BINOCULAR INTERACTION: FUSION OR SUPPRESSION

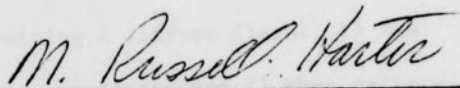OF THE VISUALLY EVOKED POTENTIAL

TO DICHOPTIC STIMULATION

by

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Approved by

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In this study averaged visually evoked potentials were used to examine the nature of binocular processing of the visual system. Two different hypotheses have been proposed by earlier writers. The first assumed that the information from any one is suppressed at a given time, while the information from the other eye dominates in perception. An alternative hypothesis proposes that all information is processed and fused into a single percept.

These two hypotheses were studied by manipulating the between line distances of grid patterns presented to the two eyes. Previously, characteristic responses have been found for the various pattern sizes. Again these differences were substantiated and were used to determine the contribution of each eye's input to the binocular responses. Pattern sizes presented to one eye were varied while holding constant the size of the pattern presented to the other. Three scalp recording sites were used: a midline occipital and two lateral occipital locations. Only the midline data was presented here. Averaged Visually Evoked Responses were obtained to each condition in a Binocular, Right, Binocular, Left flash order.

Evoked Potential amplitude was measured at two latencies after stimulus presentation: approximately 100 (N-100) and 200 (P-200) msec. It was found that for conditions containing a diffuse flash: 1) the amplitude of the binocular response was suppressed and 2) when pattern was presented to one eye, the contribution of the pattern appeared to dominate the binocular evoked response. When two patterns were presented, it was found that the earlier N-100 measure gave the greatest amplitude

responses to dichoptic presentation, i.e. two dissimilar patterns. On the other hand the P-200 measure showed the greatest response to dioptic conditions, the same pattern to both eyes.

Data obtained provided support for both of the preceeding hypotheses. It was found that both fusion and suppression type mechanisms may be operating at the level of visual processing measured by the evoked potential, the particular mechanism depending on the stimuli presented.

APPROVAL

This thesis has been approved by the following committee of the Faculty of the Graduate School at The University of North Carolina at Greensboro.

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Introduction

The body has two eyes yet the mind has but one. Humans are born with two eyes and each of these eyes has a slightly different spatial location. Thus the view of the world that these two organs receive is never the same. Each eye communicates a separate view of the visual field to the cortex; yet, our perception is of only one world. Somehow and somewhere these two dissimilar inputs are changed into one.

This paradox of the visual system has captured the interest of men since earliest time. Grecian myths told of Cyclopian creatures which were endowed with external anatomies more in tune with the obvious capacities of their mental worlds. In the second century B.C. Galen, the famous physician, dealt with this very problem in his work "On The Use Of The Parts Of The Human Body." He assumed that the humors from the two eyes flowed in separate channels, the optic nerves, until they were finally united deeper in the head. Phenomenologically, he described the intricacy of the perception with the following example: when looking at a column and shutting each eye in succession, the following will be observed. When the right eye is shut, some of those parts of the column which were formerly seen by the right eye on the right side, will now now be seen by the open left eye. Conversely, when the left eye is shut, that portion formerly seen by this eye will not be visible to the now open right eye.

Another early treatise on this subject by Leonardo da Vinci, described an apparent transparency of objects when viewed binocularly.

In his treatise on painting, he states that although a painting be done with the utmost of skill, it can never really show a relief similar to that of the real objects. This can be demonstrated by viewing a small sphere with both eyes. It appears that the sphere, especially when close and relatively small, hides nothing of the scene behind it. This same sphere represented in a picture must necessarily hide all.

Porta in 1593 realized that Galen and da Vinci were implying a union of the two dissimilar monocular pictures. However, he believed this to be an impossible accomplishment for the visual system and further proposed that only one of the two eyes perceived at any one time, with a rapid alternation between the two eyes. Thus we have a first attempt to "explain" what is known today as binocular rivalry.

Not soon after this proposition, Aquilonius proposed in 1613 the concept of horopter in an attempt to account for a way in which fusion of the two inputs could be explained. He described a horopter as the locus of the points where images fall on corresponding places of the retinas for constant positioning of the eyes. Whatever is viewed by the two eyes is joined by common sense into a single percept.

Later Charles Wheatstone (1838), the inventor of the stereoscope, realigned past thinking as to the nature of binocular vision in his work "Some Remarkable Phenomenon of Binocular Vision." He states that the union of the two different views of an object presented to the two eyes is not the problem, but rather it is the explanation of binocular space perception. Past writers had failed to recognize the fact that the differences between two images presented to the retina of the eyes can arouse an impression of distance. The way in which this

retinal disparity is related to the perception of depth, is related to

the notion of correspondence. He reasoned

... if each sense modality can be identified by its terminus in the brain,
so too can each retinal receptor. In short, it seems that each point
in the retina transmits a message to the brain, which 'tags' its point
of origin. Finally, and most conveniently, the central organization of
termination points preserves the spatial organization of retinal points.
There can be, then, a one to one correspondence between a pattern of
retinal stimulation and a pattern of brain activity. To be the pattern
of brain activity to an external visual object that is spatially local-
ized, it remains only to relate the retinal pattern to the stimulating
object. (Wheatstone, 1964, p. 130)

Helmholtz (1896) found it necessary to review the theories of

binocular vision when he was compiling his Handbuch der Physiologischen

Optik. He concluded that past theorists too readily presupposed various

kinds of anatomical structures in their theories of vision. Examples

of such thinking can be found in "intuitive theories," all of which

share the following common beliefs that a) the mind is supposed to have

some direct knowledge of the dimensions of the retina, and b) the mind

is innately endowed with these capacities and from the first moments of

sensation attributes these certain characteristics to the stimuli.

The following are examples of intuitive theories. Muller (1826)

proposed that the mind is endowed with a concept of space with which it

interprets various sensations. Even with the eye closed, it still

senses itself as a position in a dark space. Kant also proposed that

original inherited dimensions play a major role in perception. For him

these dimensions were both time and space. Hering (1864) stated that

the mind was able to determine directly the distance between a pair of

retinal points. Because this capacity allowed for judgments along a

single plane, it was the contributing factor to the illusion of mono-

cular localization. These ideas of original endowments of localization

all implied a concurrent knowledge of which points on the retina give rise to the same localization as other points on the opposite retina, identical points.

It remained for Panum (1859) to modify these theories and consolidate the notions of corresponding retinal points. His proposition is as follows: for every point 'a' on one retina, there exists an identical point and corresponding circle of sensation 'A' on the other retina. If the images of a given object fall within 'A' and 'a', then it gives rise to a single percept. The phenomenon of depth was said to be caused by exactly which point within the 'A' circle 'a' fell. Likewise, he attempted to account for rivalry by stating that contours had a dominating influence in the common fields. Rivalry takes place mainly between dissimilar colours or contours; likes tend to fuse. Panum (1861) further elaborated his theory by assigning four attributes to the eyes: "a binocular energy of colour mixing," which allowed different colours seen binocularly to be united into the mixed colour; a "binocular synergy of alteration," which allowed colours to come into conflict; disparate images were said to be united by a third attribute "synergy of single vision by corresponding circles of sensation"; and "synergy of the binocular parallax" was said to account for perceptions of depth. (Again Panum stressed that contours were particularly strong stimuli to the nervous system causing rivalry.) These mechanisms were physiological in nature and were not to be considered as psychic forces.

Another major intuitive theory of bonocular vision was proposed by Hering (1864). He felt that when individual points of the retina are in a state of stimulation, there exists three different kinds of

space feelings besides the colour sensations. They are a) altitude values (Höhenvert) of the site of retinal stimulation, b) azimuth values (Breitenvert), and c) a special kind, which has equal but opposite values for each pair of identical retinal points, and which has equal values but of the same sign for pairs of retinal points which are symmetrically situated. Together these three values give rise to a feeling of direction. Once again Hering has proposed the doctrine of identity: stimulation of equal or unequal intensity on the same points gives rise to the same values and excites only one sensation. Hering's theory differs from Panum's in that he assumed a psychological basis for these values. Practice and training allows fusion of the two impressions into a total sensation which has the mean value of both the direction and depth.

Helmholtz (1896) disagreed with intuitive explanations of binocular vision. He proposed that we seldom see double, mainly due to eye movements towards contours. These ocular movements enable us to find the local signs in the sensations which are characteristic of contiguous points. Presumably through learning of these local signs combined with other conscious factors which allow us to ignore subjective impressions, the perception of midline visual direction and single vision is gained. Although we see double at every point other than that which is fixated, the line of fixation in normal vision is always directed to the same objective place as that of attention. Thus the phenomenon of rivalry depends on the conscious characteristics that prevent us from taking in more than one impression at a time. In summary Helmholtz states,

The form of union of the impressions in the visual fields of the two eyes is the apperception of material things. Where this does not succeed on account of the nature of the two images, the attention will waiver, as shown by the rivalry between the two visual globes, unless attention is riveted by sharply defined outlines in one of the fields. (Helmholtz, 1962, p. 541)

Before proceeding into a review of current thinking regarding binocular visual processes, it would be instructive to see what phenomena these theories must account for and the nature of these as described by earlier writers. The process of union of the inputs of the two eyes has been explored from many experimental positions. Among them is the interest in thresholds when comparing monocular to binocular rivalry.

In 1860 Fechner described a paradoxical phenomenon. When both eyes are open in the daylight, and then one of them is shut, it can be noticed that there is little, if any, change in the brightness of the surroundings. Again if that eye were opened, no change in brightness is noticed. Fechner has shown, however, that if a dense filter is placed before one of the two open eyes and then the eye with the filter is closed, there is an increase in subjective illumination.

