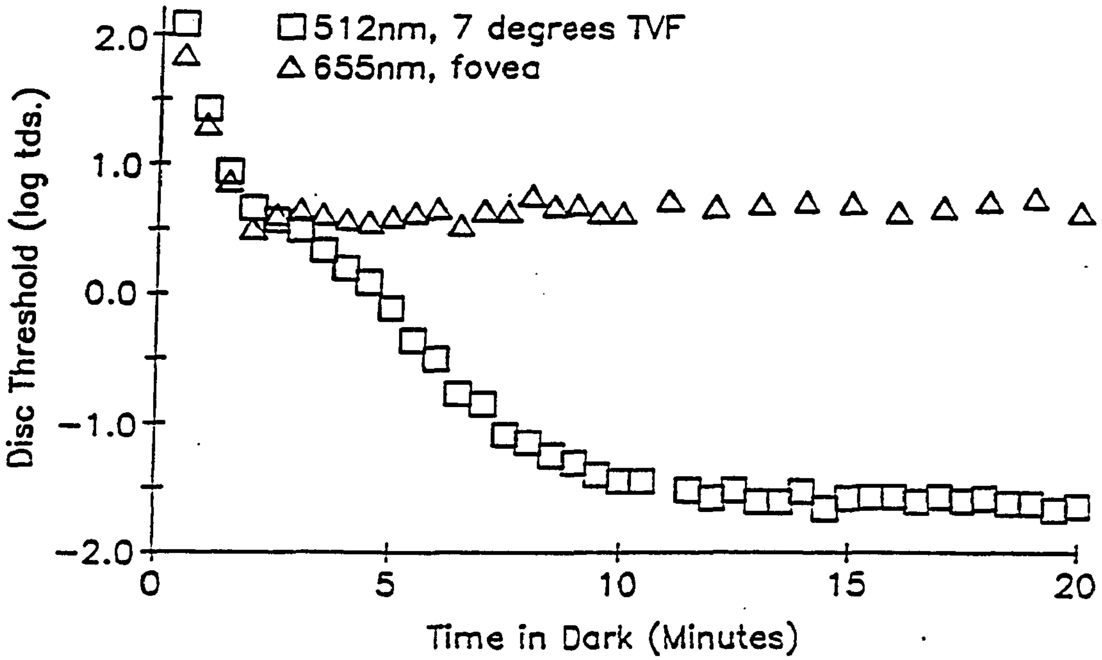
B. Is Rod and/or Cone Adaptation Involved with TIS Effects?

1. Low Spatial Frequencies

The results presented in chapter 3 show TIS influences upon 2 or 5 cpd gratings using background luminance levels as dim as 0.0001 cd/m^2 (for observer TEF, figure 11). Specific aspects of these data suggest that it is the adapted state of rods alone which determines contralateral sensitivity to spatial frequencies <5 cpd. For these low spatial frequencies, the TIS influence is maximal with the dimmest rod-stimulating backgrounds employed, and does not increase with further increases in background luminance (e.g., see figure 3). For example, as seen in figure 6, presentation of a background of 0.001 cd/m^2, which stimulates rods alone, clearly influences spatial sensitivity to 2 cpd. This luminance level is considerably less than that reflected off a "white" surface illuminated by a full moon on a clear night (Leibowitz, 1987) and is considerably dimmer than the most liberal estimate of cone absolute threshold (Wysecki & Stiles, 1967). Further increase in the background luminance to 100 cd/m^2 produces no further improvement in sensitivity. This latter luminance is about 3 $\log_{10}$ units above cone threshold, and is greater than reflected off a white paper in a modern college classroom.

In order to establish more clearly the photoreceptor type whose adaptational state is responsible for TIS, several dark adaptation experiments were performed. In all of these, the right ("adapting") eye was first exposed to a bleaching source of white light of approximately 800 cd/m^2 for 60 sec. Then this bleaching source was extinguished and the observer tracked changes in sensitivity to one of several different stimuli for a 20 minute period of dark adaptation. The top portion of figures 44 and 45 (for observers ND and TEF, respectively) shows changes in detection threshold in the right ("adapting") eye, i.e., a conventional dark adaptation curve for observer ND. Thresholds for either a foveally presented red 655 nm stimulus (triangles) or a parafoveally presented 512 nm stimulus (squares) are plotted as a function of time in the dark. These stimuli were chosen to track the state of either cones (triangles) or rods and cones (squares) throughout the time period of dark adaptation. With the relatively feeble bleaching source used, cone recovery occurs quite quickly, and foveal cone threshold remains quite stable after 3 minutes in the dark for observer ND and 5 minutes for observer TEF; the parafoveal data show a clear rod-cone break at about 3 minutes in the dark. Rod sensitivity remains quite stable after about 13 minutes in the dark for ND (and 16 minutes for TEF). Additional control data (not shown) indicated that this adapting stimulus had no influence upon either rod or cone detection threshold in the contralateral ("test" or left) eye as this eye remained at absolute threshold levels. The lower set of data in figures 44 and 45 (for observers ND and TEF, respectively) plot log percent modulation thresholds for a 2 cpd grating of 10 cd/m^2 luminance presented to the left ("test") eye as a function of time in the dark. The time scale for these data is identical to that used to plot the detection threshold

Figure 44. Disc threshold as a function of time in the dark is plotted for a 1° stimulus of 512 nm presented 7° in the TVF or for a 655 nm stimulus presented in the fovea for observer ND in the upper plot. The lower plot shows log percent threshold modulation as a function of time in the dark when a 2 cpd, 3.2° x 2.4°, 10 cd/m^2 stimulus is presented to the left fovea after an adapting field of approximately 800 cd/m^2 presented for 60 sec to the left eye was extinguished. The curve is fitted with a 4th order regression line.


□ 512nm, 7 degrees TVF
△ 655nm, fovea
Disc Threshold (log tds.)
2.0
1.0
0.0
−1.0
−2.0
0
5
10
15
20
Time in Dark (Minutes)

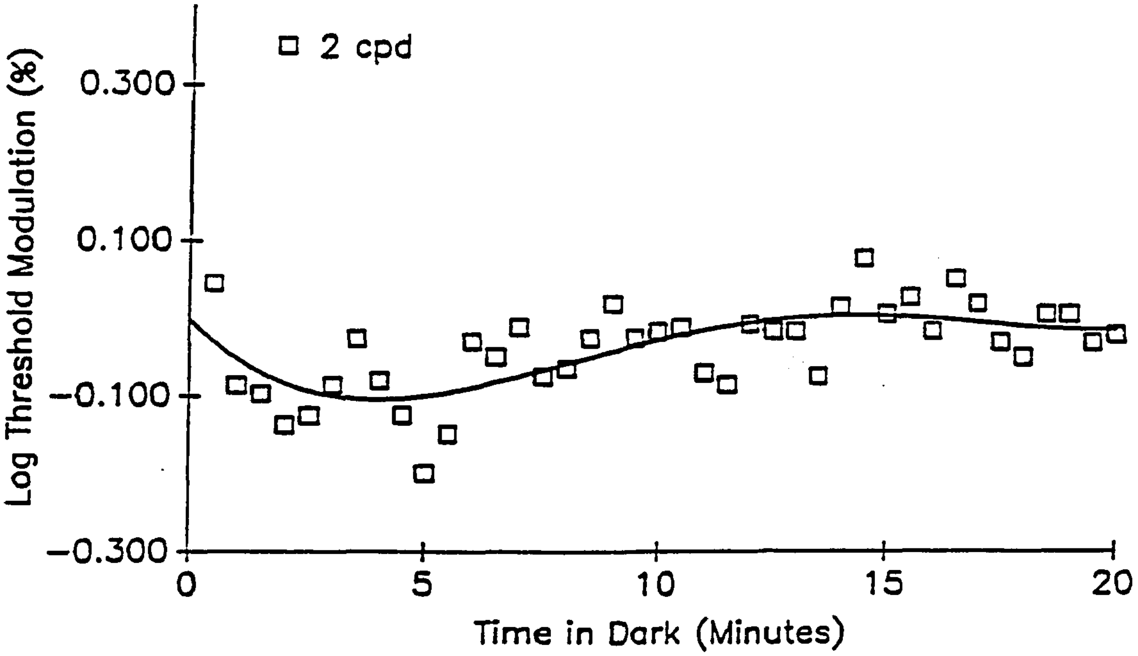
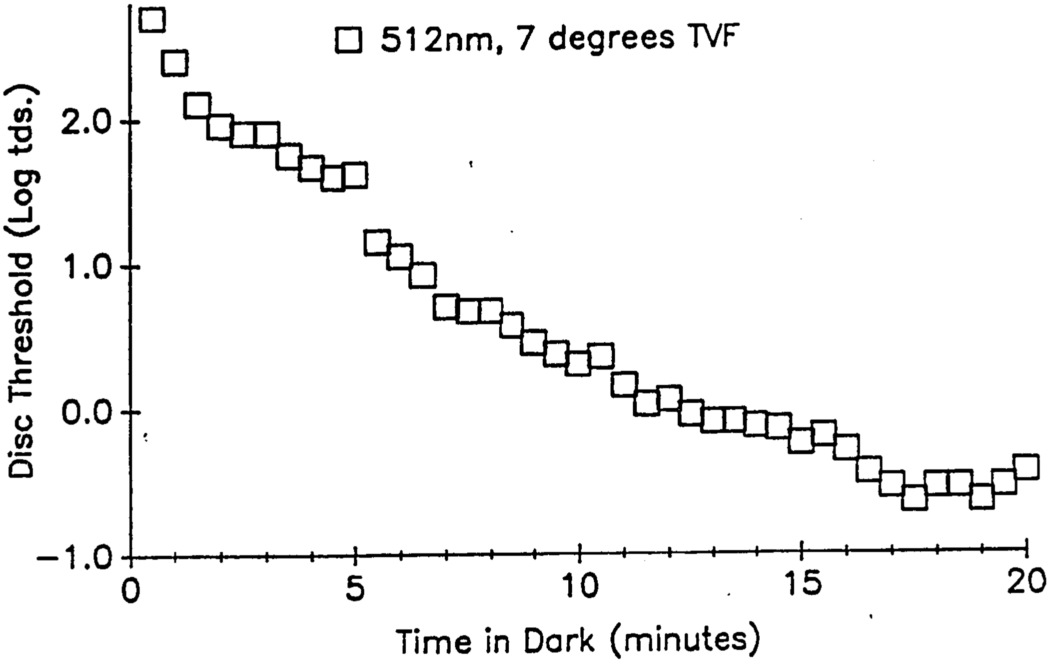
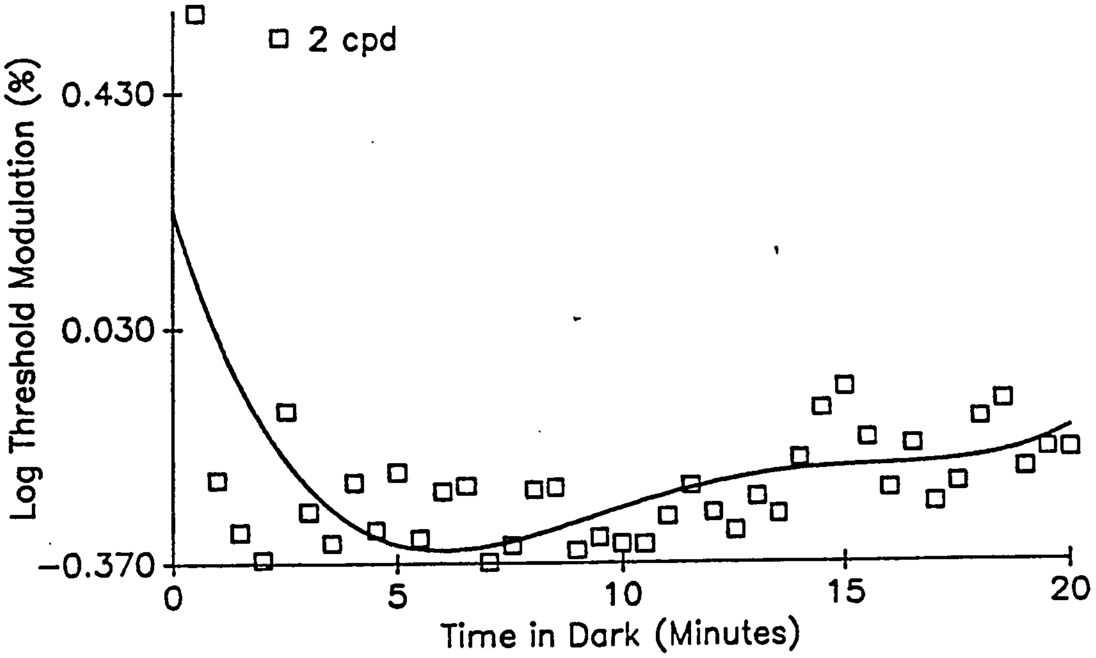

□ 2 cpd
Log Threshold Modulation (%)
0.300
0.100
−0.100
−0.300
0
5
10
15
20
Time in Dark (Minutes)

Figure 45. Disc threshold as a function of time in the dark is plotted for a 1° stimulus of 512 nm presented 7° in the TVF for observer TEF in the upper plot. The lower plot shows percent log threshold modulation as a function of time in the dark when a 2 cpd, 3.2° x 2.4°, 10 cd/m^2 stimulus is presented to the left fovea after an adapting field of approximately 800 cd/m^2 presented for 60 sec to the left eye was extinguished. The curve is fitted with a 4th order regression line.


