THE EFFECT OF INTERMITTENT PHOTIC STIMULATION ON VISUAL RESOLUTION

THESIS FOR THE DEGREE
OF PH. D.

MICHIGAN STATE UNIVERSITY
CHARLES M. BOURASSA
1962

This is to certify that the

thesis entitled

THE EFFECT OF INTERMITTENT

PHOTIC STIMULATION ON

VISUAL RESOLUTION

presented by

CHARLES MARK BOURASSA

has been accepted towards fulfillment
of the requirements for

PhD. degree in Psychology

S. Howard Bartley
Major professor

Date November 20, 1962

ABSTRACT

THE EFFECT OF INTERMITTENT
PHOTIC STIMULATION ON
VISUAL RESOLUTION

by Charles M. Bourassa

Under the proper conditions sub-fusional intermittent photic stimulation produces a level of perceived brightness greater than continuous illumination of the same intensity level. This is called brightness enhancement (BE). To account for this and other related phenomena the alternation-of-response theory has been put forward. The theory maintains that with adequate target size and luminosity sub-fusional photic pulses tend to produce a large synchronous discharge of cortical neurons. It was hypothesized that a neuronal discharge of this type would also act to destroy the neural timing and interaction believed to be necessary for fine visual resolution.

The hypothesis was tested by using two illuminated targets in an otherwise dark field. The targets, when overlapped provided a uniform visual surface. The targets were adjusted away from one another until the observers perceived a gap between them. By comparing the change in gap-size from continuous to intermittent illumination relative changes in visual resolution could

be measured. Brightness matches were obtained by having the observers adjust a continuously illuminated target of the same size as the acuity targets to an intensity which would equal the brightness of the acuity targets.

Intermittency was produced by two episcotisters which provided PCFs of 1/4 and 3/4. In general, five readings of perceived brightness were obtained at pulse rates producing fusion and at 20, 15, 10, and 5 pulses/second and also under steady illumination. Then five readings of visual resolution were obtained under the same conditions. Replications were made in many of the conditions. Medians of the five readings were used to present the data in graphical form.

In general the findings may be summarized as follows. At intensities below about 1 c/ft^2 the targets failed to produce BE. The perceived brightness produced by PCF 3/4 was always greater than the brightness produced by PCF 1/4. At these intensities visual resolution was positively related to perceived brightness in that visual resolution was better with PCF 3/4 than with PCF 1/4. At intensities between 1 and 10 c/ft^2 PCF 3/4 provided for only small changes in perceived brightness. In this intensity range PCF 1/4 produced fairly large changes in brightness. With a target size of about $1^{\circ}16'26''$ BE occurred and visual resolution was correspondingly worsened. With a target size of about $0^{\circ}30'33''$ the findings were similar, although a somewhat higher level of intensity was needed to produce

BE. It was also found with this target size that when the intensity level was about 1500 c/ft^2 no BE occurred. With a target subtending about 0°4'20" of visual angle it was found that increases in the intensity of continuous (uninterrupted) illumination adversely affected visual resolution. These small targets produced no BE but reductions in pulse rate adversely affected visual resolution.

In all cases in the present study BE was found to be maximal at 5 pulses-per-second. Whenever BE occurred the same stimulus conditions adversely affected visual resolution. In some cases in which BE did not occur but where the intermittent stimulus conditions produce relatively large brightness changes, acuity is worsened. It was concluded that a high degree of synchronization of neural impulses, as reflected in changes in intermittent brightness, act to eliminate the fine gradations in neural timing or frequency which in ordinary circumstances provide a basis for some forms of perceptual discrimination. In some cases the changes in brightness produced by intermittency acted in the same way as did brightness changes produced by manipulating intensity. This is believed to occur when intermittent stimulation produces only a very small degree of cortical synchronization. Other aspects of the data were discussed and areas for further research were suggested.

APPROVED: S. Howard Bartley.

DATE: Nov 20, 1962.

THE EFFECT OF INTERMITTENT PHOTIC STIMULATION ON VISUAL RESOLUTION

By

Charles M. Bourassa

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Psychology

1962

G 25500
6/12/63

ACKNOWLEDGMENT

I deeply appreciate the continuous help, criticism, and patience of Dr. S. Howard Bartley during the formulation and execution of this study.

I wish to thank the other members of my committee: Dr. W.D. Collings, Dr. Charles Hanley, and Dr. M. Ray Denny.

Dr. Thomas Nelson and Mr. Richard Ball must receive thanks for their donation of time and effort, both as observers and critics.

I also wish to gratefully acknowledge the many hours of time that my wife gave to this study in her role as data recorder and typist.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure | Page

INTRODUCTION

<u>Preliminary statement</u>.-The present study concerns the effect of sub-fusional intermittent photic stimulation on visual acuity. Briefly stated, the background of the study is this. To account for the increased brightness of a flickering source over that of a steady source of the same intensity, Bartley has put forward the alternation-of-response theory. This theory has not attracted wide notice, nor has it until recently been utilized in any way other than to account for brightness increases at sub-fusional flicker rates. Within the last few years however it has been demonstrated that sub-fusional flicker produces changes in saturation and hue of colored targets. Certain deductions from the alternation-of-response theory have been used to explain these phenomena. It is appropriate to ask whether this explanation will predict results in other situations. The measurement of visual acuity under conditions of sub-fusional photic stimulation provides an excellent testing ground since, as will be explained later, the predictions of the theory are entirely different than common sense expectation. It is this type of experimentation that will be reported here. In the present study such experimentation is carried out over a range of intensities and target sizes.

By this means it is hoped to present the data relating brightness, visual acuity, intensity, and flicker in a more comprehensive fashion than has been attempted hitherto, to deal more clearly with the possible mechanisms involved, and to relate the whole to the broader aspects of brightness perception.

Alternation-of-response theory.-Before discussing the present study it is necessary to present information relevant to the alternation-of-response theory. This discussion, when coupled with the description of acuity phenomena, will lay the foundations for the formulation of the hypotheses to be tested in the present work. It will also demonstrate that past work concerning sub-fusional stimulation and acuity has not only suffered from the use of inappropriate stimuli but that the experimenters were looking for effects exactly the opposite of those to be expected. It will also be pointed out that the use of acuity measurements provides a much more quantitative technique for the assessment of the perceptual effects of flicker than the technique used in the study of color changes under flicker.

We have already explained that the alternation-of-response theory was formulated to deal with brightness increases of sub-fusional intermittent photic stimulation (6,7,8,11,12,13). The general sort of relationship reported in a number of studies is shown diagramatically in Figure 1. The relative effectiveness of an intermit-

tent source is ascertained by matching a steady source to the intermittent one. When pulse rate is rapid enough the target is perceived as fused, i.e., steady. The point at which the intermittent target passes from one which is perceived as flickering to one which is perceived as steady, or vice versa, is known as the critical flicker frequency (CFF). The brightness of the intermittent target at CFF is determined by the percentage of the stimulus cycle (a cycle being the time from onset of one photic pulse to the onset of the next) occupied by the pulse. The percentage of the cycle length occupied by the pulse is represented by the pulse-to-cycle fraction (PCF). A PCF of one-half means that half the stimulus cycle is illuminated and half not illuminated. In Figure 1 we have assumed that the PCF is one-half. The brightness at CFF, i.e., Talbot level brightness, is one-half of the brightness of a steady target of the same intensity. If the PCF were one-quarter, the Talbot level would be one-quarter of the steady. In other words, the brightness at fusion is equivalent to the brightness that would be produced by spreading the photic pulse evenly over the entire cycle length (7,44,51).

As shown in Figure 1, when pulse rate is reduced brightness begins to rise above the Talbot level and eventually exceeds the brightness of the steady target. The area in which brightness of the intermittent target is above Talbot's level, but below the level of the steady target, is referred to as the intermediate range (IR) of

brightness (16). Brightness enhancement (BE) occurs when the intermittent target exceeds the brightness of the steady target. The pulse rate which produces the maximum enhancement, subject to the qualifications to be discussed shortly, is around eight to twelve per second (6).

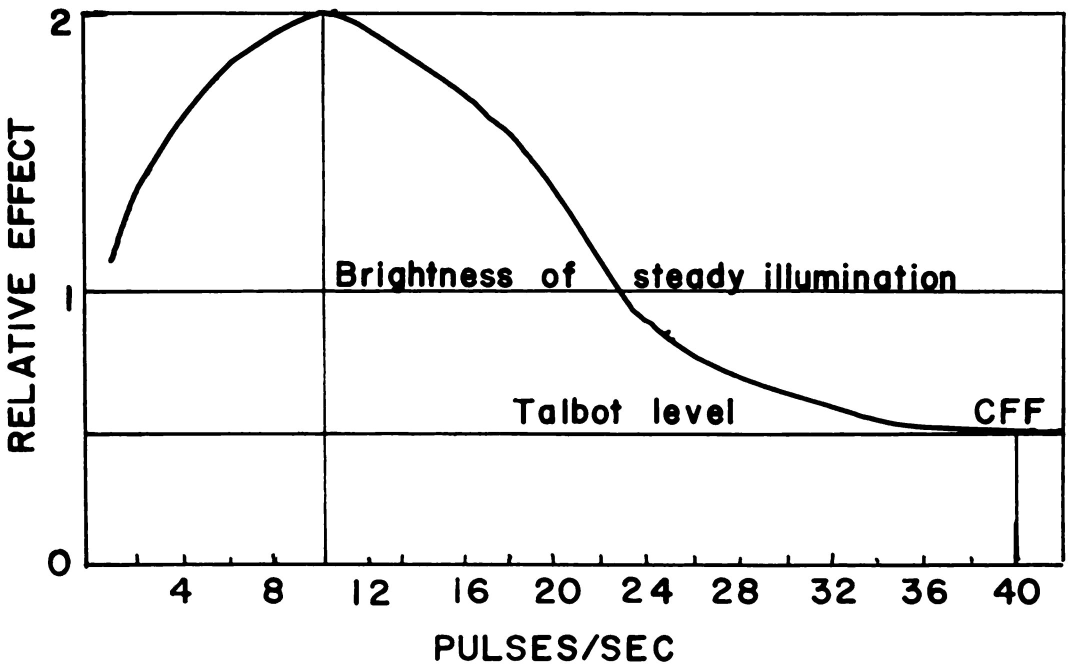

Fig. 1.--The general relation between pulse rate and perceived brightness when the source of illumination is interupted by an episcotister with a PCF of .5. See text for a complete account.

It should be pointed out that while lower PCFs have lower Talbot levels of brightness they produce correspondingly greater BE (7,16).

To account for the phenomena of Figure 1 the alternation-of-response theory was put forward by Bartley (6,8, 11,12). We may now briefly summarize the salient features of this theory. The alternation-of-response theory maintains that there are separate and relatively indepen-

dent parallel channels from retina to cortex. Each of these channels has its own latency, thresholds, and recovery time. When stimulation is maintained for some time the channels will recover and fire again in a 'random' fashion. When stimulation is intermittent each pulse of radiation will activate a certain number of channels. If the photic pulse is a relatively long one then, after an initial discharge of the retinal elements, some of the channels will recover and fire again as previously described. If the photic pulse is shortened there will occur an interval in which the photic pulse will be long enough to activate a large number of receptors but the pulse will go 'off' before the channels recover. Further, if the repetition of the pulse is at the proper rate the next pulse will fire a number of recovered channels. Not all channels may have recovered by the time the second pulse is delivered but by the time the third pulse occurs some of the lagged channels plus perhaps a few of the channels which recover rapidly from the second pulse will fire. Channels will thus rotate activity so that while no one pulse fires all possible channels each pulse will fire the maximum number of recovering channels thereby allowing for maximal utilization of the retino-cortical pathway. Furthermore, neurophysiological investigation has disclosed that certain rates of delivery of nervous impulses to the cortical visual system result in a maximal cortical response (4,7,8,36,38). Within the

framework of the alternation-of response theory this latter point is of prime importance since,

> No matter what the discharge rate in the retina happens to be, the imput has to be favorably received by the cortex before sensory effects will be maximal and be expressions of brightness enhancement (12).

It must be pointed out that not all conditions of stimulation produce the results shown in Figure 1. From the alternation-of-response theory it is possible to predict that low target intensities and/or small target sizes may reduce or eliminate BE. This follows from the fact that small targets or low intensities are not able to fire enough channels to result in a large cortical response. This is, of course, in accord with information concerning the relation of visual acuity, brightness discrimination, and CFF to changes in target size and/or intensity(7,44,51,67).

It has also been shown that with some combinations of target size and intensity, brightness of the intermittent target will continue to increase below ten pulses per second (p/s),i.e., intermittent brightness reaches a maximum at pulse rates below 10 p/s (10,21,22). Unfortunately such studies have not been systematic enough to disclose exactly the crucial parameters influencing the results.

There are other factors which will also influence the BE function. The effect of PCF has already been briefly described. According to the alternation-of-response theory the advantage of low PCFs lies in the assumption

that smaller PCFs tend to produce a more uniformly maximal response, whereas longer PCFs allow enough time for some of the initially stimulated channels to go out of action before the pulse is ended.

Another major factor thought to influence BE is the amount of stray light present on the retina. If the stray illumination is supra-liminal it will stimulate some of the neural channels which would otherwise be utilized by the photic pulse (17).

Yet another factor considered to influence BE is the rate of onset and rate of decay of the photic pulse. There has been no systematic exploration of this variable but since wave form can vary from square to an elongated sine we can expect some influence on BE. There is no way to hypothesize the exact nature of this influence without experimental data, although we might expect square pulses to produce a maximal neural response (37).

We must also mention a concept which can be deduced from the alternation-of-response theory and which has received substantiation from both physiological and psychological experimentation. This concept is that of the cortical reorganization period and it states that before rythmic stimulation reaches full effectiveness a certain amount of time must elapse in order to allow the neurons to group responses (15). That is, there must be a period of time for the various channels to fall into line and organize the responses. Functionally, this means

that intermittent stimuli must be observed for some small but appreciable time before the rythmic nature of the impingements produces brightness enhancement. Thus we must not expect extremely short exposures of the intermittent target to result in BE.

This brief account of the data concerning BE and of the mechanisms proposed to account for BE may be supplimented by reference to various papers already cited in which a more complete account is given.

Extension of alternation-of-response theory.—For many years the alternation-of-response theory has been limited to an account of sub-fusional brightness changes. Recently however Nelson and Bartley have utilized this theory to help explain the wash-out or desaturation of various hues viewed at sub-fusional intermittency rates. For details the reader may consult the original publications (14,53, 55). We may summarize the matter here by saying that it is hypothesized that the rythmic neural firing underlaying BE destroys the timing of the neural impulses which determine the perception of color. Perhaps because of the strong emphasis placed on cortical activity by the alternation-of-response theory, the authors have emphasized cortical timing as the major factor in wash-out.

Whatever the locus of the mechanisms, the alternation-of-response theory has been tentatively extended to deal with phenomena other than brightness increases. A major deficiency of the wash-out research lies in the fact that

for various good reasons, the investigators were unable to use a matching target. Thus the reports of desaturation and brightness changes are largely qualitative. While there is no doubt that desaturation phenomena occurs there may be some doubt that the conditions used produce BE. It is, moreover, clear that the wash-out takes place over a much wider range of pulse rates than does BE. There is no question that use of a matching source would allow a much stronger case to be made. It is to be expected however that desaturation is likely to occur before BE. That is, brightness perception seems to be a primitive response to stimulation and it is likely that relatively larger stimulus changes will have to occur before brightness changes take place whereas spectral discrimination will be affected by smaller changes in the conditions of stimulation. Thus wash-out may be a more sensitive indicator of alterations in neural timing than brightness.

Visual resolution.-Before extending the alternation-of-response theory to problems of visual resolution it is necessary to briefly discuss visual acuity. Acuity is expressed as the reciprocal of the minimum visual angle, in minutes, which the observer is able to resolve under a given set of conditions. Thus as the numbers representing acuity get larger, visual acuity improves. However, it is usually the minimum resolvable visual angle which is measured, and as this angle increases acuity decreases.

The difference between acuity and minimum angle of resolution (MAR) must be understood because both terms are used here; since, as Ludvigh and Weymouth point out, the minimum angle of resolution is of primary importance (69), most of the experimental data presented later are plotted in terms of MAR.

We may begin this examination by considering the perception of a point source. Although in reality no source can be a point, since a point has no area, we may for the present accept the common definition of a point source as one whose distance is very great in relation to its size (28,48,64,66). When a point source is barely liminal the observer perceives a dimensionless point. As intensity is raised the perceived point gains radial offshoots, at first short and then longer (58). The radial offshoots are due to inhomogeneities in the refracting media of the eye. Such inhomogeneities are often classed as aberrations (spherical aberrations, astigmatism etc.) (28,42,48,64,66). It should be noted that such phenomena are aberrations only in terms of an already articulated theory of optics and are not necessarily aberrations in terms of visual perception (58). The reader may also consult Walls who points out that many of the so-called aberrations do not hinder, but may aid perception (68).

If the intensity of the point source remains constant and the surrounds are gradually made luminous, perception

of the point is at first unaffected, but it will eventually lose the weakest rays and the longer ones will shorten. This occurs, in part, because the increased illumination results in a decrease in pupil size which will reduce some of the irregularities of the ocular media through which the radiation must pass (29,42,51,58,64,68). Reducing the aperature will also act, initially at any rate, to decrease the retinal illumination hence causing some of the radiation to become sub-liminal.

