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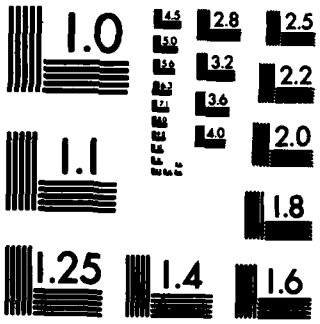

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A three part evoked potential (EP) study was undertaken in an attempt to better understand the neural mechanisms undelying vernier acuity. Results indicated: (a) VEPs evoked by vernier offset stimuli couldbe used to estimate psychophysical threshold, (b) VEP amplitude was affected by interference lines in the same way as psychophysical sensitivity (c) origin of the VEPs (and the associated neural mechanism) may be outside of striate cortex.

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ELECTROPHYSIOLOGICAL CORRELATES OF VERNIER ACUITY IN HUMAN VISUAL CORTEX

CPT Richard Zak
HQDA, MILPERCEN
200 Stovall Street
Alexandria, VA 22332

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in partial fulfillment of the requirements for the degree of Master of Science.

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THE FLORIDA STATE UNIVERSITY

COLLEGE OF ARTS AND SCIENCES

ELECTROPHYSIOLOGICAL CORRELATES OF VERNIER ACUITY IN HUMAN VISUAL CORTEX

by

RICHARD ZAK

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Department of Psychology
in partial fulfillment of the
requirements for the degree of
Master of Science

Approved:

Professor Directing Thesis

Jack E. Hokanson

Howard D. Baker

April, 1984

DEDICATION

To my wife, Dee, who has been patient, understanding and there when needed.

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The thesis presented here would not have been possible without the expertise and patience of Dr. Mark Berkley. His work as advisor and subject are much appreciated. More importantly, he has been an excellent teacher who has given me a true appreciation for the elegance of good research.

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INTRODUCTION

The resolving power of the human visual system, when considered in light of its optics and anatomy, is estimated to be slightly less than one minute of visual angle (Westheimer, 1979). Psychophysical studies, using experimental techniques to bypass optical limitations, have reported resolution thresholds as low as 30-35 seconds (Westheimer, 1979). These values coincide with predictions based on the physical properties of the eye and the grain of the receptor mosaic. There exists, however, another class of acuities which give the visual system an ability to detect extremely small differences of one object's position in space relative to another. These acuities have been collectively dubbed hyperacuities (Westheimer, 1975) and represent the limits of spatial resolution exhibited by the neural processors of visual information.

Recent investigations of hyperacuity have usually used a vernier stimulus which requires the detection of an offset between two abutting or slightly separated features. The offset is in a direction normal to an actual or implied line connecting the two features when

they are aligned. Tests of such acuity generally show that thresholds of detection are in the range of 4-10 seconds and lie well below the resolution limit of the retinal mosaic.

Specific stimulus features have an effect on vernier thresholds. For example, when the stimulus consists of abutting lines, increasing their length decreases threshold up to a line length of 5 minutes, beyond which no further effect is seen. Comparably lower thresholds, however, are found with lines of any length separated at the point of offset by 2.5-5 minutes (Westheimer and McKee, 1977a). The lowest threshold was not line dependent as similar values were obtained for detecting misalignment of two dots separated by a 2.5-5 minute interval (Sullivan et al., 1972; Westheimer & McKee, 1977a; Beck & Schwartz, 1979). Hyperacuity has also been demonstrated with a variety of other stimulus configurations by Westheimer and McKee (1977a): misalignment of dissimilar features (e.g., apex of a chevron and a vertical line segment), implied features (e.g., gaps in parallel line segments), and for features lacking high frequency contour information (e.g., brightness gradients superimposed on uniformly illuminated bars).

While hyperacuities appear to be spatial in nature, they also have temporal properties. Apparent offsets, with appropriate thresholds, can be in induced by pre-

senting two aligned segments asynchronously (Burr, 1979). Also, hyperacuity thresholds are not degraded even when the vernier target is moving up to a velocity of 4 degrees sec^{-1} (Westheimer & McKee, 1977; Morgan, 1981). These studies suggest that the mechanism processing positional information has a time constant allowing judgements of spatial location to occur even when the information must be temporally summed.

The spatial limit within which this location processor works has been estimated with a paradigm in which irrelevant contours are presented close to the offset and interaction effects noted. Presentation of line stimuli on the flanks of a vernier offset interferes with detection of the offset (Westheimer & Hauske, 1975). The strongest spatial interference occurred when the additional lines, oriented either vertically or horizontally, were presented within 2.5-5 minutes of visual angle on each side of the offset (Westheimer & Hauske, 1975). In the same experiment, strongest temporal interference was induced by interference lines, coincidental with the direction of offset, lagging stimulus presentation by 50 msec and positioned within a 2.5-5 minute spatial interval. These studies of spatial and temporal interference suggest that spatial position processing occurs within a zone of 5-10 minutes diameter and has a temporal storage limit of about 50 msec.

Several theories have been put forth to account for hyperacuity. They share the common idea that the visual system's ability to make such fine spatial discrimination depends upon a mechanism which enables it to reconstruct the continuity of an object image from its relatively coarse retinal image. For example, the centroid theory of Westheimer (1979 & 1981) suggests a mechanism which precisely locates the luminance centroid of a visual feature. The centroid of an object image is defined by Morgan et al. (1983) to be the point in the luminance distribution positioned so that the sum of distances of points from the centroid, weighted by their luminance, is the same in any direction. This scheme relies on the assumption that retinal input produces a response in a population of cortical neurons whose distributional center of mass can be determined with the precision necessary to account for the hyperacuities. The detection mechanism is likened to a differential amplifier which can specify differences between two points but ignores input common to both. Input to this mechanism must be unencumbered within a zone of 5-10 minutes of visual angle to achieve maximum precision. In another model, Barlow (1979) accounts for hyperacuity by noting that an object's image function is sampled by foveal cones at a frequency high enough to allow for accurate reconstruction of the image function at a later time.

