

## INFORMATION TO USERS

The most advanced technology has been used to photograph and reproduce this manuscript from the microfilm master. UMI films the original text directly from the copy submitted. Thus, some dissertation copies are in typewriter face, while others may be from a computer printer.

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 copyrighted 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 oversize page is available as one exposure on a standard 35 mm slide or as a 17" x 23" black and white photographic print for an additional charge.

Photographs included in the original manuscript have been reproduced xerographically in this copy. 35 mm slides or 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.



300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA

Order Number 8801748

**Binocular interactions in humans: An evoked potential and psychophysical study**

Pinkhasov, Elizabeth I., Ph.D.

City University of New York, 1987

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

**PLEASE NOTE:**

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark .

1. Glossy photographs or pages \_\_\_\_\_
2. Colored illustrations, paper or print \_\_\_\_\_
3. Photographs with dark background \_\_\_\_\_
4. Illustrations are poor copy \_\_\_\_\_
5. Pages with black marks, not original copy
6. Print shows through as there is text on both sides of page \_\_\_\_\_
7. Indistinct, broken or small print on several pages
8. Print exceeds margin requirements \_\_\_\_\_
9. Tightly bound copy with print lost in spine \_\_\_\_\_
10. Computer printout pages with indistinct print \_\_\_\_\_
11. Page(s) \_\_\_\_\_ lacking when material received, and not available from school or author.
12. Page(s) \_\_\_\_\_ seem to be missing in numbering only as text follows.
13. Two pages numbered \_\_\_\_\_. Text follows.
14. Curling and wrinkled pages \_\_\_\_\_
15. Dissertation contains pages with print at a slant, filmed as received \_\_\_\_\_
16. Other \_\_\_\_\_  
\_\_\_\_\_  
\_\_\_\_\_

**U·M·I**

**Binocular Interactions in Humans:  
An Evoked Potential and Psychophysical Study**

by


*Elizabeth Pinkhasov*

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

1987

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

9/21/87  
date

  
Chairman of Examining Committee  
Prof. James Gordon

9/21/87  
date

  
Prof. Vance Zemon

9/22/87  
date

  
Executive Officer

Dr. Martin Chodorow

Dr. Stanley Novak

Dr. William Seiple  
Supervisory Committee

**Abstract****BINOCULAR INTERACTIONS IN HUMANS:  
AN EVOKED POTENTIAL AND PSYCHOPHYSICAL STUDY**

by

**Elizabeth Pinkhasov****Advisers: Professor James Gordon****Professor Vance Zemon**

In the present study visual evoked potentials (VEPs) and psychophysical techniques were used to determine the site of binocular interactions. Spekreijse and Oosting in 1970 offered a three-stage model of processing information in the visual system. In their model one linear filter precedes and another linear filter follows a static nonlinearity. To test the site of binocular interaction with respect to this nonlinearity two models of binocular interaction were examined. In one model, binocular summation occurs prior to the nonlinearity (rectification of the neural signals). In the other model binocular summation occurs after rectification.

Gratings of sinusoidal and square-wave spatial profiles were viewed dichoptically. Spatial frequencies of these gratings were 0.4-3.2 cycles per degree, and they were contrast-reversed at 2-6 Hz. The gratings presented to the two eyes were identical in spatial and temporal frequencies, but their relative temporal phase was varied parametrically: 0, 45, 90, 135, and 180 degrees. These stimuli elicited visual evoked potentials that contained a prominent component at twice the stimulus frequency (second harmonic). The amplitude and phase of this component depended on the relative temporal phase between the dichoptic stimuli. The two models make distinct predictions concerning this dependence.

The results indicate that the major contribution to the VEP arises from summation of monocular signals subsequent to the essential nonlinearity. A small but significant contribution, however, appears to originate from a binocular pathway that contains summation of monocular signals prior to the nonlinearity.

In the psychophysical part of the study, subjects used the method of adjustment to control the temporal phase of the second grating. They were instructed to bring both gratings in-phase to see it sharply, or out-of-phase to cancel the percept.

Results showed that responses depended on the fundamental temporal frequency component when the spatial frequency of the stimulus was low, but more upon the second harmonic component when the spatial frequency was high.

## ACKNOWLEDGMENTS

The experimental part of this research was performed at the Biophysics Laboratory of The Rockefeller University. I wish to express my gratitude to all the members of the laboratory for their continuous support, encouragement and patience.

## Table of Contents

|  |           |
|--|-----------|
| Title page.....  | i         |
| Approval page.....   | ii        |
| Abstract.....  | iii       |
| Acknowledgements.....  | v         |
| Table of Contents.....   | vi        |
| List of Tables.....  | viii      |
| List of Figures.....   | ix        |
| <b>INTRODUCTION.....</b>   | <b>1</b>  |
| <b>I. Psychophysical Evidence for Binocular Interaction.....</b>       | <b>1</b>  |
| <b>II. Electrophysiological Evidence for Binocular Interaction</b>     |           |
| Single cell recording.....   | 5         |
| Visual evoked potential studies.....                                   | 7         |
| <b>III. System Analysis.....</b>                                       | <b>10</b> |
| Models of binocular interaction to be tested in the present study..... | 14        |
| <b>METHOD</b>  |           |
| Subjects.....  | 16        |
| Stimulating Apparatus.....   | 16        |
| General Procedure.....   | 19        |
| Recordings.....  | 19        |
| <b>EXPERIMENT 1</b>  |           |
| Introduction.....  | 21        |
| Method   |           |
| Procedure.....   | 21        |
| Data acquisition and analysis.....                                     | 22        |
| Results and Discussion.....  | 22        |

**EXPERIMENT 2**

|   |           |
|---|-----------|
| <b>Introduction.....</b>                  | <b>37</b> |
| <b>Method</b>                             |           |
| <b>Subjects.....</b>                      | <b>47</b> |
| <b>Procedure.....</b>                     | <b>47</b> |
| <b>Data acquisition and analysis.....</b> | <b>48</b> |
| <b>Results and Discussion.....</b>        | <b>48</b> |

**EXPERIMENT 3**

|   |           |
|---|-----------|
| <b>Introduction.....</b>                  | <b>83</b> |
| <b>Method</b>                             |           |
| <b>Apparatus.....</b>                     | <b>84</b> |
| <b>Procedure.....</b>                     | <b>84</b> |
| <b>Data acquisition and analysis.....</b> | <b>85</b> |
| <b>Results and Discussion.....</b>        | <b>85</b> |

|                        |            |
|------------------------|------------|
| <b>APPENDIX A.....</b> | <b>106</b> |
|------------------------|------------|

|                        |            |
|------------------------|------------|
| <b>APPENDIX B.....</b> | <b>118</b> |
|------------------------|------------|

|                        |            |
|------------------------|------------|
| <b>REFERENCES.....</b> | <b>120</b> |
|------------------------|------------|

**LIST OF TABLES**

|  |           |
|--|-----------|
| <b>Table I - Estimated values of monocular and binocular contributions and phases for each subject.....</b>      | <b>61</b> |
| <b>Table II - Calculated binocular indices (ratios of binocular to monocular responses) of each subject.....</b> | <b>65</b> |

## LIST OF FIGURES

|  |    |
|--|----|
| Figure 1 - Three-stage model of information processing in the visual system offered by Spekrejse and Oosting.....                          | 12 |
| Figure 2 - General view of experimental setting.....   | 17 |
| Figure 3 - Spatio-temporal tuning curves of Subject B.F.....   | 23 |
| Figure 4 - Spatio-temporal tuning curves of Subject J.W.....   | 25 |
| Figure 5 - Spatio-temporal tuning curves of Subject M.C.....   | 27 |
| Figure 6 - Spatio-temporal tuning curves of Subject C.R.....   | 29 |
| Figure 7 - Spatio-temporal tuning curves of Subject E.P.....   | 31 |
| Figure 8 - Comparison of the response amplitudes to the different viewing conditions for the subjects group.....                           | 35 |
| Figure 9 - Binocular interaction, Model 1.....   | 39 |
| Figure 10 - Bbinocular interaction, Model 2 .....  | 41 |
| Figure 11 - Predicted output of the Model 1.....   | 43 |
| Figure 12 - Predicted output of the Model 2.....   | 45 |
| Figure 13 - Second harmonic of VER for Subject E.P.....  | 49 |
| Figure 14 - Second harmonic of VER for Subject C.R.....  | 51 |
| Figure 15 - Second harmonic of VER for Subject M.C.....  | 53 |
| Figure 16 - Combined model of binocular interaction.....   | 56 |
| Figure 17 - Predicted output of the Combined model calculated for different binocular contributions and phases.....                        | 58 |
| Figure 18 - Predicted output of the Combined model calculated for different monocular contributions in absence of any binocular input..... | 60 |
| Figure 19 - Response choices of Subject E.P. in the psychophysical experiment.....   | 70 |
| Figure 20 - Response choices of Subject C.R. in the psychophysical experiment.....   | 72 |

**Figure 21 - Response choices of Subject E.P. in the psychophysical  
experiment.....74**

## INTRODUCTION

The basic characteristic of binocular vision in humans is the fusion of two separate monocular inputs. The binocular pathway provides spatial visual information not available from either monocular pathway alone. When the visual system processes information that comes from only one eye, it does an astonishingly large amount of encoding. The three-dimensional world around us forms two two-dimensional images on the retinas, which are not merely point-by-point representations. Rather the information is filtered both spatially and temporally. This processed signal is transmitted along the optic nerve to the brain. Subsequently, after additional filtering in the lateral geniculate nucleus (LGN), the image is sent to the primary visual cortex (striate, area 17) and undergoes additional processing in the striate and extrastriate cortices (areas 18,19) (Shapley and Lennie, 1984). Hubel and Wiesel in the 1960's, conducted electrophysiological studies of the visual system of cat (1962) and monkey (1968), and showed that the convergence of the inputs from two eyes upon one cell is one of the primary functions of the striate cortex. They suggested that binocular "interaction is minimal for simple cells, distinctly more for complex cells and possibly still more for hypercomplex" cells {p. 7}.

These findings provide a foundation for electrophysiological investigations of binocular interaction in humans since they can help to pinpoint the anatomical sources of the evoked potentials specific to binocular and dichoptic stimulation.

The aims of this investigation were to study the relations between the *binocular interactions in humans and linear and nonlinear stages of neural processing known to occur in the visual system.*

### I. Psychophysical Evidence for Binocular Interaction.

In a large body of psychophysical literature, a variety of perceptual phenomena are associated with manifestations of binocular interaction in the

human visual system. Much of this literature was reviewed by Blake and Fox in 1973, and then updated in 1981 (Blake, Sloane, and Fox, 1981).

In 1903, Piper measured monocular and binocular absolute thresholds which occur in the peripheral retina at various times during the course of dark adaptation. He found that, under equal conditions, the binocular threshold was lower than the monocular. In 1906 Sherrington, reported that, according to his introspective observations, the brightness of a target viewed binocularly was "somewhat, but not far, above the arithmetic mean of two values of two monocular components as expressed by the measures of the physical stimuli yielding them" {p.373}. Subsequent psychophysical studies revealed, that in many visual tasks, such as detection of very dim lights (absolute thresholds), increments of light flashed on lit backgrounds (increment thresholds), and contrast and flicker perception, humans benefit by using both eyes simultaneously, rather than by using one eye alone. This phenomenon is known as a "binocular summation" (Dawson,1913). However, it was not until the 1940's that theoretical interpretations of superior binocular performance were proposed.

In 1943 Pirenne suggested a probability-summation hypothesis, which stated that the improvement in binocular performance could be explained by the independence theorem of probability. This theorem states that the probability of occurrence of two independent events is equal to the sum of their individual probabilities minus the product of their probabilities. Thus, if the probability of detection using the left eye is .5 and the probability of detection using the right eye is .5, the probability of detection using both eyes will be 0.75 (i.e.,  $0.5 + 0.5 - (0.5 \times 0.5)$ ).

This hypothesis was adjusted by Green and Swets in 1966 in the light of the signal detection theory.

Later, Keeley and Doherty (1972) presented another model of binocular

summation, which implied that, in multiple observation situations, a subject's response is independent of previous responses.

Blake and Fox (1973) reported that binocular interactions might result not only as an enhancement but sometimes as a reduction of binocular responses compared to monocular responses. They identified four outcomes of binocular stimulation by analogy with the neural interaction found in spinal reflexes: 1) Any binocular response which is greater than the sum of the two monocular responses, was labeled facilitation. 2) Any binocular response which is equal to the sum of the two monocular responses, was called linear summation. 3) When the binocular response is less than the sum of the two monocular responses, yet greater than the response of a single input, it was called occlusion. 4) When the binocular response is equal to, or less than the response of the monocular input, it is called inhibition.

The magnitude of binocular performance depends upon spatial and temporal characteristics of the stimuli. Improvement of binocular over monocular performance requires a close match of temporal properties of the stimuli. Maximum enhancement of the binocular response usually occurs with simultaneous stimulus conditions (Thorn and Boynton, 1974). However, asynchrony in light flashes of greater than 100 msec, and in gratings of greater than 50 msec, produce the binocular response that is expected from a probability summation model (Westendorf, Langston, Chambers, and Allegretti, 1978).

Recently grating patterns of different spatial and temporal characteristics, stimuli commonly used in monocular vision research, have been applied to the study of binocular interaction as well. Research into the spatial attributes of the stimuli showed that in order to obtain binocular summation, the spatial frequencies of the two monocular inputs should be very close (Arditi et al., 1981; Blake and Rush, 1980; Rose, 1978). The magnitude of summation, however declines with increasing spatial frequency (Blake, Sloane, and Fox, 1981). Bacon (1976) also found, that

when monocular stimuli differ in relative spatial phase, the binocular response decreases. Phase-specific summation was reported also by Green and Blake (1981). Blake and Levinson (1977) found that binocular sensitivity depends upon the orientation of gratings presented to each eye. When the orientation between gratings differs by more than 15 degrees, the magnitude of response falls to a monocular level.

In addition to spatial and temporal attributes the degree of retinal correspondence of stimuli also effects the range of binocular detection. Westendorf and Fox, (1977), Blake, Martens, and Di Gianfillipo, (1980), Harwerth, Smith, and Levi, (1980) found that facilitation of binocular response occurred within retinal disparities of 1 to 4 minutes of arc. Stimulation of non-corresponding areas of the retinas would yield a binocular response only in a range of probability summation.

Another important factor controlling the extent of binocular performance concerns the differences between the eyes of a subject. Humans exhibit different degrees of ocular dominance, and it appears that binocular summation takes place only if both eyes of the observer are relatively balanced in sensitivity (Blake and Fox, 1973).

Facilitation of the binocular response which is much greater than statistical probability summation, must arise from some form of physiological interaction. This interaction was called "neural summation" by Blake, Martens, Garret, and Westendorf (1980), a term which suggests the existence of a specific pathway responsible for the manifestation of the phenomenon of binocular facilitation.

Finally, it should be noted that binocular facilitation is probably very closely related to stereopsis. Ogle in 1963, and Ross and Hobgen in 1974 pointed out that, for stereopsis, the temporal interval between successive presentation of half-images must not exceed 100 msec; the same amount of time that is critical for the

occurrence of enhanced binocular detection (Westendorf, Langston, Chambers, and Allegretti, 1978).

The area of retinal correspondence of stimuli essential for the manifestation of binocular facilitation lies in the disparity range of less than 10 min of arc. It is known that, for small disparities, an object presented separately (dichoptically) to each eye is seen as a single object (Barlow and Mollon, 1985).

It was also shown, that stereoblind humans (Lemma and Blake, 1977; Levi, Harwerth, and Manny, 1979) and stereoblind cats (von Grunau, 1979) also lack binocular summation, another fact indicating similarity between both processes.

## II. Electrophysiological Evidence for Binocular Interaction.

### Single cell recording

The lateral geniculate nucleus of the thalamus (LGN) is the first neural structure receiving inputs from both eyes. However, there is no significant convergence of the inputs from the two eyes in monkey LGN nor, most probably, in human LGN. Each of the six layers of the LGN receives input from only one eye. Studies of the cat's LGN has shown only minimal interaction across the layers (Sanderson, Darian-Smith & Bishop, 1969; Guillery, 1966). Lund, Lund, Hendrickson, Bunt, and Fuchs (1975), using the anatomical technique of retrograde transport of horseradish peroxidase, found that layer VI of the monkey's visual cortex, which has many binocular cells, sends a strong projection to the LGN. Their finding raises the possibility of an indirect influence on some geniculate cells from both eyes.

From the LGN, pathways associated with each eye terminate in separate clusters in layer IV of the striate cortex. Therefore, inputs from the two eyes converge on neurons in the superficial cortical layers II and III, and deep cortical layers V and VI only through intracortical connections. Studies in 1962 and 1968 by

Hubel and Wiesel, found some cells in the visual cortex of cat and monkey that responded to stimulation of one eye alone, but not to stimulation of the other eye. Other cells, however, responded only when both eyes were stimulated simultaneously. They reported that the receptive fields of all binocularly influenced cortical cells were similar in each eye. The only differences that existed between the two fields were related to the relative strength of each eye: identical stimuli to the two eyes evoked identical responses only in some cells; in others, stimulation of one eye would evoke a stronger response than an equal stimulation of the other eye. The authors subdivided all observed cells into seven groups according to the degree of ocular dominance. Group one consisted of cells responding only to stimulation of the contralateral eye. Group two responded much more to the stimulation of the contralateral eye than to stimulation of the ipsilateral eye. Cells in the group three were only slightly more responsive to stimulation of the contralateral than ipsilateral eye. Cells of the fourth group did not show "obvious difference in the effects exerted by the two eyes". For the cells of the fifth group, stimulation of the ipsilateral eye was slightly more effective than stimulation of contralateral eye. Group six was even more responsive to stimulation of the ipsilateral than contralateral eye. Finally, cells of the seventh group were "exclusively ipsilateral".

In 1967, Barlow, Blakemore, and Pettigrew, and in 1968 Pettigrew, Nikara and Bishop found binocular cells in the cat's cortex that respond to the various degrees of separation between their receptive fields (binocular disparity). Some of those cells have fields in exact binocular correspondence, while others have fields with convergent or divergent disparity (Poggio, 1979). All of these findings suggest that cortical neurons influenced by binocular stimulation are probably involved in stereoscopic depth perception (stereopsis).

In 1984, Gardner demonstrated the relationship between ocular dominance and disparity sensitivity in the cells of area 18 and the border between areas 17 and

18 of the cat. Gardner showed that cells which were thought to be monocular by other investigators (categories 1 and 7 according to classification of Hubel and Wiesel, 1962) are indeed the binocular cells with greatest sensitivity to retinal disparity. Units driven equally by either eye were the least sensitive to disparity. She also found larger binocular interactions among the units dominated by ipsilateral eye input in comparison to the units dominated by contralateral eye input. Her findings may allow several conclusions. First, it is possible that the retinal receptive fields of cells of categories 1 and 7 (by Hubel and Wiesel classification, 1962) are different for each eye. Second, it may suggest that the input from the contralateral eye has synapses on the cells connected to the input from the ipsilateral eye.

Compared to the animal studies, it is more difficult to identify where binocular interaction takes place in the human's cortex. Nevertheless, similarities in the visual pathways of humans and monkeys might suggest that the results of monkey studies could be extended to humans.

#### Visual evoked potential studies

Using dichoptic stimulation, characteristics of the binocular interactions in humans can be measured by recording electrophysiological responses (visually evoked potentials, VEP's) from the surface of the head. Creutzfeld and Kuhnt (1967) viewed visually evoked potentials (VEP) as a synthesis of compound excitatory postsynaptical potentials and inhibitory postsynaptical potentials of cortical cells, as well as of synchronous afferent and efferent fiber activity. VEPs are often elicited by contrast-reversing spatial patterns such as gratings and checkerboards.

Despite the fact that a large number of VEP studies have been concerned with binocular interaction, there is no VEP data which is as clear cut as that obtained in single unit studies.

White and Bonelli in 1970, and Harter, Seiple and Salmon in 1973, have reported that, under conditions where identical patterns were presented to both eyes, binocularly elicited VEPs were greater in amplitude than monocularly elicited VEPs. Comparing monocularly and binocularly elicited VEPs Harter (1977) suggested that when the amplitude of binocular VEPs is greater than the amplitude of monocular VEPs it is binocular summation, and when the amplitude of binocular VEPs is less or equal to the amplitude of monocular VEPs it is binocular suppression. He called this latter phenomenon interocular suppression and showed that it occurs when the dichoptic images falling on the retinas are not perceptually fused. His dichoptic stimuli consisted of spatial patterns of different sizes, or different orientations, or of patterns presented to non-corresponding retinal points. In addition, he found that patterned light presented dichoptically under conditions of retinal disparity elicited VEPs with amplitudes greater than those elicited with non-disparate conditions. He suggested that binocular interaction in humans is mediated by cortical mechanisms analogous to single cortical units described by Hubel and Wiesel (1968), and Pettigrew et al. (1968).

Harter, Seiple and Musso (1974) showed that the degree of binocular summation depends on the nature of the stimulus presented to each eye. When only one eye viewed a square-wave grid pattern of 15', 30', or 60' of visual subtense and the other eye viewed diffuse light, the amplitude and the waveform of the VEP elicited by this kind of binocular stimulation was equivalent to that of the monocular VEP elicited by the eye receiving the pattern. VEP amplitudes were greatest when when both eyes were presented with identical patterns.

In a paper published later, Harter, Conder, and Towle (1980) investigated interocular orientation effects on VEP amplitude, stimulating one eye by flashes of either diffuse light or square-wave gratings (0 or 45 degrees) and other eye by the diffuse light of continuously changing luminance, or by continuously presented

square-wave gratings of 0, 15, or 45 degrees of orientation. They found that increasing the similarity of orientation of the flashed and continuously presented grids reduced the amplitude of the VEP. The authors suggested that orientation-specific interocular suppression indicates the presence in the human visual cortex of orientation-specific channels, which are located "at or more central to the point of binocular convergence". They proposed that activity of complex and hypercomplex cells located in layers II, III, V, and VI of striate cortex mediates the binocular orientation channels.

Ellenberger and Shuttlesworth (1978) tried to identify wave components of the VEP generated by flashed patterns. They found differences in the amplitude of a late component (150 msec) between binocular and monocular presentation. For an early component (70 msec) of the VEP, no effects of binocular summation were found.

Apkarian, Nakayama, and Tyler (1981) investigated the influence of different spatial frequencies, as well as contrast, orientation of gratings and retinal disparity on the VEP. The level of binocular interaction, which they measured as the ratio of binocular response (B) to the sum of the means of two monocular responses (2M) was expressed numerically and varied in range from inhibition ( $B < M$ ) to facilitation ( $B > 2M$ ). Apkarian et al (1981) found that spatial frequency tuning occurred at 1.7 c/deg and at 4.3 c/deg for the binocular, and at 1.0 c/deg and 5.0 c/deg for the monocular responses. Increase of stimulus contrast did not produce saturation of binocular, but produced saturation of monocular responses. The authors also suggested that binocular facilitation was related to stereoscopic processing based on the results of the disparity experiments.

Tyler and Apkarian (1985), studying monocular and binocular VEPs as a function of stimulus contrast under a range of spatio-temporal conditions, concluded that binocular responses may be interpreted as a combination of monocular and

purely binocular (stereoscopic) responses. They suggested also that binocular VEPs are a product of several kinds of pattern-specific mechanisms, each having different spatio-temporal response characteristics (e.g., ocularity, orientation tuning and contrast gain). Another interesting finding of this study was non-correspondence of the threshold found by the means of electrophysiological techniques with psychophysical threshold at any spatial or temporal frequency used by the researchers.

In summary, it should be noted that, as a result of different recording techniques and stimulus conditions, the magnitude of reported binocular interactions ranges from inhibition to facilitation. However, it is generally agreed that amplitude of binocular response increases when such physical characteristics of stimuli as temporal and spatial frequencies, luminance, contrast and orientation are similar. It is also noted by many authors that binocular interaction is related to stereoscopic depth perception, and Apkarian et al. (1981) found some correlation between VEPs and fusion, rivalry and stereopsis.

### III. Systems Analysis

The VEP technique can be described as the technique of applying deterministic input signals to a system showing some intrinsic activity. This approach is characteristic of systems analysis, which views any biological system as a collection of components arranged and interconnected in a definite way (Basar, 1976). Each system has an input and an output, and it is the relationship between those two that is under study. If only input and output signals of the system are known, the system is considered a black box. Thus, we can refer to the visual system rather as a grey box, since we have at least partial knowledge about some of its elements.

Important characteristics of any system are linearity or nonlinearity. A linear system obeys the principle of superposition, which states that if one stimulus,  $S_1$ , elicits a response,  $R_1$ , and another stimulus,  $S_2$ , elicits a response,  $R_2$ , then the sum of the first two stimuli,  $(S_1 + S_2)$ , elicits a response that is the sum of the first two responses,  $(R_1 + R_2)$ . A sinusoidal signal applied to the input of a linear system would elicit a sinusoidal response of the same frequency. No novel frequencies can be generated by a linear system; only amplitude changes and phase shifts are introduced. The response of this system to any arbitrary signal can be predicted using its transfer function, which is represented by plots of the ratio of output to input amplitude (gain) and relative position of output compared to input (phase) versus frequency.

The analysis of a nonlinear system is more difficult. Nonlinearity generates response components at frequencies which are multiples (harmonics) of the original (fundamental) frequencies, and combinations (intermodulations) of these frequencies. Therefore, measuring the responses of such a system to a set of single sinusoidal inputs will not enable us to predict the response of that system to an arbitrary input.

It should be noted here that VEPs, elicited by counterphase luminance modulation, reflect nonlinear responses of the system. Any linear response from one group of cells would be canceled at the recording site by an equal magnitude, but out-of-phase response from an adjacent group of cells.

In 1970, Spekreijse and Oosting offered a three-stage model of information processing in the visual system (fig 1). In their model, one linear filter, (L1) precedes, and another linear filter, (L2), follows, a static nonlinearity, (N).

**Figure 1. Three-stage model of information processing in the visual system offered by Spekreijse and Oosting (1970).**

**S - stimulus**

**L1 - first linear filter**

**N - rectifier-like nonlinearity**

**L2 - second linear filter**

**VEP - visual evoked potential**

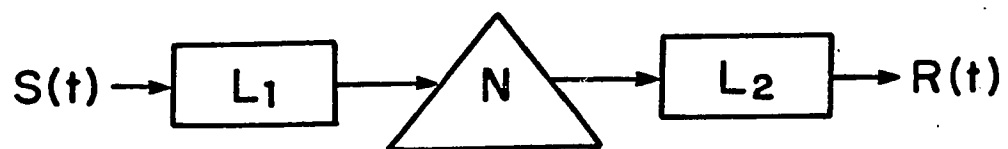


Figure 1

The initial linearity of the visual system is supported by the results of several studies involving single cell recording. A large population of retinal cells are the "X" type with a linear characteristic (Enroth-Cugell et al., 1966; Hochstein and Shapley, 1976; Kaplan and Shapley, 1982).

The particular nonlinearity in the visual system is thought to be some kind of a rectifier (Spekreijse and Oosting, 1970; Clynes, 1961). It has been shown that, presumably as a result of the strong inhibitory influence, cortical cells lack spontaneous activity. Thus, a change of a stimulus sign can not modulate a maintained discharge below its resting level. This results in half-wave rectification of the input signal. Most "simple" cortical cells show this the type of response (De Valois, Albrecht, and Thorell, 1982; Spitzer and Hochstein, 1985a; Spitzer and Hochstein, 1985b).

The second linear filter is probably responsible for the differences between sum and difference intermodulation responses observed in the VEP (Zemon, 1984; Zemon and Ratliff, 1984; Zemon et al., 1985).

As a first approximation, the three-stage or "sandwich" model seems to be a good, parsimonious explanation of processing in the visual system, not only for evoked potential data but for data obtained from single cell recordings as well (Victor and Shapley, 1980).

#### Models of binocular interaction to be tested in the present study

We are trying to incorporate binocular interactions into the "sandwich" model of Spekreijse and Oosting (1970). Our suggestion is that the binocular system can be viewed initially as two monocular pathways, each consisting of an identical "sandwich" system. Binocular interaction can occur sometime after the first linear filter and preceding the nonlinear stage, or can follow the nonlinear stage. Two models of binocular interaction are considered. Here we are giving only brief

explanation of both models, which will be discussed in greater details in the chapter describing experiment two (pages 27-30), and are depicted in figures 9 and 10. In the first model, binocular summation occurs after linear filter  $L_1$  and prior to the nonlinear stage  $N$  (Model 1, Fig 9). In the second model, binocular summation occurs after the nonlinear stage  $N$  (Model 2, Fig. 10). The fundamental question to be answered in this thesis is where the linear and nonlinear filters of the monocular pathways are located with respect to the locus of binocular summation. Three experiments will be discussed in this thesis: 1) The pilot electrophysiological study selecting the spatial and temporal characteristic of the stimuli and comparing different conditions of stimulus presentation. 2) An electrophysiological study describing and testing both models of binocular interaction. Here temporal phases of dichoptic stimuli were fixed when presented to one eye of the subject and were parametrically changed when presented to the other eye. 3) A psychophysical study examining what aspects of stimuli influence binocular perception.

## METHOD

### Subjects

The first experiment was performed on five subjects (three females and two males) who were members of the Laboratory of Biophysics of the Rockefeller University. The ages of the subjects ranged from 26 to 38 years. All subjects had normal stereopsis and normal, or corrected to normal, visual acuity. After initial testing, however, only three subjects, who had the highest amplitudes of evoked responses (two females and one male), were chosen for participation in the rest of the study (experiments two and three).

### Stimulating Apparatus

A two-dimensional computer-controlled visual stimulator, designed by the researchers of the Laboratory of Biophysics of The Rockefeller University, was used (Milkman, Shick, Rosetto, Ratliff, Shapley, and Victor, 1980). Sinusoidal or square wave grating stimuli were presented on a pair of cathode ray oscilloscopes (Tektronix 608, P31 phosphor). Polarizing material was placed in front of each screen so that direction of the light going through the polarizer from one screen was orthogonal with respect to the other screen. Images from the two screens were superimposed by means of a beam-splitting mirror, and were viewed dichoptically with the aid of polarizing glasses. A neutral density filter, (NDF=0.2 log units), was placed in the front of one screen to correct for the differences in luminance produced by the beam-splitter. Mean luminance of each screen was 45 ft-lamberts ( $154.18 \text{ cd/m}^2$ ) before filtering. The luminance of the apparatus after the filtering by the beam splitter and polarizing filters was equal to four foot lamberts ( $13.7 \text{ cd/m}^2$ ). The general scheme of the apparatus is shown in figure 2.

**Figure 2. The general scheme of apparatus used in the experiments.**

**crt 1 & crt 2 - oscilloscope displays 1 & 2**

**bs - beam splitting mirror**

**nf - neutral density filters**

**pf - polarizing filters**

**pg - polarizing glasses**

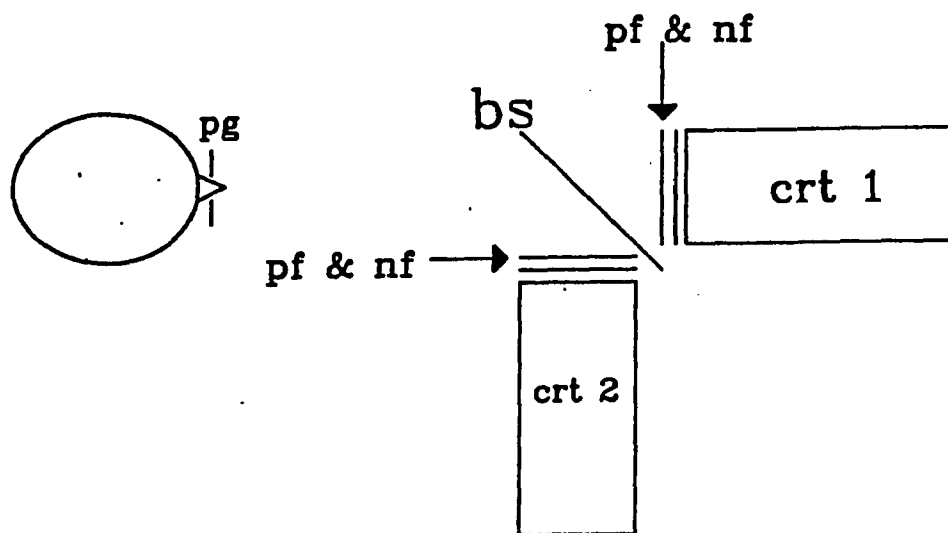


Figure 2

## General Procedure

The subjects were seated in a darkened room, lit only by the light coming from the screens. Subjects faced the screens, situated one meter from their eyes. The subject's head was on a headrest. A mask with needles ("Nonious" marks) attached to its top and its bottom was placed in front of each screen, so that the needles from the identical areas of each frame were superimposed by the beam-splitter. The subjects were instructed to fixate on these "Nonius" marks and to inform the experimenter if they observed more than two needles in their visual field. These Nonius marks were used in order to attain convergence. The visual angle of a target was 4.57 degrees.

