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Evoked Cortical Potentials in Relation to Locus of Retinal
Stimulation and Check Size.   (1971) Directed by: Dr. Robert G.
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Visually evoked cortical potentials (VERs) to checker-
board stimulation were studied as a function of locus of retinal
stimulation, check size, and relative distribution of response
over the cortex. Pattern stimuli of checks subtending 7.5, 15,
30, and 60' of arc were presented to the upper, central, lower,
and lower-peripheral visual field. Evoked responses were
recorded simultaneously from scalp electrodes located approxi-
mately 5 cm to the right or left of a point 2.5 cm above the
inion, and approximately 2.5, 7.5, and 12.5 cm above the inion.
Results obtained from the four electrode locations illustrated
the differential effect of visual field stimulation on VER wave-
form in relation to the topography of the visual cortex. When
activity was recorded from electrodes near the inion, VERs
decreased as retinal stimulation was moved from the central to
the lower-peripheral visual field. Such results indicate only
that neural activity in response to peripheral stimulation
decreased in the cortical area concerned with macular activity
and not that, in general, VERs are less to peripheral than
central visual stimulation. Responses at electrodes placed
anteriorly over the peripheral projection area increased in
amplitude as stimulation was changed from the central to the
peripheral visual field.

In general, maximal responses were obtained from lower
field stimulation across all check sizes. Checks subtending 15'

and 30' of arc exerted a more differential influence on VER wave-
form with the lower and central visual fields being more differ-
entially effected by manipulations in check size. As stimulation
moved toward the lower peripheral visual field, larger checks
evoked the greatest response.

TOPOGRAPHICAL DISTRIBUTION OF VISUALLY

EVOKED CORTICAL POTENTIALS IN
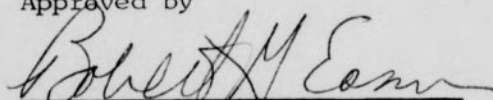
RELATION TO LOCUS OF RETINAL

STIMULATION AND CHECK SIZE

by

Pamlyn D. Atkins

A Thesis Submitted to
the Faculty of the Graduate School at
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APPROVAL PAGE

This thesis has been approved by the following committee
of the Faculty of the Graduate School at The University of
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Introduction

Systematic investigation of neural mechanisms involved in the sensations and perceptions of man has recently been facilitated by advancements in computer technology. Electronic devices that record the electroencephalogram (EEG) are now being used to differentiate EEG from averaged characteristics of time-locked cortical responses to peripheral receptor stimulation. The visual system has not only proved to be an ideal receptor for experimental manipulation but is also of utmost importance to the adaptive information processing capacities of man. A vast amount of research is developing from experimentation with electrodes placed on the scalp above the occipital lobe. These electrodes record visually evoked responses (VER). "By an evoked potential is meant the detectable electrical change of any part of the brain in response to deliberate stimulation of a peripheral sense organ" (Chang, 1959, p. 299). In the case of VER, the electrical change is recorded from the occiput and the stimulated sense organ is the eye.

Topographical Distribution of VER

Evoked potentials obtained from electrodes vary according to the location of the scalp electrode and the stimulus conditions of a particular experiment. A majority of VER research is obtained from scalp electrodes placed within 1 to 3 cm superior to the

inion (DeVoe, Ripps, & Vaughan, 1968; Dustman & Beck, 1969; Eason, White, & Bartlett, 1970; Groves & Eason, 1967; Harter, 1971; Harter & White, 1970; Rietveld, Tordoir, & Duyff, 1965). The cortical area underlying this specific electrode location is the primary visual receiving area, or the visual cortex. The anatomical distribution of retinal projections on the cortex is discussed in greater detail in following sections.

Early VER studies did not systematically investigate the effect of electrode placement on VER. It was not recognized that VER could be spatially specific as well as stimulus-specific. Later studies were concerned with electrode placement only to the extent that the electrode would obtain a maximal response to a particular phase of experimentation (Perry & Childers, 1969).

In 1964 Nagata and Jacabson obtained VERs from electrodes placed along the midline from the inion to the vertex. An optics tube was used to stimulate the retina with a sharp small focus. This was in contrast to stimuli of larger visual angles that had been used in the past (specific visual angles used in this experiment were not stated). Stray light effects were reduced by background illumination. Results showed that maximal VERs were obtained from an electrode on the midline 5 cm superior to the inion and from 3 cm lateral and 1 cm superior to the inion.

Spehlmann (1965) investigated VERs to diffuse and to patterned stimuli by varying both the interface density of the stimuli and the distribution of electrodes over the occiput. Visual stimuli subtended the central 40-60 degrees of the visual field. Spehlmann

found that the responses to both diffuse and patterned light reached their maximum in an area within 3 cm foreward and to the sides of the inion. Spehlmann's interpretation of the components of VER to patterned light initiated investigations concerned with the neural basis of the specific components of VER wave form. Spehlmann found that pattern stimuli resulted in a later (180-375 msec) maximum positive wave than did diffuse light stimuli. Spehlmann considers this "late wave" a "specific" component in that amplitude varies with the density of contrast borders. The late wave was possibly related to activity at the single unit level resulting from lateral inhibition (Hubel, 1963).

Groves and Eason (1967) recorded VERs to a dim, foveal stimulus from occipital, parietal, frontal, and temporal electrode locations. The purpose of this study was to investigate the cortical distribution of activity involved in the onset latency of the response. Results from the different electrode placements revealed that the largest VER occurred at the occipital lobe 2.5 cm above and to the right of the inion. Although VER recorded from the occiput yielded waves of maximum amplitude, onset latency was longer than that recorded from other brain areas. Groves and Eason interpreted the longer latency VER to indicate the involvement of the unspecific thalamic projection system in the evoked response.

The three studies discussed above illustrate two important factors of VER: (a) the wave form of neural activity corresponding to visual stimulation varies according to the visual quality

of stimuli and yields different components which may be related to the physical properties of that stimulus, and (b) variations in latency and amplitude of VERS are found when recording from different electrode locations. It should be remembered that maximum activity near the inion was obtained from stimulation using very small and usually foveal stimuli.

In 1965 Potts and Nagaya explicitly used VER to obtain an objective measure of foveal function. A very small (0.06^o) red stimulus, dimly illuminated, yielded VERs which were diminished at stimulation beyond 1° nasally and/or temporally. VERs were abolished at 2° stimulation. Potts and Nagata were able to obtain VERs to foveal stimulation from areas not limited to the occiput. These results were interpreted according to the anatomical distribution of foveal projection areas. VER was thought to be a response to large numbers of cortical neurons which were one or more synapses removed from the "calcarine cortex." The reasoning was that since the primary foveal projections occupy a large number of cortical cells, the secondary foveal projections must also be large.

It should be stressed that the visual cortex receives projections from two types of retinal photoreceptors: rods and cones. These biological photoreceptors contain the visual pigment which, upon light stimulation, initiates the first electrical impulses to be transmitted to the brain. The foveal centralis contains a concentration of cone receptors. The remaining retina contains both rod and cone receptors. It is at the rod-free fovea

that visual acuity is the greatest. The majority of foveal cones
have a direct electrical pathway to the optic nerve; however, in
more peripheral areas, where the rods predominate, there is a
great deal of convergence (Ganong, 1969). Figure 1 shows a
medial view of cerebral hemisphere showing projections of the
retina on the calcarine fissure in man (taken from Ganong, 1969.
Redrawn and reproduced from Brouwer, 1934).

It is thought by the author that the topographical dis-
tribution of the retina on the visual cortex and around the cal-
carine fissure plus the placement of a particular electrode on
the scalp overlying a particular projection area determines the
VER waveform obtained from a specific stimulus. Ganong (1969)
states that fibers which subserve vision in the upper portion of
each half of the visual field end on the superior lip of the cal-
carine fissure. Fibers from the inferior half of each visual
field end on the lower lip of the calcarine fissure. Macular
(foveal) projections end in the posterior part of the calcarine
fissure--posterior to the peripheral (rods and cones) projection
areas. This posterior foveal representation on the occipital
cortex insures that electrodes placed near the inion will record
photopic (cone) activity. The above anatomical facts perhaps
explain the findings that maximum VERs are obtained within 3 cm
of the inion since stimuli were presented to the foveal-macular
area as opposed to the more peripheral rod-cone areas (Rietveld,
et al., 1967; Devoe, et al., 1968; Copenhaver & Beinhocker, 1963;
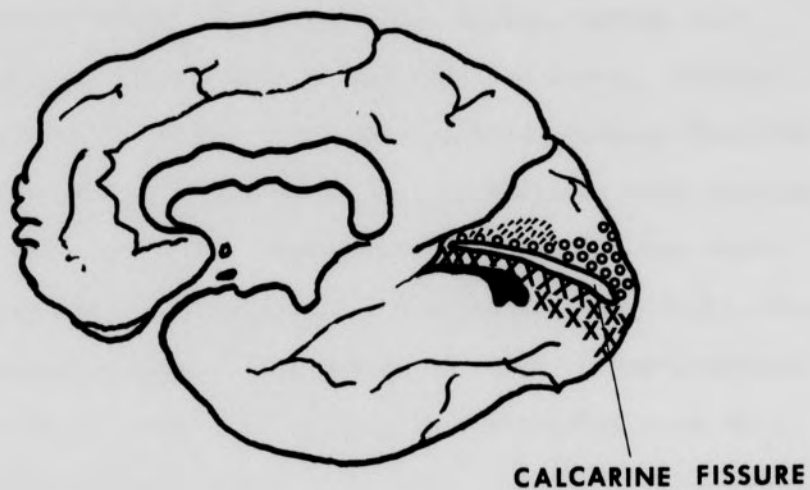
CALCARINE FISSURE

///// **UPPER PERIPHERAL QUADRANT OF RETINA**
▬ **LOWER PERIPHERAL QUADRANT OF RETINA**
o°o **UPPER QUADRANT OF MACULAR**
xXx **LOWER QUADRANT OF MACULAR**

Fig. 1. Medial view of cerebral hemisphere showing projection of the retina on the calcarine fissure in man (Ganong, 1969).

Eason, Oden, & White, 1967; Eason & White, 1967; Eason, White & Oden, 1967; Harter & White, 1968; Ciganek, 1961; van Balen, et al., 1966).

Alpern, Lawrence, and Wolsk (1967) plotted the relative contribution of visual fields to visual acuity, noting that maximal acuity is a mechanism of the rod-free fovea. Studies by Harter and White (1968, 1970) have yielded evidence that VER amplitude is related to visual acuity. Conditions that resulted in greater VERs varied for individuals depending on the least amount of refractive error for that particular individual. Since VERs were obtained from 2.5 cm above the inion, a topographical explanation is relevant. Electrodes were recording from the cortical area of foveal representation.

An inverted U-shaped function has been found between VER amplitude and check-size with maximal VERs to checks of 20' of arc (Harter & White, 1968, 1970; Rietveld, et al., 1967). This function might also be explained by a topographical hypothesis since visual acuity varies in both central and peripheral retinal fields. Harter (1971) dealt further with this problem and found that the check-size to which maximal VERs are obtained depends on the eccentricity of retinal stimulation.

Rietveld, et al., (1967) manipulated electrode placement, visual field stimulation, and contour density in relation to EPs. These manipulations, however, seem out of phase. When central and peripheral portions of the retina were stimulated, VERs were recorded from one electrode located $1\frac{1}{2}$ cm above the

inion. When electrode locations were varied, one stimulus was presented at a 20° visual angle. From these manipulations, Rietveld, et al. concluded that "the central foveal area contributes by far the greatest part to the pattern response" and that maximum VER activity is in the area $1\frac{1}{2}$ cm above the inion on the midline. Had Rietveld concurrently varied field stimulation and electrode placements he possibly would have obtained greater VERs from the more peripheral projection areas when using peripheral stimuli.

