# VISUALLY EVOKED RESPONSES AND REACTION TIMES IN MAN: EFFECTS OF INTEROCULAR AND INTRAOCULAR DISPARITY

by

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Interocular and intraocular inhibitory effects on visually evoked responses (VERs) and reaction times (RTs) in man as a function of the degree of retinal disparity were studied. Evoked potentials were recorded with scalp electrodes located on the midline and 2.5 cm to the right of the midline over the occipital area. An evoking stimulus (a transient light flash) was always viewed by the right eye while a steadily illuminated stimulus (the "inhibitory" stimulus) was viewed by either the left eye (interocular condition) or the right eye (intraocular condition).

Three hypotheses were proposed: First, that the overall amplitude of the VER would decrease and reaction time would increase when the distance between the retinal points being stimulated by the continuous stimulus and the transient stimulus is reduced; second, that the inhibitory effect would be interocular in nature; and third, that, due to the stronger inhibitory effects within the central receptive fields, the VER to foveal stimulation should more readily attenuate and RT more readily increase as the degree of disparity is decreased between the continuous and transient stimuli than would be the case if the two types of stimulation are shifted to more peripheral retinal receptive fields where inhibitory effects are less strong.

Consistent with the hypotheses, it was found that the overall amplitude of the VER was smaller when corresponding retinal points were stimulated, that the effects were more specific in the foveal rather than the peripheral retina, and that the effect was interocular. In addition, the effects were also found to be intraocular in nature.

The results of the present investigation only partially support the findings of various animal single unit investigations conducted at the cortical level concerning the effects of stimulating corresponding and noncorresponding retinal points, but show an interesting parallel to those investigations dealing with the effect at the level of the lateral geniculate nucleus.

Two mechanisms were suggested to account for the results of the present investigation: occlusion and lateral inhibition. Since the inhibitory effects occurred interocularally and intraocularally, it was suggested that the mechanism(s) responsible for such effects operated beyond the retinal ganglion cell level, most likely at the lateral geniculate nucleus.

In addition, the results of the present investigation suggested that foveal retina receptive fields are smaller than receptive fields in the peripheral retina, and that the inhibitory effects within foveal receptive fields are stronger than those in peripheral receptive fields.

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## Introduction

Suzuki and Kato (1966), using electrical stimulation of the optic nerves, reported that 49% of the geniculate cells studied were binocularly inhibited by the stimulation of the non-dominant eye optic nerve. Prior to this investigation it was commonly thought that there was a complete segregation of retinal inputs into the main lamina of the lateral geniculate nucleus (LGN), most units being, therefore, monocular in nature (Bishop, Burke, & Davis, 1959; Bishop, Kozak, Levick, & Vakkur, 1963; Hubel & Wiesel, 1965). Singer (1971) reported marked inhibition of spike activity in 78% of the LGN cells examined when a black or white bar was moved across the corresponding receptive field of the non-dominant eye. Sanderson, Bishop, and Darian-Smith (1971) found similar effects in 72% of the LGN cells investigated. In that investigation, these cells had receptive fields located in each eye at approximately corresponding retinal points. The majority of the cells had concentric receptive fields for the dominant eye, with an excitatory center and an inhibitory surround; while, at the same time also had an inhibitory receptive field for the non-dominant eye. The demonstrated inhibitory effect was, however, generally weak and was presumably mediated by interneurons having axons that crossed from one lamina to another within the LGN.

The binocular interaction in response to stimulation of binocular receptive fields of the LGN neurons reported by Sanderson, et al. (1971) was neither facilitatory nor sensitive to stimulus orientation, and did not, therefore, provide information pertaining to the question of binocular summation which is, presumably, mediated by cortical mechanisms. Barlow, Blakemore, and Pettigrew (1967), and others (Bishop, Henry, & Smith, 1970; Minke & Auerbach, 1972; Pettigrew, Nikara, & Bishop, 1968) have reported that cortical cells with binocular receptive fields respond maximally to the stimulation of slightly noncorresponding retinal points with patterns of optimal size and orientation. Less than maximal responses were found when corresponding or extremely noncorresponding retinal points were stimulated. (Barlow, et al., 1967; Bishop, et al., 1970; Pettigrew, et al., 1968).

A mechanism similar to this could account for binocular inhibition in pattern-related visually evoked response (VER) investigations dealing with the presentation of noncorresponding patterns to the same retinal points in man (Harter, Seiple, & Salmon, 1972). Harter (1972) points out that the previously mentioned single unit investigations indicate that the noncorrespondence of points of retinal stimulation is possibly "the critical variable determining the nature of binocular interaction (facilitation vs. inhibition)" as evidenced by VERs. Regan and Spekreijse (1970), Fiorentini

and Maffei (1970), and Harter, et al. (1972) have made similar suggestions. It can be noted that this variable has not been investigated in any systematic manner in human VER studies (Regan, 1972).

Some evidence from pattern-related VER investigations suggests that the stimulation of corresponding retinal areas in man produces an inhibition of VER amplitude (Cobb, Ettlinger, & Morton, 1968; Van der Tweel, Spekreijse, & Regan, 1970b) when a stationary patterned stimulus is presented to a portion of one eye's visual field while the remaining portions of that eye, and the entire visual field of the other eye were stimulated with a reversing patterned stimulus. Other investigators, however, suggest that an enhancement in the amplitude of the VER occurs when corresponding retinal points are stimulated (Cignaek, 1971; Harter, et al., 1972). In the investigation conducted by Harter, et al. (1972), for example, the dichoptic presentation of lines and grids to corresponding retinal areas evoked VERs with some components of smaller amplitude than did the dioptic presentation of identical stimulus patterns. To date, however, few investigations have dealt with the effects of varying the degree of correspondence of retinal points stimulated in man on the VER using restricted focal stimulation.

Harter (1970, 1971), and Harter and White (1968, 1970) have pointed out that the stimulus element sizes which

correspond to those which elicit the optimal stimulation of retinal ganglion cell receptive fields in animals also elicits maximal amplitude VERs in humans. Non-optimal stimulation with large stimuli elicits VERs of lesser amplitude which is believed to be due to increased amounts of lateral inhibition occurring within the receptive fields. The traditional definition of a receptive field states that it is an area of retinal surface which, when stimulated, elicits a response in the cell being investigated (Hubel & Wiesel, 1962). At any given retinal location, however, many different receptive fields of varying size, layout, and shape may coexist (Thomas, 1970).