## Recordings

Electrophysiological recordings were made using conventional EEG methodology. Gold plated cup (Grass) recording electrodes (type E5G, diameter 10 mm) were placed on the midline of scalp over the occipital area (Oz, active electrode), vertex (Cz, reference electrode), and parietal area (Pz, ground) (10-20 electrode placement system, Jasper, 1958). Resistance of the skin under each electrode was reduced by rubbing a small amount of Hewlett Packard Redux Paste onto the scalp. The electrodes were attached to the skin by the electro conductive Grass EC2 Electrode Cream.

The EEG signal was fed to an AC coupled differential amplifier. The bandwidth setting was .03 to 100 Hz, with a gain setting of 10,000. During each trial, the amplified electroencephalogram (EEG) was forwarded to an analog to digital (A to D) converter, and processed and stored by an LSI 11/23 microcomputer. The EEG was sampled at the rate of 270 Hz, and two 30 sec epochs were averaged during each experimental run. The resulting EEG record was Fourier analyzed and

the amplitudes and phases of second- and fourth-order frequency components were printed on a hard copy unit. The averaged EEG was also stored on floppy disks.

## EXPERIMENT 1

### Introduction

This experiment was designed as a pilot study with the purpose of finding out what characteristics of the stimulus provide sizable dichoptic responses. All five subjects were presented with sinusoidal or square-wave gratings of several spatial and temporal frequencies.

Sinusoidal gratings are simple stimuli containing only a single spatial frequency, which is convenient for subsequent analyses. Square wave gratings are more complex, consisting of a sum of many sine waves of different frequencies. However the sharp edges of the latter stimulus facilitate accurate accommodation and are very useful for aligning dichoptic images.

Stimuli that elicited responses of greatest amplitude were then used under binocular viewing conditions as a control for dichoptic viewing. The monocularly elicited VEP's to these stimuli were also recorded in order to compare the monocular and binocular responses.

### Method

#### Procedure

Each subject viewed dichoptically presented gratings of spatial frequencies of 0.4, 0.8, 1.6, 3.2, and 6.4 cycles/degree modulated at temporal frequencies of 2.1, 4.2, 5.3, and 6.3 Hz. Contrast, defined as the ratio  $(I_{\max} - I_{\min}) / (I_{\max} + I_{\min})$  where  $I_{\max}$  and  $I_{\min}$  are the maximum and minimal luminance of the grating, was 0.3. The spatial profile (sine or square wave) and the order of stimulus presentation was randomly assigned prior to each experiment.

Binocular VEPs were recorded when the subject viewed only one screen without polarizing glasses, and with a neutral density filter (ND = 0.5 log units)

placed in front of the screen (to equate the luminance with that under dichoptic conditions).

During monocular stimulus presentation the subjects viewed only one screen, either through the polarized filter or through the neutral density filter (ND=0.5 log units) placed in front of the screen. The second screen was turned off during this part of the experiment.

The sequence of stimulus presentation (dichoptic viewing / binocular viewing /monocular viewing through the polarizing glasses / monocular viewing through the neutral density filter ) was randomly assigned prior to the experiment and repeated twice in a counterbalanced order; thus, for monocular conditions, both eyes were tested once.

#### Data Acquisition and Analysis

Fourier analysis of second and fourth harmonics of the responses was performed at the end of each run. The vector averaged responses of the spatial and temporal "tuning" experiment were calculated and plotted by the computer, (using the program "Grapher", designed by Golden Software, Inc., P.O. Box 281 Golden, Colorado 80402).

For the second part of this study, comparing monocular, dichoptic and binocular conditions of a stimulus presentation, the vector averaged responses were calculated for each viewing condition. Mean response amplitudes and standard errors of the group were calculated and plotted as a bar graph for each condition of stimulus presentation.

#### Results and Discussion

Complete numerical results of the "tuning" experiment are presented in table 1 of Appendix A. Data for each subject are shown in figures 3, 4, 5, 6 and 7.

**Figure 3.** The response amplitudes of subject B.F. to the stimuli of different spatial and temporal frequencies.

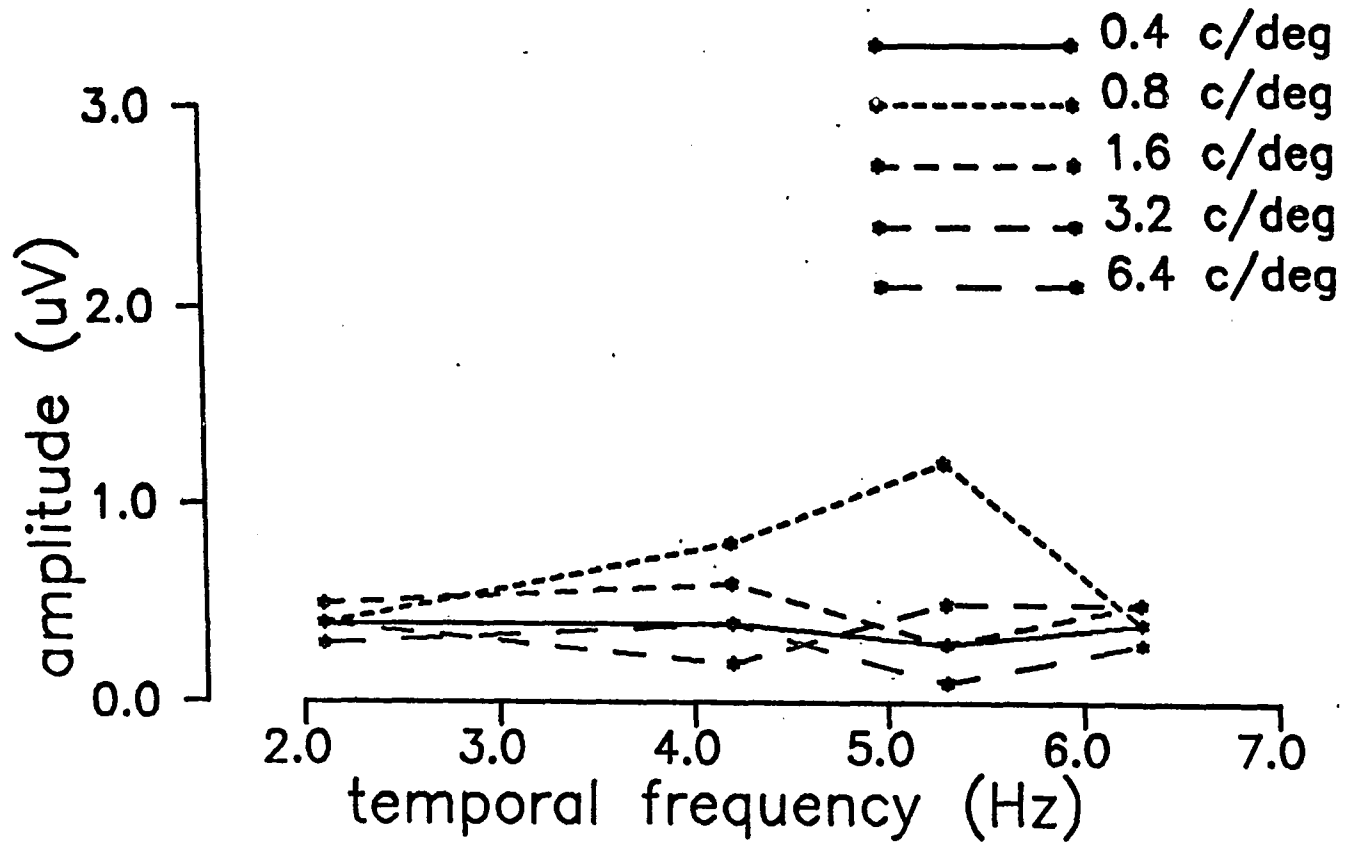


Figure 3

**Figure 4. The response amplitudes of subject J.W. to the stimuli of different spatial and temporal frequencies.**

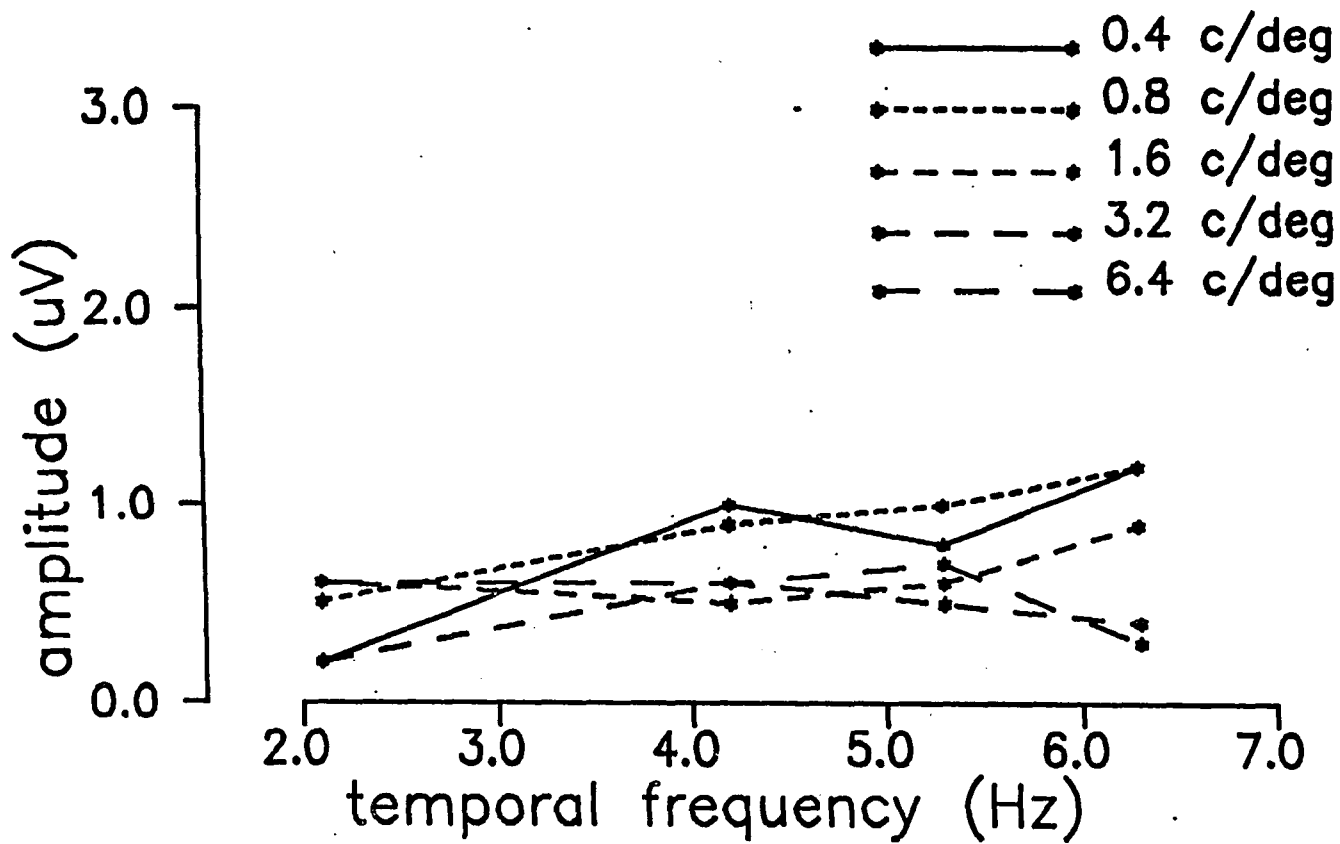


Figure 4

**Figure 5.** The response amplitudes of subject M.C. to the stimuli of different spatial and temporal frequencies.

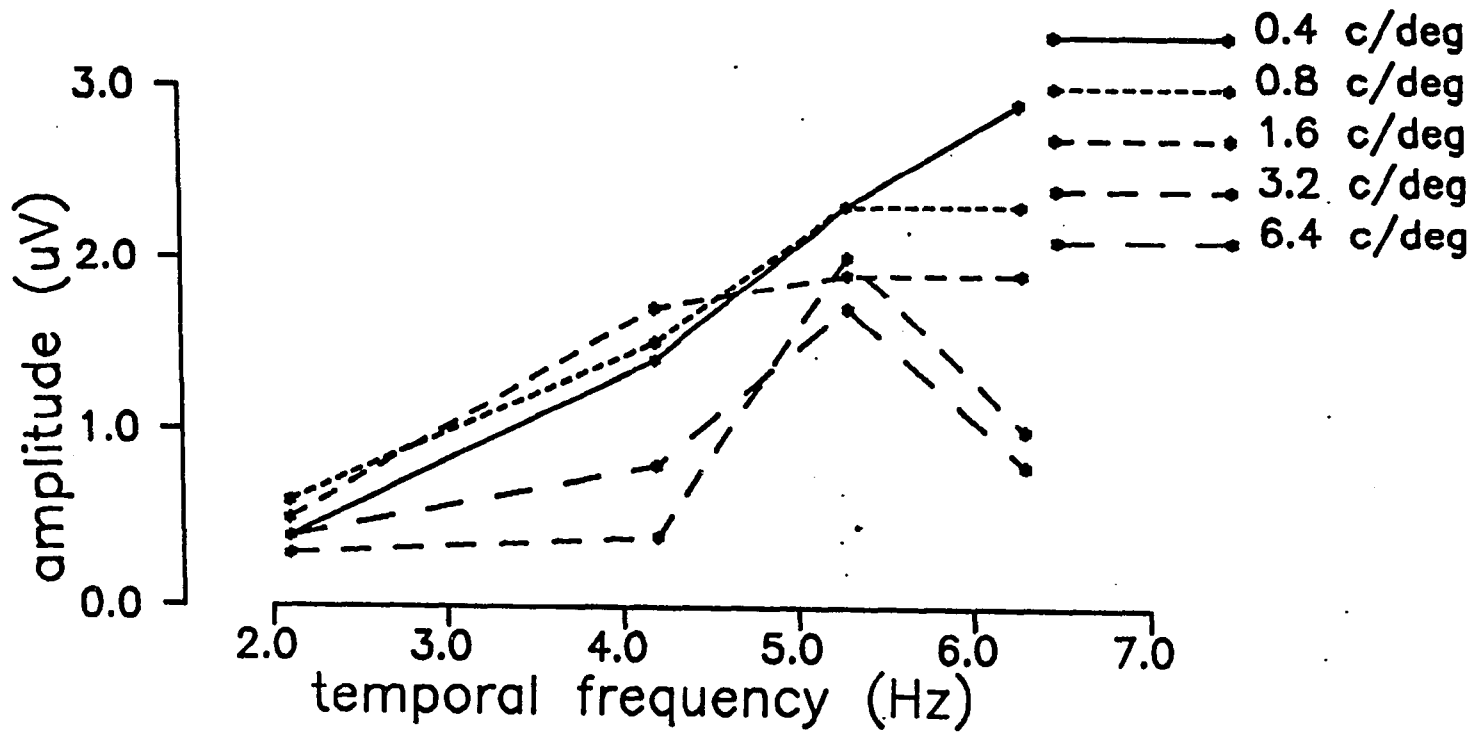


Figure 5

**Figure 6. The response amplitudes of subject C.R. to the stimuli of different spatial and temporal frequencies.**

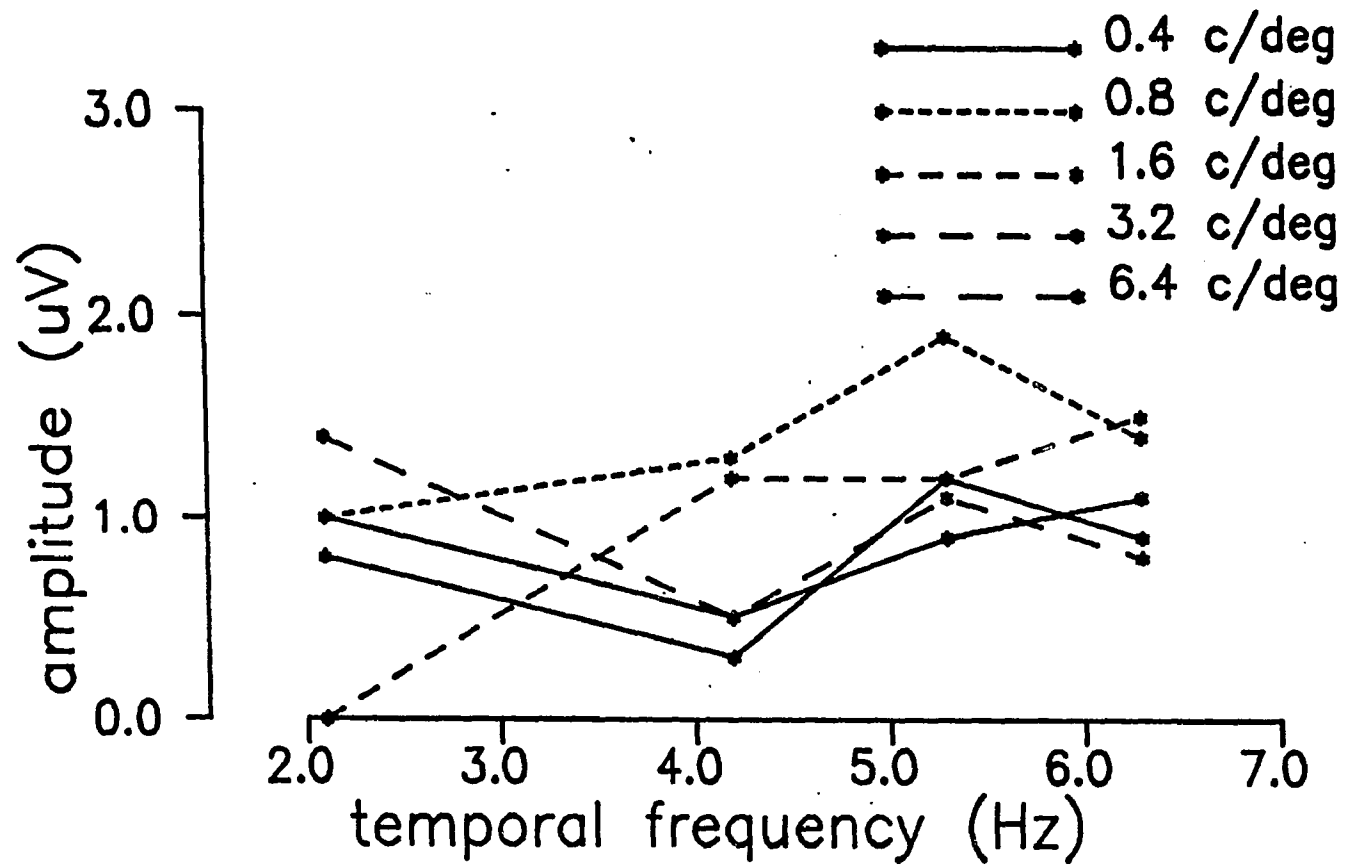


Figure 6

Figure 7. The response amplitudes of subject E.P. to the stimuli of different spatial and temporal frequencies.

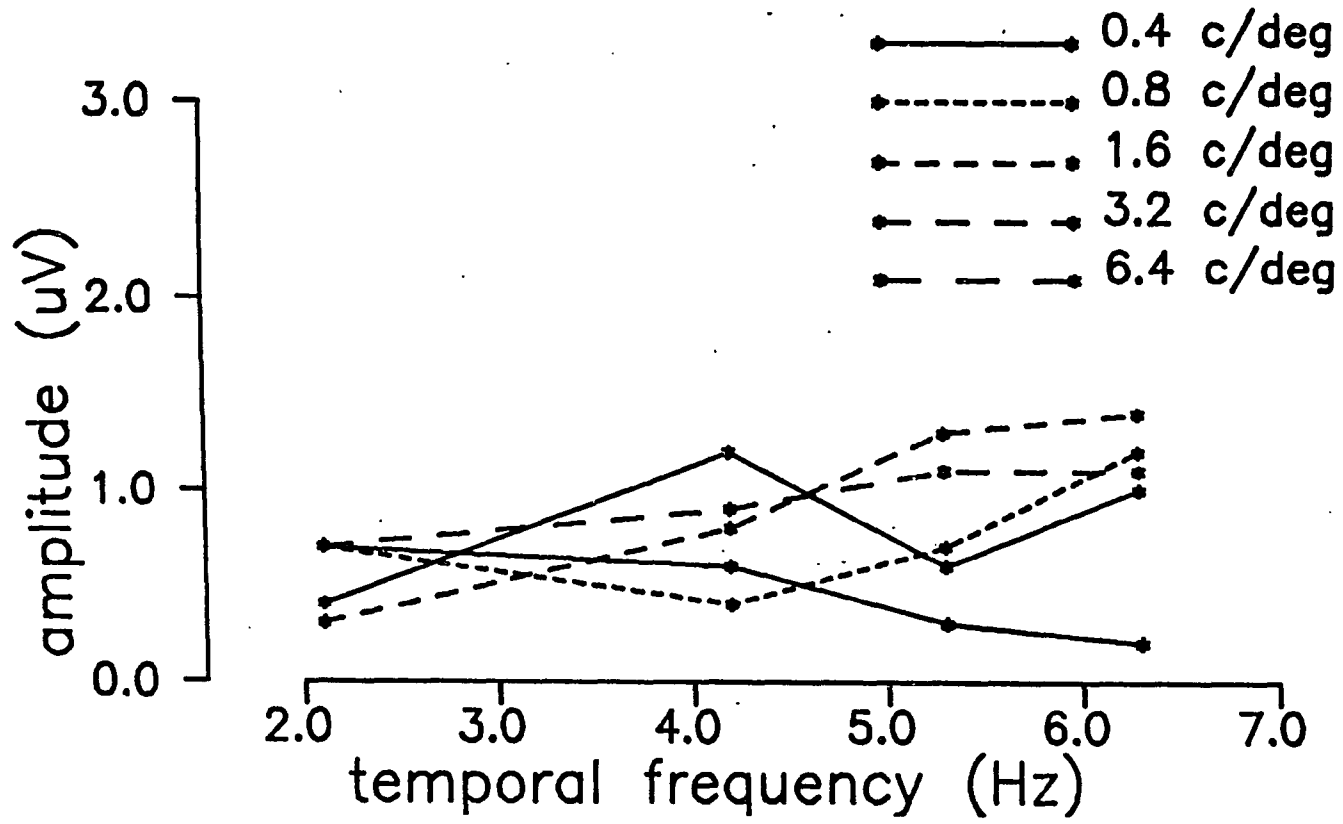


Figure 7

For each subject, responses depended critically on spatial and temporal frequencies. Response amplitudes of two subjects (B.F. and J.W.) were very small (Fig. 3 and 4).

Response amplitudes of the rest of the group did not show any common specific dependency upon spatial or temporal stimulus characteristics. One subject (M.C.) was "tuned" to a specific temporal frequency of 5.3 Hz (Fig. 5). Another subject (C.R.) was more "tuned" to the spatial than to the temporal characteristics of the stimuli. His biggest responses were to gratings of 0.8 and 1.6 c/deg (Fig. 6). Responses of the third subject (E.P.) seemed to be greatly affected by the changes of the spatial as well as by the temporal conditions of the stimuli. Her responses were greatest at 6.3 Hz in the range between 0.8 and 3.2 c/deg (Fig. 7).

Results of the tuning experiment are generally in agreement with the findings of Green (1981), who was studying the threshold of flicker detection and found that the visual system of humans is most sensitive to the range between 0.5 and 3-4 c/deg in the spatial domain and between 2 and 8 Hz in the temporal domain. All our subjects were sensitive to gratings which were less than or equal to 3.2 c/deg, in a range of temporal frequencies from 4.2 to 6.3 Hz. This is consistent also with observation of Legge (1978), that "psychophysical detection of sine wave gratings is governed by transient mechanisms at low spatial frequencies".

There is also some possibility, that dichoptic stimulation taps the visual channels responsible for stereopsis. Norcia and Tyler (1984) investigating stereopsis using random dot stimuli of different temporal frequencies found that the temporal limit for perception of apparent depth motion was approximately 6 Hz.

Results of the experiment comparing dichoptic, binocular, and monocular conditions of stimulus presentation is shown for each subject in the tables 2, 3, 4, 5, and 6 of Appendix A and in figure 8, where the averaged amplitudes of all subjects

are compared for dichoptic, binocular, and monocular responses. Under monocular viewing conditions there were two results since each subject was tested with polarizing glasses (for comparison to dichoptic viewing), and with the neutral density filter in front of the screen (for comparison to binocular viewing).

It may be seen that under dichoptic and binocular conditions the response amplitudes elicited by the sine wave gratings were somewhat lower than response amplitudes elicited by the square wave gratings. However, this difference in the response amplitudes were not in the same direction in all subjects and were not statistically significant.

Amplitudes of the dichoptic and binocular responses for the group were almost equal to twice the monocular response. This demonstrates almost complete binocular summation.

Thus, mean response amplitudes under dichoptic and binocular conditions were comparable for the group, and twice as large as response amplitudes under monocular conditions.

**Figure 8.** Comparison of the response amplitudes for the group of five subjects to the different viewing conditions.

Empty bars - response amplitudes to the stimuli of sinusoidal spatial profile.

Hatched bars - responses amplitudes to the stimuli of square spatial profile.

DICHOP - dichoptic viewing.

BINOC - binocular viewing.

MONO-G - monocular viewing through the polarizing glasses.

MONO-F - monocular viewing through the neutral density filters.

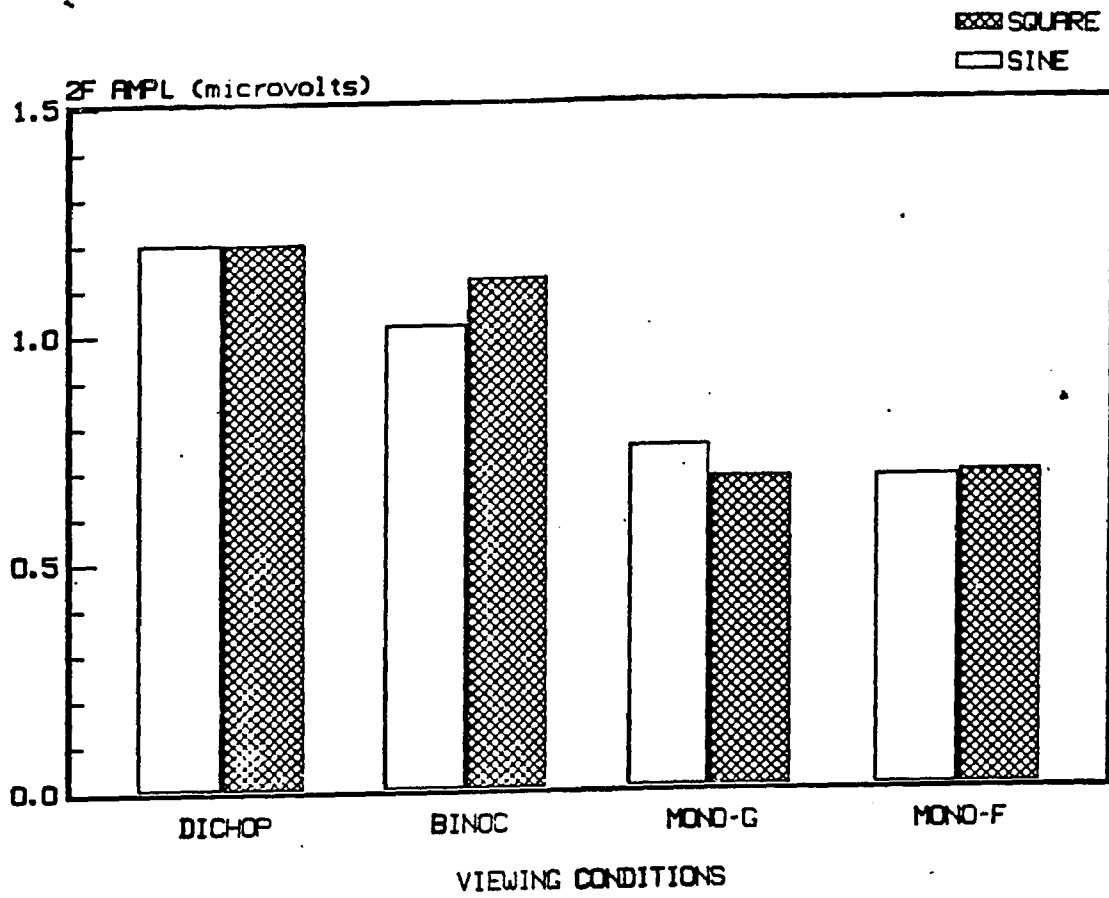


Figure 8

## EXPERIMENT 2

### Introduction

As mentioned before, we are trying to extend the "sandwich" model of Spekreijse and Oosting (1970) to find out where binocular interaction takes place.

Two models of binocular interaction are considered and they are depicted in figures 9 and 10. In the first model binocular summation occurs after linear filter L1 and prior to the nonlinear stage N (Model 1, Fig 9). In the second model binocular summation occurs after the nonlinear stage Nm (Model 2, Fig. 10). In order to test which model is employed by the visual system, temporal phases of dichoptic stimuli were fixed when presented to one eye of the subject and parametrically changed when presented to the other eye.

According to model 1, we would expect that both of the responses of the first linear outputs from the two eyes will be algebraically summed. A polar plot of the output of such a system is depicted in figure 11, where the phase of a response is equal to the angle between the X-axis and the response point, and its amplitude is equal to the distance between the point of origin and the response point.

If the input to a linear filter is phase shifted by a certain amount, the output of the same filter should be simply phase shifted by the same amount. Let's assume that outputs of the linear monocular filters L1 will always be equal for both eyes, and will have a response equal to one unit. When a dichoptic stimulus presented to both eyes has equal temporal phase (temporal phase difference 0 degree), the amplitude of response after binocular summation (at the output of the binocular adder) will be equal to two units, with the phase equal to 0, since there was no difference in the input phases. The output of the second binocular filter Lb will be equal to four units, since the output of the binocular adder goes through the nonlinear filter of the binocular pathway N, with the phase equal to 0. When a

dichoptic stimulus is presented to both eyes in opposite temporal phases (a temporal phase difference of 180 degrees), the output of L1 for the eye getting the signal at 0 degrees temporal phase will be equal to one, and the output of L1 for the other eye, getting the signal at 180 degrees will be equal to minus one. This means that the response after the binocular adder will be 0 units amplitude and 180 degrees temporal phase. The response at the output of the binocular pathway will have the same amplitude equal to 0, but its phase after the nonlinear binocular filter N will be 360 or 0 degrees. Thus, we can see that after algebraic summation the amplitude of the binocular response will be maximal where the phase difference between two temporal signals is 0 degrees, minimal when the difference in phase between those signals is 180 degrees, and will decrease monotonically with phase differences in between. The phase of the binocular response will increase with increasing temporal phase differences between the stimuli. If this model is correct we will expect the amplitude and phase of the second harmonic response to look like an asymmetrical curvilinear pattern as shown in figure 11.

