STIMULATION IN THE PERIPHERY OF
THE CONTRALATERAL EYE

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THESIS

ABSTRACT

FOVEAL CRITICAL FLICKER FREQUENCY AS A FUNCTION OF SYNCHRONOUS STIMULATION IN THE PERIPHERY OF THE CONTRALATERAL EYE

By Terry Lee Hickey

A number of studies have indicated that, under certain conditions, visual thresholds of one eye are affected by stimulation of the other eye. Of most relevance to the present investigation were those studies dealing with critical flicker frequency. The majority of these studies report a depressive effect when the stimulation in the two eyes is out-of-phase and a summative effect when the two sources of stimulation are in-phase.

The purpose of the present study was to systematically investigate the effects of in-phase stimulation of various points along the periphery of one eye on the CFF thresholds measured at the fovea of the other eye.

The method of serial exploration was used to present two synchronous, intermittent stimulus targets to three subjects. Each subject made CFF determinations at the fovea of the left eye for each of the following points of stimulation: fovea-left eye only; fovea-left eye, fovea-

right eye; fovea-left eye, 10 degrees-right eye; fovea-left eye, 20 degrees-right eye; fovea-left eye, 30 degrees-right eye; fovea-left eye, 40 degrees-right eye; fovea-left eye, 50 degrees-right eye; fovea-left eye, 60 degrees-right eye; and fovea-left eye, 70 degrees-right eye.

The results of the present study were in agreement with earlier investigations. The greatest summative effect was found when both eyes were stimulated foveally; the greatest depressive effect, at 10 degrees. Beyond 10 degrees, the slight summative effect found was attributed to differences in the latencies of the rods and cones.

The results of the present study were interpreted as a further indication of the effects of timing of inputs on the visual system and, thus, afforded further evidence that alternation of response can occur in the visual system.

Approved: Sidney Bentley

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By

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INTRODUCTION

Since the early work of such people as Sherrington (1904), Abney and Watson (1916), Piper (1904), and McDougall (1901), investigators have been concerned with the possibility that the central convergence of the pathways from the two retinae may exert some influence on binocular perception.

> "Since homonymous halves of both retinae are connected with the same half of the cerebrum, it is usually assumed that corresponding points upon the two retinae outside of the fovea are represented in the visual projection areas of the cortex by single patterns. It is therefore generally accepted that the two retinae function integratively, i.e., that the singleness of vision with binocular observation is made possible by the unity of their central connections." (DeSilva and Bartley, 1930; 241).

While comparing the brightness of an object seen both monocularly and binocularly, DeSilva and Bartley (1930) demonstrated that in order for the object seen monocularly to appear just as brilliant as the object seen binocularly, it must be 1.27 to 1.44 times as bright. Fry and Bartley (1933) presented further evidence that binocular vision results in an increase in brilliance over monocular vision. They accounted for the fact on the hypothesis "that pathways from each pair of corresponding points in the two retinae converge upon a common pathway in the brain and that summation takes place." (Fry and Bartley, 1933; 693). Several other investigators (Valerius; Piper; Aubert; and McDougall) have proposed and shown a facilitative, or summative, effect upon brightness resulting from the unity of the central projections.

A summative, and inhibitive, effect has also been demonstrated with temporally manipulated stimuli. It has been shown that synchronous flashes delivered to corresponding points on the two retinae yield a higher critical flicker frequency (CFF) than is obtained with monocular regard or with binocular regard and alternate flashes. Sherrington (1904) studying binocular summation by the flicker method, concluded that:

> "As far as sensual (sic) effect goes, the light phases at the one eye practically do not, therefore, interfere or combine at all with the coincident dark phases at the other; and conversely. Nor do they, in the alternate left and right arrangement, add themselves as a series of additional stimuli to the like series of stimuli applied at the other eye." (Sherrington, 1904; 37).

The mechanical device employed by Sherrington lacked precision and Ireland (1950) partially replicated it utilizing more modern electronic equipment. Ireland tested twenty-four subjects under four conditions of stimulation:

(a) monocular flicker, dominant eye; (b) monocular flicker, non-dominant eye; (c) binocular flicker, out-of-phase; and (d) binocular flicker, in-phase. The results clearly indicated the CFF for binocular in-phase stimulation was reliably higher than the monocular. In view of the differences between monocular and binocular stimulation, Ireland postulated some interaction between the two eyes which appeared possible only by way of some central mechanism of the brain.

Thomas (1954) was interested in determining the effect of interocular differences in intensity on CFF values reported with binocular regard. His measures were made with both in- and out-of-phase flashes in the two eyes with the stimuli located centrally and 10 degrees peripherally from the fovea. The results indicated a general subtractive effect of a less intense stimulus in one eye on the CFF of a brighter stimulus on the corresponding area of the other eye. He found the subtractive effect to be even greater when both light sources were placed 10 degrees peripherally from the fovea.

Thomas (1955) reported comparing CFF measured under three conditions: uniocular regard; binocular regard, flashes in-phase; and binocular regard, flashes out-of-phase.

He postulated that if the impulses arriving from each eye were additive, then the synchronous stimulation should yield a visual effect identical to doubling the flash luminance of a stimulus projected on a given region of one retina. His results showed that over the range of luminance studied, binocular CFF with synchronous flashes was significantly higher than the binocular CFF with out-of-phase flashes or the uniocular CFF. The difference was small "being only about one half to one third as much as would result from doubling the flash luminance of a stimulus viewed with one eye." (Thomas, 1955; 52-53). The magnitude of summation was independent of flash luminance and flash frequency.