Pattern-related VER studies in man have suggested that the receptive fields of ganglion cells in the macular region of the retina are relatively small, having centers with diameters of approximately 10' to 30' of arc subtense (Harter, 1970, 1971; Harter & White, 1968, 1970; Jeffreys, 1969; MacKay, 1969; MacKay & Jeffreys, 1969; Regan, 1972, pp. 59-61; Regan & Richards, 1971; Rietveld, Tordoir, Hagenouw, Lubbers, & Spoor, 1967; Spekreijse, 1966; Van der Tweel, Regan, & Spekreijse, 1970a). Various stimulus manipulations, however, appear to influence the size of both the center and surrounding portions of a receptive field in both man and animals (Barlow, Fitzhugh, & Kuffler, 1957; Glezer, 1965; Hallett, 1963; Ikeda & Wirght, 1971, 1972; Kuffler, 1952, 1953; Levick, Oyster, & Davis, 1965; McIlwain, 1964, 1966).

In addition, both the size of receptive field centers and surrounds appear to increase in a somewhat linear fashion with retinal eccentricity in animals (Enroth-Cugell & Robson, 1966; Fischer & May, 1970; Hubel & Wiesel, 1965; Leicester & Stone, 1967; Wiesel, 1970; Wiesel & Hubel, 1966), and there appears to be a correlation between changes in receptive field size and variations in the convergence of receptors onto ganglion cells with eccentricity (Ikeda & Wright, 1972; Stone, 1965). Pattern-related VER studies suggest that the same relationship exists in the human retina (Harter, 1971). It may also be noted that the inhibitory effects within central receptive fields have been found to be somewhat stronger than similar effects in more peripheral retinal receptive fields in animals (Cleland, Dubin, & Levick, 1971; Ikeda & Wright, 1972).

The present investigation deals with how VERs and reaction times to intermittent stimulation of one retinal point are influenced by continuous stimulation of adjacent retinal points in man as a function of (a) the distance between the points of retinal stimulation, (b) whether the two stimuli are presented to the foveal or peripheral retina, and (c) whether both stimuli were presented to the same eye (monoptic stimulation) or one was presented to one eye and the other to the other eye (bioptic stimulation).

While acknowledging the risk of overgeneralizing from animal single unit investigations to human VER

investigations, and assuming, as Creutzfeldt, Rosina, Ito, and Probst (1969) and Minke and Auerbach (1972) point out, that gross slow potentials and single unit activity are systematically related, several basic predictions can be made on the basis of the single unit, human psychophysical, and VER investigations cited above: First, when the distance between the points of retinal stimulation is reduced, a reduction in the overall amplitude of the VER and an increase in reaction time is expected to occur since the continuous stimulation of one eye in response to stimulation of corresponding retinal points in the other eye has been found to inhibit single unit activity in animals and lead to a reduction of the amplitude of the VER in humans; second, if the inhibitory effect is binocular in nature, as suggested by animal (Sanderson, et al., 1971; Singer, 1971), and human (Cobb, et al., 1968; Van der Tweel, et al., 1970b) studies, binocular (bioptic) viewing conditions should show the suggested inhibitory effect on both VERs and reaction time; and third, the VER and reaction time to foveal stimulation should more readily attenuate and increase respectively due to the inhibitory effects than the VER elicited by peripheral stimulation since the inhibitory effects within centrally located retinal receptive fields have been found to be stronger than those found in more peripheral retinal receptive fields.

## Method

### Experimental Design

The experimental design for this investigation is presented in Table 1. The independent variables of the experiment were: (a) electrode recording positions ($O_Z$ and $O_2$), (b) eccentricity of retinal stimulation (foveal vs. $5^o$ eccentricity), (c) behavioral task (reaction time vs. count), (d) stimulus presentation, or viewing conditions (monoptic vs. bioptic), and (e) the distance of retinal stimulation of the steady (constant) stimulus above or below the fixed flashing stimulus (+50', +30', +20', +10', 0', -10', -20', -30', -50' of arc subtense respectively). The various distances were presented in orders 1 or 2 according to the presentation order designated in Table 2. The latter variable will be expressed in terms of min of arc of noncorrespondence since this measure is appropriate for the bioptic viewing conditions. The $O_2$ electrode position was selected because evidence has been presented indicating that binocular interaction in humans may be mediated in the right cerebral hemisphere (Benton & Hecaen, 1970). The $O_Z$ electrode position was selected because it overlies the foveal projection location of both fovea on visual cortex.

Two tasks were employed (reaction time and counting) in order to obtain an overt behavioral measure of the effects

# TABLE I

## EXPERIMENTAL DESIGN

| RECORDING POSITION | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $O_z$ | | | | | | | | $O_2$ | | | | | | | |
| ECCENTRICITY | | | | | | | | | | | | | | | |
| 0° | | | | 5° | | | | 0° .. | | | | 5° | | | |
| BEHAVIORAL MEASURE | | | | | | | | | | | | | | | |
| RT | | C | | RT | | C | | RT | | C | | RT | | C | |
| VIEWING CONDITIONS | | | | | | | | | | | | | | | |
| B | M | B | M | B | M | B | M | B | M | B | M | B | M | B | M |
| STIMULUS PRESENTATION ORDER | | | | | | | | | | | | | | | |
| 1 2 1 2 1 2 1 2 | | | | | | | | 1 2 1 2 1 2 1 2 | | | | | | | |
| 1 2 1 2 1 2 1 2 | | | | | | | | 1 2 1 2 1 2 1 2 | | | | | | | |

Note.--Stimulus presentation orders are also replications of a given experimental condition.

# TABLE 2

## STIMULUS PRESENTATION ORDER

| STIMULUS PRESENTATION ORDER | NONCORRESPONDENCE (MIN OF ARC) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | C | 50 | 30 | 20 | 10 | 0 | -10 | -20 | -30 | -50 |
| | -50 | -30 | -20 | -10 | 0 | 10 | 20 | 30 | 50 | C |
| 2 | 0 | -10 | -20 | -30 | -50 | C | 50 | 30 | 20 | 10 |
| | 10 | 20 | 30 | 50 | C | -50 | -30 | -20 | -10 | 0 |

Note.--C refers to the control condition.

of the constant stimulus light and in order to ascertain through an implicit response measure that the results were not contaminated by the overt reaction task. The dependent measures were VER amplitude, as measured by the absolute integral of the amplitude of the VER over a period of 448 msecs after stimulation, and the median reaction time in response to each of the experimental conditions.