Reconstruction of the image is the result of an interpolation performed on the sampled information in the granule cells of cortical area 17. Estimates of granule cell density support the notion of a cell for every 3-5 seconds of the visual field. Thus, positional differences of stimulus features could arise from differences in firing rates of adjacent units comprising the fine grain reconstruction of the object image. A related model is one presented by Crick, Marr and Poggio (1980) in which they propose that accurate reconstruction of an object's image need be performed only in the vicinity of the zero crossings (contrast changes) of that function. Representation of the slope and position of the zero crossings in the fine grain cellular matrix of area 17 provides an information pool from which accurate positional information of a stimulus' features could be extracted. All three of these models are built on consideration of a restructured object image in the cortex where current cellular density estimates support the precision with which hyperacuity judgements occur. Although the proposed theories have some indirect support in studies of the anatomical connectivity of LGN to layer IV of cortex, there is no direct physiological evidence indicating that such neural mechanisms are operating. Animal behavioral studies, however, have shown substantial loss of vernier acuity associated with ablation of

area 17 (Berkley & Sprague, 1979; Berkley & Bush, 1983).

The current catalog of data on hyperacuities has been amassed using psychophysical techniques. Recently, however, an electrophysiological measure of hyperacuity has been reported opening the possibility of more direct tests of current neural theories. Levi et al. (1983 & 1983a) have recorded time-locked responses or visual evoked potentials (VEP's) to a vernier stimulus from the human scalp. When the VEP amplitudes are plotted as a logarithmic function of offset size (in seconds of visual angle), the points can be fitted with a straight line which, when extrapolated to zero voltage, accurately estimates the psychophysical threshold of vernier acuity. Although there is no previous work with VEP's and vernier acuity in the literature, similar methods have been used to accurately predict psychophysical thresholds of contrast sensitivity to a counterphased sine wave grating (Campbell & Maffei, 1970), acuity to gratings interleaved with a blank screen (Campbell & Kulikowski, 1972) as well as temporal modulation thresholds (e.g., Sternheim & Cavonius, 1972).

Replication and extension of the Levi et al. (1983 & 1983a) results would have utility in contributing to the further understanding of cortical processing of visual information. Analysis of a comparison between vernier evoked responses and other pattern evoked respon-

ses could be used to further describe and localize the hyperacuity mechanism either validating a current theory or spawning a new one. When there is correlation between perception and an objective physiological measure, information about underlying neural processes can be obtained (Regan, 1981). In addition, developmental studies would be served by such a technique in its use to estimate vernier thresholds in infants and young children (Atkinson et al., 1979; Regan, 1981). Clinical utility lies in the use of a vernier evoked responses to diagnose, in nonverbal subjects, the presence of disorders like amblyopia which appear to be a deficit in ability to make fine spatial discriminations (Newell & Ernst, 1974).

Inspired by the potential value of this technique for the study of hyperacuity, this experiment had two goals: first it undertook to assess the efficacy and reliability of VEP's as predictors of vernier acuity thresholds by replicating the Levi et al. (1983) study; second, it sought to determine whether the VEP was a direct measure of the vernier information processor or a correlated artifact. Resolution of these issues would be a step toward the validation of an explanatory model of vernier acuity.

METHODS

A. Subjects

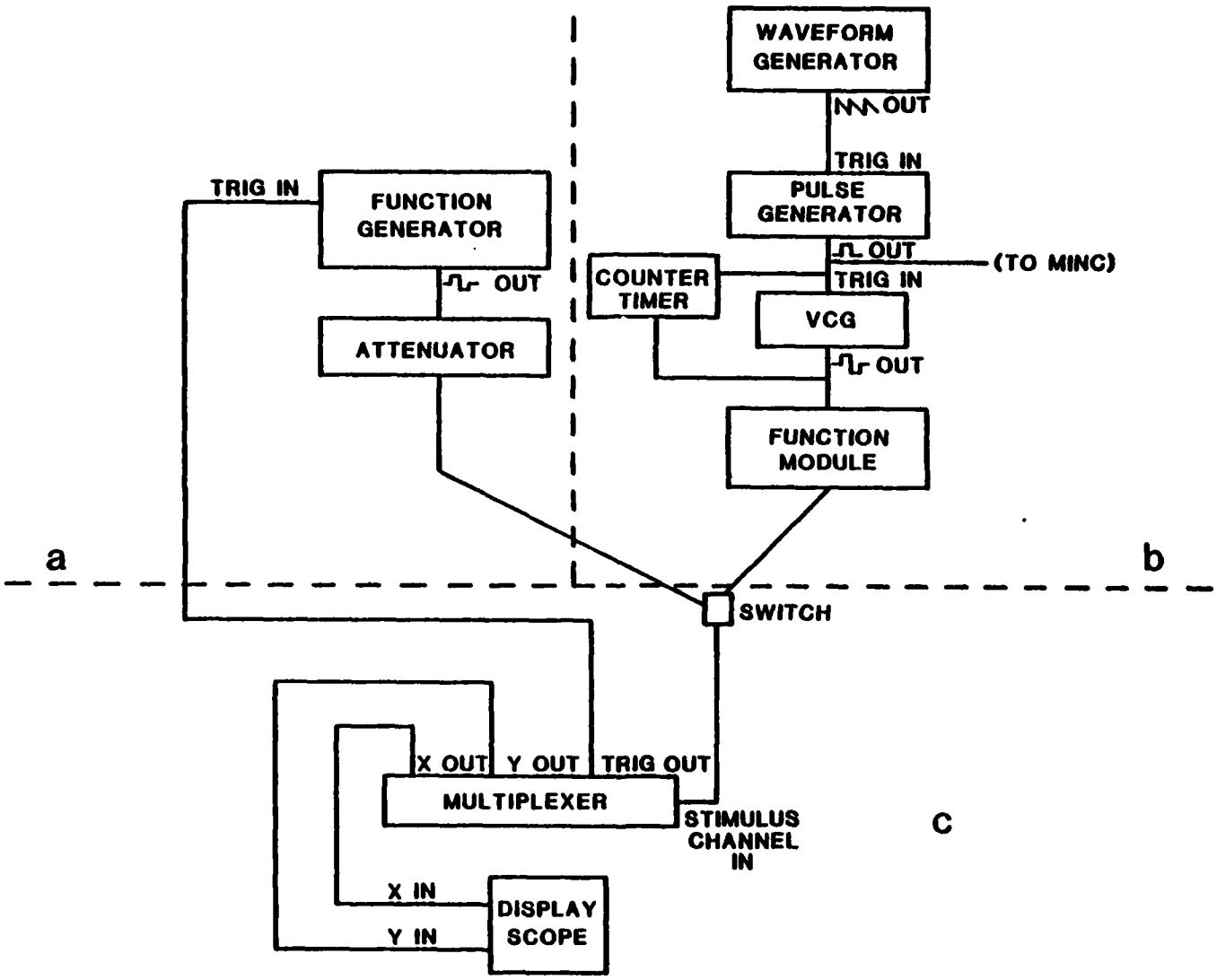
Three adult, male volunteers participated in the experiments. Subject AH was a 26 year old myope with a slight astigmatism. MB was a 46 year old myope with a moderate astigmatism and RZ was a 30 year old myope with a slight astigmatism. All subjects' vision was corrected to 20/20 with corrective lenses. Subjects RZ and MB were familiar with the hypotheses being tested, AH was initially naive as to the purpose of the experiment.