□ 512nm, 7 degrees TVF
Disc Threshold (Log tds.)
2.0
1.0
0.0
−1.0
0
5
10
15
20
Time in Dark (minutes)


□ 2 cpd
Log Threshold Modulation (%)
0.430
0.030
−0.370
0
5
10
15
20
Time in Dark (Minutes)

data. Throughout the first 3 minutes of adaptation, sensitivity to the 2 cpd grating either remains the same or increases slightly, (by approximately 30% for observer ND and 40% for observer TEF). Although these modulation data are somewhat noisy, they are sufficiently stable to indicate that sensitivity gradually decreases throughout the rod recovery period of adaptation, and that the time period corresponds roughly to the "rod-limb" of the conventional dark adaptation curve portrayed in the upper portion of the figure by the open squares. To the extent that light and dark adaptation data represent the same process (Crawford, 1947), these data strongly suggest that the adapted state of rods is responsible for TIS induced changes in sensitivity to low spatial frequencies in the contralateral eye.

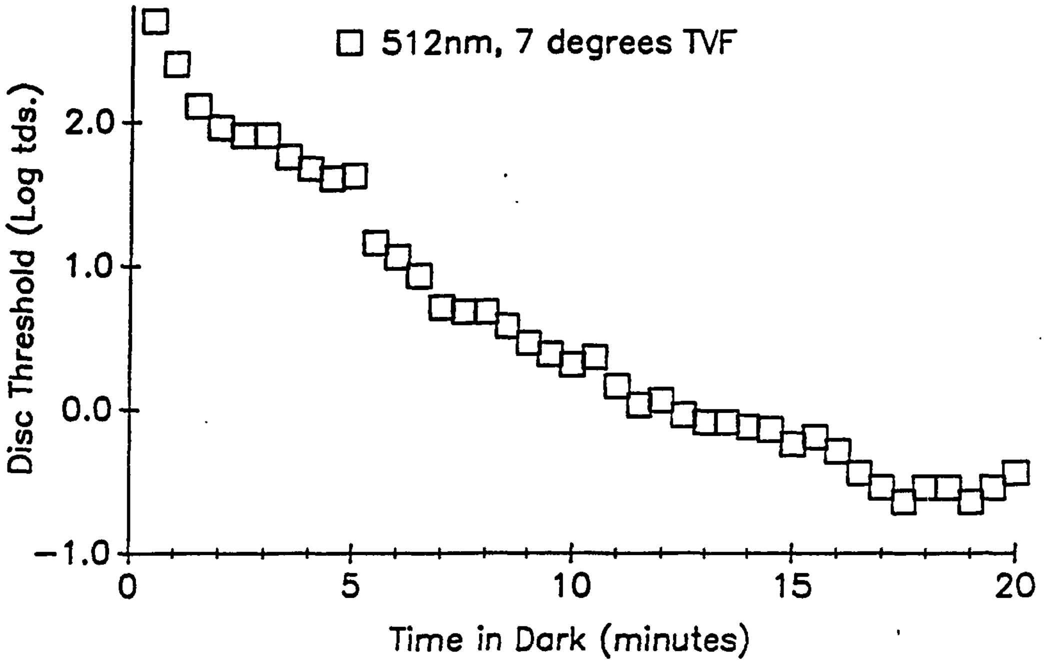
2. High Spatial Frequencies (10-20 cpd)

Cone photoreceptors alone mediate sensitivity to spatial frequencies >5 cpd, since rod-mediated vision is incapable of resolving such fine detail (Nordby & Sharpe, 1988). Moreover, such detail is probably mediated by the "parvocellular pathway" from beta ganglion cells to the parvocellular layers of the lateral geniculate body, as such detail cannot be mediated by the alpha ganglion cell-magnocellular pathway (Kaplan & Shapley, 1982).

The experiments presented in chapter 2 do not really indicate which type of photoreceptor pathways in the adapting eye causes TIS influences upon these higher spatial frequencies. Specifically, TIS influences only become clear with background levels of about 0.1 cd/m^2. Since this luminance level is also well within the operating range of rod vision, TIS could involve rod- or cone-related influences.

In order to study which type of photoreceptors mediate TIS for high spatial frequencies, a dark adaptation experiment was performed. The top portion of figure 46 again shows rod and cone detection thresholds in the adapting eye for the sake of comparison. The bottom shows log percent modulation threshold for an 11 cpd grating of 10 cd/m^2 luminance as a function of time in the dark after presentation of the same intensity adapting field, for observer ND; figure 47 shows corresponding data for observer TEF. For observer ND, sensitivity increases slightly until about 3 minutes in the dark and then slowly decreases throughout the remainder of the curve. For observer TEF, sensitivity increases for approximately 5 minutes, then decreases, but more gradually, for the remainder of the curve. This decrease follows the time course of rod adaptation. This can be more clearly seen in the replotted format for these data presented in figure 48 for observer ND and 49 for observer TEF. Thresholds representing the recovery of cones and rods from the top portions of figures 46 and 47, are replotted for each observer along with the data from the bottom portions of these curves, but magnified to show the correspondence between thresholds for the 11 cpd data and the recovery of rods. For both observers (and more clearly shown for observer TEF in figure 47), a close correspondence is obtained, indicating that for this high spatial frequency, it is the adaptational state of rods in the contralateral eye which is producing the TIS effect.

Figure 46. Disc threshold as a function of time in the dark is plotted for a 1° stimulus of 512 nm presented 7° in the TVF or for a 655 nm stimulus presented in the fovea for observer ND in the upper plot. The lower plot shows log percent threshold modulation as a function of time in the dark when an 11 cpd, 3.2° x 2.4°, 10 cd/m^2 stimulus is presented to the left fovea after an adapting field of approximately 800 cd/m^2 presented for 60 sec to the left eye was extinguished. The curve is fitted with a 4th order regression line.


□ 512nm, 7 degrees TVF
Disc Threshold (Log tds.)
2.0
1.0
0.0
−1.0
0
5
10
15
20
Time in Dark (minutes)

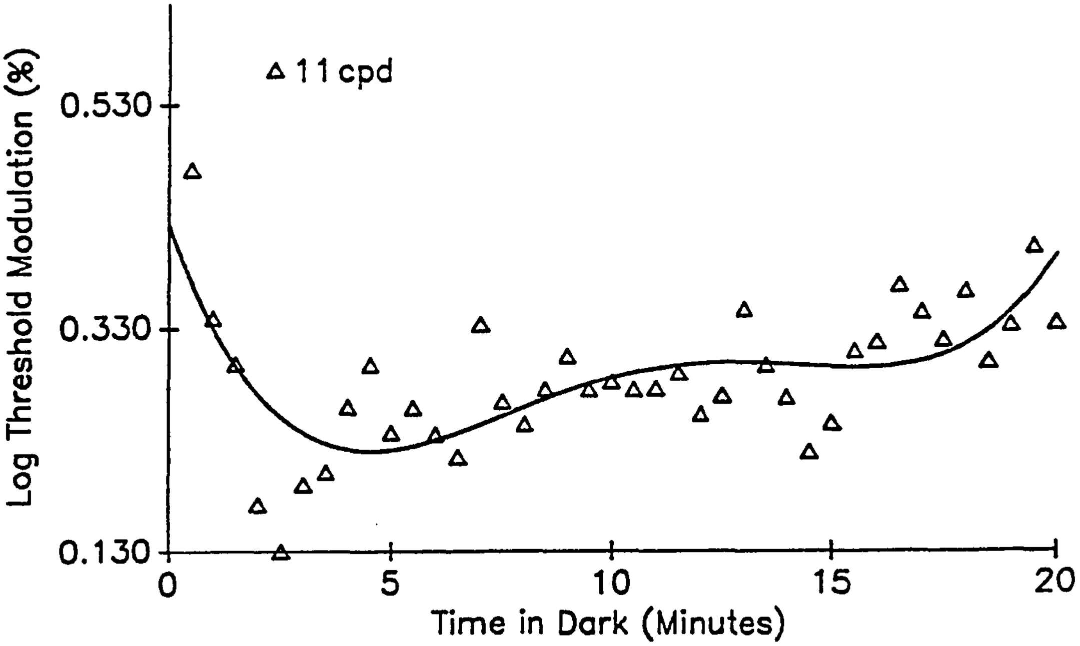
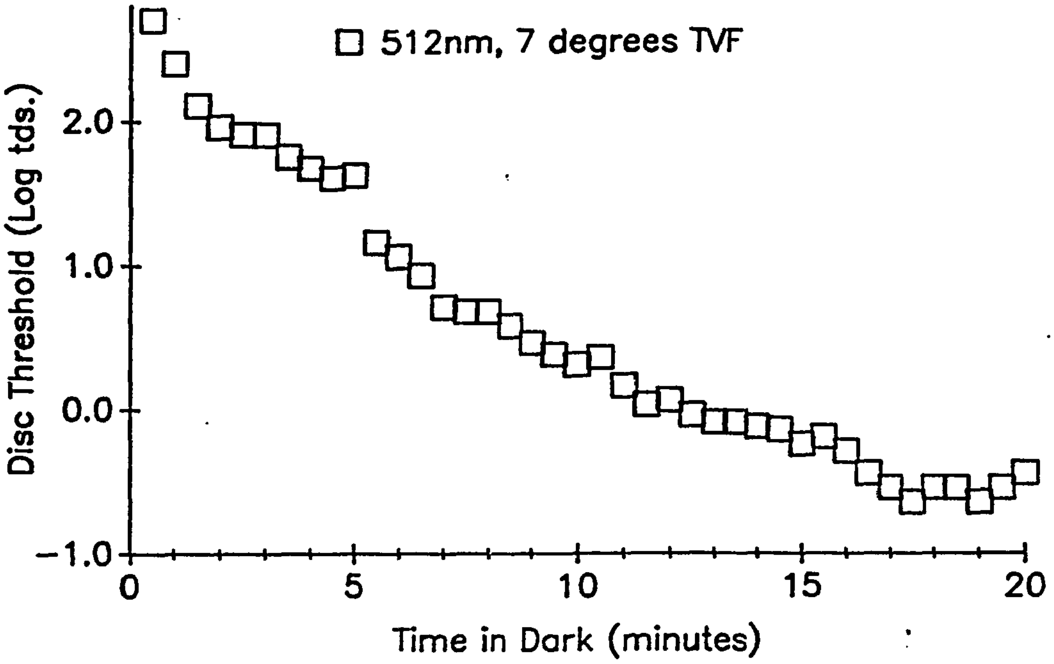

△ 11 cpd
Log Threshold Modulation (%)
0.530
0.330
0.130
0
5
10
15
20
Time in Dark (Minutes)

Figure 47. Disc threshold as a function of time in the dark is plotted for a 1° stimulus of 512 nm presented 7° in the TVF for observer TEF in the upper plot. The lower plot shows log percent threshold modulation as a function of time in the dark when a 2 cpd, 3.2° x 2.4°, 10 cd/m^2 stimulus is presented to the left fovea after an adapting field of approximately 800 cd/m^2 presented for 60 sec to the left eye was extinguished. The curve is fitted with a 4th order regression line.