For the major part of the experiment, four subjects participated in eight experimental sessions plus one control session. Electro-oculograms were recorded during the control session to insure that any unwanted eye movements did not contaminate the data. Subjects were also instructed how to minimize eye movement artifacts. An experimental session consisted of the presentation of any two of the 16 trial blocks found in Table 1 while recording simultaneously from electrode positions designated $O_Z$ and $O_2$. For example, one series of conditions consisted of the subject fixating foveally ($0^o$) while performing a reaction time task (RT), and viewing the stimulus display bioptically (B) when the distance between the stimuli was varied as indicated by order 1 in Table 2. This sequence constituted one trial block. In the second trial block of the session, the subject may have been required to fixate the peripheral fixation light ($5^o$), count (C) the number of stimulus flashes, and view the display monoptically (M) while the stimuli were presented according to order number 2.

The presentation order of the trial blocks between subjects was completely randomized with the restrictions that no two subjects received the same experimental trial blocks on the same day, nor did any subject receive a replication (presentation orders 1 and 2) of a specific condition on any one day.

The presentation order of the nine levels of noncorrespondence, expressed in terms of min of arc, and the control condition (the presentation of the evoking stimulus alone) for each trial block for replications 1 and 2 is presented in Table 2. Sixteen stimulus presentations occurred at each position designated in Table 2, so that, within a single replication, a total of 32 stimulus presentations per position of noncorrespondence and the control condition occurred. When replications 1 and 2 were combined a total of 64 stimulus presentations contributed to a single VER.

Subjects

Seven subjects from the age of 22 to 33 participated in the experiment. Four subjects (DS, RH, MM, CS) were selected to participate in all of the conditions of the experiment specified above, while the three additional subjects participated in a selected aspect of the investigation to further test the generality of the results. The refractive error for each subject was checked and corrected. All subjects had binocular visual acuities of 20/20 or better at

the time of the experiment. Of the four main subjects, only the author (DS) had not participated in evoked potential investigations prior to the start of this experiment.

Apparatus

The subjects were seated in an electrically shielded partially light- and sound-proofed 8' X 12' cubicle. The subjects were light-adapted and the illumination level of the room was .29 mL. The two stimulus displays (one for each eye) were binocularly fused by means of an American Optical Company Phoropter (Model No. 590 PC). The visual field was divided in half by a 27.5 X 225 cm black partition which extended from the center of the Phoropter to a point between the two stimulus displays. The display viewed by each eye contained a cross-like configuration composed of a series of 0.5 cm holes spaced at a distance of 0.75 cm, or 10' of arc subtense, from center to center. Eleven holes were placed in each horizontal and vertical components of the cross.

The flashing (evoking) light was presented in the central hole of the cross and was always viewed by the right eye. The steadily illuminated (constant) light was presented at various positions on the vertical portion of the cross, and was viewed by either the right (monoptic conditions) or left (bioptic conditions) eye. These two lights, subtending 2.86' of arc, were presented by means of fiber optics which

were inserted into the desired holes from the rear of the display. The evoking flashes, generated by a Grass PS-2 photostimulator, had a luminance level of 9.65 mL, a duration of 10 usec, and were presented aperiodically on a random interval schedule with a mean interval of 1.25 sec. The constant illumination light had a luminance level of 2.74 mL and was generated by an incandescent light. Both the light flashes and the constant light source were presented to the end distal to the display.

Eccentricity of stimulation was controlled by having the subjects fixate either the center of the crosses ($0^{o}$ eccentricity) or a point of light located $5^{o}$ to the right of the central portion of the cross ($5^{o}$ eccentricity). The entire stimulus display was back-illuminated with a dim incandescent light having a luminance level of 1.69 mL. This permitted the holes forming the crosses, except those containing the fiber optics, and the eccentric fixation point light source to serve as fixation references. Each of the peripheral fixation points subtended 1.5' of arc, and were easy to fixate. Prisms of 7.0 and spherical lenses of +0.25 D were positioned in the Phoropter so as to permit binocular fusion of the two displays at approximately optical infinity.

A Grason-Stadler 901B noise generator provided sufficient white noise (63 dB SPL) to mask extraneous auditory stimuli. The same noise generator served to produce an

auditory feedback click of 68 dB SPL whenever the subject failed to make a key-release response within the 500 msec interval following flash presentation under the reaction time conditions of the experiment.

Visually evoked responses were recorded monopolarly from the surface of the scalp with the active electrodes placed 2.5 cm above the inion ($O_Z$) along the midline, and 2.5 cm to the right of this electrode from the midline ($O_2$). The reference electrode was attached to the right earlobe. Electroencephalograms (and electro-oculograms during the control session) were amplified by a Grass 7WC polygraph with the $\frac{1}{2}$ amplitude high and low frequency filters set at 35 and 1 Hz respectively. Ongoing brain activity was monitored on a Dumont 708 A oscilloscope and the Grass Model 7WC polygraph.

A Computer Automation Alpha 16 mini-computer was set to sample and store 448 msecs of activity following stimulus onset. Each of the 10 channels of the computer was divided into three data arrays so that records of the VERs recorded from positions $O_Z$ and $O_2$, and the reaction time frequency distributions could be stored simultaneously. The number of stimulus presentations per position of noncorrespondence was controlled by a Lehigh Valley predetermining counter set at 16. The recorded information was displayed on a Tektronix Type RM 504 oscilloscope, photographed, and punched onto paper tape for future data analysis.

A key-release reaction time response initiated a pulse-former which generated a seven msec square pulse. This pulse was recorded in the appropriate data bin of the computer which corresponded to the latency of the reaction time response. Reaction time responses were accumulated and stored in the computer to form the reaction time distribution, and, at the end of each trial block punched onto paper tape for future data analysis.