B. VEP Stimulus

Figure 1 depicts a schematic diagram of stimulus apparatus. Stimulus display was produced on a Tektronix 602 Display Oscilliscope. The X and Y inputs came from a Tektronix Model 4701 Eight Channel Multiplexer. Input to the stimulus channel of the multiplexer was a 500 Hz square wave (minimum amplitude) generated by a Tektronix FG 501 Function Generator and was triggered by a sync pulse from the multiplexer coincidentally with its scan which was set for a period of 2 msec. This produced a display consisting of a single horizontal line with one vernier offset in the center (see Figure 2a).

Offset size was controlled with a Hewlett Packard 350D Attenuator Set. Offset was calibrated by a precision micrometer caliper. All measures were converted to

Figure 1. Schematic diagram of stimulus generating apparatus. Section a is the stimulus circuit, b is the gating circuit, c is the display circuit.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OUT
TRIG IN
PULSE GENERATOR
OUT
(TO MINC)
TRIG IN
COUNTER TIMER
VCG
OUT
FUNCTION MODULE
TRIG IN
FUNCTION GENERATOR
OUT
ATTENUATOR
a
b
SWITCH
X OUT
Y OUT
TRIG OUT
MULTIPLEXER
STIMULUS CHANNEL IN
X IN
Y IN
DISPLAY SCOPE

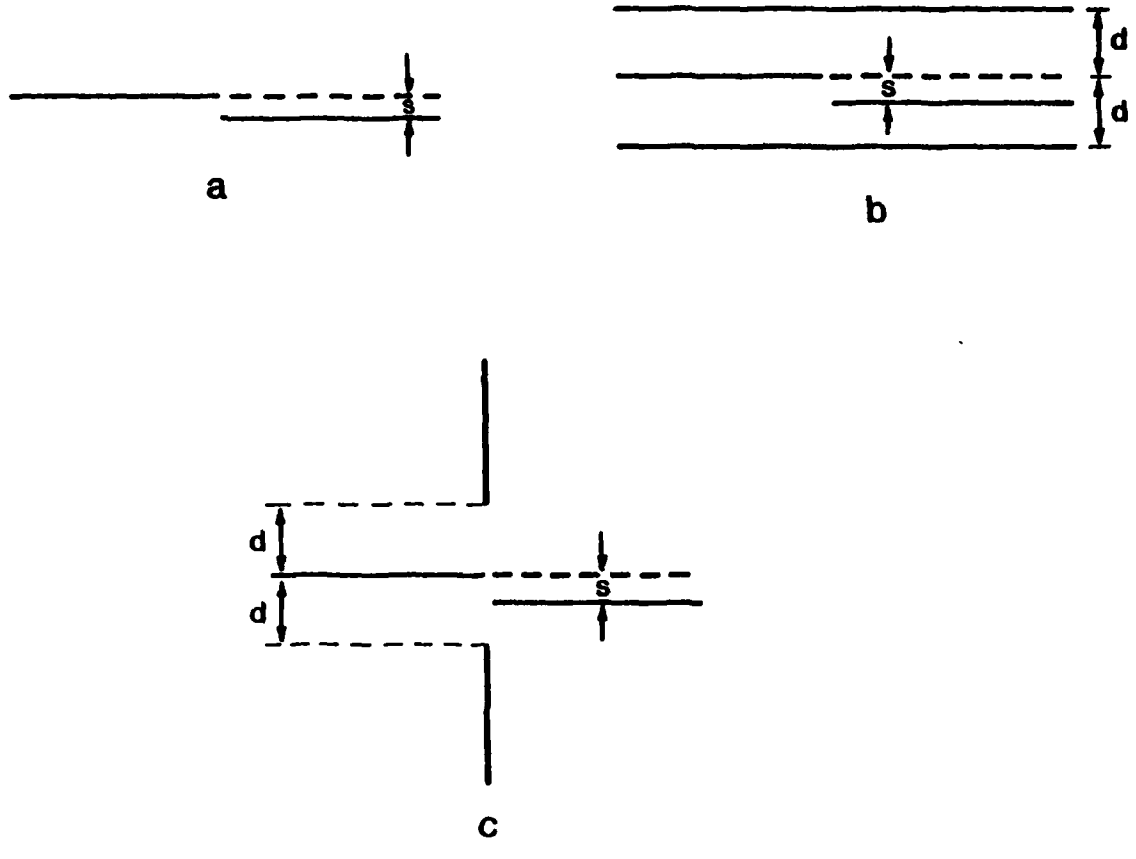
c

Figure 2. Stimulus display configurations:

a) Vernier stimulus presented alone. Right hand segment moved from an aligned position to an offset position at a rate of .67 sec^{-1} for a duration of 100 msec. Distance s was offset size chosen from a value range of 26 to 82 seconds of visual angle.