□ 512nm, 7 degrees TVF
Disc Threshold (Log tds.)
2.0
1.0
0.0
−1.0
0
5
10
15
20
Time in Dark (minutes)

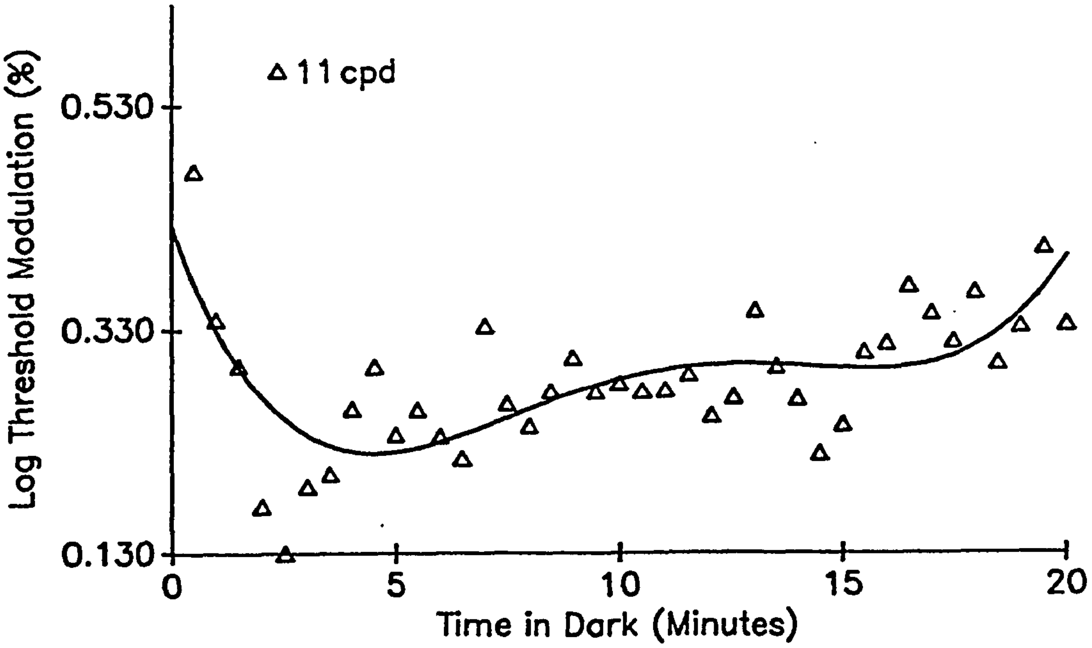

△ 11 cpd
Log Threshold Modulation (%)
0.530
0.330
0.130
0
5
10
15
20
Time in Dark (Minutes)

Figure 48. For observer ND, disc threshold as a function of time in the dark is plotted for a 1° stimulus of 512 nm presented 7° in the TVF along with log grating contrast, as a function of time in the dark when an 11 cpd, 3.2° x 2.4°, 10 cd/m^2 stimulus is presented to the left fovea after an adapting field of approximately 800 cd/m^2 presented for 60 sec to the left eye was extinguished. These data were magnified to show the correspondence between the two curves. In addition 4th order regression lines are plotted through each curve.

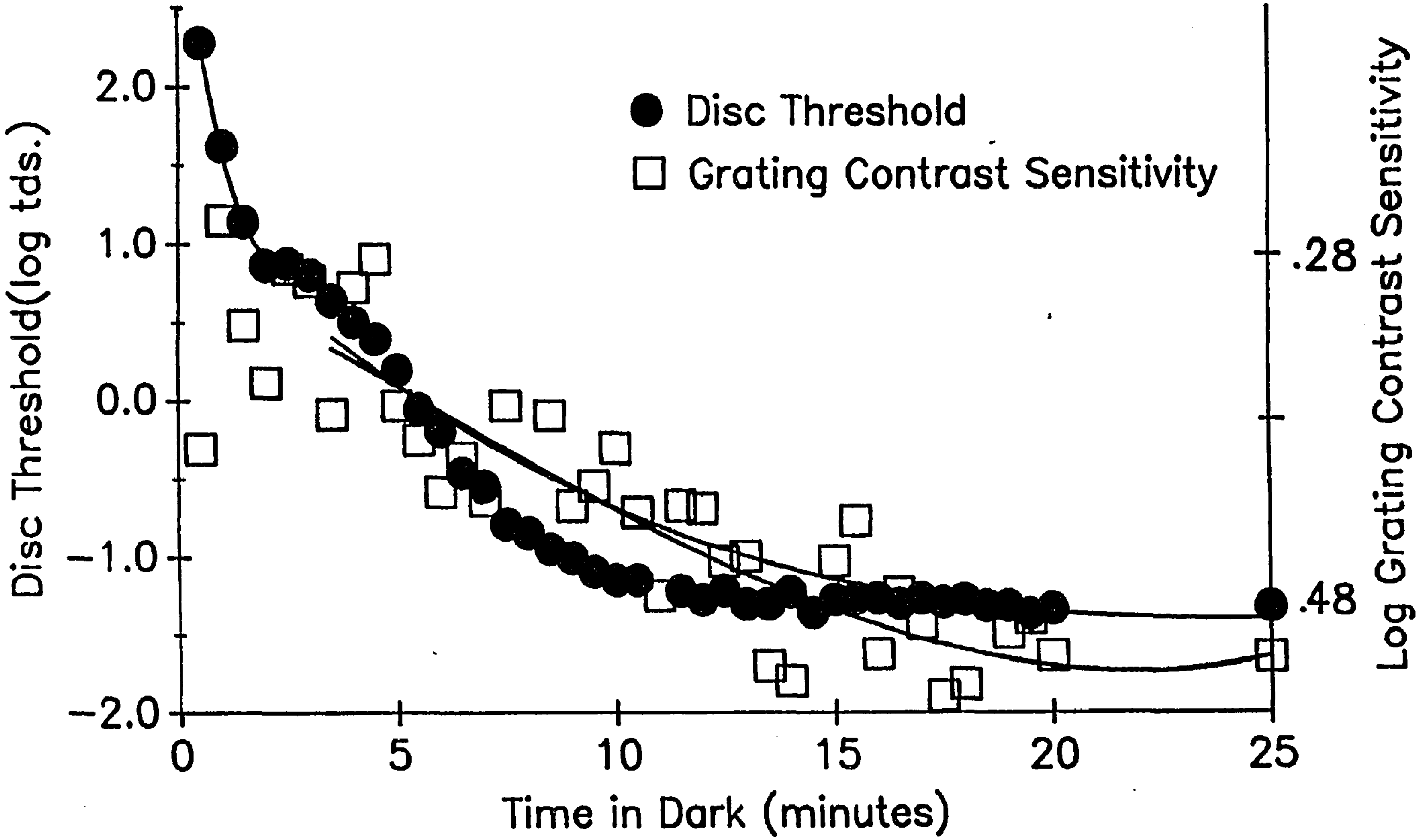
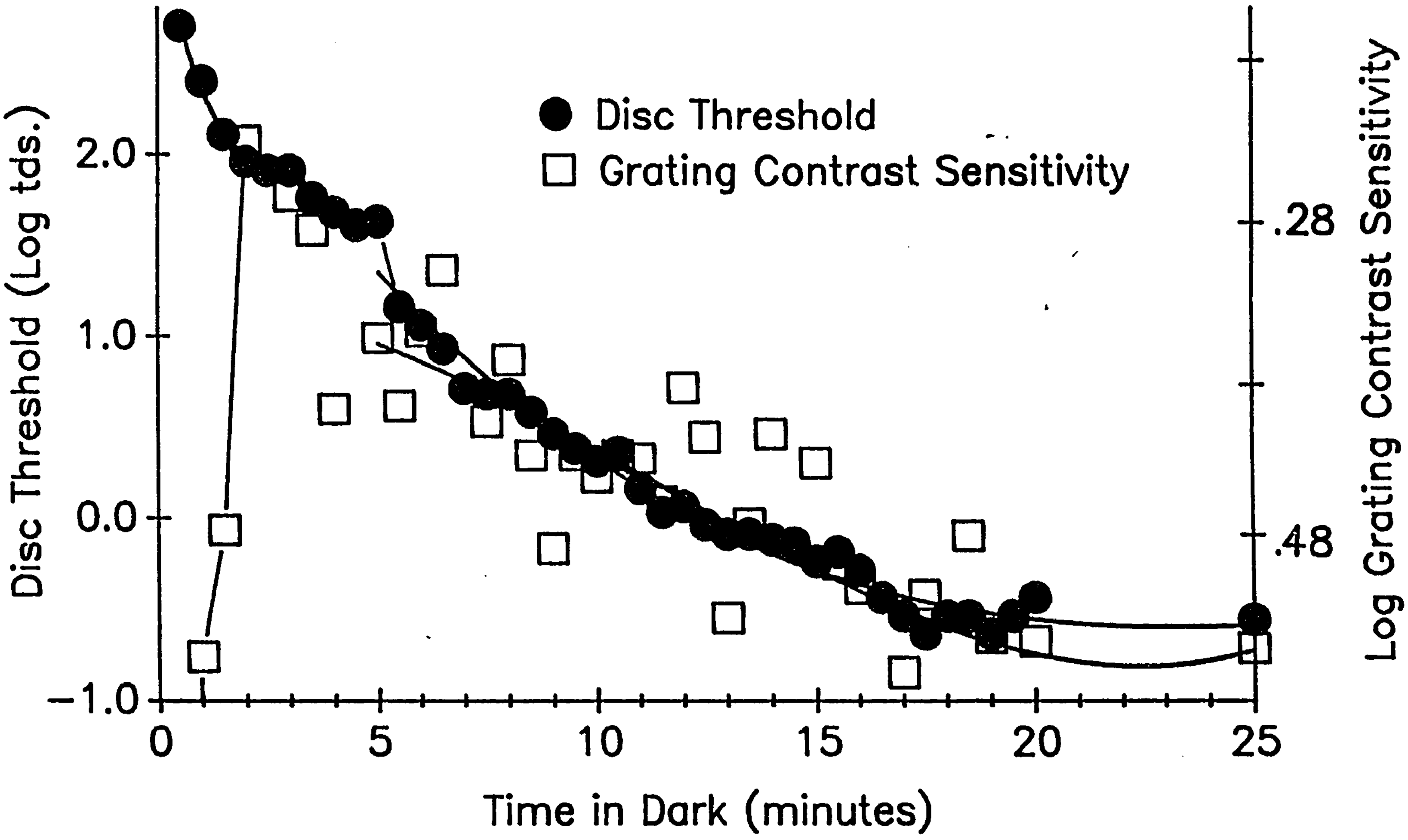

Disc Threshold
Grating Contrast Sensitivity
Disc Threshold(log tds.)
2.0
1.0
0.0
−1.0
−2.0
0
5
10
15
20
25
Time in Dark (minutes)
.28
.48
Log Grating Contrast Sensitivity

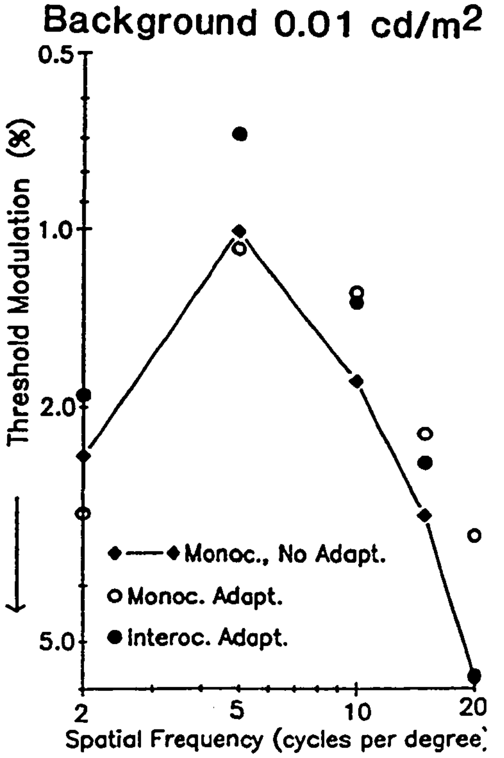
Figure 49. For observer ND, disc threshold as a function of time in the dark is plotted for a 1° stimulus of 512 nm presented 7° in the TVF along with log grating contrast, as a function of time in the dark when an 11 cpd, 3.2° x 2.4°, 10 cd/m^2 stimulus is presented to the left fovea after an adapting field of approximately 800 cd/m^2 presented for 60 sec to the left eye was extinguished. This data was magnified to show the correspondence between the two curves. In addition 4th order regression lines are plotted through each curve.