Jeffreys (1968, reviewed in MacKay, 1969; 1971) simultaneously obtained VER recordings from a 12-electrode array to whole field, upper and lower half-field patterned stimulation, eyes centrally fixated. Wave shape and polarity of VER was found to vary according to the particular visual field stimulated and the area of the cortex represented under the electrode. Results were explained on the basis of the retinotopic arrangement of the human visual cortex.

Comparisons have been made (Vaughan, 1964) between recordings taken from the scalp and the cortex of human patients undergoing occipital surgery. Scalp electrode recordings were similar to cortical recordings taken from the posterior margin of mesial occipital cortex. Similarities diminished as the recording site shifted anteriorally. Vaughan concluded that scalp electrodes overlying the occipital pole reflect the waveform of evoked responses beneath with little contribution from the more anterior striate cortex. Since the posterior pole receives projections

from the fovea, Vaughan states that the scalp VER may be expected to reflect activity generated primarily in the central area of the retina.

Visual Field Stimulation

Recently research with VER has found that components of the ER vary to differential stimulation of upper, lower, and central visual fields (Eason & White, 1967; Eason, White, & Oden, 1967; Jeffreys, 1968, 1971; Schreinemachers & Henkes, 1968; Eason, White, & Bartlett, 1970; Eason, Groves, White, & Oden, 1967).

Eason, et al. (1967) became interested in visual field effects on VER during an effort to provide further evidence for an inverse relation between reaction time (RT) and VER amplitude. Woodworth (1938), Poffenberger (1912), and Rains (1963) had obtained evidence that RT was faster to stimuli presented to the nasal than to the temporal retina. Østerberg (1935) discussed a relevant aspect of the physiology of the retina in that the nasal part of the retina is more plentifully equipped with rods and cones than is the temporal retina. Recording from 2.5 cm above the inion and to the right of the midline, Eason and White (1967) obtained smaller VERs to nasal than to temporal field stimulation of the right eye. These results were inconsistent with the existing evidence between RT and VER since RTs were shorter to temporal stimulation. Since the placement of the electrode determines the area of the brain from which activity will subsequently be recorded, VERs obtained from 2.5 cm to the

right of the midline recorded activity arising from the temporal retina of the right eye (Eason, Groves, White & Oden, 1967). An excellent illustration of the visual field and its projection in the occipital brain is given by Schreinemachers and Henkes (1968, p. 19). It is shown that binocular stimulation of the right visual field is projected to the nasal retina of the right eye and the temporal retina of the left eye. Projections of the nasal retina terminate on the left occipital lobe; whereas, those of the temporal retina terminate in the right lobe. In other words, the right visual cortex is concerned with the left half of the visual field and the left visual cortex with the right half of the visual field (Hubel & Wiesel, 1967).

In 1897, Hall and von Kries presented evidence that reaction times were faster to stimuli presented to the upper retina than to the lower retina. Rains (1963) and Payne (1967) also found shorter RTs to stimuli presented above the horizontal meridian. Payne further found that sensitivity curves for visual RTs and threshold reflect the distribution of rod and cone receptors along the horizontal and vertical meridians. This paralleled Østerberg's (1935) contention that rod and cone count is greater in the upper part of the retina than in the lower retina. Eason, White, and Oden (1967) recorded VERs simultaneously from electrodes placed one inch above the inion, to the right and to the left of the midline. Both eyes were stimulated with upper and lower field presentations. (Upper field stimuli correspond to the lower half

of the retina and lower field to the upper retinal half). Greater VERs were recorded from both the right and left lobe to stimuli occurring in the lower visual field. Latencies were also shorter under lower visual field conditions.

Eason, White, and Bartlett (1970) obtained interesting results by varying check-size within the visual field. Lower field stimulation was more sensitive to changes in check-size, with maximum amplitude recorded to checks subtending 39 min of arc. Upper field stimulation yielded a maximal response to checks of 9.4 min of arc. In summary of their results, Eason, et al. suggested that the cortical visual system is more responsive to patterned stimuli appearing in the lower visual field, but that the system is relatively more sensitive to smaller objects appearing in the upper field. Attention should be called to the fact that VERs were recorded from one electrode location, 2.5 cm above the inion on the midline, and that VER results could be specific to that cortical area. Jeffreys (1968, 1971) obtained VERs from a 12-electrode array to visual field stimulation and showed a reversal in the polarity of VER peaks to upper and lower field stimulation. As activity increased over one cortical area to upper field stimulation, activity in that cortical area decreased to lower field stimulation. These results were explained on the basis of the topography of the human visual cortex.

The polarity reversal of the upper- and lower-quadrant pattern EP's could be explained if the responses were generated in the regions of striate cortex inside the

calcarine fissure, because the cortical layers representing the upper quadrants would be inverted in relation to the overlying cortex representing the lower quadrants (MacKay, 1969, p. 214).

Check Size and VER

VER experiments were classically performed using diffuse light stimulation. In 1965 Sphelmann compared the various aspects of the response to patterned and diffuse light flashes. VER to patterned light resembled that to diffuse light only under conditions in which the contrast borders were blurred beyond recognition. Since that time, numerous studies have dealt with VER to patterned light (Rietveld, et al., 1967; John, Herrington, & Sutton, 1967; Harter & White, 1968, 1970; Harter & Suitt, 1970; Harter, 1971; Eason, et al., 1970; Clynes & Kohn, 1967).

Harter and White (1968, 1970) indicated that certain components of VER are sensitive to the size of the black and white checks used in checkerboard patterned stimulation. Check sizes subtending 10-20 min of arc produced the greatest amplitude VER under conditions of heightened visual acuity--when recording at 2.5 cm above the inion on the midline. Alpern, et al. (1967) have shown that visual acuity is maximal in the rod-free fovea and steadily decreases with an increase in rod distribution.

Hubel and Wiesel (1968) have presented physiological evidence concerning receptive field organization which may account for maximal VER responses to small check sizes (10-20 min of

arc). The receptive field of a cell in the visual system is
that area of the retina within which illumination will excite
or inhibit the firing of a particular cell (Michael, 1968).
Hubel and Wiesel have found that the optimal stimulus size which
results in maximal sensitivity corresponds to the size of the
cell's receptive field center. Receptive field centers vary
from small to large as a function of the distance of the ganglion
cells input from the area centralis (Wiesel, 1960). The spatial
discrimination abilities of the visual system are reflected by
the arrangement of inhibitory and excitatory regions in the
receptive field--foveal fields are more strongly influenced by
inhibitory-excitatory surrounds (Hubel, 1963). The finding that
VER reaches maximal amplitude in response to checks subtending
10-20' of arc plus the later finding that the check size which
evokes the greatest amplitude VER depends on eccentricity of
retinal stimulation (Harter, 1971) lends further support to the
following hypothesis: "The effectiveness of patterned stimuli in
initiating activity in cortical cells depends on the size and
shape of each cell's retinal receptive field" (Harter & White,
1970, p. 53). Eason, White, and Bartlett (1970) also speculate
using a receptive field hypothesis. Maximal VERs to different
check size, depending on the visual field stimulated, might indi-
cate differences in the receptive fields located in upper and
lower retinal area.

Retinal Eccentricity

Cortical responses recorded from approximately 2.5 cm above the inion have been shown to vary according to the eccentricity of retinal stimulation with maximal VER obtained from central stimulation (Perry & Copenhaver, 1964; DeVoe, et al., 1968; Copenhaver & Beinhocker, 1963; Rietveld, et al., 1965, 1967; Harter, 1971; Eason, Oden, & White, 1967; Potts & Nagaya, 1965; Schreinemachers & Henkes, 1968; van Balen, et al., 1966; Eason & White, 1967). Eccentricity refers to the site of retinal stimulation in relation to the fovea. Projections range from photopic (macular) to scotopic (peripheral) representation in the retina.

Perry and Copenhaver (1964) were among the first to systematically study the contribution of photopic and scotopic systems to VER. From bipolar electrodes placed on the midline and above the inion, Perry and Copenhaver found that dark adaption had no effect on VERs during 24 minutes of recording. Larger VERs were obtained from central as compared to peripheral stimulation. VER was, therefore, concluded to be primarily a photopic response; size being dependent upon two factors: (a) the type of receptor stimulated, and (b) the nearness of receptor cortical projections to the recording electrodes. When scalp electrodes are used to record cortical activity, it should be remembered that the projections of the central retina are situated at the occipital pole, thereby enhancing the likelihood of recording responses originating at the fovea (DeVoe, et al., 1968).

Although the photopic visual system has greater spatial representation in the visual cortical projection area than the scotopic system (Talbot & Marshall, 1941), the peripheral retina and not the fovea is capable of both areal and temporal summation. An increase in VER to foveal stimulation, therefore, seems to record improved visual acuity without indicating the increase in visual sensitivity that is characteristic of the scotopic system. It should also be remembered that, while it is possible to stimulate only the cones by central stimulation, peripheral stimuli excite both rod and cone receptors. Harter (1971) tested the relative sensitivities of evoked response to checks of various sizes as they were presented at different retinal eccentricities. The distance from the fovea determined the check size which would elicit the greatest response. Checks subtending angles of 15-30' of arc evoked the greatest amplitude response when the foveal area was stimulated; larger checks (with angles up to 60' of arc) evoked the greatest response when more peripheral areas of the retina were stimulated. Harter proposed that the shift in maximal VER was a function of the physiological processes which influence spatial resolution--namely spatial summation and interaction at the rod-cone ganglion level.

In a study of RTs to various eccentricities, Rains (1963) found that RT-curves to scotopic stimulation paralleled rod density versus retinal position curves. Scotopic RTs decreased to stimulation 10-20° on the side of the fovea. Eason, et al. (1967) found concomitant changes in VER latency and RT, both

decreased to stimulation 15-20° from the fovea. Beyond 20° there
was an increase in RT and a corresponding reduction in VER ampli-
tude; however, no inverse relation between amplitude and RT was
found to the 15-20° stimulus conditions. In fact, amplitude
decreased to the low intensity (scotopic) stimulation. This
finding is to be expected since VER was recorded from the corti-
cal area of foveal representation. A topographical hypothesis
would be especially true if VER amplitude reflects the number of
cortical neurons excited by a stimulus (Harter, 1971).

Several investigators have noted differential contributions
of photopic and scotopic processes to VER under conditions of
varying light intensities (Vaughan, 1964; DeVoe, et al., 1968).
Vaughan and DeVoe, et al. found that VER latency was correlated
with sensitivity functions of rods and cones. Vaughan (1964)
suggested that the initial positive component of VER (P1) repre-
sents processes necessary for the detection of a photopic stimulus
since that component was absent in responses obtained from a
patient suffering from homonymous hemianopia. When P1 latency
was plotted as a function of intensity, two limbs were gener-
ated. Short latencies occurred at higher intensities with a
break to longer latencies at cone threshold. DeVoe, et al. (1968)
concluded that, as an indicant of foveal-peripheral mechanisms,
VER latency depends on luminance level since optic nerve fibers
subserving both rod and cone receptors transmit only cone mes-
sages when the brightness of the stimulus exceeds cone threshold
(Gouras & Link, 1966). Rietveld, et al. (1965) plotted the

relative contribution of foveal and parafoveal stimulation to VER.
Latency results paralleled those of Vaughan (1964) and DeVoe, et
al. (1968) in that the latency of the B-wave (P1) was apparently
determined by elements of the central region of the retina.
Rietveld proposed that the relative obscureness of the peripheral
projection areas located on the medial face of the cerebral
hemispheres would influence the recording of activity evoked in
that area since electrodes were placed on the scalp.