In the first of a series of studies dealing with binocular CFF, Baker (1952) replicated Sherrington's (1904) study. The ranges between the synchronous and alternate flicker rates found in the Baker and Sherrington studies differed in magnitude with Baker's evidence definitely indicating the presence of some alliance and antagonism between flicker processes initiated at corresponding retinal points. Baker's results led him to the following conclusion:

> "Binocular fusion involves, in part at least, some central process which combines and inte-

> grates the neural processes arising from stimulation of corresponding retinal areas, so that the resultant sensation differs from that arising from either eye alone." (Baker, 1952; 10).

In a sequel to the first paper, Baker (1952a) described six additional experiments concerned with monocular and binocular CFF. The concensus of the six studies briefly described by Baker was that binocular fusion involved some central process which combined and integrated the neural processes arising from stimulation of corresponding, or non-corresponding, retinal areas of similar size. The resultant binocular percept is different from that arising from stimulation of either eye alone. Baker (1952b) demonstrated a central connection by utilizing "progressive" and "instantaneous" stimulus occlusion. In the first of the two experiments reported, Baker demonstrated that higher CFF values could be obtained using an "instantaneous," rather than a "progressive," source; "...the receptor and optic nerve discharge frequencies for the 'instantaneous' and 'progressive' methods of stimulus occlusion are dissimilar at similar stimulus intermittence rates." (Baker, 1952; 126). In the second experiment, Baker used an "instantaneously" occluded source of stimulation for one eye and a "progressively" occluded source of stimulation for the other. His hypothesis was that the CFF value obtained under this condition should fall somewhere between that value obtained with "instantaneous" or "progressive" occlusion alone. The experimental results confirmed the hypothesis that central factors are active in "binocularly fusing neural impulses initiated by stimulation of the respective foveas." (Baker, 1952; 128).

Perrin (1954) found that for a 2 degree visual field and dark surround, as the field luminance was varied the increase in binocular in-phase CFF was proportional to the mean critical frequency for the two eyes. Perrin was also concerned with the effect of field size on binocular summation. As would be expected, he found that increasing the stimulated area - at constant luminance - increased the critical frequency. He also noted that as the area of the stimulus target increased from 0 to 12 degrees, binocular summation increased. "Specifically, the summation for corresponding areas was about 8 percent, while for noncorresponding areas it was of the order of 0.4 percent." (Perrin, 1954; 69).

A study by Wolf and Zigler (1958) determined monocular and binocular thresholds for various points along the peripheral retina. Their measures extended from 30 degrees

METHOD

Subjects

Three students (1 male and 2 females), including the author, served as subjects. All subjects had considerable experience in making flicker discriminations.

Apparatus

The apparatus shown in Figure 1 consisted of a metal rod curved into a half circle with a radius of 16 inches; a septum which divided the left and right visual fields; and a chin rest placed just to the left of the center of the arc. This placement of the chin rest positioned the entrance pupil of the right eye exactly at the center of the arc.

Placed on the arc were two clamps each supporting a rod which held one stimulus target. Each stimulus target was a circular aperture 1/2 inch in diameter which projected a visual angle of 1^{o} 47' at 16 inches. A piece of opal glass served as the target surface. The two stimulus sources were equated for brightness by means of a Macbeth photometer. The luminance was 1.5311 candles/ft^2. The same level of luminance was maintained throughout the experiment. A small red "seed" lamp, positioned in the to the right of fixation on a horizontal meridian and on a parallel line 1.5 degrees below the meridian. They found that in the binocular curves the thresholds were high at the center, dropped to low levels between 5 and 20 degrees, and gradually rose farther in the periphery. Thresholds were maximal at approximately 17.5 degrees. The monocular curves were asymmetrical due to the blind spots in the left and right fields. They also found that the binocular thresholds were slightly lower than the monocular thresholds, indicating slight binocular summation. The Wolf and Zigler study was not, however, concerned with either CFF or intermittent stimulation.

With the exception of Thomas (1954), Perrin (1954), and Wolf and Zigler (1958), the studies previously cited were concerned only with foveal stimulation. After a more than cursory search of the literature, the present author has concluded that very little, if any, work has been done investigating binocular summation by systematically stimulating points along the peripheral retina.

PURPOSE OF THE STUDY

It is, therefore, the purpose of the present study to partially duplicate and extend the work of previous investigators dealing with binocular summation. Using intermittent light to stimulate the fovea of one eye and various points toward the periphery of the other eye it should be possible to determine the effect of peripheral in-phase stimulation on foveal CFF with binocular regard.

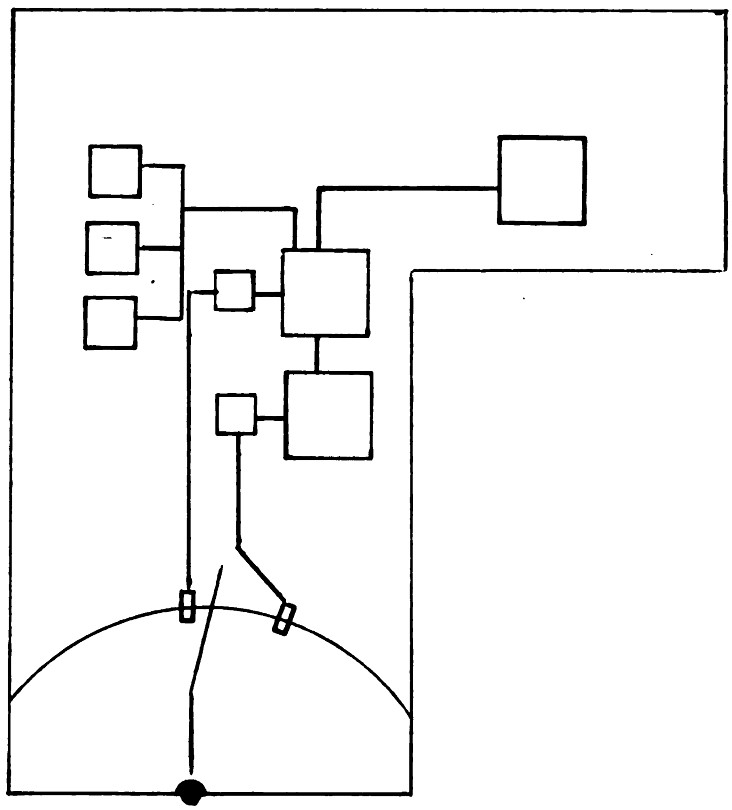

Fig. 1. Layout of experimental apparatus employed.

center of the left stimulus target, served as a fixation point.