If we resume increasing the intensity of the point source the responding retinal area will be reduced because the pupil contracts and because retinal sensitivity will decrease. On the other hand, the increasing amounts of entopic stray radiation act to increase the affected area. Over an intermediate range these two factors balance (22, 42,53,58), but eventually pupil size and sensitivity reach minimum values and further intensity increases result in dazzle or glare which reduces visual efficiency (53). This effect will occur when the target or the surround luminosity is too high and also with either point or extended sources (53).

In order to further simplify this discussion let us now consider the effect of small artificial pupils. A diameter of less than one mm will eliminate the irregularities of most eyes (58). With a small artifical pupil the energy is distributed in a diffraction pattern with a central disc of maximum brightness and rings of decreasing

intensity (53,58,64). Following Ronchi the term 'centric' will be used to refer to this diffraction pattern. The intensity of the rings of the centric are considerably less than the intensity of the central disc. Thus, while at high intensities five or six rings may be visible, at lower intensities only the central disc is perceived (53, 58).

The diameter of the central disc of the centric is inversely related to the diameter of the aperture (53,58, 64). Consideration of this relation might lead to the prediction that, since the optical image is 'sharpest' when the centric is a minimum, enlarging the aperture should produce better vision. While this is true in certain cases, e.g., the mirrors of reflecting telescopes, we have already pointed out that increasing pupil diameter uncovers more irregularities in the refracting system of the eye. Cobb was able to demonstrate that over a midrange of pupil sizes the two effects cancelled one another, i.e., acuity was unchanged over a range of pupil sizes from about 2.5mm to 4mm (22).

If, by using two artifical pupils, centrics are placed so as to coincide on the retina the only effect is to increase the brightness of the centric (53). If the centrics are placed so as to overlap slightly then brightness will increase and the observer is also likely to report that the centric is no longer round but oval (58). If we continue to add centrics, at a distance from one

another small enough so that no gap is perceived, both brightness and 'ovalness' increase. After a certain number of additions is exceeded brightness remains constant, i.e., the addition of a single centric does not contribute to the original flux, but the 'ovalness' becomes perceived as a line (58). Thus when reduction of a source produces only a brightness change it is, for that observer, a point source. We can also define linear, and by extention, extended sources (58).

Turning more directly to acuity we note that visual resolution means perception of two point sources with a darker area between them. The affected retinal zone is determined partly by intensity, but also by diameter of the artifical pupil, wavelength of the radiation, retinal threshold, etc.. In any particular case these factors can be held constant, but then we must know the sensitivity of the eye to differences in intensity. Figure 2, redrawn from Ronchi, shows the reciprocal of Weber's fraction plotted against intensity (58). The dependence of acuity on intensity can be represented by a curve which goes down at either end. It drops at high intensities because this leads to a widening of the centrics disc and because of the increase in the Weber fraction. The curve should drop at low intensities since Weber's fraction increases and also because the stimuli become subliminal.

The same considerations by and large apply to extended surfaces except that increased intensity will not lead to

the same spread of the 'image'. At high intensities a linear source is seen much wider than it 'really' is (30,59). An extended source will obviously not show the same percentage increase in apparent width (30,58).

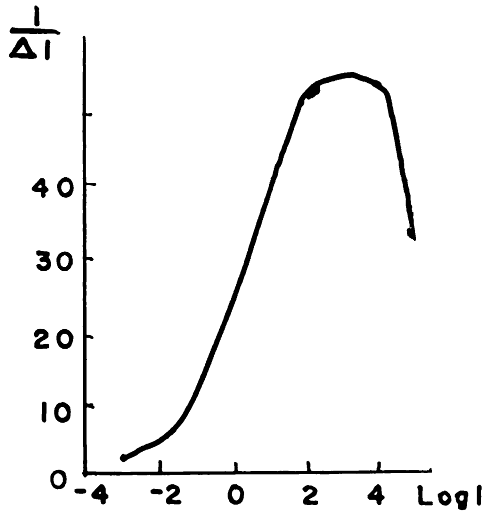

Fig. 2.--The relation between the Weber fraction and intensity of stimulation. From Ronchi (58). See text for details.

Turning now to actual data, Figure 3 shows results of several experiments relating acuity to intensity. The curve which levels off at high intensities is Konig's. The leveling off is presumably because no surround illumination was used. The other curves, with the exception of the Wilcox, and the Fry & Cobb curves, were obtained with the surround illuminated at the same level, except at the highest intensities, as the targets. Wilcox' curve was obtained using very narrow bars on a dark background (70). The visual angle subtended by the targets was about 142". The relationship here is similar to that to be expected of

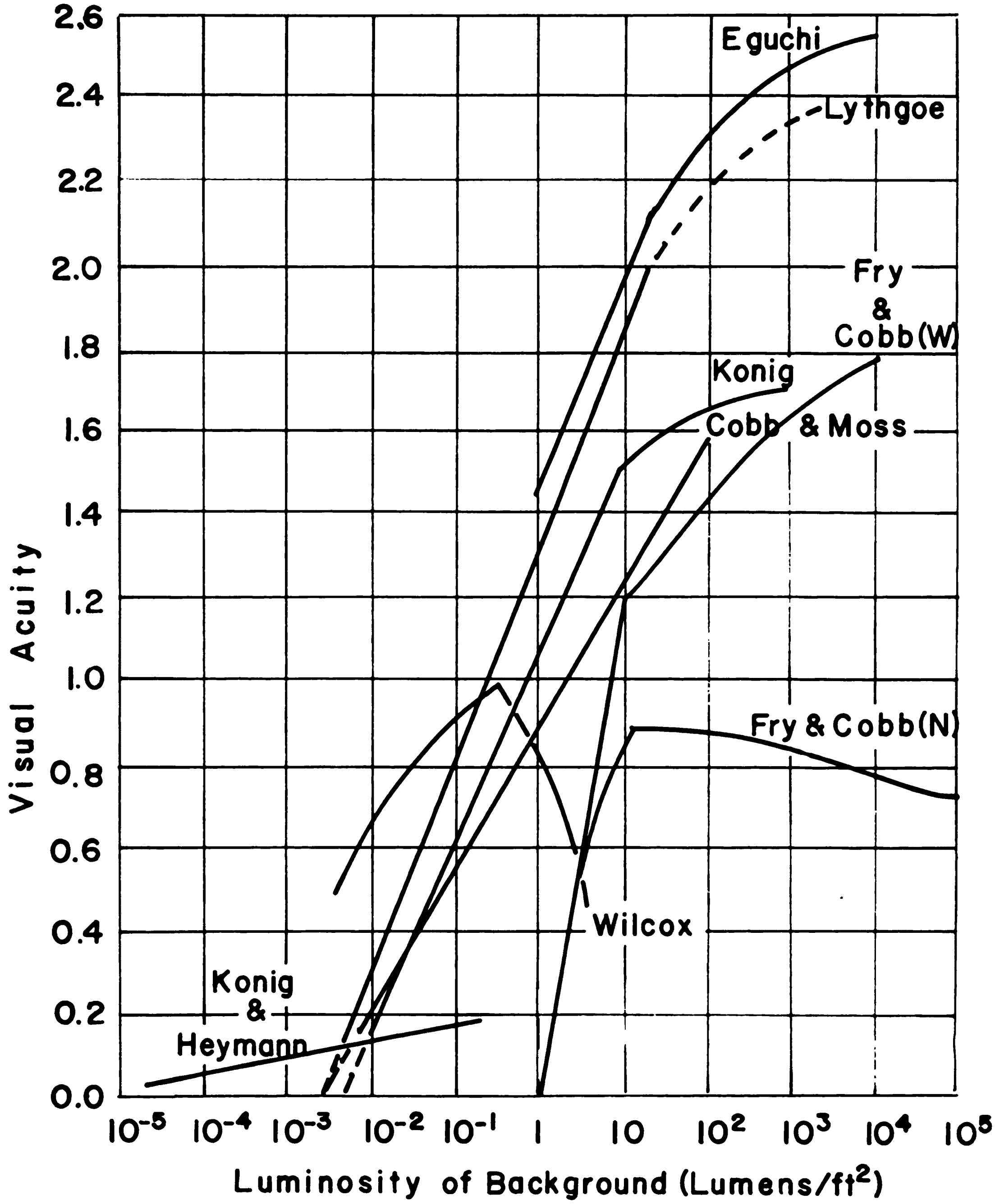

Fig. 3.--Visual acuity as a function of target luminosity. The curves of Eguchi, Lythgoe, Konig, Cobb & Moss, and Konig & Heymann are taken from Moon (51). The curves of Wilcox, and Fry & Cobb are taken from Bartley (7). See text for details.

a linear source. The curves of Fry & Cobb labelled N and W directly show the effect of target size when using illuminated targets in a dark surround(7). The N curve was obtained with targets subtending a visual angle of 168" while the W curve was obtained with target subtending 1000" of visual arc. Thus the data bear out the principles discussed earlier.

The physiological mechanisms of visual acuity are largely unknown. Several theories have been put forward from time to time and for a discussion of the most prominent of these the reader is referred to papers by Hecht, Hartridge, and Shlaer (42,44,62,63) or to the other sources listed in this section.

Recent neurophysiological investigations of the retina and optic nerves demonstrate that vision is a much more complex affair than the earlier theorists realized (2,3,7, 29,35,36,39,40,41,47,52,56). The retina, like other sensory end organs, is organized in complex sets of overlapping receptive fields. Presumably there is interaction not only within but also between receptive fields (3,6,35,39,40,41). Radiation on the retina does not start a simple neural message to the cortex. Moreover, the retina and the optic cortex are spontaneously active. Any neural impulses originating from external stimuli must be considered in relation to the ongoing activity. It must also be borne in mind that while the foveal area is limited to a small portion of the retina, foveal representation is found to

take up the largest part of the visual cortex (1,35,59,68).

Without going into detail current thought indicates that the interaction of receptive fields acts to sharpen gradients of stimulation (35). The role of spontaneous activity, by analogy with its role in other receptors, lies in its ability to indicate by deviations in either direction a more complete picture of retinal stimulation (35). That is, either an increase or a decrease in spontaneous activity is significant for perception.

So far we have been concerned with retinal mechanisms. We must now ask about cortical influences. Neurophysiological investigations of cortical 'contour processes' have yet to be carried out but there is some evidence that the processes just described in the retina are also active in the cortex (52,56). At least in man the cortex is essential for visual discrimination (59) and it seems to have been adequately demonstrated that form perception is at least partially dependent on cortical mechanisms. Evidence for this has been presented by Hebb and others (43,59). Many vertebrates, other than man, are able to discriminate light from darkness, and differences in total retinal flux (not brightness) when the cortex is eliminated (7,59). There is some justification for believing that difference in total flux is the most primitive sort of visual response (21,66). As we have already indicated, form perception seems to involve a more elegant mechanism. Presumably the perception of a

straight line falls at some intermediate point in terms of the complexity of the mechanisms involved. This assumption follows from the reports that Senden's subjects were able to distinguish an object from a ground but not able to deal with the whole object. Therefore they must have perceived some contours but were not able to follow them (43).

Table 1, taken from Moon (51), gives some average acuity values for various conditions. As might be expected the values from the various conditions differ widely. One must remember however that the conditions are not directly comparable. That is, target size, target illumination etc. cannot be equated in the various conditions so that in reality the acuity values would be expected to differ.

TABLE 1.--Resolving power of the eye under various conditions

APPROXIMATE RESOLVING POWER OF THE EYE				
Object	Minimum visual angle		Distance on retina	Visual acuity
	Minutes	Radians		
Two stars	1.0	2.9×10^{-4}	4.3microns	1
Two black bars on white ground	0.5	1.45	2.1	2
Vernier	0.15	0.43	0.65	6.67
Spider web or black wire on self-luminous background	0.13	0.38	0.57	7.69

We might ask however whether the differences in acuity values obtained by the various techniques are to be attributed solely to differences in energistic impingements. The contention here is that some of the differences arise because of a difference in physiological mechanisms employed in the discrimination. Such speculation is of course idle unless some method of testing it is found. It may be that sub-fusional intermittent stimulation will differently affect these acuity measures. Specifically, we expect the more elaborate discriminations to be more seriously affected by synchronous nervous activity than the more primitive responses (see section on extension of alternation-of response theory). A test of this hypothesis is outside the scope of the present work but indicates one interesting area for further investigation.

Effect of intermittent stimulation.-Predicting the effect of intermittent stimulation on visual acuity is somewhat difficult due to the lack of knowledge concerning the mechanisms of acuity. It is also difficult to isolate some portion of the visual nervous system as the locus for a phenomenon for disruption of any one part of the system is likely to affect other parts. As Hylkema says,

> For a good functioning of the organ of vision it is essential that all the links in the chain be sound, and this holds good for all the qualities of sight. It is generally admitted that visual acuity depends upon the eye (distinguished in refractraction system, photosensitive cells and retinal nervous tissue respectively), as well as on the nerves connecting it with the cortex cerebri and on the cortex itself.... But which organ plays the chief part cannot simply be

stated without anything further (46).

It may be possible however to point out by analogy the probable effect of intermittent stimulation if we examine some other receptor response system about which more is known. One such system involves the muscle tendon afferents. The visual receptors, i.e., rods and cones, are of course much different in structure than the muscle spindles and tendon organs, and the adequate stimuli for the two sets of receptors are very unlike. None the less the basic organization seems very similar (33,59). The afferents of muscle spindles and tendon organs converge on ganglion cells and are arranged in overlapping receptive fields. They are spontaneously active and taken together give responses similar to the 'on' and 'off' responses of the retinal ganglion cell. The muscle spindles and tendon organs 'adapt' to various states of tension just as the eye adapts to various levels of illumination. We might note however that spindle adaption to tension comes about due to efferent impulses changing the 'loading' on the receptors. Presumably the eye is little effected by efferents, although this presumption may well have to be modified.

In the normal course of events the tendon organs and muscle spindles act to aid in providing smooth, integrated muscular responses. When however a sudden strong stimulus is applied (a blow to the patellar tendon) the result is a more or less violent response. This comes about because

of a large scale synchronous discharge of the receptors, which eliminates the fine response gradients occurring under ordinary circumstances (59). It seems likely that applying sudden strong stimuli to the visual system must result in a similar state of affairs. That is strong repetitive stimuli prevent the fine gradiations of neural timing and interaction necessary for a well ordered, highly differentiated response.

Such an analogy might be extended further but it seems unnecessary to do so at this time. It is worth repeating however, that apparently in the visual system 'primitive' responses, such as perception of straight lines, movement etc. might be less affected by intermittency than more 'elegant' responses such as hue and saturation.

Previous work.-Before stating the hypothesis in an exact manner we may inspect previous work relating acuity to flicker.

Aside from the compelling reasons provided by the alternation-of-response theory and the work on washout, impetus for studying the relation between acuity and flicker has come from Crozier's work on the influence of the avian pectin on movement acuity (26). In the course of checking some of his findings in humans, Crozier reported that the intensity needed to perceive a pattern remained the same despite variations in PCF, although these manipulations of PCF caused large brightness changes (27). Crozier further pointed out that flicker studies might allow the disentan-

glement of brightness and intensity; the importance of studying the relation between form perception and flicker was emphasized (26,27). Following up the suggestion of Crozier, Senders (60) and later Nachmais (52) reported essentially similar findings, i.e., that at low intensities of illumination low PCFs provided for resolution of a grating at lower intensities than high PCFs. Nachmais demonstrated that brightness followed the Talbot level regardless of pulse rate.

The two studies just cited were concerned with BE in only an incidental fashion. The target intensities were too low for enhancement to occur. However we might note two assumptions made about BE. Both investigators believed that if BE did occur it would be maximal at about 10 p/s which as we have seen is not always true. In any case Nachmais's brightness matches dispose of the possible occurrence of BE. It may be noted in passing that Nachmais is the first to report that brightness matches at low intensities follow Talbot's law regardless of pulse rate although it must be added that Bartley, using a disc-annulus arrangement, has shown that at low intensities of intermittent stimulation, brightness may drop below the Talbot level (9).

Aside from the assumption that BE will be maximal at about 10 p/s even at low intensities, both authors also believed that increasing brightness by means of intermittent stimulation would act in the same fashion as a brightness

increase produced by raising intensity; i.e., to improve perceptual discrimination. This belief is based on the assumption that the mechanism of brightness perception, no matter how activated, will always produce the same end results. We have seen earlier that this is not necessarily the case.

Apparently only one study has been reported in which the aim was to directly assess the effect of BE on form perception. In this study Gerthewohl and Taylor assumed that if BE were operating the increased brightness should improve their subjects performance (31). To test this hypothesis they utilized a chart in which the print started out in the first line as black on white, and then, through succeeding lines the contrast decreased; i.e., the background gradually became darker. The number of lines read was used as a measure of the effect of various conditions. Using four PCFs varying from .4 to about .96, with the source at about 15.4 foot-candles and pulse rates of nine and fifteen pulses-per-second, they found that there was virtually no difference in number of lines read under the various flicker conditions. Steady illumination always produced the best results. The number of lines read at the Talbot level of brightness however was only slightly greater than the number read under the flicker conditions. Gerthewohl and Taylor concluded that the Bartley effect was not operating since if it were the pulse rates near 9 per sec should have produced increased

brightness, and therefore, according to their line of reasoning, also improved the subjects performance. No brightness matches were actually obtained.

