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The purpose of this investigation was to study the underlying physiological processes involved in the evoked potential to patterned visual stimulation. Specifically, the study was designed to assess the role of the photopic and scotopic visual systems as mediatory processes subserving occipitally elicited potentials to a series of checkerboard patterns. In addition, it was hoped that the research would provide further information with respect to the hypothetical mechanisms of lateral inhibition and receptive field size and their contribution to complex visual processes.

Six subjects participated in the experiment. Evoked potentials were recorded to a series of patterned stimuli that were illuminated with red and blue flashes presented to central and peripheral retinal sites against high and low levels of background luminance.

Statistical analysis of the data revealed significant relations between evoked potential amplitude and the main effects of background, site, and check-size. Amplitude was also significantly related to the interaction effects of background x site, check-size x background, check-size x color, and site x color x background.

Discussion of the results was in terms of the differential functional behavior of photopic and scotopic visual processes. Several comments were directed to the possible importance of lateral inhibition and receptive field size in the generation of these data.

Retinal Processes Involved in the Evoked Cortical Potential to Patterned Stimuli

by

William Franklin Greer, Jr.

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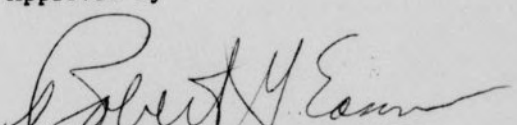

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INTRODUCTION

The use of the visually-evoked averaged cortical potential (VER) has proven to be an effective means of investigating the electrophysiology of the human visual system. Numerous parametric studies manipulating simple stimulus dimensions have shown that properties of the VER (latency, amplitude, polarity) systematically change with changes in the physical stimulus (Eason, Oden, and White, 1967; Tepas and Armington, 1962; Vanzulli, Bogacz, Handler, and Garcia-Austt, 1960). Exemplary of these studies is one by Eason, Oden, and White (1967) in which particular components of the VER were found to correlate with certain accepted facts of retinal anatomy and neural transmission. They reported, for example, that the latency of the VER increases as the locus of retinal stimulation is progressively shifted to a series of eccentric positions on the peripheral retina. This progressive latency increment parallels closely Osterberg's rod-cone density function and the established differences in the conduction velocity of these two receptor processes. There have been a number of other studies dealing with the areal and intensive dimensions of the luminous flash which have similarly revealed correlations between the characteristic features of the VER and known neurophysiological processes (Armington, 1968; Boynton and Riggs, 1951; Devoe, Ripps, and Vaughn, 1968). The communality among these studies is that they have all relied on diffuse light as the principal evoking stimulus. The influence of a patterned luminous field on the occipitocortical

potential was largely ignored until the more basic dimensional relationships could be established.

More recently, there has been a group of investigators who have focused their attention on this research problem since it is primarily information of a complex patterned nature that is transmitted to the occipital cortex under normal conditions (Harter, 1969; Harter and White, 1968; John Herrington and Sutton, 1967; Lifshitz, 1966; Reitveld, Tordoir, Hagenouw, Lubbers, and Spoor, 1967; Spehlmann, 1965). Essentially, their findings indicate that the VER is extremely sensitive to the presence and nature of the pattern in the evoking stimulus and that among its most significant features are the quantity and sharpness of the borders or edges. They have all noted with varying degrees of specificity and agreement that certain aspects of the VER waveform vary with the presence of pattern, the sharpness of the pattern, and the density of edges in the visual field. Each author has formulated tentative hypotheses as to the nature of the underlying physiological processes involved in the generation of this response. Their theoretical explanations have been couched in terms of the operations of two hypothetical retinal processes--lateral inhibition and size of receptive fields. A more detailed explication of these constructs and their application to this research will be given later.

The primary purpose of this present investigation was to analyze the underlying physiological processes involved in the coding and processing of contour stimuli, especially at the retinal level. This was accomplished by functionally varying the influence of the scotopic and

photopic systems through variation of background intensity, wavelength, and site of retinal stimulation. In addition, the experiment can be described as a parametric exploration of the main and interactive effects of background intensity, color, site of retinal stimulation, and check-size on the evoked potential. A more comprehensive analysis of the theoretical and empirical rational of this research project will be presented below.

The Evoked Potential

The procedure used to record cortically-evoked responses originated with the development by Dawson (1954) of a method of manually measuring and averaging individual evoked responses. This process was improved and advanced by Barlow and Brazier (1960) and culminated in the invention of an electronic averaging device which summated transient electrical signals initiated at sensory receptors. This method is based on the principle that the average amplitude of a response time locked to a reference point will increase in proportion to the number of samples; while fluctuating, random activity essentially cancels itself out. This extraction process permits the recording of small voltage responses ordinarily buried in the din of ongoing spontaneous activity. The technique provides a statistical record of the waveform and latency characteristics averaged for a large number of evoked responses.

Although different laboratories have often obtained conflicting results and drawn divergent conclusions, there is a general agreement that this is probably the result of small samples and variant technical

procedures such as recording methods, electrode placement, and different stimulus conditions.

Review of the Literature

A number of studies have been conducted with respect to the influence of site of retinal stimulation on the VER. Eason, Oden, and White (1967) reported changes in the amplitude and latency of the VER using red and blue flashes of one degree subtense for stimulation of the peripheral retina at a series of eccentric sites. Progressive peripheral stimulation with the red light resulted in a decrease in response amplitude beginning at 10 to 15 degrees. The amplitude to the blue light remained relatively stable at distances from the fovea of up to 40 to 50 degrees, showing indications of attenuation only at extreme peripheral loci. When stimulating retinal positions near the fovea, they found that the amplitude of the response to red light was considerably larger than that to blue light. They concluded that although changes in VER amplitude did occur, they did not seem to be related to Osterberg's rod-cone density curves or to the differential sensitivity of the photopic and scotopic systems. They also noted that the waveform of the VER to peripheral stimulation had a simpler more sinusoidal appearance than did those to identical stimulation of the fovea. Armington (1966) investigating concurrent changes occurring in the VER and ERG observed that the amplitude of both measures were of greater magnitude to foveal than to peripheral stimulation.

Some investigators of evoked potentials have proposed that cortical responses to retinal stimulation reflect primarily or

exclusively photopic or foveal activity (Armington, 1966; Devoe, Ripps, and Vaughn, 1968; Potts and Nagaya, 1965; Reitveld, Tordoir, and Duyff, 1965). Potts and Nagaya (1965) reported that the VER to a six-one hundredth degree red flash was absent at only two degrees eccentricity from the fovea. These results received confirmation in an investigation by Armington (1966) in which he found a substantial reduction in the amplitude of the VER to stimulation of an area several degrees from the fovea. These data, girded by the established disproportionate spatial representation of the macular retina in the occipital cortex, prompted Armington to conclude that VER's are principally a foveal (cone) response receiving little or no contribution from the rod system.

Reitveld, et al, (1967) conducted a study to determine the influence of a number of stimulus variables on the VER to diffuse and patterned stimuli. One phase of the research was designed to assess the extent to which the central (fovea, perifovea) and peripheral areas of the retina contributed to the cortical response to patterned stimuli. Their results indicated that cortical potentials evoked by checkerboard stimuli are predominantly of foveal origin. (Refutative evidence for this conclusion will be presented and discussed later.)

Devoe, Ripps, and Vaughn (1968) summarize the accumulated evidence for the "fovealist" position stating that:

> One fact seems reasonably certain; namely, that the evoked occipital response derives mainly from the photopic (cone) system. . . the photopic nature of the response is strengthened by recent evidence indicating that the optic nerve fibers subserving both rod and cone receptors transmit only the cone message when the stimulus exceeds cone threshold (p. 84).

This statement is inconsonant with the data reported above by Eason, Oden, and White (1967) and with our laboratory observations over the past several years. Eason has recorded rather robust evoked potentials to peripheral stimulation where the amount of stray light contaminating the response would be negligible. Van Balen and associates (1966) have attacked this issue directly attempting to demonstrate conclusively that peripheral retinal processes contribute to the VER. They used a dim flash subtending less than one degree of visual angle to minimize the influence of stray light and reported that they were able to record a response to peripheral stimulation. However, they, like several of the investigators cited above, found the amplitude of this response to be markedly less than that to foveal stimulation. It is possible that had they used a small but more intense stimulus they could have recorded larger amplitude potentials.