The stimulus target for the left eye remained stationary throughout the investigation while the stimulus target for the right eye was moved along the rod. The right hand portion of the rod was calibrated in units of 10 degrees.

Figure 2 represents a diagrammatic drawing of the stimulus presentation apparatus employed. The intermittent stimulus lights were produced by two Sylvania R1131C glow-modulator tubes activated by square-wave inputs. Two separate Model S-4 variable-frequency square-wave stimulators made by Grass Instrument Company furnished the square-wave oscillations for the two glow-modulator tubes. The rate of intermittency of both glow-modulator tubes was always equal and in-phase. The operation of the glow-modulator tubes was completely silent at all times. Adjustment of the frequency of both square-wave stimulators was always made by the experimenter. Flicker frequency was monitored by a Beckman digital counter.

The input channels were controlled by a series of Hunter Model 100-C decade relay timers. The timers activated both glow-modulator tubes simultaneously for three

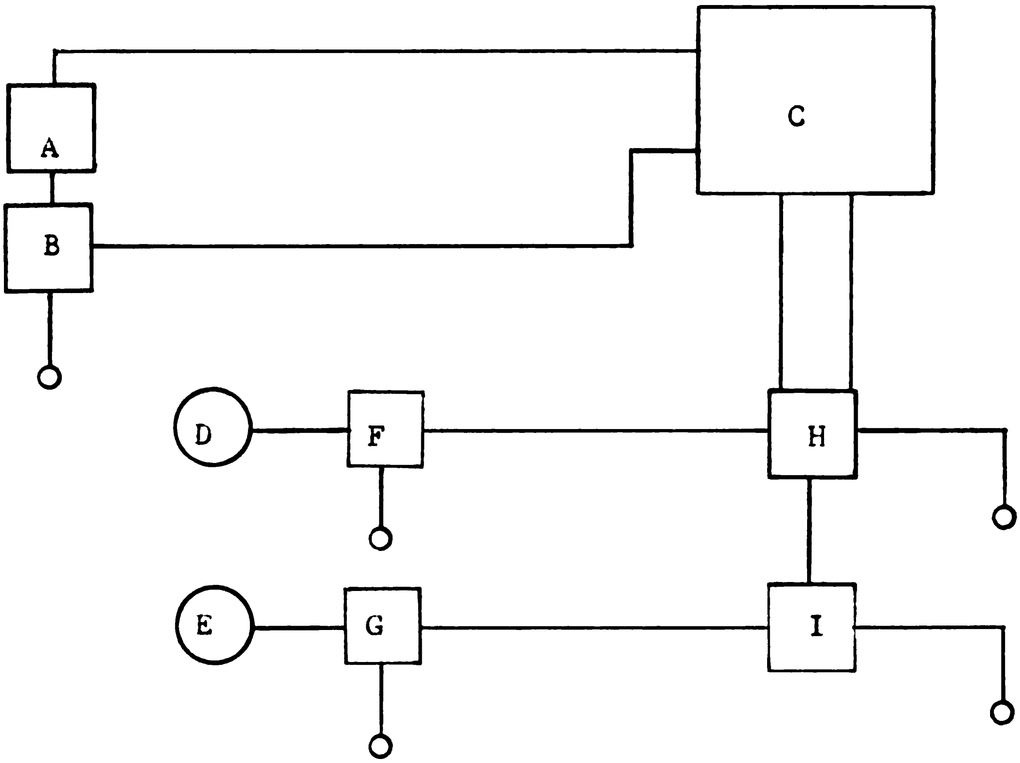

Fig. 2. Diagrammatic drawing of stimulus presentation apparatus.

A: buzzer
B: six volt transformer
C: timers
D: glow modulator
E: glow modulator
F: driver
G: driver
H: Grass S-4
I: Grass S-4

seconds, after which both tubes extinguished for seven seconds. This presentation procedure was continued throughout the experiment. The timers also controlled a buzzer which was activated 1 second prior to the activation of the two glow-modulators. This warning buzzer signaled the subject that he should fixate on the red "seed" lamp and prepare for the succeeding stimulus presentation.

Procedure

Although all subjects had previous experience in making flicker discriminations, all subjects were given several trials prior to actual experimentation in order to stabilize their criterion for CFF. During these trials only the left eye was stimulated. The data from these trials were not included in the final analysis.

Prior to each experimental session, subjects were dark adapted for one-half hour. Following dark adaptation each subject was instructed to place his head as close to the apparatus as possible with his chin in the chin rest and to fixate on the red light at the sound of the tone. The red "seed" lamp, although not as bright for the right eye due to the polaroid paper used to block out the left stimulus light, could be seen by both eyes. Following the warning signal both stimulus lights would come on for three seconds. After the stimulus lights were extinguished, the subjects were required to report their judgments as to whether the stimulus target had been steady or flickering. This judgment was reported verbally.