Procedure

Prior to the start of the investigation the correct interocular distance and necessary corrective spherical and cylindrical lenses for each subject were determined. These values were used throughout the experiment, and prior to each experimental session the Phoropter was checked to insure that the proper lenses and interocular distance for a particular subject were in position. Electrodes were placed on the scalp at positions $O_Z$ and $O_2$, care being taken to insure that skin resistance was 10,000 ohms or less, before the subject entered the experimental chamber. Subjects were then given instructions concerning the proper fixation point and behavioral task for the trial block to be presented.

A preview of ongoing electrical activity of the subject was monitored on both a Grass 7WC polygraph and a Dumont 708 A oscilloscope. The onset of white noise signaled the beginning of a stimulus trial, and preceded the onset of the

stimulus presentation by 5 secs. The evoking stimulus was then presented 16 times. The order of stimulus presentation for the steadily illuminated light was determined by the order established in Table 2. Two trial blocks were presented in each experimental session. A single trial block lasted approximately 15 min, and an entire experimental session lasted approximately 45 min. The subjects were allowed a 15 min break between trial blocks. Since the experimental conditions changed between trial blocks it was necessary to reinstruct the subject concerning fixation point and behavioral task prior to the beginning of each trial block. The recorded VER and reaction time information was punched onto paper tape for later data analysis.

The data were arranged into 30 data arrays for each trial block. Given that 10 arrays were needed for sorting the nine positions and control condition, 20 arrays were allotted for the VERs recorded at positions $O_Z$ and $O_2$, and 10 arrays were allotted for the reaction time distributions. Each trial block, which also constituted a single replication of a given experimental condition, was stored separately on paper tape and later combined with the second replication for data analysis. The combined replications were analyzed in the following manner: First, for the VER data, the algebraic integral of the amplitude of the entire VER recorded during the 448 msecs following stimulus onset was found in the Alpha 16 computer and used as the zero baseline

voltage for the VER. Following the determination of the baseline, the absolute integral over the 448 msec interval of the amplitude of the VER in reference to the baseline was found. This information was then encoded on data cards, and through the use of the Triangle University Computer Center of the Research Triangle of North Carolina's IBM-370-165 computer a 2 X 2 X 2 X 2 X 9 Bio-Med 08V repeated measures analysis of variance was performed. The Bio-Med 08V analysis of variance program is part of the University of California at Los Angeles' Bio-Med statistical package. The levels of the independent variables in the analysis corresponded to, respectively, recording positions, degree of eccentricity, behavioral task, viewing conditions, and the degree of noncorrespondence.

The reaction time distributions were analyzed in the following manner: The Alpha 16 computer was instructed to provide a digital printout of the reaction time distribution for the 448 msec recording time interval. Since each bin within the data array represented seven msecs, the resulting printout, obtained from a Fabri-Tek Model 201 High Speed Printer, provided a reference standard to which the integrated reaction time distribution for each subject for each position of noncorrespondence of stimulation could be compared. The median reaction time could then be readily determined by finding the central data point of the reaction time distribution, comparing its position within the array

with the reference, and obtaining the median reaction time for that bin in msecs. This information was placed on data cards and analyzed by a 2 X 2 X 9 Bio-Med 08V repeated measures analysis of variance program. The levels of the independent variables in this analysis corresponded to the eccentricity of stimulation, viewing conditions, and the nine levels of noncorrespondence of stimulation respectively.

## Results

A representative sample of the VERs to bioptic and monoptic foveal stimulation for two subjects (DS and RH), under conditions of reaction time response and $O_Z$ recording location, is presented in Figure 1. The VER for the monoptic 0' of arc noncorrespondence stimulus condition is missing due to the difficulty in placing both the steadily illuminated light and the evoking stimulus light at the same position in the display for this condition. Visual inspection of the data indicates that, under both foveal bioptic and monoptic conditions, there was a reduction in the overall amplitude of the VER as a function of the degree of correspondence of retinal stimulation, the smallest amplitude VERs being evoked when the stimuli were in correspondence, and the larger amplitude VERs being evoked when the stimuli were in various degrees of noncorrespondence.

Figure 2 presents the individual and group data for each of the positions of noncorrespondence and the control condition (C), under both bioptic and monoptic stimulus conditions at fixation points corresponding to $0^{\circ}$ (foveal) and $5^{\circ}$ (peripheral) eccentricity. The analysis of variance conducted on the absolute intergral of the amplitude of the VERs as a function of the correspondence of stimulation indicated a single significant effect, viz., the degree of