b) Vernier stimulus with horizontal interference lines. Separation distance d was measured form the center of the stationary line to the center of each interference line. Values of d were chosen from among 0, 2.5, 3.75, 5.0 and 7.5 minutes of visual angle.

c) Vernier stimulus with vertical interference lines. Separation distance d was measured from the center of the stationary line to the medial endpoint of each interference line. All lines subtend 40 seconds of visual angle at viewing distance of 2 meters.

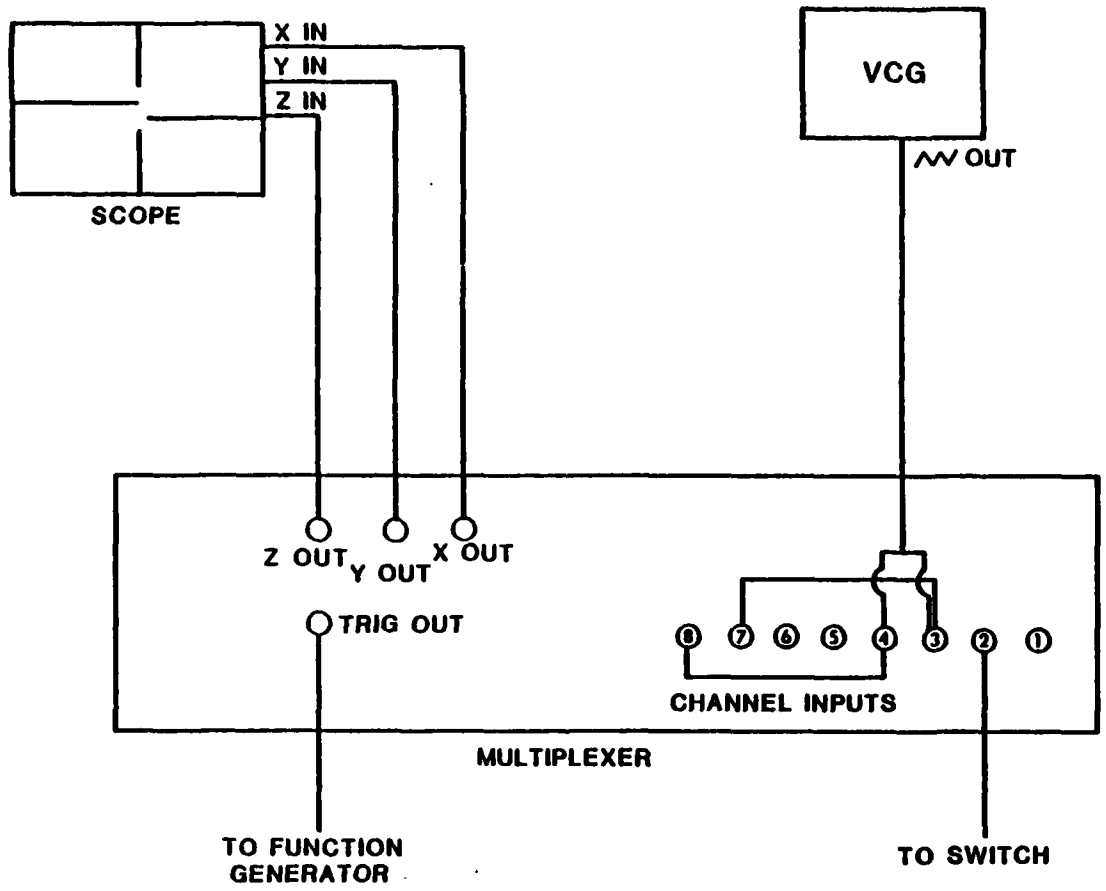

s
a
d
s
d
b
d
s
d
c

units of visual angle based on a viewing distance of 2 meters.

The offset was induced in a straight line with a specific period and duration which were controlled by an electronic switch. A master timer (Tektronix Type 162 Waveform Generator) originated a gating signal and directly determined stimulus period. This signal was used to trigger a Tektronix Type 161 Pulse Generator which produced a pulse initiating the data acquisition sweep (see paragraph D) and triggering a Wavetek Model 112 Triggered VCG. The VCG was used to produce a positive square wave which was the gate for the electronic switch on the display circuit. One half the square wave period determined stimulus duration. A Transistor Specialties Model 385-R Counter/Timer was used to accurately measure stimulus duration and period.

Two experimental conditions required the introduction of either horizontal or vertical interference lines to the stimulus display (see Figures 2b and 2c). Horizontal lines were generated by activating two additional channels of the multiplexer. Vertical lines were introduced by using four multiplexer channels in the paired mode (see Figure 3). A Wavetek Model 112 Triggered VCG was used to input a triangular signal in each of the two channel pairs. This resulted in the appearance of two vertical lines on the display scope.

Figure 3. Vertical interference line apparatus. Multiplexer channels 3 and 4 were paired with 7 and 8 respectively. A 5000 Hz signal was used to produce the vertical interference lines. Remainder of the circuit was identical to Figure 1.