There has been a sparsity of studies relating changes in the wavelength of the stimulus to changes in the VER. Shipley, Jones and Frye (1965), reported a color specificity in the waveform of the VER using Maxwellian-view stimulation. The red response, with a prominent positive deflection at about 200 msec. after stimulation and a large negative trough at 325 msec., stood strikingly apart from potentials evoked by the other colors. The response to blue was characterized by its small oscillatory waveform with one principal descending component. He cautions that such specificity in waveform to different spectral stimuli has been obtained only when using the Maxwellian-view method of retinal stimulation. Comparing spectral sensitivities of the ERG and

VER, Armington (1966) found that maximal amplitude potentials were obtained with red, rather than blue, especially at the fovea. He also observed that the largest ERG and VER responses were obtained with stimulation of intermediate wavelengths. This is consistent with the psychophysical studies of spectral sensitivity. Lennox and Madsen (1955) found that evoked responses elicited by different wavelengths in anesthetized cats differed in their characteristics, especially those related to latency.

White and Eason (1966), using a Ganzfeld apparatus to investigate the effects of stimulus intensity and background level on the VER, found that the overall amplitude was diminished by either lowering the flash intensity or raising the background level. Increasing background level while holding flash intensity constant resulted in a selective increase and decrease in the amplitude of certain components. They also reported that different components of the VER varied as a function of stimulus color and that these differences were accentuated by variations in background level.

On the basis of the behavior of certain components of the VER under bright and low background conditions they speculated that specific waves reflected scotopic and photopic activity. They further hypothesized that the multiphasic waveform of the VER to Ganzfeld stimulation may reflect the arrival at the cortex of impulses from exclusive scotopic and photopic retinocortical pathways.

Venzulli, et al, (1960) observed similar variations in waveform of the VER to changes in background illumination.

The influence of patterned light flashes in contrast to diffuse ones on the VER was studied by Spehlmann (1965). Cardboards with a white surface and various geometric patterns including checks were used as visual stimuli. Diffuse light was obtained by illumination of a blank white square. He varied the number of contrast borders in the stimulus pattern as well as the geometric character of the stimuli. He found that a "late wave" (185-375 msec.) reliably distinguished the presence of pattern in the visual field. This wave showed a progressive increase in amplitude with decreasing check-size. The amplitude of the VER to patterned stimuli was always greater than that to diffuse flashes. He further found that the "typical" wave in response to patterned stimuli reverts to the shape observed to diffuse light when induced refractive changes degrade the retinal image. Spehlmann summarizes his results stating that

> . . . when checkerboard patterns were used which reflected the same amount of light (as the diffuse light) the "late wave" could be shown to depend only on the density of interfaces (edges) (p. 565).

He made no further attempt to investigate and refine this observation.

Reitveld and associates (1967) discuss a dissertation by MacKay (1966) who investigated the effects of a series of checkerboard patterns on the VER. The response obtained to patterned stimulation was similar to that described by Spehlmann. He failed to observe, however, an increase in the amplitude of the main positive wave with a decrease in check-size. He did not investigate the effects of defocusing.

John Herrington and Sutton (1967) were interested in the

relation between the perceptual content of the visual stimulus and the VER. Their evoking stimuli were a series of geometric shapes and words. They found that the waveform of the VER to a diffuse stimulus was different than that to a geometric form. When identical geometric shapes of unequal area were presented, no appreciable differences were discernible in the VERs. However, different geometrical shapes of equal area evoked different VER waveforms. The waveform was also influenced by the presence of two different words equated for total letter area. Shape, they posit, is a more important determinant of VER waveform than is size. It is the authors' contention that the informational or perceptual content inherent in the evoking stimulus must be considered in order to give a complete account of the factors influencing the waveform of the response. This assumption is based on the observation that changes can be obtained in the waveform of the VER without concommitant change in the physical energy in the evoking stimulus. The research of Hubel and Weisel (1963) would suggest an alternative hypothesis based on the selective responses of different cortical cells to the orientation of the evoking stimulus.

An extensive analysis of the effects of patterned versus diffuse stimuli on the VER was undertaken by Reitveld, et al (1967). Their findings corroborated that of the preceding investigators in that the VER to checkerboard stimuli could easily be distinguished from that to diffuse light. They noted, as did Spehlmann, a surface positive component (180-250 msec.) whose amplitude was greater than that of the largest positive wave in response to diffuse stimuli. Also in

agreement with the findings of Spehlmann was the progressive increment in amplitude of the VER as the size of the patterned elements was decreased. Continued dimunition of check-size, however, resulted in a precipitous decrease in amplitude. There was some variability among the Ss as to the check-size giving the largest amplitude response. This was probably due to resolution differences among the Ss.

In an attempt to analyze the particular property of the checkerboard stimuli essential for the generation of the pattern response, they compared the VER to checks with that to striped patterns. The striped patterns evoked a response similar to that of diffuse light. They concluded that the presence in the pattern of intersecting borders is crucial. Along this same line, they asked if changes in the angle of the intersections would change the response. They found that a diamond shaped border evoked a response similar to that of checks but of diminished amplitude. As the angle of the contours became less acute, the amplitude of the response decreased. The authors assert that it is the presence in the patterned stimulus of acute or right angles that is essential for the evocation of the "typical" response. A research investigation in progress in our laboratory in which circles have been substituted for checkerboard squares has shown that it is the distance between edges that is critical and not their angular configuration as Reitveld has presumed.

One of the most systematic investigations of the effects of check-size and sharpness of contours on the VER was conducted by Harter and White (1968). They had their Ss view different size

checkboard patterns through a graduated series of ophthalmic lenses. They found, as have Spehlmann (1965) and Reitveld, et al (1967) that the amplitude of the VER increases with a decrease in check-size. The reduction in check-size resulted in a gradual accentuation of the early components of the response. As the checks became imperceptible, the VER reverted back to a simple sinusoidal response. More importantly, they discovered that certain components of the VER were sensitive to the sharpness of contour of the patterned stimulus. The amplitude of a component occurring at a latency of 90-100 msec. became less negative while a later component (latency 180-200 msec.) became less positive with degradation of the stimuli. They were able to accurately estimate the degree to which the pattern had been defocused by plotting changes in amplitude of certain components as a function of degradation. In a subsequent study, Harter and White (in press) demonstrated that the degree of refractive error determined the check-size which would result in the largest amplitude response, the relationship between amplitude and check-size being curvilinear. In the absence of refractive error, checks of 10-20' subtense gave maximal amplitude responses.

In an unpublished study, Harter (1969) investigated the relationship between check-size and locus of retinal stimulation. The results showed that with increasing peripheral stimulation the peak amplitude of the response was evoked by larger and larger checks. This is probably related to the fact that visual acuity is substantially reduced in the peripheral retina. This is tantamount to

artificially defocusing the image and is in agreement with the observed reduction in amplitude of VERs to degraded visual stimulus (Harter and White, 1968). In an interesting extension of these results, Eason, in his NSF research proposal, has speculated that

> the responses obtained to peripheral retinal stimulation (to a one degree spot of light) resemble those evoked by foveally presented defocused stimuli. Thus, the simple, sinusoidal character of the peripherally evoked response may be due to the fact that visual acuity drops off rapidly from the fovea and the flashes therefore become defocused (p. 8).

It will be remembered that Reitveld and associates reported that they were unable to evoke a response in the peripheral retina with checkerboard stimuli and that as result they assumed the potentials to be primarily mediated by the cone system. The research by Harter and White suggests that the reason they were unsuccessful in eliciting a peripheral response with checks was not the result of an intrinsic excitatory inefficacy of the stimuli but rather a consequence of their failure to use checks large enough to compensate for reduced peripheral acuity. The Ss may have simply been unable to clearly resolve the presence of edges in the small checks and therefore were responding to defocused stimuli. Had they used checks of a larger subtense, they may have been able to record peripheral responses.

The implications of this literature for the present investigation will be considered under the purpose section of the introduction.

Lateral Inhibition and Receptive Field: A Review of the Research

Of the stimulus information continuously being processed by the visual system, that related to the presence of contours and edges

in the visual field is of primary importance. Stimuli of a constant intensity are of limited moment to the system rapidly adapting the receptors upon which they impinge (Riggs, Ratliff, Cornsweet, and Cornsweet, 1953). The visual system is maximally sensitive to changes in illumination. Microelectrode studies of isolated ganglion cells in lower vertebrates show that maximum neural activity occurs when the stimulus changes its position or intensity. Steady illumination produces slight or no discharge of impulses in a large proportion of retinal ganglion cell axons (Hartline, 1940).

Contrast phenomena such as that of color and brightness are intimately associated with the general importance of borders in perception. Contrast is defined by the fact that an area appears brighter if it has a dark surround and that colors surrounded by their complementary appear more intense. The process exaggerates and enhances differences between two stimuli. In this regard, Thomas and Kovar (1965) investigated the relationship between perceived brightness and contour sharpness. They found that as the stimulus edges were gradually defocused the perceived brightness of the stimulus decreased monotonically. This study illustrates the importance of contrast as a determining influence in brightness perception and, as the authors suggest, may reflect the critical nature of retinal inhibition and receptive fields in visual sensation.