Disc Threshold
Grating Contrast Sensitivity
Disc Threshold (Log tds.)
2.0
1.0
0.0
−1.0
Log Grating Contrast Sensitivity
.28
.48
0
5
10
15
20
25
Time in Dark (minutes)

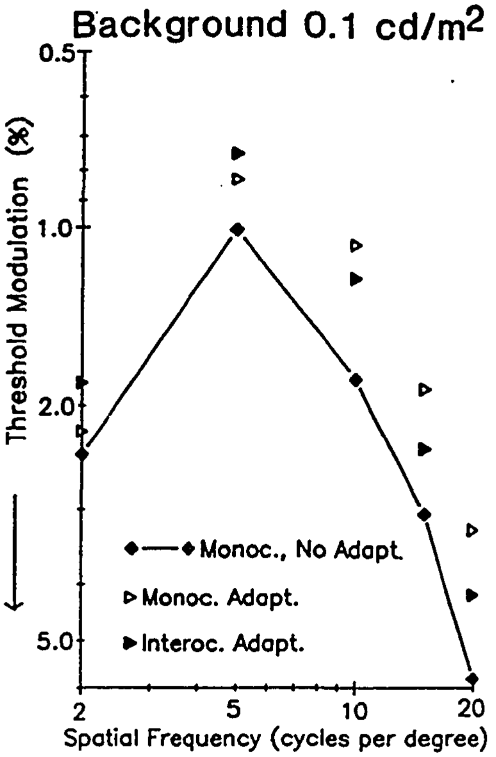
3. Direct Comparison of Monocular (SRCI) and Interocular (TIS) Adaptation Effects upon Grating Visibility

The foregoing results indicate that TIS effects upon grating visibility often involve rod-cone interaction. Previous work (Naarendorp, Denny & Frumkes, 1988; Naarendorp & Frumkes, 1991) has described a suppressive rod-cone interaction (SRCI) influence upon spatial and temporal resolution which is thought to be mediated within the distal retina. Therefore, the influence of monocular and interocular adapting fields upon visibility was compared for 1° test gratings of 10 cd/m^2 average luminance, presented foveally. Figure 50 shows the effects of four different luminance backgrounds upon contrast sensitivity, while derived figure 51 plots percent enhancement as a function of background luminance. These data show that monocular adaptation influences (SRCI) are only evident for higher spatial frequencies (10-20 cpd) and that dim monocular adapting fields (between 0.01 and 0.1 cd/m^2) optimize spatial resolution. In contrast, interocular adaptation influences (TIS) are evident for all spatial frequencies between 2 and 20 cpd; for spatial frequencies >5 cpd, the highest luminance interocular background used (10 cd/m^2) optimized spatial resolution. The different nature of these functional relationships prove that TIS cannot be considered a "stray light SRCI artifact," and that TIS and SRCI involve considerably different mechanisms. In other words, the TIS effect is interocular and not due to stray light from the adapting field "leaking" into the test eye.

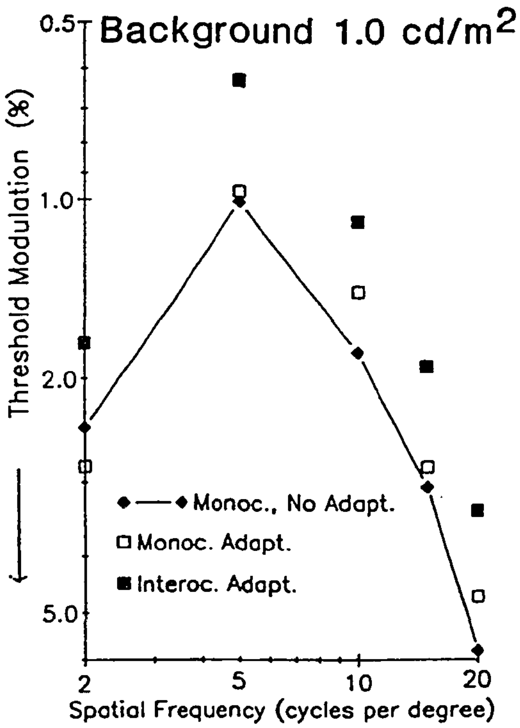
Figure 50. Percent threshold modulation as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m², 1° sine wave grating presented to the left fovea. The background was 20.8° x 15° and presented either monocularly (to the same eye as the stimulus) or interocularly, and was either 0.01 cd.m² (upper left plot), 0.1 cd/m² (upper right plot), 1.0 cd/m² (lower left plot), or 10.0 cd/m² (lower right plot).



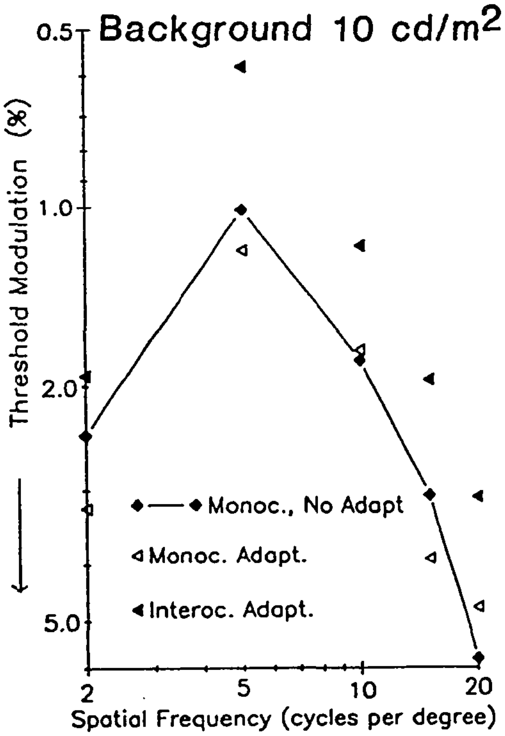
Background 0.01 cd/m2



Background 0.1 cd/m2

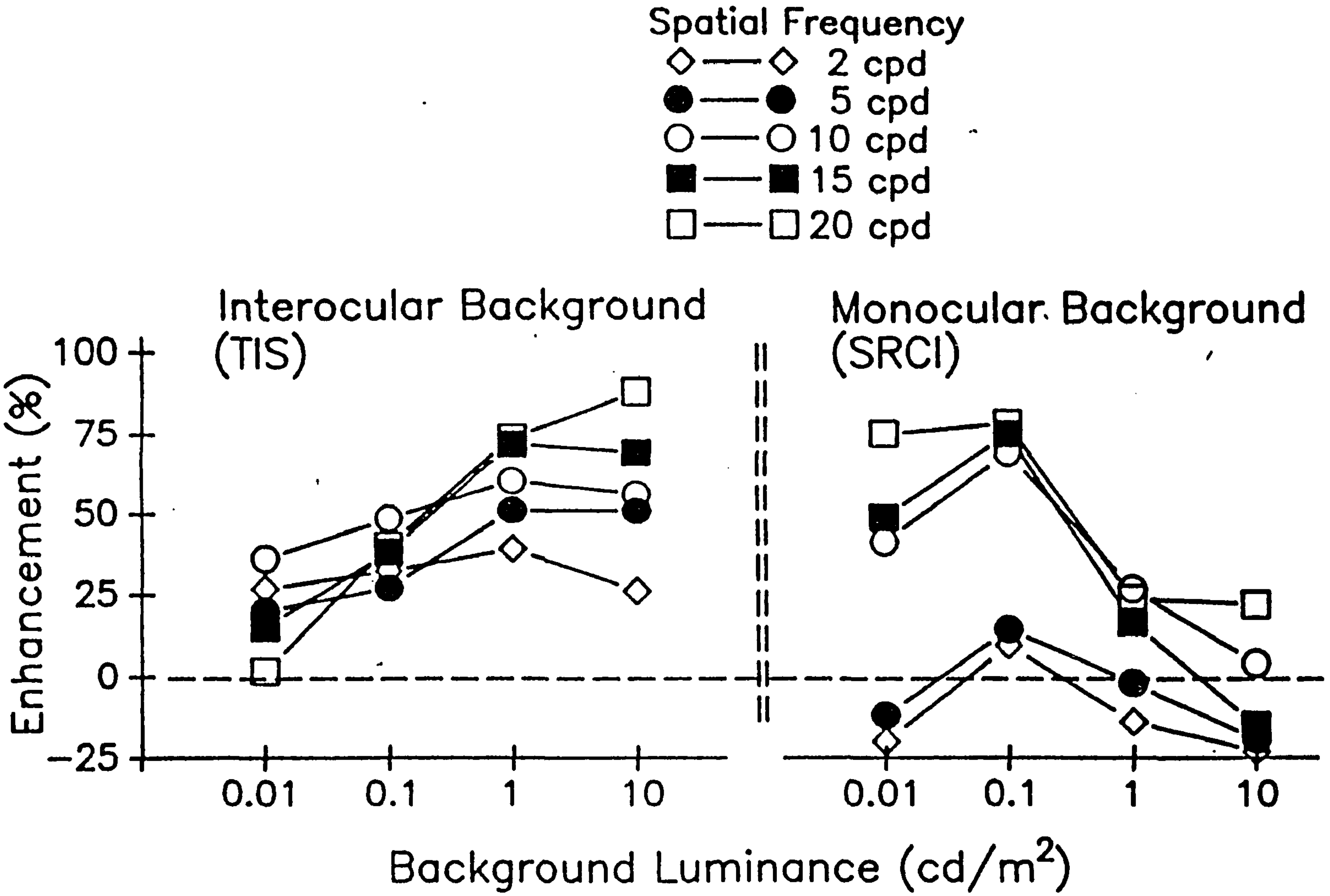


Background 1.0 cd/m2



Background 10 cd/m2

Figure 51. Percent enhancement in sensitivity as a function of background luminance is plotted for observer ND. These data were collected according to a method of adjustment procedure. The stimulus was a 10 cd/m^2, 1° square sine wave grating presented to the left fovea. The background was 20.8° x 15° and presented either monocularly (to the same eye as the stimulus) (right set of coordinates) or interocularly (left set of coordinates), and was either 0.01 cd.m^2, 0.1 cd/m^2, 1.0 cd/m^2, or 10.0 cd/m^2.


Spatial Frequency
◇—◇ 2 cpd
●—● 5 cpd
○—○ 10 cpd
■—■ 15 cpd
□—□ 20 cpd
Interocular Background (TIS)
Monocular Background (SRCI)
Enhancement (%)
100
75
50
25
0
−25
0.01
0.1
1
10
0.01
0.1
1
10
Background Luminance (cd/m²)

There are no private rod-pathways in the mammalian optic nerve. However, most evidence suggests that magnocellular cerebral pathways have considerably more rod-input than parvocellular pathways (Purpura, Kaplan & Shapley, 1988). This suggests that TIS involves an influence of magnocellular pathways from one eye upon both parvocellular and magnocellular signals conveyed from the other eye.