During the seven seconds the stimulus lights were off, the experimenter recorded the subject's response and changed the rate setting for the next trial. Between series of trials the subject was given a brief rest period while the experimenter changed the stimulus setting along the rod. This procedure was continued throughout the investigation.

The method of serial exploration, with five ascending and five descending trials, was used for the presentation of the various rates of intermittencies at each stimulation point. The order of presentation of the various stimulation points was randomly determined during each experimental session. The following conditions were used for subjects: (1) fovea-left eye only; (2) fovea-left eye, fovea-right eye; (3) fovea-left eye, 10 degrees-right eye; (4) fovea-left eye, 20 degrees-right eye; (5) fovea-left eye, 30 degrees-right eye; (6) fovea-left eye, 40 degrees-right eye; (7) fovea-left eye, 50 degrees-right eye; (8) fovea-left eye, 60 degrees-right eye; and (9) fovea-left eye, 70 degrees-right eye.

Each experimental session lasted approximately two hours including the one-half dark adaptation period. A total of five sessions on consecutive days was conducted for each subject.

RESULTS

The flicker contours plotted in cycles per second are shown in Fig. 3. Open squares represent thresholds for subject 1; solid squares, subject 2; open circles, subject 3. Each point for the curves is the mean of 50 CFF determinations. The points denoted by solid circles represent thresholds averaged over the three subjects and represent 150 CFF determinations each. It is apparent that CFF thresholds measured with foveal stimulation of both eyes are consistently a little higher than the thresholds determined with either peripheral stimulation of right eye or with stimulation of the left eye only: There is also evident a general depressive effect for all subjects when the right eye is stimulated between 10 degrees and 20 degrees in the periphery. Beyond 20 degrees the CFF thresholds remain fairly constant at approximately the threshold level for the left eye alone. In the curves of two subjects there is a drop in the thresholds beyond 60 degrees; however, this tendency is reversed in the curve of the third subject.

The results of a five-way analysis of variance computed are presented in Table I. All of the main effects with the exception of "trials" were significant at the .01 level. One three-way interaction, days x trials x pre-

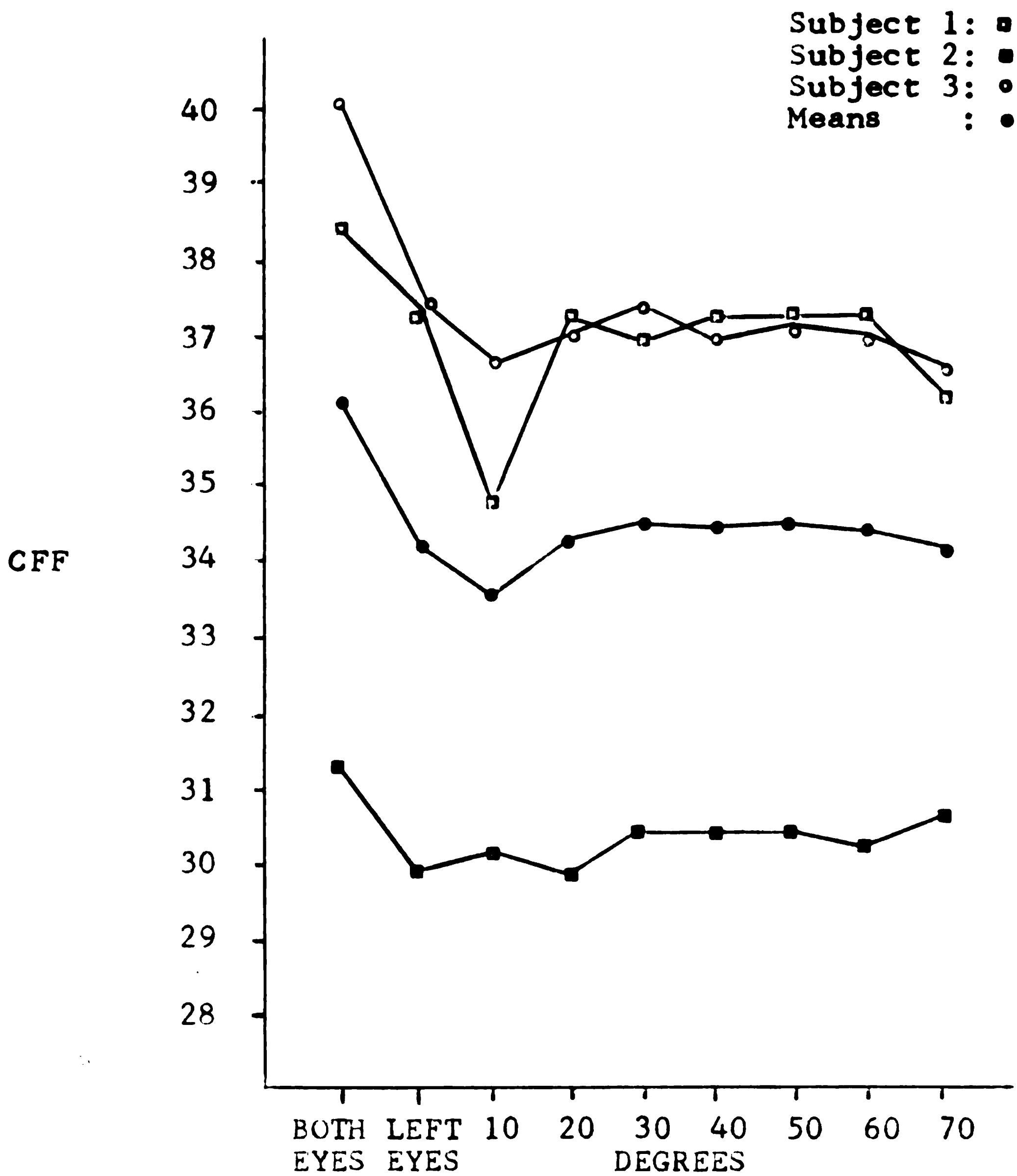

Fig. 3. Critical flicker frequency determinations for individual subjects and determinations averaged over subjects.