This was a badly mismanaged experiment and it is perfectly clear that the authors did not at all understand the nature of the phenomenon they set out to investigate. We have already pointed out that the initial hypothesis is likely to be wrong. Also the level of illumination was relatively low to begin with and, since the reflectance of the chart decreased line by line, target illumination became quite feeble. Hence if BE did occur, which because of the low illumination is not likely, it would make itself felt at some pulse rate below 9 per sec. Moreover the fact that Gerthewohl and Taylor did not obtain brightness matches is almost inexcusable in an experiment where perceived brightness is supposed to be the major factor under investigation.

Senders examined the data of Gerthewohl and Taylor and claimed that their findings supported her own in that low PCFs did not reduce acuity more than the higher PCFs (61).

<u>Present study</u>.-With this background information in hand we may proceed to a discussion of the present study. It is well known that an increase in target intensity tends to improve most visual functions. Usually target intensity is increased by increasing the amount of luminous flux reaching the eye from the target. This usually results in

the target being perceived as brighter. As we have seen some experimenters have assumed if the target is made brighter by means of BE that this should also improve visual discriminations. From the material discussed in the previous sections of this paper we know that this assumption is erroneous. In fact, if BE occurs, visual discrimination should become worse. Thus there exists here a clear cut difference between theoretical and common sense understandings of BE which may be put to test.

In the present study, the effect of intermittent photic stimulation on visual acuity is to be measured. Such measurements will prove to be significant in a number of ways, one of which was mentioned in the preceeding paragraph. It will be possible by the selection of proper stimulating conditions to systematically vary the factors of target size and intensity, which as indicated earlier, are major factors in BE and also, since brightness matches are to be directly obtained, it will be possible to state with certainty, and in a quantitative fashion, the relation of BE to acuity. Moreover, it will be possible to separate with some certainty effects due to impingements per second from the effects associated with BE, thus allowing a more positive statement of the relationship of BE and acuity than it has been possible to make concerning BE and washout.

In order to be able to obtain meaningful brightness matches the type of target must be chosen with some care. In this case it was decided to use two illuminated targets

in a dark field. The targets could be adjusted toward or away from each other. The size of the interspace which the observer found necessary in order to perceive a separation between the targets provided a direct measure of visual resolution. This method was employed by Wilcox who found that with extremely narrow targets increasing brightness caused an increase and then a decrease in acuity (70). This effect does not occur with larger targets (7).

With this technique direct measures of acuity under a wide intensity range may be obtained. Brightness matches can be obtained by use of a second target equal in size to the combined area of the acuity targets.

Although the hypotheses to be tested have been implicit throughout we may now state them in a formal manner. The following predictions are made:

1. Small target sizes combined with low intensities will not produce BE at any pulse rate.

2. Combinations of moderate target size and intensity will produce maximal BE at a pulse rate lower than 10 per second.

3. Large targets combined with high intensities will produce maximal BE at 10 pulses per second.

Concerning the effect on visual acuity of sub-fusional flicker, we have already mentioned that the type of acuity measure used is very close to involving 'pure' visual resolution and is very much akin to, in Hebb's terminology, a primitive figure ground perception. Thus it is likely to be much less effected by neural timing than hue and we therefore make the following predictions.

1. When BE does not occur there will be little difference between acuity measured at various pulse rates.

2. When BE does occur acuity will be worst at the same pulse rates that result in BE.

METHOD

APPARATUS

The apparatus is shown diagramatically in Figure 4.

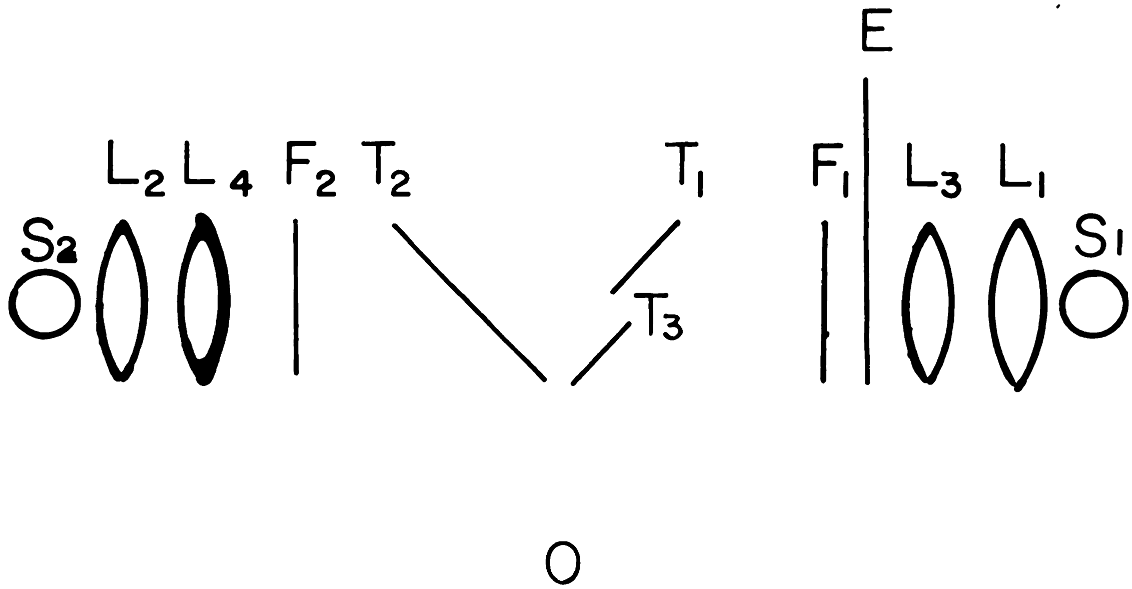

Fig. 4.--Schematic diagram of the apparatus. S_1 & S_2 are light sources. L_1, L_2, L_3 & L_4 are lens. F_1 & F_2 represent filter holders. T_1, T_2, & T_3 are first surface mirrors used as targets. The episcotister is at E. The observer is seated at O.

The sources (S_1, S_2) are 200 watt frosted lamps contained in lamp houses. The lens L_1 and L_4 are used to collimate the radiation from the sources. Lens L_2 and L_3 could be used to bring the beam of radiation to a focus. L_3 is used to focus the beam at the plane of the episcotist-

er E. The targets (T_1, T_2, and T_3) are first surface mirrors of various sizes. The intensity of the illumination falling in the targets can be controlled by Variac and by inserting opal glass filters at F_1 and F_2. The entire apparatus, excepting T_1, is rigidly mounted. T_1 is fixed to a lathe micrometer head in such a way that movements of the micrometer slide T_1 to the right or left. Measurements of movement could be made easily to the nearest .02 mm.

Target sizes.-Three target sizes are used. The smallest targets are each 4 mm wide. The medium size targets are each 22 mm wide and the largest targets are each 5.5 cm wide. In order to provide uniform illumination of the large targets it was necessary to modify the apparatus in the following way. Project-o-chart projectors are used to illuminate plane mirors which are placed at the S_1 and S_2 positions in Figure 4. The radiation is then reflected to the targets. The lens are not used in this case.

The visual angles subtended by the targets, each target alone and by both targets combined, i.e., T_1 and T_3, at viewing distances of 100 cm and 350 cm, are given in Table 2 on the next page.

Episcotister.-Two episcotisters are used giving PCFs of 1/4 and 3/4. Episcotister speed was measured by a Weston tachometer and controlled by Variac.

Illumination.-As already indicated illumination was provided

by either project-o-chart projectors or 200 watt lamps. In either case the voltage to the sources was controlled by Variac and constantly monitored by means of an AC voltmeter. All electrical equipment was run on line voltage. The level of the target illumination was measured by a McBeth Illuminometer.

Table 2.--Visual angles subtended by the targets at two viewing distances.

Large targets			
Together		One	
100 cm	350 cm	100 cm	350 cm
4°27'	1°16'26"	2°13'30"	0°38'13"
Medium targets			
Together		One	
100 cm	350 cm	100 cm	350 cm
1°46'50"	0°30'33"	0°53'37"	0°15'19"
Small targets			
Together		One	
100 cm	350 cm	100 cm	350 cm
0°19'27"	0°4'20"	0°9'44"	0°2'46"

OBSERVERS

Three observers, including the author, were used. All have had extensive experience as observers in similar psychophysical experimentation.

PROCEDURE

The procedure was determined by the recommendations given by Crozier (23,24,25), and Nelson, Bartley, and DeHardt (54). For a full rationale the reader may consult the original papers.

Observers were seated at the viewing distance to be used; i.e., either 100 cm or 350 cm and dark adapted for a length of time dependent on the level of illumination to be used. At the lowest level of illumination dark adaptation extended for a 45 minute period whereas at higher intensities a 10 minute period was used.

Brightness matches were made starting with steady targets, then at the highest rate of intermittency (fusion), and at 20, 15, 10 and 5 p/s. PCF 1/4 was tested first. To make brightness matches, the observer manipulated a Variac attached to S_2. Five brightness matches were made at each pulse rate and also under steady illumination.

In obtaining acuity readings the only illumination came from S_1. The observer fixated the target and the experimenter, starting from a position with the targets overlapped, gradually moved T_1 outward away from T_3. When the observer reported a gap between the targets the experimenter recorded the micrometer-head reading. Five acuity readings were obtained under the same conditions described for the brightness matches. It should be noted that there is no way to determine with high accuracy the point at which the two acuity targets are just adjacent to each other. Thus it is not possible to determine an

'absolute' visual acuity. In some cases this point was estimated and used to calculate a rough approximation of 'absolute' acuity. This feature of the apparatus is not a serious drawback in the present study since interest is on changes in visual resolution rather than on acuity per se. As will be seen later the most convenient presentation of the data is in the form of deviations from the MAR under conditions of steady illumination.

A 3 mm artifical pupil was used throughout and the observers wore an eye patch over the unused left eye.

RESULTS

<u>Preliminary investigations</u>.-Before collecting too much data it was necessary to evaluate the influence of factors such as the diameter of the artifical pupil, viewing distance, observer versus experimenter manipulation of brightness and acuity, etc. on the final outcome of the experiment. Not all of these factors required extensive data collection. For example, the author discovered that a pupil diameter of 2 mm was the limiting factor in acuity for him by moving about the room while examining the targets through the artifical pupil and also by making acuity readings with and without his corrective lens. With a 2 mm artifical pupil neither of these manipulations changed acuity, and since without the corrective lens the authors nearpoint is 15 inches, it became clear that the artifical pupil determined acuity. Similar investigations with various pupil sizes showed that the 3 mm diameter pupil used in the experiment is close to the minimal size permitting the 'eye' to determine acuity (see also Schlaer 62,63).

In the matter of viewing distance several factors had to be taken into account. It is almost traditional in acuity studies to view the targets from a distance of

about 20 feet. The reason is presumably that an 'average' observer does not accomodate for objects at this distance. In the present case however several matters prevented the use of this 'ideal' distance. The length of the experimental room was insufficient, and more importantly, the size of targets necessary to cover an appreciable portion of the observers retina at this distance becomes too great to allow the targets to be used in the experimental apparatus. The most important factor however was that the authors' eye glasses are 'over-corrected' and the other two subjects are slightly hyperopic. Thus the viewing distance necessary to eliminate accomodation would be closer to 30 than to 20 feet. The viewing distance finally chosen, i.e., 350 cm, was a compromise between providing for fairly large changes in acuity while still maintaining adequate retinal image size. Data will be presented later showing a comparison between measurements at 100 and 350 cm.

A method sometimes used to allow the observer to be near the targets, but which still eliminates accomodation, is to introduce lenses between the observer and target in such a way as to provide for parallel beams of light at the observers eye. In the present case several objections to the use of this method arise. First, placing lenses between the observer and target introduces additional sources of error, i.e., chromatic aberration, spherical aberration, diffraction etc., into acuity measurements. Second, the lenses will reduce illumination. Third, in the

present experimental situation the use of lenses makes it exceedingly difficult if not impossible to meaningfully calculate magnification (58). Fourth, the lenses act to introduce stray light. Other objections might also be raised. The author investigated a number of lens systems and met with the difficulties just described. It also became apparent that small changes in lens placement, as can be calculated, cause large changes in the diopters of accomodation necessary to focus the radiation on the retina. Often very slight changes in lens position made proper accomodation so difficult that observations could be made for only a few minutes at a time. Moreover it is very difficult at times to localize the targets. For example, if the radiation from the target reaches the eye in parallel beams then, in theory, the targets should be seen at infinity, whereas in fact they are always seen where the observer knows them to be. The disparity between the conditions of stimulation and knowledge of location, while perhaps not affecting either accomodation or acuity is reflected on the phenomenological side by a feeling of conflict or tension when observing the targets. It is worth noting that Wilcox (70), who used a lens system to 'place' his targets at 20 feet, reports large variability in his acuity readings, whereas in the present study, in which no lens system is used, the data are very stable and consistent.

It was felt that problems arising from shifts in

accomodation were largely avoided by the use of short experimental sessions and by allowing the observer to relax momentarily between sets of five readings.

It was found both more rapid and less tiring on the observer if he were allowed to manipulate the intensity of the matching source, i.e., to make the brightness matches himself. On the other hand, it was more pleasant for the observer to simply fixate the targets and wait for a gap to appear. Therefore acuity readings were taken with the experimenter manipulating the equipment and brightness matches with the observer manipulating the appropriate Variac.

Although some of this present discussion may be considered to deal with 'merely' subjective matters the author feels that insuring comfort and calmness in the observer is a large part of the battle in obtaining reliable data rapidly.

Large targets.-The data, in all conditions, were stable and consistent. In order that the reader may see some of the data from which the graphs are constructed the following tables are presented.

Table 3 gives in raw form typical data from RB on acuity readings. The readings are in units of .02 millimeters and represent values necessary for perceiving a gap. The starting point for the readings is an arbitrary one so the values do not indicate 'absolute' acuities. The values are quite consistent. The table also gives the mean

and median for each pulse rate. Following Crozier's (23, 24,25) recommendations we have chosen to deal with medians rather than means but as can be seen there is no real difference between the values.

Table 3.--Raw data acuity readings for observer RB.

P/S	Steady	5	10	15	20
PCF	164	165	162	157	155
	160	165	160	160	157
¼	159	167	163	160	159
	158	163	161	159	157
	157	165	161	160	160
$\bar{x}$	159.6	165	161.4	159.2	157.6
Md.	159	165	161	160	157

Table 4 gives <u>brightness matching values</u> reported by CB.

Table 4.--Raw data brightness matches for observer CB.

P/S	Steady	5	10	15	20
PCF	103	87	77	71	71
	100	98	74	75	69
3/4	100	96	74	71	65
	106	92	74	76	70
	100	89	74	74	68
$\bar{x}$	101.8	92.4	73.4	74.6	68.6
Md.	100	92	74	74	69

The values here are in volts. Because of the relation of voltage to illuminance a change of five volts is equivalent to about four-tenths c/ft^2. The variance of the values is again small. The data shown in Tables 3 & 4 are typical of the rest of the data. The values chosen for display were selected randomly from the raw data sheets.

The results yielded by the larger targets are depicted in Figure 5. The intensity level was about .4 c/ft^2. Each of these targets subtended a visual angle of about 38'13", or together an angle of about 1^{o}16'26". Figure 5c & 5d shows the results of the brightness matches for the two observers. The points indicated by dots represent PCF 1/4, the PCF 3/4 being represented by crosses. It can be seen that at 20 p/s the values lie near the Talbot level for the respective PCFs. As pulse rate is decreased the brightness of the target increases. No brightness enhancement (BE) is apparent but since the values are higher than the Talbot level for pulse rates below fusion, the brightness is in the intermediate range (IR). The a and b portions of Figure 5 give the resolving power of the observers at the various pulse rates. Resolving power is given in terms of the seconds of deviation from the minimum angle resolvable under steady illumination. That is, the MAR under steady illumination is used as a zero point. Upward deflections of the curve indicate the increase in the visual angle necessary in order to perceive a separation of the two targets.

From the figure it can be seen that as apparent brightness increases there is a tendency for acuity to become worse when intermittency is produced by a PCF of 1/4, but is largely unaffected by a PCF of 3/4.