Another Classic experiment (Dove, 1850) demonstrated stereoscopic luster. He found that if two similar objects, one having a black surface and the other a white surface, are presented to the two eyes, the surface of the object seen binocularly appears to have a polished appearance. This phenomenon also holds under tachistoscopic presentation.

A third phenomenon to be described is that of retinal rivalry. Beginning with Porta in 1593, it has been reported that if two quite dissimilar images are presented to the two retinas, only one is perceived

at a time, and the perceived image alternates between the eyes in succession. As can be recalled, Helmholtz contributed this to fluctuation in eye movement and attentional states, while Hering and Panum considered it a peripheral effect due purely to the nature of the system.

The phenomenon of rivalry was extensively studied by Breese (1899) and described in his paper "On Inhibition." In summary, Breese found that all of the following manipulations could affect the nature of rivalry. The length of time a given stimulus is held in perception can be increased by direct will power, however, purposeful attempts to decrease the number of changes in a given time proved unsuccessful. He found that accompanying the will effect there were always eye movements, and with elimination of these movements there was a decrease in ability to hold either field in dominance. Again with restoration of conscious eye movements, there was a concommitant increase in time. Other conscious processes such as counting lines in either field also increased length of that field's dominance. Movement in one of the two fields also increased its length. Contraction of the muscle on either side of the body was said to increase only the pattern to the right eye. If two different sized stimuli were used, the smaller would dominate in length of time. Finally, he found that if the intensity were increased, it resulted in an increase in the rate of alteration, but not in the ratio. Breese concluded that these effects were not purely mentalistic since will power was not completely effective. But likewise, any movements of the eye affected both of them, so that motor factors were not solely in control. Logically, he postulated a mechanism controlled by incoming and outgoing motor impulses, a psycho-physiological process.

We are now in a position which allows us to look at current models and their attempts at explanation. In view of past theories and research, these theories can be placed into two primary, though not always distinctive, categories. The first to be considered are theories which claim suppressive mechanisms as the primary workings of binocular vision. The second will be those which proclaim fusional processes as the determinants of binocular vision.

Suppression theories of binocular vision have been popular in the past (Porta, 1593; Bose, 1915; Verholf, 1935; Neuhaus, 1936; and Fleisher, 1931; ref. in Le Grand, 1967), as well as in the present. The major proponent today has been Asher (1951, 1961). In order to get a clear picture of the position these theorists assumed, we will follow Asher, as he proposes experiments and examines data which support his position.

When holding up a pencil and fixating behind it, a double image of the pencil is perceived. However, if one eye is closed one pencil is seen and the background now appears in the position in which the other pencil was seen, likewise for the other eye. If again both eyes are opened, we see that two portions of the ground are missing, hidden by the two images. What this implies is a suppression of impulses from the corresponding portion of the other retina. When the object is seen as double we have double suppression. Most commonly the figure suppresses the ground. A second demonstration supporting the suppression hypothesis involves viewing two black dots in a stereoscope, one being smaller than the other. Each dot is located on a white background and when viewed stereoscoptically, the smaller dot and part of

its surroundings appear in the center of the larger dot. Asher concludes that not only is the figure endowed with suppressive powers, but that areas closely adjacent to contours also have increased powers of suppression. The reasons for figures suppressing grounds is then that by being small, each part acquires suppressive power by virtue of lying close to its own contour. For Asher the interest value of the picture was largely irrelevant. Other evidence includes such things as: the constancy of apparent monocular versus binocular brightness, and the fact that depth perception can be stimulated by disparate images.

From this evidence Asher has derived and proposed the suppression theory. According to the theory, any picture perceived by a subject is built up of some parts contributed by the image of one eye and other parts contributed by that of the other eye; no single part being a blend of images from both retinas.

Gordon Walls (1942) argues in favor of a fusion theory on naturalistic and evolutionary grounds. The mere fact that vertebrates have developed two frontal eyes instead of one is sufficient support for him. If some sort of suppression does occur, why would we have two eyes? why wouldn't animals close one eye to get a better look at things? Walls contends that the independence of the two eyes is over-rated. Motor independence does not necessarily mean sensory independence. When two independent hands grasp an object, it is perceived as only one object. Walls states his theory as follows

In ourselves, fusion is not through suppression or even a completed blending of the whole of one image within the whole of the other. Rather, it is a sort of mosaic process which is dynamic, with constant shifting of the conspicious parts of the images ... (Walls, 1942, p. 324)

Fusion for this author, then, involves parts contributed from each eye

fused into a single figure. Asher, as can be recalled, felt that the whole of the image was contributed by a single eye.

Dodwell (1970) proposes three arguments against suppression theories. First, stereoscopic images are usually perceived as being located at a median point in space and on different planes. Secondly, suppression does not have time to occur in case of briefly presented forms. And thirdly, because Asher finds instances where suppression does occur and fusion does not, this is not the same as proving suppression is a necessary condition for binocular vision. Dodwell feels that although suppression can occur, it is not the only mechanism and probably not the most important mechanism.

Anatomical Basis of Binocular Fusion

The anatomical basis of the mammalian nervous system includes two frontally located eyes and likewise two flexible optic nerve tracts running dorsally and medially from the rear of these structures. In all animals below mammals, these tracts completely cross to the opposite side of the body from their origins. In mammals, however, a partial decussation is the rule. Just anterior to the pituitary body at the base of the brain, approximately half of the fibers in the optic nerve cross over. In these animals it is the fibers from the medial portions of each retina that cross. The importance of this partial decussation has been debated and presently

The great majority of physiological opticists have ... seen in partial decussation the essential basis of fusion and stereopsis. The argument is that since there are no median end stations in the brain, fusion must occur on each side and can only do so if each half of the brain receives information from both eyes. (Walls, 1942, p. 321)

The validity of this statement would depend on whether singleness of

vision is attributed to animals where the optic tracts totally cross, with each side of the brain representing the contralateral eye. If we close one eye, it is obvious that this type of interlobal synthesis takes place, for we see one view with both lobes. If, likewise, we assume that totally decussated animals can accomplish similar fusibility of the images on the two sides of the brain, then this process cannot depend on the nature of the optic chiasm.

After crossing, the medial fibers from the contralateral retina and the lateral fibers from the ipsilateral retina proceed to either the lateral geniculate body (80%) or the superior colliculi (20%) on that side (Grossman, 1967). In the six layers of the lateral geniculate body, the fibers representing each eye are kept separate on alternating cell layers. Glees and Clark (1941) reported that each fiber from the retina ends in a spray of five or six branches and each of these terminates on an end bulb. Each one of these buttons then contacts with the body of only one geniculate cell. In no cases that they reported, did more than one end button contact with one geniculate cell. Later evidence (Bishop, et al., 1959) reported approximately 8% of over 100 geniculate cells tested could be fired by optic nerve fibers from either eye. It would seem from this anatomical evidence that most of the nervous pathways originating from separate eyes remain relatively distinct until they reach the cortical level. The axons from the geniculate cells then go to the cortex forming the optic radiation.

Studies of the striate cortex of lower animals (Hubel & Wiesel, 1962) have shown up to 85% of cortical cells are binocularly driven. Hubel and Wiesel (1968) have described the architectonic structure of

the monkey striate showing a distinct segregation of binocular cells. Horizontal layering showed that binocularly driven cells were most commonly found in the upper layers, II and III, and the lower layers, V and VI. The middle layer IV was composed of simple cells, or axons from the geniculate cells, and were driven monocularly. One eye was found to dominate at the beginning of a penetration with the other eye contributing slightly to the response. Proceeding downward, the non-dominate eye's influence gradually dropped out until at the fourth layer these cells were driven solely by the dominant eye. As they proceeded through V and VI binocular responding again reappeared. The column, nevertheless, favored the same eye through the entire penetrations. Adjacent columns, however, were found to favor alternating eyes. They generally found that binocular interaction increased from simple to complex to hypercomplex cells. More binocular cells were found for the monkey than in the cat. Another point made that will later prove interesting, is that only a small proportion of cells are likely to be influenced at any one time, since inappropriate orientation or diffuse light has little or no effect.

Another study by Burns and Pritchard (1968) has shown binocular summation in all twenty-six single cell recordings that they tested in the cat's visual cortex. They also found that these cells were most excited by contours of similar orientation and aligned through representative districts on each retina. Stimulation meeting these conditions produced dramatic summation. Aligned boarders within the two receptive fields produced greater responses than misaligned boarders. Experiments with human subjects reported in this same study, have given some further perceptual data. When two similar patterns were misaligned

more than fifteen munutes of visual arc, fusion was no longer reported. However, when the patterns presented to the eyes differed only in reversal of the position of the black-white fields, no instances of fusion were reported even with no misalignment. In these instances the subjects reported a five minute black or white bar on a grey background. Since the visual system was obviously not seeking a minimum number of perceived contours during binocular viewing, these experimenters proposed that the system has as its goal some maximum cortical response as suggested by the single cell data from the cats.

Although these studies suggested the locus of anatomical fusion, they have added little to the understanding of binocular vision as a whole. What would be more instructive is to consider the total picture. It is not necessary to assume a homonculus in the occipital lobe, who has to look at two pictures and choose between them, or decide to fuse them. Again two hands holding an object give but a single percept. Another way of studying the cortical response would be to look at the patterns of neuronal responses to varying physical stimuli, for it would seem that binocular stimulation could be better represented in patterns of aggregate neuron activity. For, although single unit activity may well represent activity in response to isolated stimulation, it does not necessarily mean that the type of process involved in producing binocular perceptions are the same.