Table I. Summary of Analysis of Variance

	Source	SS	DF	MS	F
1.	Subjects	9824.4	2	4912.2	354.9*
2.	Point	309.9	8	38.7	4.6*
3.	Day	1196.2	4	299.0	9.3*
4.	Trial	3.2	4	.8	.8
5.	Presentation	109.9	1	109.9	422.6*
6.	Point X Day	198.3	32	6.1	.8
7.	Point X Trial	8.7	32	.2	.6
8.	Point X Presentation	1.9	8	.2	2.0
9.	Day X Trial	3.0	16	.1	.6
10.	Day X Presentation	13.3	4	3.3	.2
11.	Trial X Presentation	3.7	4	.9	3.1
12.	Point X Day X Trial	36.7	128	.2	1.1
13.	Point X Day X Presentation	7.7	32	.2	.8
14.	Day X Trial X Presentation	4.7	16	.2	2.2**
15.	Point X Day X Trial X Presentation	17.3	128	.1	.7

* Significant at .01 Level

** Significant at .05 Level

sentations, was significant at the .05 level. A test of individual comparisons was not made due to the small number of subjects.

Figure 4 shows the "learning" or "practice" effect over days. Each point is the mean of 270 CFF determinations. Note the curve becomes asymptotic at about day four. The significant "days" main effect was attributed to the rise in CFF thresholds over days. This shift in the CFF curve agrees with data presented by Ireland (1950).

Figures 5, 6, and 7 show CFF curves for subjects 1, 2, and 3, respectively. Open circles represent an average of the CFF determinations during the first two days of the experiment; solid circles represent averages for the last two days. Note that although the curves for the last two days are typically displaced toward the higher frequencies, the overall shapes of the curves are generally similar. These curves tend to indicate that rather than differences in the general shape of the curve occurring over days, the subjects, as a whole, become more sensitive, as evidenced by the higher CFF determinations.

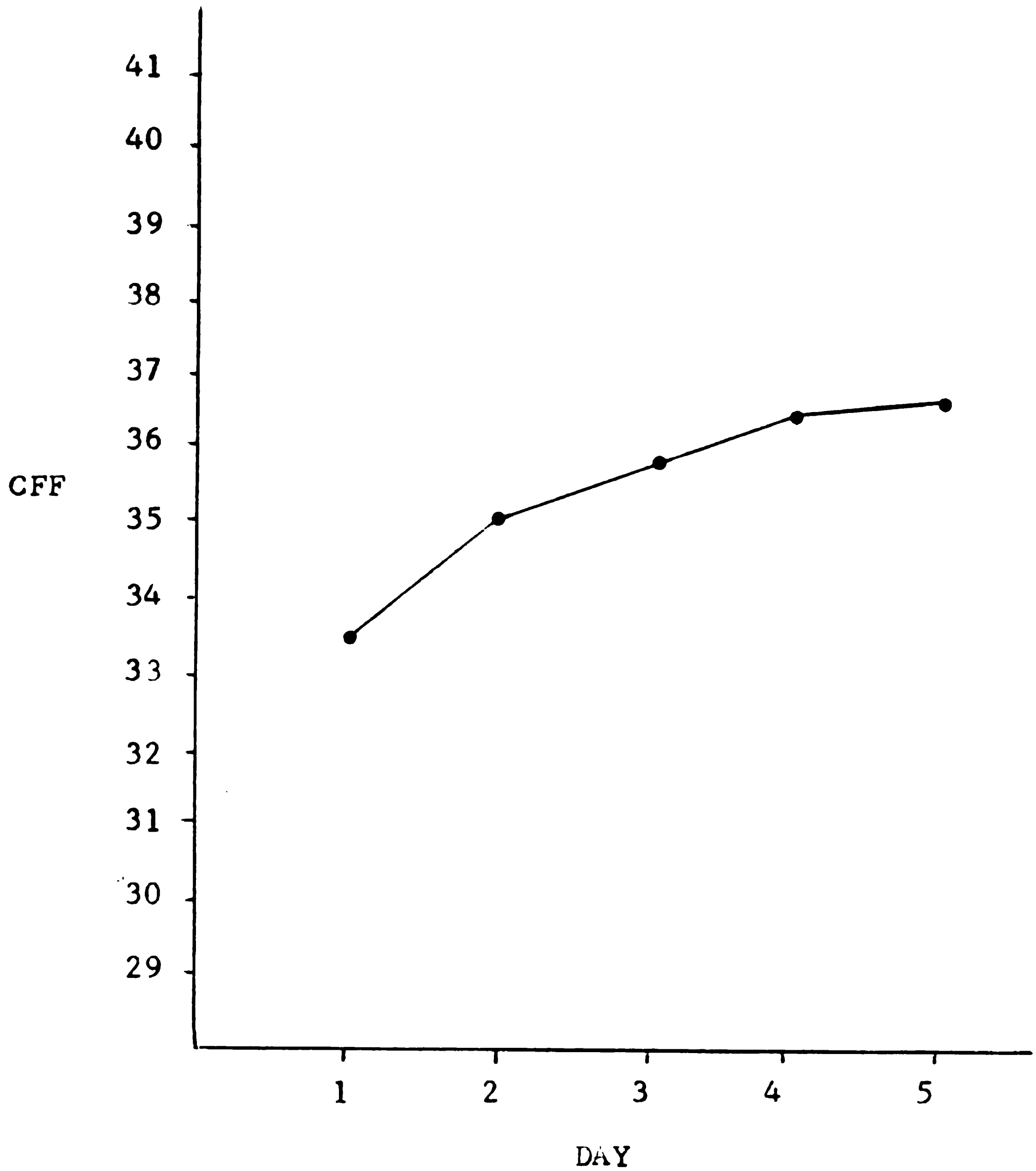

Fig. 4. Learning or practice effect over days averaged over subjects.