Figure 6 gives the data obtained with a higher illumination level of about 4 c/ft^2. The same features

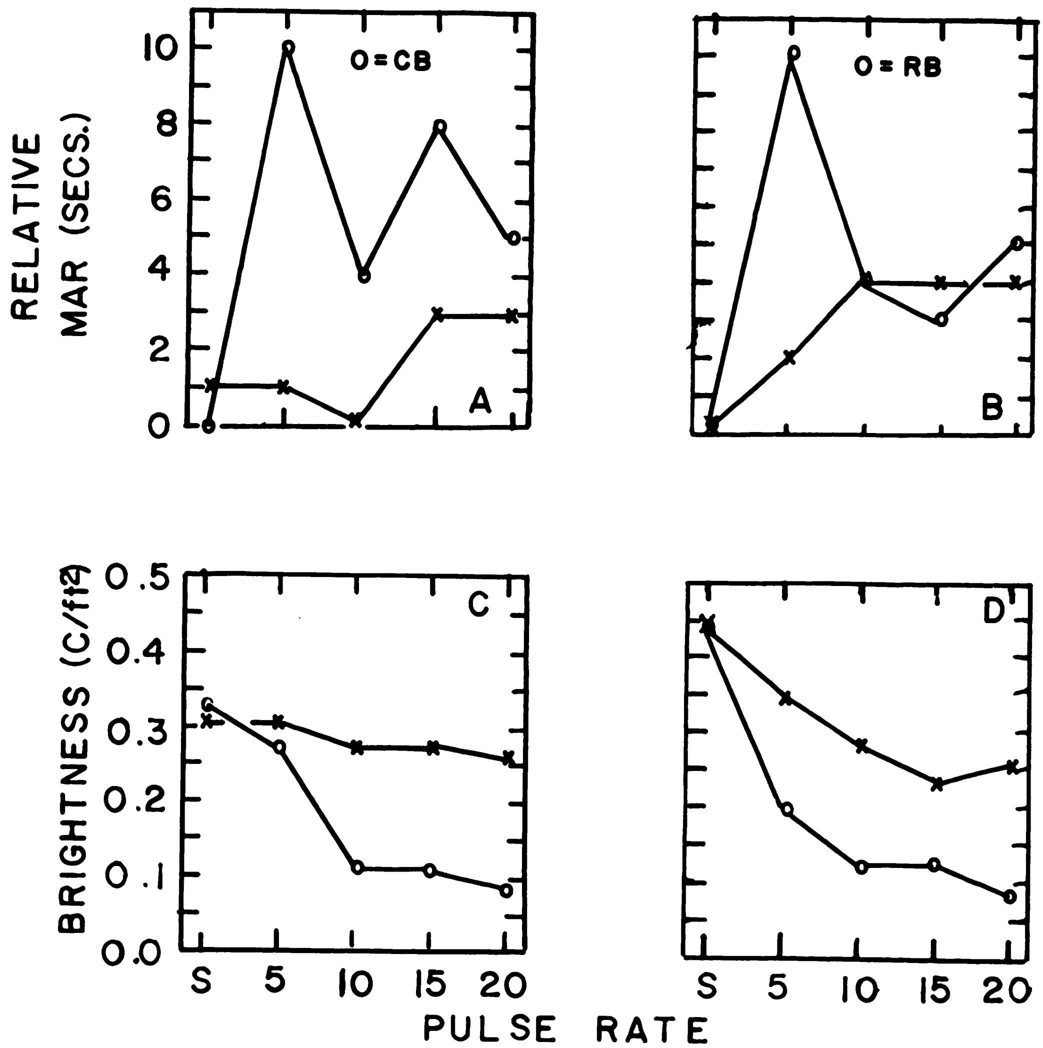

Fig. 5.--The c and d portions of the figure show the brightness matches given by the indicated observers, under conditions of steady illumination (S), and under intermittent illumination at 5, 10, 15, and 20 pulses/sec. The dots represent data using a 1/4 PCF, the crosses 3/4 PCF. The a and b portions show, for each observer, the change in minimum angle of resolution (MAR) necessary in order to perceive a gap under the intermittent stimulus conditions as compared to MAR under steady illumination. MAR is in seconds of visual angle.

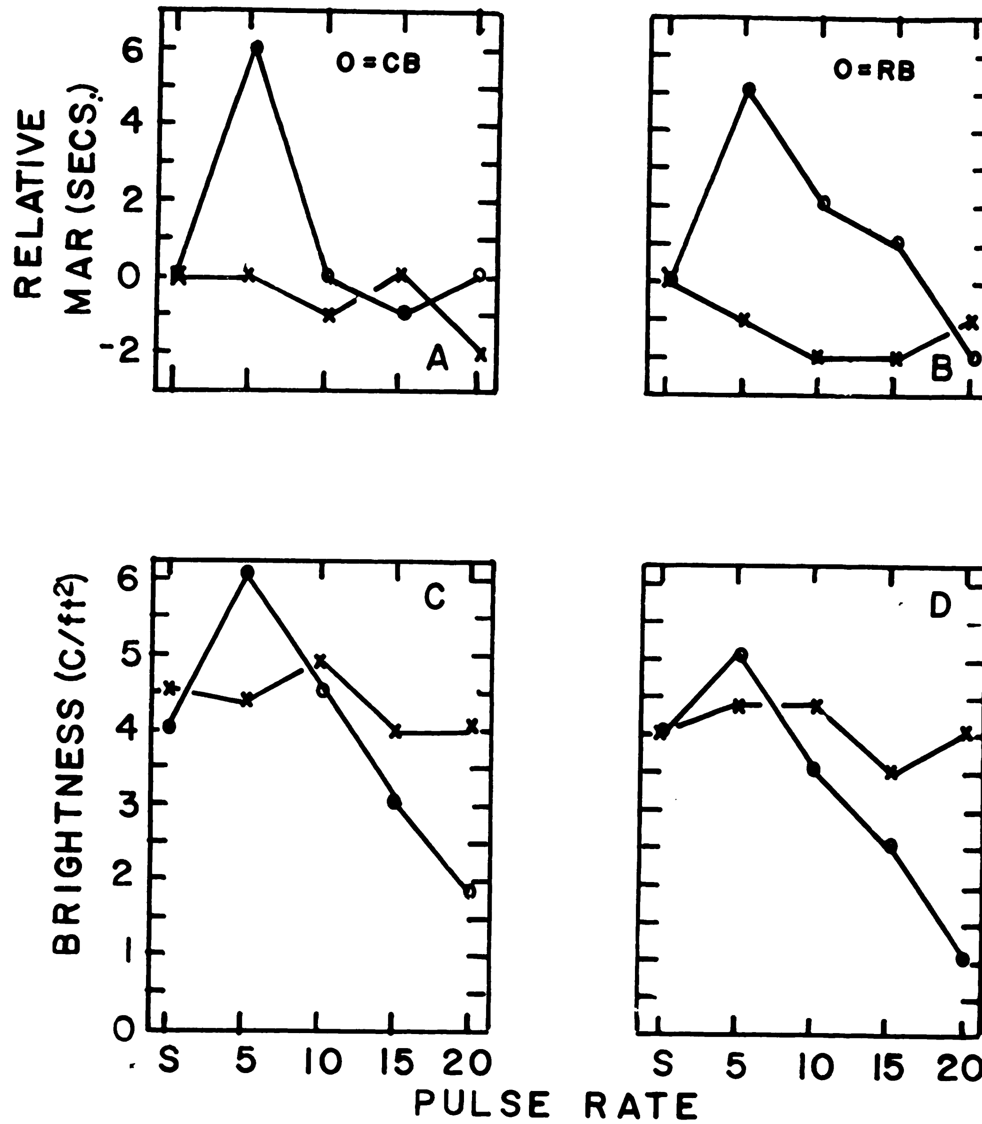

Fig. 6.--The c and d portions of the figure show the brightness matches given by the indicated observers, under conditions of steady illumination (S), and under intermittent illumination at 5, 10, 15, and 20 pulses/sec. The dots represent data using a 1/4 PCF, the crosses 3/4 PCF. The a and b portions show, for each observer, the change in minimum angle of resolution (MAR) necessary in order to perceive a gap under the intermittent stimulus conditions as compared to MAR under steady illumination. MAR is in seconds of visual angle.

described earlier are apparent here also, with the addition that a small amount of BE is apparent at 5 p/s.

The data clearly indicate that pulse rates of 5 per second produced by a PCF of 1/4 adversely affects acuity, whereas the PCF of 3/4 largely results in acuity equal to or better than that of steady illumination. The PCF of 1/4 also results in a higher brightness increase above Talbot level than does the PCF of 3/4. Replications a few days later produced essentially similar data.

The data tend to support the hypothesis that conditions which are favorable to the occurence of BE are detrimental to acuity. It can be seen from Figure 6 that BE occurs under these conditions at 5 p/s and that acuity is worst at this pulse rate. On the other hand it should be noted that in the low intensity condition (Figure 5) the brightness changes due to intermittency are small while the acuity changes are large; whereas at a higher intensity (Figure 6) the brightness changes are large but the acuity changes are small.

It might be argued that the differences in acuity are due to differences in total luminous flux, but such arguements are contravened by the fact that acuity becomes greatly worse only at 5 p/s, whereas if the difference were due to the PCF of 3/4 passing more total flux than the PCF of 1/4 it should be equally observable at all points. It is likely however that with low intensities of illumination the superiority of PCF 3/4 is due to the

larger flux passed by this PCF in comparison with PCF 1/4. This can be more clearly seen with the medium size targets.

<u>Medium targets</u>.-With targets subtending visual angles of $0^{o}30'33''$ data were gathered which revealed the perceived brightness at various pulse rates and also the corresponding visual resolution. The results are displayed in the next series of figures. Figures 7c & 7d show the perceived brightness for two observers under steady illumination and also at 5, 10, 15, and 20 pulses/second, when target luminosity is at about .2 c/ft^2. At this intensity level 20 p/s is sufficiently rapid to produce fused targets. It can be seen that the brightness of the PCF 3/4 is always greater than the brightness with PCF 1/4. The perceived brightness of PCF 1/4 increases as pulse rate decreases and thus, below fusion, lies in the intermediate range. The PCF 3/4 produces only a slight brightness increase as pulse rate is reduced.

Figure 7a & 7b give the minimum angle of resolution necessary in order to perceive a gap. The angle is expressed as seconds of deviation from the MAR in steady illumination. Thus values greater than zero indicate the number of seconds of arc by which the targets had to be separated, over and above the separation under conditions of steady illumination, in order to perceive a gap. For example a value of 10 indicates that the observer found it necessary to increase the separation between the targets

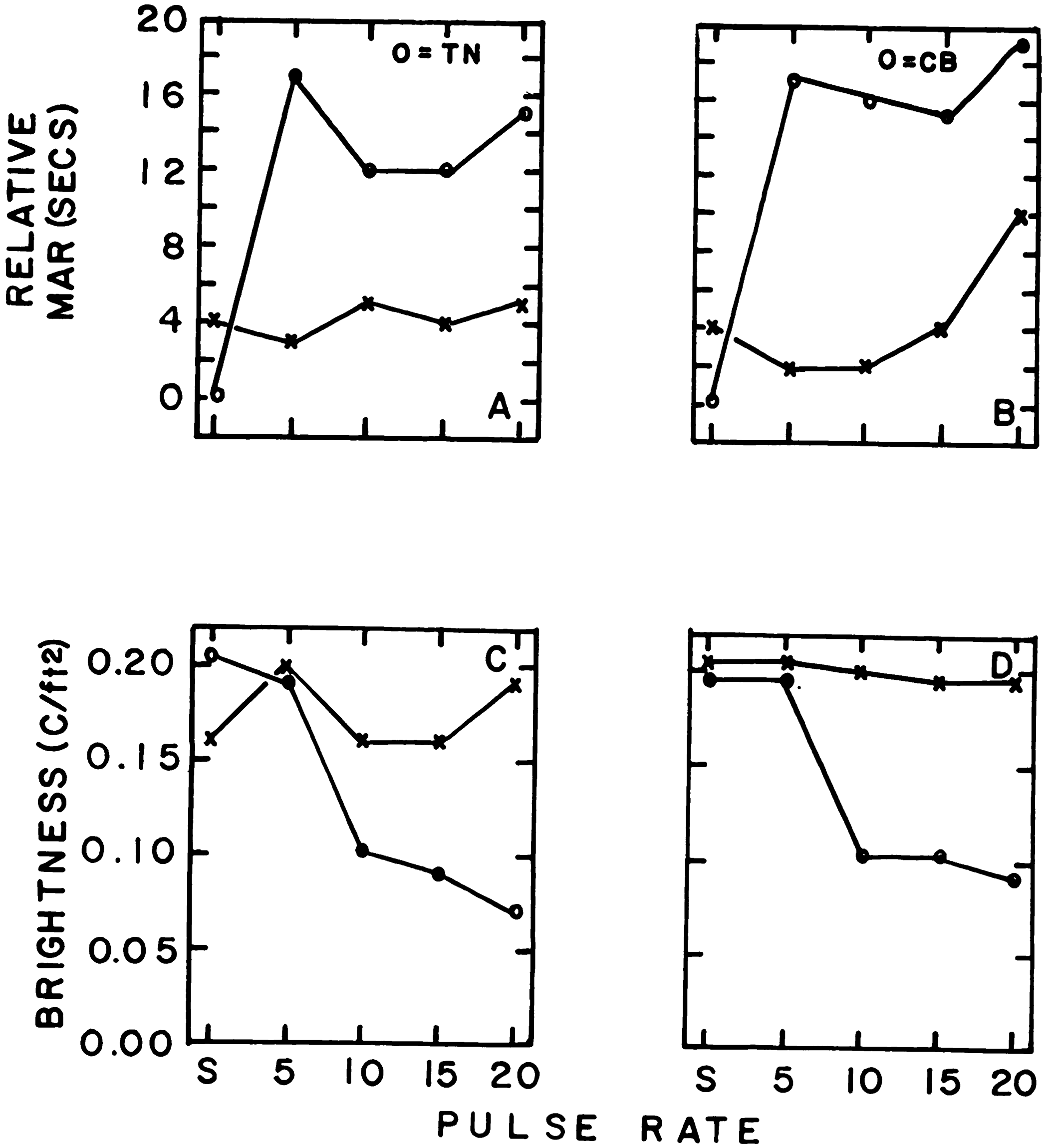

Fig. 7.--The c and d portions of the figure show the brightness matches given by the indicated observers, under conditions of steady illumination (S), and under intermittent illumination at 5, 10, 15, and 20 pulses/sec. The dots represent data using a 1/4 PCF, the crosses 3/4 PCF. The a and b portions show, for each observer, the change in minimum angle of resolution (MAR) necessary in order to perceive a gap under the intermittent stimulus conditions as compared to MAR under steady illumination. MAR is in seconds of visual angle.

by 10 seconds of arc more than the separation under steady illumination. Figures 7c & 7d show that, for both observers visual resolution was much superior with the PCF of 3/4. This is largely attributable to the fact that PCF 1/4 reduces the luminous flux to such an extent that the observations are made at an almost scoptic level. That is, the decrease in brightness produced by PCF 1/4 is great enough to place the final, i.e., retinal, flux at a level near the limit of cone sensitivity. It is to be noted however that although at lower pulse rates the brightness increases, there is no corresponding improvement in acuity. It is quite clear that increasing phenomenal brightness does not act to improve acuity in this case.

In Figure 8 the results of using slightly higher levels of target illumination are shown. In this case the intensity is at 1.75 c/ft^2 for CB and about 1.75 c/ft^2 for TN. The data show much the same relations as just described for the lower level illumination. Here however the increases in apparent brightness produced by PCF 1/4 are greater between 10 and 5 p/s than at the lower intensity.

In Figure 9, at a higher intensity, observer TN gives evidence that BE occurs at 5 p/s. Once again we see that increases of perceived brightness are not accompanied by improved acuity. The steady illumination for TN was at an intensity of about 3 c/ft^2 while for CB it was at 5 c/ft^2. For observer TN the apparent brightness produced by PCF 1/4 greatly exceeds the brightness produced by PCF

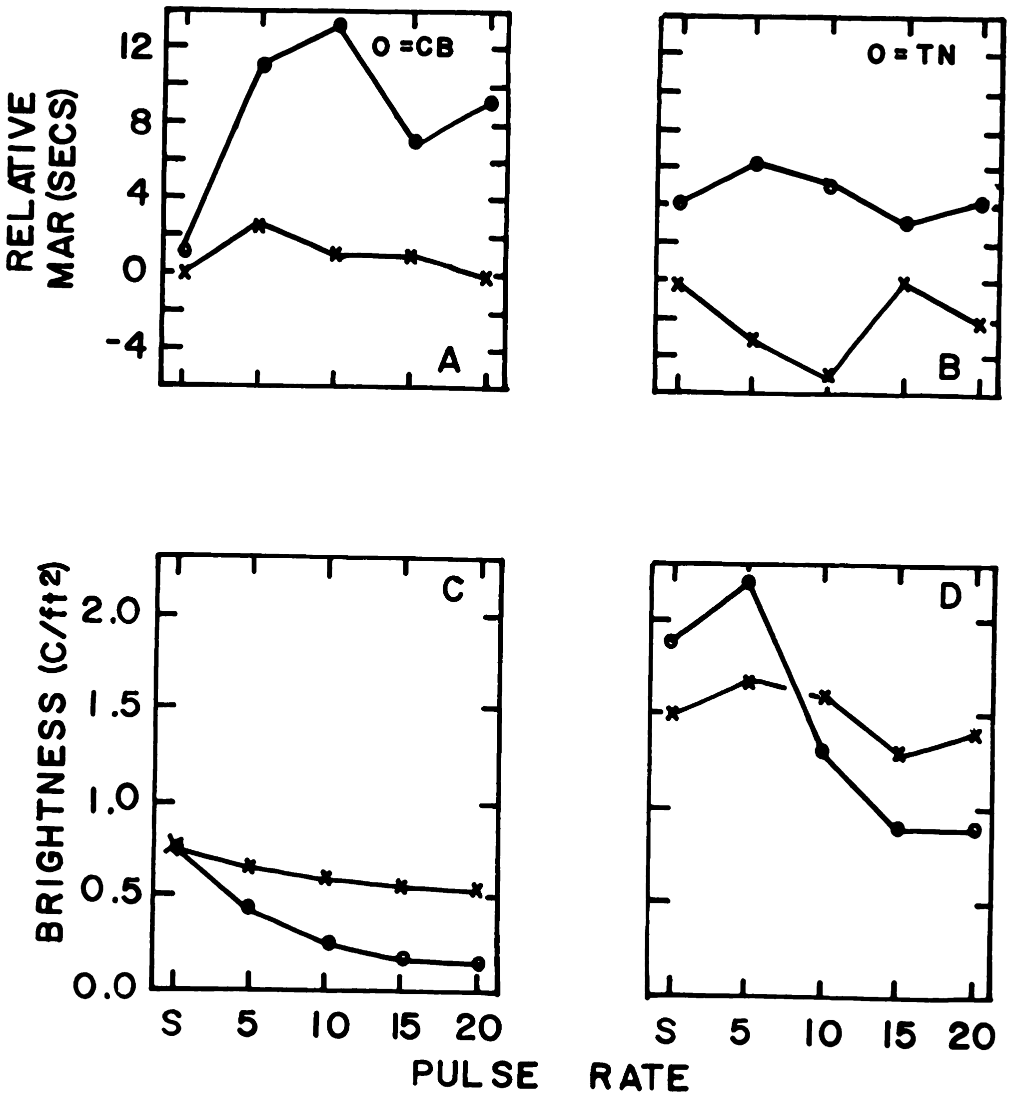

Fig. 8.--The c and d portions of the figure show the brightness matches given by the indicated observers, under conditions of steady illumination (S), and under intermittent illumination at 5, 10, 15, and 20 pulses/sec. The dots represent data using a 1/4 PCF, the crosses 3/4 PCF. The a and b portions show, for each observer, the change in minimum angle of resolution (MAR) necessary in order to perceive a gap under the intermittent stimulus conditions as compared to MAR under steady illumination. MAR is in seconds of visual angle.