The problem in vision, then, is how the detection and enhancement of contours is attained in a system composed of essentially identical units of neural activity. Hartline and Ratliff (1957) have

proposed an empirical model to explain this process based on their detailed experimental analysis of the functional properties of neural networks in the lateral eye of the Limulus. The fundamental integrative process governing the behavior of this system is reciprocal inhibition among adjacent neural units. The receptor elements exert an influence on one another via a plexus of lateral interconnections. As their measure they used the frequency of discharge of impulses in an optic nerve fiber of one ommatidium. The principal findings of their research were: 1) inhibition of the test receptor increased as the intensity of light on neighboring cells was increased; 2) the larger the number of adjacent cells illuminated, the greater the inhibition on the test receptor; 3) inhibition of the test receptor was a decreasing function of the distance of illuminated neighboring cells; 4) the absolute influence exerted by a receptor depends on its own activity which in turn depends on the activity of surrounding cells. Thus, the discharge maxima and minima of receptor cells occur at the sides of the transition from one luminance level to another sharpening the neural representation of the contour.

The concept of a receptive field will now be considered since its interplay with lateral inhibition is of seminal importance to Harter's interpretation of the differential effects of check-size on the amplitude of the VER. The construct was first introduced by Adrian (1928) for tactile sensation and since has been extended to the retinal surface. Retinal receptive fields are based on the anatomical organization of the receptor cells there being a convergence

of many such units on each bipolar cell and several bipolars on each ganglion cell. For the visual system, then, a receptive field of a given ganglion cell may be defined as the area of the retina that when stimulated by a spot of light will cause firing in its axon. The more retinal receptors converging their impulses on a single ganglion cell the larger the size of the receptive field. Glezer (1965) has shown that the size of receptive fields progressively increases from the fovea outward, the rod or scotopic system having large numbers of cells converging their impulses on a given optic fibers. His experimentation further demonstrated the dependence of receptive field size on background luminance, their size increasing with decreasing ambient intensity. He also hypothesized that visual acuity may be determined by receptive field size since the system cannot discriminate spatially discrete events arising in the same optic fiber. Acuity is maximum in the fovea according to his model since many foveal cones have direct linkages with ganglion and cortical cells.

Investigating the functional properties of receptive fields in frogs, Hartline (1938) observed three characteristic patterns of impulse discharge in the optic fibers subserving these fields. He described them as "on" fibers which emit a brief burst of impulses upon stimulation; "off" fibers which gave a burst of impulses only when the stimulus was terminated; and "on-off" fibers which emit impulses only when the stimulus was turned on and off.

Kuffler (1953) investigating the receptive fields of ganglion cells of cats found that the pattern of discharge obtained when

stimulating the field varied as a function of the locus of stimulation. Some of the receptive fields had cells that responded only when their center was excited while stimulation of the peripheral surround resulted in an "off" response. Intermediate regions of the field gave an "on-off" discharge pattern upon illumination. Other cells had a distribution of discharge patterns that was exactly the opposite of this. Baumgartner and Hakas (1959) have identified cells in the occipital cortex whose receptive fields resembled those described by Kuffler for retinal ganglion cells. They also reported that the diameter of receptive fields of cortical neurons are substantially smaller than those of geniculate and ganglion cells. In addition, they have found cortical neuronal correlates of pattern vision. Cells which they have labeled B neurons respond differentially to variations in luminance while the activity of D neurons correlates with darkness information.

Hubel and Weisel (1962, 1963, 1965) have applied microelectrode techniques to the analysis of the organization of visual information at the cortical level. Their preparation was an anesthetized cat situated so that it could observe a screen onto which forms were projected. They recorded extracellularly from single cells in the striate cortex. They discovered first, that cells in the visual cortex did not have concentric receptive fields as do ganglion cells but rather rectangular or "edge" shaped ones. The specificity of these cortical cells was reflected by their firing only to edges of boundaries of particular shapes, sizes, positions, and orientations. Many cells

would simply not fire to diffuse stimuli. They also found a columnar organization of the visual cortex i.e., stimuli with different orientations initiate activity in different columns of cells.

In another study, Hubel and Weisel (1961) recorded the activity of cells in the lateral geniculate nucleus of a cat. They found that the discharge characteristics of ganglion cells ("on", "off", "on-off") were present as far in the visual system as the lateral geniculate body.

From the evidence presented it is clear that activity generated in any optic fiber depends not only on the excitation of specific receptor cells but also upon the spatial and temporal arrangement of the stimulation. The principal role of interaction among retinal cells is the accentuation of contrast at sharp spatial and temporal gradients.

Purpose of This Study

Based on known relationships between pattern stimulation and VERs and information garnered from retinal field studies, Harter (1968, 1969) raised a number of important questions: (1) Why is there a curvilinear relationship between check-size and VER amplitude? (2) Why do checks of 10-20' subtense produce the largest amplitude responses in the absence of refractive error? (3) Why is there a peak shift in VER amplitude to increasing peripheral stimulation?

A tentative theoretical explanation for these questions has been proposed by Harter based upon the behavior of two physiological processes assumed to underlie the coding of patterned stimuli--lateral

inhibition and receptive field size. He posits that when the checks subtend angles equivalent to the size of the receptive fields stimulated, lateral inhibition is minimized and the excitation in the subserving optic fiber is maximal. The result is that the amplitude of the VER is maximal. However, when two or more checks fall within the same receptive field the neural activity initiated in one area of the field inhibits activity in adjacent regions of the field thus reducing the total discharge output of the connecting optic fiber. As the between edge distance is further reduced inhibition increases. This results in smaller amplitude VERs.

Furthermore, he speculated that a functional correlate of receptive field size may be reflected by the check-size generating maximal amplitude responses. It was also suggested that receptive field size may be a critical determinant of visual acuity.

The purpose of the present study was to analyze further the construct of receptive fields and their relationship to evoked responses with particular attention being given to the extent to which the photopic and scotopic visual systems contribute to the VER to checkerboard stimuli.

The contribution of the functionally distinct photopic and scotopic systems was investigated in three ways. Firstly, two visual displays were used for presentation of the checkerboard patterns onto equal areas of the central and peripheral retina where the cones and the rods (the receptors forming the anatomical basis of the photopic and scotopic systems) are maximally dense. Secondly, red and blue

flashes were used to take advantage of the differential spectral sensitivity of the rods and the cones, the former having a low threshold to blue and the latter to red. Thirdly, two levels of background luminance were used one being a low condition for accentuation of rod function and the other a high condition for maximum cone function.

Since the size of a receptive field theoretically depends on the number of rods and cones converging their impulses on a given ganglion cell, and the proportion of these cells pooling their input is greater for the scotopic than for the photopic system, it is assumed that variation of the above conditions generates variation in receptive field size.

The smallest checks would be expected to generate the largest responses when the fovea is stimulated by the red light against a high intensity background. Larger checks should be required to give the same amplitude responses when the periphery of the retina is stimulated by a blue light against a dark background.

METHOD

Subjects

Six subjects, five males and one female, ranging from 22 to 40 years of age served in the experiment. Three of the Ss were experienced in electrophysiological research of this nature while the other three had no such previous experiences. The visual acuity of each subject was established prior to the experiment since certain components of the VER are known to be sensitive to the sharpness of focus of patterned stimuli (Harter and White, 1968). No S's acuity was less than 20/20 corrected. This control prevented resolution differences from confounding with the experimental variables. It was assumed that all Ss had normal color vision.

Experimental Design

This experiment was a four factorial repeated measures design containing thirty-two separate stimulus conditions. These thirty-two treatments were generated by stimulating central and peripheral retinal loci with four red and blue illuminated patterned stimuli superimposed against high and low levels of background illumination. Each stimulus condition was presented in separate blocks of 50 trials, with the blocks being counterbalanced in an ABAB-BABA-BBAA-AABB sequence for the four experimental sessions with no more than one session being run per day for any one S. One session consisted of recording 16 evoked potentials. Every subject was administered each of the thirty-two conditions, two replications being obtained for each condition.

One-hundred responses were summed for each recorded VER. Four experimental sessions were required to obtain a complete set of data for each S.

During the low background condition, the Ss dark adapted for approximately 20 minutes before the start of the experiment by wearing a pair of red goggles. The low background intensity was sufficient for the Ss to perceive the fixation point located in the center of the displays. The intensity of the stimulus flash was set so that it was about one log unit above threshold under both levels of background illumination.

The Ss were seated relaxed in the shielded cubicle and were given a few moments to adjust to the experimental setting prior to commencement of the actual experiment. They were instructed to fixate binocularly a small point in the center of the target during each trial and to count each flash in order to maintain a relatively constant level of internal arousal.