According to Model 2, introducing a phase shift into the nonlinear device produces a phase shift which is twice as large in the second harmonic output of that device, and a phase shift four times as large in the fourth harmonic output. When the temporal phase difference of the stimulus is 0 degrees, the outputs of the nonlinear monocular inputs  $N_m$  from both eyes will both be equal to one unit of amplitude and 0 degree phase. Amplitude of the output of the binocular adder will be equal to two, with 0 degrees phase. When the stimulus' temporal phase difference is 180 degrees, the output of the nonlinear filter N of the eye receiving the phase shifted signal, will be equal to one unit of amplitude and 360 or 0 degrees phase. Therefore, when the temporal phase difference of the stimulus is 0 or 180 degrees, the input to the site of binocular interaction will consist of two signals each containing second and fourth harmonic components completely in phase, and the

**Figure 9. Model 1 of binocular interaction where binocular summation occurs after linear filter L1 prior to nonlinearity.**

**S1 - stimulus viewed by one eye (the temporal phase of this stimulus is always constant)**

**S2 - stimulus viewed by other eye (the temporal phase of this stimulus is changing with the reference to S1)**

**L1 - first linear filter**

**- putative site of binocular summation**

**N - major nonlinearity**

**Lb - linear filter of the binocular pathway**

# MODEL 1

*BINOCULAR SUMMATION BEFORE NONLINEARITY*

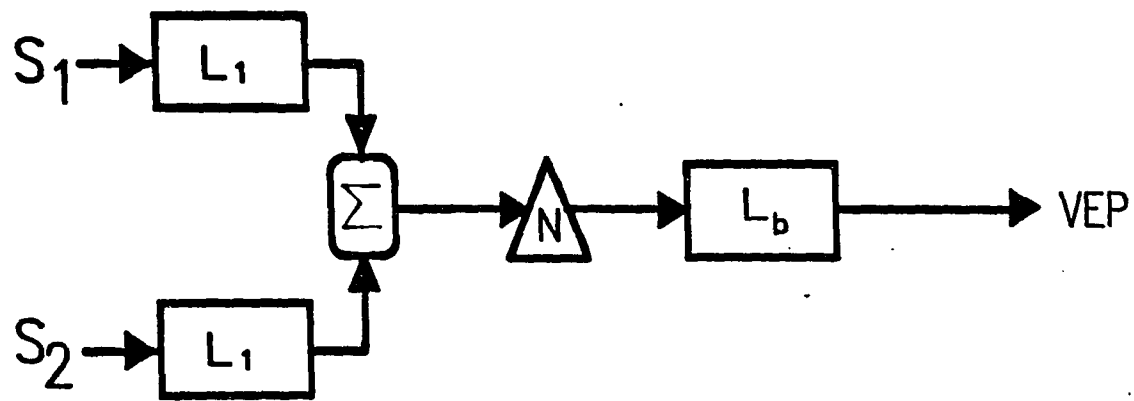


Figure 9

**Figure 10. Model 2 of binocular interaction where binocular summation occurs after nonlinear stage.**

**S1 - stimulus viewed by one eye (the temporal phase of this stimulus is always constant)**

**S2 - stimulus viewed by other eye (the temporal phase of this stimulus is changing with the reference to S1)**

**L1 - first linear filter**

**- putative site of binocular summation**

**N - major nonlinearity**

**Lb - linear filter of the binocular pathway**

# MODEL 2

## *BINOCULAR SUMMATION AFTER NONLINEARITY*

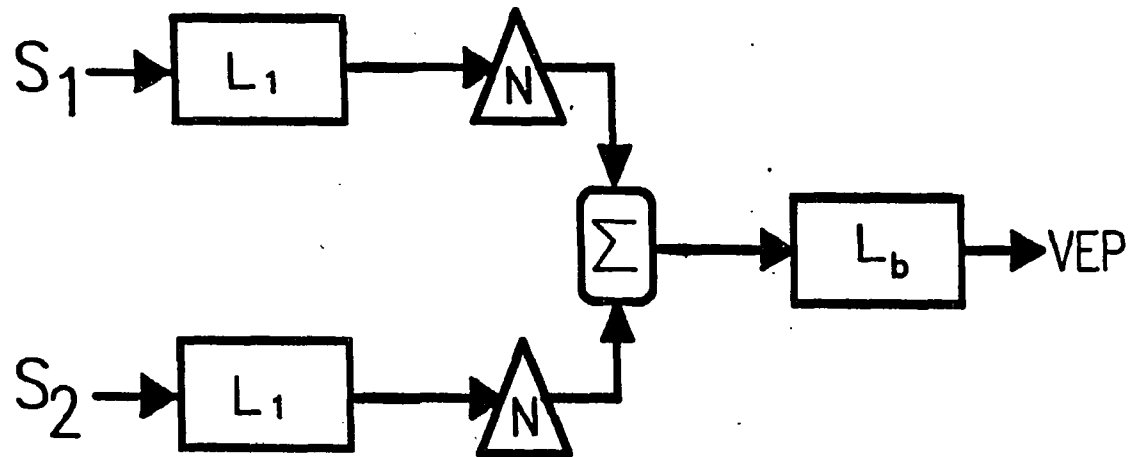


Figure 10

**Figure 11. Polar plot of the predicted output of the Model 1.**

**0, 45, 90, 135, 180 - relative temporal phase differences between the gratings viewed dichoptically.**

## PREDICTED FUNCTION

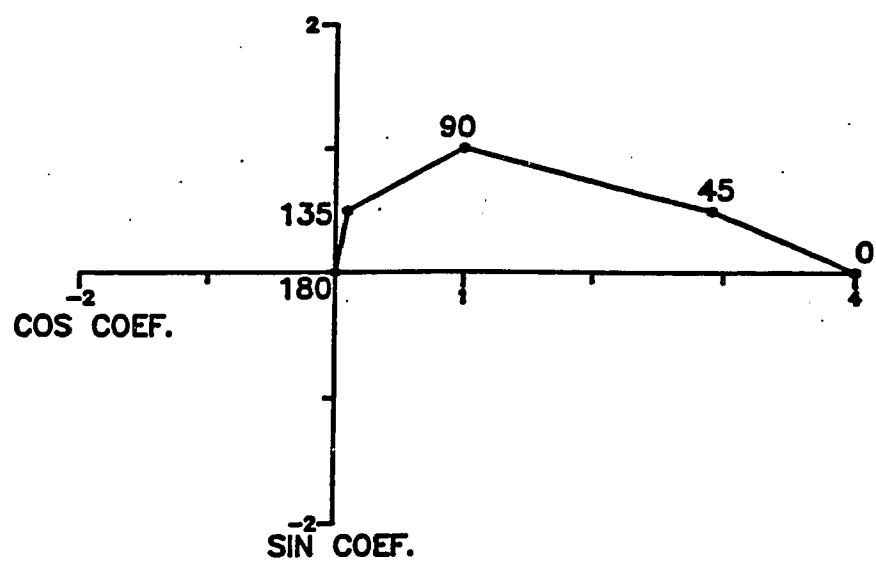


Figure 11

**Figure 12. Polar plot of the predicted output of the Model 2.**

**0, 45, 90, 135, 180 - relative temporal phase differences between the gratings viewed dichoptically.**

## PREDICTED FUNCTION

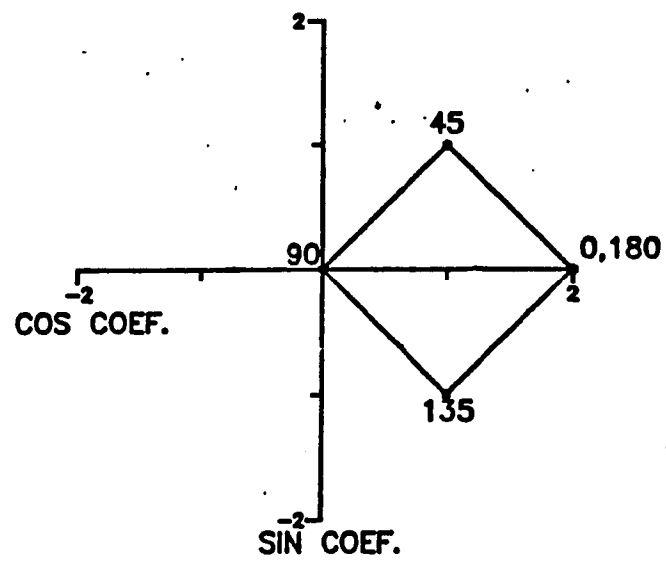


Figure 12

output of the binocular pathway will be of maximal amplitude and 0 degrees phase. When the stimulus temporal phase difference is 90 degrees, the two outputs of the monocular nonlinear filters N will be completely out of phase (180 degrees), and cancel each other. This means that the amplitude and the phase at the output of the binocular pathway will be 0. Stimulus temporal phase differences of 45 and 135 degrees would result in second harmonic outputs of intermediate amplitude, phases of which will be 45 and 315 degrees, respectively. Thus the second harmonic of the binocular response would be depicted on a polar coordinates plot as a square-like pattern shown in figure 12.

#### Method

#### Subjects

The three subjects who had the largest amplitude of visual evoked responses in the first series of experiments were used for this series.

#### Procedure

Each subject was presented with stimuli of several spatial and temporal frequencies which had elicited the greatest responses in the previous series (chosen for each individual).

Two gratings of the same spatial and temporal frequencies were contrast-reversed sinusoidally with one presented to each eye. Both sinusoidal and square wave gratings were tested. The grating presented to one eye was fixed in initial temporal phase 0, and the grating presented to the other eye was randomly set at 0, 45, 90, 135, and 180 degrees temporal phase, relative to the fixed grating. All other parameters were analogous to the conditions described above.

## Data Acquisition and Analysis

Each trial was repeated twice. The averaged response amplitudes and phases are plotted on polar coordinates for each subject.

## Results and Discussion

A numerical presentation of the results for all subjects is shown in the tables 7, 8, and 9 of Appendix A. As it can be seen from figures 13, 14 and 15, the response amplitudes of all subjects were maximal when the stimulus phase difference was 0 degrees, and 180 degrees. The response amplitudes were minimal for the stimulus phase difference of 90 degrees. Phase differences of 45 and 135 degrees produced intermediate response amplitudes.

In addition, it should be noticed, that the VEP amplitude elicited by a 0 degrees phase difference was always greater than the amplitude elicited by a 180 degrees phase difference. Phases of both responses were also always different.

The same observation holds for the responses elicited by stimulus phase shifts of 45 and 135 degrees. The responses to a phase difference of 45 degrees were greater than responses elicited by a stimulus phase difference of 135 degrees. Phases of both responses were also different.

Graphically the responses look like pentagons, open at the base, with their point representing the response amplitudes to a stimulus phase difference of 90 degrees.

Experimental data showed that response amplitudes were maximal when elicited by the stimulus phase differences of 0 and 180 degrees, and minimal when elicited by the stimulus phase differences of 90 degrees. However, the amplitudes and the phases of responses elicited by stimulus phase differences of 0 and 180 degrees were never equal.

Figure 13 a,b,c,d,e. Polar plots of the response amplitudes and phases of subject E.P.

Spatial profile, and spatial and temporal frequencies are indicated in the right upper corner of each plot.

0, 45, 90, 135, 180 - relative temporal phase differences between the gratings viewed dichoptically.

E.P. 5/12/86  
square profile  
0.4 c/deg 4.2 Hz

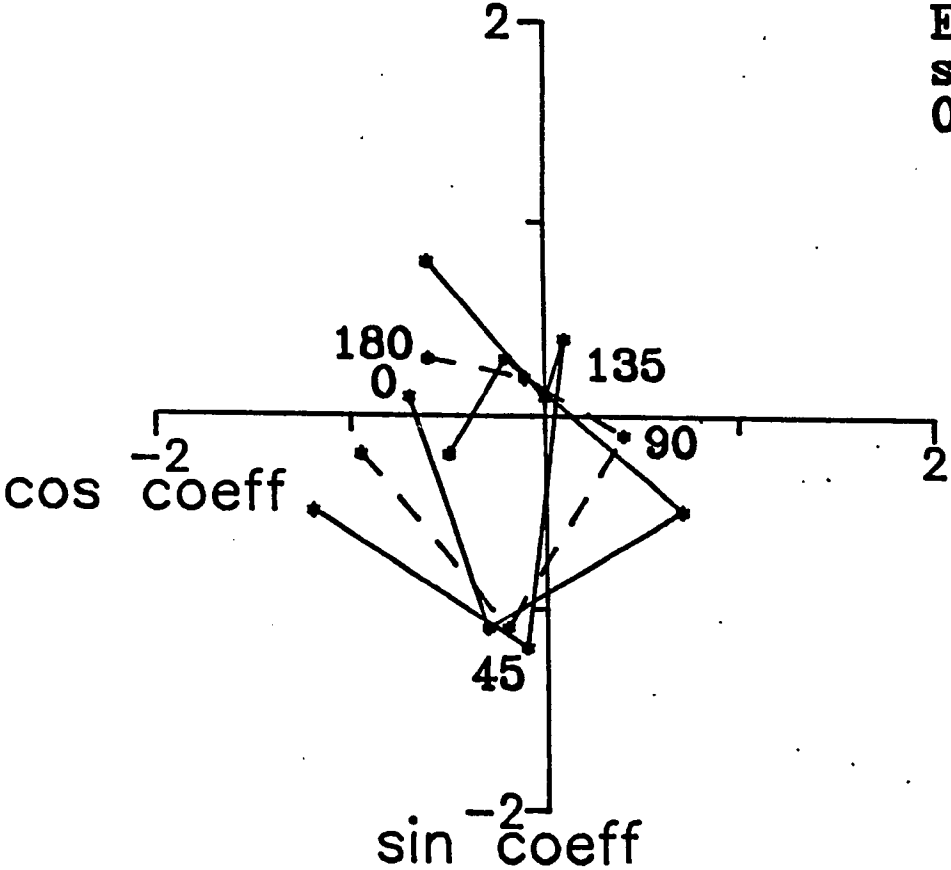


Figure 13a

E.P. 5/12/86  
sine profile  
0.8 c/deg 6.3 Hz

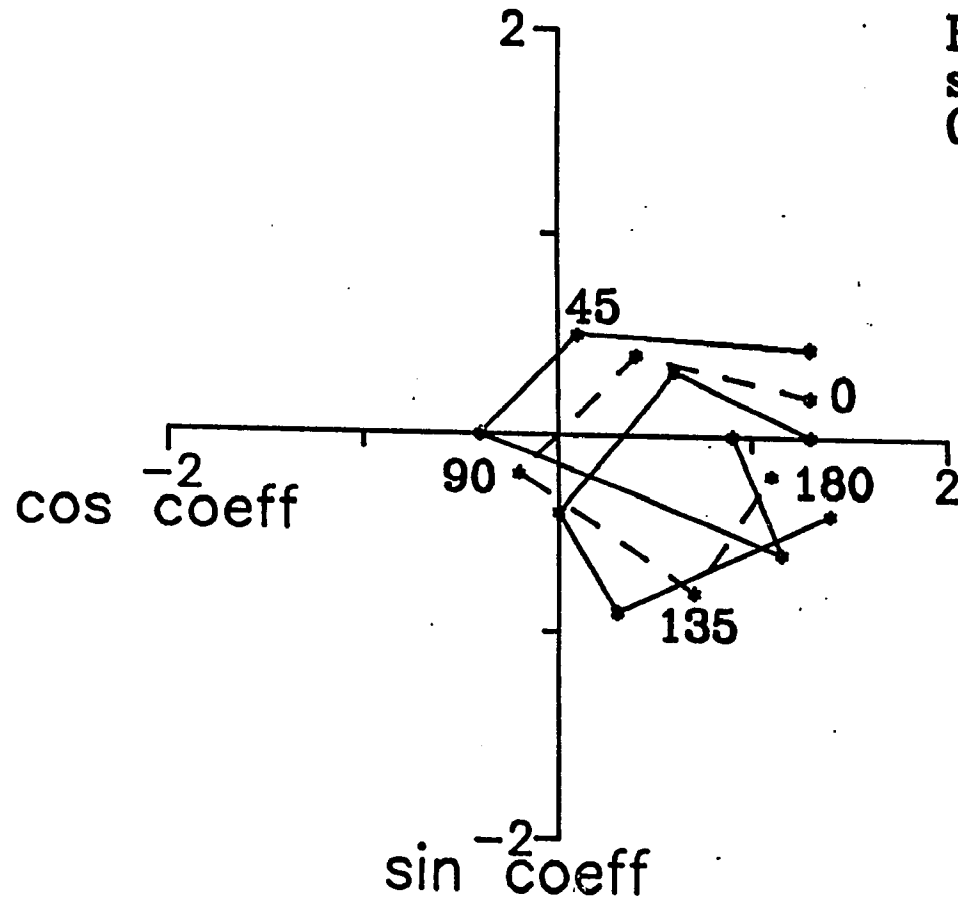
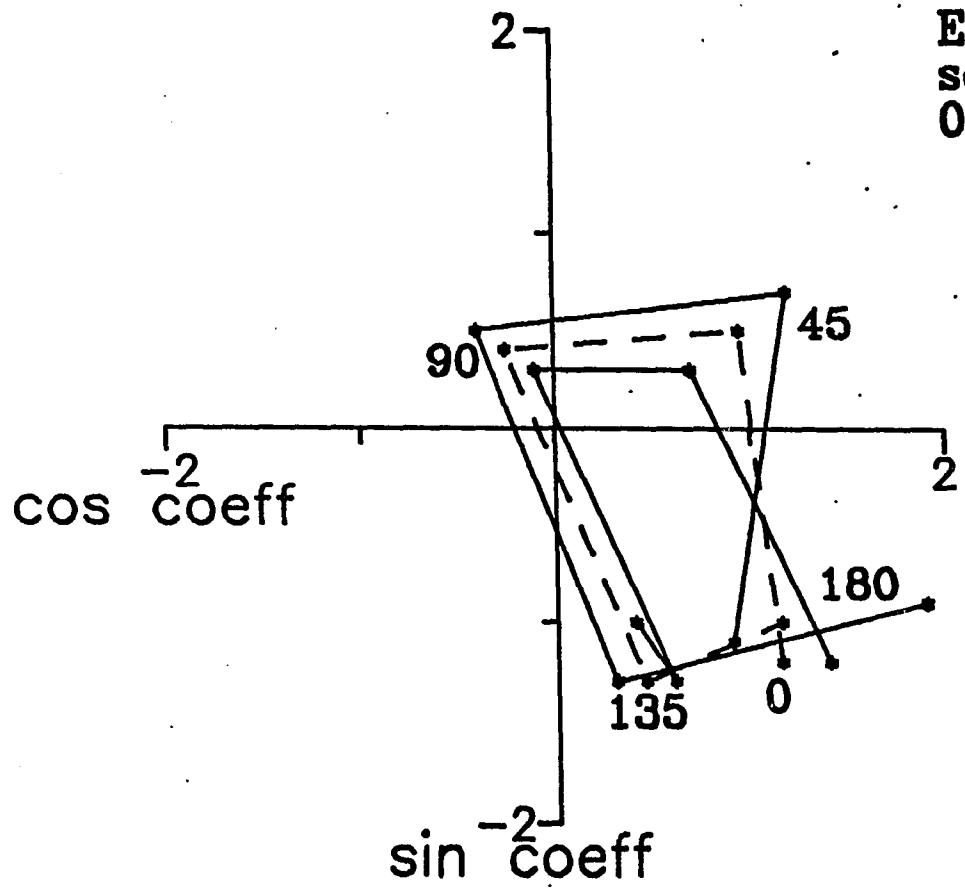


Figure 13b



E.P. 5/12/86  
 square profile  
 0.8 c/deg 6.3 Hz

Figure 13c

E.P. 5/12/86  
sine profile  
1.6 c/deg 6.3 Hz

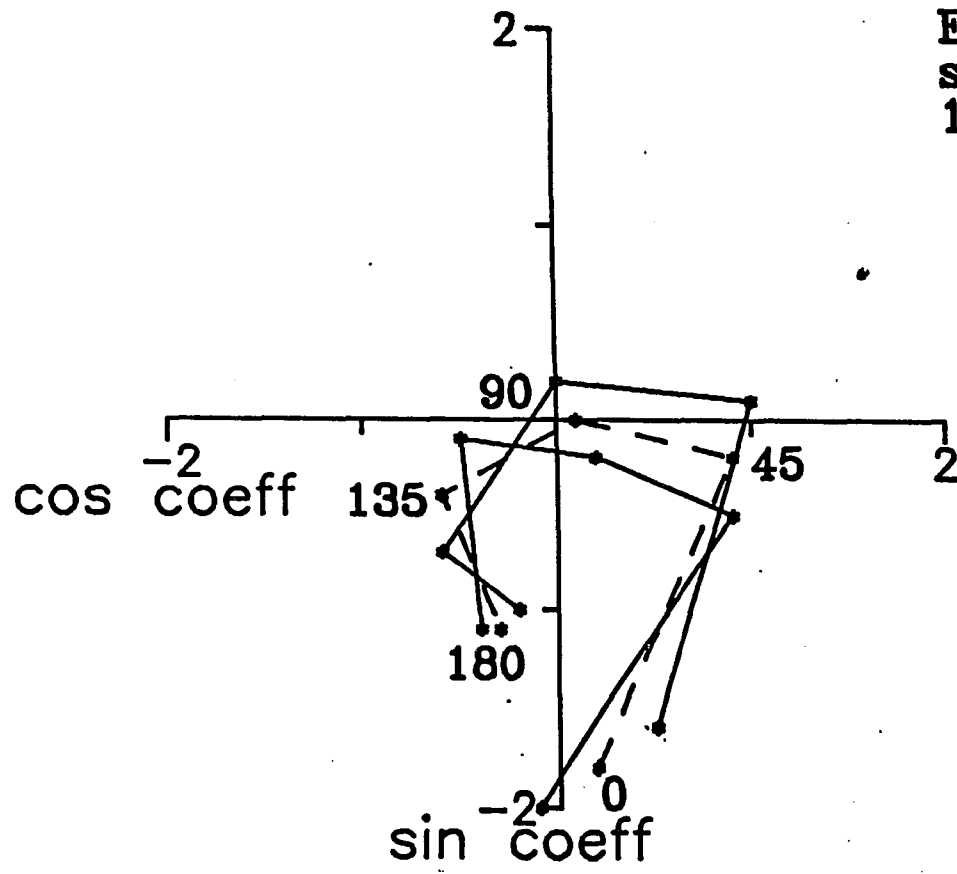


Figure 13d

E.P. 5/12/86  
square profile  
1.6 c/deg 6.3 Hz

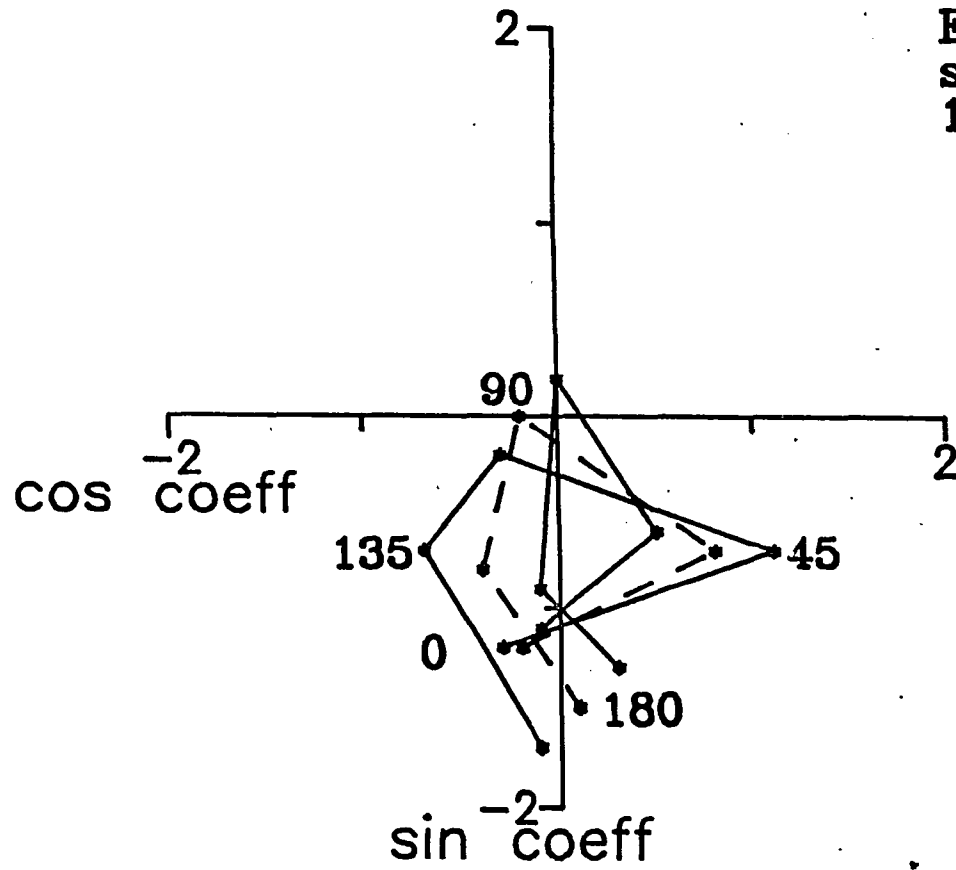


Figure 13e

Figure 14. Polar plots of the response amplitudes and phases of subject C.R. Spatial profile, and spatial and temporal frequencies are indicated in the right upper corner.

0, 45, 90, 135, 180 - relative temporal phase differences between the gratings viewed dichoptically.