Chapter 6

General Discussion

The results of the present study show that spatial sensitivity in one eye is influenced by the adapted state of the contralateral eye. In general, light adapting one eye increases sensitivity to spatial sine wave gratings presented to the other eye and this sensitivity increase appears at low spatial frequencies when dim interocular test stimuli are presented interocularly up to approximately 50%. Brighter interocular backgrounds increase sensitivity to all frequencies above 1 cpd, for the two higher stimulus luminance levels and for all frequencies for the dimmest stimulus level. The increase in sensitivity produced by the brighter interocular backgrounds can be greater than 100%. Providing the test grating is not small and restricted to the fovea, this effect can be observed at any retinal position studied but seems to increase with parafoveal displacement. The results of the experiments presented in chapter 3 show that this interocular adaptation effect involves a tonic interocular suppression (TIS) from a dark adapted eye. Removal of this suppression by light adapting one eye results in improved grating visibility in the contralateral test eye. Finally, the results of the present study question claims for binocular summation which are based exclusively upon the greater visibility obtained with binocular as opposed to monocular grating presentation. The present study shows that binocular stimulation or interocular adaptation can reliably enhance visibility by more than the 100% value expected based upon a perfect summation model. As a consequence, it seems likely that instead of (or in addition to) summation, TIS accounts for the superiority of binocular over monocular visibility.

A. Comparison of TIS Influences upon Grating Visibility with other Interocular Adaptation Effects

1. Detection Threshold Experiments

a. The Lansford-Baker Effect

Several early studies (Lythgoe & Phillips, 1930; Mitchell & Liaudansky, 1955; Wolf & Zigler, 1955) showed that interocular light adaptation can exert a slight influence upon detection threshold for small, brief spots of light. More recently, Lansford and Baker (1969) and subsequent investigators (Auerbach, Dörrenhaus & Cavonius, 1991; Auerbach & Peachey, 1984; Makous, Teller & Boothe, 1976; Paris & Prestrude, 1975; Prestrude, 1976; Reeves, Peachey & Auerbach, 1986) demonstrated the "Lansford-Baker effect" or other interocular effects which may be examples of this particular effect, where interocular light adaptation leads to an increase in sensitivity. There are several similarities between the present grating visibility studies and the Lansford-Baker effect. 1) As described in chapter 4, both effects seem to involve rod-cone interaction (Auerbach & Peachey, 1984; Paris & Prestrude, 1975; Reeves, Peachey & Auerbach, 1986). However, the present study shows that rod-adaptation exerts an influence upon both rod- and cone-related grating visibility, while the Lansford-Baker effect may exclusively involve rod-cone interaction. 2) Both involve a TIS mechanism (Makous, Teller & Boothe, 1976, and chapter 3 of this thesis). 3) Both apparently increase with the degree of parafoveal displacement (see results in chapters 2 and 4; also, Auerbach, Dörrenhaus & Cavonius, 1991). 4) The Lansford-Baker effect is apparently absent in stereoblind individuals (Lansford & Baker, 1969). Frumkes and DeMatteo (personal communication) find that the present interocular effect is absent in "stereo-impaired" individuals who are amblyopic in one eye. These observers were tested for Snellen acuity in each eye separately, while wearing optimal spectacle correction. In two observers with equal Snellen acuity in both eyes, an interocular light adaptation effect, as shown here, occurred. In two other observers, however, in which there was discrepancy in the Snellen acuity between the two eyes, different results were obtained. If the eye with better acuity was used for test stimulation, interocular adaptation had an insignificant effect upon grating visibility. However, if the eye with poorer acuity was used for test stimulation, interocular backgrounds improved grating visibility.

On the other hand, the TIS influence upon grating visibility described in the present study appears to be much more robust than the Lansford-Baker effect. The Lansford-Baker effect is highly dependent upon the size, retinal position, and degree of spatial overlap between the test and adapting stimuli (Auerbach, Dörrenhaus &

Cavonius, 1991; Lansford & Baker, 1969; Makous, Teller & Boothe, 1976; Reeves, Peachey & Auerbach, 1986). Moreover, the luminance ratio between the adapting stimuli is a critical variable for determining the extent of the Lansford-Baker effect (Makous, Teller & Boothe, 1976). Although the present grating effect was not observed with small foveal stimuli, it was observed with any other combination of test and adapting stimuli providing the test and interocular adapting stimuli were presented to corresponding retinal loci. Moreover, at least for 2-5 cpd gratings, the present TIS effect can be observed with any luminance adapting field between 0.0001 and 100 cd/m^2 and occurs for all luminances of the test grating examined.

b. Demonstrations of Interocular Visual Masking

A large number of studies have demonstrated interocular visual masking, i.e., light adapting one eye increases threshold in the contralateral eye. At first glance, these results seem to contradict the present results which usually show that contralateral light adaptation lowers grating thresholds. However, two types of previous studies perhaps suggest that these visual masking studies hold some relevance for the present results. Firstly, Battersby and colleagues (Battersby & Wagman, 1962; 1964; Battersby, Oesterreich & Sturr, 1964) demonstrated interocular masking to be greatest when the test and adapting stimuli were approximately equal in size. In the present study, when a 0.5° test grating was presented foveally, presentation of an interocular adapting stimulus depressed grating visibility, an effect which was greatest when test and adapting stimuli were equal in size. Secondly, Auerbach, Dörrenhaus & Cavonious (1991) showed that the influence of an interocular adapting stimulus upon detection threshold is highly dependent upon retinal position. In particular, interocular adaptation depresses foveal grating sensitivity, has no effect at an intermediate retinal position from the fovea, but enhances sensitivity when the stimulus is in the far periphery. As suggested in the discussion in chapter 4, these results suggest that an interocular adapting stimulus produces two separate influences upon grating visibility: 1) A mechanism involving masking is most prevalent in the fovea and decreases with distance from the fovea; and 2) A TIS mechanism which is absent in the center of the fovea but increases with the amount of parafoveal displacement.

2. Other Visual Tasks

Since a tonic interocular suppressive mechanism plays a role in determining detection threshold (Makous, Teller & Boothe, 1976) as well as grating visibility (chapter 3), it may seem reasonable to propose that a single TIS mechanism effects all aspects of visual sensitivity. However, two types of evidence indicate that this is unlikely to be the case. Firstly, the results reported in chapter 2 show that with larger test stimuli, large backgrounds increase both grating visibility and subjective brightness; same-sized backgrounds similarly increase grating visibility but "average" apparent brightness according to Fechner's Paradox. Secondly, interocular light adaptation does not enhance, but depresses flicker sensitivity (Lipkin, 1962; Perrin, 1954; Vernon, 1934). Collectively, these results suggest that there may be several TIS mechanisms which independently influence different aspects of vision.

B. Comparison of TIS with Other Contralateral Suppressive Effects

The idea of a tonic suppressive contralateral influence has been well documented within motor system development (Govind, 1989) and functioning (Taub & Berman, 1968) as well as in the development of vision (Crewther, Crewther & Pettigrew, 1978; Hoffmann & Cynader, 1977; Smith, Spear & Kratz, 1978). In these examples, the suppressive influence is generally believed to involve an active inhibitory mechanism. Evidence has been provided that the effects of monocular visual deprivation are due to a contralateral tonic GABAergic inhibitory influence from the non-deprived eye onto the deprived eye (Duffy, Snodgrass, Burchfiel & Conway, 1976). Since such tonic inhibitory influences are well established within the entire visual pathway from distal retina (Eysteinsson & Frumkes, 1989) through the inner retina (Frumkes, Miller, Slaughter & Dacheux, 1981) and through the cerebrum (Singer, Gruenau & Rauschecker,1979), TIS may reflect the operation of a tonic inhibitory mechanism.

On the other hand, the TIS effect shows some similarities to results of studies on masking level differences (the "cocktail party effect") in audition (Jeffress, 1972). This type of tonic interaural suppression is usually explained as a change in signal-to-noise relationships, and is not attributed to inhibition. According to a signal-to-noise explanation, the factor which would limit grating visibility would be intrinsic noise, which most likely exists within the cerebrum. Contralateral light adaptation does not change the size of the signal but instead reduces noise.

At the conclusion of the studies summarized in chapters 2-5, Frumkes, Zhu, and the author planned experiments to determine whether TIS is more likely to involve an inhibitory or a change in signal-to-noise mechanism. Probability of seeing functions would be determined (by the method of constant stimuli) for monocularly presented gratings in the presence and absence of an interocular adapting stimulus. According to high threshold theories (e.g., Blackwell, 1963), a change in signal-to-noise ratio would result in a change in the overall shape of a probability of seeing function. In contrast, a reduction in signal size would result in a change in the mean of a probability of seeing function without altering its shape. This type of study would be a logical continuation of the present findings.

C. General Model for TIS

It is proposed that at least three separate types of interactions dominate binocular vision. One is predominantly excitatory and is likely to play a role in stereopsis. A second is inhibitory and is likely to play a role in binocular rivalry when the contours of the stimuli presented to the two eyes are sufficiently different. A third mechanism involves TIS, a mechanism which does not depend upon specific spatial contours. Presumably, this is a weaker mechanism then either the excitatory or rivalry mechanism. It will predominate when there are no striking differences in the contours presented to the two eyes and it depends upon the state of adaptation of the eye. Since this suppression is not specific for stimulus features, it may very well occur at an early stage of the cerebral visual pathway, perhaps at the level of the lateral geniculate nucleus, although interaction within the cortex cannot be excluded as a possibility. For example, Ohzawa and Freeman (1986a, b) found that approximately 8% of complex cells appear monocularly driven but show an inhibitory input from the "silent" eye. Similar results have been found by other investigators (Henry, Bishop & Coombs, 1969; Ferster, 1981). These cells could account for the present TIS effect.

It is further proposed that although this TIS inhibitory effect does not depend upon specific contours, it is largely limited to corresponding retinal areas. This is supported by the fact that with large foveally centered stimuli, interocular backgrounds of the same size as the test grating are as effective in influencing grating visibility as larger backgrounds, and annular backgrounds are ineffective (e.g., see figures 15 and 16). It accounts particularly well for the similar influences on grating sensitivity of binocular viewing (i.e., most evidence for "binocular summation") and interocular adaptation with large test gratings centered in the fovea. The importance of retinal position in determining the effect of adapting stimulus shape and size on TIS may relate to other well known features of binocular vision which are known to be influenced by retinal position. For example, Panum's fusional area is smallest in the fovea and increases with the extent of parafoveal displacement (Mitchell, 1988). Along these lines, annular backgrounds are ineffective in producing sensitivity increases foveally but quite effective in the periphery.

Just how the TIS mechanism interacts with other mechanisms in the binocular visual system is not known. For example, TIS output could feed into the stereopsis mechanism or it could operate in parallel to it. Although it does not suggest a definitive answer, the spatial arrangement of stimuli producing the TIS effect also produced a vivid sensation of depth with the test grating appearing in front of the adapting field.

D. Related Phenomena

This suppressive influence may also explain the phenomena of perceptual blankout of a Ganzfeld stimulus, since this blankout is prevented with binocular viewing (Bolanski & Doty, 1987), particularly if they are equal in luminance. In addition, alternating strabismics fail to show blankout when presented with a monocular Ganzfeld. Perceptual blankout of a Ganzfeld does not occur for stimuli presented in the monocular temporal crescent and is also prevented by pressure blinding the contralateral eye (Alpern & Campbell, 1963). This blankout phenomenon is an example of the Troxler effect, where with steady fixation, images in the periphery show a tendency to disappear and then reappear when the eye is moved. The present TIS effect could account for these phenomena. During monocular viewing, TIS from the dark adapted eye may cause the disappearance in the periphery.