Preparation of Subjects and Electrode Placement

Occipitocortical responses recorded from the scalp are known to be attenuated by the impedence characteristics of the overlying cranial tissue. To reduce this resistence to less than 10,000 ohms the placement site for each S was rubbed with Redux Electrode Paste. The active commercial gold plated electrode was filled with electrode paste and placed securely in position on the midline one inch superior to the inion. It was held firmly against the scalp by an adjustable rubber headband. The reference electrode was then filled with

electrode paste and fastened to the right earlobe.

Instrumentation for Electroencephalogram and Evoked Potential Recording

One channel of a Grass six-channel Model 7 Polygraph was used to amplify and record each S's EEG. The channel contained a model 7 P5A, Wide Band A.C. EEG Preamplifier and a model 7 DAC D.C. Driver Amplifier. The polygraph was calibrated by feeding a known signal through the system, and then noting the amount of pen deflection.

To record the evoked potentials the amplified output from the polygraph was fed into a Mnemotron 400B Computer of Average Transients (CAT) for summation. The analysis time during the experiment was 0.5 sec. However, the Stimulus Switch was placed in the ORD. 20 position so that a delay of 0.1 sec. existed between the time that the analysis sweep began and the flash was presented. Consequently, the photo-flash unit was being triggered by the CAT at 100 msec. following the onset of the analysis sweep. This meant that the CAT was integrating and averaging the spontaneous cortical activity during the 100 msec. interval prior to stimulus onset. Therefore, only the last 400 msec. of each record contained the averaged evoked response to the flash stimuli. This enabled E to sample the Ss's averaged spontaneous EEG for indications of alpha rhythm that might be summating with the VER. It also provided a standardized baseline for subsequent quantification of the data. The evoked potentials stored in the CAT were plotted on graph paper with a Mosely X-Y Recorder, Model 2D-2, providing a permanent record of the Ss' responses. A Grason-Stadler 901B Noise

Generator was used to mask the clicks generated by the discharge of the flash tube. This prevented acoustical artifacts from contaminating the data. A schematic representation of the experimental instrumentation is shown in Fig. 1.

Apparatus

The Ss were placed in an electrically shielded cubicle to eliminate extraneous electrical interference. They binocularly fixated a dot located in the center of each display. The displays were mounted over a translucent screen placed at a distance of 36 in. from the Ss. They were illuminated from behind by a 10 msec. red or blue stimulus flash generated by a Grass Model PS-2 Photo Stimulator. The flash intensity was set at positions 2 and 4 under the low and high background conditions respectively. The flashes were presented at random intervals by a programmed tape. The average interstimulus interval was about 1 sec.

Color.--- The chromatic flashes were obtained by transmitting the light through one of two relatively narrow band Kodak Wratten filters with peak transmission at 450 and 640 mu respectively (numbers 29 and 45A). The filters were placed directly over the luminance source. E was responsible for changing the filters during the experimental session.

Background Illumination.--- Two levels of background illumination were included in the experiment. A 150W bulb regulated by a variable voltage control (VARIAC) provided the only source of

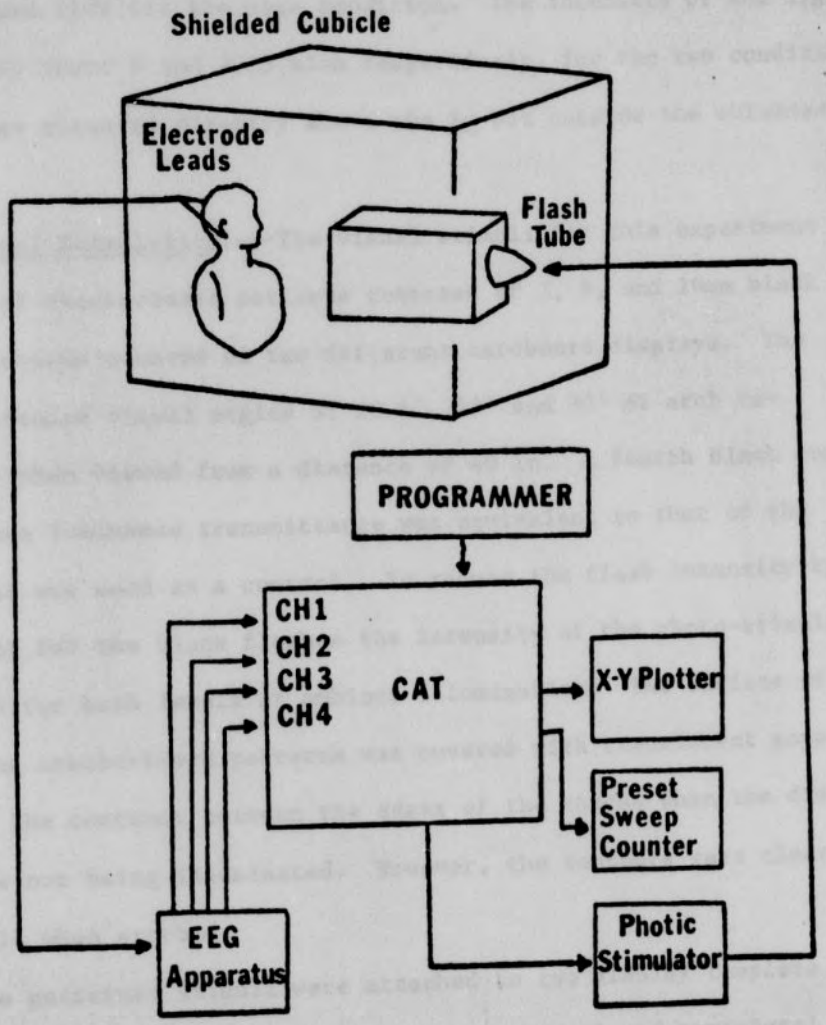


Figure 1. A schematic representation of the experimental instrumentation.

ambient illumination. The VARIAC was set at 19V for the low background condition and 110V for the high condition. The intensity of the light was slightly above 0 and 2.15 mlam respectively, for the two conditions. The lamp was situated directly above the Ss but outside the shielded cubicle.

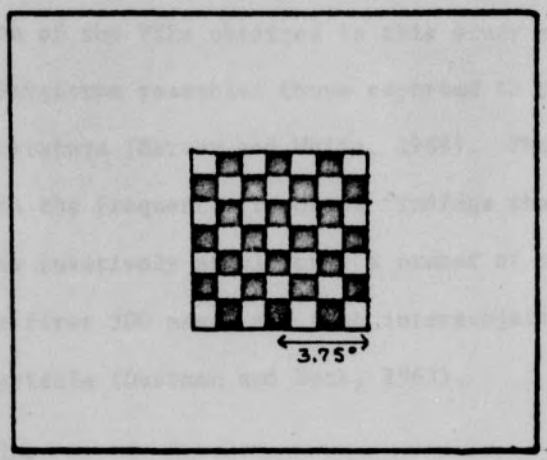
Visual Stimulation.---The visual stimuli for this experiment consisted of checkerboard patterns composed of 3, 8, and 16mm black and white checks mounted on two different cardboard displays. The checks subtended visual angles of 22.5', 45' and 90' of arch respectively when viewed from a distance of 40 in. A fourth blank condition where luminance transmittance was equivalent to that of the other three was used as a control. To reduce the flash intensity by 50 per cent for the blank flashes the intensity of the photo-stimulator was halved for both levels of ambient illumination. The surface of each of the checkerboard patterns was covered with translucent paper to reduce the contrast between the edges of the checks when the displays were not being illuminated. However, the contours were clearly discernible when strobed.

The patterned stimuli were attached to two display templets which henceforth will be referred to as the central and peripheral displays. The central display exposed a 9 sq. in. section of patterned elements and subtended 7.5 degrees of visual angle for stimulation of the fovea and perifovea. The peripheral display was in the form of a square subtending 1.5 degrees of visual angle. The annular border of elements was projected to a retinal area equivalent

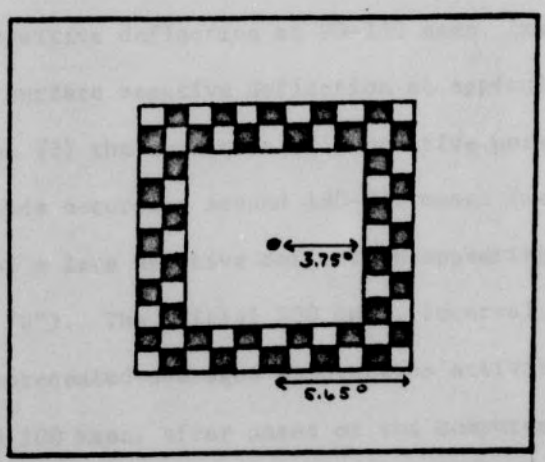
to that stimulated by the central display. Figure 2 provides a pictorial representation of the two displays described above including their respective dimensions.