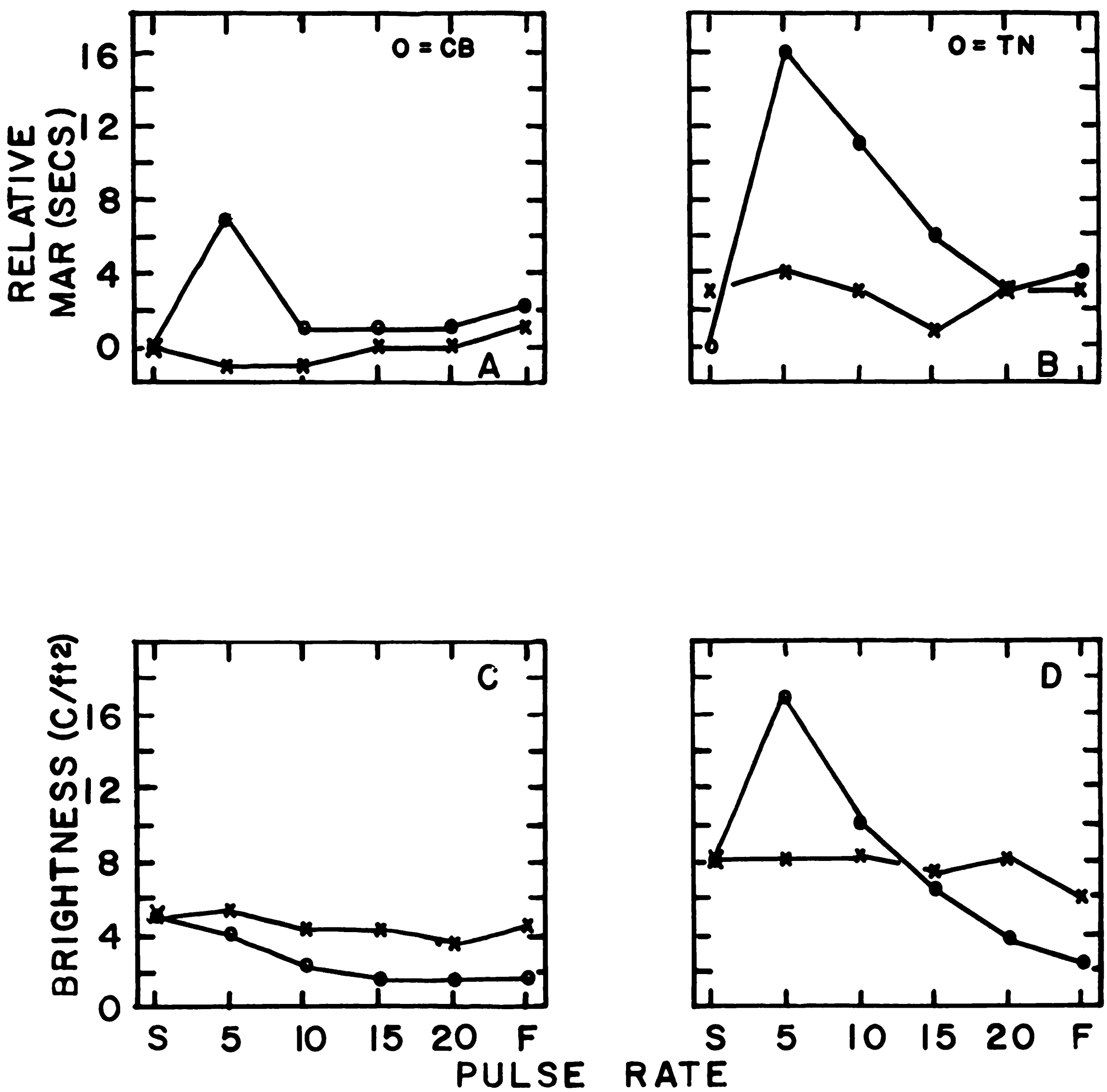

Fig. 9.--The c and d portions of the figure show the brightness matches given by the indicated observers, under conditions of steady illumination (S), and under intermittent illumination at 5, 10, 15, and 20 pulses/sec., and also at a pulse rate high enough to produce fusion (F). The dots represent data using a 1/4 PCF, the crosses 3/4 PCF. The a and b portions show, for each observer, the change in minimum angle of resolution (MAR) necessary in order to perceive a gap under the intermittent stimulus conditions as compared to MAR under steady illumination. MAR is in seconds of visual angle.

3/4 at lower pulse rates. For observer CB the brightness produced by PCF 1/4 is still in the intermediate range. For both observers the brightness maximum under intermittent stimulation is at 5 p/s.

The acuity data in Figure 9a & 9b also reflect the differences in the observers response to intermittent stimulation. We may note first however that now the difference in flux produced by the two PCFs is not great enough to cause correspondingly large differences in visual resolution. That is, the difference in acuity with PCF 1/4 and 3/4 at fusion is much smaller than the differences reported earlier at lower intensities. We see that now decreasing pulse rate acts, with PCF 1/4, to cause an increase in MAR, i.e., to cause a worsening of acuity. On the other hand PCF 3/4 produces little or no change in acuity at any pulse rate. The increase in MAR closely follow the increase of apparent brightness. It is also easily seen that the observer reporting the greatest brightness increase also demonstrates the greatest increment in MAR. Clearly this lends strong support to the hypothesis that conditions of intermittent stimulation which act to increase apparent brightness will also act to reduce visual acuity.

The data obtained with still higher levels of target illumination are shown in Figure 10. The same relations prevail here that were evident in Figure 9 and the same remarks apply. It might also be pointed out that now CB

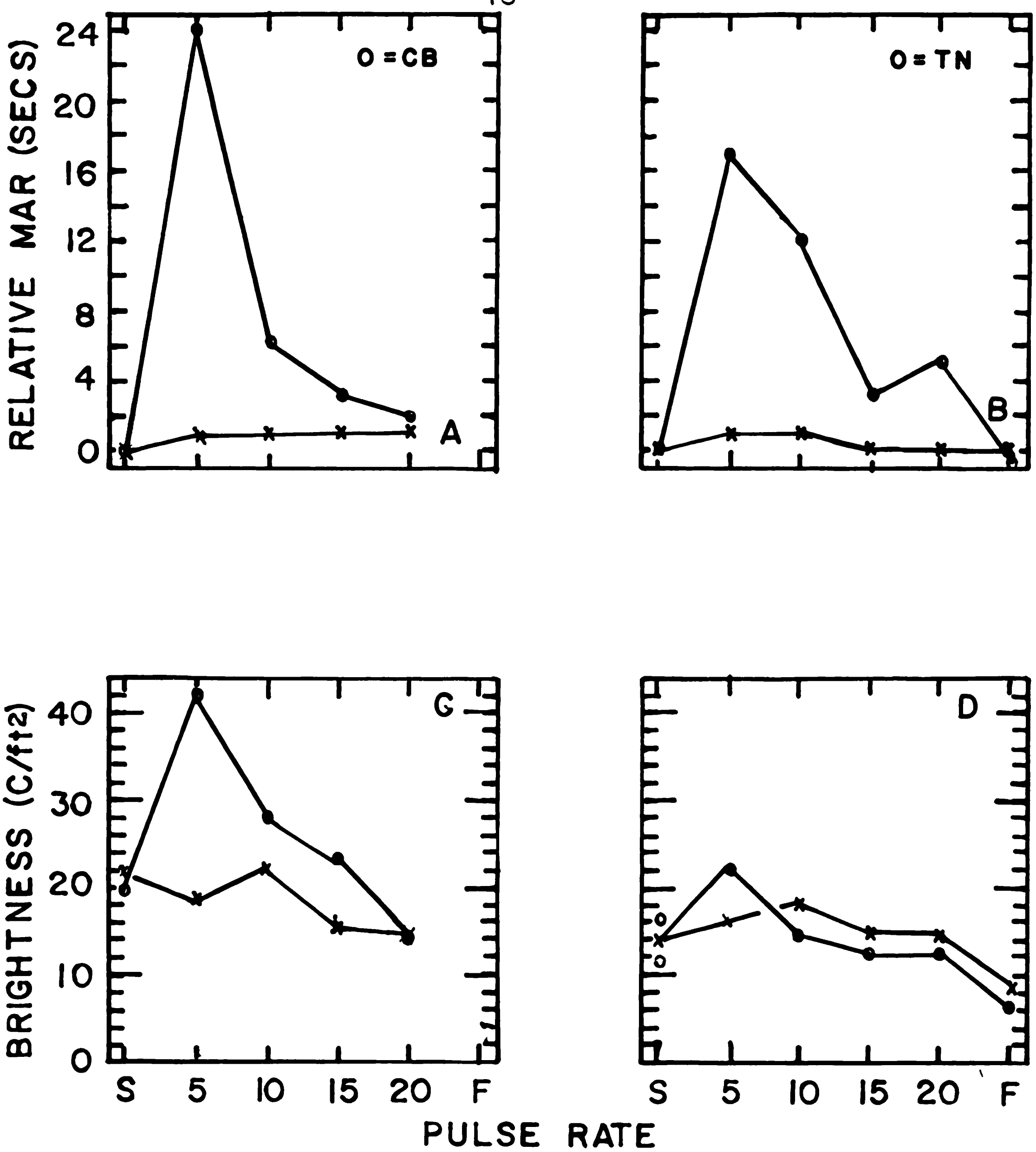

Fig. 10.--The c and d portions of the figure show the brightness matches given by the indicated observers, under conditions of steady illumination (S), and under intermittent illumination at 5, 10, 15, and 20 pulses/sec., and also at a pulse rate high enough to produce fusion (F). The dots represent data using a 1/4 PCF, the crosses 3/4 PCF. The a and b portions show, for each observer, the change in minimum angle of resolution (MAR) necessary in order to perceive a gap under the intermittent stimulus conditions as compared to MAR under steady illumination. MAR is in seconds of visual angle.

shows greater BE than does TN and CB's increment in MAR is correspondingly greater than TN's.

An attempt was made to obtain data at an even higher intensity level. The results are shown in Figure 11. Each observer was run at a slightly different level of target illumination. All observers mentioned that both the brightness matches and the acuity judgements were extremely difficult to make. This subjective estimate of the observers was borne out by an increased variability in the data. For instance it can be seen that TN reported three fairly different intensities to give equal brightness under steady illumination. Also all observers indicate, with one or the other PCF, that brightness at fusion was greater than brightness at 20 p/s, which is extremely unlikely. None of the observers indicate any BE with PCF 1/4 and as the curve for visual resolution shows, acuity is also not affected to any great extent. CB and RB perhaps display some small amount of BE with PCF 3/4 although because of the unreliability of the data this is not at all certain. Because of the difficulty in obtaining accurate photometric information concerning the luminance at such high intensity levels, the brightness matching data are reported in terms of voltages. The approximate intensity levels are: for observer RB 1500 c/ft^2, for TN 1650 c/ft^2, and for CB 1750 c/ft^2.

The findings that no BE occurs when high levels of intensity are coupled with small target sizes has been predicted by the alternation-of-response theory.

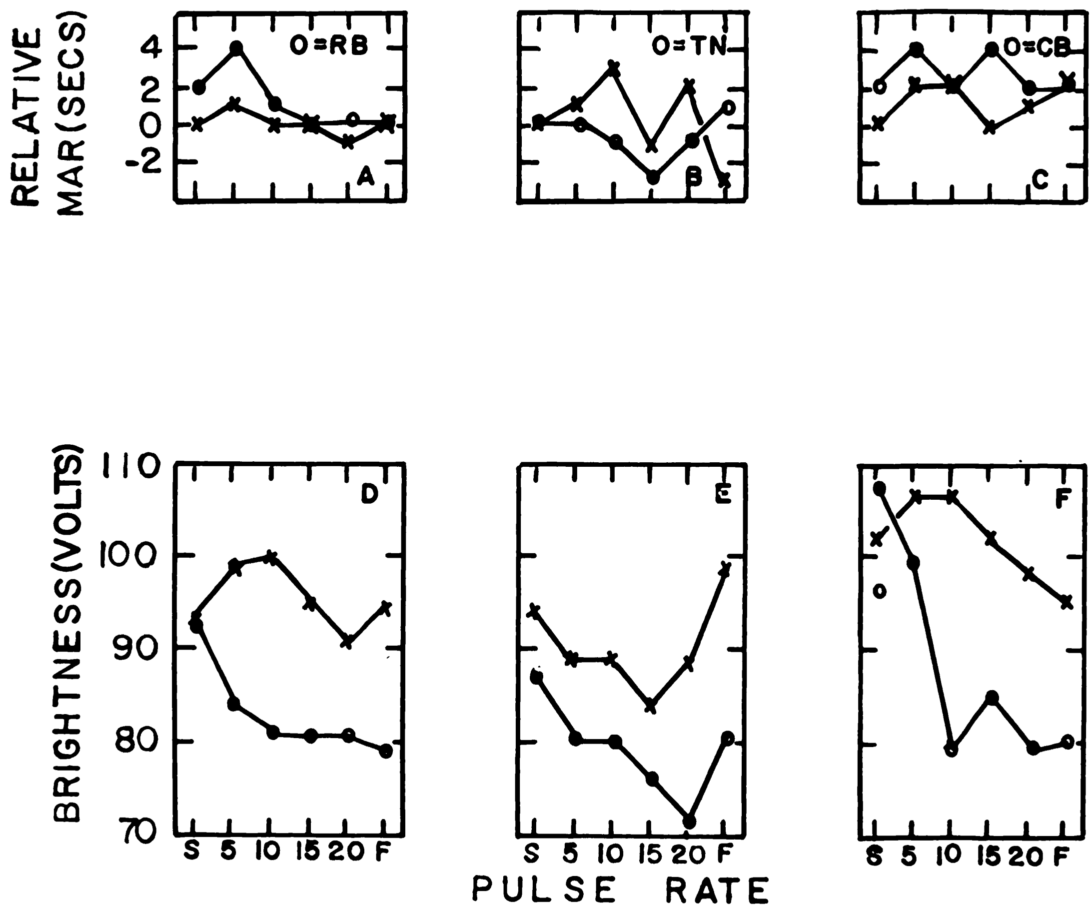

Fig. 11.--The d, e, and f portions of the figure show the brightness matches given by the indicated observers, under conditions of steady illumination (S), and under intermittent illumination at 5, 10, 15, and 20 pulses/sec., and also at a pulse rate high enough to produce fusion (F). The dots represent data using a 1/4 PCF, the crosses 3/4 PCF. The a, b, and c portions show, for each observer, the change in minimum angle of resolution (MAR) necessary in order to perceive a gap under the intermittent stimulus conditions as compared to MAR under steady illumination. MAR is in seconds of visual angle.

The data again support our hypothesis, however, in that no large changes in intermittent brightness occur and acuity is likewise unaffected.

In order to insure that increased brightness due to flicker did not act to decrease acuity in the same manner that increased intensity reduced acuity in Wilcox' experiment (see Figure 3), acuity readings were obtained under steady illumination at intensity levels producing brightness equal to and higher than the brightnesses produced by intermittent stimulation. The data is shown in raw form for TN in Table 5.