Evoked Potentials

Recent electrophysiological work has provided researchers with a convenient method of studying cortical processes in healthy and intact human subjects. The Averaged Evoked Potentials recorded from the

scalp and time locked to a sensory stimulus have become an important measure of these sensory processes. Visually Evoked Potentials (VERs) have been shown in previous work to be related to such varied phenomena as attention (Eason, Harter, & White, 1969), pattern size (Harter, 1971; Harter & White, 1970; Uenoyama, 1971), and visual acuity (Harter & White, 1968).

For our purposes the property of the VER that lends itself best to our needs in studying binocular processing, is pattern size. Previous work on VERs has shown that the waveform and amplitude of various components are extremely sensitive to pattern size. A diffuse pattern produces a response of lower amplitude with the first component around 100 msec being predominately positive. As pattern is introduced, the amplitude of the VER becomes enhanced and the measure at 100 msec becomes increasingly negative. This continues until an optimum size pattern (20 to 10 min. of visual arc) is reached, then the response again decreases. Harter and White (1970) have proposed that this curvilinear relationship is reflecting the modal size of the receptive fields in the visual system.

Numerous investigators have reported that a type of binocular dominance occurs in the waveform of the VER (Ciganek, 1971; Cobb, Morton, & Ettlinger, 1967; McKay, 1968; and Lansing, 1964). In all these reports, however, the dominance found was that of a pattern stimulus waveform dominating the waveform of the diffuse. When two pattern stimuli were presented dichoptically (Fiorentini & Maffei, 1970; Regan & Spekreijse, 1970) reports have been primarily concerned with showing an increase in amplitude with disparate presentations. In no case did these designs

allow for identification of particular pattern, or eye contributions to
the binocular response.

The present study, then, will attempt to determine the nature of
binocular interaction with both diffuse and pattern stimuli. The nature
of the response to different patterns will be used to determine the
contribution of each eye's input to the binocularly evoked potential.
If suppression processes are at work, we should see the dominance of a
given waveform over the suppressed waveform. If fusion occurs, it
would be expected that the binocular waveform would look similar to the
sum of the two different pattern waves.

Method

Experimental Design

Independent variables in this experiment consisted of pattern
size and eye of stimulation. The patterns were photographically
reproduced grids with between line distances subtending 15, 30, and
60 minutes of visual arc. These were white crossed lines on trans-
parent film. The fourth pattern, a diffuse stimulus, was made with
Kodak Neutral Density Filter which was selected to pass an amount of
light equivalent to the pattern stimuli. The "eye of stimulation"
variable consisted of three levels: right eye stimulated alone, left
eye stimulated alone, and binocular stimulation. The dependent
measures were amplitude measures of the waveform of the visually evoked
potential and will be described in detail below.

Each of five subjects participated in four experimental sessions.
An experimental session consisted of the presentation of all sixteen
experimental conditions. Within one session a given eye was presented

the four patterns, while the other eye constantly received a single
pattern for four conditions. After four conditions, the pattern to
the constant eye was changed and again the other four patterns were
sequentially presented to the other eye. This procedure was followed
until all possible combinations of patterns and eyes, sixteen in all,
were presented. Exact presentation order was determined using a
Latin Square design (Table I). One session for each subject was held
per day for four days until four replications were completed. During
any given experimental condition, 64 flashes were presented to the
right eye, 64 to the left eye, and a total of 128 were presented bi-
nocularly. The stimuli were presented at a rate of 1.96 cps, and the
order of presentation was binocular, right, binocular, left, and so on.

Subjects

Five subjects from the age 22 to 31 were chosen for this study,
each of whom participated in all four experimental sessions. All
subjects had had prior experience as subjects in evoked potential
studies. All subjects had right hand and right eye dominance, as
determined by a visual sighting test. They were also required to
wear corrective lenses when necessary to insure normal visual acuity
during testing.

Task and Stimuli

During stimulus presentations subjects were required to perform
a synchronous tapping task. This task consisted of releasing a micro-
switch key within an 80 msec epoch (40 msec prior or consequent to the
onset of a flash). If the subject responded by releasing a key during
this interval, a reinforcement click was presented over the white

noise system. Although this task was difficult for some subjects to learn, all became proficient. This task requirement was used to assure attention to the stimulus presentations, while at the same time, occurring at a position which could not produce contamination of the sensory potential by the motor response. Later control data have shown that neither the motor nor sensory click response influenced the visual response recorded at the midline occipital electrode.

Stimulus patterns were presented using a haploscopic arrangement. The patterns were held in 3¼" x 4" slide holders and placed separately in each side of the stereoscope. This arrangement allowed for dichoptic presentations, that is, placement of different patterns to each eye. Continuous back illumination was provided by standard 40 watt light bulbs connected separately to two Variacs. This continuous illumination allowed any dominance or rivalry phenomenon in the situation to be present at all times. The intensity of the back illumination was matched for each side and measured at 1 log unit above threshold. An overhead 40 watt light bulb was used to illuminate the experimental room between stimulus conditions. The actual illumination of the stimulus patterns was accomplished using the two Grass PS-2 Photostimulators, one located behind the pattern to each eye. The stimulus flash was 10 microseconds in duration and was 3.3 log units above threshold at the intensity setting used (I-4).

The subjects, stimulus display apparatus, and the response key were all located inside an electrically shielded room. This enclosure also attenuated extraneous sound and light. A Grason-Stadler model 901B noise generator supplied white noise over a speaker located inside

the room. All other stimulus presentation and electrical recording equipment was located outside of this room in an adjacent area.

Measurement of Visually Evoked Response

The recordings of EEG activity were obtained using three Grass gold cup electrodes grounded through a yoked ear arrangement. In order to get the best recordings from the scalp, Redux electrode paste was used. This paste contains an abrasive which cleans the scalp of dead epithelial cells, and ionic salts which increase conductivity. This procedure allowed resistance to be lowered to at least 10,000 ohms.

The placement of electrodes was standardized for each subject by using the following procedure. A midline occipital placement was obtained by locating the inion and placing the electrode 2.5 cm. above this cranial landmark. Two lateral electrodes (5 cm. lateral to midline), one over each occipital lobe, were then placed at the same height as the midline electrode (the data from the lateral electrodes are not contained in this report).

After the electrodes were affixed, the subject was taken into the experimental room and seated in front of the haploscope and the response key was given to him. He was informed as to the nature of the response task and allowed to practice. He was also instructed to minimize eye blinks and excessive head movements in order to keep these influences from contaminating the recordings. Finally, he was told to turn the overhead light off during experimental presentations, and back on during the inter-trial interval. This procedure allowed subjects to be able to change patterns in the haploscope. The electrode leads were then plugged into a Grass Electrode Selector Panel located inside the room.

Electroencephalogram activity from each of the three electrode positions was fed into three separate channels of a Grass Model 7 polygraph. All channels used Model 7P5A Wide Band A.C. EEG Pre-Amplifiers. The ½ amplitude low frequency filter was set at 1 Hz and the time constants at .1 Model 7DAC D.C.

Amplifiers were used in connection with these pre-amplifiers. The amplifier's ½ amplitude high frequency filters were set at 35 Hz. These amplifiers were calibrated using the internal calibration pulse and the appropriate pens were set to a zero voltage baseline. Sensitivity was set at 20 microvolts per centimeter.

The amplified signals were then fed into a Fabri-Tex Model 1062 averaging computer. The memory of this computer was divided into four channels allowing averaging af all three EEG records and of the response task simultaneously. Sweep time for averaging was set a 2000 msec. The sweep was triggered by the binocular condition following the left monocular condition and the activity for the following 2000 msec was averaged. This interval included the presentation of four stimulus conditions: binocular, right, binocular, and left. In this manner averaged evoked potentials were obtained for each of the four eye stimulation conditions. Automatic stop of the computer was set on 64, and a visual readout of the average of these 64 sweeps was displayed on a Textronic oscilloscope Model RM504. A written record of these averages was then obtained using a Hewlett Packard X-Y Plotter Model 7035B. This graph was drawn by connecting values for each bin in the computer memory. Figure 1 presents a typical printout for one experimental condition. While averaging EEGs, ongoing activity was also monitored by a Hewlett Packard oscilloscope Model 141A.

Fig. 1.   Typical printout for one condition for one replication.
Data presented shows midline (O_z), right (O_1), left (O_2) records and
reaction time distribution for subject MRH.