The usefulness of VER for interpreting neural and visual
processes involved in photopic and scotopic mechanicms, visual
acuity, retinal eccentricity, visual field, and pattern vision
has been shown in the research survey section above. A majority
of the studies reported interpreted findings in terms of scalp
electrodes placed from 1 to 3.0 cm superior to the inion. It
is proposed that (a) the topographical distribution of the retina
on the visual cortex, and (b) the placement of electrodes on these
retinal representation areas determines the electrical activity
that will subsequently be recorded. Visual stimulation of retinal
areas whose projections end on the posterior occipital cortex will
result in maximum VERs when scalp electrodes are placed superior
to the inion. Thus activity arising from certain types of retinal
stimulation will be maximally recorded while that arising from
other aspects of stimulation will be obscured. By placing elec-
trodes over several areas of the cortex, one might be able to
record activity arising from the upper and lower, and anterior

retinal projection areas. One would then be able to adequately extend interpretations of VER to peripheral field stimulation.

The purposes and general questions to be fostered in the forthcoming research are as follows:

(a) to simultaneously record electrical activity arising from both the horizontal and vertical planes of the occiput in response to various manipulations of the visual field. Will activity be differentially affected by stimulus parameters and will the effect be in accordance with cortical topography?

(b) to further investigate the differential sensitivity of retinal visual fields to check-size. How is the interaction between visual field and check-size affected by patterned light presentation at different eccentricities?

(c) to lend further support to the receptive field hypotheses by recording EPs from cortical locations representing both photopic and scotopic projection areas. As electrical activity increases in areas receiving macular projections, will activity decrease in the cortical areas receiving more peripheral projections? Is this interaction dependent on receptive field centers represented by checks of various sizes?

(d) to investigate the specificity of research that has been based on VER recordings taken from 1 to 3.0 cm above the inion. How specific to the recording site

is the finding that lower visual field stimulation
yields maximal VERs? Will maximal VERs to checks
subtending angles of 15-20' of arc be obtained from
all electrode locations? How does eccentricity affect
VERs when visual field and check size are concurrently
manipulated?

Method

Subjects

Data were obtained from four psychology graduate students
at the University of North Carolina at Greensboro. Subjects ranged
from 23 to 45 years of age.

Experimental Design

The foregoing research was concerned with change in the
amplitude of specific components of VERs as affected by three
variables: (a) electrode location, (b) locus of retinal stimu-
lation, and (c) check-size.

VERs and electrode placement. VERs were recorded from
four electrodes, three of which were aligned along the midline
from the occiput to the vertex and one along a horizontal plane
with respect to the occipital lobe. The midline electrode place-
ments were approximately 2.5 (occipital), 7.5 (parietal), and
12.5 (vertex) cm above the inion; the temporally placed electrode
was approximately 5 cm to the right or left of the occipital
electrode. Simple counterbalancing across sessions was used to
obtain VERs from the two sides of the inion. Visually evoked

responses were recorded simultaneously from the four electrodes

thus enabling an analysis of activity arising from four different

cortical areas to any given visual stimulation. All scalp record-

ings were obtained monopolarly. The reference signal consisted

of the combined output of two electrodes placed on the right and

left ear lobes.

Each S's EEGs were monitored continuously with a Grass

polygraph as a check for the adequacy of electrode contact and

for detecting body movement and other artifacts. The input from

the four electrode locations to the polygraph amplifier channels

was counterbalanced over sessions to nullify any slight differ-

ences in the gain level of the amplifiers.

Locus of retinal stimulation. Evoked potentials to bin-

ocular stimulation of upper, central, lower, and lower-peripheral

visual fields were recorded. Site of stimulation was varied by

having Ss fixate one of four points differentially positioned with

respect to the 8 x 8 cm stimulus display. The display remained

stationary over all experimental sessions. Depending on the

experimental condition Ss were required to fixate: (a) the mid-

point of the lower edge of the stimulus display (Condition A),

(b) the center of the display (Condition B), (c) the midpoint of

the upper edge of the display (Condition C), and (d) a point $5^{\circ}19'$

above the midpoint of the upper edge of the display (Condition D)

(see Figure 2). Except for Condition B, the fixation points were

small white squares subtending approximately 10 min of visual

angle. During Condition B, Ss fixated the intersection of two

A
UPPER
0 - 5° 19'

B
CENTRAL
0 - 2° 40'

C

D

LOWER
0 - 5° 19'

LOWER -
PERIPHERAL
5° 19' - 10° 33'
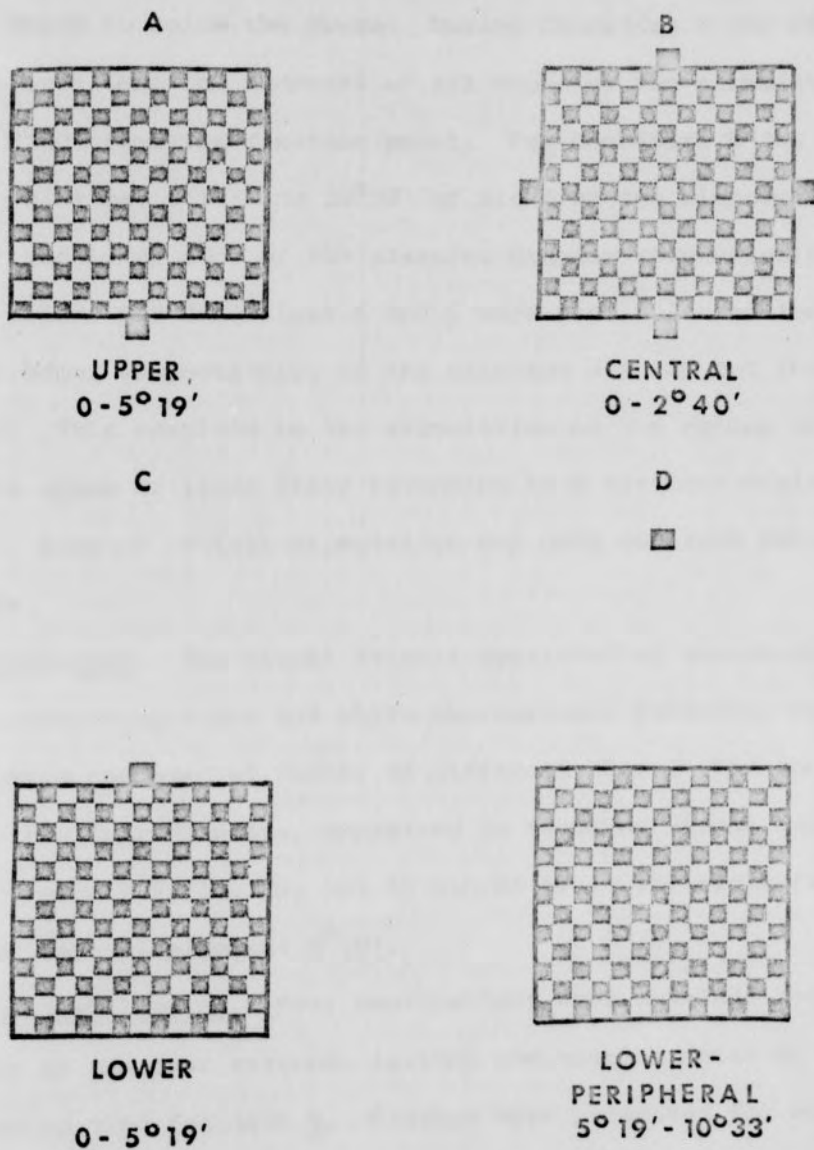
Fig. 2. Stimulus displays for the four areas of
retinal stimulation. Degree of eccentricity in relation
to each fixation point is given in degree of arc.

imaginary lines connecting the midpoints of each side of the display. Thus the retina was stimulated at four locations ranging from above to below the fovea. During Condition B the fixation point was such that the midpoint of all edges of the stimulus display was $2^o40'$ from the fixation point. For Condition D the fixation point was $5^o19'$ and $10^o33'$ of arc from the midpoint of the upper and lower edge of the stimulus display respectively. Fixation points for Conditions A and C were such that the lower and upper edge, respectively, of the stimulus display cut through the fovea. This resulted in the stimulation of the retina in either the upper or lower field extending to a vertical distance of $5^o19'$. Area of retinal stimulation was held constant for all conditions.

Check-size. The visual stimuli consisted of square-shaped displays containing black and white checkerboard patterns, each display being composed of checks of different sizes. The check sizes for the four displays, expressed in terms of visual angle subtended, were 7.5, 15, 30, and 60 min of arc. The width (and height) of each display was $5^o19'$.

Counterbalancing. Four replications were obtained for each S with one of the four sessions lasting one hour; a total of four hours running time for each S. Flashes were presented for each condition in blocks of 50. The order of stimulation for each retinal locus and check-size was presented according to a Graeco-Latin square design such that every retinal location occurred once and only once with every check-size during one experimental session.

Control. White noise was used to mask any extraneous sounds that might evoke auditory cortical potentials or be distracting to Ss.

Methods for Data Collection and Stimulation

Visual stimulus apparatus. Patterned light flashes of approximately 10 μsec duration were presented binocularly to each S at a rate of about 1 Hz. Flashes were generated by a Grass PS - 2 Photostimulater. Flash intensity level was set at 2 on the Photostimulator with subjective intensity approximately 3 log units brighter than the background luminance level, which was approximately 0.5 millilamberts. Fixation points were clearly visable under all conditions.

Subjects were seated at a distance of 86 cm from the visual stimulus in an electrically shielded room. Electrodes were placed on the scalp before Ss entered the experimental cubical.

Data collection. VER recordings from the four electrode locations were amplified by a multichannel Grass Model 7 Polygraph equipped with 7P 1 Preamplifiers and summed through four channels of a Mnemotron 400B Computer of Average Transients (CAT). At the completion of each of the 16 experimental conditions, the on-line records were written out by a Moseley X-Y plotter for graphical analysis.

Subject's instructions. Binocular fixation was required for all Ss. Points of fixation were varied for each experimental condition (16 times per session). To save experimentation time

Ss were asked to change the stimulus display after each condition. During this time the experimenter obtained the on-line VER records. To insure that Ss were attending to the stimulus, they were asked to count each light flash and to report the number counted at the end of each condition. Flash number was varied from run to run in order that Ss could not anticipate the number to be presented; however, VERs to exactly 50 flashes were consistently recorded during each run.

Data analysis. Quantification of VER waveform was made by measuring the average height in millimeters of each waveform within the second, third, fourth, and fifth 50-millisecond intervals following stimulus presentation. Average height was measured by algebraic summation with respect to a common baseline representing zero voltage level (i.e., the average voltage level of the first 50-millisecond interval). The average distance of each deflection from the baseline, as well as the location of the baseline, was determined by visual inspection in such a way that one-half of the total area within a 50-millisecond interval fell above as well as below a line drawn to fit that particular waveform. To expedite the statistical analysis a constant was added to each amplitude measure so as to make all measures positive. The measures thus obtained for each S were subjected to an analysis of variance using a repeated measures design.