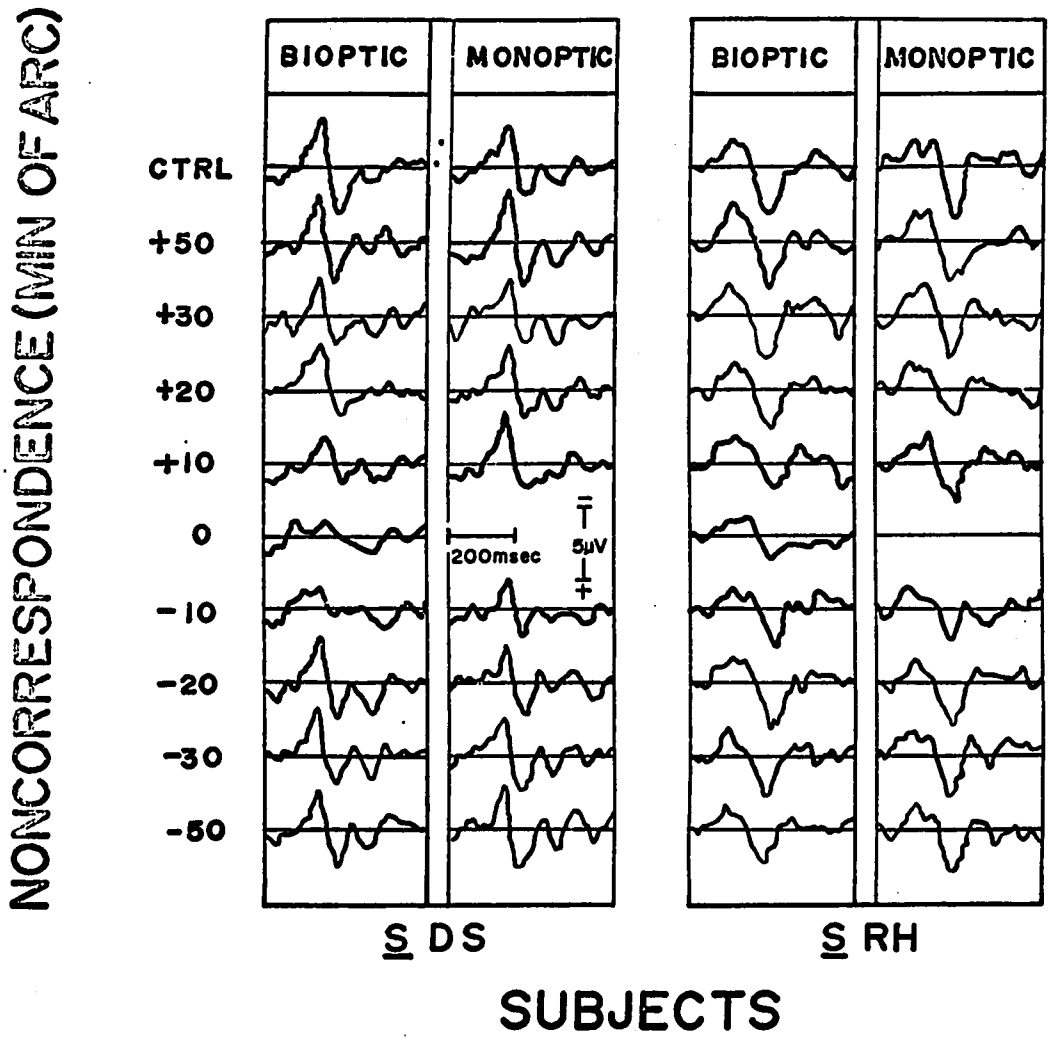


Fig. 1. Averaged evoked responses to foveal bioptic and monoptic stimulus conditions as a function of the noncorrespondence of retinal stimulation for two subjects under reaction time tasks and Oz recording location. The 0' of arc position of noncorrespondence under the monoptic viewing conditions is not shown due to the difficulty of placing both the evoking and steadily illuminated stimulus at the same position under these conditions.

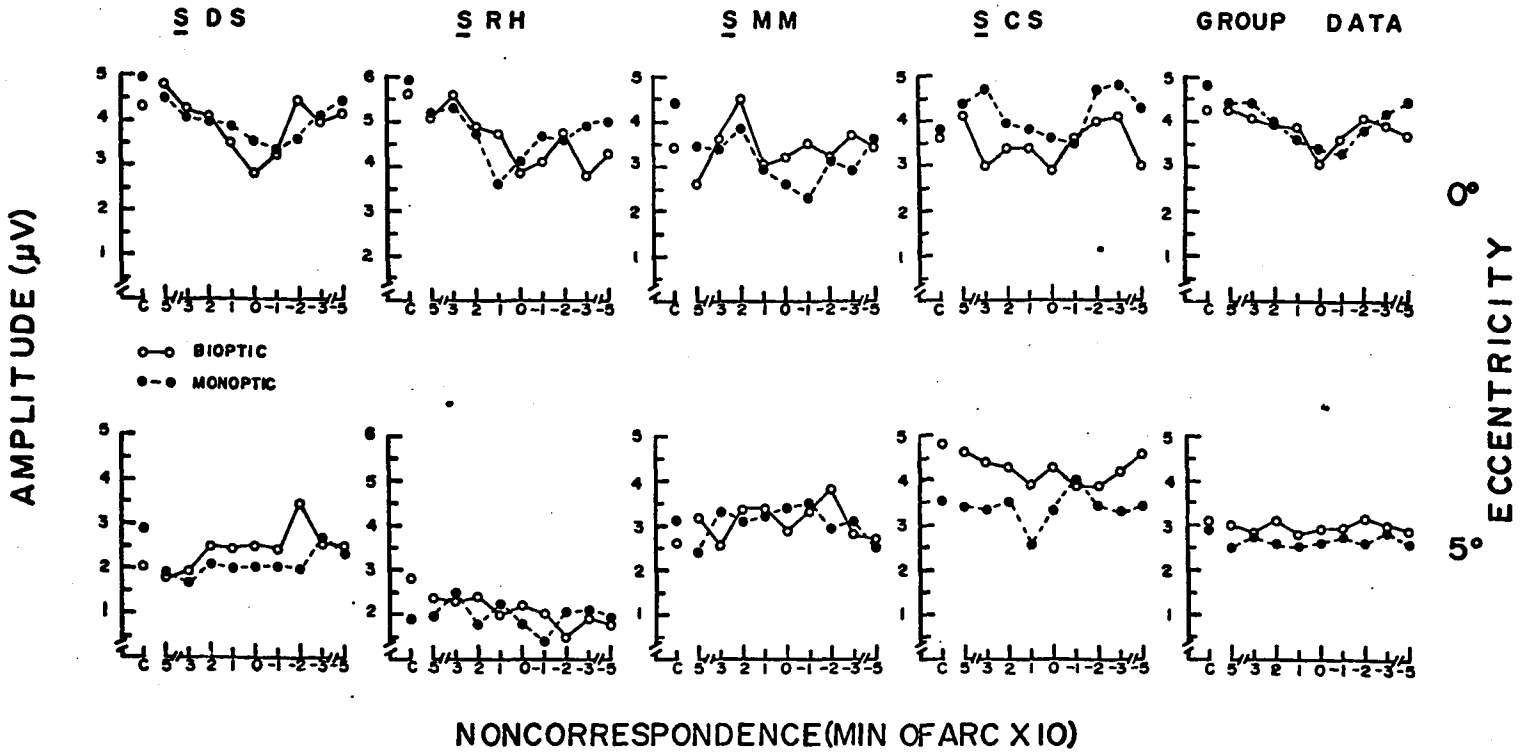


**Fig. 2.** Amplitude of the visually evoked responses for individual subjects and group data under foveal ($0^{o}$) and peripheral ($5^{o}$) viewing conditions for both monoptic and bioptic stimulus conditions as a function of the noncorrespondence of retinal stimulation. The 0' of arc values for the monoptic conditions are interpolated.

noncorrespondence of stimulation ($p < .05$); whereas all other factors and their interactions were nonsignificant. The degree of noncorrespondence of stimulation effect indicated that when the steadily illuminated light and the evoking stimulus light were in positions of noncorrespondence ($\pm$10' -- $\pm$50' of arc subtense) larger amplitude VERs were found than when the two light sources were in correspondence (0' of arc). Both the group and individual data indicated that this effect was most pronounced under the foveal ($0^{o}$) fixation condition. The peripheral fixation conditions showed little evidence of VER amplitude variations as a function of positions of noncorrespondence of retinal stimulation. Although the interaction between foveal and peripheral viewing conditions and the degree of noncorrespondence was evident in the data from all subjects, it only approached significance at the .05 level. The failure of this interaction to reach statistical significance was due to the variable degree to which the interaction was evident in the individual subjects.