X IN
Y IN
Z IN
SCOPE
VCG
OUT
Z OUT
Y OUT
X OUT
TRIG OUT
8 7 6 5 4 3 2 1
CHANNEL INPUTS
MULTIPLEXER
TO FUNCTION GENERATOR
TO SWITCH

Position of all displays was adjusted using the channel gain controls on the multiplexer front panel and calibrated by a precision micrometer caliper.

In all experiments, the stimulus was viewed through a white circular mask of 32.5 cm diameter with a centrally placed rectangular viewing field subtending 1.5° x 2° of visual angle. Stimulus line brightness was measured at 20 ft-lamberts in Experiments 1 and 3 and 23 ft-lamberts in Experiment 2. The stimulus line width subtended 40 seconds of visual angle. Ambient light was maintained at a photopic level (33 ft-lamberts).

Stimulus time parameters were determined in pilot studies. Although an experimental goal was to replicate the Levi et al. (1983 & 1983a) results, the stimulus was modified to make a segment of these results directly comparable to the psychophysical data obtained by Westheimer and Hauske (1975). A series of pilot recording sessions were conducted in an attempt to find a set of parameters to meet this requirement. A stimulus period of 1.5 sec and duration of 100 msec in the single offset configuration already described was found to reliably evoke a response in the pilot subject and were sufficiently close to those used by Westheimer and Hauske (1975) to permit comparison of the results (see Discussion for justification of the comparison).

C. Psychophysical Stimulus

The vernier stimulus used in the psychophysics study (Experiment 3) had an identical generation scheme with the exception that the gating circuit was triggered by the subject manipulating a mechanical switch. Thus, stimulus onset was under the subject's control but duration and vernier offset size were still controlled electronically. During the psychophysical measurements an audio signal accompanied stimulus onset.

D. VEP Recording

Subjects were seated 2 meters from the stimulus display. A chin rest was used to assist the maintenance of steady gaze. One Beckman miniature scalp electrode (sintered silver) was used to record activity at the surface of the scalp. The placement site was on the midline approximately 1.5 cm above the inion. Removal of scalp hair from a 2 cm circle at the recording site and cleansing with alcohol preceeded electrode placement. An AgCl plate electrode was placed on the right earlobe for reference. Burdick electrode paste was used at both placement sites. Ground was the subject's right hand.

Prior to stimulus presentations, subjects were told the offset would appear in the center of the viewing field, however, no fixation point was present on the target and the subjects were not given any additional viewing instructions. They were also instructed to

attend to the presentation of the offsets but to avoid counting or engaging in any other rhythmic mental activity which could result in artifact recording. Instructions were periodically reviewed and subjects questioned with regard to their compliance.

When the subject was ready a recording epoch was initiated. Recorded signals were amplified 2×10^4 times using a Grass P511 pre-amplifier and low pass filtered with a Krohn-Hite Model 3202 filter, the low pass corner frequency being 30 Hz as suggested by May and Reed (1983). Overall bandpass of the system was 3-30 Hz. Filtered signals were led to a Digital Modular Instrument Computer (MINC) and summed.

Each recording epoch consisted of 200 stimulus presentations at the rate of .67 sec^{-1}. Recording samples consisted of 256 bins and lasted 1 sec (4 msec/bin). Each sample was initiated by the electronic pulse which also controlled the stimulus gating circuit (see paragraph B). All response data was digitized by the MINC and stored on floppy disk for off line analysis.

E. Experiment 1

This experiment investigated the use of VEP amplitude, evoked by different size vernier offsets, to estimate the psychophysical threshold of vernier acuity and was a modified replication of the Levi et al. (1983) study.

1. Procedure.

A VEP recording session consisted of six epochs, five recorded the response to a suprathreshold vernier offset of size ranging from 82 to 21 seconds of visual angle and a sixth control epoch recorded the response to a stimulus line displacing, in its entirety, the distance determined by one offset size. Order of trials was haphazard. Each session was replicated three times for each subject.

The stimulus configuration used had several unique features which could result in an evoked response unrelated to the presence of a vernier offset. With the subject fixating on the point of offset, the moving line segment's image fell on the temporal half of the left eye and the nasal half of the right. As a result, the moving image was projected onto a single hemifield. To control for an artifact response to this condition, responses to the following configurations were recorded: a moving line presented in a single hemifield (the other being masked), a stimulus with two vernier offsets spaced 9 minutes apart with the center segment moving, a stimulus with two offsets spaced at 9 minutes and the outside segments moving, and to a stimulus in which both segments displaced half the offset distance. Also, the offsets used throughout the experiment were oriented vertically. Control for an orientation artifact was an epoch recorded

to an offset oriented horizontally (see Figure 4). These epochs were distributed randomly through the series of recording sessions.

Subjects also participated in a control session during which responses were recorded to the whole stimulus line displacing (no offset) at five different displacement sizes within the previously specified range. A sixth epoch recorded the response to a vernier offset in the same size range. Comparison of these epochs was used to ascertain the magnitude of response to stimulus movement alone. A response to movement, per se (without an offset), has been reported to be minimal (Levi et al., 1983a).

2. Data Analysis.

The response measured was a relatively large negative to positive deflection found in the first 300 msec of the record. VEP amplitude and latency were derived from the recorded response by computer. Amplitude was calculated as the difference between the two largest adjacent peaks in each epoch. The latency measure was the implicit time associated with the first peak of the response. Time to the second peak was also computed (see Figure 5).

The derived response amplitude was plotted as a function of the base 10 logarithim of the offset size for each session. A least squares regression line was then

Figure 4. Stimulus configurations for control epochs: a) offset was oriented horizontally, b) two offsets were presented with a spacing of 9 minutes, c) same as b except outer segments displaced, d) both segments displaced. Arrows indicate displacing segment and direction of movement.