Results

Evoked responses obtained under all 16 experimental conditions for $\underline{S}$ PA are given in Figure 3. Superimposed tracings of VERs, made directly from X-Y plots, represent replications for each experimental condition and illustrate the high degree of VER consistency. As indicated on the abscissa, the VER waveforms in Figure 3 have been divided into 100 millisecond intervals. The four major divisions along the ordinate represent check size which is expressed in terms of visual angle (minutes of arc). Visual inspection across each column reflects the effect of stimulating the retina with checkerboard patterns positioned progressively lower in the visual field. It should be remembered that stimuli presented to the upper visual field impinges on the lower half of the retina; the lower field impinges on the upper half. Visually evoked responses recorded from different electrode locations are shown on the ordinate with V_z, P_z, O_z, and T_5-T_6 representing vertex, parietal, occipital, and temporal lobe activity respectively. Each VER for this particular $\underline{S}$ had an average frequency of about 10 Hz. The reader is reminded that each averaged waveform was based on a summation of 50 responses.

Main Effects

Effects of retinal stimulation site on VER. The effect of locus on retinal stimulation on VER is shown in Figure 4.

Fig. 3. Averaged evoked cortical responses for S PA
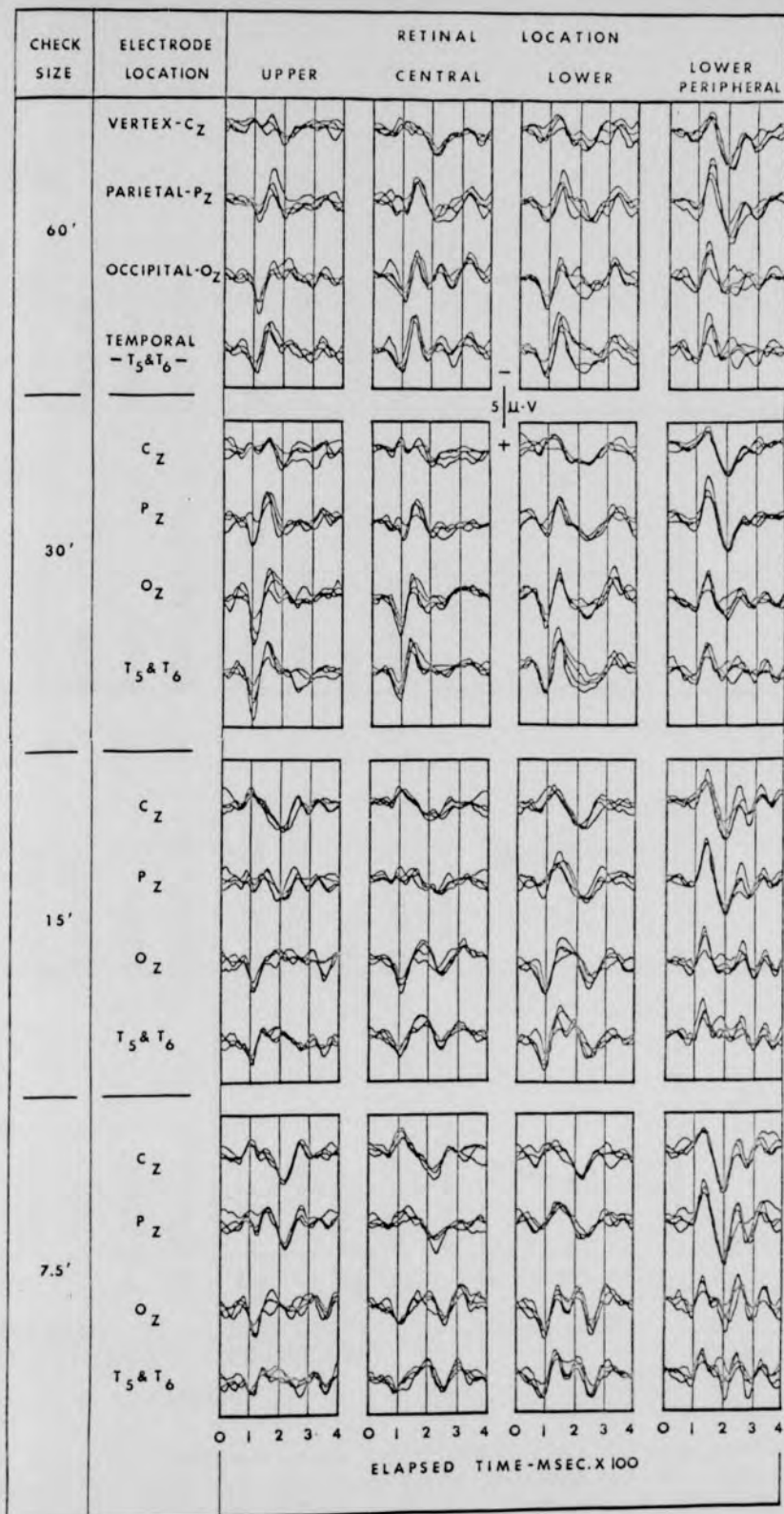recorded from four electrode placements to various check sizes
(in min of arc) presented to various retinal locations. Each
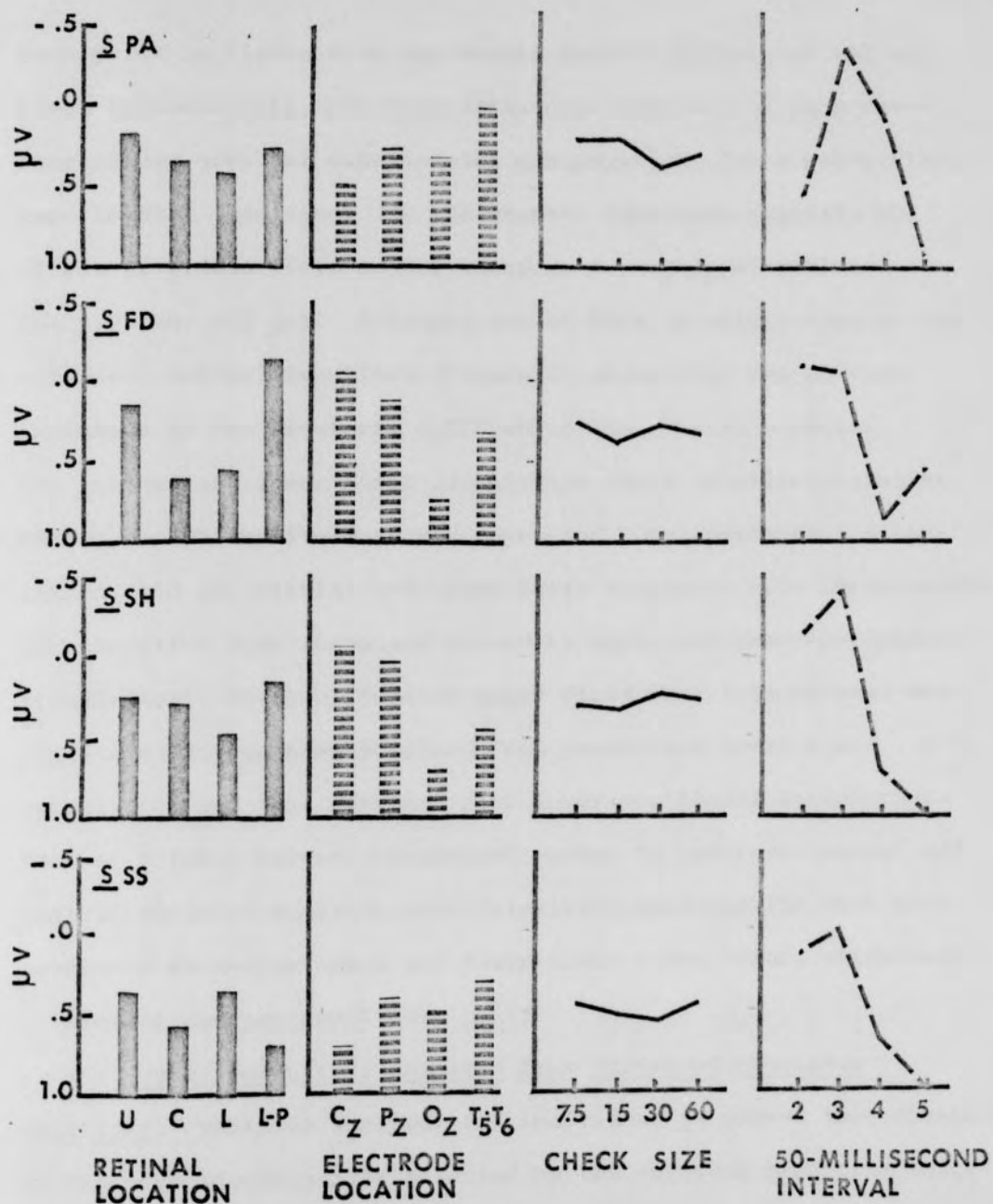superimposed tracing represents the summation of 50 responses.

Fig. 4. Average (see text) amplitude of quantified components of VERs for the four Ss illustrating the main effects of retinal location, electrode location, check size, and 50-millisecond interval.

Each point in Figure 4 is representative of the average voltage level in microvolts, per 50-millisecond interval, of each waveform summed over all experimental manipulations for a particular experimental condition. As the graphic functions suggest, the effect of visual field on VER waveform is highly significant ($p < 0.01$ for all $\underline{S}$s). A comparison of VERs to stimulation at the different retinal locations (Figure 4) shows that the average amplitude of the waveforms differed in two general aspects: (a) central and lower field stimulation had a relatively similar effect on VER amplitude, as did upper and lower-peripheral stimulation, and (b) central and lower field responses were consistently more positive than responses evoked by upper and lower-peripheral stimulation. The amplitude of upper field VERs fell between the amplitude of responses obtained from central and lower field stimulation and that obtained from lower-peripheral stimulation. For one $\underline{S}$ (SS), however, responses evoked by lower-peripheral and central field stimulation were relatively more similar than were responses evoked by upper and lower field stimulation, which were of similar average amplitude.

Evoked potentials obtained from different electrode locations. Variance analyses for individual $\underline{S}$s showed that changes in VER were significantly affected by the cortical area from which activity was recorded ($p < 0.01$); however, graphical representations of the data (see Figure 4) show differential effects between $\underline{S}$s. For $\underline{S}$s FD and SH, responses became progressively more positive as the recording site was shifted from a more anterior (V_z) to a more

posterior (O_z) location along the midline. Maximum positivity was recorded from electrodes placed over O_z. Responses obtained from T_5-T_6 fell between those obtained from electrodes over O_z and P_z areas. For Ss PA and SS maximum positivity was recorded from the V_z electrode, with positivity decreasing at sites O_z and P_z. Minimum positivity was recorded at the T_5-T_6 electrode. These effects are discernable in the waveform tracings of S PA (see Figure 3).

The effect of check size on VER. Both graphic (see Figure 4) and variance analyses revealed that VERs were not differentially affected by changes in check size for three of the four Ss. Although the main effect of check size was not significant, inter-actions between check size and other experimental conditions were extremely significant (first-order interactions will be dealt with in a later section). The main effect of check size was significant at the 0.01 level of probability for S PA. Relative positivity increased to stimulation with checks subtending visual angles of 30 and 60' of arc.

VERs occurring within 50-millisecond intervals. As was expected, variation in VER waveform was dependent upon the point in time that a particular component occurred following the onset of light stimulation. Differences in potential over the second, third, fourth, and fifth intervals were significant for all Ss ($p < 0.01$). In general, the most positive response occurred within the fifth 50-millisecond interval following retinal stimulation, with least positivity (negative component) occurring during the third 50-millisecond interval (see Figure 4).

First-Order Interactions

Locus of retinal stimulation X 50-millisecond intervals.
Variance analysis revealed significant interactions between visual
field and 50-millisecond intervals ($p < 0.01$). With respect to
locus of retinal stimulation, VERs obtained from upper visual
field stimulation were of relatively opposite polarity when com-
pared to responses obtained from lower visual field stimulation
within a particular 50-millisecond interval. In general, polarity
inversions between upper and lower field responses were readily
apparent within the second 50-millisecond interval. Maximum
differences were manifested within third and fourth 50-millisecond
intervals. Figures 3 and 5 illustrate this polarity inversion
effect.