Figure 3 presents the median reaction time data for both the individual and group data for each of the positions of noncorrespondence of stimulation under both bioptic and monoptic stimulus conditions at fixation points corresponding to $0^{o}$ and $5^{o}$ eccentricity. The analysis of variance conducted on the reaction time data indicated two significant main effects: First, that foveal stimulation resulted in faster

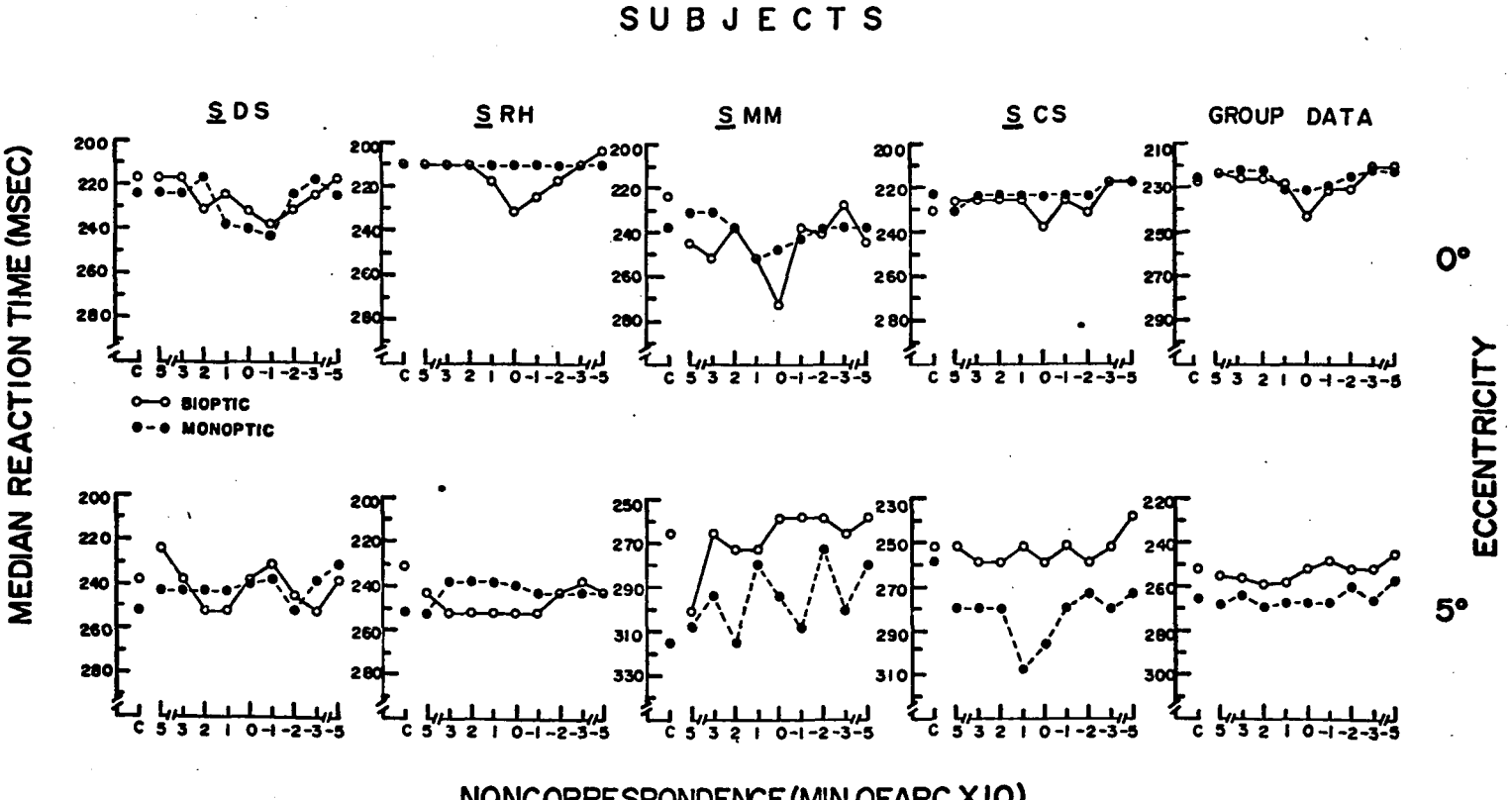


Fig. 3. Median reaction time in msecs for individual subjects and group data under foveal ($0^{o}$) and peripheral ($5^{o}$) viewing conditions for both bioptic and monoptic stimulus conditions as a function of the non-correspondence of retinal stimulation. The 0' of arc monoptic values are interpolated.

reaction times than peripheral stimulation ($p < .05$); and second, that reaction times varied as a function of the positions of noncorrespondence of retinal stimulation ($p < .01$). An analysis of the individual data implies that reaction times under foveal conditions increased as the steadily illuminated light was moved closer to the flashing stimulus. Under the peripheral conditions, however, relatively little change in reaction time occurred as a function of the stimulation of corresponding and noncorresponding retinal points.

Individual differences suggested two subjects (CS and MM) showed consistent differences between the peripheral monoptic and bioptic conditions of the experiment. The remaining two subjects (DS and RH) showed no differences in their reaction times to peripheral monoptic and bioptic stimulation.

Three additional subjects were added to further substantiate the generality of the foveal monoptic and bioptic reaction time and VER results of the main part of the experiment. A 2 X 2 X 9 analysis of variance was conducted on the VER information for all seven subjects in the experiment. The levels of the independent variables were electrode position, monoptic and bioptic viewing conditions, and the nine levels of noncorrespondence of points of retinal stimulation. Reaction time information was analyzed by a 2 X 9 analysis of variance with the levels of the independent variables

corresponding to monoptic and bioptic stimulus conditions and the nine levels of noncorrespondence of retinal stimulation. The results of both analyses supported the findings of the major part of the present investigation.