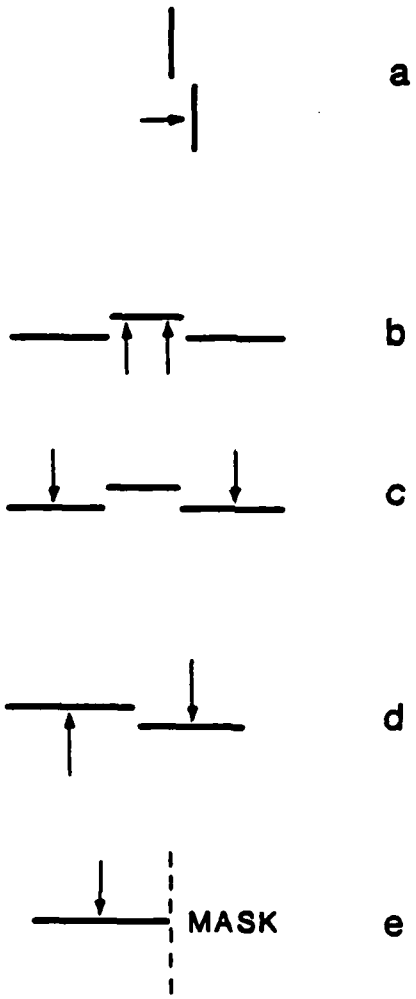
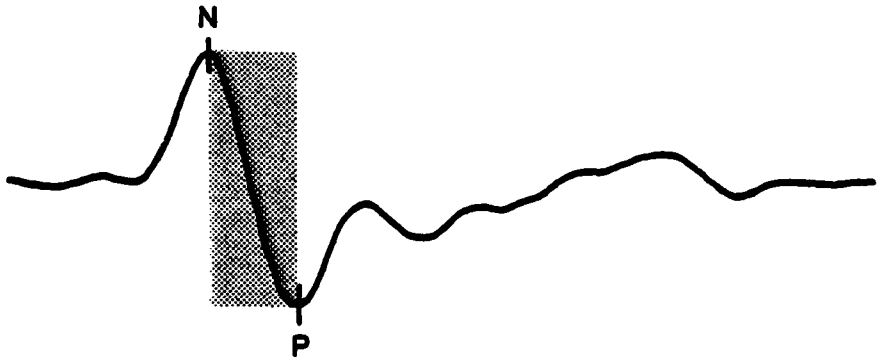

a
b
c
d
MASK
e

Figure 5. VEP time and amplitude measures. Amplitude of the response was measured as the long axis of the shaded area. Derived latency was taken as the time to N, the negative peak. Time to P was also measured for analysis. All values were computed from digitized data stored on floppy disk by the MINC.


N
P

fit to this data and extrapolated to zero volts amplitude. This intercept was used as an estimate of vernier acuity threshold (Levi et al., 1983 & 1983a). Time to each peak was plotted as a function of offset size for use as a measure of response consistency.

F. Experiment 2

The second experiment had the intent of assessing the effect of spatial interference lines on vernier offset VEP amplitude for comparison with interference effects reported in the psychophysical experiments of Westheimer and Hauske (1975).

1. Procedure.

In this experiment, each recording session also consisted of six epochs, five were responses recorded to a vernier offset flanked by either horizontal or vertical interference lines placed at various distance from the offset (see Figures 2b and 2c) and a sixth recorded to a vernier offset alone. Size of the offset was constant through the session. Distance from the stimulus line to the interference line was measured from the center of the stationary stimulus line to the center of each of the interference lines with values chosen haphazardly from 0, 2.5, 3.75, 5.0, 7.5 minutes of visual angle across each session. The 0 minute condition had the interference lines superimposed on the stimulus offset. Three sessions were recorded for each orientation from all

subjects.

2. Data analysis.

Derivation of amplitude and latency measures was identical to Experiment 1. Amplitude of the offset induced response was plotted as a function of interference line distance and the resulting curves examined for effects analogous to those found by Westheimer and Hauske (1975) using psychophysical methods.

G. Experiment 3

The final experiment was conducted to measure vernier acuity threshold by psychophysical means for comparison with the VEP estimate.

1. Procedure.

Viewing conditions were identical to those used in Experiment 1 with the exception that the subject controlled stimulus presentation. A single stimulus, forced choice procedure employing the method of constant stimuli was used with 10 trials for each stimulus value. Three sessions were conducted for each subject.

2. Data analysis.

Threshold was defined as the offset size yielding a 50% detection rate. The value used for comparison was the computed mean of the three session thresholds.

RESULTS

A. General

The VEP recordings for 2 of 3 subjects revealed a consistently identifiable response associated with the presentation of a vernier offset stimulus. Response characteristics varied systematically with stimulus size and their relationship was useful in estimating threshold which was compared to the psychophysical thresholds obtained in the final experiment. In the second experiment, interference lines were found to attenuate response amplitude. Detailed results of all three experiments are presented below.

B. Experiment 1

Results of Experiment 1 show a clear evoked response to a vernier offset and no reliable response to moving line stimuli. Amplitude and latency of the vernier VEPs varied systematically with offset size.

Records obtained during the moving stimulus session are shown in Figure 6A-C. Inspection reveals the absence of a substantial response to presentation of a line stimulus moving through distances equal to offset sizes. The small amplitude responses to displacements greater than 40 seconds of visual angle are not readily distinguishable from background noise. Absence of a noteworthy response is especially obvious in light of the

Figure 6A. VEP's recorded to movement stimuli for subject AH. The first five epochs in the series are responses recorded to the entire stimulus line displacing the indicated distance. The sixth epoch is the response to vernier offset of indicated size, recorded during the same session. Order of stimulus presentation was haphazard. Stimulus duration and period were 100 msec and 1.5 sec respectively.