These two display configurations permitted E to vary check-size and locus of retinal stimulation while holding the total area of illumination constant. This technique enabled E to differentially stimulate rod and cone receptor processes.

In summary, a series of eight different displays, four for stimulation of the central (fovea, perifovea) retina and four for stimulation of the peripheral retina, composed the visual stimuli for this experiment. All eight displays were illuminated with red and blue flashes superimposed upon high and low levels of background luminance.



CENTRAL DISPLAY



PERIPHERAL DISPLAY

Figure 2. Pictorial representation of the visual displays used to differentially stimulate the central and peripheral retina.

RESULTS

The Evoked Potential

Visual inspection of the VERs obtained in this study showed that, in general, the waveforms resembled those reported to patterned stimuli in previous literature (Harter and White, 1968). They were also in conformance with the frequently reported findings that an individual's response is relatively stable over a number of replications, especially the first 300 msec. and that intersubject waveforms may be highly variable (Dustman and Beck, 1963).

Measurement of Amplitudes

Figure 3 illustrates the general latency and polarity characteristics of the VER to patterned stimuli and the amplitude measures used. Four amplitude measures were made on each VER: (1) the amplitude of an early positive deflection at 90-120 msec. (measure "A"); (2) the amplitude of a surface negative deflection at approximately 120-160 msec. (measure "B"); (3) the amplitude of a positive potential of relatively large magnitude occurring around 180-210 msec. (measure "C"); and (4) the amplitude of a late negative deflection appearing about 240-300 msec. (measure "D"). The initial 100 msec. interval, as pointed out earlier, represented averaged spontaneous activity since the flash was presented 100 msec. after onset of the computer sweep. The final 100 msec. of the VER was composed of a series of low voltage oscillations of approximately 10 cps.

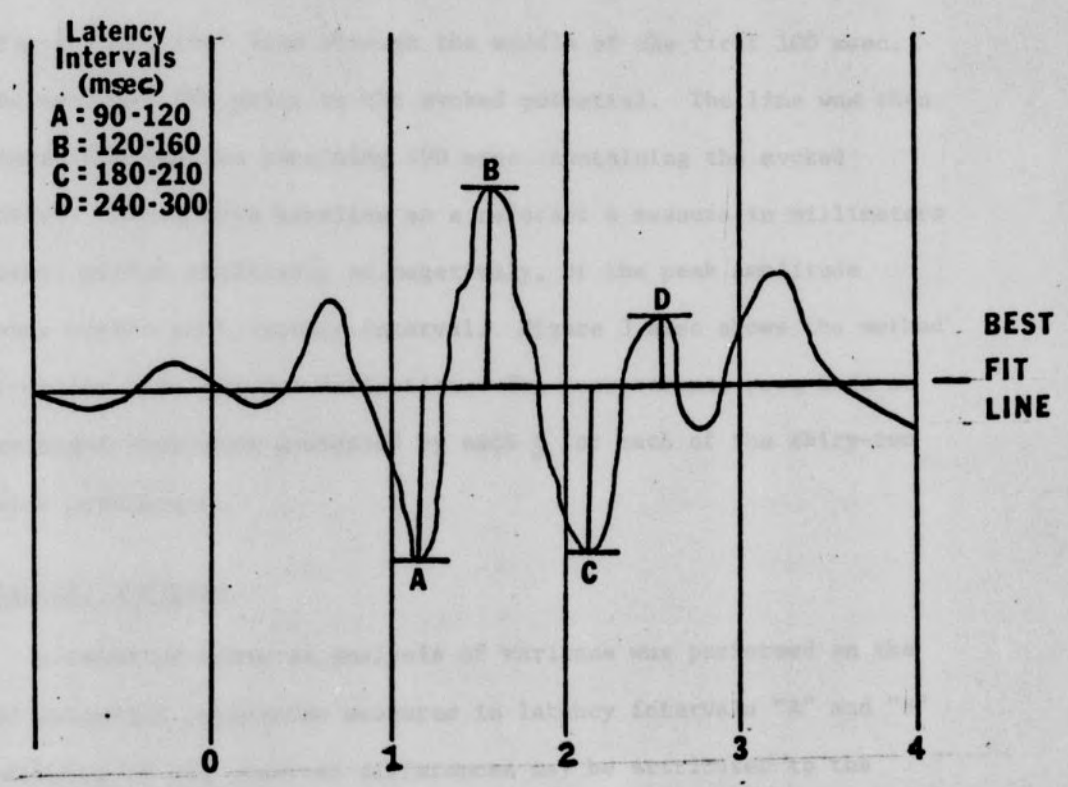


Figure 3. Latency and polarity characteristics of a representative evoked potential and the method used to determine the maximum deflection within each latency interval.

Only measures "A" and "B" were included in the statistical analysis of this study since they are known to be particularly sensitive to visual stimuli of the type used in this experiment (Harter and White, 1968).

The procedure for the measurement of amplitudes began by drawing a "best-fit" line through the middle of the first 100 msec. of the averaged EEG prior to the evoked potential. The line was then continued through the remaining 400 msec. containing the evoked potential. Using this baseline as a referent a measure in millimeters was made, either positively or negatively, of the peak amplitude response within each latency interval. Figure 3 also shows the method to determine this maximum deflection. The measurements were made on two averaged responses generated by each S for each of the thiry-two stimulus conditions.

Statistical Analysis

A repeated measures analysis of variance was performed on the evoked potential amplitudes measured in latency intervals "A" and "B" to determine if the observed differences may be attributed to the experimental variables or random variation.

Measure "A". The results derived from measure "A" are summarized in Table 2 (Appendix). As can be seen from this tabular summary, this measure proved to be a rather insensitive index of variation in the stimulus conditions. The only significant differences in the amplitude of "A" were related to the main effects of background intensity, color, and site of retinal stimulation ($p < .01$). The

amplitude of "A" was greatest when the checks were illuminated against the low (2.15 mlam) luminance background and when the central rather than the peripheral retina was stimulated. Also, the amplitude of measure "A" was of a larger magnitude when the checks were illuminated with the red instead of the blue stimulus flash. Graphic representation of these significant effects will not be presented since measure "A" contributed so little to the interpretation of the experiment.

Measure "B". The analysis of variance performed on measure "B" resulted in a number of significant main and interaction effects (Table 2, Appendix). The change from a background luminance of 2.15 mlam to one of less than one mlam produced a significant reduction in the amplitude of measure "B" ($p < .05$). The effect was rather marked. Furthermore, the effect of site of stimulation was significant for this measure, the potentials evoked by flashes to the periphery being of larger amplitude than those evoked central ($p < .05$). The direction of this difference was unexpected and will be discussed later. Figure 4 shows the amplitude of "B" plotted as a function of background and site of stimulation.

The effect of check-size on the amplitude was "B" was highly significant ($p < .001$). Figure 5, where average amplitude is plotted against check-size, shows that when the size of the elements was decreased from 90-22.5 min. of arc the amplitude of "B" increased. The amplitude to the diffuse flash dropped steeply although it remained slightly larger than the evoked by the check subtending 90 min. of arc.