BINOC   RIGHT   BINOC   LEFT
15 MIN   30 MIN
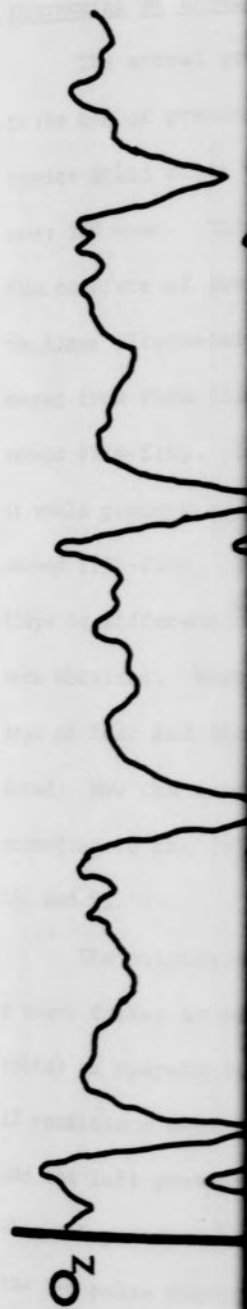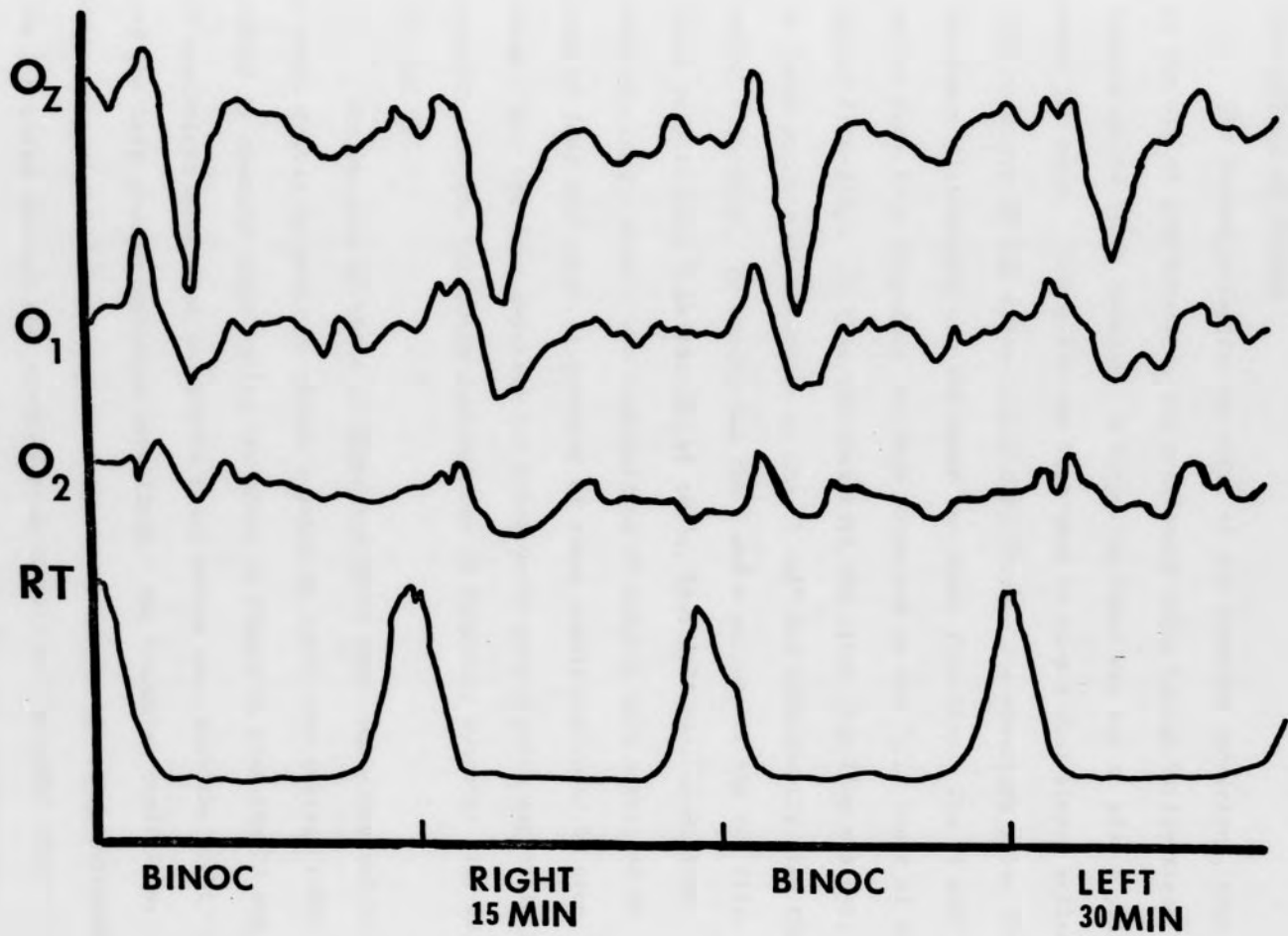
Programming of Events

The actual presentation order of the stimulus conditions, that is the eye of presentation, was programmed using Lehigh Valley Electronics solid state modules. A recycling timer was set to give a pulse every 520 msec. This pulse was then used to step a dual binary scaler. This consists of two cross-couple flip-flops. The momentary pulse from the timer alternately set and reset the first flip-flop. The "1 out" output from this flip-flop was then connected to the "ICL" input of the second flip-flop. In this way each time the first flip-flop was set, it would produce an assertion at the "1 out" and subsequently step the second flip-flop. By connecting the 1 and 0 outputs of the two flip-flops in different combinations of two's, four different conditions were obtained. When these combinations of outputs were connected to legs of four And Gates, a decoding of these conditions could be produced. Now the four separate And Gates would give a pulse sequentially according to the following combinations of flip-flop outputs: 11, 00, 10, and 01.

The outputs of three of these And Gates were then connected to a power driver in order to obtain a pulse of sufficient voltage (-28 volts) to operate relay coils. As shown in Figure 2, when the 10 and 11 conditions were used to operate relay number one, both the right and the left photostimulators were fired - the binocular conditions. When relay number two was operated by the 01 state, the relay switched the S-8 pulse through the normally open contact to the right photostimulator. When neither relay was operated, 00, the second relay rested on normally closed and the pulse was delivered to the left
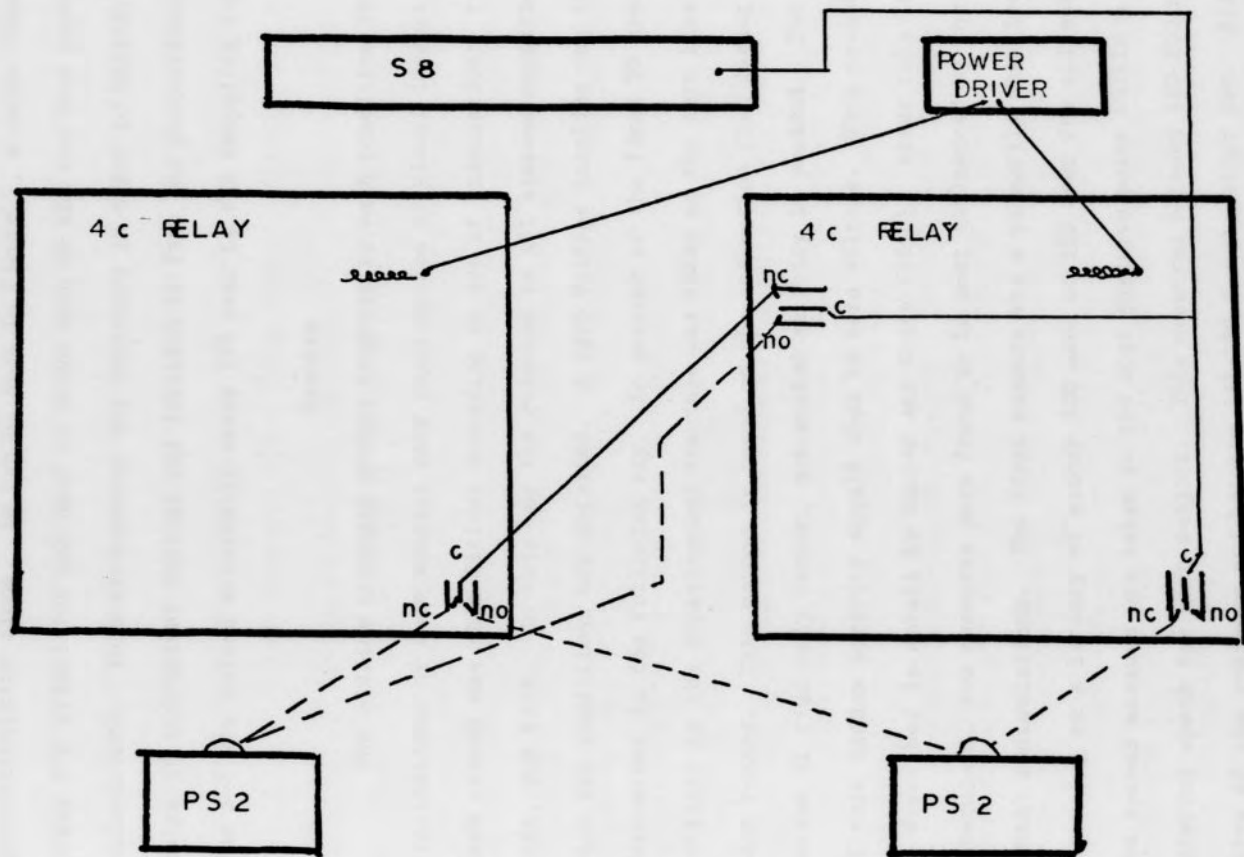
Fig. 2. Relay Wiring

photostimulator alone. As can be seen in Figure 2, a pulse from a Grass S-8 stimulator was used to drive each of the two PS-2 photostimulators. This arrangement was necessary in order to deliver a pulse of sufficient voltage and duration to fire the photostimulator. The S-8 was pulsed externally every 520 msec by the recycling timer.