For two of the four Ss (PA and FD), there was a systematic
change in waveform polarity among the four 50-millisecond inter-
vals as stimulation was moved from the lower-peripheral to the
upper visual field. For example, within the third 50-millisecond
interval, responses for PA show a progressive shift from maximum
positivity to negativity as stimulation progressed from upper, to
central, to lower, to lower-peripheral visual fields. By the
fourth 50-millisecond interval, maximum positivity was evoked
from lower-peripheral field stimulation with positivity steadily
decreasing as stimulation was moved to the upper visual field.
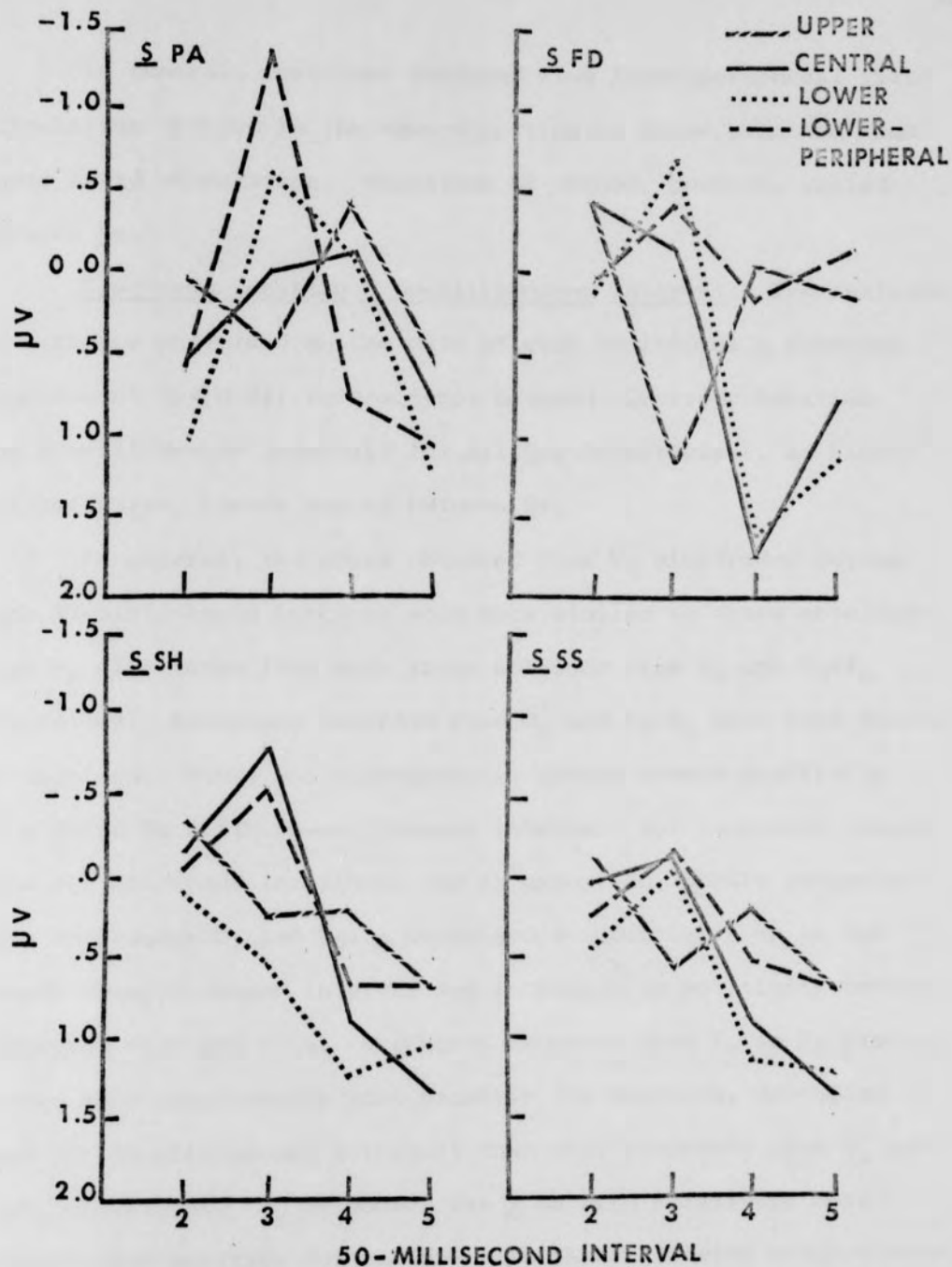This change-over effect is evident in the tracings of Figure 3.

Fig. 5. Interaction effects for each S of locus of retinal stimulation and 50-millisecond interval on the average amplitude of quantified components of VERs (see text).

In general, functions obtained from lower-peripheral field stimulation changed in the same direction as those obtained from lower field stimulation. Magnitude of change, however, varied between $\underline{S}$s.

$\underline{\text{Electrode location}}$ X $\underline{\text{50-millisecond interval}}$. The analysis of variance performed on the data of each individual $\underline{S}$ revealed significant (p$<$0.01) interactions between electrode location and 50-millisecond intervals for all $\underline{S}$s; nevertheless, as Figure 6 illustrates, trends varied between $\underline{S}$s.

In general, responses obtained from V_z electrodes during each 50-millisecond interval were more similar to those obtained from P_z electrodes than were those obtained from O_z and T_5-T_6 electrodes. Responses recorded from O_z and T_5-T_6 were also similar in waveform. There was a progressive change toward positivity from third to fifth 50-millisecond intervals for responses taken from all electrode locations. As an exception, $\underline{S}$ PA's responses from electrodes O_z and T_5-T_6 decreased in positivity up to the fourth 50-millisecond interval and increased in positivity between intervals four and five. Responses recorded from V_z to P_z electrodes were consistently more negative (or positive, depending upon the 50-millisecond interval) than were responses from O_z and T_5-T_6 electrodes. P_z responses for $\underline{S}$ SS were relatively more negative and positive during intervals three and five respectively than responses obtained from other electrode locations. O_z responses for $\underline{S}$s FD and SH shifted toward negativity earlier (fifth 50-millisecond) than did those for $\underline{S}$s PA and SS. O_z and

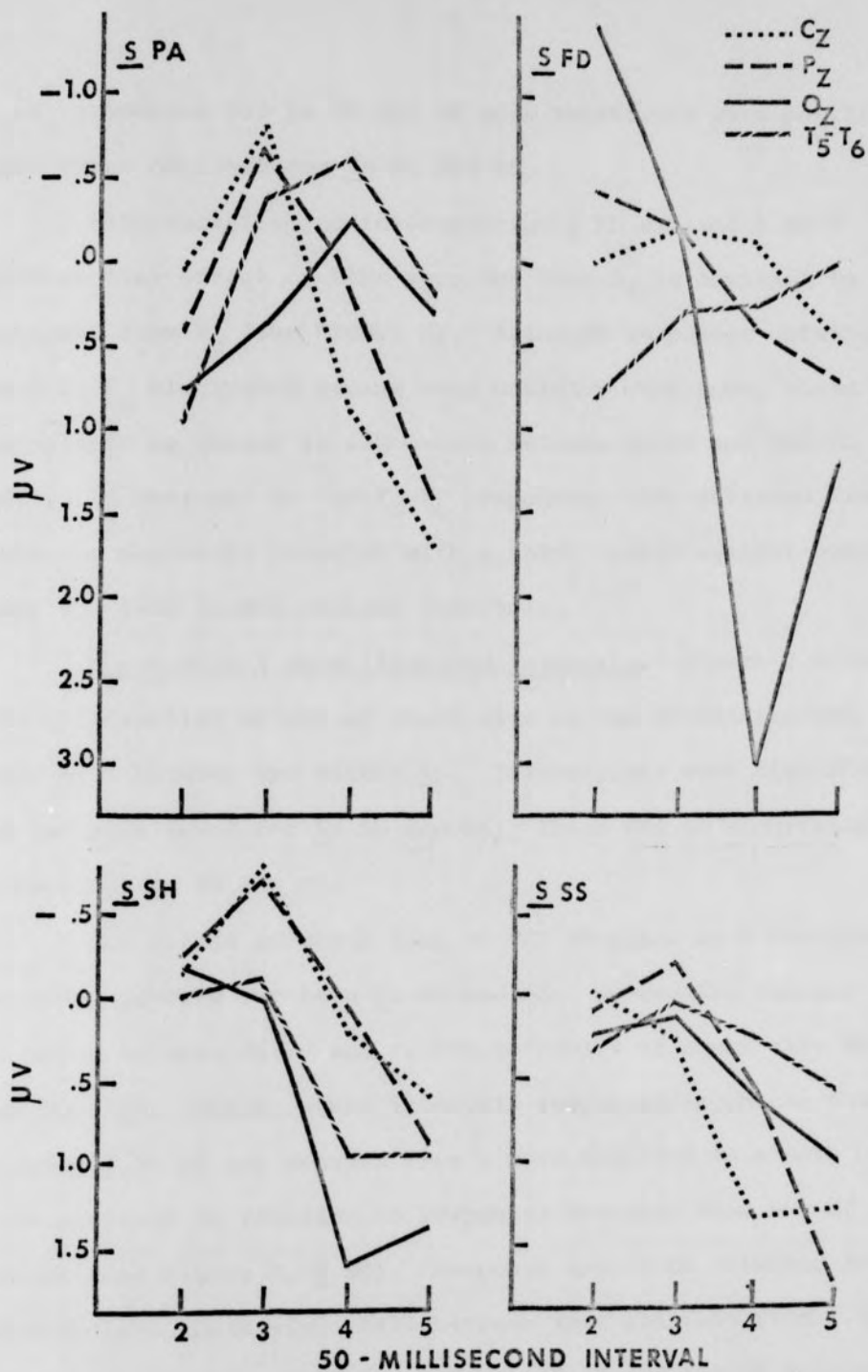Fig. 6. Interaction effects for each S of electrode location and 50-millisecond interval on the average amplitude of quantified components of VERs (see text).

T_5-T_6 responses for $\underline{S}$s FD and SH were relatively more positive than those obtained for $\underline{S}$s PA and SS.

Fifty-millisecond intervals for $\underline{S}$ FD exerted a more differential effect on VERs recorded from O_z in contrast to those recorded from V_z (see Figure 6). Although responses obtained from T_5-T_6 electrodes became less positive over time, there was relatively no change in components between third and fourth intervals. In contrast to the T_5-T_6 responses, VERs obtained from P_z showed a monotonic relation with a shift toward maximal positivity over the four 50-millisecond intervals.

Check size X 50-millisecond intervals. Figure 7 illustrates the differential effect of check size on the 50-millisecond intervals both between and within $\underline{S}$s. Interactions were significant at the 0.01 level for $\underline{S}$s SH and SS. There was no significant effect for $\underline{S}$s FD and PA.