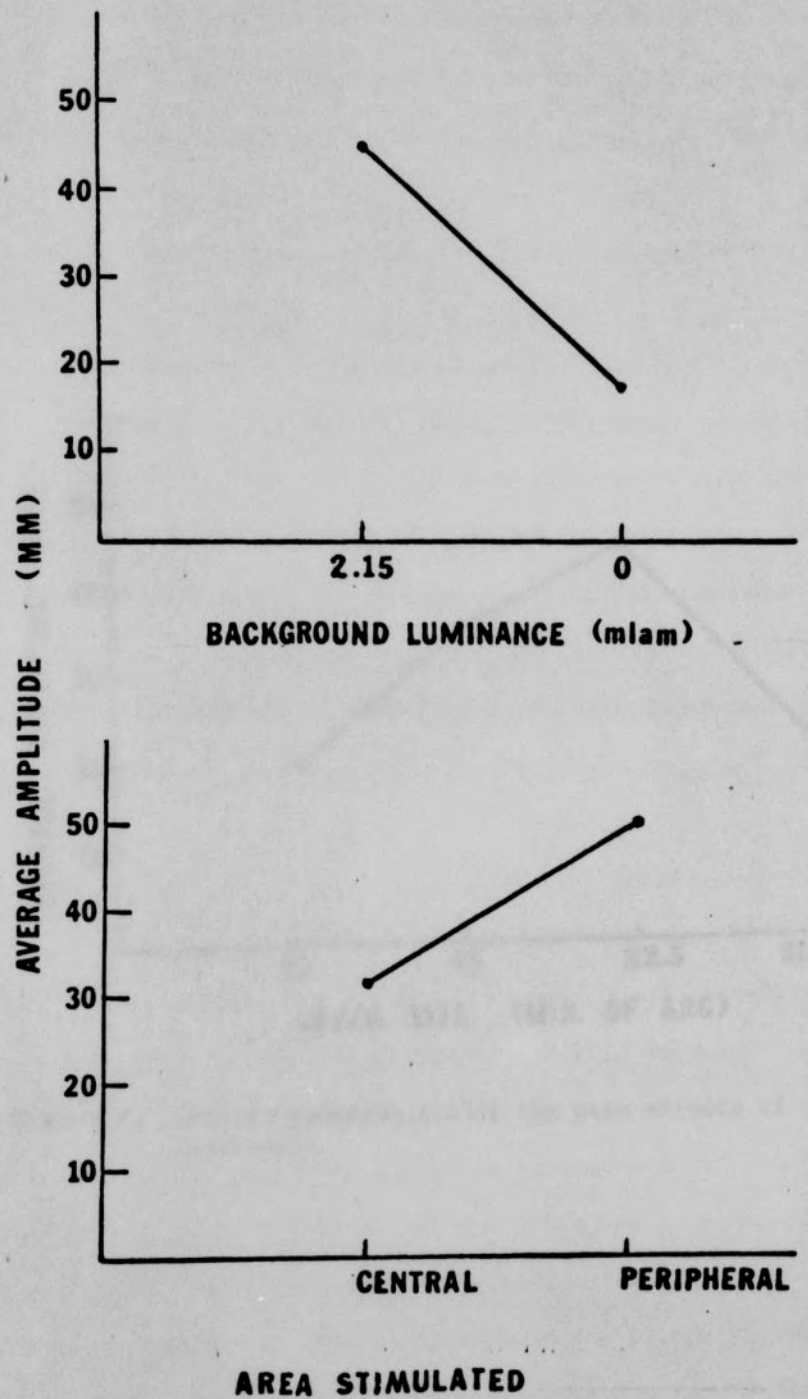


Figure 4. Graphic presentation of the main effects of background luminance and site of retinal stimulation.

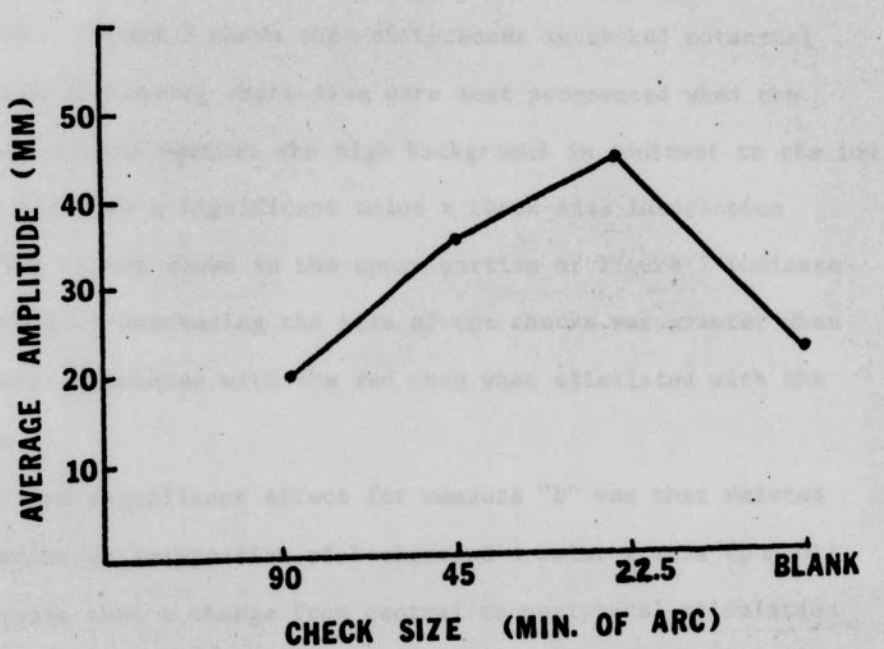


Figure 5. Graphic presentation of the main effects of check-size.

A significant background x site interaction ($p < .05$) occurred indicating that differences in the amplitude of the potential under high and low levels of background luminance were greater for the central than for the peripheral site (Figure 6). Changing the background from a high to low intensity had a greater decremental amplitude effect when the central site was stimulated.

Background luminance also interacted significantly with check-size ($p < .05$). Figure 7 shows that differences in evoked potential amplitude with decreasing check-size were most pronounced when the elements were viewed against the high background in contrast to the low one. There was also a significant color x check-size interaction ($p < .05$). The curves shown in the upper portion of Figure 7 indicate that the effect of decreasing the size of the checks was greater when the retina was stimulated with the red than when stimulated with the blue flashes.

The final significant effect for measure "B" was that related to the second-order interaction of background x color x site ($p < .01$). Figure 8 reveals that a change from central to peripheral stimulation generates differences in VER amplitude which are quite dependent on the color of the flash. A change from central to peripheral stimulation under the low luminance condition generates about the same degree of change in evoked potential amplitude for both red and blue flashes. However, under the high background condition color exerts considerable influence. The difference in the slopes of the two curves under this luminance condition seem to be due to the fact

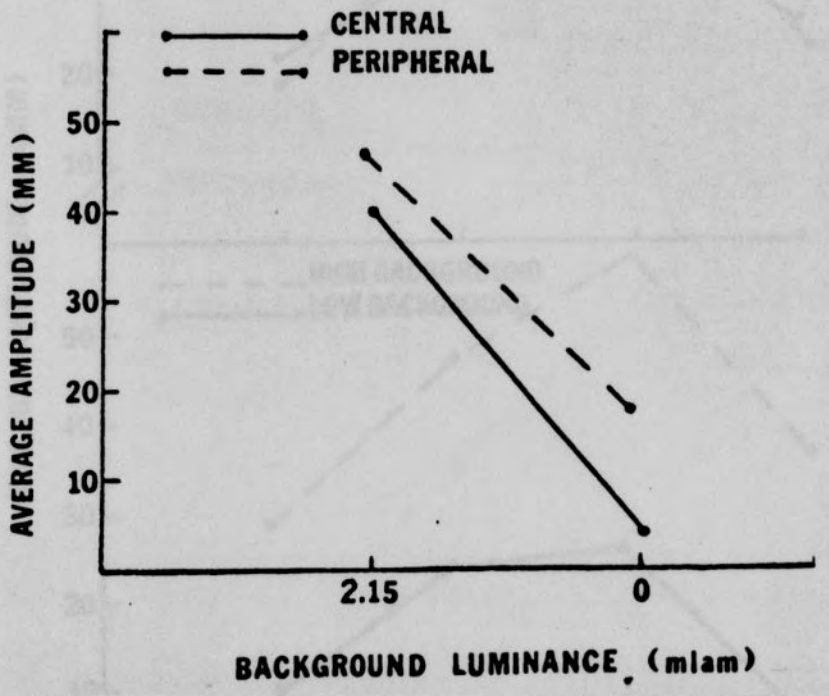


Figure 6. Graphic presentation of the interaction effects of background and site of retinal stimulation.