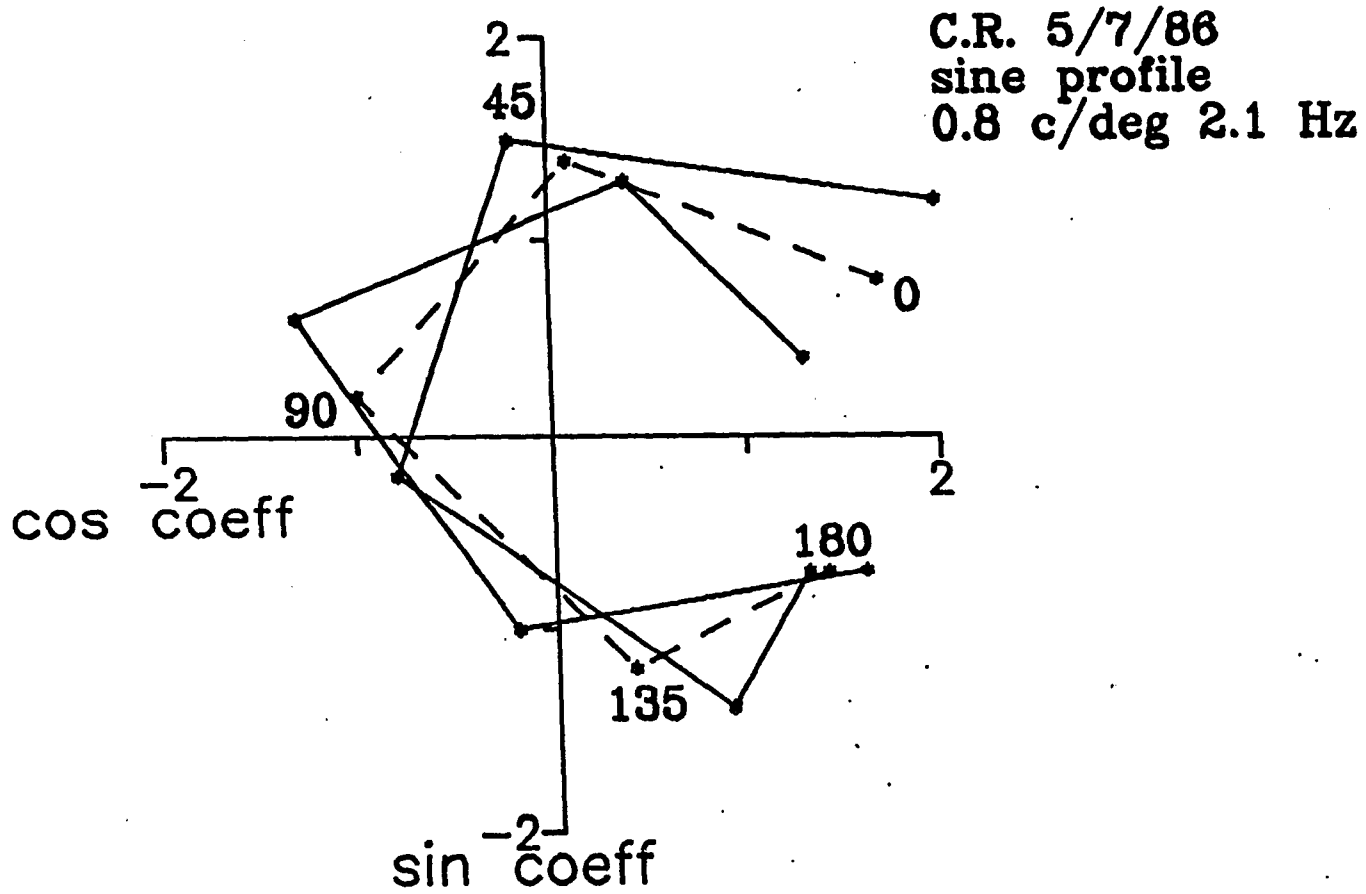


Figure 14

**Figure 15 a,b,c,d,e,f. Polar plots of the response amplitudes and phases of subject M.C.**

**Spatial profile, and spatial and temporal frequencies are indicated in the right upper corner of each plot.**

**0, 45, 90, 135, 180 - relative temporal phase differences between the gratings viewed dichoptically.**

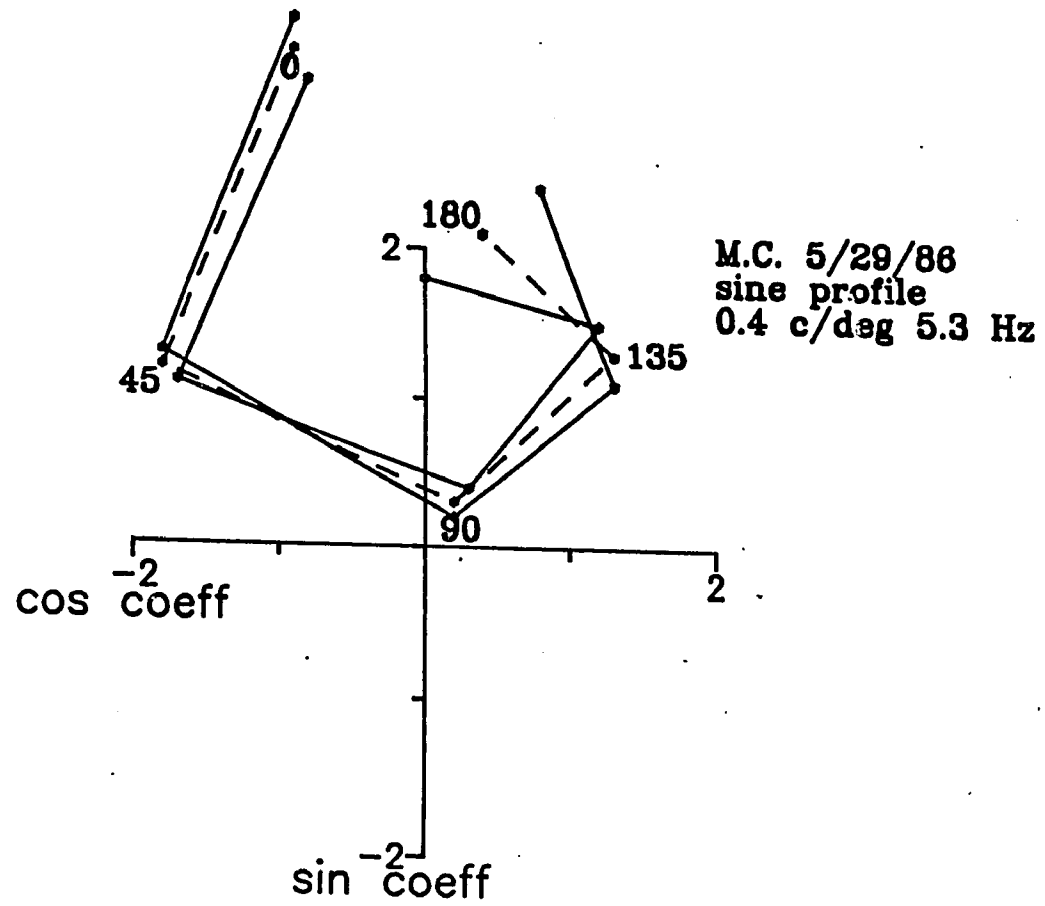


Figure 15a

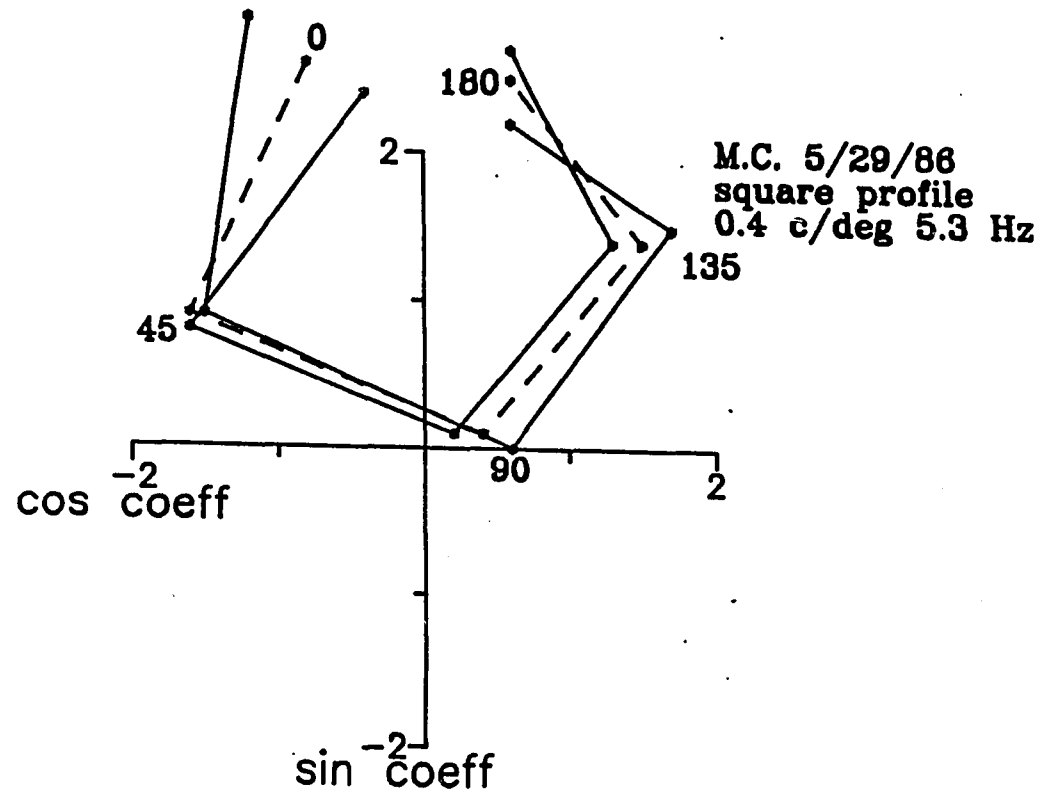


Figure 15b

M.C. 5/29/86  
sine profile  
1.6 c/deg 5.3 Hz

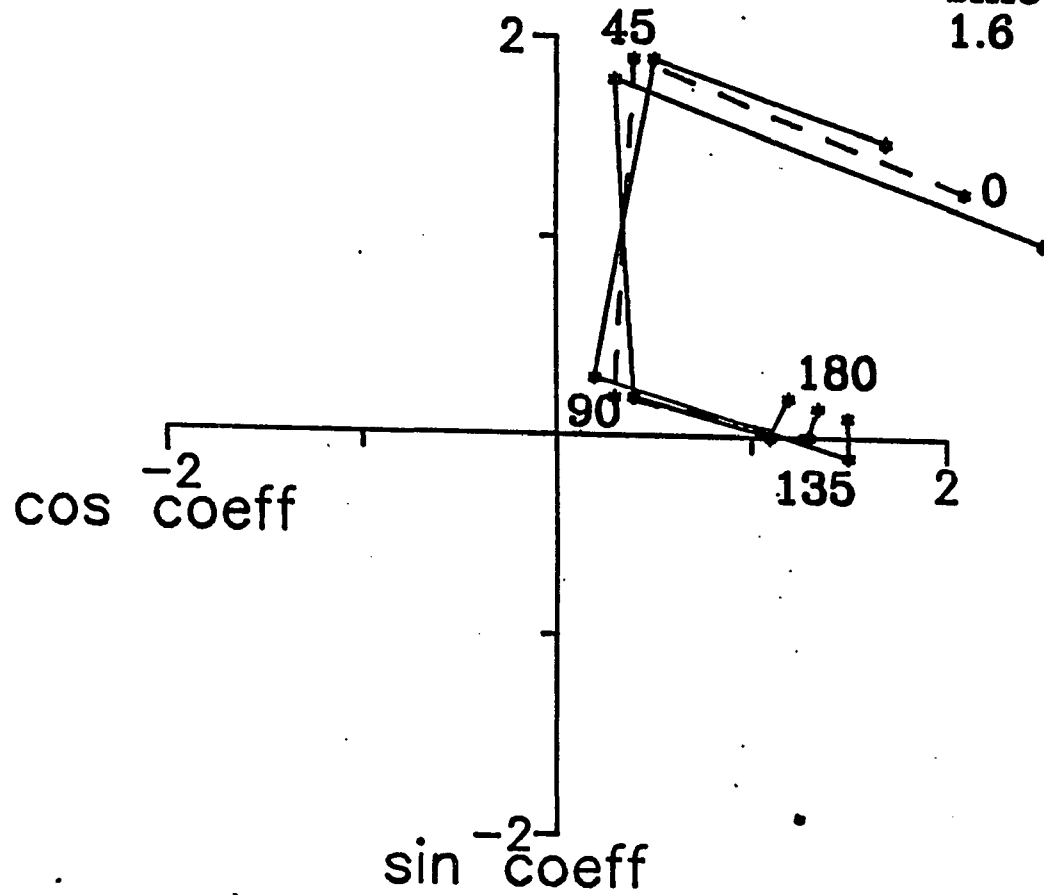


Figure 15c

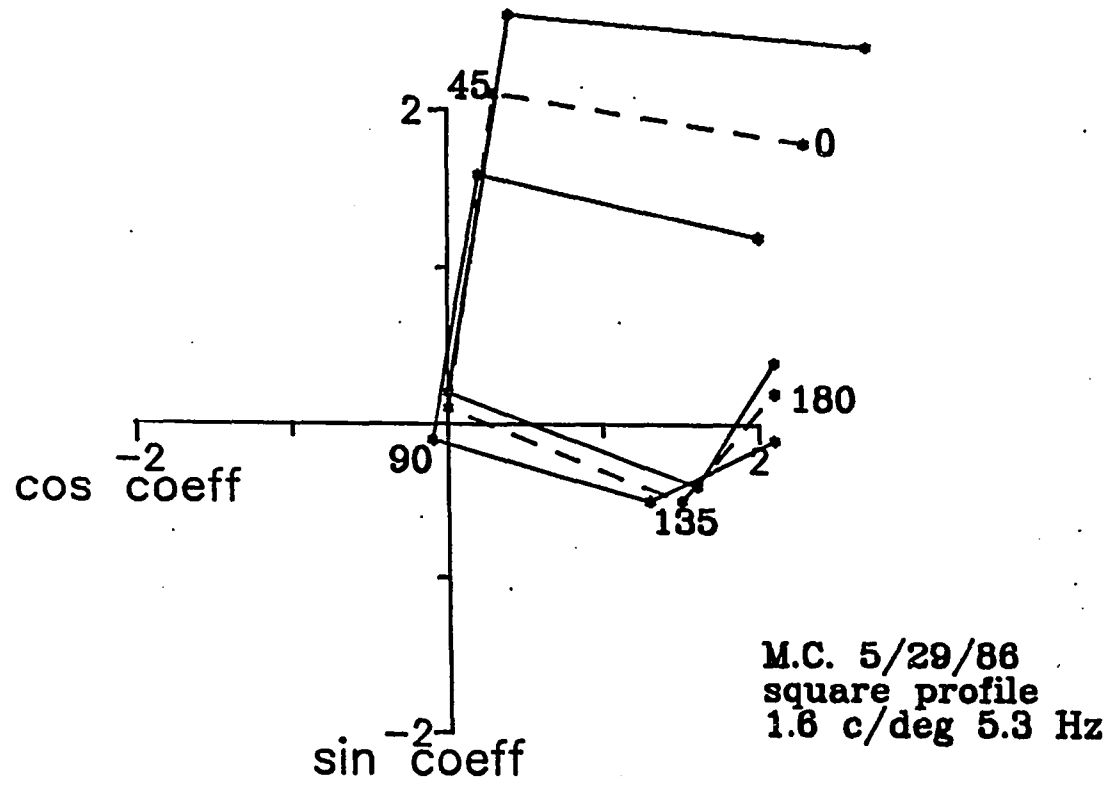


Figure 15d

M.C. 5/29/86  
sine profile  
6.4 c/deg 5.3 Hz

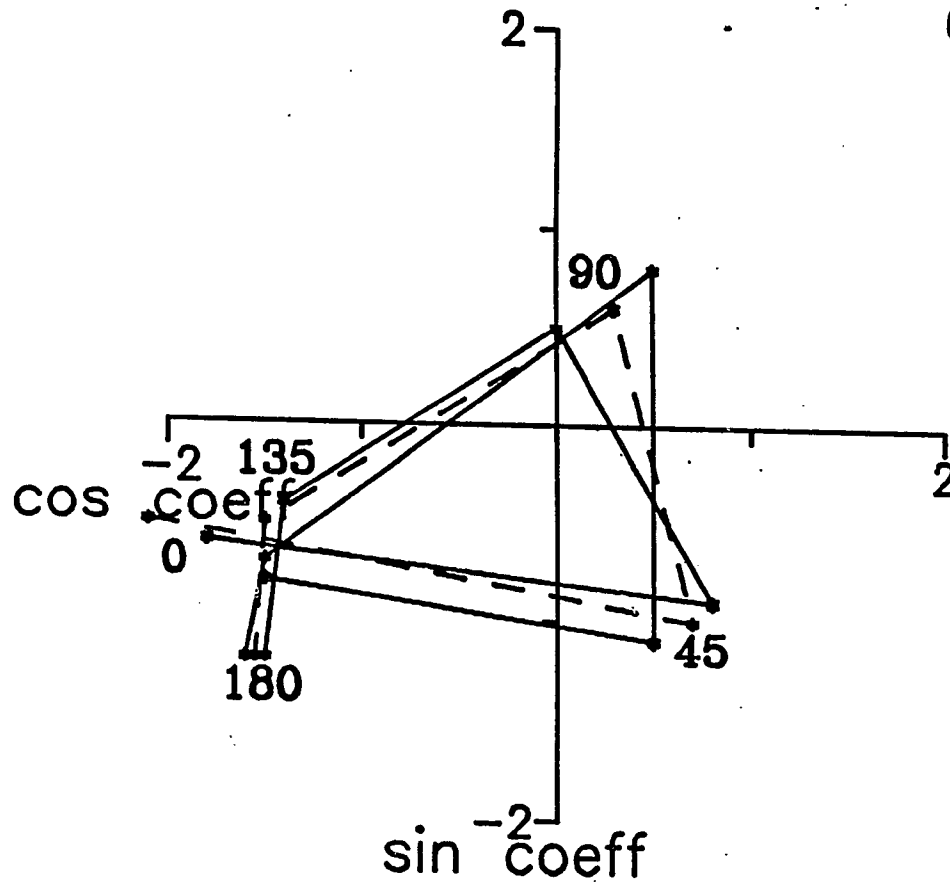


Figure 15e

M.C. 5/29/86  
square profile  
6.4 c/deg 5.3 Hz

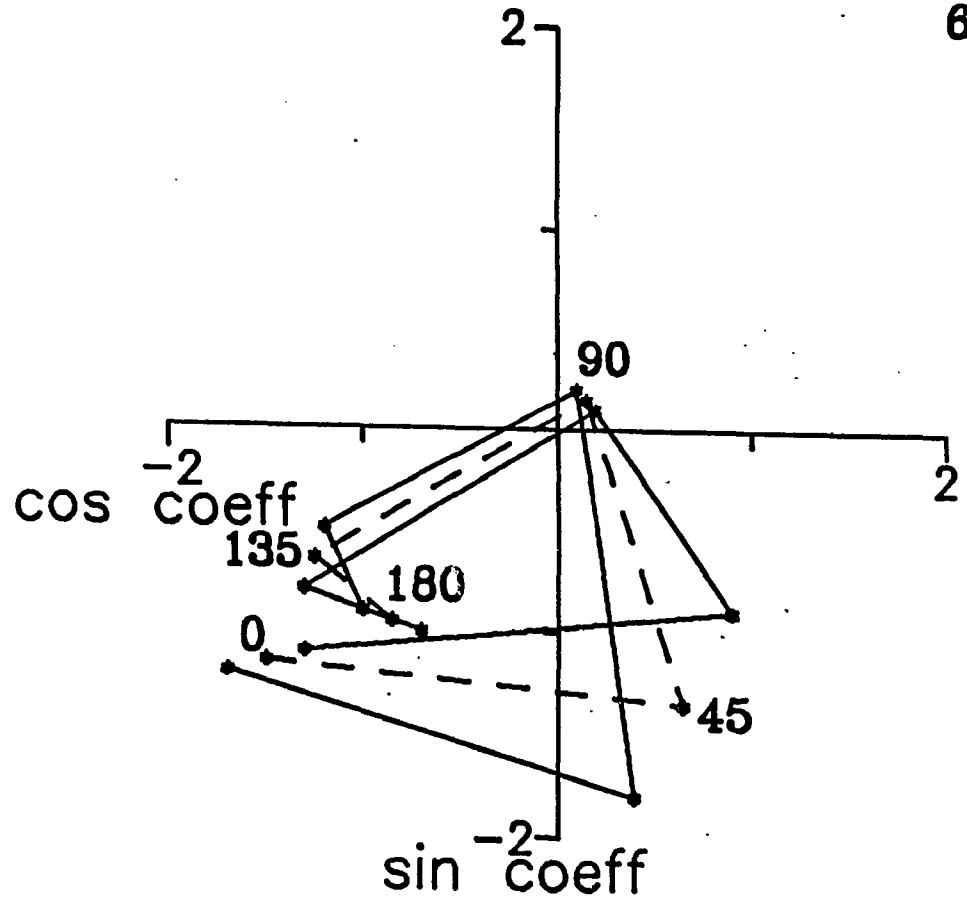


Figure 15f

Model 2 (summation after the non-linearity) does not predict any difference in the amplitude and phase of responses elicited by stimuli differing in their temporal phase by 0 or 180 degrees. Furthermore, it should be noted that just the summation of the outputs of only monocular pathways will produce the same results as Model 2. In that sense Model 2 really is synonymous with the monocular system, since it does not differentiate between purely monocular and purely binocular contributions to the visual system.

The shape of the experimental curves appears as though the data reflect a combination of the two models. It may be a manifestation of some combined activity from the two binocular pathways, or binocular and monocular pathways, each one representing different phase and amplitude ratios.

Our next step was to simulate a system which would combine both these models. A computer program, which was used to model the behavior of such a system was written, using the BASICA computer language (Appendix B). In this program it was taken into account that monocular (or binocular pathways described in Model 2) and binocular pathways, and changes of their angular phases could provide different contributions and change the output of the whole system. It was assumed that the linear filters would just introduce some additional gain in the response amplitude or change its phase, while the nonlinear filters would rectify response (square response amplitude and double its phase). The program calculated sine and cosine coefficients on the output of the binocular system, which were then plotted. Several graphs, showing responses predicted by this model and computed for the binocular contributions ranging from 0.1 to 0.6, and changes

**Figure 16. Combined model of binocular interaction.**

**S1 - stimulus viewed by one eye (the temporal phase of this stimulus is always constant)**

**S2 - stimulus viewed by other eye (the temporal phase of this stimulus is changing with the reference to S1)**

**L1 - first linear filter**

**- putative site of binocular summation**

**N - major nonlinearity**

**Lb - linear filter of the binocular pathway**

# COMBINED MODEL

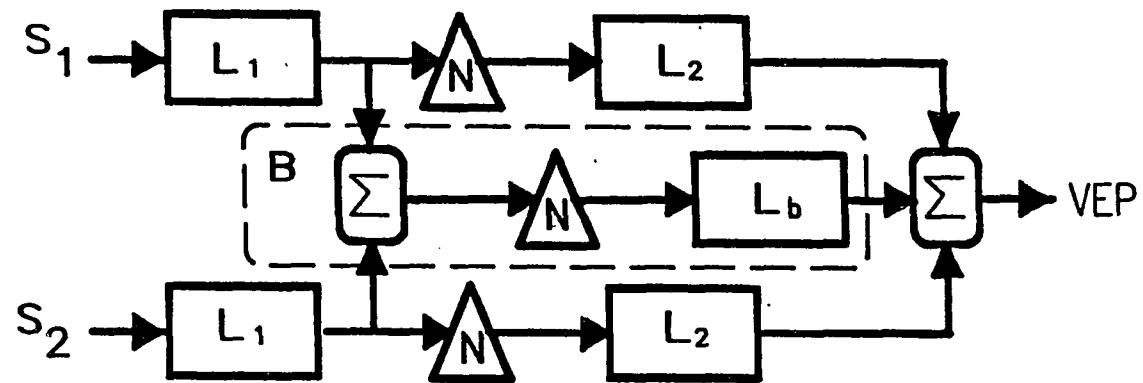


Figure 16

**Figure 17 a,b,c,d,e,f. Polar plots of the predicted output of the combined model calculated (by the computer program) for different binocular contributions and binocular phases.**

**Monocular and binocular contributions, and monocular and binocular phase shifts are indicated on the top of each plot.**

**0, 45, 90, 135, 180 - relative temporal phase differences between the gratings viewed dichoptically.**

monocular contribution  $M_1=M_2=1$ , monocular phase shift is 0  
binocular contribution = .1, binocular phase shift 0-180 in 45 deg steps

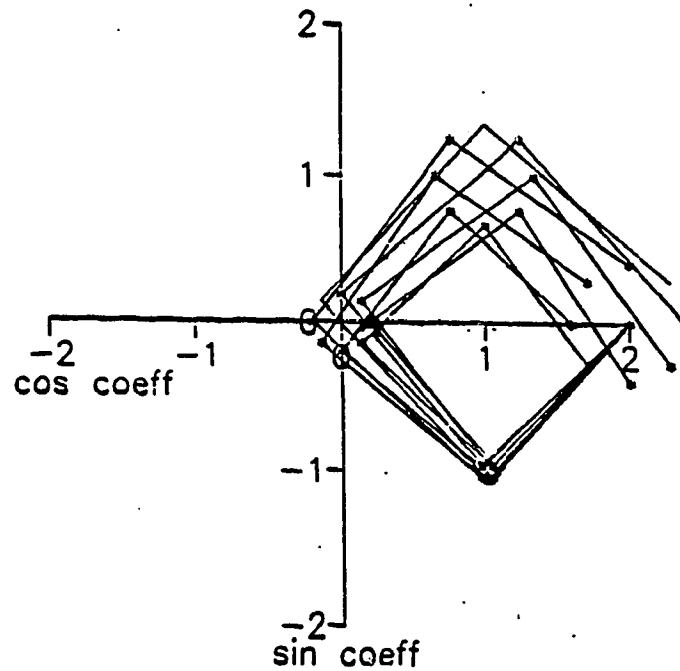


Figure 17a

monocular contribution  $M_1=M_2=1$ , monocular phase shift is 0  
binocular contribution = .2, binocular phase shift 0-180 in 45 deg steps

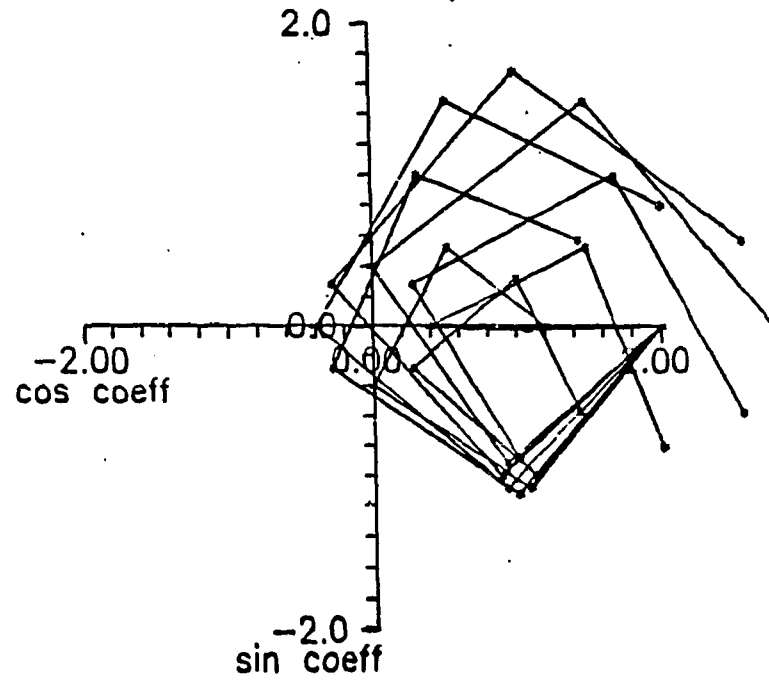


Figure 17b

monocular contribution  $M_1=M_2=1$ , monocular phase shift is 0  
binocular contribution = .3, binocular phase shift 0-180 in 45 deg steps

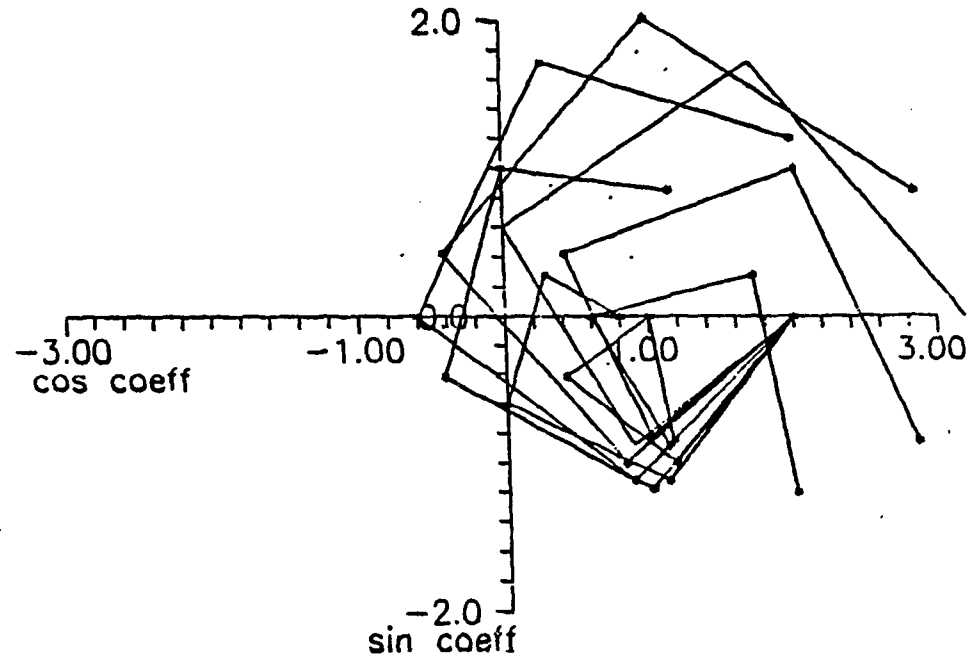


Figure 17c

monocular contribution  $M_1=M_2=1$ , monocular phase shift is 0  
binocular contribution = .4, binocular phase shift 0-180 in 45 deg steps

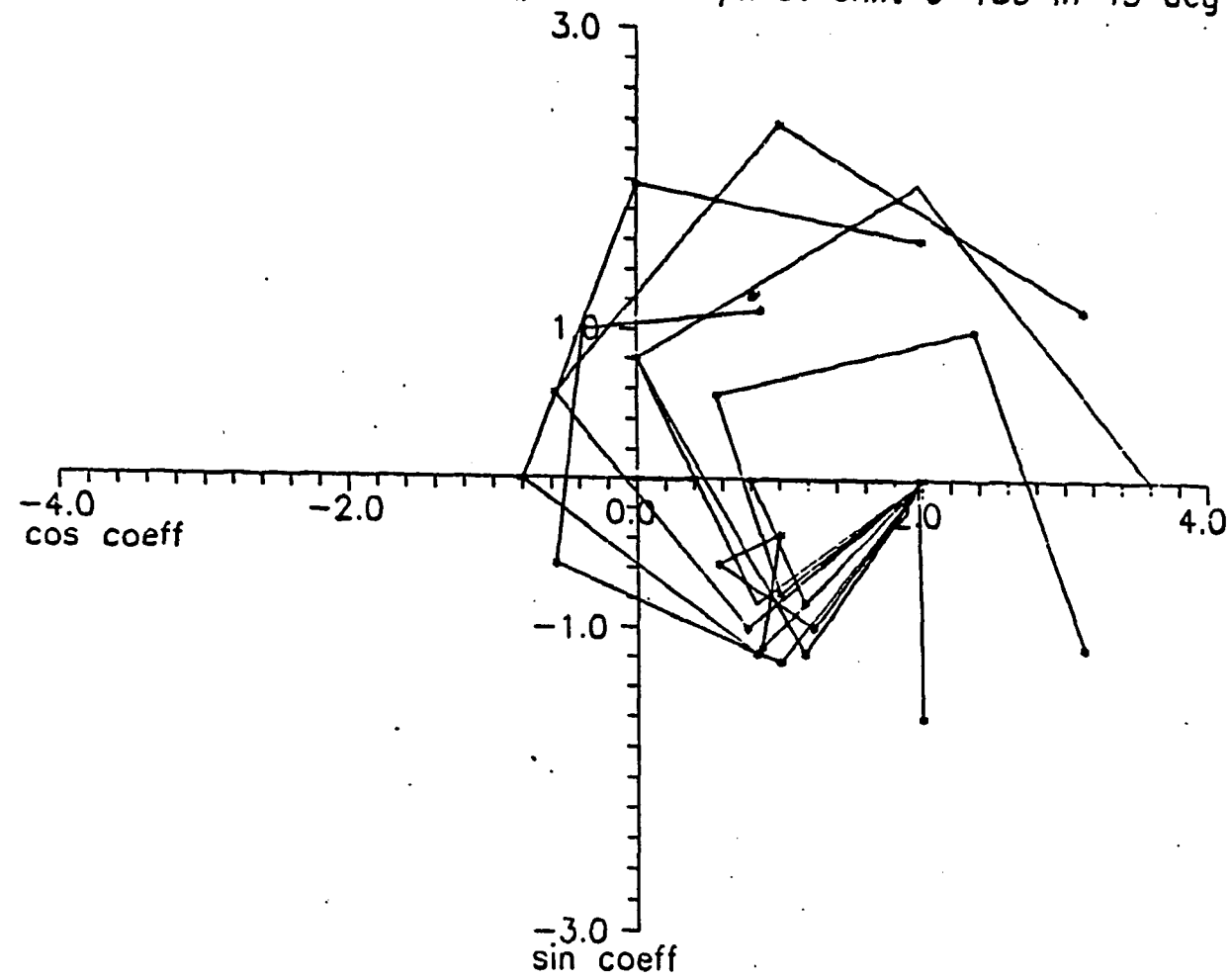


Figure 17d

monocular contribution  $M1=M2=1$ , monocular phase shift is 0  
binocular contribution = .5, binocular phase shift 0-180 in 45 deg steps

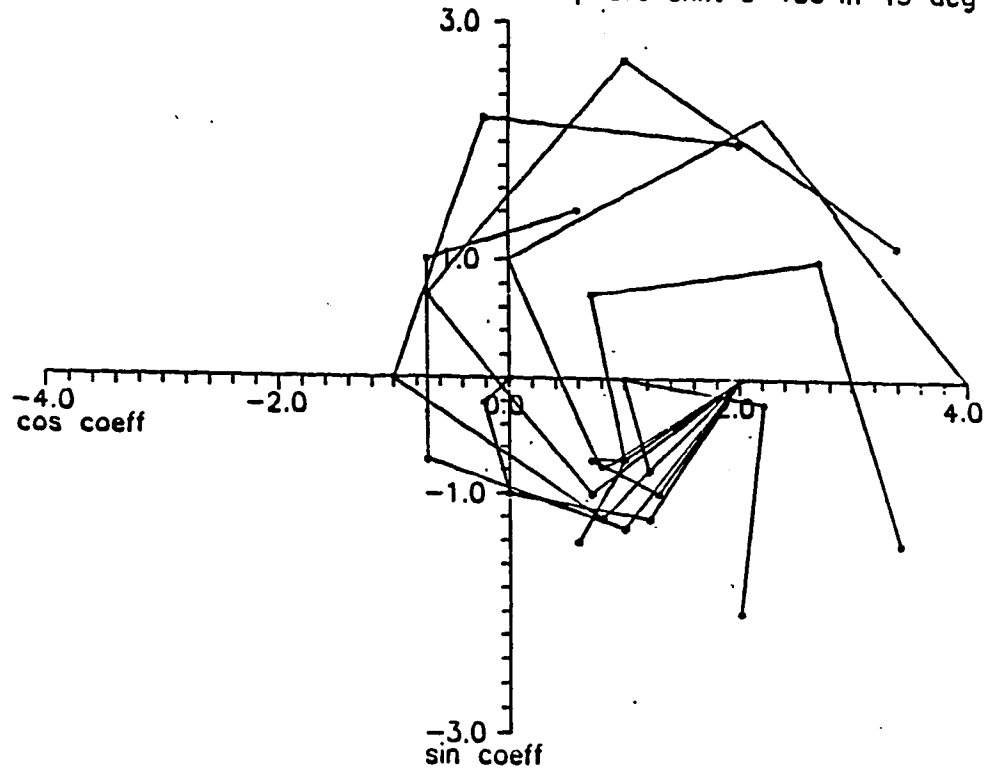


Figure 17e

monocular contribution  $M_1=M_2=1$ , monocular phase shift is 0  
binocular contribution = .6, binocular phase shift 0-180 in 45 deg steps

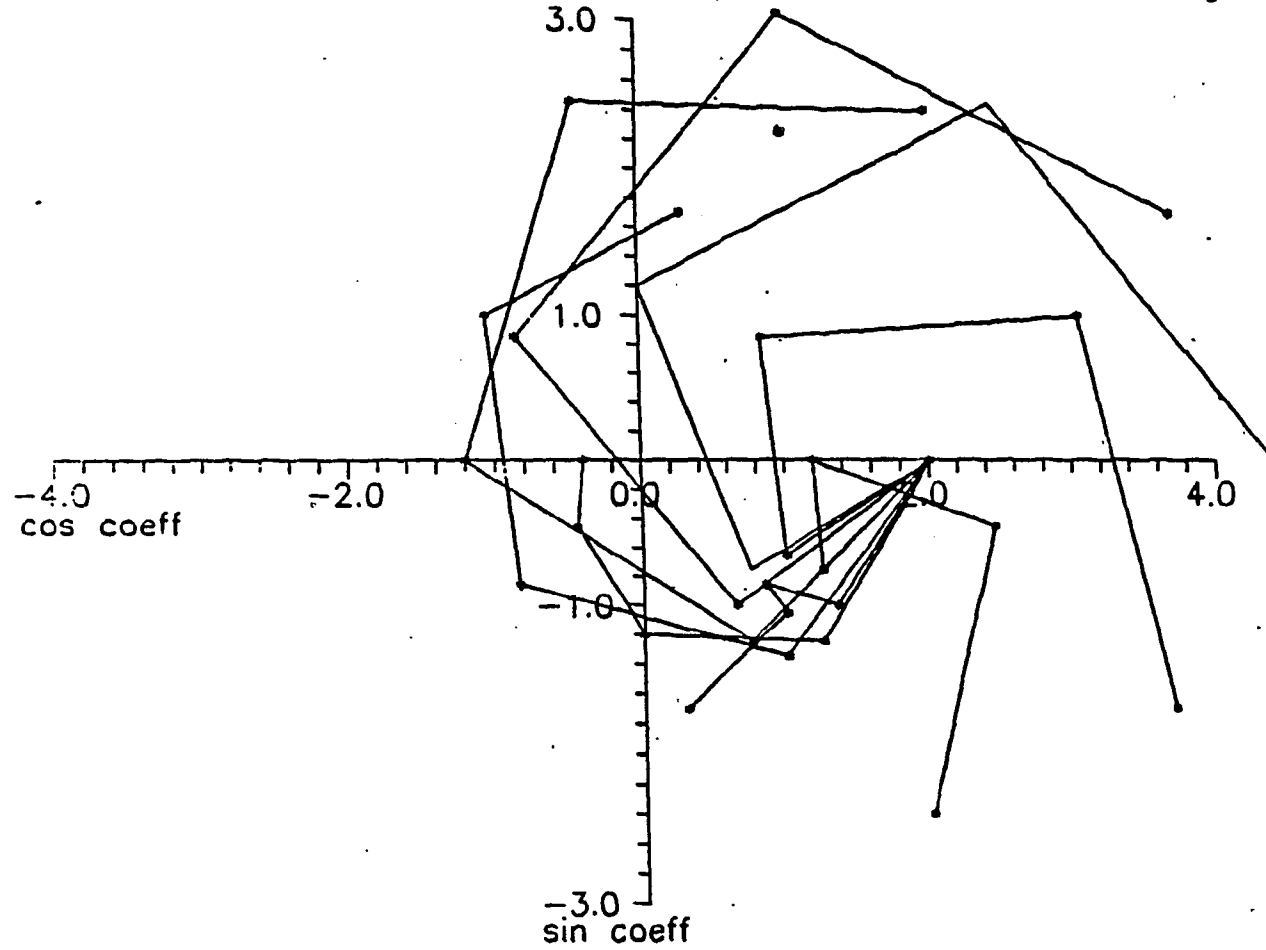


Figure 17f

**Figure 18 - Predicted output of the Combined model calculated for different monocular contributions in absence of any binocular input.**

## PREDICTED FUNCTIONS

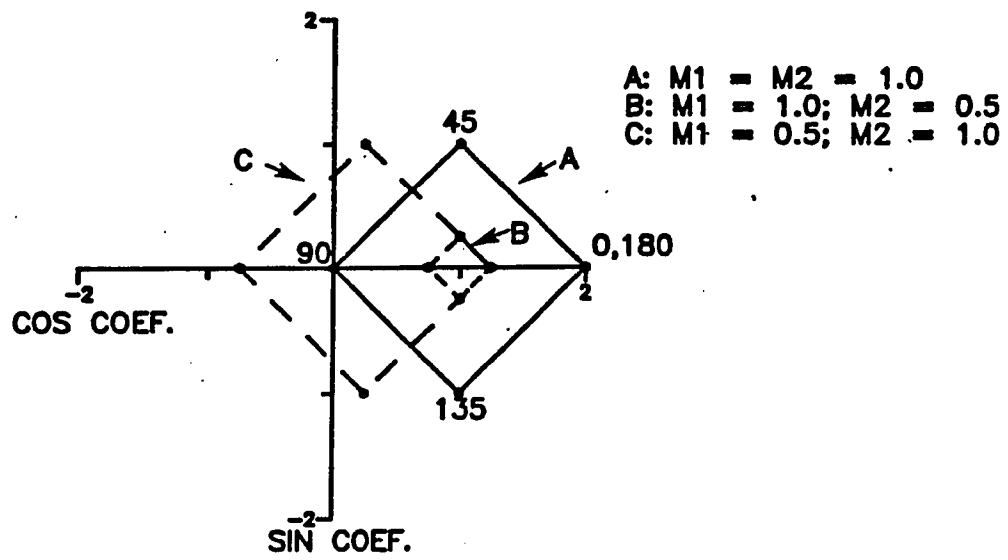


Figure 18

in the binocular phase from 0 to 360 degrees in the steps of 45 degrees are displayed in fig. 16.