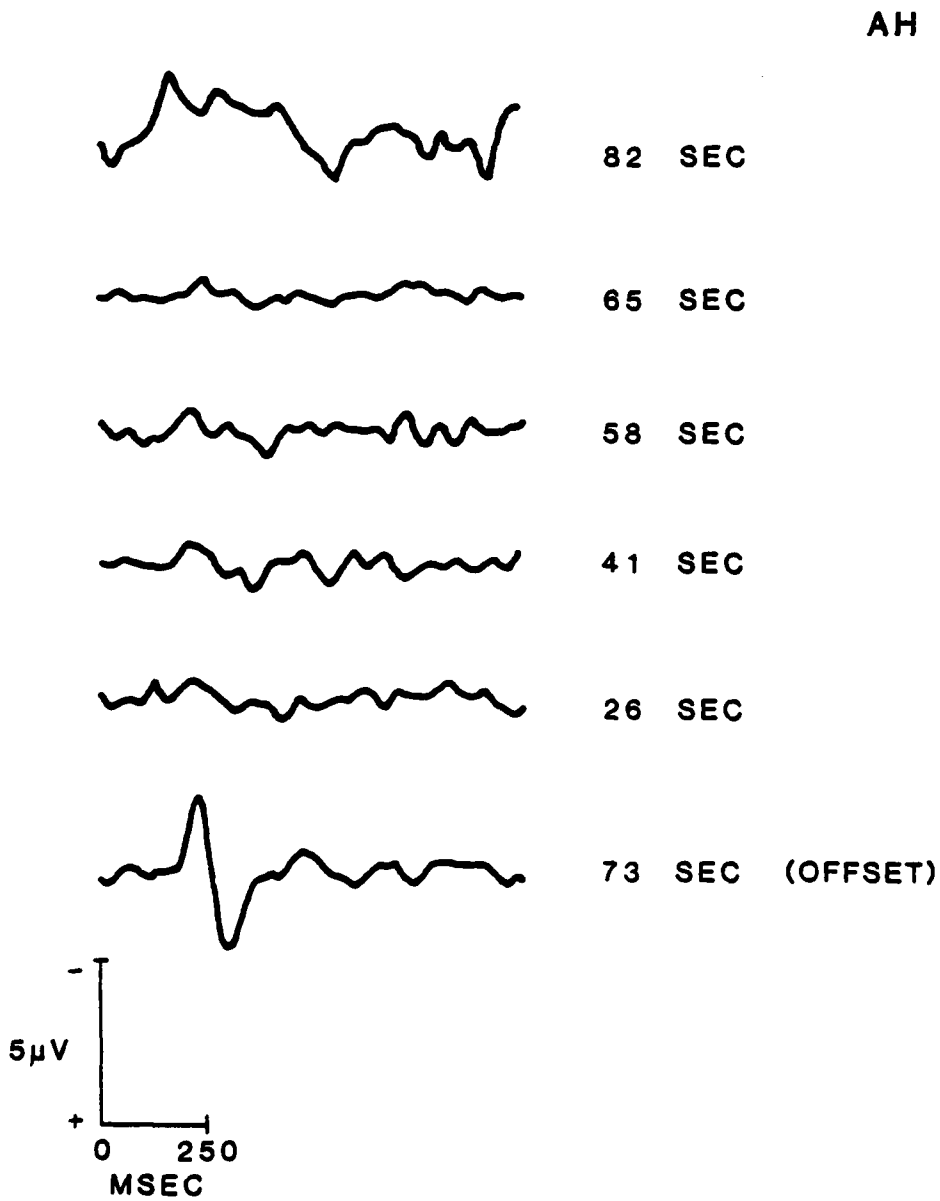

AH
82 SEC
65 SEC
58 SEC
41 SEC
26 SEC
73 SEC (OFFSET)
-
5μV
+
0
250
MSEC

Figure 6B. VEP's recorded to movement stimuli for subject MB. Refer to Figure 6A for details.