The effect of check size on VER waveform as a function of time was orderly for both $\underline{S}$s SH and SS. Systematic changes occurred between third and fourth intervals as check size varied for both $\underline{S}$s. During these intervals responses to checks subtending 7.5' of arc changed from a more negative to a more positive position in relation to responses obtained from 60' of arc checks (see Figure 7, $\underline{S}$ SH). Response magnitude obtained from intermediate check sizes fell between that obtained from 7.5 and 60' of arc checks. Rotation between third and fourth intervals for $\underline{S}$ SS resulted in a greater degree of change for checks subtending 30 and 60' of arc than for 7.5 and 15' checks. Responses to
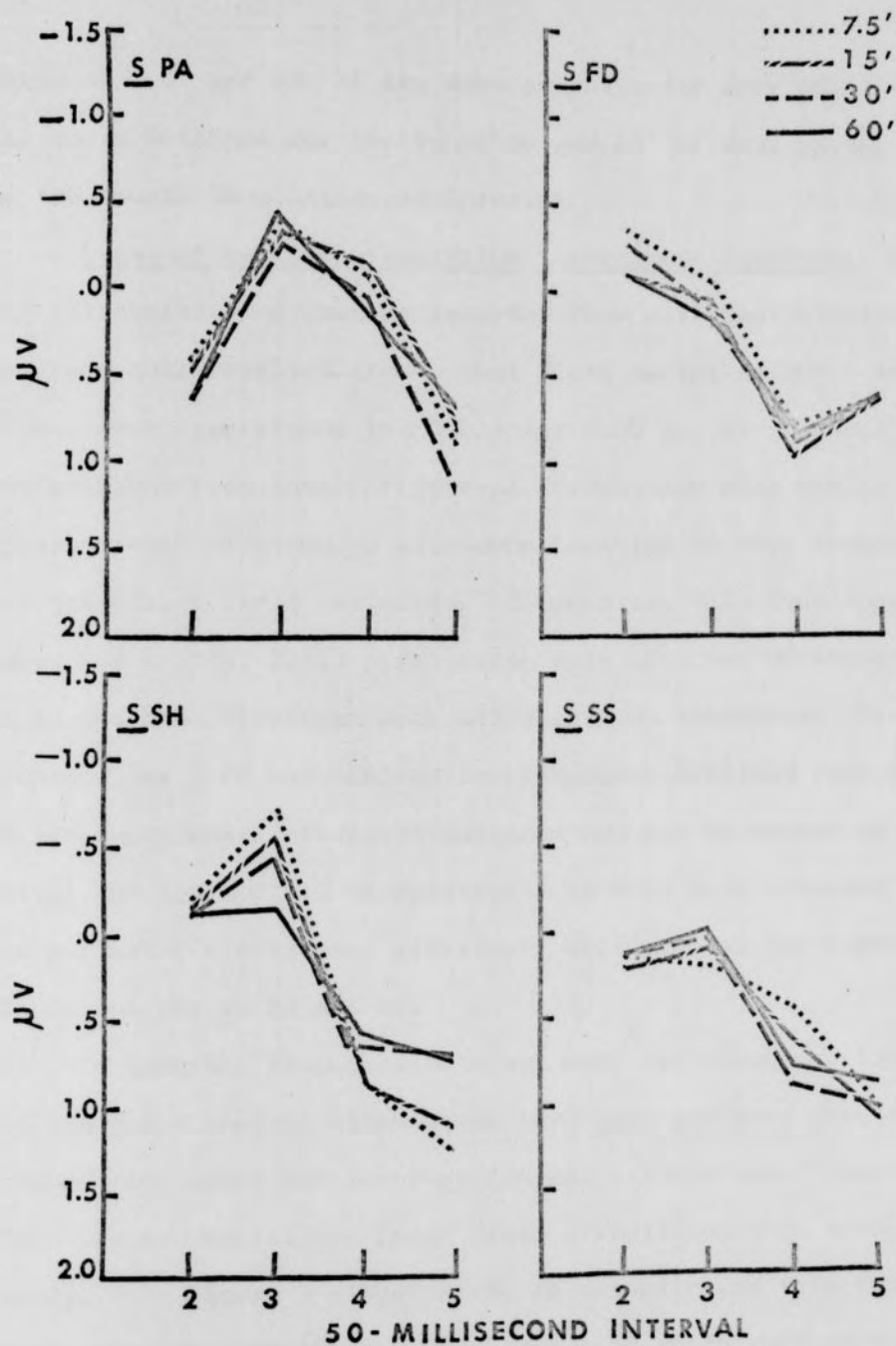
Fig. 7. Interaction effects for each S of check size
and 50-millisecond interval on the average amplitude of
quantified components of VERs (see text).

checks of 7.5' and 15' of arc were consistently more positive than those obtained for checks of 30 and 60' of arc, except during the fourth 50-millisecond interval.

Locus of retinal stimulation X electrode location. Figure 8 is illustrative of changes recorded from different electrode locations that resulted from visual field manipulations. Interactions were significant (p < 0.01) for each S. It is clear that VERs obtained from lower-peripheral stimulation were not as differentially affected by electrode location as were responses to other visual field variables. In general, VERs from upper, lower, and central field stimulation were affected differentially but in the same direction over all electrode locations. Direction of change for S PA was similar for responses obtained from upper and lower-peripheral field stimulation and for responses to central and lower field stimulation. As VERs were recorded from more posterior electrodes, positivity decreased to lower-peripheral stimulation for Ss PA and SS.

In general, responses obtained over all electrode locations from lower and central stimulation were more positive than those obtained from upper and lower-peripheral stimulation. Largest potentials to central and lower field stimulation were recorded from O_z. As Figure 3 illustrates, an exception to this finding was the lower-peripheral VERs from S PA which were more positive at V_z than were responses from upper, central, or lower stimulation. Responses obtained from all visual field manipulations became progressively less negative as the recording site

Fig. 8. Interaction of effects for each S of electrode placement and retinal location on the average amplitude of quantified components of VERs (see text).

shifted from P_z to O_z. From O_z to T_5-T_6 values moved in a direction of lesser positivity.

Retinal locus of stimulation X check size. Response relations between locus of retinal stimulation and check size are shown in Figure 9. Interactions between these variables were significant at the 0.01 level for all Ss except FD ($p < 0.10$). Over check size, responses from central stimulation changed in directions which were opposite those obtained to lower-peripheral stimulation. At all retinal locations, checks subtending 15 and 30' of arc had a more differential effect on VERs than did checks of smaller or larger visual angles. A greater degree of change occurred between check size presentations to central and lower visual fields than to upper and lower-peripheral fields. S PA, however, showed a differential change in upper field VERs in response to smaller checks subtending 7.5 and 15' of arc. Lower field responses to all check sizes were consistently more positive than responses recorded to other retinal locations for this particular S.

Electrode location X check size. With respect to the statistical analysis, electrode location and check size inter-actions were significant for only one of the four Ss (SH: $p < 0.01$). Graphical representations of these results nevertheless show interesting functions for all Ss. Although the analysis of variance revealed a significant interaction between check size and electrode location for S SH, the error variance for this particular S was extremely low (M.S. = 7.88; df, 768), and
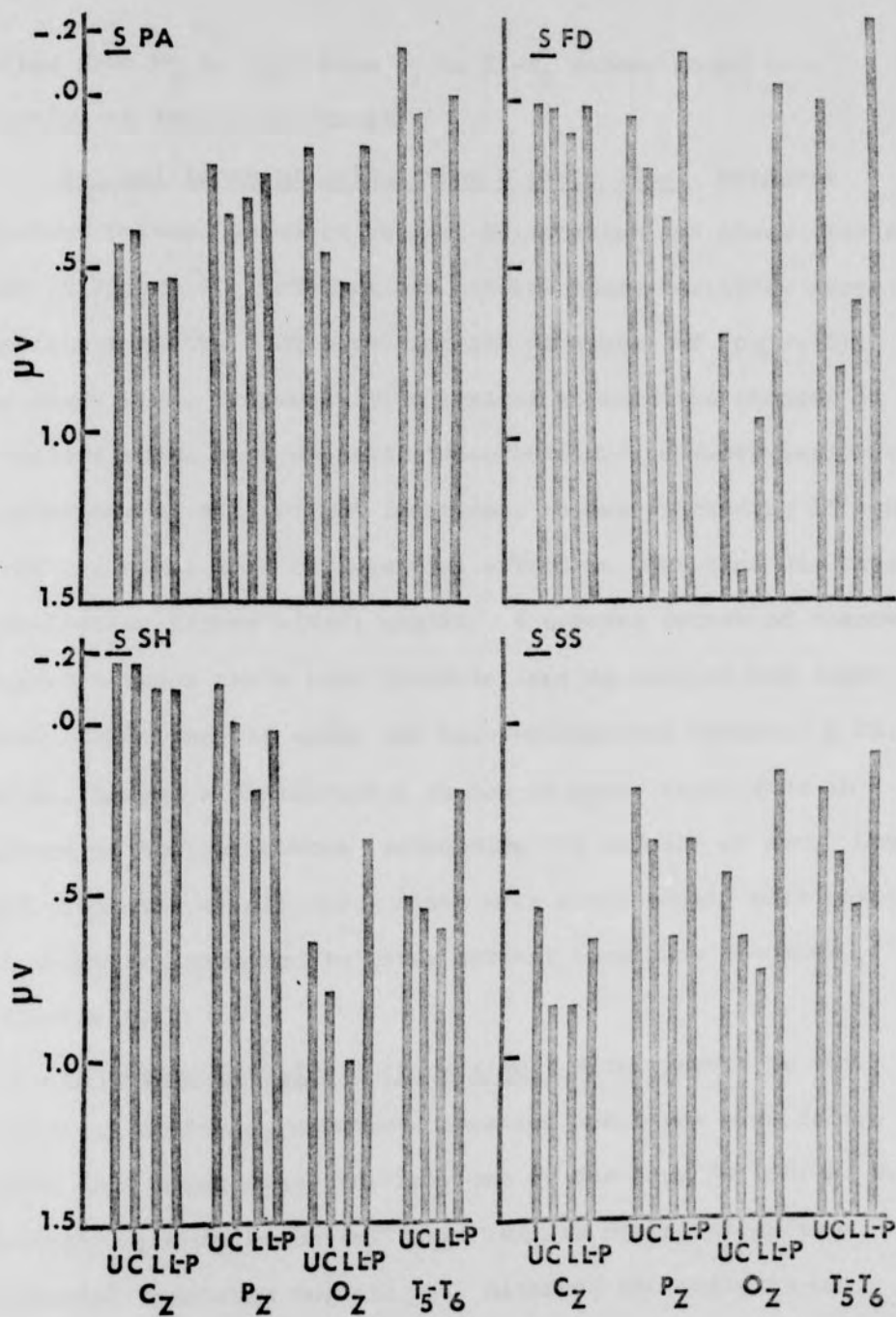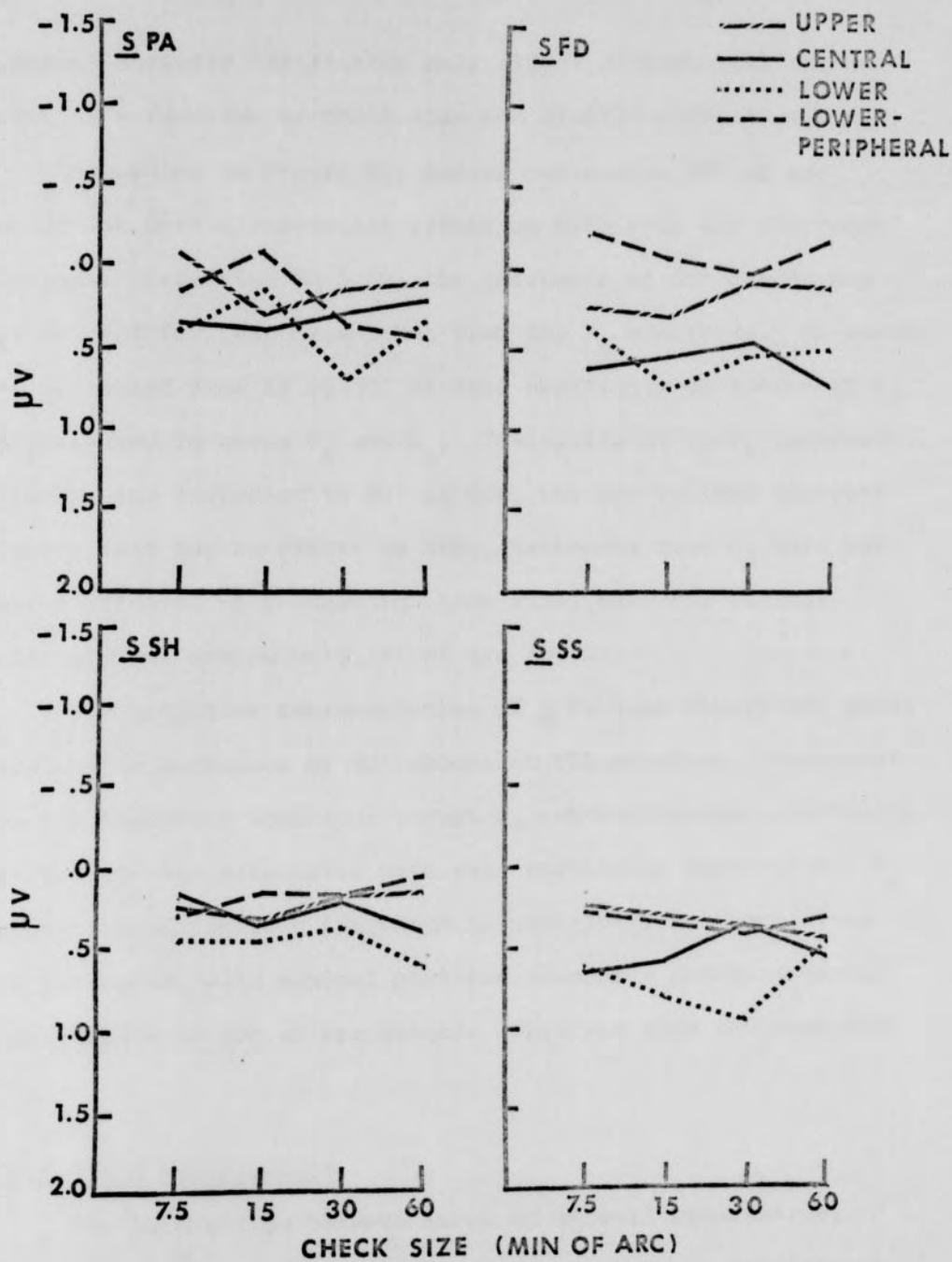
Fig. 9. Interaction effects for each S of check
size and retinal location on the average amplitude of
quantified components of VERs (see text).