Results

The midline averaged evoked response to each condition for all four replications of each subject were superimposed by visual inspection. Each record was then divided according to eye of stimulation: right, left, and both. In this way the response to all sixteen conditions for each eye conditions was obtained. A zero voltage baseline was then determined in the following way. An average of the first 50 msec of activity in the superimposed tracings was taken as the zero line for each record. This method is based on the assumption that during this period of time only random, non-evoked activity is present. The average of this random activity should thus be zero voltage. This procedure is described in detail by Harter and White (1968). After this line was determined, two measures were found to be most influenced by the experimental manipulations. The first measure was a primarily negative peak occurring at a latency of either 100 msec or 120 msec for all subjects. The second measure was taken at the most positive point within a 10 msec interval epoch for each subject. This occurred between 180-200 msec for three of the subjects and between 160-180 for the other two. All records were measured in microvolts from the zero baseline. Another manipulation was then made. The superimposed tracings reflecting the four replications of a given condition were then averaged by visual

inspection to obtain a simplified representation of the data (Figure 3). This procedure allowed an interpretation of the contribution of each of the monocular waveforms to the waveform of the binocular presentation.

As can be seen in Figure 3, which presents data from one subject, a dominance of waveform appears to occur in all binocular conditions containing a diffuse pattern. This trend held consistently for all subjects. By looking across the top and along the left hand column of this figure, we can see that it is the waveform of the monocular response to pattern that is most similar to the binocular waveform. When two pattern stimuli are presented, a different process appears to be working. In these cases none of the monocular response waves dominates. Instead, there seems to be a summation of the two monocular responses in the binocular wave and amplitude.

In order to examine the nature of these interactions, the aforementioned latency measures were made on the raw data and statistically analysed. The two monocular conditions were analyzed separately from the binocular conditions. This was done in order to reduce the complexity of the statistical computations. The monocular analysis consisted of three main factors: eye stimulated (A), pattern to eye flashed (B), and pattern to eye not flashed (C). For the group analysis on the N-100 measure, only factor (B) was found to be statistically significant (.001). For the monocular P-200 measure analysis (B), and the interactions of eye by pattern to eye flashed (AB) were both found to be significant at the .05 level (Tables II and III). These data will be described in detail later.

Fig. 3. Simplified waveforms. Figure presents simplified waves for one subject (BS). Monocular waves to pattern presented to right eye and to pattern to left eye are compared to the waveform obtained when they are presented binocularly.

PATTERN TO RIGHT EYE
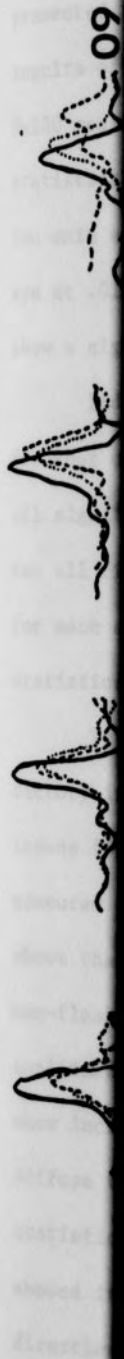
PATTERN TO LEFT EYE
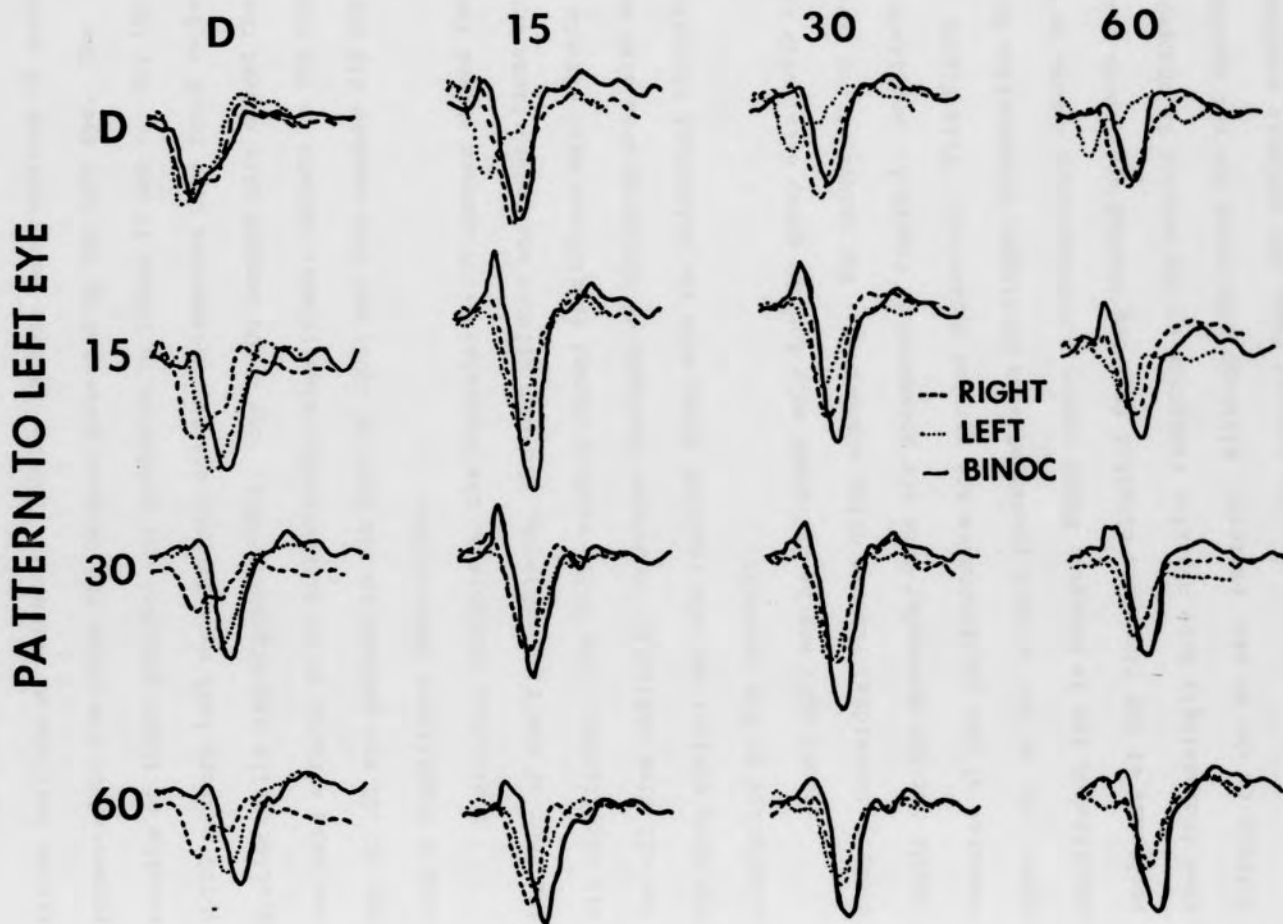
--- RIGHT
····· LEFT
— BINOC

The binocular conditions were separately analyzed using a two factor Analysis of Variance. The two factors here consisted of pattern presented to the right and pattern presented to the left eye. The results of these analyses are presented in Tables IV and V. For the N-100 measure both main factors and the interaction were found to be statistically significant (.001). The P-200 measure also showed the two main effects to be statistically significant, pattern to the right eye at .01 and pattern to the left at .005; but this measure did not show a significant interaction.

Individual analysis on the binocular N-100 measure showed that for four of the five subjects, the main effects and interactions were all significant. The P-200 measure showed significant main effects for all five subjects. Monocular Analysis of Variances were also done for each subject and are reported along with the individual binocular statistics in the appendix.