## Discussion

The VER and reaction time data support the following hypotheses: (a) a reduction in the distance between the points of retinal stimulation would result in increased inhibition -- that is, the presentation of the continuous stimulus in close correspondence to the intermittent stimulus would decrease the response to the intermittent stimulus; (b) the presentation of the continuous stimulus to one eye would inhibit the response to stimulation of the other eye, indicating that the inhibitory effect is binocular in nature. The hypothesis that the inhibitory effect would be more pronounced under foveal than peripheral conditions of stimulation was supported when trends in individual data were considered. On the basis of the information presented in the following discussion, it is proposed that the reported changes in VER amplitude, as well as related reaction time changes, most likely reflect the effects of mechanisms operating at the geniculate level of the visual system.

As noted in the introduction, various animal single unit investigations (Barlow, et al., 1967; Bishop, et al., 1970; Pettigrew, et al., 1968) have indicated that binocularly driven cortical units generally show increased, or facilitated activity when receptive fields of both retinas are stimulated. Other investigators (Burns & Pritchard, 1968; Noda, Creutzfeldt, & Freeman, 1971) have found similar

results. The degree of facilitation, however, depends on the correspondence of points of retinal stimulation. As disparity varied in these animal experiments, an inverted "U"-shaped function was generated; maximal activity occurring when the disparity falls within 10' to 6° of arc, depending on the unit being measured; minimal activity occurring when extremely disparate retinal points are stimulated; and an intermediate level of activity occurring when corresponding retinal points are stimulated.

The results of the present investigation are only partially consistent with this inverted "U"-shaped function. A compatible finding was that VER amplitude was greater when slightly noncorresponding (optimal) as compared to corresponding retinal points were stimulated. Although only indirectly related, the faster reaction times obtained under the former conditions are in agreement with the electrophysiological findings. Unlike the single unit data, stimulation of the most disparate noncorresponding points (the control condition when the continuous stimulus was withheld) resulted in VERs (and reaction times) which were quite similar to those found when less disparate ("optimal") noncorresponding retinal points were stimulated. In other words, with increasing disparity, an increase in facilitation was not followed by a decrease as would have been predicted from the inverted U-shaped function for the single unit data. It appears, therefore, that the VER results, as well as the

reaction time data, obtained in the present investigation cannot be readily explained in terms of the types of mechanisms postulated to account for the activity of single units at the cortical level.

It may be noted that a reduction in VER amplitude to transient stimulation of one eye due to continuous stimulation of the other eye has been reported by other investigators (Lansing, 1964; Lehmann & Fender, 1967, 1968; Riggs & Whittle, 1968; Shipley, 1969; Spekreijse, Van der Tweel, & Regan, 1972). Such stimulation appears to result in binocular or interocular suppression. On the other hand, a number of human VER investigations have indicated that an enhancement or facilitation of VER amplitude occurs when a transient stimulus is presented to both eyes (Bartlett, Eason, & White, 1968; Ciganek, 1970; Harter, et al., 1972; Perry, Childers, & McCoy, 1968; White & Bonelli, 1970). It appears, therefore, that the nature of binocular interaction depends in large measure on the type of stimulation being applied to the two eyes. If the stimulus applied to both eyes is transitory, binocular facilitation will occur; if continuous stimulation is applied to one eye and a transient stimulus to the other, the evoked potential to the transitory stimulus may be suppressed.

Investigations of single unit activity at the cortical level in animals typically have not studied the effects of presenting continuous stimulation to one eye on the

transient response to flash stimuli presented to the other eye. This paradigm, however, has been employed to investigate the binocular receptive fields of single units in the LGN of the cat (Sanderson, et al., 1971). The LGN single unit data reflect trends similar to those observed in the present study, and suggest a possible explanation.

Sanderson, et al. (1971) found that, to a considerable extent, the spontaneous activity of binocular units within the main lamina of the LGN, and, to a lesser extent, the driven activity due to the stimulation of the dominant eye, was inhibited by the stimulation of the non-dominant eye. The inhibitory effect was maximal when approximately corresponding retinal points were stimulated. Inhibition progressively decreased when the stimulus presented to the non-dominant eye was presented to increasingly noncorresponding retinal points. The decrease in VER amplitude obtained in the present study could reflect, through presynaptic cortical activity, the same inhibitory mechanisms noted at the LGN by these investigators. The longer RTs associated with reduced VERs may be a behavioral consequence of such inhibition.

Such inhibitory binocular interaction (due to the stimulation of corresponding retinal points) could result from a form of binocular occlusion. Binocular occlusion occurs when the stimulation of one eye drives a cell at a sufficiently high rate that additional stimulation of the other

eye is less effective in further increasing the response level of the cell (Noda, et al., 1971; Pettigrew, et al., 1968). In the present study, the attenuation in the evoked response (and longer RTs) to transient stimulation of a given retinal area of one eye, which resulted from stimulation of the corresponding area of the other eye, may reflect binocular occlusion. That is, continuous stimulation of one eye could activate that part of the cortex which also must respond to a transient stimulus presented to the other eye. As the response to continuous stimulation approaches saturation level, the extent to which that particular cortical area could respond to additional transient stimulation of the other eye would be reduced.

When noncorresponding retinal points are stimulated, the cortical area activated by continuous stimulation of one eye may be appreciably different from that activated by the transient stimulation of the other eye. Thus, occlusion would not be expected to result. If in fact occlusion did occur in this experiment, the data suggest that substantially different populations of cells were involved when the degree of noncorrespondence of the points of retinal stimulation reached 50' of arc. The control condition, which theoretically represented the stimulation of widely disparate retinal points, produced VERs and reaction times similar to those obtained with stimulation of 50' of arc disparity.

Another equally possible mechanism which may have been responsible for the results of the present investigation is lateral inhibition. The presentation of the steadily illuminated light source to corresponding retinal points may have produced maximal amounts of lateral inhibition in binocular single units at the LGN level. The amount of lateral inhibition would be expected to increase as the disparity or distance between the two stimuli is reduced, as was the case in the present experiment. The data of the present experiment suggest that virtually all inhibition occurred when the degree of noncorrespondence was less than 50' of arc subtense. The control condition indicated that beyond 50' of arc disparity, no further changes in evoked responses were found.