It should be noted that the calculations shown in figure 16 are true only in cases where each monocular pathway contributes equally to the response and without any relative changes in the monocular phase. Thus, another important factor could be the difference between the contribution from each eye.

As it can be seen from figure 17, in the absence of any binocular contribution, when the contribution of the first monocular pathway is twice the contribution of the second monocular pathway, the resulting curve will be greatly compressed in comparison to the curve which would be obtained if both eyes contributed equally to the response. When the opposite case is true, and the contribution from the first monocular pathway is half the contribution from the second, the resulting curve will be greatly expanded.

It can be seen that the experimental data (figs 13-15) look more or less like the theoretical data (fig 16). The best approximation is for values of the binocular scale factor that are less than 0.5.

Because of the complexity of the model, we used the theoretical curves depicted in figures 16 and 17 as templates for estimates of the parametrical values for each of the experimental curves. Those values are shown in table I.

Examining the data of table I, we can see some correlation between changes in spatial and temporal frequencies of the stimuli and changes in monocular and binocular phases of the responses. It seems that increase of the spatial frequency of the stimuli correlates with the shift of the monocular phase (introduced by the L1 filter as it was described in the Model) in the counterclockwise direction.

**Table I. Estimated values of monocular and binocular contributions and phases for each subject.**

**S.F. - stimulus spatial frequency**

**T.F. - stimulus temporal frequency**

## ESTIMATED VALUES OF MONOCULAR AND BINOCULAR CONTRIBUTION

| A                    | B            | C                           | D               | E                           | F               |
|----------------------|--------------|-----------------------------|-----------------|-----------------------------|-----------------|
| S.F.<br>(c/deg)      | T.F.<br>(Hz) | MONOC<br>PHASE<br>(degrees) | MONOC<br>FACTOR | BINOC<br>PHASE<br>(degrees) | BINOC<br>FACTOR |
| C.R.                 |              |                             |                 |                             |                 |
| sine-wave gratings   |              |                             |                 |                             |                 |
| 0.4                  | 2.1          | 57.0                        | 0.7             | 8.0                         | 0.05            |
| 0.8                  | 5.3          | -12.5                       | 0.9             | 90.0                        | 0.4             |
| square-wave gratings |              |                             |                 |                             |                 |
| 0.4                  | 2.1          | 55.0                        | 0.6             | -34.0                       | 0.1             |
| 0.8                  | 5.3          |                             |                 |                             |                 |
| E.P.                 |              |                             |                 |                             |                 |
| sine-wave gratings   |              |                             |                 |                             |                 |
| 0.4                  | 4.2          | -33.5                       | 0.4             | -164.0                      | 0.4             |
| 0.8                  | 6.3          | -5.0                        | 0.8             | 90.0                        | 0.2             |
| 1.6                  | 6.3          | -58.0                       | 0.7             | 90.0                        | 0.4             |
| square-wave gratings |              |                             |                 |                             |                 |
| 0.4                  | 4.2          | 1.0                         | 0.7             | 44.0                        | 0.2             |
| 0.8                  | 6.3          | -19.5                       | 0.9             | -5.0                        | 0.1             |
| 1.6                  | 6.3          | -46.0                       | 0.7             | -8.0                        | 0.1             |
| M.C.                 |              |                             |                 |                             |                 |
| sine-wave gratings   |              |                             |                 |                             |                 |
| 0.4                  | 5.3          | 39.5                        | 1.1             | 45.0                        | 0.4             |
| 1.6                  | 5.3          | 9.5                         | 0.9             | -45.0                       | 0.2             |
| 6.4                  | 5.3          | -72.0                       | 1.0             | -15.0                       | 0.1             |
| square-wave gratings |              |                             |                 |                             |                 |
| 0.4                  | 5.3          | 39.0                        | 1.1             | 112.0                       | 0.4             |
| 1.6                  | 5.3          | 4.0                         | 1.1             | 90.0                        | 0.4             |
| 6.4                  | 5.3          | -66.0                       | 0.8             | 8.0                         | 0.3             |

Table I

For the subject M.C., change of spatial frequency from 0.4 c/deg to 1.6 c/deg to 6.4 c/deg corresponds to the monocular phases shift from 39.5 degrees to 9.5 degrees to -72.0 degrees respectively. For C.R., as the spatial frequency changed from 0.4 c/deg to 0.8 c/deg, the monocular phases of his responses changed from 57 degrees to -12.5 degrees, respectively. For E.P. changes of spatial frequency from 0.4 c/deg to 0.8 c/deg to 1.6 c/deg correlate with changes of the monocular phases from 75 degrees to -19.5 degrees to -46 degrees respectively.

Increase of the temporal frequency of stimuli may somehow correlate with changes in the binocular phase of the responses. The binocular phases of responses of the subject C.R. changed from 8 degrees to 51.5 degrees, as the temporal frequency of the stimuli changed from 2.1 Hz to 5.3 Hz. The binocular phases of the responses of the subject E.P. changed from 44 degrees to -5 degrees, as the temporal frequency of the stimuli changed from 4.2 Hz to 6.3 Hz. However, for stimuli of the same temporal frequency, but different spatial frequencies, the binocular phase of her responses was almost in the same range from -5 degrees to -8 degrees. The stimuli presented to the subject M.C. were all modulated at the same temporal frequency of 5.3 Hz; the binocular phases of her responses were 32 degrees, 8 degrees, and 31 degrees.

If we assume equal contribution from each eye, then according to the model, response amplitudes obtained at stimulus phase shifts of 90 degrees should represent contributions of only the binocular pathways, because the monocular responses would be canceled after monocular nonlinear filters.

On the other hand, keeping the same assumption of equal contributions from each eye to the VEP, the amplitude of the responses obtained at stimulus phase shifts of 180 degrees should represent contributions of only the monocular pathways, since the binocular pathway should be canceled at the binocular summer by the

signals coming in counterphase. Thus, we can compare relative contributions of the binocular and monocular pathways in these experiments by calculating the ratios of amplitudes of binocular to monocular responses for these phases (Table II). We will call this value the "binocular index".

Comparing both tables one can clearly see that values of binocular indices in table II do not coincide with the values of the coefficients of binocular interaction in table I. One of the most parsimonious explanations would be unequal contributions of both eyes: in this case the outputs of the monocular inputs into the binocular adder won't cancel each other at the stimulus temporal phase difference 90 degrees.

It may be concluded that the contribution to the VEP of the binocular pathway is always less than that of the monocular pathways, for all subjects.

We can compare our results to the data of anatomical studies done by Powell and Hendrickson (1981); they showed that in area 17 of the monkey's visual cortex equal number of cells occupy monocular and binocular regions. We may safely suggest then that the binocular coefficient in the formula should therefore be less than one. This number will be reduced even more taking into account data on ocular dominance reported by Hubel and Wiesel (1962). According to them, in the cat's visual cortex only about one fourth of the cells are driven equally by both eyes (group 4).

Using single-unit recording, Ohzawa and Freeman (1986a, 1986b) showed that linear summation is characteristic of the majority of the simple and complex binocular cells in the striate cortex of a cat.

**Table II. Calculated Binocular Indices (ratios of binocular to monocular responses) of each subject.**

**S.F. - stimulus spatial frequency**

**T.F. - stimulus temporal frequency**

**Binocular input - response amplitudes for the stimuli phase shift of 90 degrees**

**Monocular input - response amplitudes for the stimuli phase shift of 180 degrees**

## BINOCULAR INDICIES

| A<br>S.F.<br>(c/deg) | B<br>T.F.<br>(Hz) | C<br>BINOCULAR<br>INPUT<br>( $\mu$ V) | D<br>MONOCULAR<br>INPUT<br>( $\mu$ V) | E<br>BINOCULAR<br>INDEX |
|----------------------|-------------------|---------------------------------------|---------------------------------------|-------------------------|
| C.R.                 |                   |                                       |                                       |                         |
| sine-wave gratings   |                   |                                       |                                       |                         |
| 0.4                  | 2.1               | 0.24                                  | 0.84                                  | 0.29                    |
| 0.8                  | 5.3               | 1.04                                  | 1.60                                  | 0.65                    |
| square-wave gratings |                   |                                       |                                       |                         |
| 0.4                  | 2.1               | 0.60                                  | 1.14                                  | 0.53                    |
| 0.8                  | 5.3               | 0.08                                  | 0.72                                  | 0.11                    |
| E.P.                 |                   |                                       |                                       |                         |
| sine-wave gratings   |                   |                                       |                                       |                         |
| 0.4                  | 4.2               | 0.67                                  | 0.39                                  | 1.72                    |
| 0.8                  | 6.3               | 0.29                                  | 1.14                                  | 0.25                    |
| 1.6                  | 6.3               | 0.09                                  | 1.10                                  | 0.08                    |
| square-wave gratings |                   |                                       |                                       |                         |
| 0.4                  | 4.2               | 0.40                                  | 2.12                                  | 0.19                    |
| 0.8                  | 6.3               | 0.34                                  | 1.43                                  | 0.24                    |
| 1.6                  | 6.3               | 0.65                                  | 1.95                                  | 0.33                    |
| M.C.                 |                   |                                       |                                       |                         |
| sine-wave gratings   |                   |                                       |                                       |                         |
| 0.4                  | 5.3               | 0.40                                  | 2.12                                  | 0.19                    |
| 1.6                  | 5.3               | 0.34                                  | 1.43                                  | 0.24                    |
| 6.4                  | 5.3               | 0.65                                  | 1.95                                  | 0.33                    |
| square-wave gratings |                   |                                       |                                       |                         |
| 0.4                  | 5.3               | 0.10                                  | 0.27                                  | 0.37                    |
| 1.6                  | 5.3               | 0.24                                  | 0.99                                  | 0.24                    |
| 6.4                  | 5.3               | 0.45                                  | 1.15                                  | 0.39                    |

Table II

## EXPERIMENT 3

### Introduction

In this experiment we examined some of the characteristics of our stimuli that actually influence perception by human observers. Our question was, what is important for the observers when under dichoptic viewing conditions they adjust the relative temporal phase one of the gratings so that they can see the stimulus as having maximal or minimal apparent contrast. If they report seeing the stimulus sharply, or of maximal apparent contrast, when the temporal phase difference between the gratings is 0 degrees, and report seeing it with minimal apparent contrast, when the temporal phase difference is 180 degrees, it means that they use the fundamental temporal frequency of the stimulus for perception. If they report seeing the stimulus sharply, or with maximal apparent contrast, when the temporal phase difference is 0 and 180 degrees, and report it as fuzzy, or with minimal apparent contrast, when the temporal phase difference is 90 or 270 degrees, then we would conclude that subjects use the second harmonic of the stimulus for perception.

The VEP data from the second experiment, described earlier, yield a prediction for the psychophysical experiment. In this experiment, the amplitude of VEPs was smallest when the temporal phase difference between two gratings was 90 degrees. This means that under dichoptic viewing conditions the second harmonic of the stimulus is "important" for the generation of the VEPs.

In the present experiment, subjects will be asked to maximize or minimize apparent contrast changing the perception of the stimulus by adjusting the temporal phase of one of the gratings (to make the gratings clearest or fuzziest). Will they use the fundamental or the second harmonic of the stimulus in their judgement? In particular, will it be possible to differentiate between primarily monocular and

binocular inputs, and determine which input controls the appearance of the stimulus?

### Method

#### Apparatus

The computer controlled visual stimulator used in the three previous experiments was interfaced with a keypad, which enabled the subject to adjust values of various stimulus parameters. Three keys were operational in the present experiment. Pressing one key decreased the temporal phase shift of the variable grating, pressing another key increased it, and pressing the third key recorded the response. All temporal phase values chosen by the subjects were stored in the computer's memory and printed at the end of each trial.

#### Procedure

Square- and sine-wave gratings of identical spatial and temporal frequencies and 0.3 contrast were viewed by the subjects under two conditions: dichoptic and binocular. Spatial and temporal characteristics of the stimuli were optimized for each subject and were the same as in the previous two experiments; C.R. was presented with gratings of 0.4 c/deg and 3.2 c/deg modulated at 2.1 Hz, and 0.8 c/deg modulated at 5.3 Hz. E.P. was presented with gratings of 0.4 c/deg modulated at 4.2 Hz; 0.8 c/deg modulated at 6.3 Hz, and 1.6 c/deg modulated at 6.3 Hz. M.C. was presented with gratings of five spatial frequencies (0.4, 0.8, 1.6, 3.2, and 6.4 c/deg), all modulated at 5.3 Hz.

Psychophysical measurements were done using the method of adjustment. At the beginning of each session the subjects received instruction to adjust the relative temporal phase between the two gratings to "make perception of gratings appear clear" (in phase adjustment), or "make perception of gratings appear fuzzy"

(out of phase adjustment). Each adjustment was repeated twenty times. The initial temporal phase differences, at the start of each trial, were randomly set by the computer.

### Data Acquisition and Analysis

The recorded values of adjusted temporal phases were plotted on polar coordinates. The response from each of the twenty trials is represented by a vector, the phase of which corresponds to the value of the temporal phase difference between dichoptic stimuli set by the subject. The amplitudes of all vectors, since they are not a part of the subject's response, were arbitrarily made equal.

### Results and Discussion

The binocular responses of all subjects are clustered around 0 degrees when they were asked to make stimuli look clear (representing adjustment in phase), and around 180 degrees when asked to make stimuli appear "fuzzy" (representing responses out of phase). This can be seen in the figures 19-I, 20-I, and 21-I.

Dichoptic responses are clustered less, and in some cases scattered all around. This could mean that adjustment of temporal phases under binocular conditions was an easier task than adjustment of temporal phases under dichoptic conditions.

Under binocular conditions subjects could more accurately bring both gratings out of phase ("to make the screen look fuzzy" - null adjustment) than in phase ("to make screen look clear" - peak adjustment). As can be seen in figure 19-1a-e (subject E.P.), 20-1a-d (subject C.R.), and in figure 21-1a-f (subject M.C.), scatter around 0 degrees was larger than the scatter around 180 degrees.

**Figure 19 a,b,c,d,e. Response choices of subject E.P. in binocular (I) and dichoptic (II) viewing conditions of psychophysical experiment.**

**Spatial profile, and spatial and temporal frequencies of stimulus indicated in the right lower corner.**

**"clear" - subject was asked to bring both gratings in phase**

**"fuzzy" - subject was asked to bring both gratings out of phase**

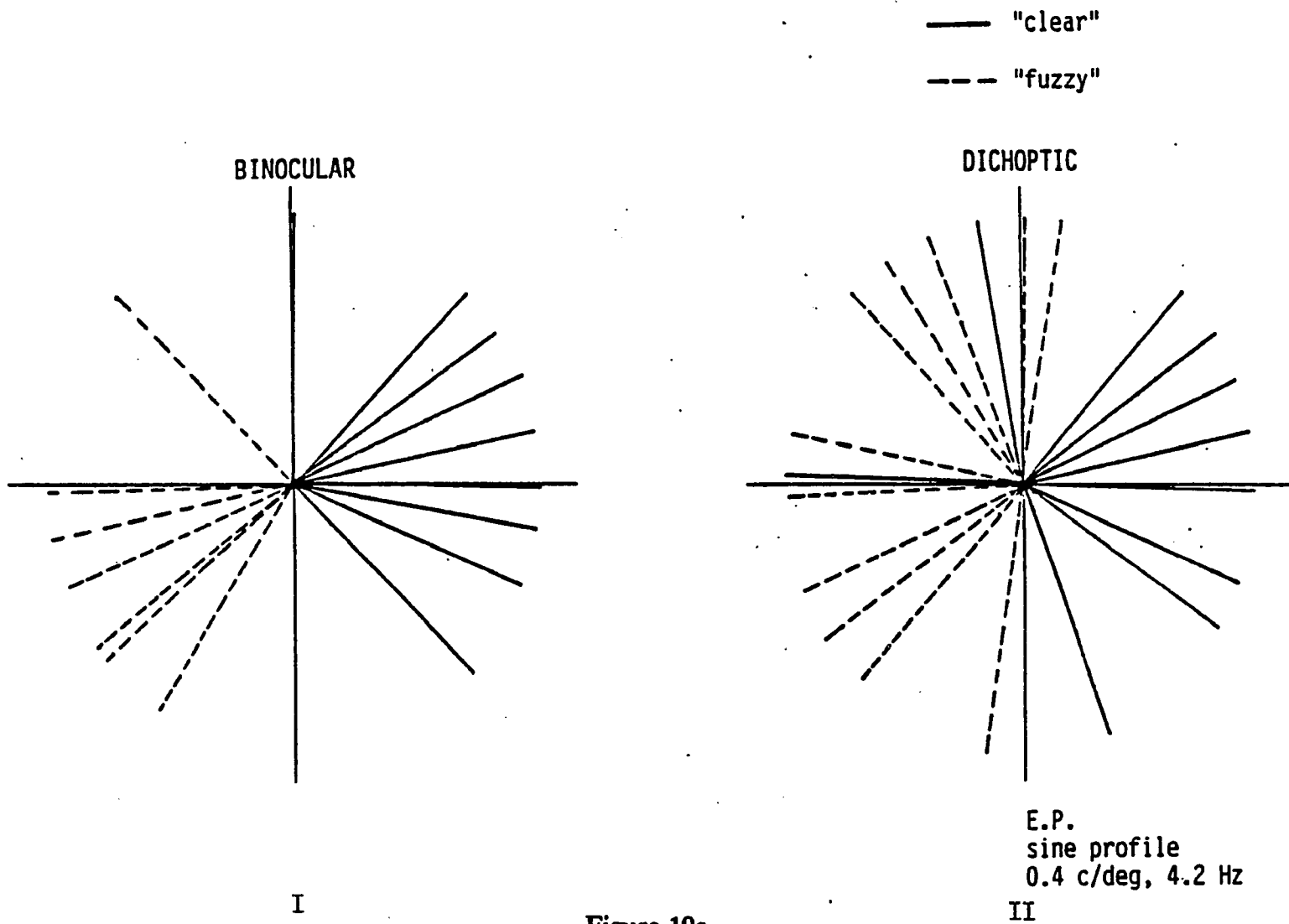
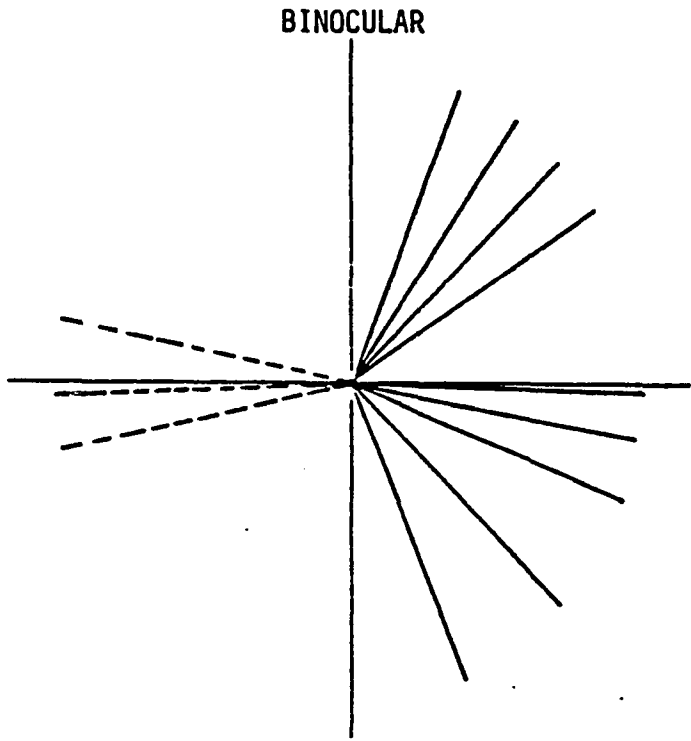


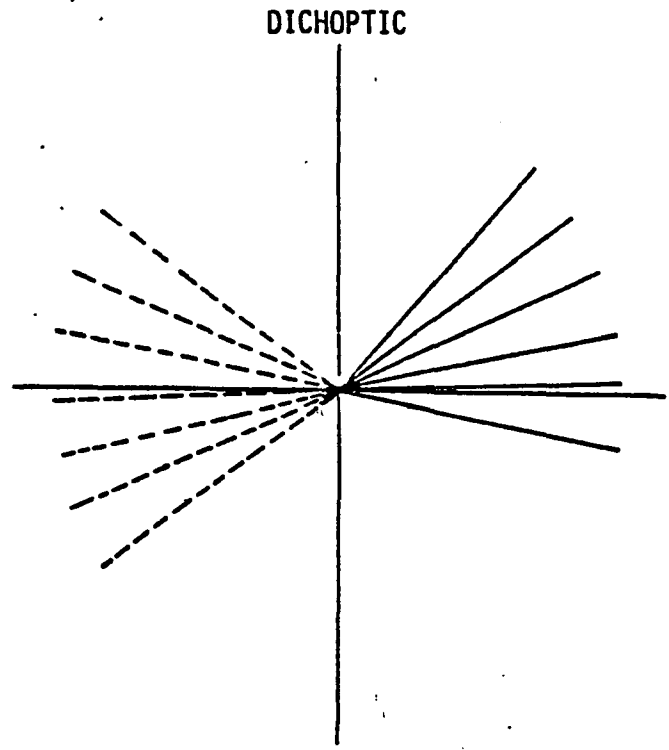
Figure 19a



I

Figure 19b

— "clear"  
 - - - "fuzzy"



E.P.  
 square profile  
 0.4 c/deg, 4.2 Hz  
 II

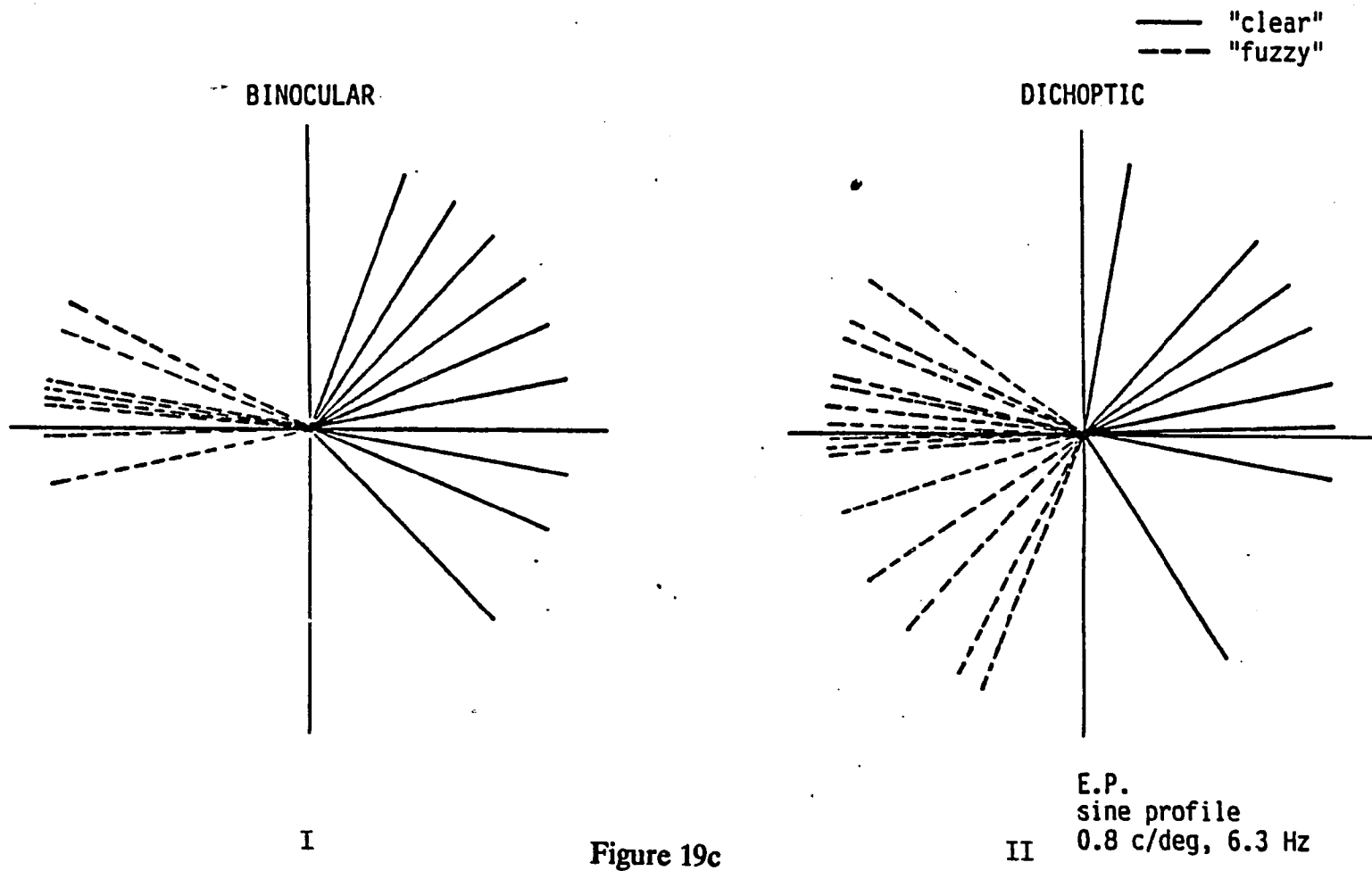
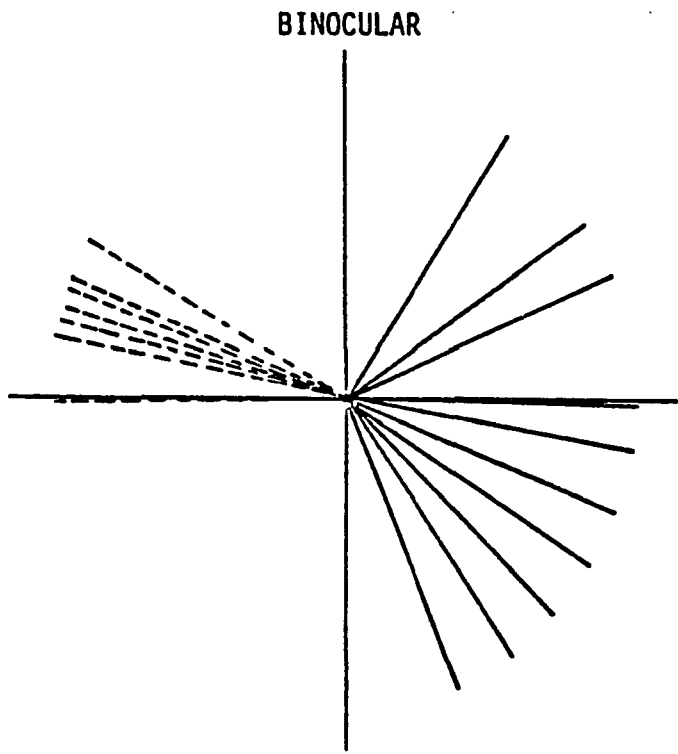
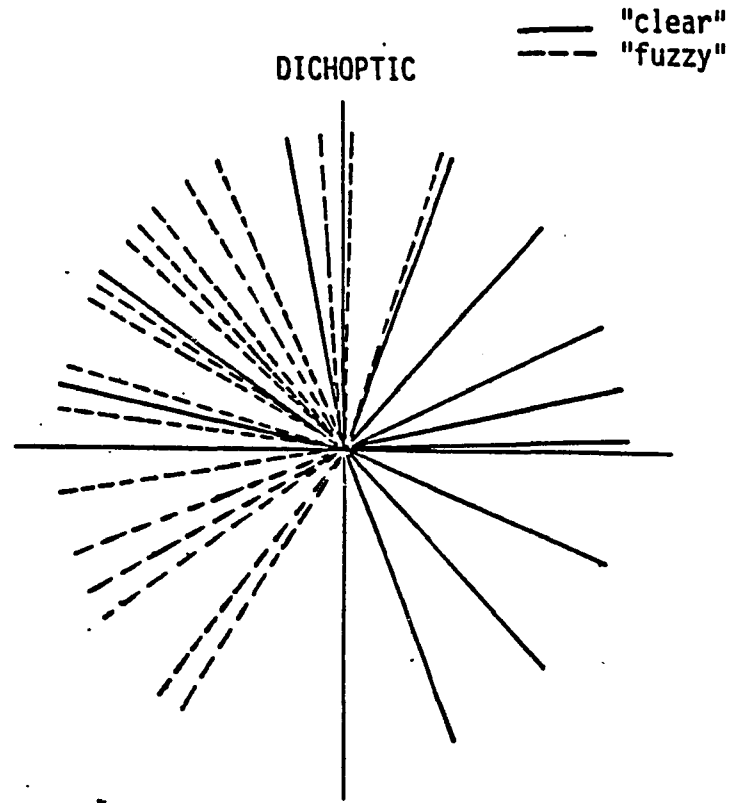