Table 5.--Raw data from observer TN for acuity at various intensities of target illumination.

	Intensity					
c/ft^2	2.5	4.4	7.5	22	36	50
	303 304 306 303 305	304 303 303 298 300	298 302 300 301 302	300 304 300 298 297	302 302 304 299 300	298 306 298 301 301
Md	304	303	301	300	302	301

As can be seen the intensity increases fail to produce any large changes in acuity. We may conclude that the Wilcox effect is not responsible for the acuity changes produced by intermittent stimulation.

Figure 12 gives the results obtained by CB with the medium sized targets at a viewing distance of 100 cm. The visual angle of the acuity target is about 1°46'50". The d, e, & f portions of Figure 12 show the brightness

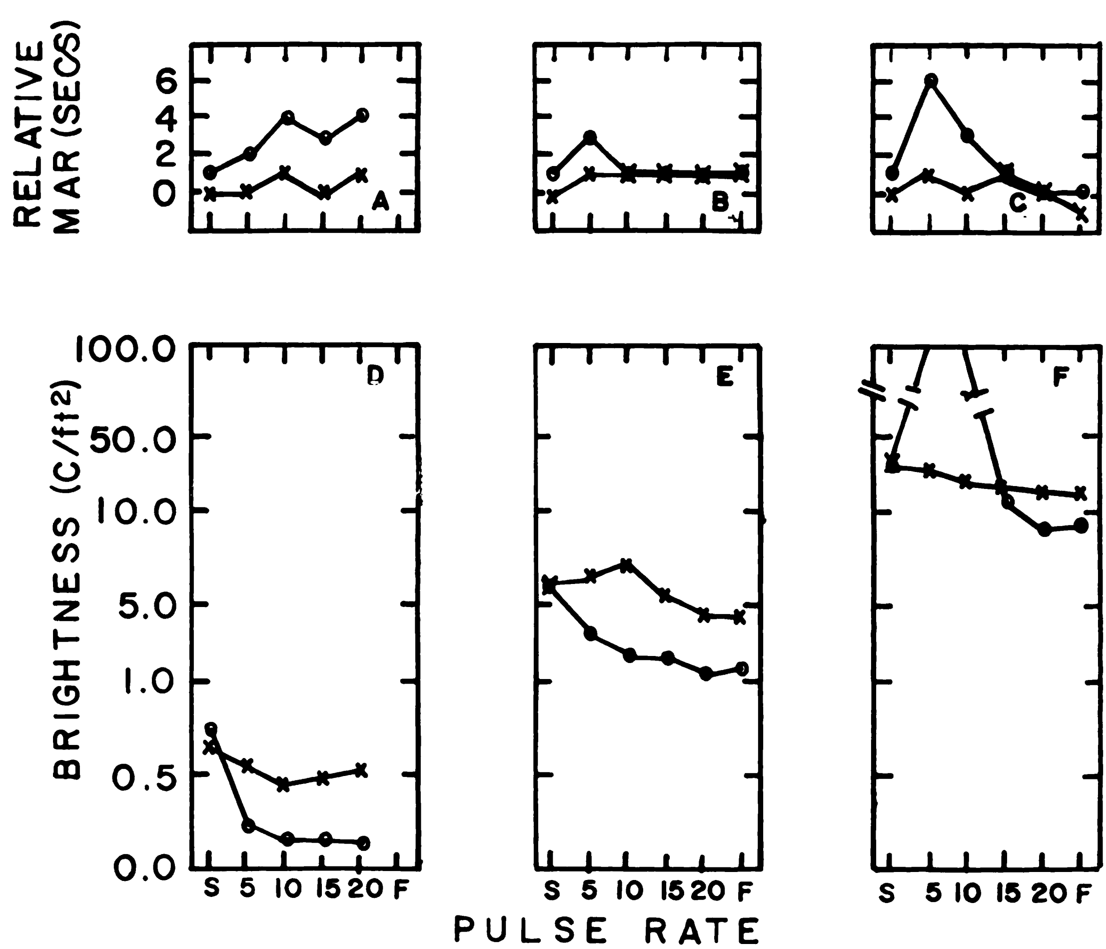

Fig. 12.--The d, e, and f portions of the figure show the brightness matches given by the indicated observers under conditions of steady illumination (S), and under intermittent illumination at 5, 10, 15, and 20 pulses/sec., and also at a pulse rate high enough to produce fusion (F). The dots represent data using a 1/4 PCF, the crosses 3/4 PCF. The a, b, and c portions show, for the observer, the change in minimum angle of resolution (MAR) necessary in order to perceive a gap under the intermittent stimulus conditions as compared to MAR under steady illumination. MAR is in seconds of visual angle.

matching data. In order to display the intensity range more clearly the brightness matches are all drawn to the same scale on a logarithmic axis. The brightness matchings show much the same phenomena as previously described. At the highest intensity of target illumination a large amount of BE occurs and there is a corresponding worsening of acuity as shown in 12c. It should be noted that the amount of BE was so great that the matching source could not be raised to an intensity high enough to match the intermittent target. The points above the interruption in the curve are therefore arbitrary. As can be seen however the change in acuity is relatively small. Figure 12b & 12e shows that at an intermediate intensity a very small worsening of acuity takes place at 5 p/s. The type of data displayed at the low intensity as shown in Figure 12a & 12d has already been thoroughly discussed. In essence the effects are similar to those already reported; because the visual angle of the targets is greater, BE is correspondingly greater than at 350 cm. Acuity changes are smaller because the visual angle subtended by the targets is greater than at 350 cm and also because the visual angle created by any given lateral displacement of the targets will be greater at 100 cm than at 350 cm.

Small targets.-The results obtained with the smallest targets are shown in Figure 13. These targets subtended visual angles of about 4'20". As can be seen from the brightness matches no enhancement is produced by these

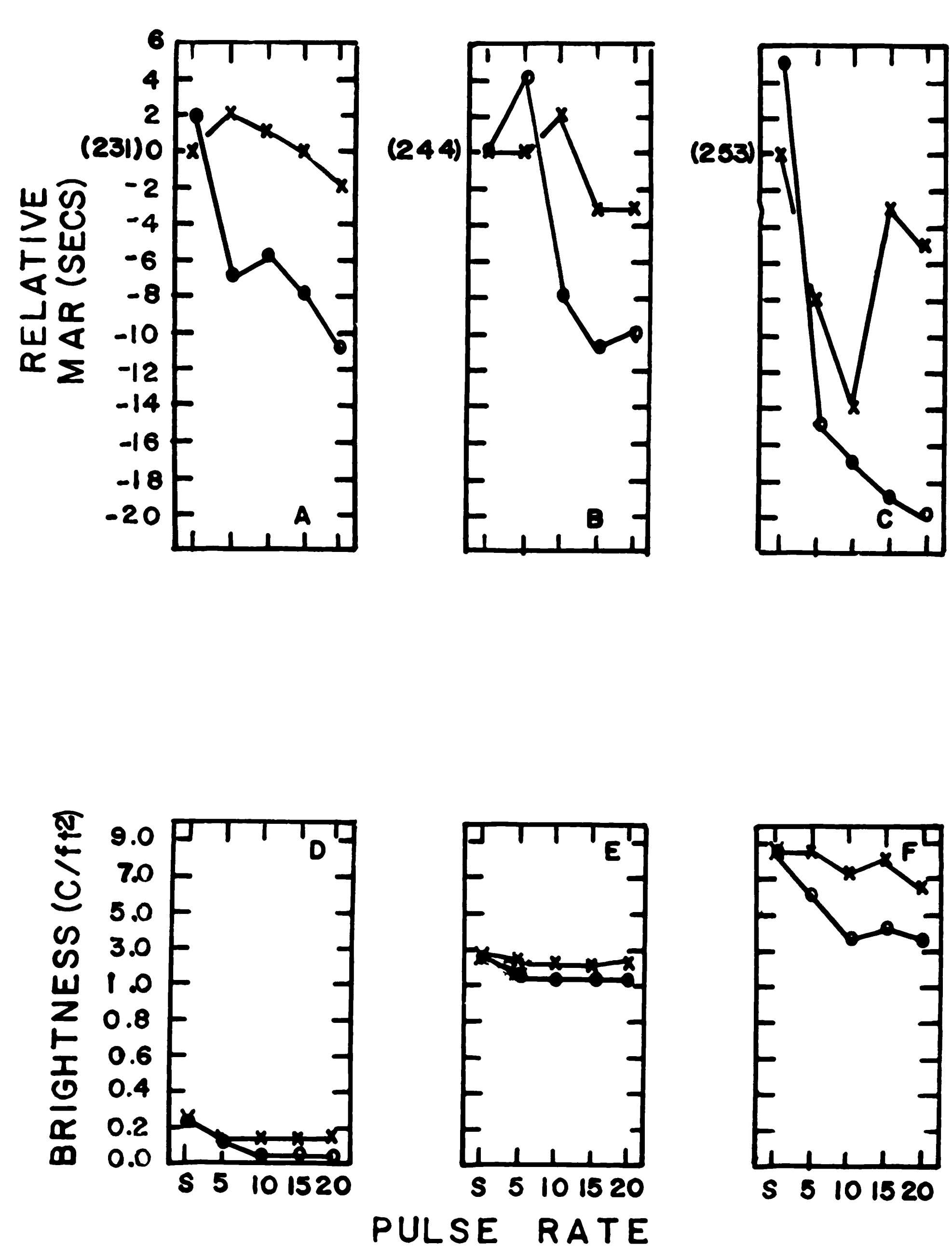

Fig. 13.--The d, e, and f portions of the figure show the brightness matches given by observer CB, under conditions of steady illumination (S), and under intermittent illumination at 5, 10, 15, and 20 pulses/sec. The dots represent data using a 1/4 PCF, the crosses 3/4 PCF. The a, b, and c portions show, for the observer, the change in minimum angle of resolution (MAR) necessary in order to perceive a gap under the intermittent stimulus condtions as compared to MAR under steady illumination. MAR is in seconds of visual angle.

targets. Many features of the curves have been seen in the data presented earlier and need not be discussed again at this point. It might be noted that at the lowest intensity level the perceived brightness of the intermittent targets remains at the Talbot level down to between five and ten p/s. This is accounted for by the fact that the fusion point also occurs at these low pulse rates and may help to explain Nachmais's observation that at low intensities the perceived brightness of intermittent targets tends to remain at the Talbot level regardless of pulse rate.

The acuity data, as can be seen in 13 a, b, & c, is quite different from that previously presented. It can easily be seen, in contrast to earlier effects, that now intermittency acts in general to improve resolving power, i.e., acuity actually is better when viewing the intermittently illuminated targets than when viewing the targets under steady illumination. It can also be seen that PCF 1/4 results in far better resolution for pulse rates above 5 p/s than does PCF 3/4.

It was obvious that with targets of the size used here, increasing target intensity resulted in a perceptual widening of the targets. This effect was described in an earlier section of this paper. The increase in perceived width of the targets as intensity is increased is likely to cause visual resolution to become worse at higher intensities; i.e., at higher intensities, due to their

increase in perceived width, the targets will have to be moved further apart in order that the observer perceives a gap between them. That this is, in fact, the case has been shown by Wilcox (70) and by Fry and Cobb (7).

In determining the visual resolution at various levels of steady illumination it is found that resolution becomes progressively worse as intensity is increased. The micrometer head readings are given opposite the zero point on the a, b, & c portions of Figure 13. Clearly, increasing the intensity of the illumination adversely affects visual resolution.

It is now clear that changes in perceived brightness act in the same fashion as changes in intensity; PCF 1/4 producing greater changes in visual resolution than PCF 3/4 since the brightness changes provided by PCF 1/4 are much greater than those provided by PCF 3/4.

The data presented here regarding these very small targets bears a superficial resemblence to the data already presented with regard to the larger target sizes in that all data indicate that reducing the pulse rate of the intermittently illuminated targets results in a worsening of visual resolution.

The data presented earlier regarding larger targets indicated that at moderate intensity levels the difference in perceived brightness produced by PCF 1/4 and 3/4 did not materially affect resolution except at pulse rates which are capable of producing brightness enhancement.

However with the present small target size it is clear that decreasing brightness acts to improve acuity, and for this reason we may not conclude that the present data lend support to our original hypothesis.

Brightness.-The fact that numerous replications were made has already been alluded to. In each case the data were essentially similar to those already reported. In addition observer CB obtained brightness matches with target sizes other than those involved in the measurement of acuity. Some of this data is displayed in Figure 14. The data in any one column represent a single visual angle. The level of intensity is lowest at the bottom of the column and increases as one moves up the column. The intensity levels across columns are only roughly equivalent in some cases, but enough data are displayed so that major trends are evident. The lowest intensities, regardless of target size, show no indication of BE. PCF 3/4 always is more effective than PCF 1/4. At moderate intensities, i.e., one to ten c/ft^2, the same is true for the smaller targets but now the largest target, subtending a visual angle of $4^{o}27'$ produces a small amount of BE. The maximum enhancement is at 5 p/s, but some enhancement is also seen at 10 p/s. At intensities between 10 and 20 c/ft^2 the $1^{o}46'50''$ target now also produces enhancement. Again maximum enhancement is at 5 p/s. At 10 p/s brightness lies in the intermediate range. The smallest target still shows no indication of BE.

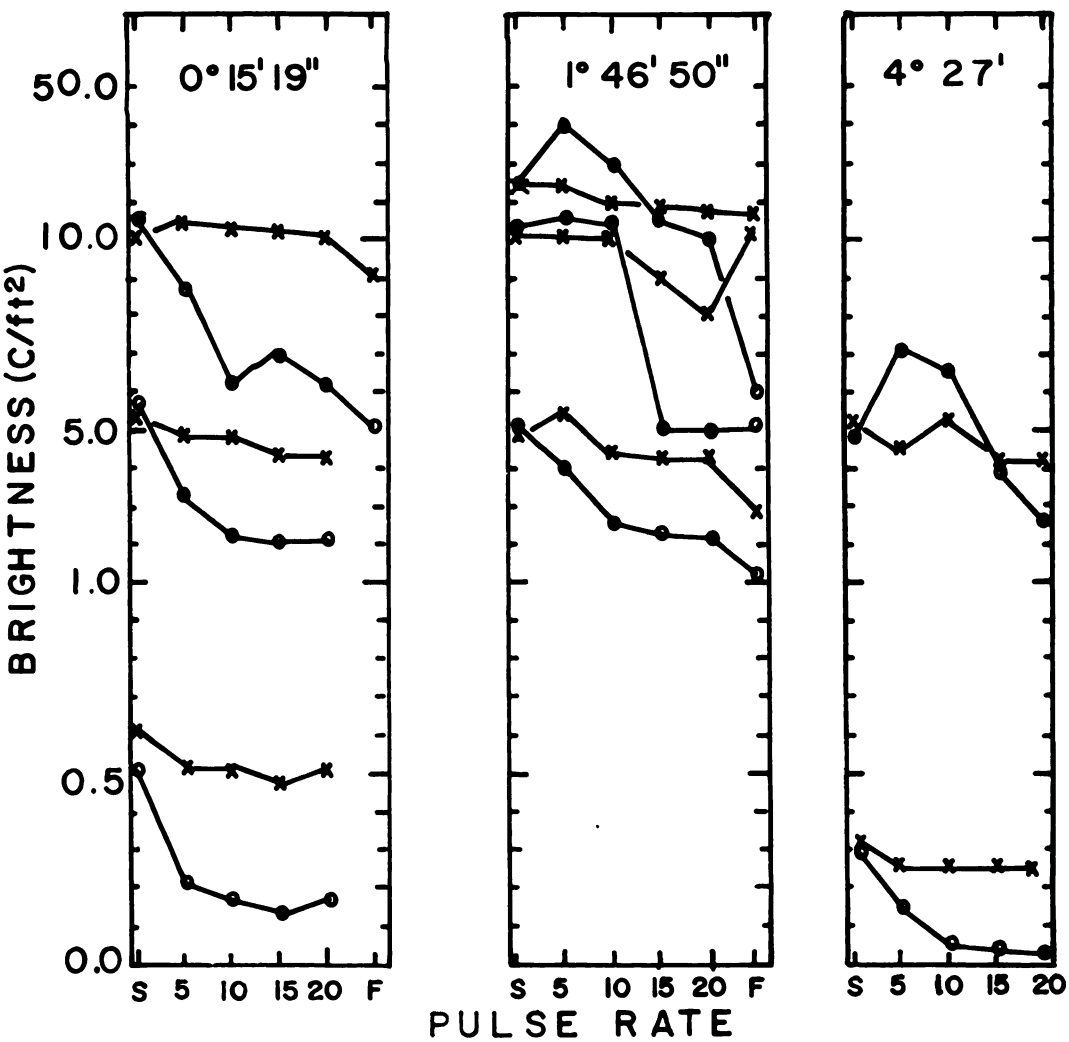

Fig. 14.--Brightness matches obtained under steady illumination (S), at 5, 10, 15, and 20 pulses/sec. and at fusion (F). The visual angle of the targets is given at the top of each column. The points represent PCF 1/4, the crosses PCF 3/4. The data are from observer CB.