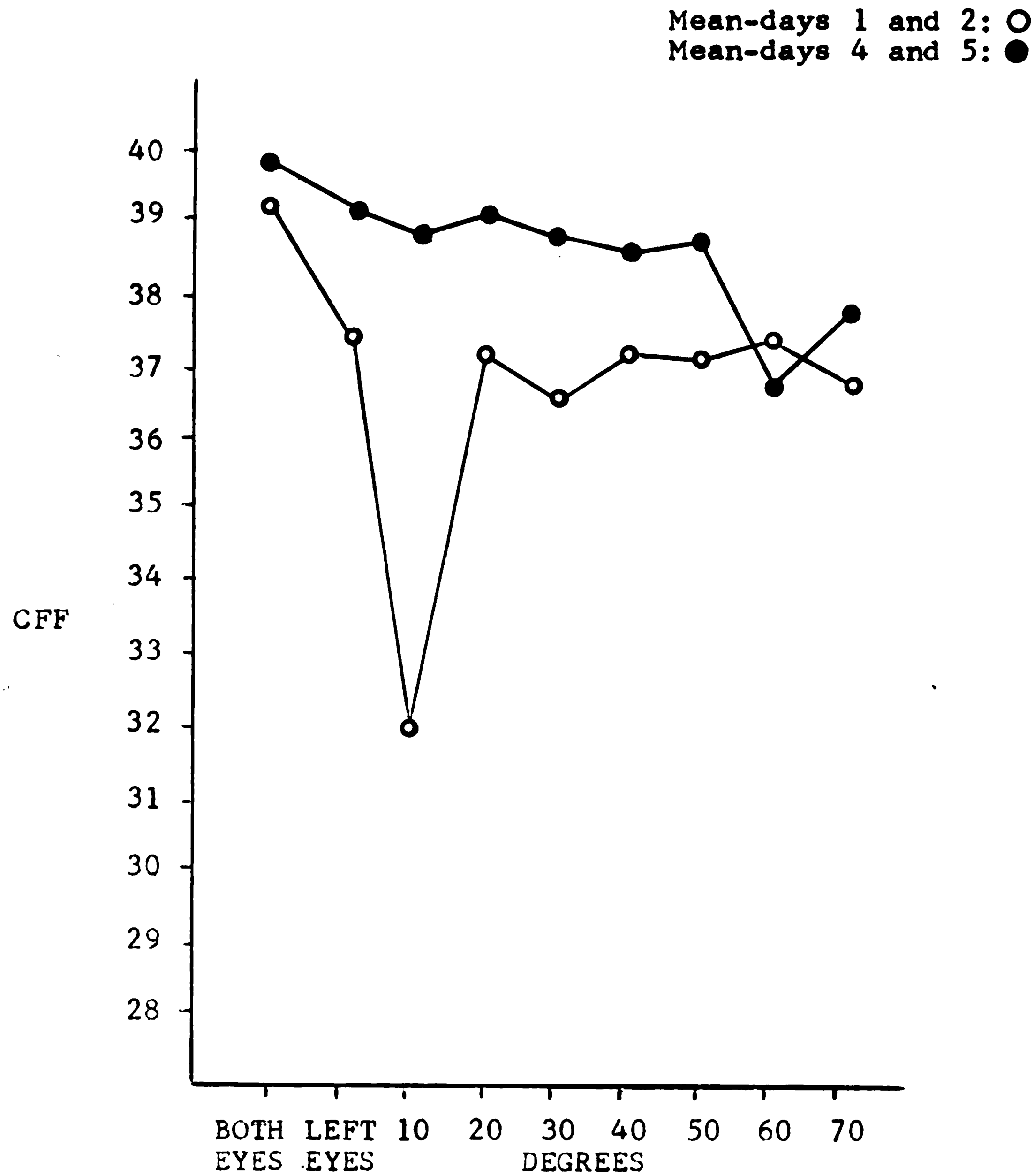

Fig. 5. CFF determinations for subject 1.