Fechner's paradox represents an averaging effect of the two eyes. When different luminance levels are presented to each eye, brightness appears to be an average of the two. A contralateral suppressive influence could also explain such averaging.

E. The Importance of TIS

It is proposed that the TIS mechanism studied here exists to prevent the changes which develop during monocular deprivation during the critical period from occurring in situations involving short term visual deprivation. After monocular deprivation during the critical period in cats, changes in physiological responsiveness occur in neurons in the visual cortex such that considerably fewer cells are driven by the deprived eye (Hubel & Wiesel, 1970; Kratz, Spear & Smith, 1976; Hubel & Wiesel, 1965). Competitive interactions are proposed to account for these changes (Kratz, Spear & Smith, 1976). In addition, it has been shown that the deprived eye is tonically suppressed by the undeprived eye in studies where removal of the undeprived eye results in an increase in responsiveness of the visual cortex to stimulation of the previously deprived eye (Crewther, Crewther & Pettigrew, 1978;

Hoffmann & Cynader, 1977; Kratz, Spear & Smith, 1976; Smith, Spear & Kratz, 1978).

It is suggested that during this critical period, under normal viewing conditions, both eyes exert a mutual tonic suppressive influence upon one another. When one eye is occluded, it gradually dark adapts. As it does so, it exerts a relatively greater suppression upon the contralateral eye--just as occurs in the present TIS effect. However, as the monocular deprivation continues, the suppression from the deprived eye onto the undeprived eye fatigues and the suppression from the viewing eye eventually becomes relatively greater. This could be the mechanism which accounts for the competitive interactions mentioned above. Thus, TIS as studied here exists as a means to keep an occluded eye physiologically active under conditions of short term deprivation. When the deprivation becomes long term, competitive interactions (TIS) cause a decrease in responsiveness of the deprived eye, which represents an expression of the plasticity which exists in the developing visual system.

F. Relationship to Existing Theories of Binocular Vision

Many investigators propose the coexistence of several different binocular processes. For example, physiological evidence clearly indicates the existence of three types of units which respond in quite different fashions to retinal disparity (Poggio & Fischer, 1977). In a similar fashion, psychophysical models often propose the existence of several different binocular processes (Wolfe, 1986; Blake, 1989; Cogan, 1987).

The present effect is most compatible with a two-channel theory of binocular vision proposed by (Cogan, 1987). According to his model, there are no independent monocular contributions to psychophysical visual responses. There are three processes, including an excitatory process which acts in a multiplicative fashion for fused stimuli (binocular) and two bilateral processes comprising ipsilateral excitation and contralateral inhibition The final response is a sum of those processes. The bilateral excitatory and inhibitory processes are "stimulus specific" in terms of orientation frequency, energy and contrast but insensitive to spatial phase. In this model, inhibition is assumed to be proportional to the strength of the stimulation in the contralateral eye. Cogan states that the model explains Fechner's Paradox. He also states that this inhibition can be used to explain the decrease in interocular transfer of aftereffects since the adapted eye would send inhibitory signals to the other eye which decay gradually. This theory does not permit the types of alternation in perception seen in rivalry or unperceived alternating suppression during normal vision. The inhibition here occurs between stimuli which are similar in each eye, occurs at the same time as does excitation and only serves to weaken contralateral signals. These ideas could be compatible with a TIS mechanism.

The present study shows that regardless to its relation to other mechanisms, TIS is a robust phenomenon which contributes to binocular visual perception and may relate to the plasticity seen in early visual development. TIS should be considered in the functioning of the visual system along with other phenomena such as stereopsis and binocular rivalry, and should be considered as an explanation for "binocular summation". The specific relationship of TIS to other aspects of binocular vision such as stereopsis and binocular rivalry, as well as influences upon brightness, color, and detection threshold, can only be determined by means of further experimentation.

Appendix A

Comparison of Results obtained with 3 Psychophysical Methods

As indicated in chapter 2, three different psychophysical methods were used, and data collected with these were lumped together throughout this thesis. Approximately 15 months after the experimental data reported in chapters 3-6 were collected, data similar to those shown in figure 3 were collected with all 3 psychophysical methods in two experimental sessions for observer ND. Figure 52 shows the influence of a large interocular background of 10 cd/m^2 luminance upon the visibility of a full sized 10 cd/m^2 test grating. These data are replotted in figure 53 with percent change in contrast sensitivity plotted as a function of grating frequency. Figure 53 shows that regardless of which of the three psychophysical methods were used, background presentation tended to produce a similar increase in grating visibility. Figure 52 more clearly shows that for any spatial frequency grating and regardless of psychophysical method, the lowest sensitivity datum obtained with a background was higher than the highest sensitivity datum obtained without a background. This control experiment indicates that the results in this study are robust and do not result from use of one particular psychophysical method.

Figure 52. Percent threshold modulation as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure, a yes/no method of adjustment procedure and a lternative forced-choice staircase procedure. The stimulus was a 10 cd/m^2, 3.2° x 2.4° sine wave grating presented to the left fovea. The background was 20.8° x 15° and presented to the right eye at 10.0 cd/m^2.

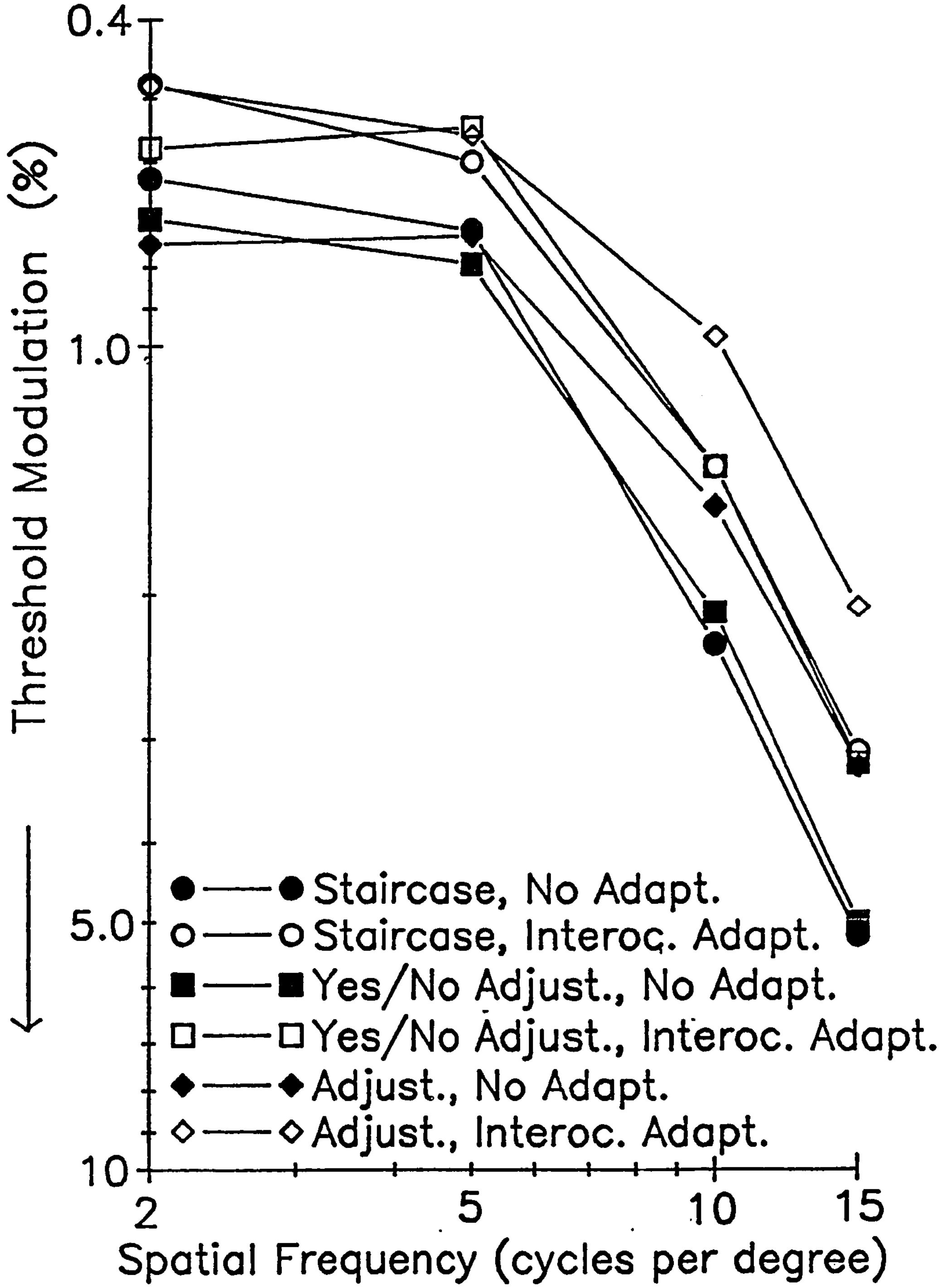
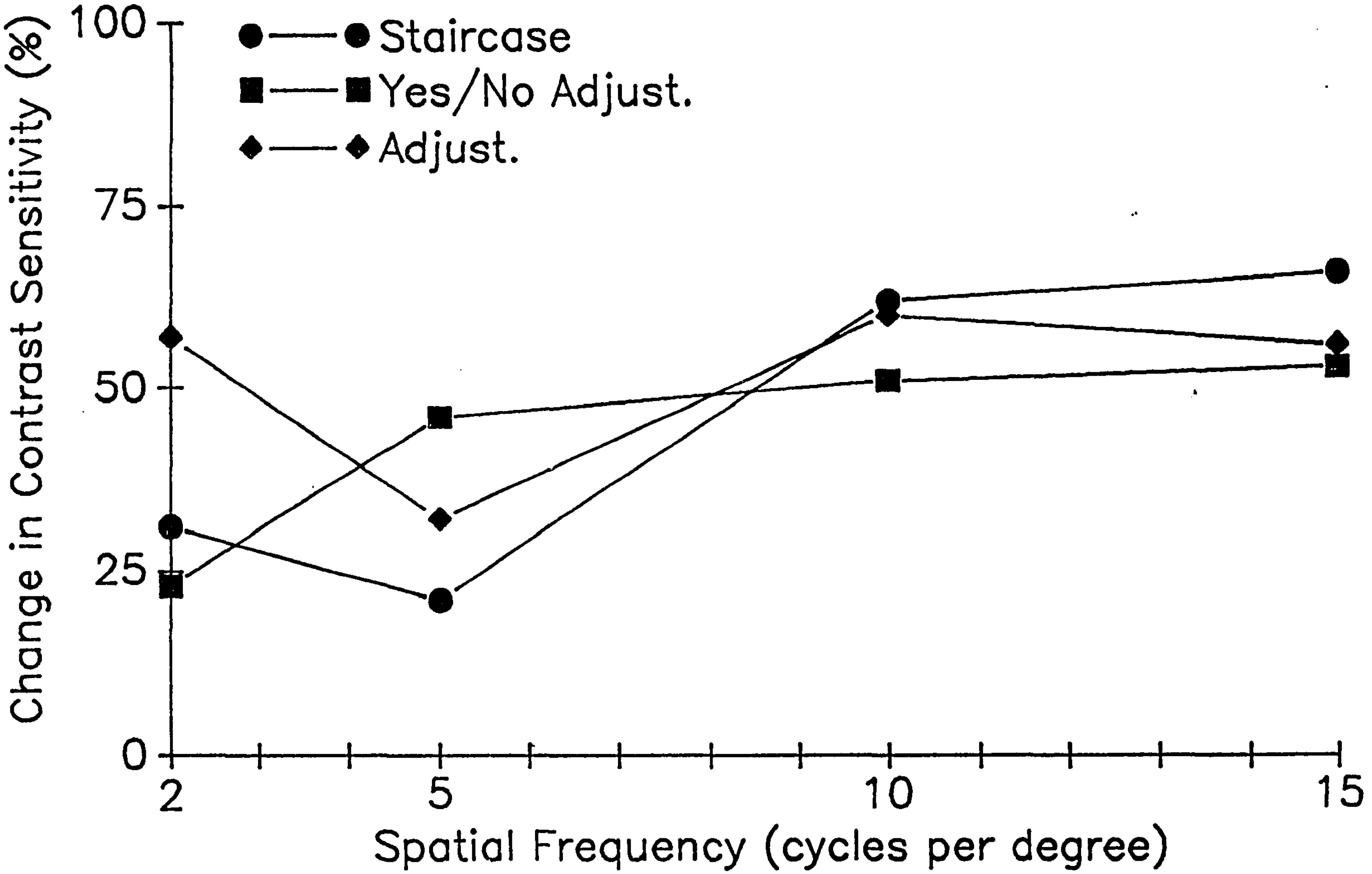

0.4
1.0
5.0
10
Threshold Modulation (%)
2
5
10
15
Spatial Frequency (cycles per degree)
● —— ● Staircase, No Adapt.
○ —— ○ Staircase, Interoc. Adapt.
■ —— ■ Yes/No Adjust., No Adapt.
□ —— □ Yes/No Adjust., Interoc. Adapt.
◆ —— ◆ Adjust., No Adapt.
◇ —— ◇ Adjust., Interoc. Adapt.