In Figure 15 are displayed the combined brightness curves for all observers and all replications. No attempt has been made to keep the various target sizes separate in the graph. It can be seen that intensity is a major factor in changing the shape of the curves. It is clear that PCF 3/4 does not act in any striking way to alter perceived brightness. In Figure 16 are 'idealized' curves which are meant to represent the major aspects of Figure 15. Only PCF 1/4 is considered since PCF 3/4, as has been seen, does not display any striking changes with intermittency.

The 'idealized' curves of Figure 16 display the salient features of brightness changes caused by intermittency. At the lowest intensities intermittent brightness is always less than steady brightness. At high intensities, pulse rates of 5 per second produce maximum brightness and also pulse rates of 10 per second result in perceived brightnesses greater than a steady target of the same intensity. At an intermediate intensity level, between approximately 1 and 10 c/ft^2, BE sometimes occurs and sometimes does not. The present data show that the largest target, which subtended a visual angle of about 4.5°, always produced BE at this intensity level, whereas the smallest target never produced BE at the same intensity level. The targets which subtended visual angles between 30' and about 2° sometimes gave enhancement and at other times failed to produce BE. It has not previously been

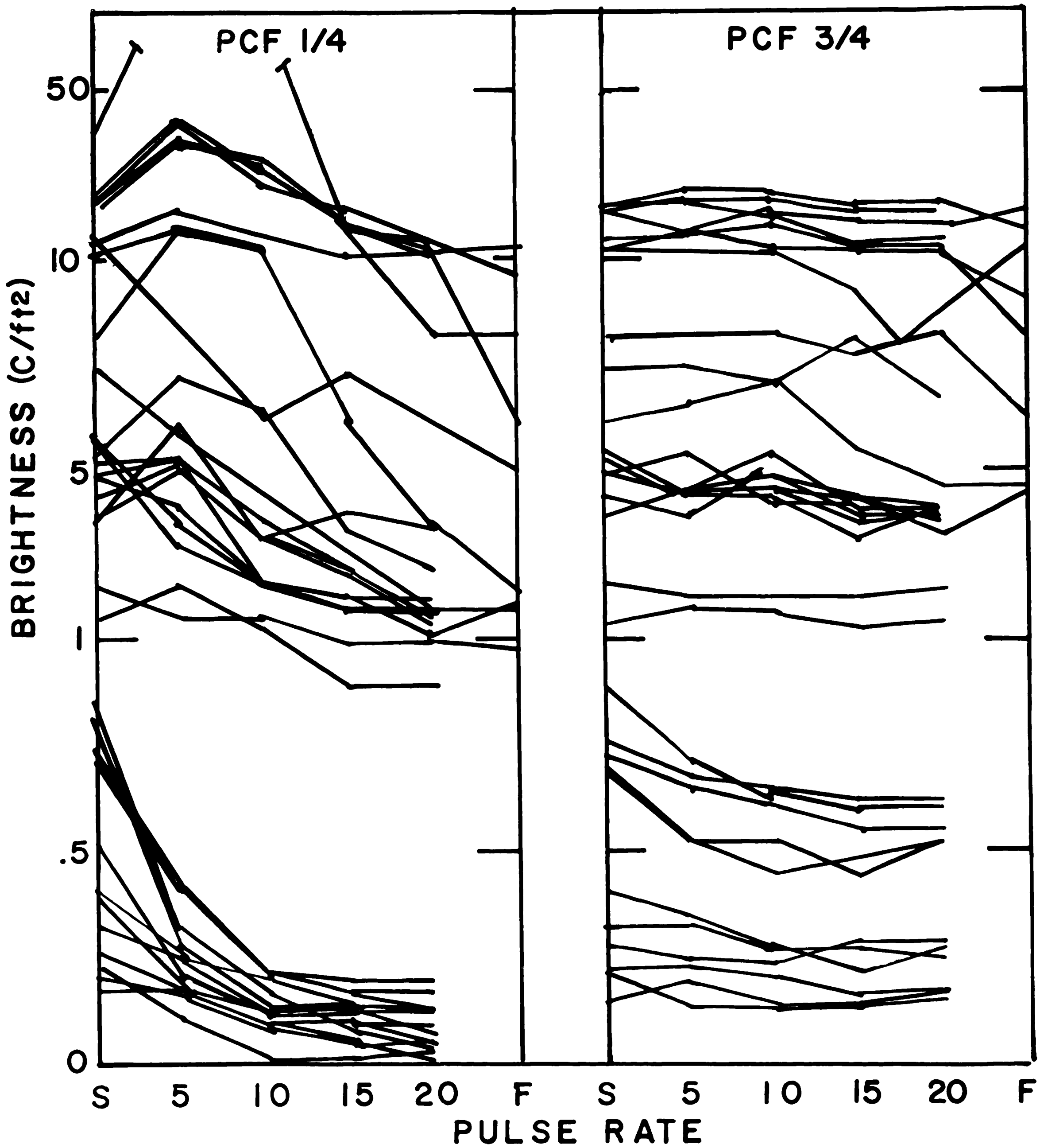

Fig. 15.--Combined data for all replications and all observers. The curves represent brightness matches under steady illumination (S), at 5, 10, 15, and 20 pulses/sec., and also at fusion (F). The data represent all target sizes. The two PCFs are plotted separately as indicated.

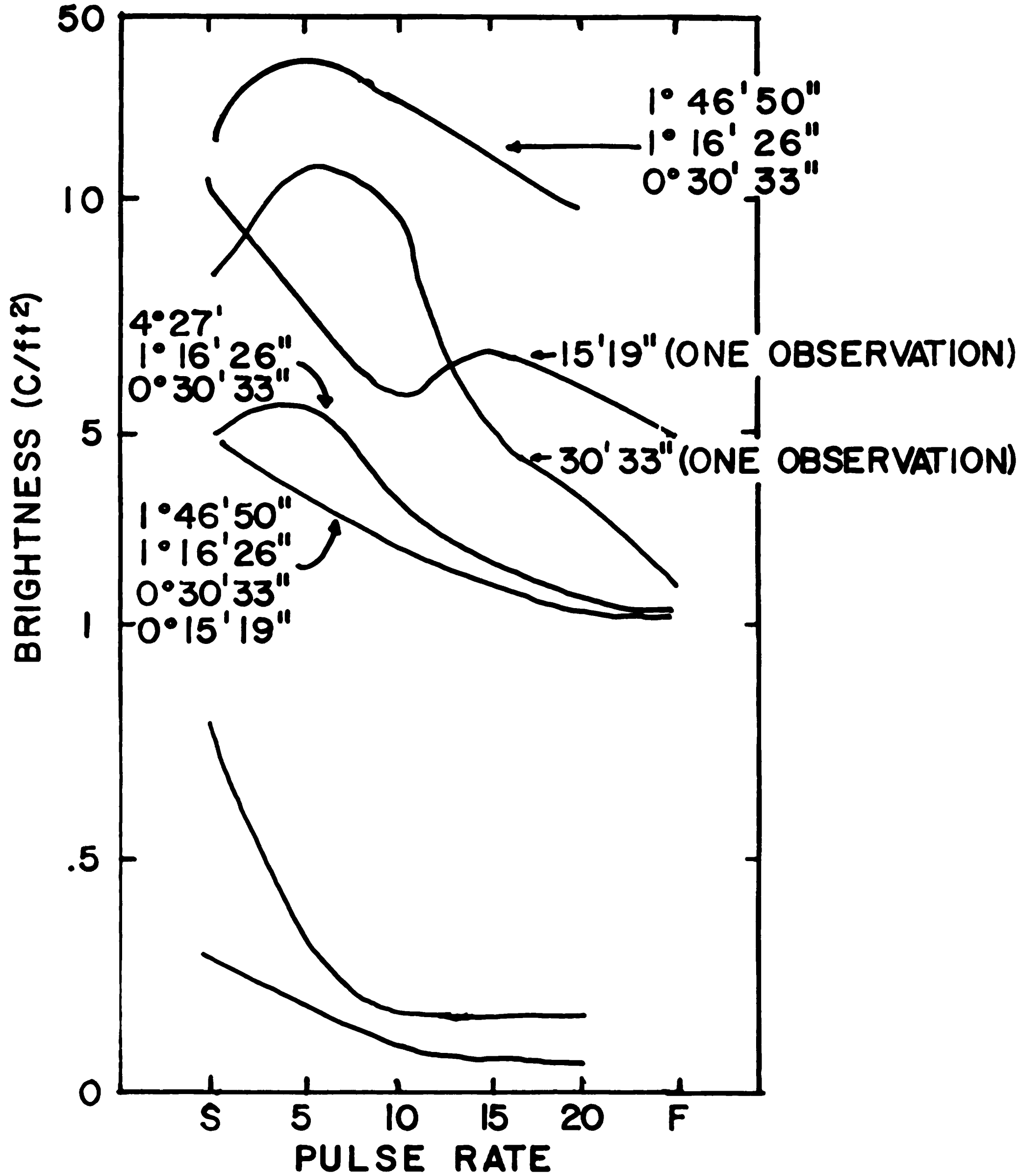

Fig. 16.--Idealized form of curves from Figure 15. The target sizes which produced the curves are indicated in the figure. The data is only for PCF 1/4.

demonstrated that the same subject faced with the same task will sometimes display brightness enhancement and at other times not display it, but since Bartley (10) has shown that not all subjects respond alike, there seems to be no reason why a variation in a population of subjects will not also be reflected, to a certain extent, in the variation from time to time in one subject (23,24,25). In any case the degree of BE at this intensity level is quite small, at most a matter of only 2 c/ft^2.

DISCUSSION

Two sets of hypotheses were involved originally in this study. One set involved the probable influence of target size and intensity on BE, and the other set involved the effect of BE on visual resolution. The former set of hypotheses will be considered first.

The hypotheses were somewhat naively expressed in that the author failed to make a clear distinction between target size and intensity. It will be recalled that the first hypothesis is that small target sizes combined with low intensities will not produce BE at any pulse rate. While this was amply confirmed over the range of target sizes used, it is also probably true that at a sufficiently low intensity no target, no matter how large, will give BE. In the present cases, targets ranging from slightly over four minutes of visual angle to slightly over four degrees of visual angle fail to produce any sign of BE at intensities below about 1 c/ft^2. The perceived brightness of intermittent targets at these low intensities is, with targets subtending less than 30 seconds of visual angle, usually near the Talbot level; whereas with targets subtending larger visual angles intermittent brightness is often, especially at five p/s, in the intermediate range.

The prediction of the alternation-of-response theory that low intensities of target illumination will not produce BE is amply verified. Examining the question of the target size per se we find that the smallest target, i.e., the target subtending 4'20" of visual arc, does not produce enhancement at any of the intensities used in this experiment.

It is, of course, not possible to conclude that there is no intensity level at which this target will provide enhancement but the findings presented here are certainly a strong confirmation of the prediction made by the alternation-of-response theory that small target sizes will not produce BE.

The second hypothesis states that combinations of moderate target size and intensity will produce maximal BE at a pulse rate lower than ten p/s. We must again differentiate the effects due to intensity and the effects due to target size, although we may ignore the smallest targets having disposed of them in the preceeding paragraphs. It is now possible to attach some operational, not to say rational, meaning to the rather indefinite qualifer 'moderate' used in the formulation of the hypothesis.

In the present study a 'moderate' level of intensity seems to be between 1 and 10 c/ft^2. In this range the target subtending 4°27' always produces BE and the enhancement was maximal at 5 p/s. Targets subtending a visual angle of 15 seconds or less never produced BE

whereas targets subtending visual angles intermediate between those mentioned sometimes produced BE and sometimes did not. Whether or not BE occurred intermittent brightness was always above the Talbot level at pulse rates below fusion and was always maximal at 5 p/s. It is thus demonstrated that in some conditions BE is maximal at a pulse rate less than 10 p/s.

The third hypothesis states that large targets and high intensities will produce maximal BE at 10 p/s. Unfortunately it was not possible to use the larger targets at intensities above about 10 c/ft^2 and we must therefore conclude that this hypothesis is not fully explored in the present study, although we know from other work that it is true (5). In the present case all target sizes, always excepting the smallest, produce enhancement when the intensity is around 20 to 30 c/ft^2, but again, as at lower intensities, the maximal brightness is at 5 p/s. We thus see that with the target sizes investigated, all of which were foveal, relatively high levels of target intensity still produce maximal enhancement at 5 p/s. The conclusion which may be tentatively drawn from this data is that foveal targets will always produce maximal intermittent brightness at pulse rates lower than ten per second. The statement must be tentative because, of course, it may well be that targets subtending retinal areas greater than the fovea may also show maximal intermittent brightness at 5 p/s at the intensity levels in

concern here and we have, in fact, seen that this is the case at lower levels of intensities. It is tempting to speculate that the inability to obtain maximum intermittent brightness at 10 p/s with the foveal targets is due to a difference in response of the foveal as opposed to the more peripheral retinal elements. Such speculation however is idle since the question may be answered very easily by further research.

One aspect of BE which does not seem to have been predicted is the finding that at the highest intensity levels used, i.e., about 3 log c/ft^2, no enhancement occurs, whereas at lower intensities it is very much in evidence. Quite probably this finding can be explained by assuming that at such high intensities the neural response is already almost maximal so that intermittency can not effectively act to alter perceived brightness. Some credence is lent to this supposition by experimentation dealing with CFF, visual acuity, and contrast sensitivity in which it was shown that in situations utilizing illuminated targets in dark surrounds, a 'leveling-off' of the tested function occurred at high intensities (7,51). Further it has been demonstrated that if the targets are placed in a surround illuminated at an intensity equal to that of the targets the leveling-off disappears and the functions continue to climb. This suggests the need of utilizing an illuminated surround at high intensity levels in the present experiment, in order to determine whether

the high intensity targets will then produce BE. The outcome of such an experiment is difficult to predict since the alternation-of-response theory states that increasing the amount of stray radiation, which is what the illuminated surround will do, should act to decrease the amount of BE. None the less such experimentation certainly seems worthwhile.

Let us turn now to the hypotheses relating to acuity and intermittent photic stimulation. It will be recalled that the second hypothesis stated that whenever the stimulus conditions produced BE acuity would become worse under those same conditions. This hypothesis is completely supported by the data presented here. In every case in which BE occurred the same stimulus conditions produced a decease in acuity.

The significance of this evidence is simply that the factors which underlie and produce BE also act to adversely affect visual resolving power. As we have seen in earlier sections the occurrence of BE can be taken to indicate a large synchronous neural discharge at the cortical level and perhaps also at the retina. The assumption is that this mode of discharge eliminates the fine gradations in timing and frequency which are necessary in order to have optimal perceptual discrimination.

The first hypothesis concerning acuity and intermittency predicted that in cases where no BE occurred visual acuity would be uneffected. As we have seen there

are several cases in which, when intermittent brightness was in the IR, acuity became worse. Therefore we may conclude that the first hypothesis is not confirmed.

In order to assess the significance of the observation that acuity is adversely effected under the same conditions that produce brightness in the IR we must examine briefly the interpretation of the IR.

It will be recalled that IR is the range in which intermittent brightness is above the Talbot level but below the brightness of the steady illumination. It has been shown in this study and also in numerous other studies (5,7) that brightness in the IR is, in many cases, a much more pervasive phenomena than BE. That is, BE, when it occurs, is usually limited to a relatively narrow range of pulse rates whereas brightness in the IR occurs over a much wider range of pulse rates. Presumably greater or lesser degrees of perceived brightness indicate greater or lesser degrees of synchronized cortical activity. Put another way, maximal BE can be taken to indicate that the visual cortex is responding maximally to each photic pulse; i.e., there is a massive synchronized discharge in the cortex to each input from the retina. As stimulus conditions deviate away from those producing this maximal response the degree of cortical synchronization should become less. Perceptually the lessening of the cortical response should be reflected in a diminishing of subjective brightness. Thus brightness in the IR indicates a degree

of cortical synchronization greater than that produced by a fused or steady source but less than that provided by conditions producing BE.

We may now return to the hypothesis relating acuity to intermittent photic stimulation. The hypothesis stated that acuity would become worse only when BE occurred and would be unaffected when BE did not occur. The hypotheses were stated in this way because it was assumed that the type of discrimination called for was relatively a 'primitive' one and would therefore be disturbed only by a high degree of cortical synchronization. But since acuity is decreased by conditions which provide for intermittent brightness in the IR, we must conclude that it is not necessary for the synchronous nervous discharge to be maximal in order to affect acuity. It would be desireable to make a more exact statement of the relationship between cortical activity and changes in visual resolution but such a statement can be made only after extensive neurophysiological investigation.

Turning to more general considerations we have pointed out that there are two ways in which changes in brightness may affect acuity. Brightness may be altered either by changing intensity or by making the target intermittent. We have seen that in using intermittency, brightness may be either increased or decreased depending upon the conditions of stimulation, i.e., target size, pulse rate, PCF, etc. The question which is now raised is this, how do

the changes in brightness produced by intensity changes affect acuity, as compared to the affects on acuity of brightness changes produced by intermittent stimulation.