Figure 19c



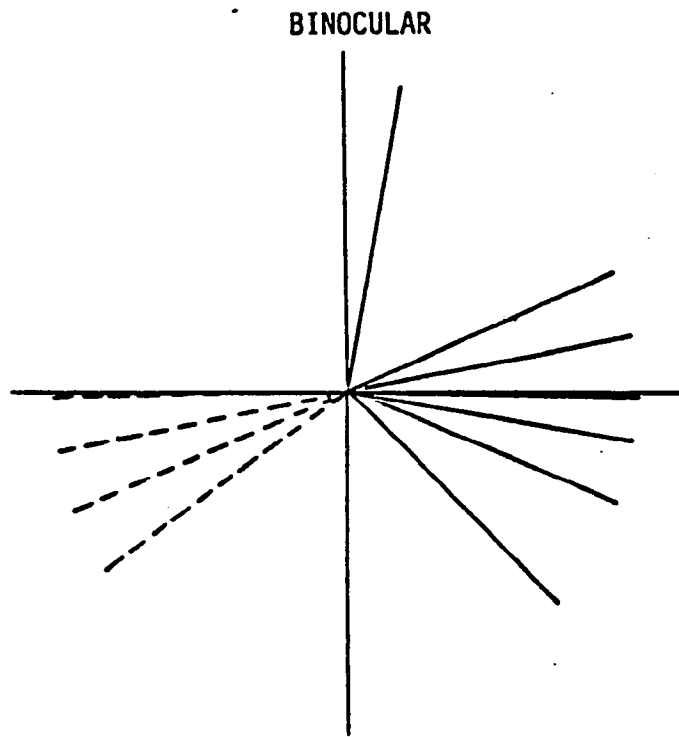
II

Figure 19d



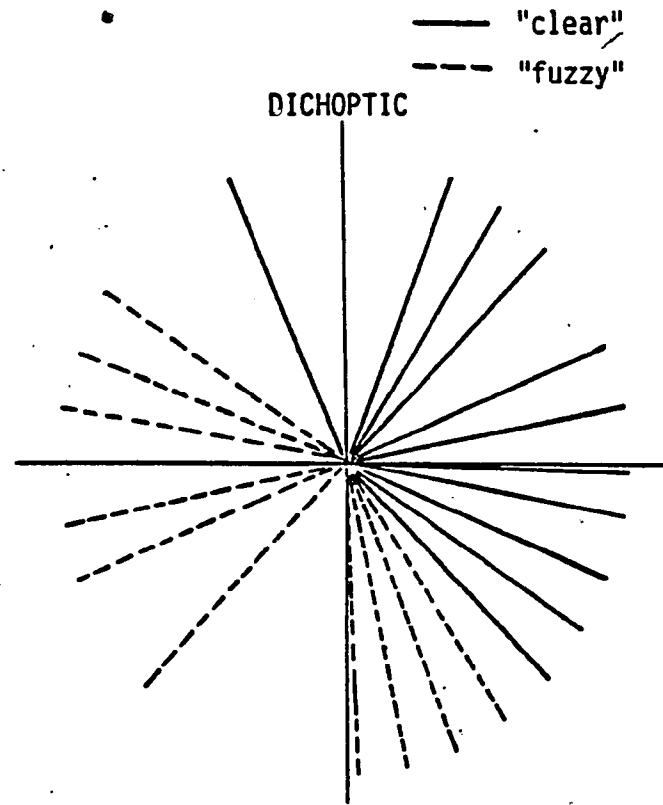
E.P.  
 sine profile  
 1.6 c/deg, 6.3 Hz

II



I

Figure 19e



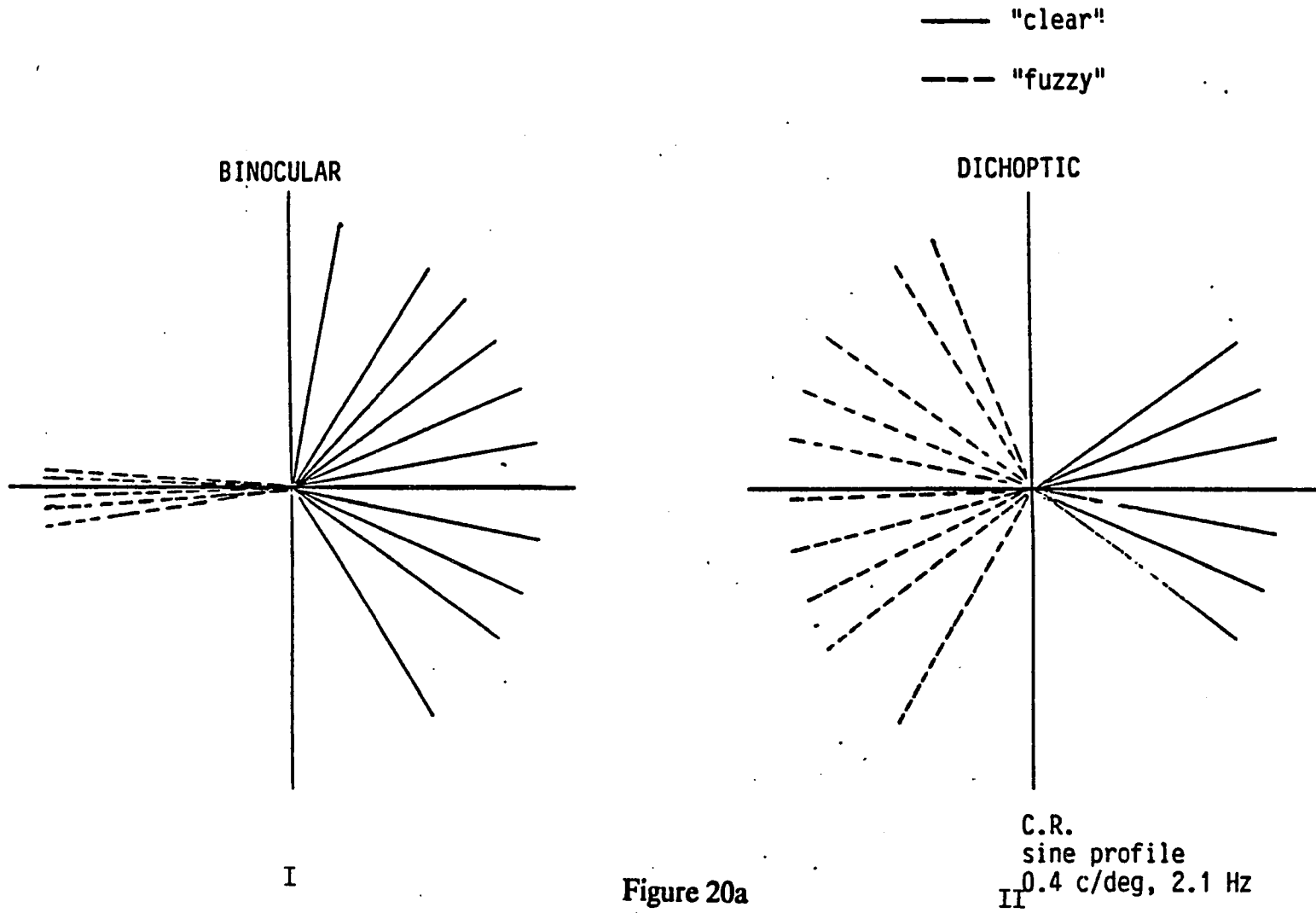
E.P.  
square profile  
1.6 c/deg, 6.3 Hz

II

**Figure 20 a,b,c,d. Response choices of subject C.R. in binocular (I) and dichoptic (II) viewing conditions of psychophysical experiment. Spatial profile, and spatial and temporal frequencies of stimulus indicated in the right lower corner.**

**"clear" - subject was asked to bring both gratings in phase**

**"fuzzy" - subject was asked to bring both gratings out of phase**



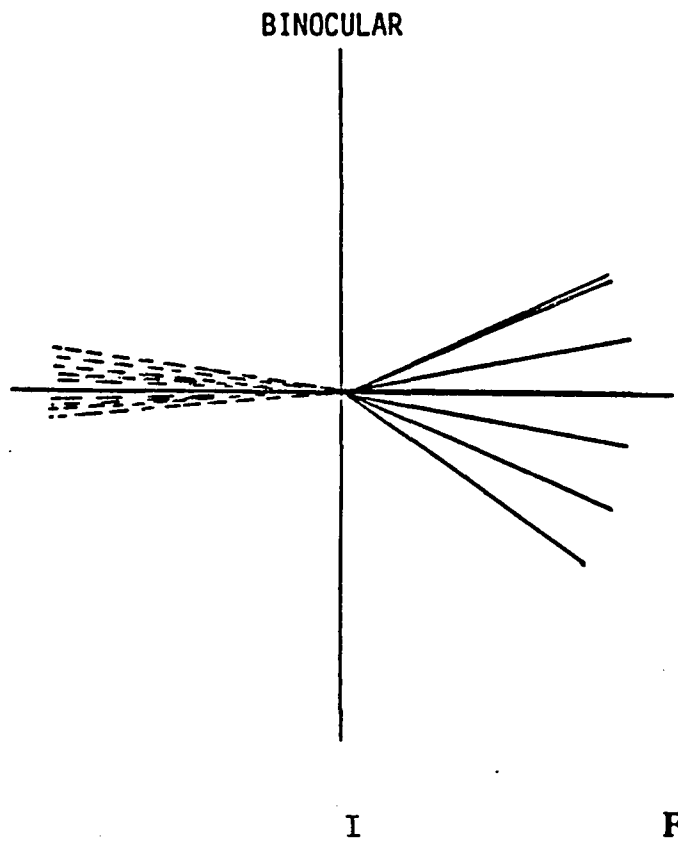
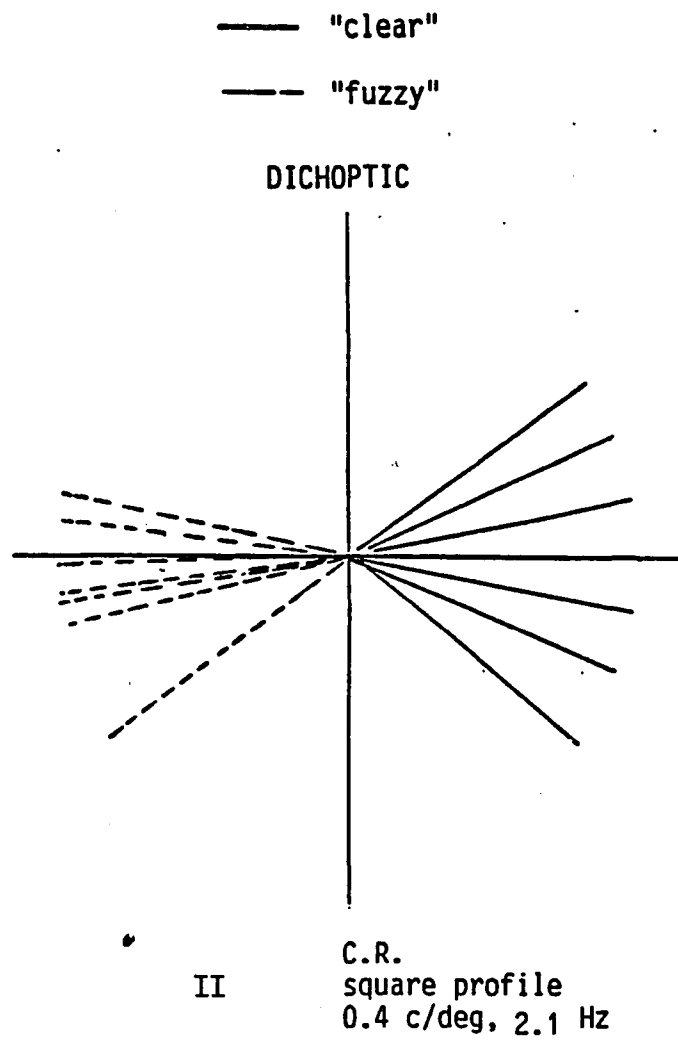
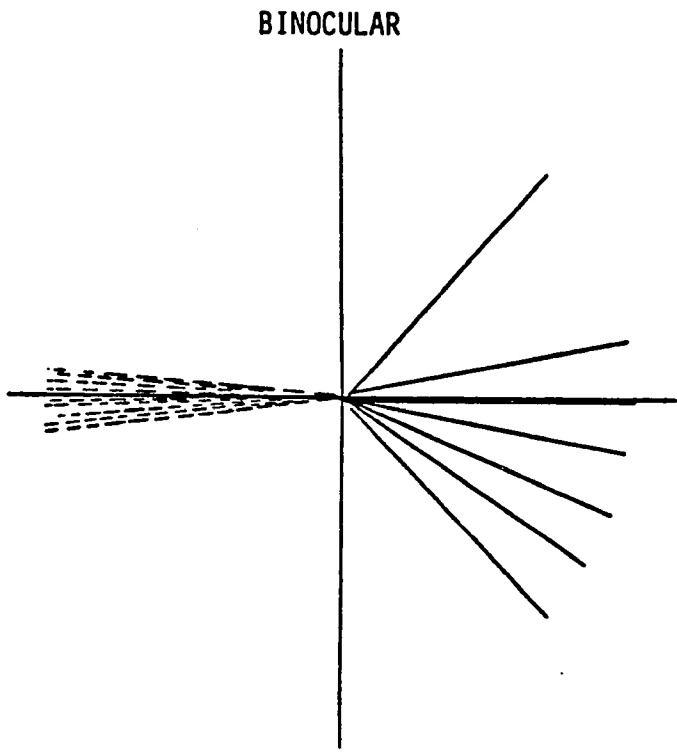


Figure 20b

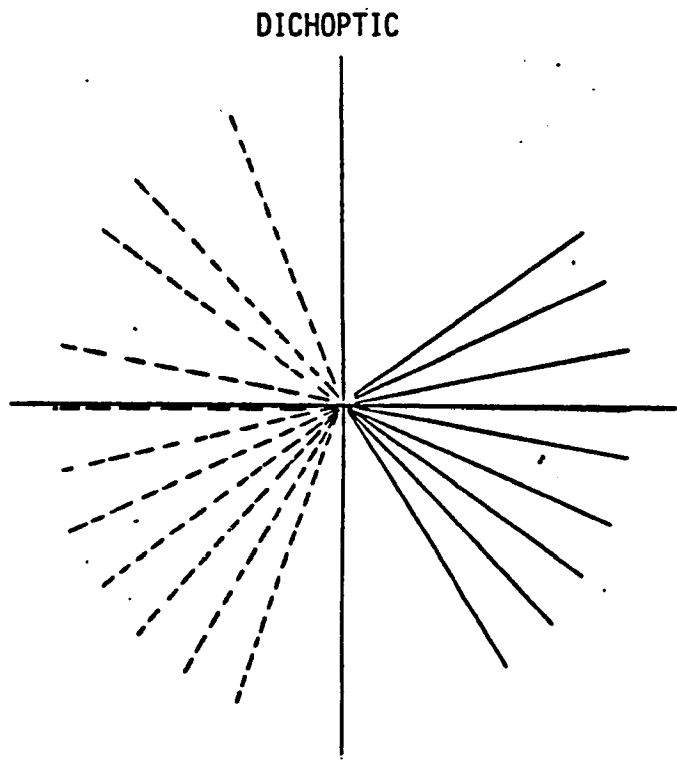




I

Figure 20c

— "clear"  
 - - - "fuzzy"



C.R.  
 sine profile  
 II 0.8 c/deg, 5.3 Hz

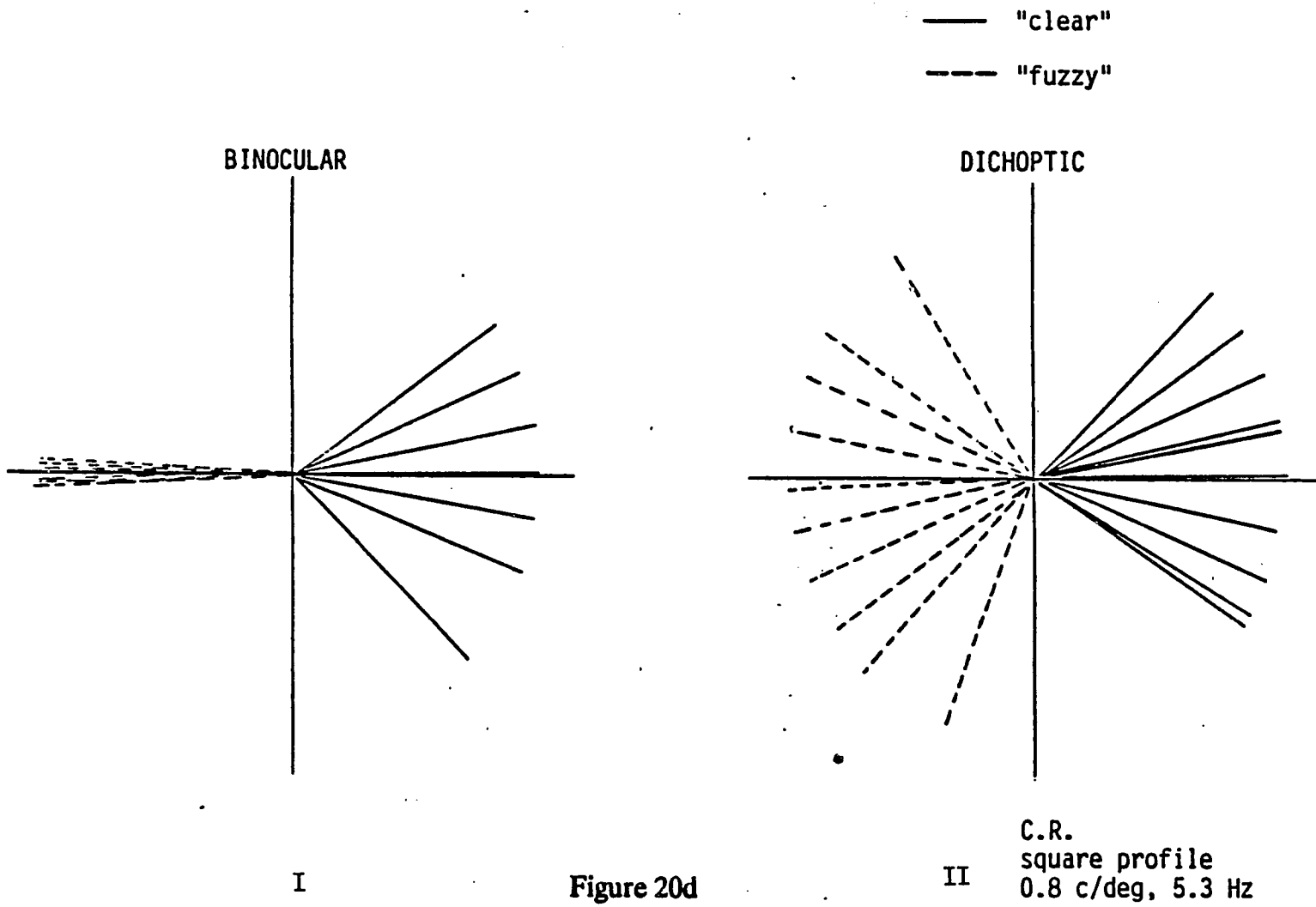


Figure 21 a,b,c,d,e,f. Response choices of subject M.C. in binocular (I) and dichoptic (II) viewing conditions of psychophysical experiment.

Spatial profile, and spatial and temporal frequencies of stimulus indicated in the right lower corner.

"clear" - subject was asked to bring both gratings in phase

"fuzzy" - subject was asked to bring both gratings out of phase

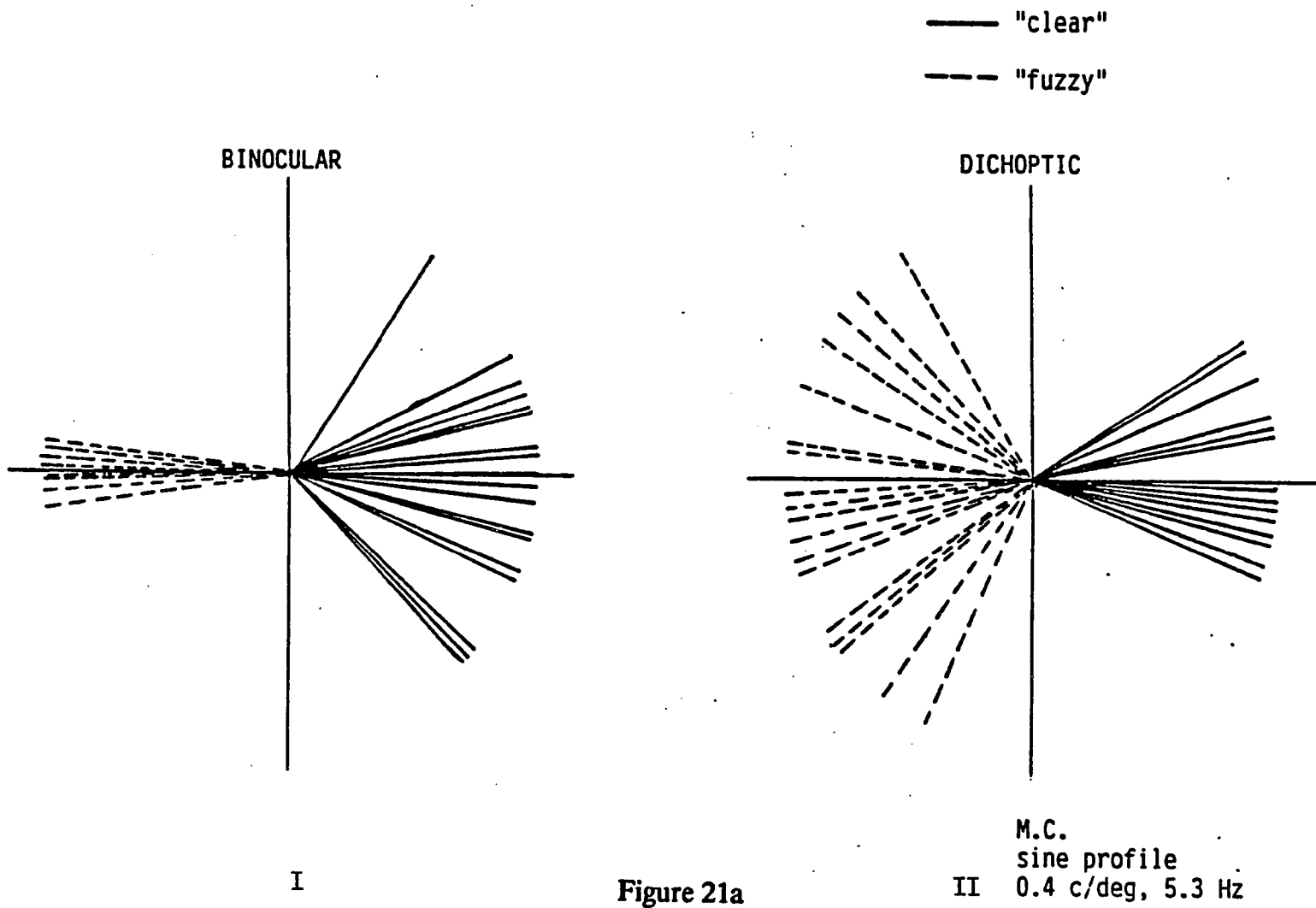
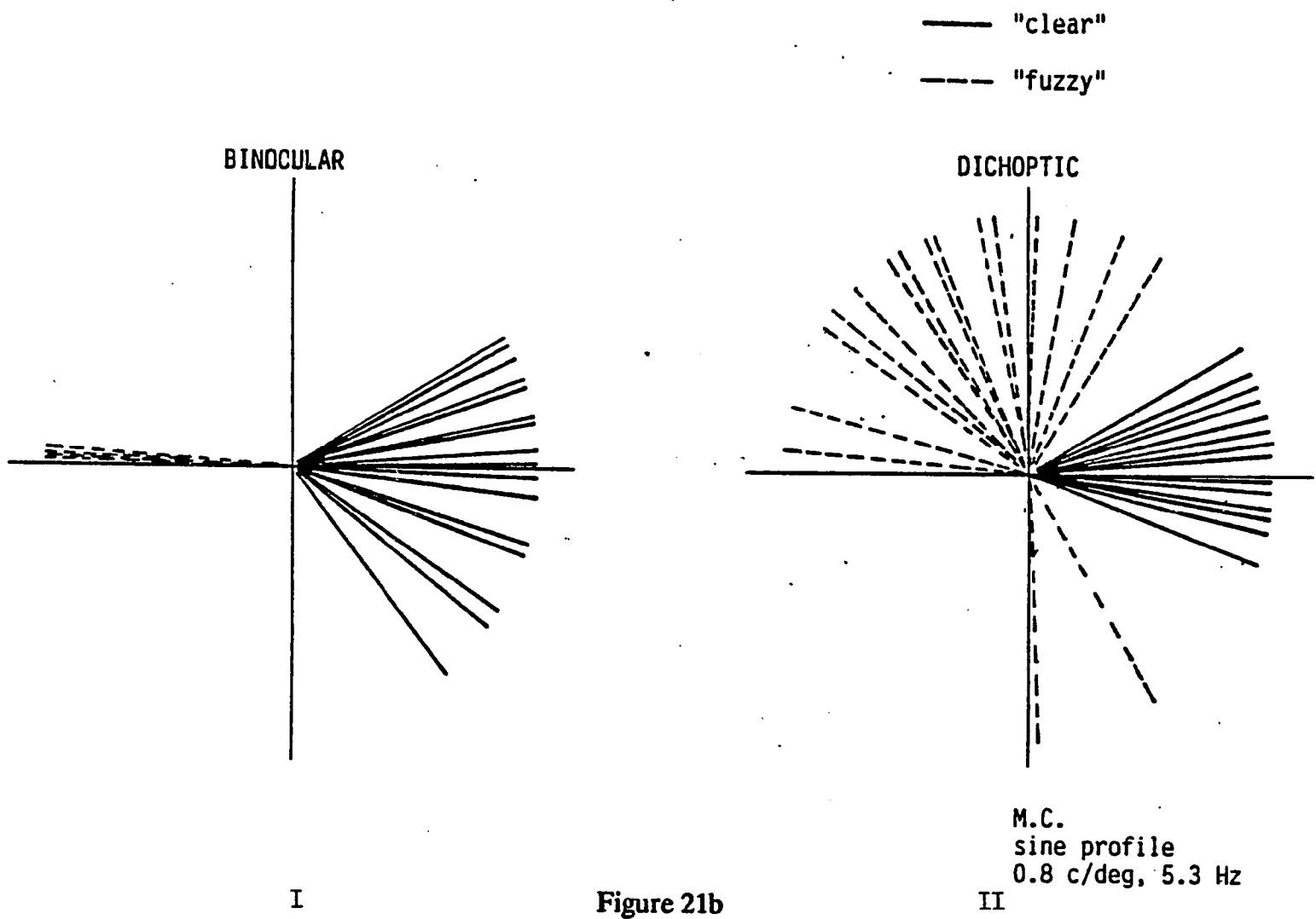