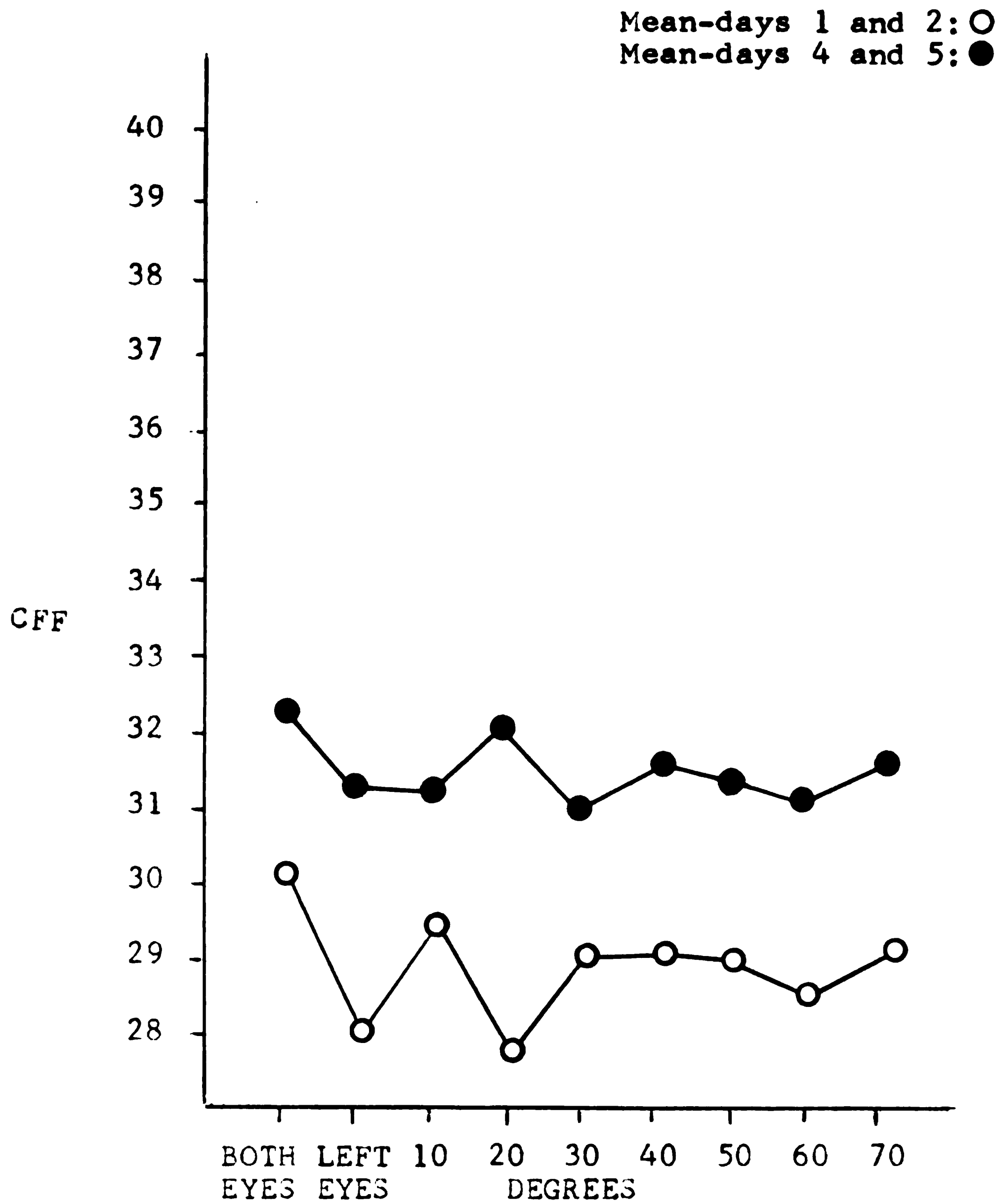

Fig. 6. CFF determinations for subject 2.