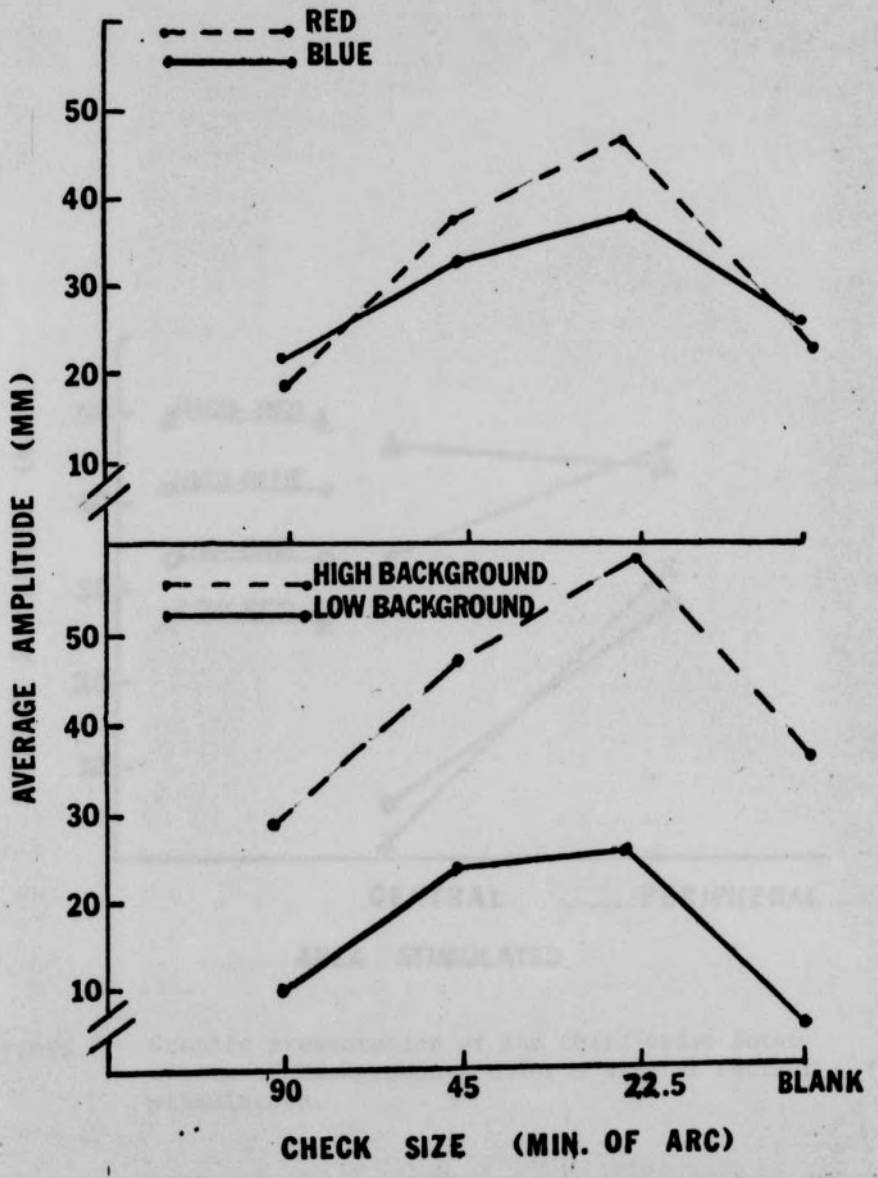


Figure 7. Graphic presentation of the interaction effects of check-size x background and check-size x color.

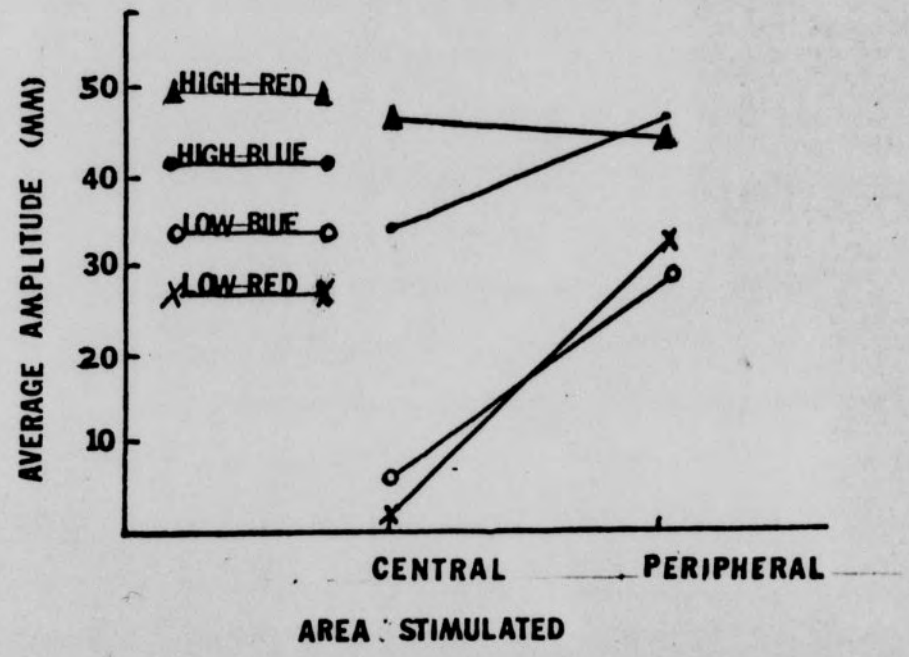


Figure 8. Graphic presentation of the third-order interaction of background x color x site of retinal stimulation.

the amplitude to the centrally presented blue flash is attenuated, whereas that for the red is not. At the peripheral site there was little differential effect as a result of stimulation with the red and blue flashes.

DISCUSSION

The Main Effects of Measure "B"

The discussion of this experiment will be restricted to measure "B" except where otherwise noted. This decision was based on the relative insensitivity of measure "A" to the stimulus conditions.

Effects of Background Luminance. When viewing checkerboard patterns, changing the background illumination from a high to low intensity had the effect of reducing markedly the amplitude of measure "B". This result supports Shipley's observation of a progressive amplitude decrement during the first 8-10 min. of dark-adaptation. Although Shipley stimulated the retina with diffuse instead of patterned flashes, the decrement in both cases is probably related to the differential influence of photopic and scotopic processes.

The data also corroborate Harter's finding (1969) of a decrease in amplitude of the evoked potential to increasing peripheral stimulation with checkerboard patterns. The rationale for this conclusion rests on the fact that photopic and scotopic vision are generally conceded to represent central and peripheral retinal processes. Therefore, shifting from one system to the other by increasing or decreasing background luminance is tantamount to changing the locus of stimulation to either the central or peripheral retina.

The physiological basis of this reduction in amplitude appears to be related to the difference in function of these two visual systems. Lowering the intensity of the background increases rod sensitivity, and

hence reduces visual acuity. This, in effect, partially defocuses the checks causing the visual system to respond as though diffuse light were impinging upon the retina. As noted previously by Harter and White (1968), the waveform of the VER progressively resembles that given to diffuse light when the checks are gradually defocused. The amplitude decrement may be attributed to the absence in the evoking stimulus of sharp spatial gradients whose presence is critical for generation of large amplitude potentials.

Effects of Site of Retinal Stimulation. Differential stimulation of the central and peripheral retina with checkerboard patterns resulted in an unexpected difference in the direction of amplitude change. The peripheral potentials were, on the average, of greater amplitude than those generated by stimulation of the central retina.

At first blush, this result seems incompatible with the previous research in this area by Harter (1969). However, closer analysis reveals several tenable hypotheses which may adequately account for this apparent discrepancy. It will be remembered that Harter has recently shown that the generation of a peak amplitude response depends on the presence in the evoking stimulus of an optimal amount of edge. By its very nature, the square annulus used to elicit peripheral potentials contains more edge than does the central display. The presence of this extra edge may have been sufficient to evoke larger peripheral potentials. Another factor enhancing this effect may have been stray light exciting receptors to either side of the annular retinal image thus functionally enlarging the total area of stimulation. Such areal enlargement would

have been less for the central display since stray light could influence receptors to only one side of its border. The net effect of these two extraneous factors may have been responsible for this anomalous finding.

Effects of Check-Size. The effect of decreasing check-size from 90.0-22.5 min. of arc was a progressive increase in the amplitude of measure "B". This amplitude increment to a reduction in check-size confirms the findings of a number of research investigators (Harter and White, 1968; Reitveld, et al, 1967; Spehlmann, 1965). In addition, the data seem to provide electroencephalographic evidence for Hartline's observation (1938) that only a small proportion of optic fibers are excited when the retina is stimulated with diffuse light, the preponderance of excitation occurring in response to a patterned luminous field. The data are also in agreement with the limited cortical excitation to diffuse light reported in cats by Hubel and Weisel (1951).

The general significance of this amplitude-check-size relationship is its further substantiation of the critical nature of the density of edge in the evoking stimulus. Had a wider range of check-sizes been used, the typical curvilinear relationship reported by several investigators (eg., Harter and White, 1968 and Reitveld, et al, 1967) would probably have been found.

Since the theoretical explanation of these phenomena based on the interplay of lateral inhibition and receptive field size was presented in the introduction it will receive no further elaboration.

Interaction of the Stimulus Variables

Background with Site. Changing the background intensity from a high to low level resulted in a larger decrease in the amplitude of the central potentials than in the amplitude of the peripheral ones. When the background intensity is reduced to the level used in the experiment, the photopic system is functionally abolished so that the flashes were near threshold initiating impulses in only a limited number of cones. Consequently, fewer neural impulses reached the occipital cortex generating a smaller amplitude response. Since the cones are maximally sensitive when the retina is light adapted, the larger central potentials evoked under this retinal condition may simply reflect this increased photopic activity. The amplitude of the potentials to peripheral stimulation decreased to the reduction in background luminance although less steeply than those centrally evoked. The larger potentials evoked by peripheral stimulation under the high luminance condition is an unanticipated result and is difficult to account for within the context of differential central and peripheral processes. However, as predicted, the low background peripheral responses were of greater magnitude than were central ones obtained under this background condition. This was to be expected since the scotopic system was highly sensitive and functionally dominant.

Background with Check-Size. Changing the background intensity from a high to low level had a dramatic influence on the effects of check-size for measure "B". When the checks were viewed against the

high background, decreasing the size of the elements resulted in a pronounced increase in the amplitude of the potentials whereas under the low condition this increment was less marked.