It is difficult to determine which of these two mechanisms, lateral inhibition or binocular occlusion, best accounts for the present data. One would expect lateral inhibition to extend over considerable distances (as measured in the visual field). Considering the size of the stimulus spot of light and the effects of diffusion of light in the optical system of the eye, the areal extent of the inhibitory effect was relatively small. This gives some support to binocular occlusion, in contrast to lateral inhibition, as the better explanation of the results.

If it is assumed that a binocular occlusion type mechanism was operating in the present study, then the present data

are consistent with previous data obtained in studies of the areal extent of receptive field centers in the foveal retina in man. Indirect evidence has been offered indicating that receptive field centers in man range in diameter from 10' to 30' of arc in the fovea (Bryngdahl, 1966; Harter, 1970, 1971; Harter & White, 1968, 1970; Jeffreys, 1969; MacKay, 1969; MacKay & Jeffreys, 1969; Regan, 1972, pp. 59-61; Regan & Richards, 1971; Rietveld, et al., 1967; Spekreijse, 1966; Van der Tweel, et al., 1970a). In the present study, the stimulation of corresponding receptive field centers could have produced the inhibitory effect due to occlusion, while the stimulation of noncorresponding regions of the receptive field (central portion of one eye and surround of the other eye) could not have produced this effect.

Evidence has been offered that the size of receptive field centers and surrounds increase with retinal eccentricity in animals (Enroth-Cugell & Robson, 1966; Fischer & May, 1970; Hubel & Wiesel, 1965; Leicester & Stone, 1967; Wiesel, 1960; Wiesel & Hubel, 1966), and in man (Bryngdahl, 1966; Hallett, 1963; Harter, 1970; Rietveld, et al., 1967). The lack of differentiation in VER amplitude as a function of the degree of noncorrespondence in retinal points in the peripheral retina in the present study may have been due to the larger size of receptive fields in the peripheral retina. The larger size of receptive fields in the peripheral retina may have resulted in an extremely small percentage of the

total area of the field being stimulated. This could have reduced the magnitude of the inhibitory effect to a level beyond the sensitivity of the VER measure used. A second possibility is that had the range of retinal stimulation been increased beyond the 50' of arc distance for the peripheral viewing conditions, some differentiation in VER amplitude, and perhaps even reaction time, would have been found. Such a suggestion is based on the assumption that the inhibitory effects within receptive fields at $5^{o}$ eccentricity would be sufficient to allow for some differentiation in activity to occur as a function of the noncorrespondence of retinal stimulation. A third possibility is that the mechanisms underlying the inhibitory effect were not operating in the peripheral area of retinal stimulation.

In view of the above discussion, the hypothesis that the inhibitory effect would be found under the bioptic condition, indicating that it was post-chiasmal in nature, appears to be supported by the results of the present investigation. It should be noted, however, that inhibitory effects due to the distance between the two stimuli were evident when both stimuli were presented to the same eye (monoptic viewing conditions). Thus, an intraocular type inhibitory mechanism could have been operating at the retinal and/or ganglion cell level of the visual system. However, since the inhibitory effect was very similar under both the monoptic and bioptic viewing conditions, it would

be more parsimonious to propose that the inhibitory effect was operating beyond the ganglion cell level, most likely at the LGN as discussed above.

## Summary

Interocular and intraocular inhibitory effects on VERs and reaction times were studied as a function of the degree of disparity of retinal stimulation. The degree of disparity was manipulated by presenting a steadily illuminated stimulus light in various positions above and below an evoking stimulus light. The evoking stimulus light was always viewed by the right eye, while the continuous (steadily illuminated) stimulus light was viewed either by the left eye (bioptic condition) or the right eye (monoptic condition).

Three hypotheses were proposed: First, that the overall amplitude of the VER would decrease, and reaction time increase, when the distance between the retinal points being stimulated was reduced; second, that the inhibitory effect would be interocular in nature; and third, that, due to stronger inhibitory effects within central retina receptive fields relative to inhibitory effects within peripheral retina receptive fields, the VER would more readily attenuate, and reaction time more readily increase, under foveal conditions of stimulation than under peripheral conditions of stimulation.

Various cortical single unit investigations in animals have suggested that an inverted "U"-shaped function would occur when the degree of retinal disparity was varied. The stimulation of corresponding retinal points has been found to produce an increase in single unit activity, while the stimulation of slightly disparate retinal points produces an additional enhancement, or facilitation of single unit activity. The stimulation of widely disparate retinal points produces the least amount of facilitation of single unit activity in the cortex. At the LGN the stimulation of corresponding retinal points produces a decrease in single unit activity, while the stimulation of increasingly disparate retinal points produces a progressive increase in activity. The stimulation of widely disparate retinal points, however, apparently does not produce further decreases in single unit activity at this level of the visual system.

The results of the present investigation only partially support the trends suggested by cortical single unit investigations, and appear to more readily reflect what is occurring at the LGN. When corresponding retinal points were stimulated a decrease in the amplitude of the VER, and an increase in reaction time was observed. When noncorresponding retinal points were stimulated VER amplitude was enhanced, and faster reaction times occurred. The stimulation of widely disparate retinal points, however, failed to

produce a further decrease in VER amplitude as would have been expected on the basis of cortical single unit activity. In addition, such stimulation did not significantly affect reaction times in comparison with the stimulation of slightly disparate retinal points. Two mechanisms were suggested to account for the results of the present investigation: occlusion and lateral inhibition. Both mechanisms appear to be equally possible alternatives.

The second hypothesis, that the inhibitory effect was interocular in nature, was supported by the results of the present investigation. But, the inhibitory effect was also found to occur intraocularally. If one parsimoniously postulates a single mechanism to account for both the interocular and intraocular inhibitory effects, it would have to be operating beyond the ganglion cell level, most likely at the LGN.

The third hypothesis was partially supported by the results of the present investigation. The VER to foveal stimulation more readily attenuated, and the reaction time more readily increased, than did VERs and reaction times to peripheral stimulation. This suggests, perhaps, that the inhibitory effects within central retina receptive fields were stronger than those found in more peripheral retina receptive fields. In addition, these findings indirectly suggest that the size of foveal receptive fields are considerably smaller than the size of peripheral receptive fields,

not only in overall areal extent, but also in regard to the relative size of receptive field centers and surrounds.

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