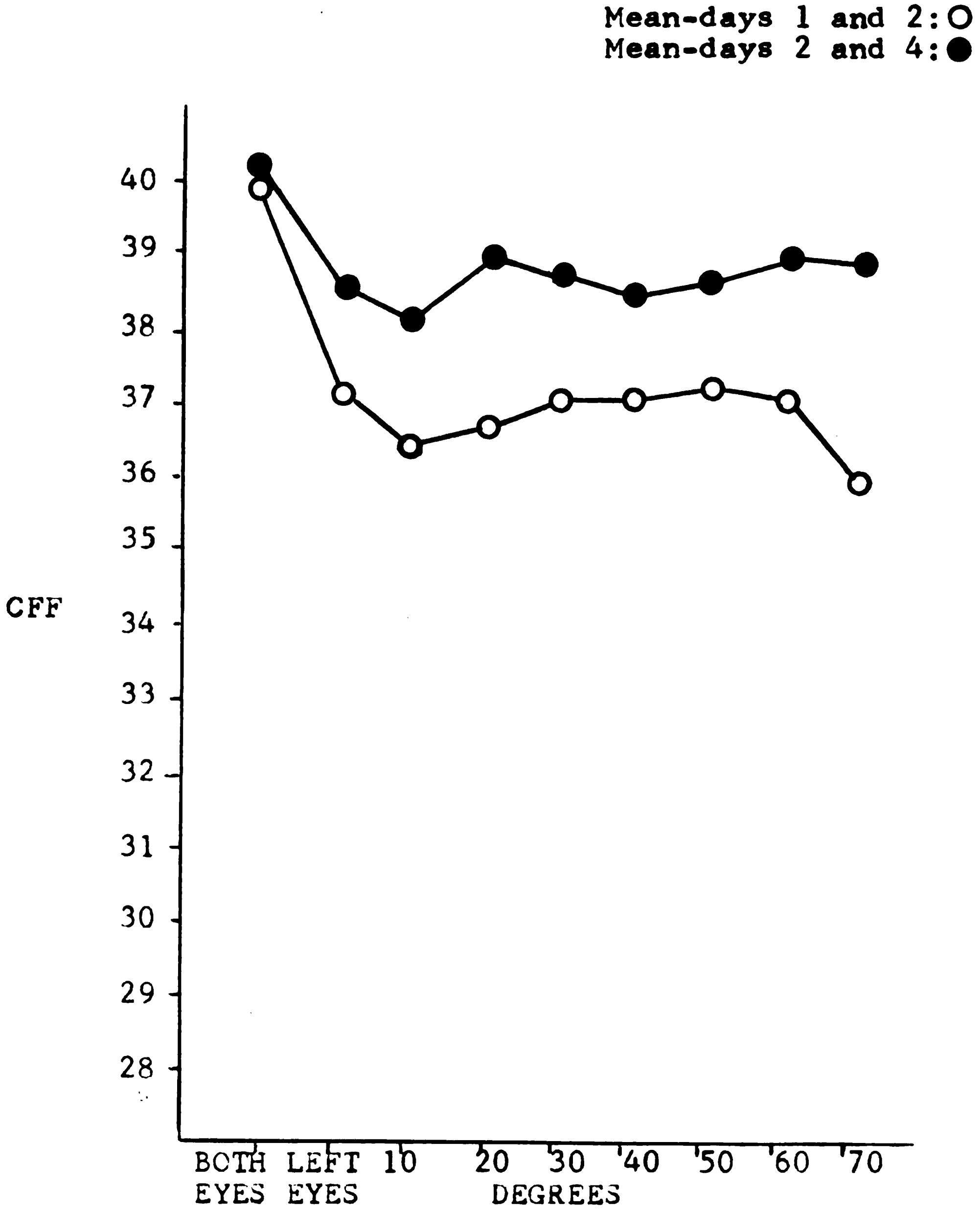

Fig. 7. CFF determinations for subject 3.

DISCUSSION

The finding that synchronous stimulation of the foveas of both eyes yields a significantly elevated CFF agrees with the results obtained by several authors (Ireland, 1950; Thomas, 1955a, 1955b; and Baker, 1952a, 1952b, 1952c). These results, along with the results of the present study, indicate a certain degree of binocular summation.

Thomas (1955) reported average differences of 1.37 and 0.89 flashes per second between binocular and uniocular CFF thresholds. In the present study, the value obtained for the same comparison - 1.78 flashes per second - closely resembles those reported by Thomas.

The depressive effect found at 10 degrees in the present study at first appears to coincide with the depressive effect reported by Thomas (1954). However, in comparing the results from the two studies, certain procedural differences must be kept in mind. Thomas was concerned with CFF thresholds as a function of stimulus intensity and the depressive effect he reported was due to differences in intensity of the stimulus targets. Also in the Thomas study, both stimulus patches were displaced 10 degrees, whereas, in the present study only the right target was displaced and the CFF determinations were always made at the fovea of the left eye. The fact, however, that Thomas did find a greater depressive effect at 10 degrees than at the fovea appears to coincide with the results of the present study.

Ross (1936) determined CFF thresholds at the fovea and at 5, 10, 20, 30, and 45 degrees in the retinal periphery using a single stimulus target. He found that fusion frequency values decreased as the stimulus target was moved toward the periphery. His curves showed that at 45 degrees the CFF values were about 50% as large as they had been at the fovea, with the greatest drop occurring between 0 and 10 degrees. Beyond 10 degrees the curve continued to drop but more gradually. In contrast to the curves presented for binocular thresholds in the present study, the curves presented by Ross indicate no increase in CFF thresholds beyond 10 degrees. The increase in threshold values beyond 10 degrees found in the present study would, thus, appear to indicate some degree of binocular summation occurring during peripheral stimulation.

Since the proportion of rods to cones increases toward the periphery of the eye, the points of stimulation beyond 10 degrees may be viewed as stimulation to two different populations of receptors. Although the stimulus inputs to the two populations of receptors were synchronous in the present study, it is unlikely that their inputs to any central processes mediated by the receptors would be synchronous. Bartley (1942), working with single flashes of light, found that when the area of the stimulus target was increased, the subject reported seeing two flashes. Bartley deduced from his finding that the two flashes were obtained "when both the rod and the cone populations are activated, and that the one population reacts more quickly than the other population." (Bartley, 1958; 127). Gouras (1966) presented electroretinogram records showing rod and cone threshold response latencies in the dark adapted retina of the Rhesus monkey. The records indicated a considerable (100 msec.) time delay between the cone and rod responses with the cone response being the faster. Therefore, if there is a difference in the latencies of the rods and cones, as there well appears to be, then the points beyond 10 degrees on the curve in Fig. 3 may actually represent CFF determinations under cortical out-of-phase stimulation rather than under synchronous stimulation as was originally assumed. Such an interpretation would seem plausible in light of the following data. Perrin (1953) found that with a 2 degree field, subjects' monocular CFF threshold values were approximately midway between the binocular thresholds with alternate flashes and those with synchronous flashes. Thomas (1954) also reported that binocular thresholds with out-of-phase flashes tended to be the same as the uniocular thresholds, and in some cases lower.

The results of the present study indicate that the timing of stimulus inputs, and thus the receptor outputs, has a considerable influence on processes within the visual system. Baker (1952c) interpreted his results as offering additional evidence that alternation of response can occur in the visual system. Baker states that:

> "...the central factors active in effecting binocular vision can perform their task when non-corresponding retinal points are stimulated, for, within any fovea, the receptors (corresponding points) alternate in responding to intermittent stimulation." (Baker, 1952c; 129).

An interpretation of the results of the present study along the lines of the interpretation given by Baker appears reasonable.

The present study is taken to be another example of the fact that certain gross temporal features of input to the cortex exercise a demonstrable effect on sensory outcome.

It is, therefore, another example of the temporal factor that has received so much study in this laboratory.

SUMMARY

The method of serial exploration was used to determine CFF thresholds for three subjects. With stimulation being supplied synchronously by two Sylvania glow-modulator tubes, the subjects made CFF determinations at the fovea of the left eye under the following nine conditions: fovea-left eye; fovea-left eye, fovea-right eye; fovea-left eye, 10 degrees-right eye; fovea-left eye, 20 degrees-right eye; fovea-left eye, 30 degrees-right eye; fovea-left eye, 40 degrees-right eye; fovea-left eye, 50 degrees-right eye; fovea-left eye, 60 degrees-right eye; and fovea-left eye, 70 degrees-right eye.

A five-way analysis of variance was computed and the results presented in tables and graphs. The basic findings were in accord with previous studies dealing with binocular summation and inhibition.

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