graphical analysis illustrates only slight differential changes in VER as a function of check size and electrode location.

According to Figure 10, checks subtending 30' of arc exerted the most differential effect on VERs over all electrode locations. Referring to $\underline{S}$ FD, the influence of 30' checks was most evident for responses taken from the P_z electrode. As check size increased from 15 to 30' of arc, negativity decreased at P_z and increased in areas V_z and O_z. Positivity at T_5-T_6 increased as check size increased to 30' of arc, but any further increase in check size had no effect on VER. Responses from O_z were not greatly affected by changes in check size; however, maximal positivity was evoked with 15' of arc checks.

The graphical representation of $\underline{S}$ PA (see Figure 10) shows a systematic influence of 30' checks on VER waveform. Responses from all electrode locations except V_z reached maximal positivity when the eye was stimulated with this particular check size. V_z responses progressively increased in positivity as check sizes were increased, with maximal positive responses obtained during stimulation with 60' of arc checks. This was also the case with $\underline{S}$ SS.

Higher-Order Interactions

The interaction between locus of retinal stimulation, electrode location, and 50-millisecond interval was significant ($p < 0.01$) for all $\underline{S}$s. The significance of this and other second-order interactions suggests the tremendous sensitivity of VER to
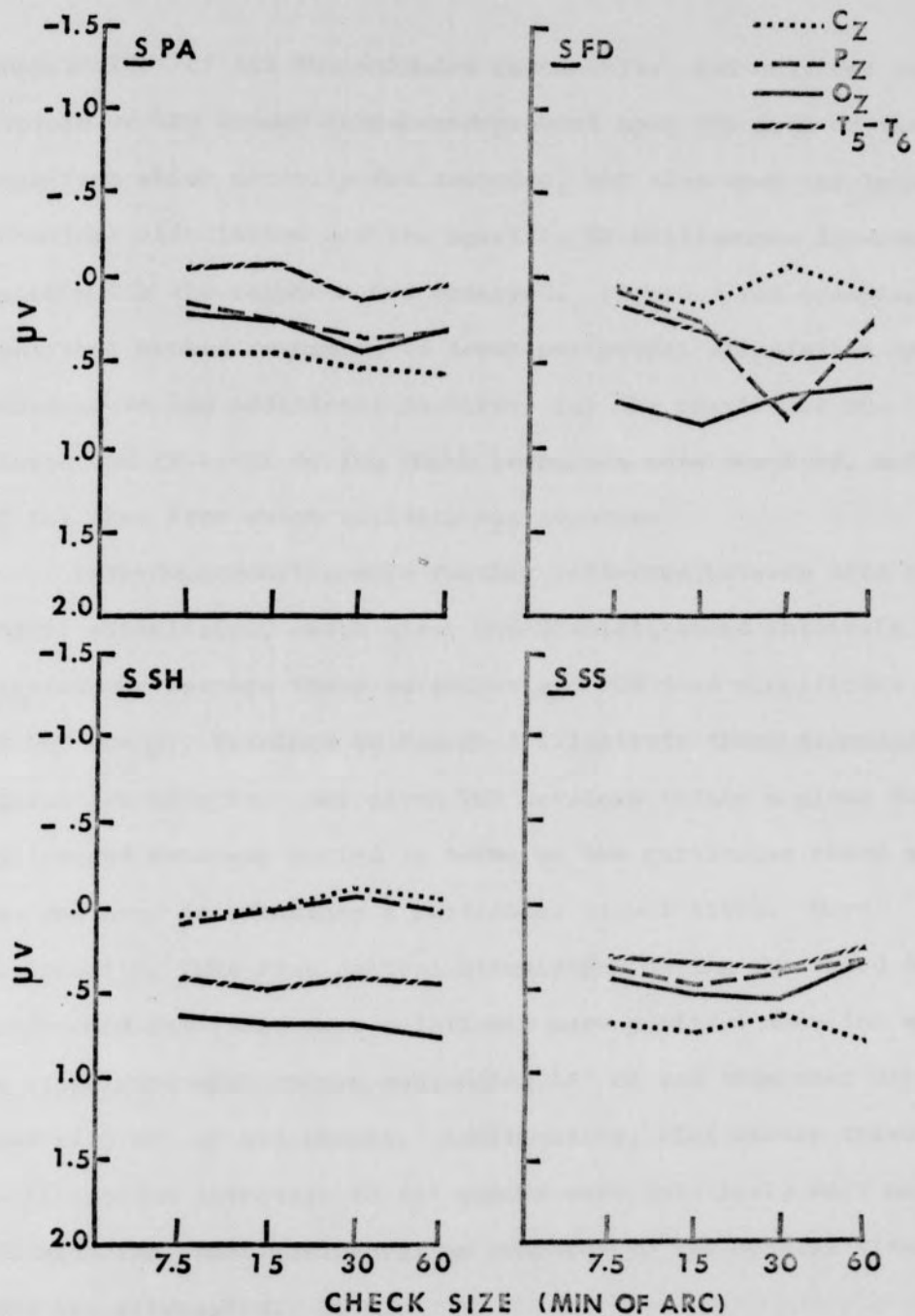
Fig. 10. Interaction effects for each S of electrode location and check size on the average amplitude of quantified components of VERs (see text).

manipulations of all the stimulus parameters. Not only was the waveform of the evoked response dependent upon the area of the brain from which activity was recorded, but also upon the locus of retinal stimulation and the specific 50-millisecond interval during which the response was observed. Figure 3, for example, shows that evoked responses to lower-peripheral stimulation varied according to two additional factors: (a) the particular 50-millisecond interval during which responses were observed, and (b) the area from which activity was recorded.

Interdependencies were further reflected between site of retinal stimulation, check size, and 50-millisecond intervals. Interactions between these variables and VER were significant for all but one $\underline{S}$. Tracings in Figure 3 illustrate these second-order interaction effects. Any given VER waveform within a given 50-millisecond interval varied in terms of the particular check size that was used to stimulate a particular visual field. More specifically, VERs from central stimulation during the third 50-millisecond intervals were relatively more positive when the eye was stimulated with checks subtending 15' of arc than when stimulated with 60' of arc checks. Additionally, VERs within third 50-millisecond intervals to 15' checks were relatively more negative when the lower-peripheral as compared to the central visual field was stimulated.

Second-order interactions between electrode location, check size, and 50-millisecond intervals were significant for three $\underline{S}$s at the 0.01 probability level and for $\underline{S}$ SS at the 0.05 level.

Figure 3 shows that response magnitude during the fourth 50-millisecond interval yielded one function when responses to 60' of arc checks were obtained from the O_z electrode and a relatively different function when the retina was stimulated with 15' of arc checks, or when all variables were held constant except electrode location.

Significant interactions ($p < 0.01$) between retinal location, electrode location, and check size were found for one Ss (FD). Third-order interactions were significant ($p < 0.01$) for S SH. This interaction indicated that VERs for a particular S were dependent upon the interval of time following flash presentation, the retinal site of stimulation, the particular size of the check used in stimulating the retina, and the cortical location from which activity was recorded.

Discussion

VERs in Relation to Topography of the Visual Cortex

The observed variation in VER waveform to stimulation at different retinal locations may be interpreted in terms of the retinotopically-arranged visual cortex. Retinal projections around the calcarine fissure (see Figure 1) are arranged in such a manner that macular projections end posteriorally on the occipital pole with respect to the more anterior peripheral projections. In relation to the occipital lobe, the calcarine fissure extends on a horizontal plane with its lower extremities reaching toward the occipital pole (Jeffreys, 1971). Lower visual

field projections lie mainly above the calcarine fissure in contrast to upper visual field projections which extend below the calcarine fissure. Electrodes placed differentially around this area would therefore maximally, or minimally, record potentials evoked by stimulation of underlying retinal projection areas.

Polarity inversions obtained in this study between corresponding components (second, third, and fourth 50-millisecond intervals) of VERs to upper and lower field stimulation are possibly indicative of differences in the anatomical origin of those responses in that lower field projections around the calcarine fissure are inversely oriented in relation to those of upper field projections. When VERs were recorded from 2.5 cm above the inion (O_z), response inversions were readily noticeable; however, as the recording site shifted to areas farther removed anteriorly from the calcarine fissure, responses obtained from upper field stimulation progressively decreased in magnitude. In general, lower field VERs from C_z were more positive or more negative than responses to upper field stimulation with polarity inversions either missing or less apparent at C_z. These findings are inconsistent with those of Jeffreys (1971) who found upper VERs to reach a maximum 5-10 cm foreward of the occipital protuberance and lower field 2-5 cm foreward of the occiput. This discrepancy indicates a high degree of complication within the electrophysiological processes underlying VER and suggests the need for further research.