We have already partially answered this question by pointing out that whenever the intermittent conditions produced BE, acuity became worse; whereas when the intensity of a steady target was increased so as to yield a 'steady' brightness equivalent to that produced by the intermittent targets, no changes in acuity occurred. Hence in these cases an increase in intermittent brightness did not act in the same way as an intensity increase. The probable reasons for this have already been discussed. It has also been pointed out that in some cases where BE did not occur, but large changes in the intermittent brightness took place, acuity became worse. Again intensity changes in a steady target could not have produced corresponding changes in acuity. Thus in the cases just mentioned alterations in brightness produced by intermittent stimulation act in a different fashion than alterations in brightness produced by intensity manipulations.

When we consider the acuity data pertaining to the small targets however, the outcome is different. With the smallest targets it was found that decreasing intensity aided acuity and raising the intensity worsened acuity. Under intermittent conditions it was found that decreasing brightness improved acuity and that intermittent brightness increases, although in all cases being rather small,

decreased acuity. Thus with the smallest targets intensity and intermittent brightness act in the same way. However these data are not conclusive because in the other circumstances mentioned in the preceeding paragraph the findings are much the same; i.e., reducing pulse rate, which serves to increase intermittent brightness, also causes a decrease in acuity. In other words, when pulse rate is reduced intermittent brightness is increased; this increase in brightness may affect acuity in the same way as an intensity increase, or if the increased brightness causes a sufficient degree of neural synchronization, this synchronization may affect acuity. It is possible that both factors may operate together but such a contingency is unlikely since, in fact, intermittent acuity never becomes much worse than steady acuity whereas if both factors were working together we would expect a large decrement in intermittent acuity.

It is possible to clarify the issue somewhat by refering to the low intensity condition with the medium target sizes. It will be recalled that in those circumstances a drop in intensity would adversely affect acuity and it was also found that decreasing brightness by means of intermittency caused a decrease in acuity. However, as pulse rate was reduced from the fusion frequency there was no marked increase in acuity although the increased brightness provided by the reduction in pulse rate should have acted in that direction. Presumably the small amount

of neural synchronization produced by reducing pulse rate worked against any increase in acuity that might be caused by brightness increases per se.

The assumption underlying this discussion is that intermittent brightness may be affected by factors other than an increase in synchronous neural discharge. But it is, in fact, not necessary to assume that brightness is affected, but only to assume that in some cases where the degree of neural synchronization is not great that decreasing the pulse rate may aid visual discrimination. For example a decrease in pulse rate from 20 to 5 p/s increases the pulse length by a factor of four. Thus with PCF 1/4, reducing the pulse rate from 20 p/s to 5 p/s increases the pulse length from 12.5 ms to 50 ms. The increase in length of the pulse may act to improve, i.e., make finer, visual discrimination as suggested in the work on critical duration (20,32,33,34,50). Such speculations can only be checked by neurophysiological investigation.

An additional point should be made in reference to the work just cited (20,32,33,34,50). In these studies it was found that if the exposure time of the stimulus was dropped below a certain critical value it was necessary to increase the intensity of the stimulus to produce a visual effect equivalent to that yielded by a longer exposure time. In other words dropping exposure time below a critical value adversely affects visual discrimination.

These findings have little relevance to the present study, except in the context mentioned above, since in the present study, discrimination is adversely affected at the longer rather than the shorter pulse rates.

To conclude and summarize it may be said that several predictions of the alternation-of-response theory have been verified in this study. It was found that larger targets produce more BE than smaller targets and that BE will occur at lower intensities with the larger targets than with the smaller. It was also found that the smallest target used did not produce BE at all.

Concerning the effect of intermittency on visual resolution we may say that conditions which produce BE will adversely affect visual acuity. With the technique used in this study we have also seen that in some cases in which BE does not occur, but where the intermittent stimulus conditions produce brightness in the IR, acuity is worsened. The implication to be drawn is that a high degree of synchronization of neural impulses in the cortex act to eliminate the fine gradations in neural timing or frequency which in ordinary circumstances provide a basis for some forms of perceptual discrimination. In some cases the changes in brightness produced by intermittency acted in the same way as did brightness changes produced by manipulating intensity. This is believed to occur when intermittent stimulation produces only a very small degree of cortical synchronization.

SUMMARY

Under the proper conditions sub-fusional intermittent photic stimulation produces a level of perceived brightness greater than continuous illumination of the same intensity level. This is called brightness enhancement (BE). To account for this and other related phenomena the alternation-of-response theory has been put forward. The theory maintains that with adequate target size and luminosity sub-fusional photic pulses tend to produce a large synchronous discharge of cortical neurons. It was hypothesized that a neuronal discharge of this type would also act to destroy the neural timing and interaction believed to be necessary for fine visual resolution.

The hypothesis was tested by using two illuminated targets in an otherwise dark field. The targets, when overlapped provided a uniform visual surface. The targets were adjusted away from one another until the observers perceived a gap between them. By comparing the change in gap-size from continuous to intermittent illumination relative changes in visual resolution could be measured. Brightness matches were obtained by having the observers adjust a continuously illuminated target of the same size as the acuity targets to an intensity which would equal the brightness of the acuity targets.

Brightness matches, over the intensity range used, demonstrated that larger targets produce more BE than smaller targets, and also that BE will occur at lower intensities with the larger targets. In all cases in the present experiment BE was found to be maximal at 5 pulses/second. At the highest intensity used (about 1500 c/ft^2) BE failed to occur even though the same target sizes had provided BE at lower intensities. Whenever the stimulus conditions produced BE the same stimulus conditions adversely affected visual resolution. In some cases visual resolution was also adversely affected by conditions which provided for intermittent brightness at a level somewhat lower than that afforded in BE. Explanations have been discussed and areas for further research indicated.

BIBLIOGRAPHY

1. Allen, F. "The Visual Apparatus as an Optical Instrument," Sci. Mon., 72, (1951), 71-74.

2. Barlow, H. B., Fitzhugh, R., and Kuffler, S. W. "Resting Discharge and Dark Adaptation in the Cat," J. Physiol., 125, (1954), 28p-29p.

3. Barlow, H.B., Fitzhugh, R., and Kuffler, S.W. "Change of Organization in the Receptive Fields of the Cats Retina During Light and Dark Adaptation," J. Physiol. 137, (1957), 338-54.

4. Bartley, S.H. "Temporal and Spatial Summation of Extrinsic Impulses with the Intrinsic Activity of the Cortex," J. Cell. Comp. Physiol., 8, (1936), 41-62.

5. Bartley, S.H. "Some Effects of Intermittent Photic Stimulation," J. Exp. Psychol., 25, (1939), 462-80.

6. Bartley, S.H. "Some Factors in Brightness Discrimination," Psychol. Rev., 46, (1939), 337-58.

7. Bartley, S.H. Vision. New York: D. Van Nostrand Company, Inc., 1941.

8. Bartley, S.H. "Visual Sensation and its Dependence on the neurophysiology of the Optic Pathway," Biol. Symposia, 7, (1942), 87-106.

9. Bartley, S.H. "B.E. in Relation to Target Intensity," J. of Psychol., 32, (1951), 57-62.

10. Bartley, S.H. "Intermittent Photic Stimulation at Marginal Intensity Levels," J. of Psychol., 32, (1951), 217-23.

11. Bartley, S.H. "Some Facts and Concepts Regarding the Neurophysiology of the Optic Pathway," A.M.A. Archives of Ophthal. Part II, 60, (1958), 775-91.

12. Bartley, S.H. "A Clarification of Some of the Procedures and Concepts Involved in Dealing with Optic Pathway," The Visual System: Neurophysiology and Psychophysics, (Symposion Freiborg, 1960, Verlag/ Berlin).

13. Bartley, S.H. "Central Mechanisms of Vision," Handbook of Neurophysiology, Chap. XXX, 713-40.

14. Bartley, S.H., Nelson, T. "Certain Chromatic and Brightness Changes Associated with Rate of Intermittency of Photic Stimulation," J. Psychol., 50, (1960) 323-32.

15. Bartley, S.H., Nelson, T.M., and Ranney, J. "The Sensory Parallel of the Reorganization Period in the Cortical Response in Intermittent Retinal Stimulation," J. Psychol. 52, (1961), 137-47.

16. Bartley, S.H., Paczewitz, G., and Valsi, E. "Brightness Enhancement and the Stimulus Cycle," J. of Psychol., 43, (1957), 187-92.

17. Bartley, S.H. and Wilkinson, E. "Brightness Enhancement When Entoptic Stray Light is Held Constant," J. Psychol., 33, (1952), 301-305.

18. Battig, W.F., Voss, J.F., and Brogden, W.J. "The Effect of Frequency of Target Intermittence upon Tracking," J. Exp. Psychol., 49, (1955), 244-48.

19. Battig, W.F., Voss, J.F., and Brogden, W.J. "Effect of Frequency of Intermittence upon Perceived Brightness," J. Comp. Physiol. Psychol., 50, (1957), 61-64.

20. Booman, M.A. and Van Der Verlden, H.A. "The Two Quanta Explanation of the Dependence of the Threshold Values and Visual Acuity on the Visual Angle and the Time of Observation," J. of Opt. Soc. of Amer., 37, (1947), 908-19.

21. Bridgeman, C.S. and Smith, K.V. "The Absolute Threshold of Vision in Cat and Man with Observation on its Relation to the Optic Cortex," Amer. J. Physiol., 136, (1942), 463-73.

22. Cobb, P.W. "The Influence of Pupillary Diameter on Visual Acuity," Amer. J. Physiol., 36, (1915), 335-346.

23. Crozier, W.J., Wolf, E., and Zerrahn-Wolf, G. "On Critical Frequency and Critical Illumination for Response to Flickered Light," J. Gen. Physiol., 20, (1936), 211-28.

24. Crozier, W.J., Wolf, E., and Zerrahn-Wolf, G. "Critical Illumination and Critical Frequency for Response to Flickered Light in Dragon Fly Larvae," J. Gen. Physiol., 20, (1936), 363-92.

25. Crozier, W.J. and Wolf, E. "Theory and Measurement of Visual Mechanisms IV. Critical Intensities for Visual Flicker, Monocular and Binocular," J. Gen. Physiol., 24, (1941), 505-33.

26. Crozier, W.J. and Wolf, E. "Theory and Measurement of the Visual Mechanisms X. Modifications of the Flicker Response Contour and the Significance of the Avian Pectin," J. Gen. Physiol., 27, (1944), 287-313.

27. Crozier, W.J. and Wolf, E. "Theory and Measurement of the Visual Mechanisms XI. On Flicker with Subdivided Fields," J. Gen. Physiol., 27, (1944), 401-32.

28. Fincham, W.H.A. Optics. Sixth Edition. London: Hatton Press Ltd., 1951, pp 426.

29. Fitzhugh, R.A. "A Statistical Analyser for Optic Nerve Messages," J. Gen. Physiol., 41, (1958), 675-692.

30. Fry, G.A. Blur of the Retinal Image. Columbus: Ohio State University Press, 1955, pp 120.

31. Gerathewohl, S.J. and Taylor, W. "Effect of Intermittent Light on the readability of Printed Matter under Conditions of Decreasing Contrast," J. Exp. Psychol., 46, (1953), 278-82.

32. Graham, C.H. and Margaria, R. "Area and the Intensity-time Relation in the Perpheral Retina," Amer. J. Physiol., 113, (1935), 299-305.

33. Graham, C.H. and Kemp, E.H. "Brightness Discrimination as a Function of the Duration of the Increment in Intensity," J. Gen. Physiol., 21, (1938), 635-650.

34. Graham, C.H. and Cook, C. "Visual Acuity as a Function of Intensity and Exposure Time," Amer. J. Psychol., 49, (1937), 654-661.

35. Granit, R. Receptors and Sensory Perception. New Haven: Yale University Press, 1955, pp 366.

36. Grusser, O.J., and Creutzfelft, O. "Eine Neurophysiologische Grundlage des Brucke-Bartley-Effektes: Maxima der Impulse-frequenz Retinaler und Corticaler Neurone bei Flimmerlickt Mittlerer Frequenzen," Pflugers Archiv fur Ges. Physiol., 263, (1957), 668-681.

37. Gulick, W.L. "Brightness Enhancement with Microsecond Pulses," Psychol. Rec., 11, (1961), 249-56.

38. Halstead, E.C., Knox, G.W., Wooly, J.L., and Walker, A. "Effects of Intensity and Wave Length on Driving Cortical Activity in Monkeys," J. Neurophysiol., 5, (1942), 483-86.

39. Hartline, H.K. "The Receptive Fields of Optic Nerve Fibers," Am. J. Physiol., 130, (1940), 690-99.

40. Hartline, H.K. and Ratliff, F. "Inhibitory Interaction of Receptor Units in the Eye of Limulus," J. Gen. Physiol., 40, (1957), 357-76.

41. Hartline, H.K., Wagner, H.g., and Ratliff, F. "Inhibition in the Eye Limulus," J. Gen. Physiol., 39, (1956), 651-73.

42. Hartridge, H. Recent Advances in the Physiology of Vision. London: J. & A. Churchil Ltd., 1950, pp 401.

43. Hebb, D.O. The Organization of Behavior. New York: John Willey & Sons Inc., 1949, pp 335.

44. Hecht, S. Vision:II. The Nature of the Photoreceptor Process. in C. Murchison (Ed.). Handbook of Experimental Psychology. Worchester, Mass.: Clark University Press, 1934, pp 704-829.

45. Hecht, S. and Mintz, E. "The Visibility of Single Lines at Various Illuminations and the Retinal Basis of Visual Resolution," J. Gen. Psychol., 22, (1939), 593-611.

46. Hylkema, B.S. "Fusion Frequency with Intermittent Light under Various Circumstances," Acta Ophthal., 20, (1942), 180.

47. Kuffler, S.W., Fitzhugh, R., and Barlow, H.B. "Maintained Activity in the Cats Retina in Light and Darkness," J. Gen. Physiol., 40, (1957), 683-702.

48. LeGrand, Y. Light, Color and Vision. New York: Dover Publications, Inc., 1957, pp 512.

49. Marshall, W.H. and Talbot, S.A. "Recent Evidence for Neural Mechanisms in Vision Leading to a General Theory of Sensory Activity," Biol. Symp., 7, (1942), 117-64.

50. McDougall, W. "The Variation of the Intensity of Visual Sensation with the Duration of the Stimulus," Brit. J. Psychol., 1, (1904), 151-189.

51. Moon, P. The Scientific Basis of Illuminating Engineering. New York: Dover Publications, Inc., 1961, pp 608.

52. Nachmais, J. "Brightness and Visual Acuity with Intermittent Illumination," J. of Opt. Soc. of Amer., 48, (1958), 726-30.

53. Nelson, T. and Bartley, S.H. "The Role of PCF in Temporal Manipulations of Color," J. Psychol., 52, (1961), 457-77.

54. Nelson, T. Bartley, S.H., and DeHardt, D. "A Comparison of Variability of Three Sorts of Observers in a Sensory Experiment," J. Psychol., 49, (1960), 3-11.

55. Nelson, T., Bartley, S.H., and Mackavey, W. "Responses to Certain Pseudoisochromatic Charts Viewed in Intermittent Illuminance," Perceptual and Motor Skills, 13, (1961), 227-31.

56. Ochs, S. "Organization of Visual Afferents Shown by Spike Component of Cortical Response," J. Neurophysiol., 22, (1960), 2-15.

57. Polyak, S. The Vertebrate Visual System. Edited by H. Kluver. Chicago: University of Chicago Press, 1957.

58. Ronchi, V. Optics the Science of Vision. Translated and revised by E. Rosen. New York: New York University Press, 1957.

59. Ruch, T.C. Physiology and Biophysics. Edited by T.C. Ruch and J.F. Fulton. Philadelphia: W.B. Saunders Company, 1960, Chapters 7,8,19,20.

60. Senders, V.L. "Visual Resolution with Periodically Interrupted Light," J. Exp. Psychol., 39, (1949), 453-65.

61. Senders, V.L. "On Reading Printed Matter with Interrupted Light," J. Exp. Psychol., 47, (1954), 135-36.

62. Shlaer, S. "The Relation Between Visual Acuity and Illumination," J. Gen. Physiol., 21, (1937), 165-88.

63. Shlaer, S., Smith, E.L., and Chase, A.M. "Visual Acuity and Illumination in Different Spectral Regions," J. Gen. Physiol., 25, (1942), 553-69.

64. Shortley, G. and Williams, D. Elements of Physics. Second Edition. New York: Prentice-Hall Inc., 1955, 375-541.

65. Smith, K.V. "The Postoperative Effects of Removal of the Striate Cortex upon Certain Unlearned Visually Controlled Reactions in the Cat," J. Genet. Psychol., 50, (1937), 137-56.

66. Southall, J.P.C. Introduction to Physiological Optics. New York: Dover Publications Inc., 1961.

67. Steinhardt, J. "Intensity Discrimination in the Human Eye I the Relation of I/I to Intensity," J. Gen. Physiol., 20, (1936), 185-209.

68. Walls, G.L. The Vertebrate Eye. Bloomfield Hills: The Cranbrook Press, 1942, pp 785.

69. Weymouth, F.W. "Visual Sensory Units and the Minimal Angle of Resolution," Amer. J. Ophthal., 46, (1958), 102-113.

70. Wilcox, W. "The Basis of the Dependence of Visual Acuity on Illumination," Proc. Nat. Acad. Sci., 18, (1932), 47-56.