Figure 21a



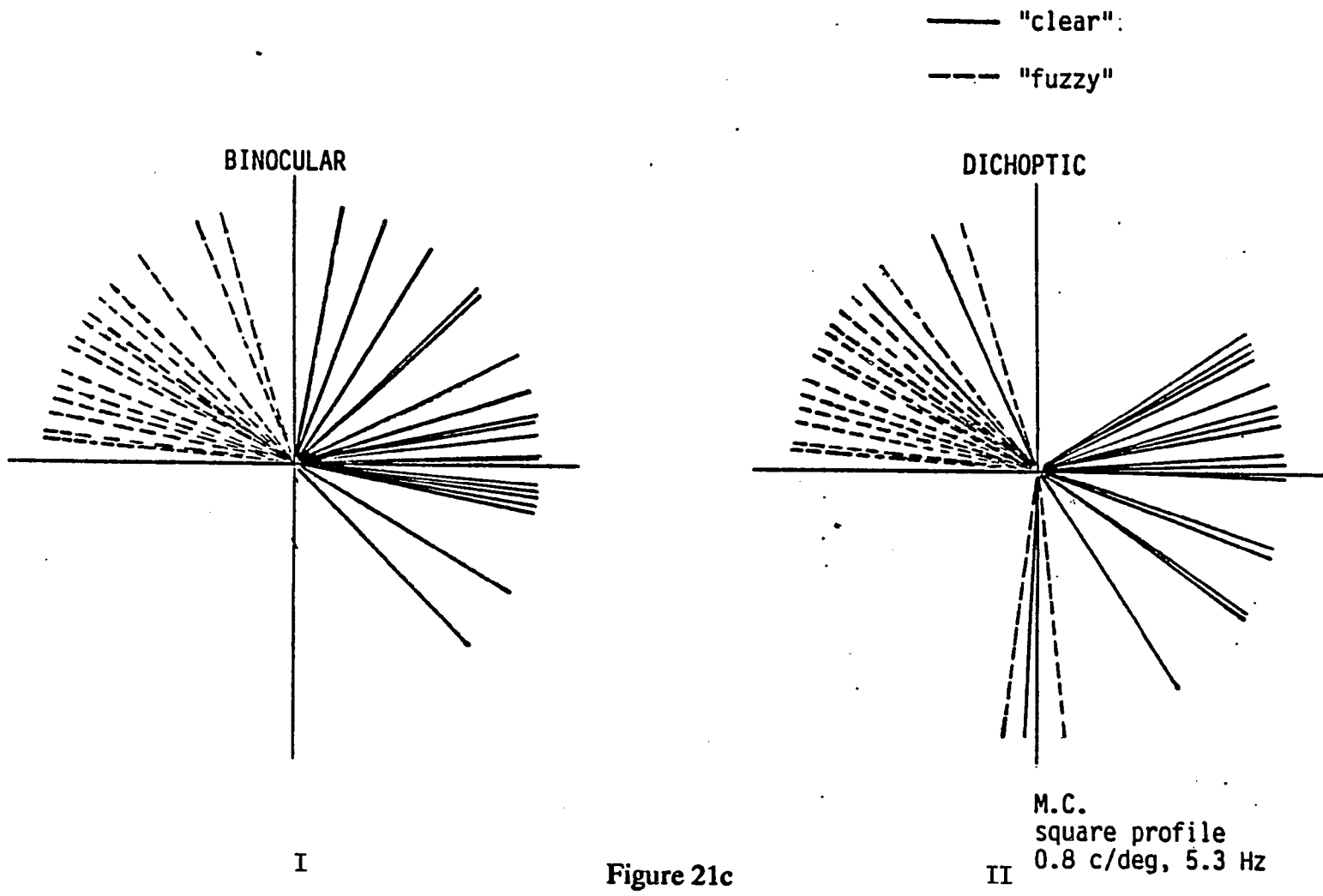
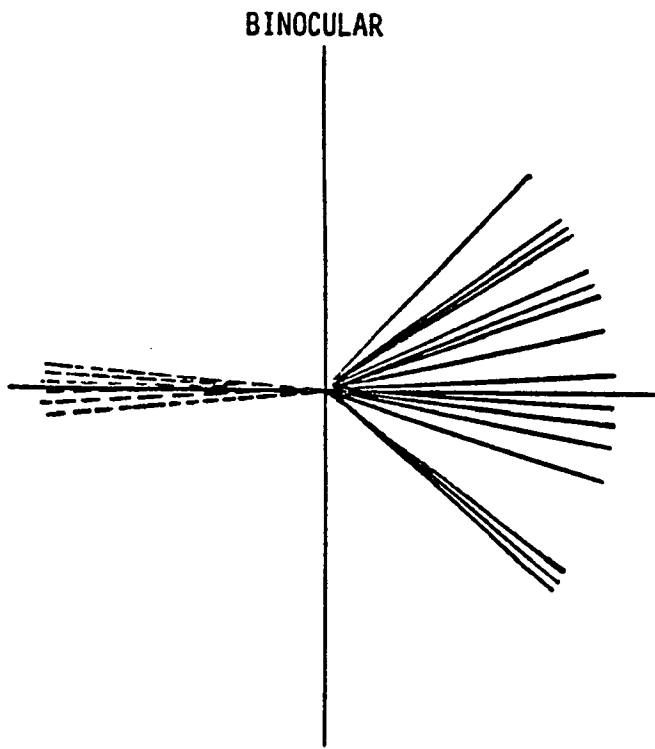
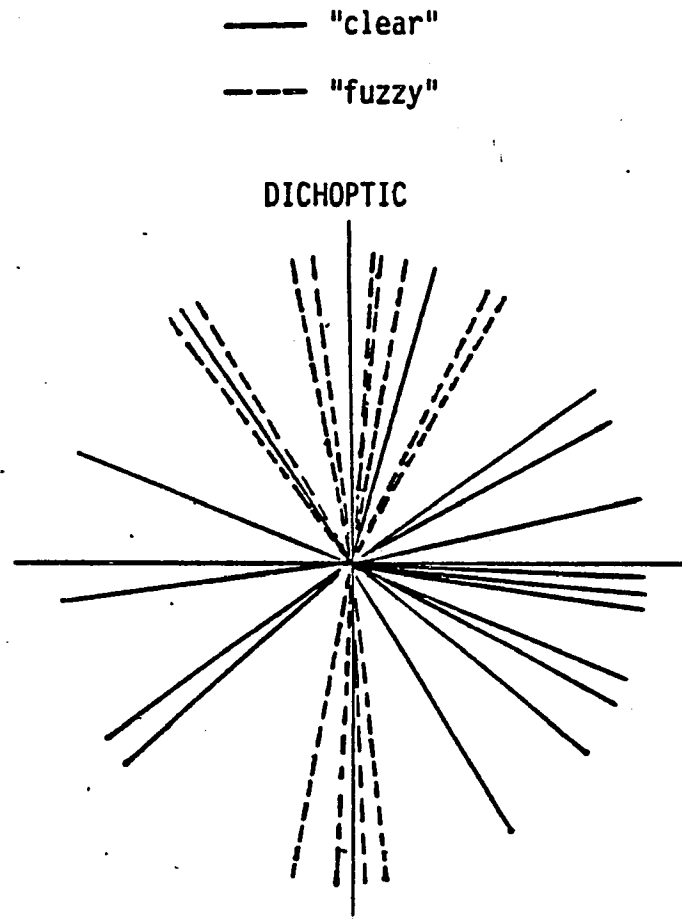


Figure 21c



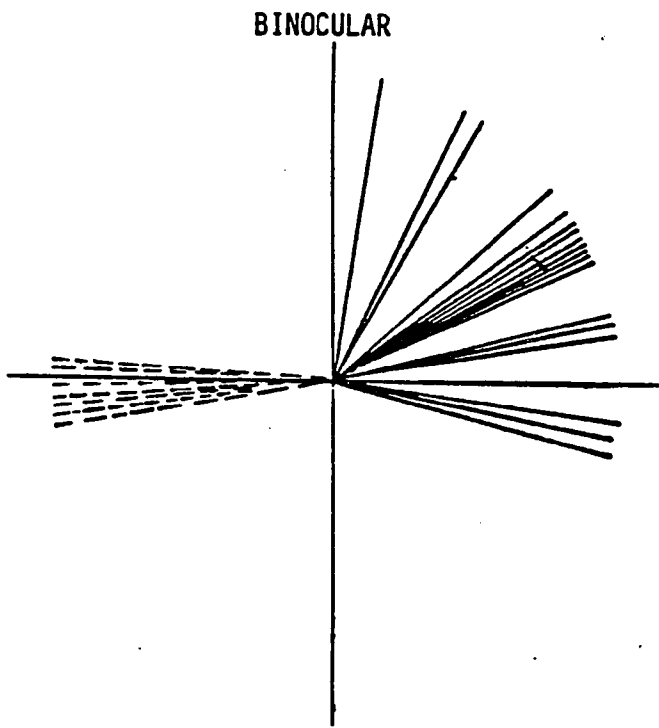
I

Figure 21d



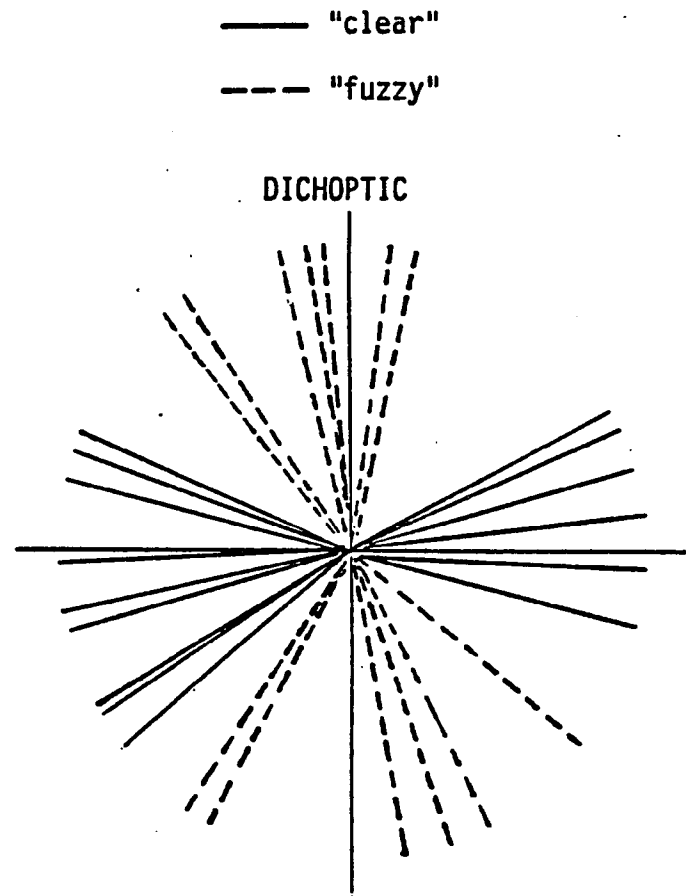
M.C.  
 sine profile  
 3.2 c/deg, 5.3 Hz

II



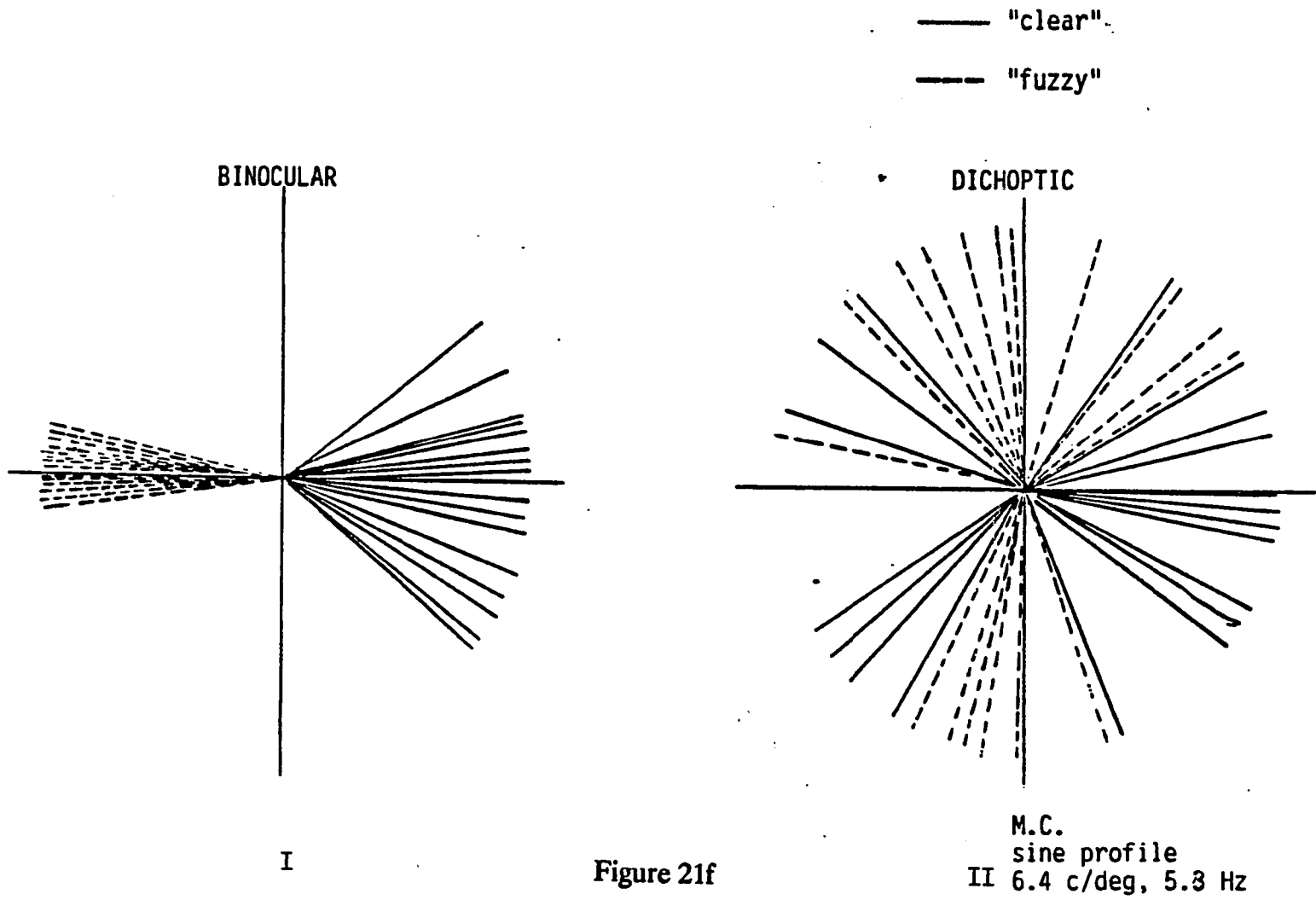
I

Figure 21e



M.C.  
 square profile  
 3.2 c/deg, 5.3 Hz

II



With respect to the changes in spatial profile under binocular conditions, two of the subjects (E.P. and C.R.) showed less scatter for square wave than for sine wave gratings. This is consistent with our personal observation that alignment of a square wave gratings is easier than sine wave gratings.

Under dichoptic viewing conditions for low spatial frequencies the results were similar to binocular conditions. The peak (clear) settings were around 0 degrees and the out of peak (fuzzy) settings were around 180 degrees. When subjects were asked to make stimuli look "fuzzy" or to make stimuli look "clear" there were no real differences between the ranges of the scatters around 180 and 0 degrees, for the gratings of low spatial frequencies. However, as spatial frequencies of stimuli were increased, responses of two subjects (E.P. and C.R.) became more and more scattered for both the "clear" and "fuzzy" conditions (figures 19-2,d-e; and 20-2,e). For subject M.C., increasing the spatial frequency had an even more dramatic effect. As it can be seen in figure 21b and 21c, choices of her adjustments when she was asked to make stimuli look "fuzzy" were scattered close to and around 90 and 270 degrees, and around 0 and 180 degrees when she was asked to make stimuli look "clear" for the gratings of 3.2, and 6.4 c/deg.

We can conclude from this results that under binocular viewing conditions perception of the stimuli depends upon the fundamental frequency of the stimuli or the binocular pathway. It seems that under dichoptic viewing conditions subjects' responses also depend on the fundamental frequency when the spatial frequency is low, but more upon the stimuli second harmonic of the stimuli as the spatial frequency increases. Returning to our models of binocular interaction (pages 39-46, figs. 9-12), we may suggest that the low spatial frequency results are in accord with model 1, in which summation is before the nonlinearity. As spatial frequency increases, the contribution of the binocular pathway, (described by the model 1) becomes smaller; this is in agreement with the psychophysical results as well.

We did not find in this study strong correspondence between response amplitudes in the VEP's and subject's choices in adjusting stimulus phase. So far, we do not know of any studies showing connections between the psychophysical and VEP characteristics. Musselwhite and Jeffreys (1985) found that although increase in spatial frequency of the stimulus increased the latency of the reaction times, it did not correspond to the changes in the peak latency of the initial VEP component. Some additional experiments are needed before we may conclude that changes in the VEP amplitude observed in this study reflect psychophysical perception of a signal.

**APPENDIX A**

Table 1  
Spatial and Temporal Tuning  
Experiment # 1

| Subjects<br>Spatial<br>profile | M.C        |           | B.F          |           | C.R          |           | E.P          |           | J.W.         |           |              |
|--------------------------------|------------|-----------|--------------|-----------|--------------|-----------|--------------|-----------|--------------|-----------|--------------|
|                                | sine       |           | sine         |           | sine         |           | square       |           | square       |           |              |
| S. f<br>c/d                    | T. f<br>Hz | Amp<br>uV | Phase<br>deg | Amp<br>uV | Phase<br>deg | Amp<br>uV | Phase<br>deg | Amp<br>uV | Phase<br>deg | Amp<br>uV | Phase<br>deg |
| .4                             | 2.1        | .4        | -17.1        | .4        | 154.5        | .8        | 133.6        | .4        | 74.1         | .2        | 159.1        |
| .4                             | 4.2        | 1.4       | -143.9       | .4        | -148.7       | .3        | -144.1       | 1.2       | -123.3       | 1.0       | 158.6        |
| .4                             | 5.3        | 2.3       | 104.5        | .3        | 44.0         | 1.2       | 7.0          | .6        | 106.7        | .8        | 26.4         |
| .4                             | 6.3        | 2.9       | 13.7         | .4        | -30.2        | .9        | -55.9        | 1.0       | 16.1         | 1.2       | -59.0        |
| .8                             | 2.1        | .6        | 3.7          | .4        | 119.3        | 1.0       | 138.0        | .7        | 68.6         | .5        | 60.7         |
| .8                             | 4.2        | 1.5       | -165.2       | .8        | 155.8        | 1.3       | -178.3       | .4        | 111.0        | .9        | 143.5        |
| .8                             | 5.3        | 2.3       | 72.6         | 1.2       | -2.8         | 1.9       | 4.3          | .7        | 43.7         | 1.0       | 14.8         |
| .8                             | 6.3        | 2.3       | -35.1        | .4        | -118.9       | 1.4       | -76.4        | 1.2       | -23.9        | 1.2       | -87.6        |
| 1.6                            | 2.1        | .5        | -60.0        | .5        | 118.7        | .0        | -121.5       | .3        | -152.5       | .6        | 22.6         |
| 1.6                            | 4.2        | 1.7       | 173.9        | .6        | 145.9        | 1.2       | 172.1        | .8        | 40.8         | .5        | 94.2         |
| 1.6                            | 5.3        | 1.9       | 25.1         | .3        | -58.9        | 1.2       | -93.0        | 1.3       | -2.9         | .6        | 2.9          |
| 1.6                            | 6.3        | 1.9       | -134.3       | .5        | 160.7        | 1.5       | -108.5       | 1.4       | -79.7        | .9        | -101.7       |
| 3.2                            | 2.1        | .3        | -3.9         | .4        | 133.0        | 1.4       | 111.5        | .7        | 167.7        | .2        | -140.3       |
| 3.2                            | 4.2        | .4        | 140.0        | .2        | -166.4       | .5        | 32.9         | .9        | 2.9          | .6        | -44.3        |
| 3.2                            | 5.3        | 2.0       | -31.5        | .5        | -120.7       | 1.1       | -110.2       | 1.1       | -86.4        | .5        | -169.2       |
| 3.2                            | 6.3        | 1.0       | -165.5       | .5        | 68.9         | .8        | -159.9       | 1.1       | -175.5       | .4        | 23.3         |
| 6.4                            | 2.1        | .4        | -99.7        | .3        | 77.0         | 1.0       | 66.3         | .7        | 150.6        | .6        | -172.4       |
| 6.4                            | 4.2        | .8        | -30.5        | .4        | 135.4        | .5        | 11.0         | .6        | -60.7        | .6        | -48.9        |
| 6.4                            | 5.3        | 1.7       | -132.5       | .1        | -115.9       | .9        | -176.2       | .3        | 175.3        | .7        | -167.8       |
| 6.4                            | 6.3        | .8        | 81.2         | .3        | 169.6        | 1.1       | 73.9         | .2        | 75.7         | .3        | 126.3        |

Table 1

B.F. 3/12-17/86

Binocular and monocular control  
Sine and square profiles

| Spatial<br>frqncy<br>(c/degree) | Temporal<br>frqncy<br>(Hz) | Amplitude<br>(uV)                        | Phase<br>(degrees) | Amplitude<br>(uV)              | Phase<br>(degrees) | Amplitude<br>(uV)   | Phase<br>(degrees) | Amplitude<br>(uV)                                 | Phase<br>(degrees) |
|---------------------------------|----------------------------|--|--------------------|--------------------------------|--------------------|---|--------------------|---|--------------------|
|                                 |                            | Dichoptic viewing<br>(polarized glasses) |                    | Binocular viewing<br>(NDF=0.5) |                    | Monocular viewing<br>(algebraic sum)<br>(polarized glasses) |                    | Monocular viewing<br>(algebraic sum)<br>(NDF=0.5) |                    |
| Sine profile                    |                            |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                 |                            |  |                    |                                |                    |   |                    |   |                    |
| 3.20                            | 6.30                       | .72                                      | 82.15              | .64                            | 32.64              | 1.40  | 82.00              | .20   | 20.65              |
| 3.20                            | 4.20                       | .49                                      | -166.58            | .23                            | -179.72            | .80   | -108.80            | .40   | -57.28             |
| 1.60                            | 6.30                       | 1.08                                     | 159.61             | .54                            | 92.07              | 1.10  | 130.17             | .30   | 69.10              |
| .80                             | 5.30                       | .80                                      | -5.49              | .58                            | -10.34             | 1.70  | 50.86              | .70   | -73.22             |
| .80                             | 4.20                       | .75                                      | 177.02             | .90                            | 134.94             | 1.00  | 162.71             | 1.20  | 113.70             |
| fourth harmonics                |                            |  |                    |                                |                    |   |                    |   |                    |
| 3.20                            | 6.30                       | .45                                      | 178.13             | .24                            | 81.02              | .40   | 137.30             | .20   | 33.55              |
| 3.20                            | 4.20                       | .39                                      | -107.65            | .20                            | -142.07            | .60   | -148.85            | .30   | 128.36             |
| 1.60                            | 6.30                       | .24                                      | -116.35            | .20                            | 90.00              | .20   | -164.55            | .10   | -104.15            |
| .80                             | 5.30                       | .20                                      | -29.85             | .11                            | -101.77            | .20   | -83.71             | .20   | -151.25            |
| .80                             | 4.20                       | .29                                      | -158.45            | .20                            | 164.86             | .40   | 150.30             | .20   | 161.30             |
| Square profile                  |                            |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                 |                            |  |                    |                                |                    |   |                    |   |                    |
| 3.20                            | 6.30                       | .75                                      | 60.94              | .75                            | 71.67              | .30   | 9.80               | .60   | 50.90              |
| 3.20                            | 4.20                       | .39                                      | -160.33            | .57                            | -158.28            | .20   | -119.39            | .60   | -146.28            |
| 1.60                            | 6.30                       | .59                                      | 155.17             | .68                            | 149.50             | .40   | 129.38             | .70   | 78.47              |
| .80                             | 5.30                       | 1.05                                     | 10.89              | 1.44                           | -17.95             | .40   | -6.15              | 1.50  | -32.50             |
| .80                             | 4.20                       | .88                                      | 160.20             | .47                            | 88.28              | 1.80  | 142.46             | 1.70  | 141.50             |
| fourth harmonics                |                            |  |                    |                                |                    |   |                    |   |                    |
| 3.20                            | 6.30                       | .24                                      | 160.56             | .25                            | 139.36             | .40   | -174.30            | .30   | 173.24             |
| 3.20                            | 4.20                       | .26                                      | -133.35            | .27                            | -72.70             | .30   | -148.14            | .20   | -176.30            |
| 1.60                            | 6.30                       | .14                                      | -128.69            | .15                            | 139.56             | .10   | -168.90            | .10   | 64.25              |
| .80                             | 5.30                       | .05                                      | -72.20             | .07                            | 12.05              | .10   | -10.85             | .10   | -19.93             |
| .80                             | 4.20                       | .35                                      | 171.51             | .16                            | 116.26             | .20   | 179.44             | .30   | 159.74             |

Table 2

C.R. 4/8/86

Binocular and monocular control  
 Sine and square profiles

| Spatial<br>freqncy<br>(c/degree) | Temporal<br>freqncy<br>(Hz) | Amplitude<br>(uV)                        | Phase<br>(degrees) | Amplitude<br>(uV)              | Phase<br>(degrees) | Amplitude<br>(uV)   | Phase<br>(degrees) | Amplitude<br>(uV)                                 | Phase<br>(degrees) |
|----------------------------------|-----------------------------|--|--------------------|--------------------------------|--------------------|---|--------------------|---|--------------------|
|                                  |                             | Dichoptic viewing<br>(polarized glasses) |                    | Binocular viewing<br>(NDF=0.5) |                    | Monocular viewing<br>(algebraic sum)<br>(polarized glasses) |                    | Monocular viewing<br>(algebraic sum)<br>(NDF=0.5) |                    |
| Sine profile                     |                             |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                  |                             |  |                    |                                |                    |   |                    |   |                    |
| .80                              | 5.30                        | 1.45                                     | -11.76             | 2.04                           | -23.87             | 2.45  | -25.90             | 2.90  | -48.00             |
| .40                              | 2.10                        | .93                                      | 139.48             | .75                            | 140.17             | 1.40  | 122.00             | 1.36  | 87.50              |
| fourth harmonics                 |                             |  |                    |                                |                    |   |                    |   |                    |
| .80                              | 5.30                        | .15                                      | 31.90              | .05                            | -46.40             | .29   | 24.10              | .18   | 174.20             |
| .40                              | 2.10                        | .38                                      | 175.04             | .30                            | -4.20              | .18   | 129.60             | .78   | 9.10               |
| Square profile                   |                             |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                  |                             |  |                    |                                |                    |   |                    |   |                    |
| .80                              | 5.30                        | 2.04                                     | 27.58              | 2.00                           | 1.22               | 2.97  | -11.20             | 2.80  | -45.90             |
| .40                              | 2.10                        | 1.18                                     | 112.10             | 1.28                           | 94.75              | 1.39  | 92.00              | 2.10  | 74.20              |
| fourth harmonics                 |                             |  |                    |                                |                    |   |                    |   |                    |
| .80                              | 5.30                        | .15                                      | 20.22              | .15                            | -33.54             | .14   | 36.20              | .20   | -57.90             |
| .40                              | 2.10                        | .42                                      | -90.25             | .46                            | -61.85             | .30   | 63.20              | 1.60  | -19.30             |

Table 3

E.P.5/1-2/86

Binocular and monocular control  
Sine and square profiles

| Spatial<br>frqncy<br>(c/degree) | Temporal<br>frqncy<br>(Hz) | Amplitude<br>(uV)                        | Phase<br>(degrees) | Amplitude<br>(uV)              | Phase<br>(degrees) | Amplitude<br>(uV)   | Phase<br>(degrees) | Amplitude<br>(uV)                                 | Phase<br>(degrees) |
|---------------------------------|----------------------------|--|--------------------|--------------------------------|--------------------|---|--------------------|---|--------------------|
|                                 |                            | Dichoptic viewing<br>(polarized glasses) |                    | Binocular viewing<br>(NDF=0.5) |                    | Monocular viewing<br>(algebraic sum)<br>(polarized glasses) |                    | Monocular viewing<br>(algebraic sum)<br>(NDF=0.5) |                    |
| Sine profile                    |                            |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                 |                            |  |                    |                                |                    |   |                    |   |                    |
| .40                             | 4.20                       | .45                                      | -98.61             | .30                            | -91.38             | .50   | -97.70             | .90   | -72.30             |
| .80                             | 6.30                       | 1.24                                     | -21.03             | .83                            | -53.98             | 1.10  | -54.20             | .30   | -39.60             |
| 1.60                            | 6.30                       | 1.10                                     | -91.66             | .98                            | -134.02            | .80   | -144.20            | .60   | -172.70            |
| fourth harmonics                |                            |  |                    |                                |                    |   |                    |   |                    |
| .40                             | 4.20                       | .44                                      | -147.92            | .60                            | -179.00            | .10   | 54.10              | .10   | 48.10              |
| .80                             | 6.30                       | .29                                      | -129.10            | .10                            | 103.20             | .10   | -85.10             | .10   | -148.40            |
| 1.60                            | 6.30                       | .17                                      | 158.22             | .05                            | 35.70              | .20   | 172.00             | .10   | -109.90            |
| Square profile                  |                            |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                 |                            |  |                    |                                |                    |   |                    |   |                    |
| .40                             | 4.20                       | 1.21                                     | -134.20            | .80                            | -167.12            | .60   | -157.40            | 1.00  | 178.60             |
| .80                             | 6.30                       | 1.48                                     | -27.84             | .83                            | -53.12             | 1.20  | -17.50             | 1.00  | -18.60             |
| 1.60                            | 6.30                       | 1.39                                     | -80.80             | 1.29                           | -117.32            | 1.40  | -120.90            | .50   | -178.60            |
| fourth harmonics                |                            |  |                    |                                |                    |   |                    |   |                    |
| .40                             | 4.20                       | .38                                      | -130.18            | .25                            | -141.34            | .30   | -49.40             | .50   | -110.80            |
| .80                             | 6.30                       | .30                                      | -73.87             | .26                            | -146.71            | .30   | -113.70            | .20   | -144.60            |
| 1.60                            | 6.30                       | .49                                      | -162.20            | .30                            | 148.83             | .10   | 101.60             | .00   | 90.00              |

Table 4

J.W. 3/8-14-19/86

Binocular and monocular control  
Sine and square profiles

| Spatial<br>freqncy<br>(c/degree) | Temporal<br>freqncy<br>(Hz) | Amplitude<br>(uV)                        | Phase<br>(degrees) | Amplitude<br>(uV)              | Phase<br>(degrees) | Amplitude<br>(uV)   | Phase<br>(degrees) | Amplitude<br>(uV)                                 | Phase<br>(degrees) |
|----------------------------------|-----------------------------|--|--------------------|--------------------------------|--------------------|---|--------------------|---|--------------------|
|                                  |                             | Dichoptic viewing<br>(polarized glasses) |                    | Binocular viewing<br>(NDF=0.5) |                    | Monocular viewing<br>(algebraic sum)<br>(polarized glasses) |                    | Monocular viewing<br>(algebraic sum)<br>(NDF=0.5) |                    |
| Sine profile                     |                             |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                  |                             |  |                    |                                |                    |   |                    |   |                    |
| .40                              | 6.30                        | .40                                      | -171.87            | .10                            | -132.60            | .67   | 63.40              | .70   | -17.28             |
| .80                              | 6.30                        | 1.04                                     | -88.34             | .90                            | -133.75            | .87   | -104.92            | .70   | -145.26            |
| 3.22                             | 6.30                        | .85                                      | -70.78             | .94                            | -93.73             | .90   | 168.20             | 1.10  | -86.45             |
| fourth harmonics                 |                             |  |                    |                                |                    |   |                    |   |                    |
| .40                              | 6.30                        | .12                                      | -174.40            | .07                            | -136.98            | .45   | 14.30              | .30   | -60.70             |
| .80                              | 6.30                        | .13                                      | 158.42             | .15                            | 99.37              | .19   | 168.20             | .17   | 93.80              |
| 3.22                             | 6.30                        | .08                                      | -147.85            | .05                            | 71.80              | .17   | -151.30            | .04   | -14.50             |
| Square profile                   |                             |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                  |                             |  |                    |                                |                    |   |                    |   |                    |
| .40                              | 6.30                        | .15                                      | 131.92             | .01                            | -82.50             | 1.75  | 42.80              | .35   | 67.02              |
| .80                              | 6.30                        | 1.28                                     | -78.20             | 1.17                           | -122.16            | 1.06  | -63.88             | 1.00  | -139.84            |
| 3.22                             | 6.30                        | 1.17                                     | -44.10             | 1.21                           | -95.54             | .91   | -45.23             | 1.47  | -90.41             |
| fourth harmonics                 |                             |  |                    |                                |                    |   |                    |   |                    |
| .40                              | 6.30                        | .29                                      | -142.20            | .25                            | 168.27             | .20   | 15.93              | .30   | -12.20             |
| .80                              | 6.30                        | .25                                      | -151.16            | .19                            | 159.20             | .29   | -160.47            | .00   | 90.00              |
| 3.22                             | 6.30                        | .10                                      | 5.80               | .05                            | 137.80             | .20   | -35.50             | .10   | 155.50             |