Figure 53. Percent change in contrast sensitivity as a function of spatial frequency is plotted for observer ND. These data were collected according to a method of adjustment procedure, a yes/no method of adjustment procedure and alternative forced-choice staircase procedure. The stimulus was a 10 cd/m², 3.2° x 2.4° sine wave grating presented to the left fovea. The background was 20.8° x 15° and presented to the right eye at 10.0 cd/m².


Staircase
Yes/No Adjust.
Adjust.
Change in Contrast Sensitivity (%)
100
75
50
25
0
2
5
10
15
Spatial Frequency (cycles per degree)

References

Abadi, R. V. (1976). Induction masking--a study of some inhibitory interactions during dichoptic viewing. Vision Research, 16, 269-275.

Alexander, K. R., & Fishman, G. A. (1984). Rod-cone interaction in flicker perimetry. British Journal of Ophthalmology, 68, 303-309.

Allen, F. (1923). On reflex visual sensations. Journal of the Optical Society of America, 7, 583-626.

Anderson, P. A., & Movshon, J. A. (1989). Binocular combination of contrast signals. Vision Research, 29, 1115-1132.

Apkarian, P. A., Nakayama, K., & Tyler, C. W. (1981). Binocularity in the human visual evoked potential: Facilitation, summation and suppression. Electroencephalography and Clinical Neurophysiology, 51, 32-48.

Arden, G. B., & Frumkes, T. E. (1986). Stimulation of rods can increase cone flicker ERGs in man. Vision Research, 26, 711-721.

Asher, H. (1953). Suppression theory of binocular vision. British Journal of Ophthalmology, 37, 37-49.

Auerbach, E., Cavonius, C. R., & Dörrenhaus, A. (1987). Human visual sensitivity during light adaptation of the contralateral eye. Journal of Physiology, 138P.

Auerbach, E., Dörrenhaus, A., & Cavonius, C. R. (1991). Visual Neuroscience, in press.

Auerbach, E., & Peachey, N. S. (1984). Interocular transfer and dark adaptation to long-wave test lights. Vision Research, 24, 1043-1048.

Baitch, L. W., & Levi, D. M. (1988). Evidence for nonlinear binocular interactions in human visual cortex. Vision Research, 28, 1139-1143.

Barris, M. C., & Frumkes, T. E. (1978). Rod-cone interaction in human scotopic vision-IV. Cones stimulated by contrast flashes influence rod threshold. Vision Research, 18, 801-808.

Bartlett, N. R., & Gagné, R. M. (1939). On binocular summation at threshold. Journal of Experimental Psychology, 25, 91-99.

Battersby, W. S., Oesterreich, R. E., & Sturr, J. F. (1964). Light adaptation kinetics: The influence of spatial factors. Science, 143, 1029-1031.

Battersby, W. S., & Wagman, I. H. (1962). Neural limitations of visual excitability IV. Spatial determinants of retrochiasmal interaction. American Journal of Physiology, 203, 359-365.

Battersby, W. S., & Wagman, I. H. (1964). Neural limitations of visual excitability VII. Nonhomonymous retrochiasmal interaction. American Journal of Physiology, 206, 1181-1188.

Bauer, G. M., Frumkes, T. E., & Nygaard, R. W. (1983). The signal to noise characteristics of rod cone interaction. Journal of Physiology, 337, 101-119.

Blackwell, H. R. (1963). Neural theories of simple visual discriminations. Journal of the Optical Society of America, 53, 129-160.

Blake, R. (1989). A neural theory of binocular rivalry. Psychological Review, 96, 145-167.

Blake, R., & Fox, R. (1973). The psychophysical inquiry into binocular summation. Perception & Psychophysics, 14, 161-185.

Blake, R., Sloane, M., & Fox, R. (1981). Further developments in binocular summation. Perception & Psychophysics, 30, 266-276.

Bolanowski, S. J. (1987). Contourless stimuli produce binocular brightness summation. Vision Research, 27, 1943-1951.

Bolanowski, S. J., & Doty, R. W. (1987). Perceptual "blankout" of monocular homogeneous fields (Ganzfelder) is prevented with binocular viewing. Vision Research, 27, 967-982.

Boynton, R. M., & Wisowaty, J. J. (1984). Selective color effects in dichoptic masking. Vision Research, 24, 667-675.

Braccini, C., Gambardella, G., & Suetta, G. (1980). A noise masking experiment in grating perception at threshold: The implications on binocular summation. Vision Research, 20, 373-376.

Burchfiel, J. L., & Duffy, F. H. (1981). Role of intracortical inhibition in deprivation amblyopia: reversal by microiontophoresis of bicuculline. Brain Research, 206, 479-484.

Campbell, F. W., & Green, D. G. (1965a). Optical and retinal factors affecting visual resolution. Journal of Physiology, (London), 181, 576-593.

Campbell, F. W., & Green, D. G. (1965b). Monocular versus binocular visual acuity. Nature, 208, 191-192.

Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analyses to the visibility of gratings. Journal of Physiology (London), 197, 551-566.

Cavonius, C. R. (1979). Binocular Interactions in flicker. Quarterly Journal of Experimental Psychology, 31, 273-280.

Cogan, A. I. (1987). Human binocular interaction; Towards a neural model. Vision Research, 27, 2125-2139.

Coletta, N. J., & Adams, A. J. (1984). Rod-cone interaction in flicker detection. Vision Research, 24, 1333-1340.

Collier, G. (1954). Probability of response and intertrial association as functions of monocular and binocular stimulation. Journal of Experimental Psychology, 47, 75-83.

Collier, G., & Kubzansky, P. (1958). The magnitude of binocular summation as a function of the method of stimulus presentation. Journal of Experimental Psychology, 56, 355-361.

Cook, T. W. (1934). Binocular and monocular relations in foveal dark adaptation. Psychological Monograms, 45, 1-86.

Crawford, B. H. (1947). Visual adaptation in relation to brief conditioning stimuli. Proceedings of the Royal Society of London, B, 134, 283-302.

Crewther, D. P., Crewther, S. G., & Pettigrew, J. D. (1978). A role for extraocular afferents in post-critical period reversal of monocular deprivation. Journal of Physiology, 282, 181-195.

Daw, N. W., Jensen, R. J., & Breinhun, W. J. (1990). Rod pathways in mammalian retinae. Trends in Neuroscience, 13, 110-115.

Denny, N., Frumkes, T. E., Barris, M. C., & Eysteinsson, T. (1991). Tonic interocular suppression and binocular summation in human vision. Journal of Physiology, 437, 449-460.

Denny, N., Frumkes, T. E., & Goldberg, S. H. (1990). Comparison of summatory and suppressive rod-cone interaction. Clinical Vision Sciences, 5, 27-36.

De Silva, H. R., & Bartley, S. H. (1930). Summation and subtraction of brightness in binocular perception. British Journal of Psychology, 20, 241-250.

de Weert, Ch. M. M., & Levelt, W. J. M. (1976). Comparison of normal and dichoptic colour mixing. Vision Research, 16, 59-70.

Duffy, F. H., Snodgrass, S. R., Burchfiel, J. L., & Conway, J. L. (1976). Bicuculline reversal of deprivation amblyopia in the cat. Nature, 260, 256-257.

Eysteinsson, T., Denny, N., & Frumkes, T. E. (1990). Tonic suppressive influence from the dark adapted eye. Society for Neuroscience (abstract), 16, 104.

Eysteinsson, T., & Frumkes, (1989). Physiology and pharmacological analysis of suppressive rod-cone interaction in Nectures retina. Journal of Neurophysiology, 61, 866-873.

Fechner, G. T. (1860). Elemente der Psychophysik. Leipzig: Breitkopf & Härtel.

Ferster, D. (1981). A comparison of binocular depth mechanisms in areas 17 and 18 of the cat visual cortex. Journal of Physiology, 311, 623-655.

Foster, D. H. (1976). Rod cone interaction in the after-flash effect. Vision Research, 16, 393-396.

Foster, D. H. (1977). Rod- and cone-mediated interactions in the fine-grain movement illusion. Vision Research, 17, 123-127.

Foster, D. H., & Mason, R. J. (1977). Interaction between rod and cone systems in dichoptic visual masking. Neuroscience Letters, 4, 39-42.

Fox, R., Blake, R., & Bourne, J. R. (1973). Visual evoked cortical potentials during pressure-blinding. Vision Research. 13, 501-503.

Frumkes, T. E. (1990). Classical and modern psychophysical studies of dark and light adaptation and their relationship to underlying retinal function. In K. N. Leibovic (Ed.): The Science of Vision: A Convergence of Disciplines. Berlin: Springer-Verlag.

Frumkes, T. E. (1991). Suppressive rod-cone interaction. In G. B. Arden, B. & Heckenlively (Eds.), Clinical Visual Electrophysiology. St. Louis: Mosby.

Frumkes, T. E., & Denny, N. (1987). Types of rod-cone interactions. Die Farbe, 34, 79-81.

Frumkes, T. E., & Eysteinsson, T. (1988). The cellular basis for suppressive rod-cone interaction. Visual Neuroscience, 1, 263-273.

Frumkes, T. E., Miller, R. F., Slaughter, M. M., & Dacheux, R. F. (1981). Physiological and pharmacological basis of GABA and glycine action on neurons of mudpuppy retina. III. Amacrine-mediated inhibitory influences on ganglion cell receptive-field organization; a model. Journal of Neurophysiology, 45, 783-804.

Frumkes, T. E., Sekuler, M. D., Barris, M. C., Reiss, E. H., & Chalupa, L. M. (1973). Rod-cone interaction in human scotopic vision-I. temporal analysis. Vision Research, 13, 1269-1282.

Frumkes, T. E., & Sturr, J. F. (1968). Spatial and luminance factors determining visual excitability. Journal of the Optical Society of America, 58, 1657-1662.

Frumkes, T. E., & Wu, S. M. (1990). Independent influences of rod adaptation on cone-mediated responses to light onset and offset in distal retinal neurons. Journal of Neurophysiology, 63, 1043-1054.

Fry, G. A., & Bartley, S. H. (1933). The brilliance of an object seen binocularly. American Journal of Ophthalmology, 16, 687-693.

Goldberg, S. H., Frumkes, T. E., & Nygaard, R. W. (1983). Inhibitory influence of unstimulated rods in the human retina: Evidence provided by examining cone flicker. Science, 221, 180-182.

Gouras, P., & Link, K. (1966). Rod and cone interaction in dark-adapted monkey ganglion cells. Journal of Physiology, 184, 499-510.

Govind, C. K. (1989). Asymmetry in lobster claws. American Scientist, 77, 468-474.

Graham, C. H. (1930). An investigation of binocular summation: I. The fovea. Journal of General Psychology, 3, 494-510.

Graham, C. H. (1931). An investigation of binocular summation: II. The periphery. Journal of General Psychology, 5, 311-327.