The differential effect of check-size under the two luminance conditions may also be related to photopic and scotopic processes. Under the high luminance background it is hypothesized that the cones were the principal determinants of the response since the rods were, for the most part, insensitive. As many experiments have shown, visual acuity is optimal when the cone system is mediating the stimuli (Hect, 1934). Since the sharpness of the retinal image and hence the ability to discriminate detail is optimized under this condition, the amplitude of the potential should be quite sensitive to variation of check-size. Under the low background condition variation in check-size should have limited effect on the amplitude of the potential since resolution of detail is reduced in the rod system. The results cited above are consistent with this analysis.

The remarkable drop in amplitude of measure "B" to diffuse stimulation under both high and low levels of background luminance emphasizes the crucial importance of pattern on cortical activity. In this regard, Gregory states that "it is primarily the existence of borders which are signaled to the brain, while regions of constant intensity do not need much information" (p. 76).

Background with Color. This experiment demonstrated that the effect of a particular check-size on the amplitude of measure "B" was a function of the color with which the displays were illuminated. The

blue flashes evoked the largest amplitude potentials to the largest check and to diffuse pattern while those to the red were greatest to the checks subtending 45 and 22.5 min. of arc.

This differential chromatic effect on the amplitude of the evoked potential to patterned stimuli corroborates the findings of Reitveld and associates (1967). The effects of the two colors on the potential's amplitude may reflect differences in spectral sensitivity of the photopic and scotopic visual systems since the sensitivity of the retina is known to vary with the wavelength with which it is stimulated (Woodworth and Schlosberg, 1964). Visibility curves, in which sensitivity is plotted as a function of wavelength, show that the photopic system is more sensitive to wavelengths in the red region of the visible spectrum while the scotopic system has its maximal sensitivity in the blue-green region.

When the checks were illuminated with red flashes, the curve was similar to that obtained with high background luminance. This would suggest that stimulation of the retina with red light influenced primarily the cone system enhancing the effects of check-size on the potential. Conversely, blue flashes stimulated predominately the rod system and hence diminished the effects of check-size. There was a negligible difference between the effects of the two colors on the check of 90 min. of arc and the diffuse pattern. This, again, is probably related to the density of edge in the stimulus displays.

Background with Site with Color. As predicted, the amplitude of the evoked potential was greatest when the central retina was

stimulated with red flashes against high background luminance. Since the cones are concentrated primarily in the central retina and are quite sensitive to red embedded in a bright surround, it is not surprising that the amplitude of the potential was greatest under these experimental conditions.

Color had little differential effect under the low luminance condition either at central or peripheral sites. It is possible that the blue filter may have been passing less light then the red one since their luminance transmittance was uncontrolled. This may explain, at least in part, the modulated effect of the blue as compared to the red flashes in the peripheral retina.

Relationship of Lateral Inhibition and Receptive Field Size to This Study

The interaction effect of background with check-size may be examined in the light of the theoretical processes of lateral inhibition and receptive field size. As previously noted, Glezer (1965) has demonstrated the dependence of receptive field size on the intensity of the existing background luminance. It is possible that the differential effects of check-size under the two luminance conditions may reflect changes in the size of the receptive fields stimulated and hence the capacity to resolve edges within their perimeter. Under the low background condition the effects of decreasing check-size may have been minimized since the spatially discrete events within the boundaries of the larger receptive fields was presumably lost. Under the high luminance condition where receptive field size is smaller, the visual

system transmits more sensitively to the brain the spatial information in the stimulus. The result is an increased sensitivity of VER amplitude to variation in the total amount of spatial information present in the evoking stimulus.

CONCLUSION

The present investigation indicates that the scotopic visual system is capable of mediating evoked cortical potentials to checkerboard patterns. The sensitivity of this mediatory capacity, inferred from changes in the amplitude of the VER, is somewhat less than that of the photopic system. A reduction in peripheral visual acuity determined possibly by increased receptive field size in this portion of the retina may be responsible for this inferior resolving capacity since spatially disparate events are not detected by the brain when transmitted by a single optic fiber.

This study also emphasizes the importance of strict control of background intensity when stimulating the retina and recording evoked potentials. Lack of such control may account for the contradictory results being reported by different laboratories under ostensibly similar stimulus conditions.

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APPENDIX

TABLE 1

SUMMARY OF ANALYSIS OF VARIANCE FOR MEASURE A

SOURCE OF VARIATION	SS	DF	MS	F
A. Between Columns	37,444.80	31		
1. Background	14,743.70	1	14,743.70	18.69**
2. Color	2,688.60	1	2,688.60	26.48**
3. Site	17,189.40	1	17,189.40	20.57**
4. Check-Size	511.80	3	17.26	.02
5. Background x Color	1.30	1	1.30	.0028
6. Background x Site	953.10	1	953.10	.68
7. Background x Check-Size	301.90	3	103.63	1.02
8. Color x Site	303.90	1	303.90	2.99
9. Color x Check-Size	43.80	3	14.60	.14
10. Site x Check-Size	114.50	3	38.16	.37
11. Background x Color x Site	4.00	1	4.00	.03
12. Background x Color x Check-Size	54.90	3	18.30	.18
13. Background x Site x Check-Size	425.90	3	141.96	1.39
14. Color x Site x Check-Size	81.40	3	27.13	.26
15. Background x Color x Site x Check-Size	26.60	3	8.86	.80
B. Between Rows	60,819.00	5		
C. Rows x Columns	36,215.00	155		
1. Background x Ss	3,945.60	5	789.12	4.29*
2. Color x Ss	856.20	5	171.24	.93
3. Site x Ss	4,178.10	5	835.62	4.54*
4. Check Size x Ss	4,259.00	15	283.93	1.54
5. Background x Color x Ss	2,260.70	5	452.10	4.45*
6. Background x Site x Ss	7,007.50	5	1,401.50	13.80**

TABLE 1

SUMMARY OF ANALYSIS OF VARIANCE FOR MEASURE A Continued

SOURCE OF VARIATION	SS	DF	MS	F
7. Background x Check-Size s Ss	1,952.85	15	130.10	1.28
8. Color x Site s Ss	1,129.30	5	205.80	2.02
9. Color x Check-Size x Ss	2,270.40	15	151.30	1.49
10. Site x Check-Size x Ss	1,853.30	15	123.50	1.21
11. Residual	6,602.10	65	101.50	
D. Total	133,186.10	191		

* Significant at $p < .05$
** Significant at $p < .01$

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* Significant at $p < .05$
** Significant at $p < .01$

TABLE 2

SUMMARY OF ANALYSIS OF VARIANCE FOR MEASURE B

SOURCE OF VARIATION	SS	DF	MS	F
A. Between Columns	73,693.83	31		
1. Background	32,682.42	1	32,682.42	7.27*
2. Color	165.02	1	165.02	.29
3. Site	11,859.80	1	11,859.80	13.64*
4. Check-Size	15,454.78	3	5,151.59	64.35***
5. Background x Color	819.17	1	819.17	1.03
6. Background x Site	4,700.52	1	4,700.52	11.10*
7. Background x Check-Size	1,610.76	3	536.92	3.33*
8. Color x Site	73.75	1	73.75	.33
9. Color x Check-Size	968.16	3	322.72	4.03*
10. Site x Check-Size	3,119.90	3	1,039.96	2.98
11. Background x Color x Site	1,517.53	1	1,517.53	18.96**
12. Background x Color x Check-Size	255.77	3	85.25	1.06
13. Background x Site x Check-Size	192.15	3	64.05	.80
14. Color x Site x Check-Size	79.71	3	26.57	.33
15. Background x Color x Site x Check-Size	194.39	3	64.79	.80
B. Between Rows	77,949.77	5		
C. Rows x Columns	56,187.57	155		
1. Background x Sx	22,453.16	5	4,490.63	25.52**
2. Color x Ss	2,762.56	5	552.51	3.13*
3. Site x Sx	4,345.35	5	869.07	4.93*
4. Check-Size x Ss	4,630.81	15	308.72	1.75
5. Background x Color x Ss	3,971.02	5	794.20	9.92*
6. background x Site x Ss	2,116.33	5	423.26	5.28*

TABLE 2

SUMMARY OF ANALYSIS OF VARIANCE FOR MEASURE B Continued

SOURCE OF VARIATION	SS	DF	MS	F
7. Background x Check-Size x Ss	2,416.09	15	161.07	2.01*
8. Color x Site x Sx	1,108.29	5	221.65	2.76*
9. Color x Check-Size x Ss	1,947.44	15	129.82	1.62
10. Site x Check-Size x Ss	5,233.09	15	348.87	4.35*
11. Residual	5,203.43	65	80.05	
D. Total	207,831.17	191		

* Significant at $p < .05$
** Significant at $p < .01$
*** Significant at $p < .001$