In relation to the topography of the visual cortex, electrodes recording from P_z to C_z are relatively closer to that area above the calcarine fissure than to the area below the calcarine fissure. Electrodes located on the vertex are, therefore, farther away from areas dealing with upper field responses than from those areas concerned with lower field VERs. Further, vertex electrodes are located closer to peripheral lower field projections than to lower macular projections. If a topographical hypothesis were relevant, VERs to lower peripheral field stimulation would be expected to reach maximal amplitude at recording sites closer in proximity to projections of the upper peripheral area of the retina. As the tracings in Figure 3 illustrate, progressive shifts in stimulation from the lower to the lower-peripheral field resulted in maximal VERs at P_z cortical areas. P_z electrodes were approximately directly over peripheral lower field projections in the visual cortex. The above finding is consistent with Jeffreys' data (1971) in that a progressive anterior displacement of VER distribution over the cortex was found as stimulation sites were changed from the center to the periphery of the lower visual field.

Relative Contribution of Central and Peripheral Retinal Areas to VER

Although Rietveld, et al. (1967) stated that "the central foveal area contributes by far the greatest part to the pattern response (p. 269)," the present study illustrates the profound

contribution of retinal areas other than the fovea to the pattern response. Under manipulations in four check size variables, maximal VERs depended on both the locus of retinal stimulation and the projection area underlying a particular electrode placement. Rietveld's conclusion was based on VERs obtained from bipolar electrodes 1.5 cm above the inion in response to central and perhiperal ($4^o04'$) stimulation with small checks (20.5' of arc). Tracings in Figure 3 are an example of the general finding in the present study that, as the pattern response to peripheral stimulation decreases at the O_z electrode, activity increases at the more anterior recording sites. Electrodes placed over the area 2.5 cm above the inion yield maximal VERs to central stimulation and minimal activity to peripheral stimulation. This is to be expected when the topography of the visual cortex is taken into consideration. Stimulation of the central (more foveal) retina initiates activity that is transmitted to the posterior occipital lobe. Electrodes placed over the cortical area receiving this activity record resultant potential changes. Electrodes placed at distances farther removed from the posterior pole are less likely to record activity initiated in the macular area, but relatively more likely to record activity from the more anterior peripheral projection areas of the cortex. The central foveal area, therefore, contributes the greatest part of the pattern response when pattern stimuli are being projected to the central visual field and when activity is being recorded from the area within 3 cm above the inion. When pattern stimuli are being

projected to the peripheral visual field, the greatest part of

the pattern response is contributed by the peripheral retinal

area; however, this increase in activity will be recorded only

if electrodes are placed over the more anterior cortical areas.

Interaction between Check Size and Locus of Retinal Stimulation: Effect on VER

It has been previously demonstrated that the critical check

size evoking the greatest amplitude VERs depends on the area of

the retina to which that stimulus is presented (Harter, 1971). In

general, the results of the present study obtained from O_z elec-

trodes further illustrate that (a) checks subtending 15 to 30' of

arc evoke maximal VERs when the central retina is stimulated, and

(b) as the retina is stimulated progressively more peripherally

(central to lower to lower-peripheral), check size evoking maximal

VERs increases from 30 to 60' of arc. For two $\underline{S}$s checks subtend-

ing 30 to 15' of arc evoked the greatest VERs to upper field

stimulation; 60' of arc checks evoked greatest VERs at the upper

field for the remaining two $\underline{S}$s. Further research concerning VERs

from upper field stimulation should resolve this discrepancy.

The following findings obtained from O_z electrodes were in

agreement with those obtained by Eason, et al. (1970): (a) responses

to lower field stimulation were consistently greater (more posi-

tivity) than those of central and upper field stimulation, (b)

lower and central field responses were more differentially affected

by manipulations in check size than were upper (and lower-peripheral)

field VERs, (c) upper field responses contained a second sinusoidal oscillation; however, this oscillation was present over all check sizes for two of the four Ss and absent over all check sizes for the remaining two Ss, and (d) lower field VERs were greater for the relatively large check sizes (those subtending 30 and 60' of arc), while central field responses were maximal to checks subtending 30 and 15' of arc. Eason, et al. further found upper field VERs to be more sensitive to checks subtending 9.4' of arc. Only one S (PA) showed this selective sensitivity to smaller checks in the upper field. Since differences were found between check size and lower and central field stimulation, it is plausible that the upper visual field would also be differentially sensitive to check size thus reflecting differences in the size of the centers of the retinal receptive fields. Harter (1971) and Harter and White (1968) presented evidence that suggests a correspondence between differentially effective check size on VER amplitude and the size of receptive field centers at different retinal locations. Since lower-peripheral VERs showed a slight increase to 30 and 60' checks, with sensitivity increasing to smaller (15') checks as stimulation shifted from the lower to the central visual field, it is expected that responses from a larger sample would yield maximal VERs to small checks projected to the peripheral upper visual field. This would further test the possibility of differences in receptive field centers with respect to both retinal eccentricity and topography of the visual cortex.

Previous studies have found VER to be significantly affected by check size variables (Harter & White, 1968, 1970; Harter, 1971; and Eason, White, & Bartlett, 1970); however, check size failed to exert a significant effect in the present study. The studies mentioned above were held under conditions of virtually complete darkness. In the present study scattered light from an adjacent laboratory and from the area where the experimenter was monitoring EEG could have kept adaptation level at a minimum. Perry and Childers (1969) discussed the differential effect of adaptation level on VERs in relation to photopic and scotopic processes. It is highly possible that variation in individual responses as well as the failure of check size to reach significance is related to the level of adaptation within the experimental cubical. The need for further research concerning the effects of adaptation and the relative contribution of photopic and scotopic processes on VER is evident.

Although the main effect of check size was significant for only one of four $\underline{S}$s, significant interactions obtained for some $\underline{S}$s between check size and visual field, check size and electrode location, check size and 50-millisecond intervals in addition to the second-order interactions with check size suggest the specificity of the effect of these variables on VER. The significance and specificity of the results indicates the need for further research dealing with only one or two levels of the variables used in the present study.

VER in Relation to Check Size, Locus of Retinal Stimulation,
and Electrode Location

The interaction between check size and locus of retinal
stimulation indicates that the relative contribution of check
size on VER was dependent upon the locus of retinal stimulation
and electrode location. The data reported in this study are
consistent with that of Harter (1971) in that surface-negativity
was least affected as stimulation was changed from the central
to the peripheral retina. Negativity was, therefore, the dominant
feature in the peripheral VERs.

As the recording site was shifted anteriorally to C_z,
peripheral responses were consistently greater in magnitude
than were central VERs. These findings are again in accordance
with the topography of the visual cortex.

The relationship between check size and anteriorally
recorded (in relation to O_z) VERs is not clear. It has been
shown that visual acuity gradually decreases as rod distribution
increases (Alpern, et al., 1967). As the rod count increases,
however, so does the involvement of processes such as temporal
and areal summation (Talbot & Marshall, 1941). Perhaps the
contribution of these two physiological processes cancels the
relatively minor effect of check size on VERs at the periphery.

For S PA response amplitude remained the same for peripheral
and central responses to checks of 60' of arc but responses evoked
by peripheral stimulation (5°19') were clearly different in
shape from those evoked by central stimulation. As Figure 3

shows, the peripheral 60' check size response was more negative than the central response with second sinusoidal oscillations more evident for central stimulation at O_z but consistently more evident for peripheral responses as electrodes moved anteriorally from O_z. Second and third sinusoidal oscillations were readily apparent in peripheral responses recorded from checks of 15 and 7.5' of arc, with second sinusoidal waves present at O_z from central stimulation of 7.5' checks. Eason, et al. (1970) found second sinusoidal oscillations to be characteristic of VERs evoked by large checks in the upper visual field. Since upper field responses were less sensitive to large checks in the Eason, et al. study and since second (and third) sinusoidal oscillations were apparent in those conditions for PA that have been previously found to result in lower amplitude responses, it is suggested that these oscillations following maximal evoked potentials are indicative of different physiological processes underlying the evoked response. Further research is needed to see if similar findings can be considered typical of other Ss.

Summary Statement

The data presented above have illustrated the usefulness of VER in detecting visual processes involved in the retinotopically arranged visual cortex. VERs were shown to be highly dependent upon the locus of retinal stimulation. Response variability from a particular electrode location depicted manipulations in the locus of retinal stimulation and in the amount of contour contained

within the patterned stimuli presented to a particular visual field. When both the locus of retinal stimulation and check size were held constant, systematic changes in VER were consistent with the topography of the visual cortex. The location of scalp electrodes over specific retinal projection areas around the calcarine fissure was shown to be an important factor in detecting different patterns of electrical activity concomitant with changes in the other independent variables.

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APPENDIX

TABLE 1

ANALYSIS OF VARIANCE FOR VER
WAVEFORM: S̲ PA

Source	df	MS	F
Retinal location (A)	3	173.09	6.48**
Electrode location (B)	3	581.75	21.79**
Check size (C)	3	106.48	3.99**
50-millisecond intervals (D)	3	4986.82	186.77**
A X B	9	57.76	2.16*
A X C	9	112.68	4.22**
A X D	9	1374.14	51.47**
B X C	9	9.98	.37
B X D	9	1708.26	63.98**
C X D	9	35.58	1.33
A X B X C	27	14.43	-
A X B X D	27	68.87	2.58**
A X C X D	27	103.80	3.88**
B X C X D	27	73.09	2.73**
A X B X C X D	81	21.30	-
Total within	768		

* $p < 0.05$

** $p < 0.01$

TABLE 2

ANALYSIS OF VARIANCE FOR VER
WAVEFORM: S FD

Source	df	MS	F
Retinal location (A)	3	1621.14	53.45**
Electrode location (B)	3	1368.06	45.11**
Check size (C)	3	39.18	1.29
50-millisecond intervals (D)	3	3989.22	131.53**
A X B	9	292.53	9.64**
A X C	9	55.82	1.84
A X D	9	2212.10	72.93**
B X C	9	38.95	1.28
B X D	9	3452.69	113.84**
C X D	9	19.11	-
A X B X C	27	124.33	4.10**
A X B X D	27	622.27	20.51**
A X C X D	27	100.11	3.30**
B X C X D	27	95.19	3.13**
A X B X C X D	81	31.71	1.04
Total within	768	30.33	

* $p < 0.05$

** $p < 0.01$

TABLE 3

ANALYSIS OF VARIANCE FOR VER
WAVEFORM: S̲ SH

Source	df	MS	F
Retinal location (A)	3	263.13	33.39**
Electrode location (B)	3	1931.33	245.09**
Check size (C)	3	15.68	1.99
50-millisecond intervals (D)	3	6490.59	823.68**
A X B	9	100.78	13.75**
A X C	9	42.65	5.41**
A X D	9	610.03	77.41**
B X C	9	25.77	3.27**
B X D	9	347.56	44.11**
C X D	9	196.06	24.88**
A X B X C	27	9.09	1.15
A X B X D	27	129.55	16.44**
A X C X D	27	52.24	6.62**
B X C X D	27	27.83	3.53**
A X B X C X D	81	542.14	68.79**
Total within	768		

* $p < 0.05$

** $p < 0.01$

TABLE 4

ANALYSIS OF VARIANCE FOR VER
WAVEFORM: $\underline{S}$ SS

Source	df	MS	F
Retinal location (A)	3	474.70	21.72**
Electrode location (B)	3	447.71	20.48**
Check size (C)	3	24.54	1.12
50-millisecond intervals (D)	3	3062.69	140.10**
A X B	9	42.94	1.96*
A X C	9	150.59	6.89**
A X D	9	493.31	22.57**
B X C	9	12.56	-
B X D	9	320.11	14.64**
C X D	9	66.43	3.04**
A X B X C	27	17.88	-
A X B X D	27	70.66	3.23**
A X C X D	27	29.61	1.35
B X C X D	27	34.52	1.58*
A X B X C X D	81	15.72	
Total within	768	21.86	

* $p < 0.05$

** $p < 0.01$