Graham, C. H. (1965). Vision and Visual Perception. New York, NY: John Wiley & Sons, Inc.

Graham, N. (1989). Visual Pattern Analyzers. New York, NY: Oxford University Press.

Harter, M. R., Seiple, W. H., & Salmon, L. (1973). Binocular summation of visually evoked responses to pattern stimuli in humans. Vision Research, 13, 1433-1466.

Henry, G. H., Bishop, P. O., & Coombs, J. S. (1969). Inhibitory and sub-liminal excitatory receptive fields of simple units in cat striate cortex. Vision Research, 9, 1289-1296.

Hoffmann, K. P., & Cynader, M. (1977). Functional aspects of plasticity in the visual system of adult cats after early monocular deprivation. Transcriptions of the Royal Society of London B., 278, 411-424.

Horowitz, M. W. (1949). An analysis of the superiority of binocular over monocular visual acuity. Journal of Experimental Psychology, 39, 581-596.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. Journal of Physiology, (London), 160, 106-154.

Hubel, D. H., & Wiesel, T. N. (1965). Binocular interaction instriate cortex of kittens reared with artificial squint. Journa of Neurophysiology, 28, 1041-1059.

Hubel, D., & Wiesel, T. (1970). The period of susceptibility to the physiological effects of unilateral eye closure in kittens. Journal of Physiology, London, 206, 419-436.

Jeffress, L. A. (1972). Binaural signal detection: Equalization and cancellation theory. In J. V. Tobias (Ed.), Foundations of Modern Auditory Theory (Vol. 2). New York, NY: Academic Press, pp. 349-367.

Julesz, B. (1964). Binocular depth perception without familiarity cues. Science, 145, 356-362.

Kaplan, E., & Shapley, R. M. (1982). X and Y cells in the lateral geniculate nucleus of macaque monkeys. Journal of Physiology, 330, 125-143.

Katsumi, O., Tanino, T., & Hirose, T. (1986). Objective evaluation of binocular function with pattern reversal VER III. Effect of stimulus size and localization. Acta Ophthalmologica, 64, 691-697.

Kelly, D. H. (1977). Visual contrast sensitivity. Optica Acta, 24, 107-129.

Kelly, D. H. (1978). Photopic contrast sensitivity without foveal vision. Optics Letters, 2, 79-81.

Kratz, K. E., Spear, P. D., & Smith, D. C. (1976). Postcritical-period reversal of effects of monocular deprivation on striate cortex cells in the cat. Journal of Neurophysiology, 39, 501-511.

Landolt, E. (1889). Tableau d'optotypes pour la determination de l'acuité visuelle. Soc. Francais d'ophthal. In C. H. Graham (Ed.) (1965), Vision and Visual Perception. New York, NY: John Wiley & Sons, Inc.

Lansford, T. G., & Baker, H. D. (1969). Dark adaptation: An interocular light-adaptation effect. Science, 164, 1307-1309.

Latch, M., & Lennie, P. (1977). Rod-cone interaction in light adaptation. Journal of Physiology, 269, 517-534.

Legge, G. E. (1984a). Binocular contrast summation-I. Detection and discrimination. Vision Research, 24, 373-383.

Legge, G. E. (1984b). Binocular contrast summation-II. Quadratic summation. Vision Research, 24, 385-394.

Leibowitz, H. W. (1987). Night Vision-Current Research and Future Direction, Symposium Proceedings. Washington, D. C.: National Academy Press.

Leibowitz, H., & Walker, L. (1956). Effect of field size and luminance on the binocular summation of suprathreshold stimuli. Jounal of the Optical Society of America, 46, 171-172.

Lema, S. A., & Blake, R. (1977). Binocular summation in normal and stereoblind humans. Vision Research, 17, 691-695.

Lie, I. (1963). Dark adaptation and the photochromatic interval. Documenta Ophthalmologica, 17, 411-510.

Lipkin, B. S. (1962). Monocular flicker discrimination as a function of the luminance and area of contralateral steady light. I Luminance. Journal of the Optical Society of America, 52, 1287-1295.

Livingston, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. Journal of Neuroscience, 7, 3416-3468.

Long, G. M. (1978). The unspecified role of cones and rods in grating detection: A theoretical note. Journal of the Optical Society of America, 68, 1009-1012.

Lythgoe, F. J., & Phillips, L. R. (1938). Binocular summation during dark adaptation. Journal of Physiology, 91, 427-436.

MacLeod, D. I. A. (1972). Rods cancel cones in flicker. Nature, 235, 173-174.

MacLeod, D. I. A. (1974). Psychophysical studies of signals from rods and cones. Unpublished doctoral dissertation, Cambridge University.

Maffei, L., & Fiorentini, A. (1976). Asymmetry of motility of the eyes and change of binocular properties of cortical cells in adult cats. Brain Research, 105, 73-78.

Matin, L. (1962). Binocular summation at the absolute threshold of peripheral vision. Journal of the Optical Society of America, 52, 1276-1286.

Makous, W., Teller, D, & Boothe, R. (1976). Binocular interaction in the dark. Vision Research, 16, 473-476.

Mitchell, D. E. (1988). The extent of visual recovery from early monocular or binocular visual deprivation in kittens. Journal of Physiology, 395, 639-660.

Mitchell, R. T., & Liaudansky, L. H. (1955). Effect of differential adaptation of the eyes upon threshold sensitivity. Journal of the Optical Society of America, 45, 831-834.

Naarendorp, F., Denny, N., & Frumkes, T. E. (1988). Rod light and dark adaptation influence cone-mediated spatial acuity. Vision Research, 28, 67-74.

Naarendorp, F., & Frumkes, T. E. (1991). The influence of short term adaptation of human rods and cones on cone-mediated grating visibility. Journal of Physiology, 432, 521-541.

Nelson, R. (1977). Cat cones have rod input: A comparison of the response properties of cones and horizontal cell bodies in the retina of the cat. Journal of Comparative Neurology, 172, 109-135.

Nordby, K., & Sharpe, L. T. (1988). The directional sensitivity of the photoreceptors in the human achromat. Journal of Physiology, 399, 267-281.

Ohzawa, I., & Freeman, R. D. (1986a). The binocular organization of simple cells in the cat's visual cortex. Journal of Neurophysiology, 56, 221-242.

Ohzawa, I., & Freeman, R. D. (1986b). The binocular organization of complex cells in the cat's visual cortex. Journal of Neurophysiology, 56, 243-259.

Paris, J., & Prestrude, A. M. (1975). On the mechanisms of the interocular light adaptation effect. Vision Research, 15, 595-603

Patel, A. S. (1966). Spatial resolution by the human visual system. Journal of the Optical Society of America, 56, 689-694.

Perrin, F. H. (1954). A study in binocular flicker. Journal of the Optical Society of America, 44, 60-69.

Pflug, R., & Nelson, R. (1986). Enhancement of red cone flicker by rod selective backgrounds in cat horizontal cells. Neuroscience Abstracts, 16, 402.

Pflug, R., Nelson, R, & Ahnelt, P. K. (1990). Background-induced flicker enhancement in cat retinal horizontal cells I. Temporal and spectral properties. Journal of Neurophysiology, 64,313-325.

Pirenne, M. H. (1943). Binocular and uniocular threshold of vision. Nature, 152, 698-699.

Poggio, G. F., & Fischer, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkeys. Journal of Neurophysiology, 40, 1392-1405.

Polyak, S. (1957). The Vertebrate Visual System. Chicago: University Chicago Press.

Prestrude, A. M. (1976). The interocular light adaptation effect at varying retinal locations. Vision Research, 16, 1071-1075.

Prestrude, A. M., Watkins, L., & Watkins, J. (1978). Interocular light adaptation effect on the Lie "specific threshold." Vision Research, 18, 855-857.

Purpura, K., Kaplan, E., & Shapley, R. M. (1988). Background light and the contrast gain of primate P and M retinal ganglion cells. Proceedings of the National Academy of Science, 85, 4534-4537.

Reeves, A., Peachey, N. S., & Auerbach, E. (1986). Interocular sensitization to a rod-detected test. Vision Research, 26, 1119-1127.

Rodieck, R. W., & Rushton, W. A. H. (1976). Isolation of rod and cone contributions to cat ganglion cells by a method of light exchange. Journal of Physiology, 254, 759-773.

Sherrington, C. S. (1904). On binocular flicker and the correlation of activity of 'corresponding' retinal points. British Journal of Psychology, 1, 26-60.

Sillito, A. M., Kemp, J. A., & Blakemore, C. (1986). The role of GABAergic inhibition in the cortical effects of monocular deprivation. Nature, London, 292, 318-320.

Singer, W., Gruenau, M. v., & Rauschecker, J. (1979). Requirements for the disruption of binocularity in the visual cortex of strabismic kittens. Brain Research, 171, 536-540.

Smith, D. C., Spear, P. D., & Kratz, K. E. (1978). Role of visual experience in postcritical-period reversal of effects of monocular deprivation in cat striate cortex. Journal of Comparative Neurology, 178, 313-328.

Snellen, H. (1862). Probebuchstaben zur Bestimmung der Sehschärfe. Utrecht: P. W. van de Weijer. In Graham, C. H. (Ed.) (1965), Vision and Visual Perception. New York, NY: John Wiley & Sons, Inc.

Steinberg, R. H. (1969). Rod and cone contributions to s-potentials from the cat retina. Vision Research, 9, 1319-1329.

Taub, E., & Berman, A. J. (1968). Movement and learning in the absence of sensory feedback. In S. J. Freeman (Ed.), The Neuropsychology of Spatially Oriented Behavior. Homewood, IL: Dorsey Press.

Trick, G. L., Dawson, W. W., & Compton, J. R. (1982). Interocular luminance differences and the binocular pattern-reversal visual-evoked response. Investigative Ophthalmology & Visual Science, 22, 394-401.

Vernon, M. D. (1934). The binocular perception of flicker. British Journal of Psychology, 24, 251-374.

Werner, H. (1940). Studies on contour: Strobostereoscopic phenomena. American Journal of Psychology, 53, 418-422.

Westendorf, D., & Blake, R. (1988). Binocular reaction times to contrast increments. Vision Research, 28, 355-359.

Westendorf, D. H., Blake, R. R., & Fox, R. (1972). Binocular summation of equal-energy flashes of unequal duration. Perception & Psychophysics, 12, 445-448.

Wheatstone, C. (1838). Contributions to the physiology of vision-I. On some remarkable, and hitherto unobserved, phænomena of binocular vision. Proceedings of the Royal Society of London, B, 18, 371-394.

White, C. T., & Bonelli, L. (1970). Binocular summation in the evoked potential as a function of image quality. American Journal of Optometry, 47, 304-309.

Whittle, P., & Challands, P. D. C. (1969). The effects of background luminance in the brightness of flashes. Vision Research, 9, 1095-1110.

Williams, R. (1974). The effect of strabismus on dichoptic summation of form information. Vision Research, 14, 307-309.

Witkovsky, P., Stone, S., & Tranchina, D. (1989). Photoreceptor to horizontal cell synaptic transfer in the Xenopus retina: Modulation by dopamine ligands and a circuit model for interactions of rod and cone inputs. Journal of Neurophysiology, 62, 864-881.

Wolfe, J. M. (1986). Stereopsis and binocular rivalry. Psychological Review, 93, 269-282.

Wolf, E., & Zigler, M. J. (1955). Course of dark adaptation under various conditions of pre-exposure and testing. Journal of the Optical Society of America, 45, 696-702.

Wolf, E., & Zigler, M. J. (1963). Effects of uniocular and binocular excitation of the peripheral retina with test fields of arious shapes on binocular summation. Journal of the Optical Society of America, 53, 1199-1205.

Wysecki, G., & Stiles, W. S. (1967). Color Science. New York, NY: Wiley.

Yellott, J. I., & Wandell, B. A. (1976). Color properties of the contrast flash effect: Monoptic vs. dichoptic comparisons. Vision Research, 16, 1275-1280.