Trends will now be discussed only for the group data, with contradictory individual results being elaborated. The nature of the grouped trends for the monocular data are presented in Figure 4. Amplitude measures at the two latencies are graphed separately. This figure shows that as the pattern presented with continuous illumination to the non-flashed eye is changed, there occurs a corresponding change in the amplitude of the responses elicited from the flashed eye. Both measures show increasingly more negative responses as the pattern is changed from diffuse to the 60 min. pattern. Although this trend did not approach statistical significance for the grouped data, all subjects consistently showed it. The value of the slope differed among subjects, but the direction was constant for all.
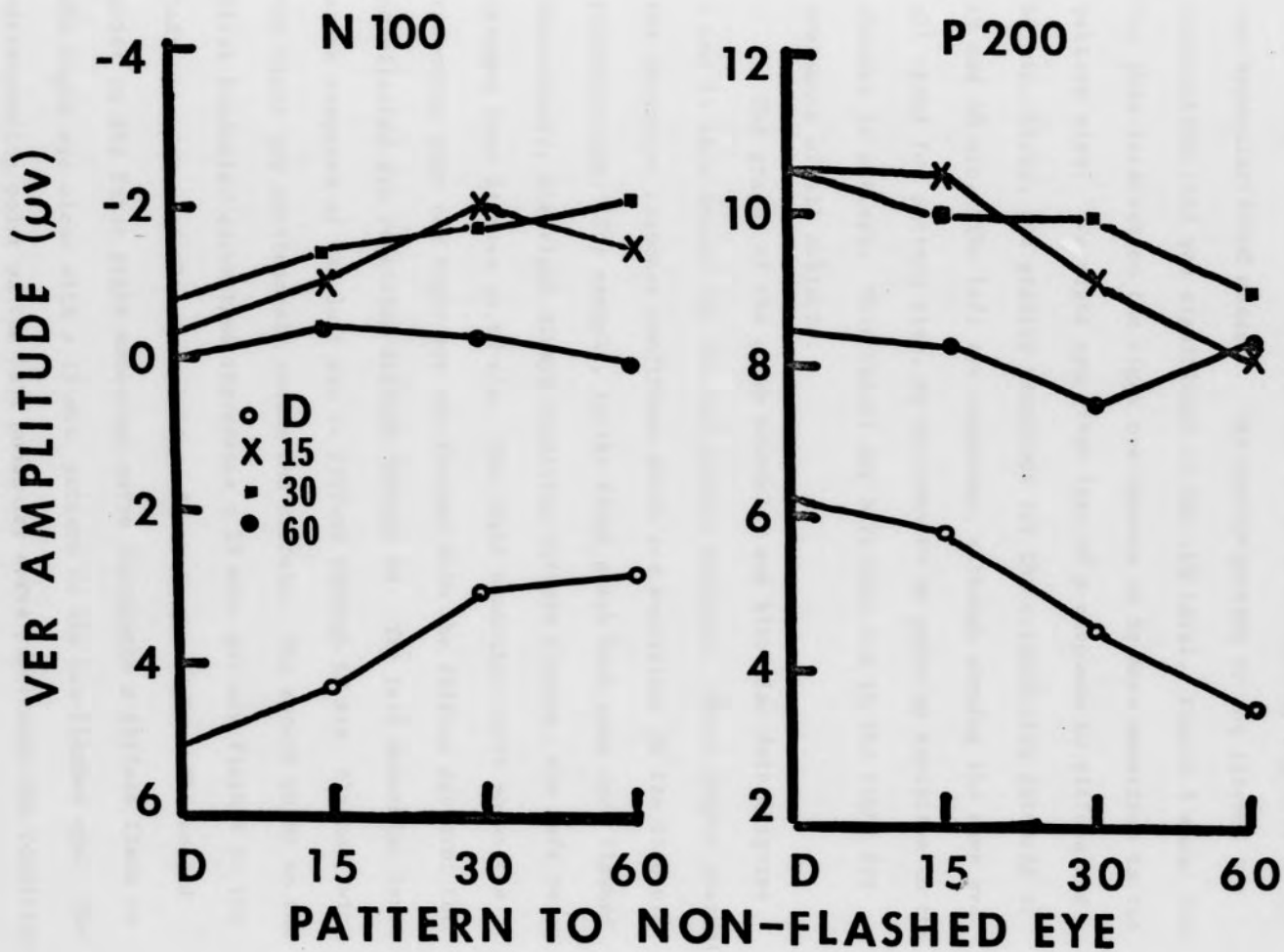
Fig. 4.   Influence of non-flashed eye.   Figure presents N-100 and P-200 responses to the flashed eye pattern as a function of pattern to other eye.   Graphs represent grouped data collapsed over flashed and over non-flashed eye.

PATTERN TO NON-FLASHED EYE

One interaction also proved to be statistically significant for the monocular P-200 measure. The eye-by-pattern to the flashed eye interaction (AB) was significant at the .05 level. Figure 5 shows that for this interaction the right eye appears to be more sensitive to the pattern size. The right eye gives less of a response to diffuse and 60 min. sizes, and greater responses for the optimal size patterns of 15 and 30 min. The left eye responses, although showing the same over-all trend for pattern size, do not seem to be quite as sensitive to the changes in pattern. This result may have been due to the right eye dominance of all subjects.

The graphs of the group monocular and binocular data (Figures 6 and 7) show trends for the two latency measures. These graphs present the monocular response conditions which are equivalent to the binocular presentations. For example, in the first graph both eyes were flashed binocularly; the right always receiving diffuse flashes, the left being changed from diffuse to 60 min. The right monocular curve shows the responses when the right eye was flashed with the diffuse pattern; the non-flashed eye receiving diffuse through 60. The left monocular curve shows response of the left eye to diffuse through 60 min. flashes, with the right eye continuously seeing the diffuse. The second point on the first binocular curve then represents a 15 min. pattern flashed to the left eye with a simultaneous diffuse flash to the right. The second point on the first right monocular curve represents a diffuse flash to the right eye alone with a 15 min. pattern to the non-flashed eye. The corresponding point on the left monocular curve represents the condition where the 15 min. pattern was flashed to this eye, the non-flashed right

Fig. 5. AB interaction, P-200. Eye-by-pattern to eye flashed interaction for measure P-200. Grouped data shows eye differences as a function of pattern flashed to that eye.

flashed

ences as

VER AMPLITUDE (μV)

RIGHT EYE
LEFT EYE

15   30   60

PATTERN TO
EYE FLASHED

30
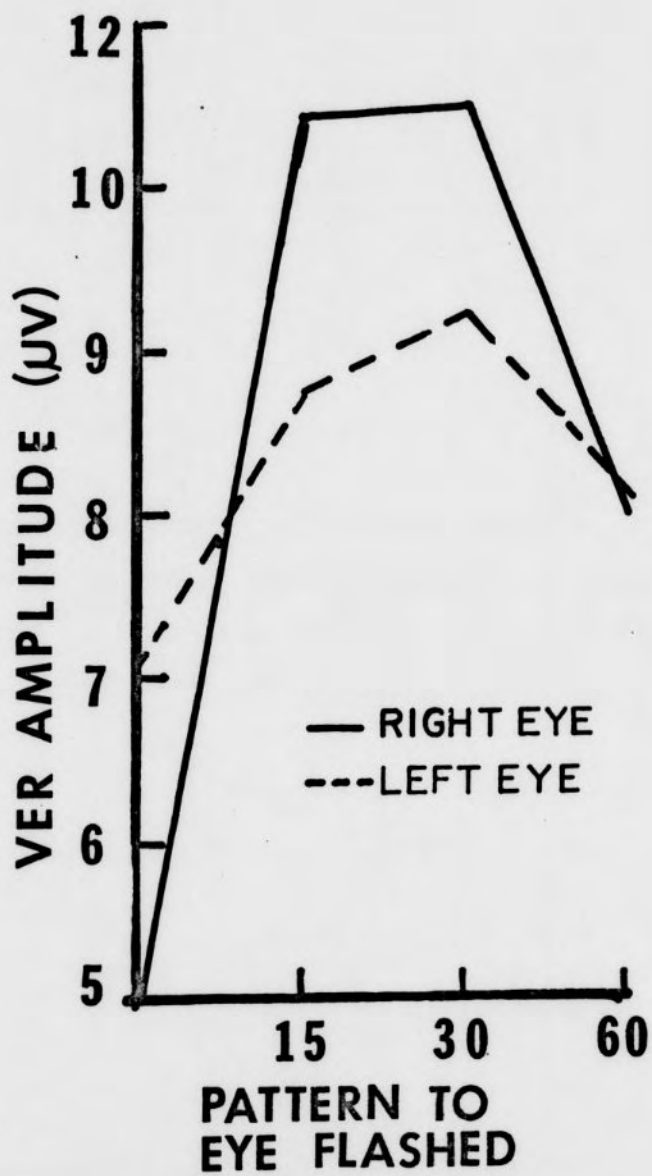
Fig. 6. Binocular summation, N-100. Group data for measure N-100 is a comparison of monocular response conditions equivalent to the binocular responses to that condition. Each graph represents a single pattern to the right eye while that to the left was changed.

measure n-100
PATTERN TO RIGHT EYE

measure n-100

PATTERN TO RIGHT EYE

PATTERN TO LEFT EYE
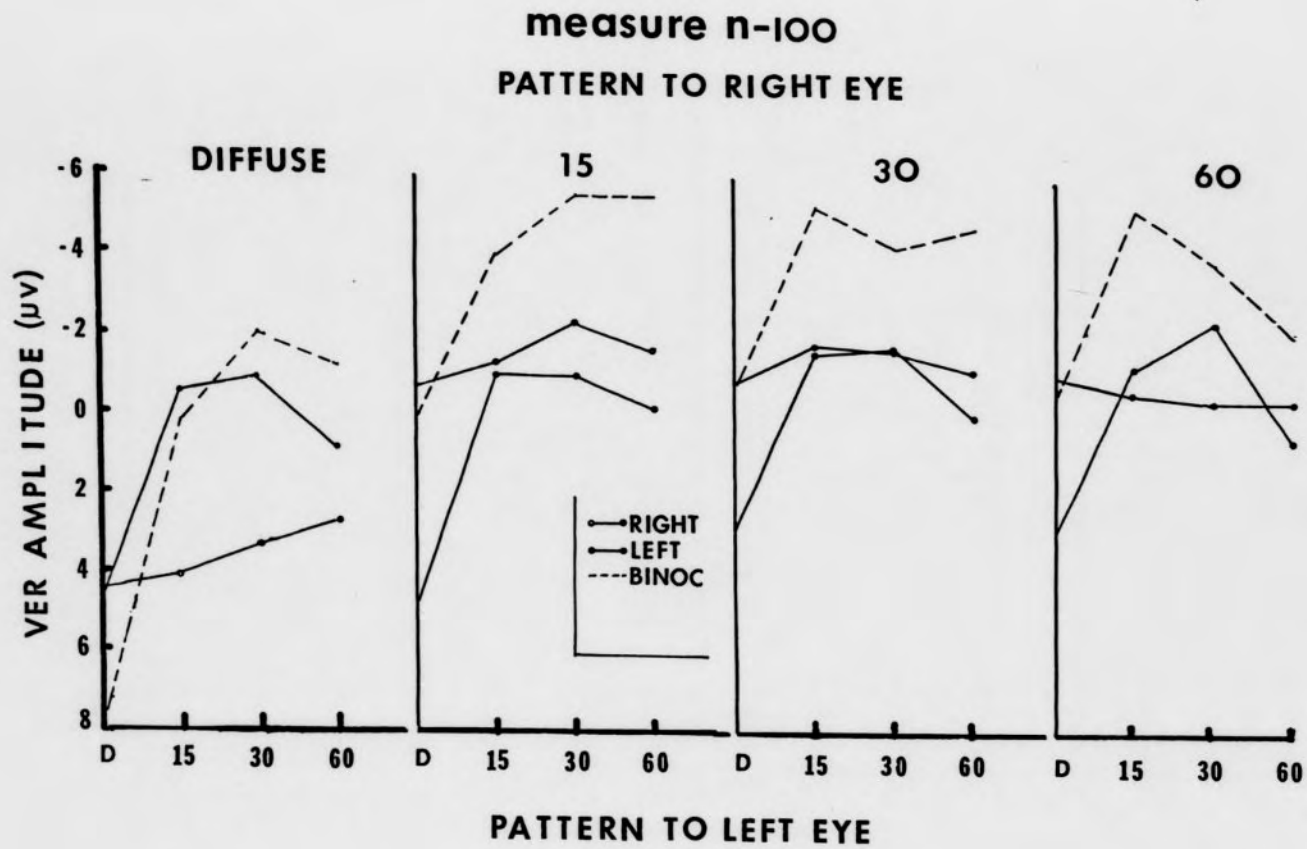
Fig. 7. Binocular summation, P-200. Group data for measure P-200 is a comparison of monocular response conditions equivalent to the binocular responses to that condition. Each graph represents a single pattern to the right eye while that to the left was changed.