Table 5

M.C. 3/12/86

Binocular and monocular control  
Sine and square profiles

| Spatial<br>freqncy<br>(c/degree) | Temporal<br>freqncy<br>(Hz) | Amplitude<br>(uV)                        | Phase<br>(degrees) | Amplitude<br>(uV)              | Phase<br>(degrees) | Amplitude<br>(uV)   | Phase<br>(degrees) | Amplitude<br>(uV)                                 | Phase<br>(degrees) |
|----------------------------------|-----------------------------|--|--------------------|--------------------------------|--------------------|---|--------------------|---|--------------------|
|                                  |                             | Dichoptic viewing<br>(polarized glasses) |                    | Binocular viewing<br>(NDF=0.5) |                    | Monocular viewing<br>(algebraic sum)<br>(polarized glasses) |                    | Monocular viewing<br>(algebraic sum)<br>(NDF=0.5) |                    |
| Sine profile                     |                             |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                  |                             |  |                    |                                |                    |   |                    |   |                    |
| 6.40                             | 5.30                        | 2.20                                     | -154.10            | 1.60                           | -164.60            | 4.20  | -139.10            | 3.20  | -168.40            |
| 6.40                             | 2.10                        | 1.30                                     | -36.90             | .80                            | -12.90             | .70   | -36.80             | .30   | 12.70              |
| 1.60                             | 5.30                        | 3.80                                     | 19.20              | 1.20                           | -18.70             | 3.10  | -17.90             | 3.50  | -17.50             |
| 1.60                             | 2.10                        | 1.30                                     | 10.70              | 1.20                           | 22.40              | 2.30  | 12.00              | 1.40  | -19.30             |
| .40                              | 5.30                        | 3.70                                     | 95.40              | 4.00                           | 62.20              | 4.30  | 84.30              | 5.40  | 5.40               |
| .40                              | 2.10                        | 1.20                                     | 44.00              | 1.40                           | 20.10              | 2.10  | 4.80               | 2.40  | -.40               |
| fourth harmonics                 |                             |  |                    |                                |                    |   |                    |   |                    |
| 6.40                             | 5.30                        | 1.80                                     | 25.40              | 1.90                           | -27.90             | 1.90  | 14.60              | 1.90  | -53.20             |
| 6.40                             | 2.10                        | 1.00                                     | -119.20            | .80                            | -142.00            | .80   | -139.10            | .90   | -157.10            |
| 1.60                             | 5.30                        | 1.60                                     | 62.40              | 1.30                           | 18.70              | 1.30  | 39.00              | 1.20  | 3.00               |
| 1.60                             | 2.10                        | 1.10                                     | -59.60             | 1.00                           | -70.90             | 1.30  | -84.30             | 1.20  | -105.10            |
| .40                              | 5.30                        | .40                                      | 134.60             | .50                            | 70.70              | .40   | 111.80             | .50   | 42.20              |
| .40                              | 2.10                        | .20                                      | 58.50              | .60                            | 116.80             | .70   | 132.70             | .60   | 91.40              |
| Square profile                   |                             |  |                    |                                |                    |   |                    |   |                    |
| second harmonic                  |                             |  |                    |                                |                    |   |                    |   |                    |
| 6.40                             | 5.30                        | 1.73                                     | -132.48            | .90                            | 171.10             | 2.50  | -140.00            | 2.40  | -165.60            |
| 6.40                             | 2.10                        | .40                                      | -99.66             | .50                            | -21.80             | 1.20  | -88.90             | .80   | -36.90             |
| 1.60                             | 5.30                        | 2.90                                     | 25.04              | 3.30                           | -10.80             | 2.50  | -.70               | 2.80  | -22.10             |
| 1.60                             | 2.10                        | .49                                      | -59.96             | .60                            | .40                | .70   | -16.00             | 1.00  | -20.80             |
| .40                              | 5.30                        | 2.25                                     | 104.53             | 2.70                           | 74.00              | 2.70  | 99.30              | 2.80  | 76.20              |
| .40                              | 2.10                        | .35                                      | -17.09             | .30                            | 51.10              | .30   | 98.60              | .30   | -134.90            |
| fourth harmonics                 |                             |  |                    |                                |                    |   |                    |   |                    |
| 6.40                             | 5.30                        | 1.30                                     | 36.95              | 1.20                           | -69.40             | 1.30  | -.50               | 1.40  | -45.70             |
| 6.40                             | 2.10                        | .47                                      | -145.35            | .50                            | -148.60            | .20   | -154.80            | .10   | 169.70             |
| 1.60                             | 5.30                        | 1.00                                     | 87.11              | .80                            | .40                | .60   | 28.10              | .60   | -2.30              |
| 1.60                             | 2.10                        | .99                                      | -77.65             | .90                            | -99.50             | .70   | -113.60            | .80   | -125.40            |
| .40                              | 5.30                        | .30                                      | 160.10             | .30                            | 79.70              | .40   | 123.70             | .60   | 98.80              |
| .40                              | 2.10                        | .11                                      | 86.49              | .30                            | 22.60              | .30   | 117.60             | .30   | 67.70              |

Table 6

C.R. 5/7/86

Temporal phases shift  
 Sine and square profile  
 Dichoptic viewing

| Spatial<br>frqncy<br>(c/degree) | Temporal<br>frqncy<br>(Hz) | Temporal<br>ph.shift<br>(degrees) | Amplitude<br>(uV) | Phase<br>(degrees) | Amplitude<br>(uV) | Phase<br>(degrees) | Averaged<br>amplitude<br>(uV) | Averaged<br>phase<br>(degrees) |
|---------------------------------|----------------------------|-----------------------------------|-------------------|--------------------|-------------------|--------------------|-------------------------------|--------------------------------|
| Sine profile                    |                            |                                   |                   |                    |                   |                    |                               |                                |
| second harmonic                 |                            |                                   |                   |                    |                   |                    |                               |                                |
| .40                             | 2.10                       | 0.00                              | .60               | 118.00             | .80               | 127.30             | .70                           | 123.32                         |
| .40                             | 2.10                       | 45.00                             | .20               | 94.30              | .20               | 34.90              | .17                           | 64.60                          |
| .40                             | 2.10                       | 90.00                             | .20               | -13.00             | .50               | 91.80              | .24                           | 68.50                          |
| .40                             | 2.10                       | 135.00                            | 1.00              | 93.60              | .70               | 78.40              | .84                           | 87.35                          |
| .40                             | 2.10                       | 180.00                            | .90               | 128.40             | .80               | 110.80             | .84                           | 120.12                         |
| fourth harmonics                |                            |                                   |                   |                    |                   |                    |                               |                                |
| .80                             | 5.30                       | 0.00                              | 2.30              | 30.60              | 1.40              | 17.90              | 1.84                          | 25.80                          |
| .80                             | 5.30                       | 45.00                             | 1.50              | 99.00              | 1.40              | 72.80              | 1.41                          | 86.36                          |
| .80                             | 5.30                       | 90.00                             | .80               | -163.50            | 1.40              | 156.60             | 1.04                          | 170.90                         |
| .80                             | 5.30                       | 135.00                            | 1.70              | -56.70             | 1.00              | -98.70             | 1.27                          | -72.02                         |
| .80                             | 5.30                       | 180.00                            | 1.50              | -29.20             | 1.70              | -22.30             | 1.60                          | -25.53                         |
| Square profile                  |                            |                                   |                   |                    |                   |                    |                               |                                |
| second harmonic                 |                            |                                   |                   |                    |                   |                    |                               |                                |
| .40                             | 2.10                       | 0.00                              | 19.0              | 20.10              | 1.50              | 47.40              | 1.65                          | 32.11                          |
| .40                             | 2.10                       | 45.00                             | 1.20              | 78.90              | 1.50              | 98.60              | 1.33                          | 89.86                          |
| .40                             | 2.10                       | 90.00                             | .60               | .60                | .80               | .60                | .60                           | .60                            |
| .40                             | 2.10                       | 135.00                            | 1.00              | 1.00               | 1.00              | 1.00               | 1.00                          | 1.00                           |
| .40                             | 2.10                       | 180.00                            | .80               | -29.40             | 1.50              | -43.40             | 1.14                          | -38.54                         |
| .80                             | 5.30                       | 0.00                              | .90               | 76.00              | 1.00              | 69.70              | .95                           | 72.68                          |
| .80                             | 5.30                       | 45.00                             | .10               | 71.70              | .60               | 94.90              | .35                           | 91.64                          |
| .80                             | 5.30                       | 90.00                             | .10               | 57.80              | .10               | -15.80             | .08                           | 21.00                          |
| .80                             | 5.30                       | 135.00                            | .60               | 24.40              | .30               | 64.90              | .43                           | 37.64                          |
| .80                             | 5.30                       | 180.00                            | .70               | 124.00             | .80               | 91.80              | .72                           | 106.80                         |

Table 7

E.P. 5/12/86  
 Temporal phases shift  
 Sine profile  
 Dichoptic viewing

| Spatial<br>frqncy<br>(c/degree) | Temporal<br>frqncy<br>(Hz) | Temporal<br>ph. shift<br>(degrees) | Sine profile |          | Amplitude<br>(uV) | Phase<br>(degrees) | Amplitude<br>(uV) | Phase<br>(degrees) | Averaged<br>amplitude<br>(uV) | Averaged<br>phase<br>(degrees) |
|---------------------------------|----------------------------|------------------------------------|--------------|----------|-------------------|--------------------|-------------------|--------------------|-------------------------------|--------------------------------|
|                                 |                            |                                    | second       | harmonic |                   |                    |                   |                    |                               |                                |
| .40                             | 4.20                       | 0.00                               | .90          | -133.40  | 1.40              | -129.50            | 1.15              | -131.03            |                               |                                |
| .40                             | 4.20                       | 45.00                              | .40          | 4.40     | 1.30              | -70.00             | .73               | -54.69             |                               |                                |
| .40                             | 4.20                       | 90.00                              | .60          | -25.10   | .80               | -56.70             | .67               | -43.21             |                               |                                |
| .40                             | 4.20                       | 135.00                             | .80          | 72.30    | 1.50              | 138.70             | .98               | 116.76             |                               |                                |
| .40                             | 4.20                       | 180.00                             | .60          | -64.90   | .20               | -89.60             | .39               | -71.00             |                               |                                |
| .80                             | 6.30                       | 0.00                               | 1.40         | 18.60    | 1.30              | -1.40              | 1.33              | 8.97               |                               |                                |
| .80                             | 6.30                       | 45.00                              | .50          | 75.40    | .70               | 28.00              | .55               | 47.52              |                               |                                |
| .80                             | 6.30                       | 90.00                              | .40          | -177.10  | .40               | -88.60             | .29               | -132.85            |                               |                                |
| .80                             | 6.30                       | 135.00                             | 1.30         | -27.70   | 1.00              | -70.30             | 1.07              | -46.09             |                               |                                |
| .80                             | 6.30                       | 180.00                             | .90          | -1.20    | 1.40              | -15.40             | 1.14              | -9.85              |                               |                                |
| 1.60                            | 6.30                       | 0.00                               | 1.70         | -71.40   | 2.00              | -93.10             | 1.82              | -83.14             |                               |                                |
| 1.60                            | 6.30                       | 45.00                              | 1.00         | 3.20     | 1.00              | -28.80             | .96               | -12.80             |                               |                                |
| 1.60                            | 6.30                       | 90.00                              | .20          | 92.30    | .30               | -53.30             | .09               | -13.37             |                               |                                |
| 1.60                            | 6.30                       | 135.00                             | .90          | -133.60  | .50               | -168.40            | .67               | -145.88            |                               |                                |
| 1.60                            | 6.30                       | 180.00                             | 1.00         | -102.20  | 1.20              | -108.30            | 1.10              | -105.53            |                               |                                |

Table 8a

E.P. 5/12/86  
 Temporal phases shift  
 Square profile  
 Dichoptic viewing

| Spatial<br>frqncy<br>(c/degree) | Temporal<br>frqncy<br>(Hz) | Temporal<br>ph. shift<br>(degrees) | Amplitude<br>(uV) | Phase<br>(degrees) | Amplitude<br>(uV) | Phase<br>(degrees) | Averaged<br>amplitude<br>(uV) | Averaged<br>phase<br>(degrees) |
|---------------------------------|----------------------------|------------------------------------|-------------------|--------------------|-------------------|--------------------|-------------------------------|--------------------------------|
|                                 |                            |                                    | Sine profile      |                    |                   |                    |                               |                                |
|                                 |                            |                                    | second            | harmonic           |                   |                    |                               |                                |
| .40                             | 4.20                       | 0.00                               | .70               | 173.30             | 1.30              | -156.10            | 1.59                          | -44.52                         |
| .40                             | 4.20                       | 45.00                              | 1.10              | -105.20            | 1.20              | -93.00             | 1.10                          | 28.34                          |
| .40                             | 4.20                       | 90.00                              | .80               | -34.80             | .40               | 69.00              | .44                           | 119.67                         |
| .40                             | 4.20                       | 135.00                             | .40               | 123.00             | .10               | 86.30              | 1.34                          | -70.91                         |
| .40                             | 4.20                       | 180.00                             | .50               | -158.00            | 1.00              | 125.70             | 1.50                          | -39.83                         |
| .80                             | 6.30                       | 0.00                               | 1.40              | -50.20             | 1.80              | -40.10             | .97                           | -166.71                        |
| .80                             | 6.30                       | 45.00                              | 1.40              | 30.30              | .80               | 24.90              | 1.14                          | -98.83                         |
| .80                             | 6.30                       | 90.00                              | .60               | 126.60             | .30               | 105.70             | .40                           | -5.93                          |
| .80                             | 6.30                       | 135.00                             | 1.30              | -76.20             | 1.40              | -66.00             | .24                           | 115.91                         |
| .80                             | 6.30                       | 180.00                             | 2.10              | -25.50             | 1.10              | -67.40             | .61                           | 149.18                         |
| 1.60                            | 6.30                       | 0.00                               | 1.10              | -95.20             | 1.20              | -103.50            | 1.15                          | -99.53                         |
| 1.60                            | 6.30                       | 45.00                              | .80               | -50.30             | 1.30              | -31.20             | 1.04                          | -38.46                         |
| 1.60                            | 6.30                       | 90.00                              | .20               | 101.30             | .30               | -145.70            | .14                           | 174.61                         |
| 1.60                            | 6.30                       | 135.00                             | .90               | -97.50             | 1.00              | -136.10            | .90                           | -117.86                        |
| 1.60                            | 6.30                       | 180.00                             | 1.30              | -76.20             | 1.70              | -93.00             | 1.48                          | -85.73                         |

Table 8b

M.C. 5/29/86  
 Temporal phase shift  
 Sine profile

| Spatial<br>freqncy<br>(c/degree) | Temporal<br>freqncy<br>(Hz) | Temporal<br>ph.shift<br>(degrees) | Phase<br>(degrees) | Amplitude<br>(uV) | Phase<br>(degrees) | Amplitude<br>(uV) | Averaged<br>amplitude<br>(uV) | Averaged<br>phase<br>(degrees) |
|----------------------------------|-----------------------------|-----------------------------------|--------------------|-------------------|--------------------|-------------------|-------------------------------|--------------------------------|
| 2.10                             | 6.40                        | 5.30                              | 0.00               | 1.70              | -152.20            | 1.88              | -160.38                       |                                |
|                                  |                             |                                   |                    |                   |                    |                   |                               |                                |
|                                  | 6.40                        | 5.30                              | 45.00              | 1.20              | -63.20             | 1.20              | -46.60                        | 1.19                           |
|                                  | 6.40                        | 5.30                              | 90.00              | .90               | 57.10              | .50               | 93.20                         | .65                            |
|                                  | 6.40                        | 5.30                              | 135.00             | 1.60              | -155.40            | 1.50              | -163.50                       | 1.55                           |
|                                  | 6.40                        | 5.30                              | 180.00             | 2.00              | -144.50            | 1.90              | -141.20                       | 1.95                           |
|                                  | 1.60                        | 5.30                              | 0.00               | 2.40              | 39.30              | 2.70              | 22.00                         | 2.52                           |
|                                  | 1.60                        | 5.30                              | 45.00              | 2.00              | 76.40              | 1.80              | 79.20                         | 1.90                           |
|                                  | 1.60                        | 5.30                              | 90.00              | .30               | 57.10              | .40               | 24.30                         | .34                            |
|                                  | 1.60                        | 5.30                              | 135.00             | 1.50              | -2.20              | 1.10              | -.80                          | 1.30                           |
|                                  | 1.60                        | 5.30                              | 180.00             | 1.70              | 27.20              | 1.20              | 8.40                          | 1.43                           |
|                                  | .40                         | 5.30                              | 0.00               | 3.20              | 104.70             | 3.60              | 104.20                        | 3.40                           |
|                                  | .40                         | 5.30                              | 45.00              | 2.00              | 147.60             | 2.20              | 144.20                        | 2.10                           |
|                                  | .40                         | 5.30                              | 90.00              | .50               | 59.40              | .30               | 47.70                         | .40                            |
|                                  | .40                         | 5.30                              | 135.00             | 1.90              | 51.30              | 1.70              | 39.60                         | 1.79                           |
|                                  | .40                         | 5.30                              | 180.00             | 1.80              | 88.70              | 2.50              | 70.80                         | 2.12                           |

Table 9a

M.C. 5/29/86

Temporal phase shift

Square profile

| Spatial<br>frqncy<br>(c/degree) | Temporal<br>frqncy<br>(Hz) | Temporal<br>ph. shift<br>(degrees) | Phase<br>(degrees) | Amplitude<br>(uV) | Phase<br>(degrees) | Amplitude<br>(uV) | Averaged<br>amplitude<br>(uV) | Averaged<br>phase<br>(degrees) |
|---------------------------------|----------------------------|------------------------------------|--------------------|-------------------|--------------------|-------------------|-------------------------------|--------------------------------|
|                                 |                            |                                    |                    |                   | second             | harmonic          |                               |                                |
| 6.40                            | 5.30                       | 0.00                               | 2.10               | -145.60           | 1.70               | -141.30           | 1.90                          | -143.68                        |
| 6.40                            | 5.30                       | 45.00                              | 1.80               | -77.00            | 1.30               | -46.70            | 1.50                          | -64.35                         |
| 6.40                            | 5.30                       | 90.00                              | .20                | 64.40             | .20                | 21.30             | .19                           | 42.85                          |
| 6.40                            | 5.30                       | 135.00                             | 1.30               | -159.10           | 1.50               | -146.80           | 1.39                          | -152.51                        |
| 6.40                            | 5.30                       | 180.00                             | 1.30               | -138.80           | 1.20               | -126.20           | 1.24                          | -132.75                        |
| 1.60                            | 5.30                       | 0.00                               | 3.60               | 41.40             | 2.30               | 32.00             | 2.94                          | 37.74                          |
| 1.60                            | 5.30                       | 45.00                              | 2.60               | 80.90             | 1.60               | 81.60             | 2.10                          | 81.17                          |
| 1.60                            | 5.30                       | 90.00                              | .20                | 76.90             | .10                | -139.70           | .07                           | 103.37                         |
| 1.60                            | 5.30                       | 135.00                             | 1.70               | -14.50            | 1.40               | -22.10            | 1.55                          | -17.93                         |
| 1.60                            | 5.30                       | 180.00                             | 2.10               | 12.00             | 2.10               | -2.20             | 2.08                          | 4.90                           |
| .40                             | 5.30                       | 0.00                               | 2.40               | 99.30             | 3.10               | 111.70            | 2.73                          | 106.29                         |
| .40                             | 5.30                       | 45.00                              | 1.80               | 152.20            | 1.80               | 148.80            | 1.80                          | 150.50                         |
| .40                             | 5.30                       | 90.00                              | .20                | 43.40             | .60                | .60               | .38                           | 10.91                          |
| .40                             | 5.30                       | 135.00                             | 1.90               | 45.90             | 2.20               | 41.10             | 2.05                          | 43.32                          |
| .40                             | 5.30                       | 180.00                             | 2.80               | 77.50             | 2.30               | 75.40             | 2.55                          | 76.55                          |

Table 9b

**APPENDIX B**

```

5 LPRINT CHR$(27);"*0"
10 REM BMOD10, binocular VEP model
12 INPUT "monocular scale factor, M1=";M1
14 INPUT "monocular scale factor, M2=";M2
16 REM M1 and M2 are L1 scale factors for eye 1 and eye 2
18 INPUT "monocular phase shift, FM=";FM
19 REM FM is a phase shift of L1
20 INPUT "binocular scale factor, B=";B
25 REM B is scale factor of L2
30 INPUT "binocular phase shift, F=";F
35 REM F is a phase shift introduced by L2
40 FOR N=1 TO 8
45 REM N changes PS (stimulus phase shift of the eye 2) from 0 to 180 deg
50 PS=PS+.7854
75 REM CC and CS are cosine and sine values of output of binocular summer
80 CC=M1*COS(FM)+M2*COS(FM+FS)
90 CS=M1*SIN(FM)+M2*SIN(FM+FS)
95 REM C and FC are amplitude and phase of output of binocular summer
100 C=(CC^2+CS^2)^.5
105 IF CC=0 THEN FC=1.5708:GOTO 125
110 FC=ATN(CS/CC)
120 IF CC<0 THEN FC=FC+3.14159
125 REM FB is phase shift at output of binoc. pathway
130 FB=F+2*FC
140 REM BD is gain of binocular output
150 BD=C^2*B
160 REM BC and BS are cosine and sine of binocular output
170 BC=BD*COS(FB)
180 BS=BD*SIN(FB)
190 REM VC and VS are cosine and sine of VEP
200 VC=M1^2*COS(2*FM)+M2^2*COS(2*(FM+FS))+BC
210 VS=M1^2*SIN(2*FM)+M2^2*SIN(2*(FM+FS))+BS
220 VC$="COSINE OF VEP, VC="
230 VS$="SINE OF VEP, VS="
240 B$="BINOCULAR SCALE FACTOR, B="
250 F$="BINOCULAR PHASE SHIFT, F="
260 M1$="MONOCULAR SCALE FACTOR, M1="
262 M2$="MONOCULAR SCALE FACTOR, M2="
264 FS$="MONOCULAR STIMULUS PHASE SHIFT, PS="
266 LPRINT FS$;FS
270 LPRINT B$;B
280 LPRINT F$;F
290 LPRINT M1$;M1
295 LPRINT M2$;M2
300 LPRINT VC$;VC
310 LPRINT VS$;VS
320 NEXT N
330 END

```

## REFERENCES

- Apkarian, P., Nakayama, K., and Tyler, C. (1977). Binocular interaction in steady state visual evoked responses. Society for neuroscience abstracts, 3, 551.
- Apkarian, P., Nakayama, K., and Tyler, C.W. (1981). Binocularity in the human visual evoked potentials: Facilitation, summation and suppression. Electroencephalography and Clinical Neurophysiology, 51, 32-48.
- Arditi, A.R., Anderson, P.A., and Movshon, J.A. (1981). Monocular and binocular detection of moving sinusoidal gratings. Vision Research, 21, 329-336.
- Bacon, J. (1976). The interaction of dichoptically presented spatial gratings. Vision Research, 16, 337-344.
- Barlow, H.B., and Mollon, J.D. (Eds.). (1985). The Senses, Cambridge: Cambridge University Press.
- Basar, E. (1976). Biophysical and Physiological System Analysis. Reading, Massachusetts: Addison-Wesley Publishing Company.
- Blake, R., and Fox, R. (1973). The psychophysical inquiry into binocular summation. Perception and Psychophysics, 14, 161-185.
- Blake, R., and Levinson, E. (1977). Spatial properties of binocular neurones in the human visual system. Experimental Brain Research, 27, 221-232.
- Blake, R., Martens, W., and Di Gianfillipo, A. (1980). Reaction time as a measure of binocular interaction in human vision. Investigative Ophthalmology and Visual Science, 19, 930-941.
- Blake, R., Martens, W., Garret, A., and Westendorf D. (1980). Estimating probability summation for binocular reaction time data. Perception and Psychophysics, 27, 375-378.
- Blake, R., and Rush, C. (1980). Temporal properties of binocular mechanisms in the human visual system. Experimental Brain Research, 38, 333-340.
- Blake, R., Sloane, M., and Fox, R. (1981). Further development in binocular summation. Perception and Psychophysics, 30, 266-276

- Barlow, H.B., Blakemore, C., and Pettigrew, J.D. (1967). The neural mechanisms of binocular depth discrimination. Journal of Physiology (London), 193, 327-342.
- Cailli, T., and Hubner, M. (1983). On the Efficient Two-Dimensional Energy Coding Characteristics of Spatial Vision. Vision Research, 23, 1053-1055.
- Clynes, M. (1961). Unidirectional rate sensitivity: a biocybernetic law of reflex and humoral systems as physiologic channels of control and communication. Annales of New York Academy of Sciences, 92, 946-969.
- Creutzfeldt, O.D., and Kuhnt, U. (1967). The visual evoked potential: Physiological, developmental and clinical aspects. Electroencephalography and Clinical Neurophysiology, 26, 29-41.
- Dawson, S. (1913). Binocular and uniocular discrimination of brightness. British Journal of Physiology, 6, 78-108
- De Valois, R.L., Albrecht, D.G., and Thorell, L.G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. Vision Research, 22, 545-559.
- Ellenberger, C., Shuttlesworth, D.E. (1978). Electrical correlates of normal binocular vision. Archives of Neurology, 35, 834-837.
- Enroth-Cugell, C., and Robson, J. (1966). The contrast sensitivity of retinal ganglion cells of the cat. Journal of Physiology (London), 187, 517-522.
- Gardner, C.J. (1984). Ocular Dominance and Disparity-Sensitivity in Cat Visual Cortex. Investigative Ophthalmology and Visual Science, 45, (Suppl. 25), 799.
- Green, M., and Blake, R. (1981). Phase effect in monoptic and dichoptic temporal integration: Flicker and motion detection. Vision Research, 21, 365-372.
- Guillery, R.W. (1966). A study of Golgi preparation from the dorsal lateral geniculate cell growth. Journal of Comparative Neurology, 128, 21-50.
- Harter, M.R. (1977). Binocular interaction: Evoked potentials to dichoptic stimulation. Visual Evoked Potentials in Man; New Developments, Ed. J. E. Desmedt, Clarendon Press, Oxford, 208-233.

- Harter, M.R., Conder, E.S., and Towle, V.L. (1980). Orientation-specific and luminance effects: Interocular suppression of visual evoked potentials in man. Psychophysiology, 17, 141-145.
- Harter, M.R., Seiple, W.H., and Salmon, L. (1973). Binocular summation of visually evoked responses to pattern stimuli in humans. Vision Research, 13, 1433-1446.
- Harter, M.R., Seiple, W.H., and Musso, M. (1974). Binocular summation and suppression: Visually evoked cortical responses to dichoptically presented patterns of different spatial frequencies. Vision Research, 14, 1169-1180.
- Harwerth, R.S., Smith, E.L., and Levi, D.M. (1980). Suprathreshold binocular interactions for grating patterns. Perception and Psychophysics, 27, 43-50.
- Hochstein, S., and Shapley, R.M. (1976). Quantitative analysis of retinal ganglion cell classification. Journal of Physiology (London), 262, 237-264.
- Hubel, D.H., and Wiesel, T.N. (1962). Receptive fields, binocular interaction, and functional architecture in the cat's visual cortex. Journal of Physiology, 160, 106-154.
- Hubel, D.H., and Wiesel, T.N. (1968). Receptive fields and functional architecture of monkey striate cortex. The Journal of Physiology, 195, 215-243.
- Jasper, H.H. (1958). The ten twenty electrode system of the international federation. Electroencephalography and Clinical Neurophysiology, 10, 371-375.
- Kaplan, E., and Shapley, R.M. (1980). X and Y cells in the lateral geniculate nucleus of the macaque monkey. Investigative Ophthalmology and Visual Science, 41, (Suppl. 19).
- Keeley, S.M., and Doherty, M.E. (1971). Bayesian prediction of multiple look identification performance from one-look data: The effect of unequal prior probabilities. Perception and Psychophysics, 10, 119-122.
- Legge, G.E. (1978). Sustained and transient mechanisms in human vision: temporal and spatial properties. Vision Research, 18, 69-81.
- Lema, S.A., and Blake, R. (1977). Binocular summation in normal and stereoblind observers. Vision Research, 17, 691-696.

- Levi, D.M., Harwerth, R.S., and Manny, R.E. (1979). Suprathreshold spatial frequency detection and binocular interaction in strabismic and anisometric ambliopia. Investigative Ophthalmology and Visual Science, 18, 714-730.
- Lund, J.S., Lund, R.D., Hendrickson, A.E., Bunt, A.H. and Fuchs, A.F. (1975) The origin of efferent pathways from primary visual cortex, area 17, of the macaque monkey as shown by retrograde transport of horseradish peroxidase. Journal of Comparative Neurology, 164, 287-304
- Matsubara, J., Cynader, M., Swindale, N.V., and Stryke, M. (1985). Intrinsic Projections within Visual Cortex: Evidence for Orientation-Specific Local Connections. Proceedings of National Academy of Sciences of the USA, 82, 935-939.
- Milkman, N., Shick, G., Rosetto, M., Ratliff, F., Shapley, R., and Victor, J. (1980). A two-dimensional computer-controlled visual stimulator. Behavior Research Methods and Instrumentation, 10, 539-545.
- Musselwhite, M.J., and Jeffreys, D.A. (1985). The influence of spatial frequency on the reaction times and evoked potentials recorded to grating pattern stimuli. Vision Research, 25, 1545-1555.
- Norcia, A.M., and Tyler, C.W. (1984). Temporal frequency limits for stereoscopic apparent motion processes. Vision Research, 24, 395-401.
- Ogle, K.N. (1963). Stereoscopic depth perception and exposure delays between images in two eyes. Journal of the Optical Society of America, 53, 1296-1304.
- Ohzawa, I., and Freeman, R.D. (1986a). The binocular organization of simple cells in the cat's visual cortex. Journal Neurophysiology, 56, 221-242.
- Ohzawa, I., and Freeman, R.D. (1986a). The binocular organization of complex cells in the cat's visual cortex. Journal Neurophysiology, 56, 243-259.
- Pettigrew, J.D., Nikara, T., and Bishop, P.O. (1968). Binocular interaction on single units in the cat striate cortex: Simultaneous stimulation by single moving slit with receptive fields in correspondence. Experimental Brain Research, 6, 391-410.
- Piper, H. (1903). Uber das Helligkeitsverhaltnis monokular und binokular ausgeloster Lichtempfindungen. Zeitschrift fur Sinnesphysiologie, 32, 161-176.

Pirene, M.H. (1943). Binocular and unocular thresholds in vision. Nature, 152, 698-699.

Poggio G.F.(1979). Mechanisms of stereopsis in monkey visual cortex. Trends in NeuroSciences, 2, 199-201.

Powell, T.P.S., and Hendrickson, A.E. (1981). Similarity in number of neurons through the depth of the cortex in the binocular and monocular parts of area 17 of the monkey. Brain Research, q216, 409-413.

Rose, D. (1978). Monocular vs binocular contrast thresholds for movement and patterns. Perception, 7, 195-200.

Ross, J., and Hogben, J.H. (1974). Short-term memory in streopsis. Vision Research, 14, 1195-1201.

Sanderson, K.J., Darian-Smith,I., and Bishop, P.O. (1969). Binocular corresponding receptive fields of single units in the cat dorsal lateral geniculate nucleus. Vision Research, 9, 1297-1303.

Shapley, R., and Lennie, P. (1984). Spatial frequency analysis in the visual system. Annual Review of Neuroscience, 8, 547-583.

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

Spekreijse, H., and Oosting, H. (1970). Linearizing:A method for Analizing and synthesizing nonlinear systems. Kybernetik, 7, 22-31.

Spitzer, H., and Hochstein, S. (1985a). A complex cell receptive field model. Journal of Neurophysiology, 53, 1281-1301.

Spitzer, H., and Hochstein, S. (1985b). Simple- and complex cell response dependences on stimulation parameters. Journal of Neurophysiology, 53, 1259-1280.

Turlejski, K., and Kossut, M. (1985). Decrease in the number of synapses formed by subcortical inputs to the striate cortex of binocularly deprived cats. Brain Research, 331, 115-125.

Thorn, F., and Boynton, R.M. (1974). Human binocular summation at absolute threshold. Vision Research, 14, 445.

- Tyler, C.W., and Apkarian, P.A. (1985). Effects of contrast, orientation and binocularity in the pattern evoked potential. Vision Research, 25, 755-766.
- Victor, J., and Shapley, R. (1980). A method of nonlinear analysis in the frequency domain. Biophysical Journal, 29, 459-484.
- von Grunau, M. (1979). Binocular summation and the binocularity of cat visual cortex. Vision Research, 19, 813-816.
- Westendorf, D., and Fox, R. (1977). Binocular detection of disparate light flashes. Vision Research, 17, 697-702.
- Westendorf, D., Langston, A., Chambers, D., and Allegretti, D. (1978). Binocular detection by normal and stereoblind observers. Perception and Psychophysics, 24, 209-213.
- White, C.T., and Bonelli, L. (1970). Binocular summation in the evoked potential as a function of image quality. American Journal of Optometry, 47, 304-309.
- Zemon, V. (1984). The VEP: Analysis of functional subsystems in the brain. Proceedings of the Sixth Annual Conference IEEE Engineering in Medicine and Biology Society, 426-431.
- Zemon, V., Conte, M., Jindra, L., and Camisa, J. (1985). Evoked potential estimates of temporal filters in the human visual system. Proceedings of the Seventh Annual Conference IEEE Engineering in Medicine and Biology Society, 431-436.
- Zemon, V., and Pinkhasov E.I. (1983). Dichoptic visual evoked potentials and nonlinear mechanisms in human vision. Journal of the Optical Society of America, 73, 1923.
- Zemon, V., and Ratliff, F. (1984). Intermodulation components of the visual evoked potential: Responses to lateral and superimposed stimuli. Biological Cybernetics, 50, 401-408.