measure P-200
PATTERN TO RIGHT EYE

measure p-200

PATTERN TO RIGHT EYE

DIFFUSE **15** **30** **60**

VER AMPLITUDE (µv)

16
14
12
10
8
6
4
2

D 15 30 60   D 15 30 60   D 15 30 60   D 15 30 60

RIGHT
LEFT
BINOC

PATTERN TO LEFT EYE
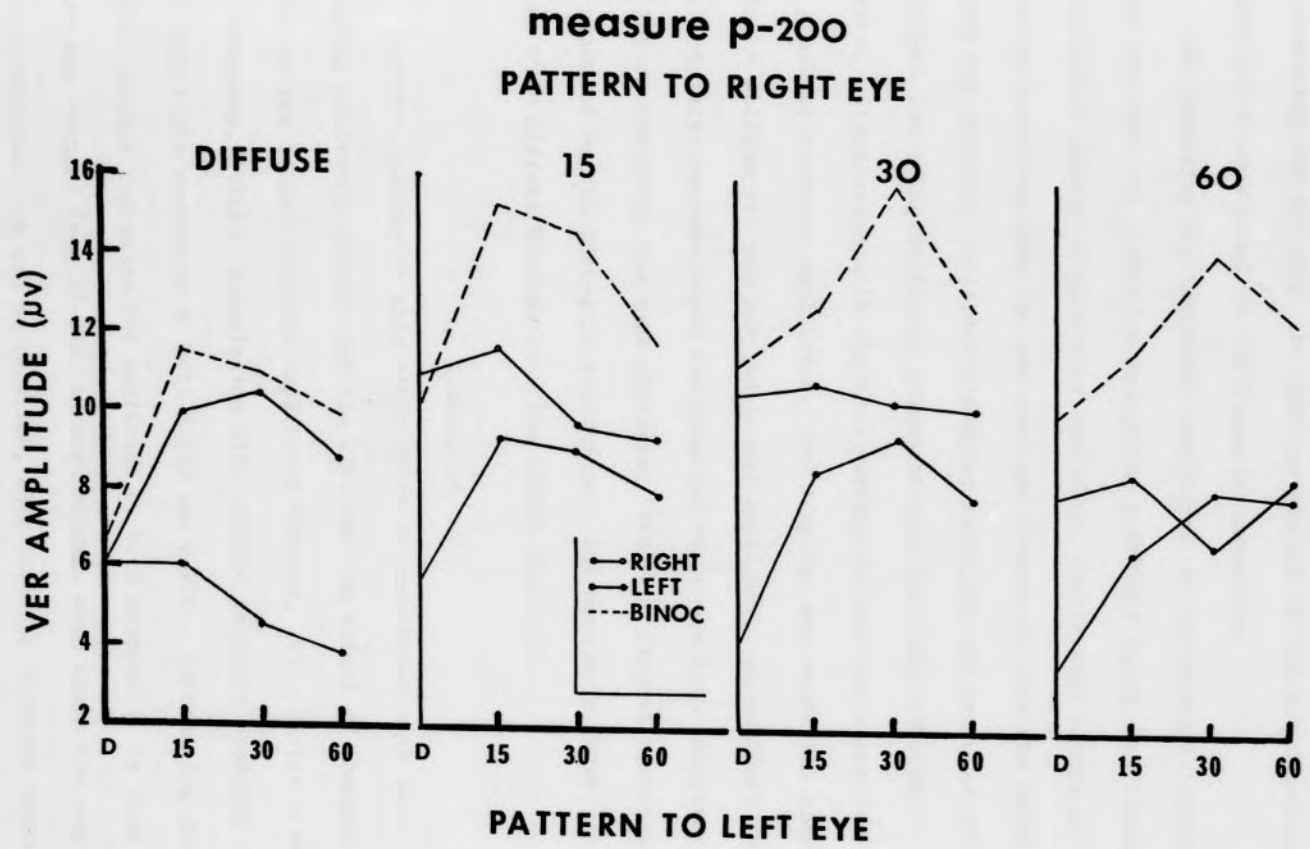
eye receiving the diffuse. In this way the sum of the two monocular flashes are always equal to the binocular condition.

In comparing the monocular amplitudes to the binocular responses, we can see that any condition containing a diffuse flash also results in the lowest amount of binocular summation, the largest amount of summation occurring when two patterns are presented. For the N-100 measure the greatest amplitude binocular responses are produced by conditions involving dichoptic presentations; i.e. two different patterns. Stimulation with the same pattern to each eye shows the next greatest response amplitudes. And finally, any condition containing a diffuse pattern has the lowest amplitude. In contrast to this, the later measure shows the greatest responses with binocular stimulation involving the same patterns. The next largest responses were produced by the dichoptic conditions. And once more those conditions with diffuse flashes were the lowest amplitude.

Discussion

A major finding of this study which is consistant with past work using patterned stimuli and the VER, was the effect of changes of pattern on the evoked response amplitudes (Harter, 1971; Harter & White, 1970; Uenoyama, 1971). Stimulation with diffuse patterns produced the lowest amplitude responses at both N-100 and P-200. Introducing patterns into the display increases the amplitude of both measures. As this pattern was changed from 15 min. through 60 min. once again the amplitudes began to decrease. As can be recalled, this inverted U shaped function has been proposed by Harter and White (1971) to reflect the modal size of the receptive fields in the visual system. The largest response being

to patterns subtending between line distances of 10 to 20 min. of
visual arc.

Further, analysis of the monocular conditions showed that
as the pattern to the non-flashed eye was changed from diffuse to the
patterns, the response amplitude in both measures increased in nega-
tivity. Previous work by Lehman and Fender (1967, 1969), has reported
that the amplitude of the evoked responses to diffuse flash decreased,
(N-100 going positive and P-200 going more negative) as the target
presented to the contralateral eye was changed from a diffuse to a.
cross to a grid. They proposed that this decrease was due to the in-
creased information load on the neurons that produced the evoked response.
The results of the present study have shown that the amplitude of the
N-100 component is increased, while that of the P-200 component is de-
creased (both going more negative). Increasing the information by
changing from a diffuse to a 15 min. pattern increases amplitude in the
same way as decreasing the information going from 15 to 60 min. patterns.
It would seem as if information is not the primary influence on ampli-
tude in this study. The design used by Lehman and Fender presented
flashes to only one eye, and always the same eye. Because of this a
purely attentional influence could account for their results. In our
design, however, both eyes were flashed in a given sequence which re-
quired that all information contained in the presentations be processed.

In binocular conditions containing a diffuse flash paired with a
pattern flash, it was found that the waveform of the binocular response
most resembled that of the monocularly evoked pattern response. These
findings support those of others using similar stimulus parameters

(Lansing, 1964; Cobb, Morton & Ettlinger, 1967; McKay, 1968; Martin, 1970; Cigánek, 1971). However, when two patterns were presented binocularly, the waveform dominance attributable to pattern stimulation seems to disappear. It would appear then, as if two different processes are occurring. The first would be a suppression of the input of the eye receiving diffuse light by the eye receiving patterned light. This type of process could only be said to occur in the diffuse flash conditions, however. In the binocular conditions containing two flashed patterns, it was seen that the waveform of the binocular response was similar to both of the monocular waveforms. Changes were found primarily in the amplitude differences between the monocular and binocular waves. The second process occurring would then involve simultaneous processing of all information and could better explain these different results. Perhaps when the system is presented with two dissimilar patterns, it must process all of the information at some minimal level. It may be this primary processing that is measured by the evoked potential.

A fourth finding of the present study is that for the first measure, N-100, dichoptic stimulation (different patterns to the two eyes) produced greater amplitude responses than dioptic (same patterns to the two eyes). The later measure, P-200, was found to show the opposite. This corroborates our earlier findings (Seiple, Harter & Salmon, 1972). This measure showed the greatest responses when the stimulation was with the same patterns presented to both eyes. Previous work (Fiorentini & Maffei, 1970; Regan & Spekreijse, 1970) has shown larger responses with disparate presentation at early latencies. This

report also shows this relationship for N-100; however, the later measure has shown the opposite effect. We propose that the greater earlier response is due to the greater number of primary simple cells excited by dichoptic presentations. Lesser earlier responses could be reflecting the redundancy of information in the dioptic conditions. The later measure would then represent the convergence of impulses on more complex cells and result in more uniform amplitude responses for both dioptic and dichoptic conditions.

In conclusion, it can be seen that in the patterned binocular conditions of the present study, the response is greater than the mean of the monocular responses; so that to some extent the fusion hypotheses are supported at the level of activity measured. However, we have also seen that diffuse flashes paired with pattern stimuli involve a process more like suppression than fusion. It would seem then that data is equivocal in its support of the two hypotheses on binocular interaction. It appears as if the visual system, at least at the level measured by these methods, is capable of using both fusion and suppression mechanisms. It was also shown that the form of information processing is very sensitive to the nature of the stimulus inputs. With stimuli containing little information, the diffuse flashes, the system seems to be able to partially suppress processing. However, when two patterned stimuli are presented all information is processed in a fusion sort of model.

The nature of processing then is determined in part by stimulus input. But it may also be influenced by higher cortical level activity, as suggested by the discrepancy of these results with those of Lehman

and Fender (1967, 1969). It was speculated that attentional set may also determine the way in which information is processed. This remains a question for further research.

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TABLE

Revised Design

APPENDIX

TABLE I

Subject Design

	Replication 1		Replication 2		Replication 3		Replication 4	
	Right Eye	Left Eye	Right Eye	Left Eye	Right Eye	Left Eye	Right Eye	Left Eye
1	30	30	15	15	60	60	Diffuse	Diffuse
2	D	30	15	60	30	60	D	15
3	60	30	15	D	15	60	D	30
4	15	30	15	30	D	60	D	60
5	30	D	60	15	60	30	15	D
6	D	D	60	60	30	30	15	15
7	60	D	60	D	15	30	15	30
8	15	D	60	30	D	30	15	60
9	30	60	D	15	60	15	30	D
10	D	60	D	60	30	15	30	15
11	60	60	D	D	15	15	30	30
12	15	60	D	30	D	15	30	60
13	30	15	30	15	60	D	60	D
14	D	15	30	60	30	D	60	15
15	60	15	30	D	15	D	60	30
16	15	15	30	30	D	D	60	60

TABLE II

Monocular Group Analysis Measure N-100

Source	SS	Df	MS	F	Significance
Total	124759.11				
Treatment	52921.21	31			
(A)Eye Flashed	329.19	1	329.19		
(B)Pattern To Eye Flashed	47822.63	3	15940.88	12.12	.001
(C)Pattern To Eye Not Flashed	2312.38	3	770.79	–	–
(A) X (B)	629.03	3	209.68	–	–
(A) X (C)	276.38	3	92.13	–	–
(B) X (C)	1500.53	9	166.73	–	–
(A) X (B) X (C)	51.08	9	5.75	–	–
Subjects	33500.29	4			
Treatment X Subjects	38337.61	124			
(A) X (S)	1323.20	4	330.8	7.51	.001
(B) X (S)	15787.25	12	1315.6	29.86	.001
(C) X (S)	8876.79	12	739.73	16.79	.001
(A) X (B) X (S)	2762.71	12	230.23	5.23	.001
(A) X (C) X (S)	1629.57	12	135.8	3.08	.01
(B) X (C) X (S)	6371.99	36	177.00	4.02	–
(A) X (B) X (C) X (S)	1586.1	36	44.06	–	–

TABLE III

Monocular Group Analysis Measure P-200

Source	SS	Df	MS	F	Significance
Total	177652.67				
Treatment	47586.47	31			
(A) Eye Flashed	1590.75	1	1590.75	1.16	–
(B) Pattern To Eye Flashed	36419.69	3	12139.90	6.30	.01
(C) Pattern To Eye Not Flashed	4679.30	3	1559.77	3.28	–
(A) X (B)	1629.17	3	543.06	4.55	.05
(A) X (C)	900.63	3	300.21	3.76	–
(B) X (C)	2039.21	9	226.58	1.24	–
(A) X (B) X (C)	327.72	9	36.41	.77	–
Subjects	85085.76	4			
Treatment X Subjects	44980.44	124			
(A) X (S)	5481.52	4	1370.38	29.02	.001
(B) X (S)	23107.37	12	1925.61	40.77	.001
(C) X (S)	5709.20	12	475.77	10.07	.001
(A) X (B) X (S)	1433.02	12	119.42	2.53	.05
(A) X (C) X (S)	958.76	12	79.90	1.69	–
(B) X (C) X (S)	6590.27	36	183.06	3.88	.001
(A) X (B) X (C) X (S)	1700.30	36	47.23	–	–

TABLE IV

Binocular Group Analysis Measure N-100

Source	SS	Df	MS	F	Significance
Total	388859.92				
Treatment	223070.42	15			
(A)Pattern To Right Eye	117421.71	3	39140.57	14.14	.001
(B)Pattern To Left Eye	77294.41	3	25764.80	14.77	.001
(A) X (B)	28354.30	9	3150.48	6.03	.001
Subjects	92835.84	4			
Treatment X Subjects	72953.66	60			
(A) X (S)	33212.43	12	2767.7	5.30	.001
(B) X (S)	20939.23	12	1744.94	3.34	.01
(A) X (B) X (S)	18802.00	36	522.28	–	–

TABLE V

Binocular Group Analysis Measure P-200

Source	SS	Df	MS	F	Significance
Total	448470.35				
Treatment	99063.55	15			
(A)Pattern To Right Eye	51493.39	3	17164.46	8.39	.005
(B)Pattern To Left Eye	36168.31	3	12056.10	6.50	.01
(A) X (B)	11401.85	9	1266.87	1.82	-
Subjects	277538.77	4			
Treatment X Subjects	71868.03	60			
(A) X (S)	24562.00	12	2046.83	2.94	.05
(B) X (S)	22241.08	12	1853.42	2.66	.05
(A) X (B) X (S)	25064.95	36	696.25	-	-

TABLE VI

Individual Monocular Analysis N-100

		Subjects				
		MRH	LS	LW	SH	BS
Conditions	Df					
(A) Eye Flashed	1	-	9.84***	1.25	1.73	1.17
(B) Pattern To Eye Flashed	3	8.74***	14.91****	22.13****	63.55****	16.75****
(C) Pattern To Eye Not Flashed	3	3.82	23.91****	7.91***	56.02****	16.12****
(A) X (B)	3	18.18****	66.01****	19.32****	39.72****	4.00*
(A) X (C)	3	15.62****	29.85****	2.76	35.60****	14.14***
(B) X (C)	9	1.33	1.52	3.30**	2.79*	-
(A) X (B) X (C)	9	7.66****	2.02	-	1.20	-
(A) X REP	3	4.48*	1.18	5.51**	1.30	3.82*
(B) X (R)	9	2.70*	2.23****	1.38	1.19	1.04
(C) X (R)	9	2.84*	1.82****	2.30	1.78	1.77
(A) X (B) X (R)	9	-	1.96****	1.08	1.51	-
(A) X (C) X (R)	9	-	1.84****	3.02*	1.44	-
(B) X (C) X (R)	27	-	1.21	-	-	-
(A) X (B) X (C) X (R)	27	-	-	-	-	-

Significance **** .001
*** .005
** .01
* .05

TABLE VII

Individual Monocular Analysis P-200

				Subjects		
		MRH	LS	LW	SH	BS
Conditions	Df					
(A) Eye Flashed	1	–	26.35****	15.22*	–	17.18*
(B) Pattern To Eye Flashed	3	–	4.90**	14.41****	50.37****	56.34****
(C) Pattern To Eye Not Flashed	3	5.14*	1.05	15.21****	26.06****	13.06***
(A) X (B)	3	20.09****	5.75*	8.77****	54.89****	59.25****
(A) X (C)	3	4.94*	3.65	16.54****	30.84****	17.10****
(B) X (C)	9	1.91	2.14*	1.17	1.27	4.23****
(A) X (B) X (C)	9	11.56****	3.64**	–	1.35	–
(A) X REP	3	24.65****	3.24	9.39****	8.10****	18.28****
(B) X (R)	9	12.90****	1.06	–	–	–
(C) X (R)	9	7.38****	2.47*	–	–	2.95*
(A) X (B) X (R)	9	10.83****	–	1.12	1.06	–
(A) X (C) X (R)	9	4.52****	2.24*	1.12	–	3.20*
(B) X (C) X (R)	27	1.67	–	–	–	–
(A) X (B) X (C) X (R)	27	–	–	–	–	–

Significance **** .001
*** .005
** .01
* .05

TABLE VIII

Individual Binocular Analysis N-100

				Subjects		
		MRH	LS	LW	SH	BS
Conditions	Df					
(A) Pattern To Right Eye	3	8.25****	1.00	40.88****	92.07****	71.60****
(B) Pattern To Left Eye	3	7.94****	.98	16.46****	49.18****	36.45****
(A) X (B)	9	5.78****	1.00	6.29****	4.77****	7.44****

Significance **** .001
*** .005
** .01
* .05

TABLE IX

Individual Binocular Analysis P-200

Conditions	Df	MRH	LS	Subjects LW	SH	BS
(A) Pattern To Right Eye	3	4.94**	4.07*	19.65****	25.27****	46.28****
(B) Pattern To Left Eye	3	10.60****	6.40***	12.59****	47.40****	41.77****
(A) X (B)	9	2.98***	3.27***	8.19****	1.81	18.42****

Significance **** .001
*** .005
** .01
* .05