MB

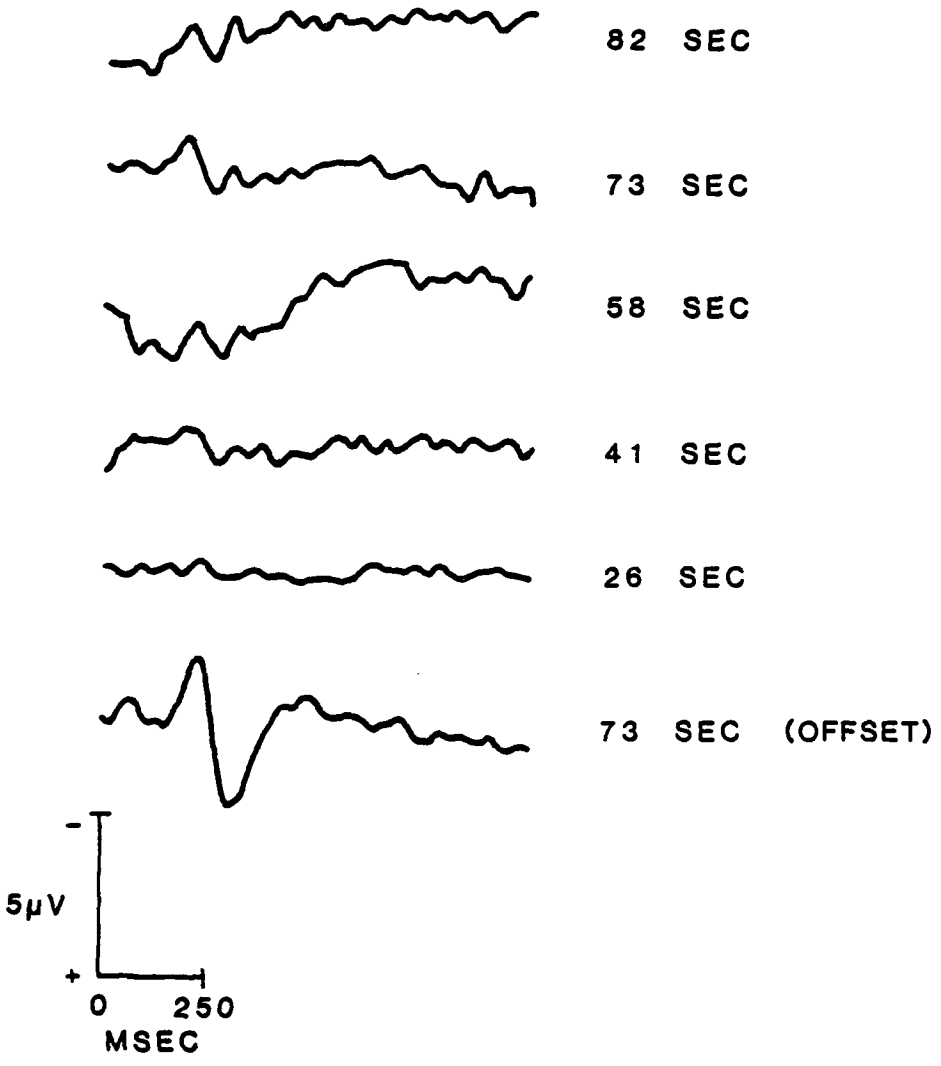
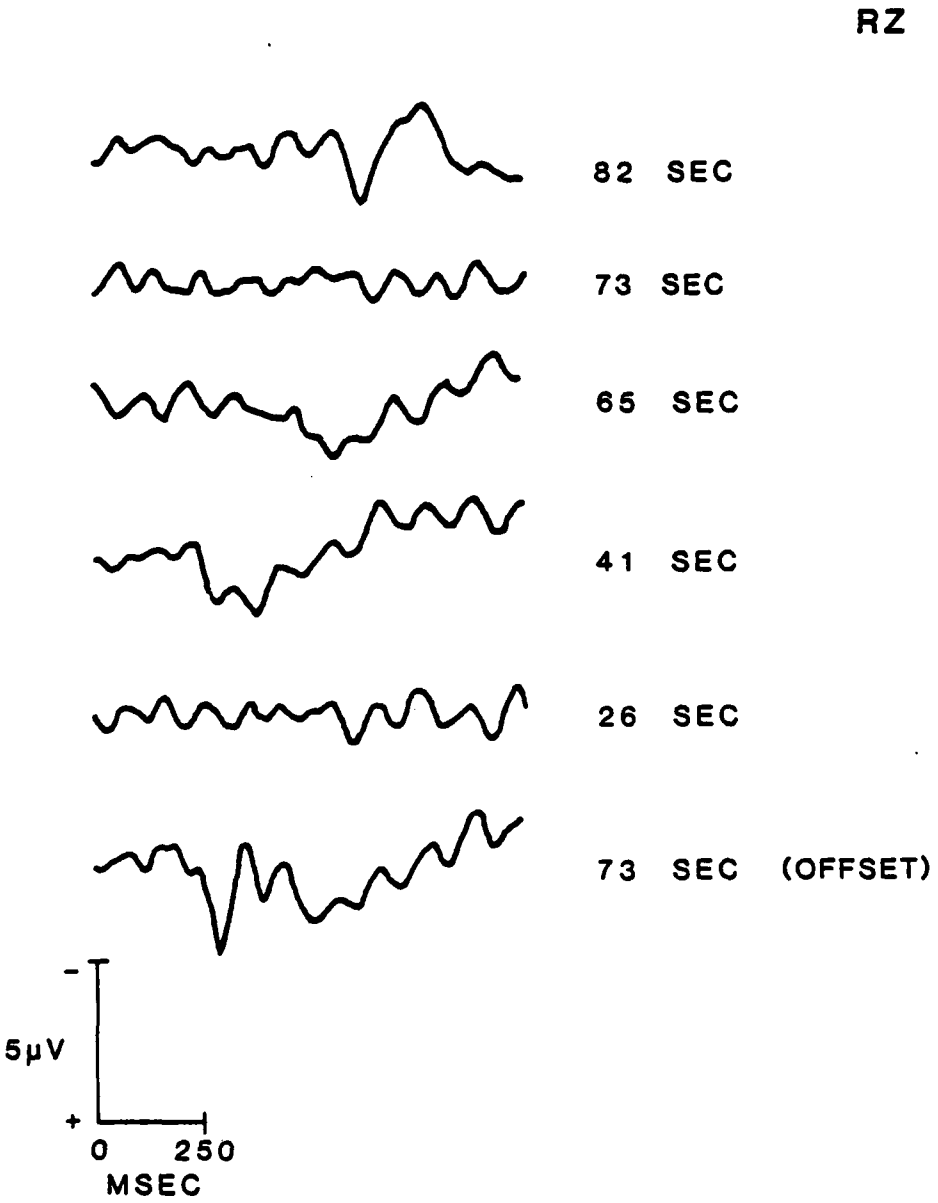


Figure 6C. VEP's recorded to movement stimuli for subject RZ. Refer to Figure 6A for details.


RZ
82 SEC
73 SEC
65 SEC
41 SEC
26 SEC
73 SEC (OFFSET)
-
5μV
+
0
250
MSEC

epoch recorded to a vernier offset during the same session in which the VEP is apparent.

Figure 7A-C illustrates typical recordings to vernier offsets of varying size. Characteristic of the responses is a negative to positive deflection with the negative peak occurring at approximately 220 msec. Although it is clear that RZ was generating a response, its unreliability becomes evident after viewing the total session record. This unreliability caused the subject's data to be excluded from further quantitative analysis.

Table 1 shows mean latencies of negative and positive peaks for the other two subjects. Negative peak latency appears to be a decreasing function of offset size although a plot in Figure 8A-B reveals considerable overlap of each measurement's standard error. Application of regression analysis to the raw data resulted in a negative correlation being significant at the .01 level for both subjects (AH: $t = -4.25$, $t(.01,13) = -2.65$; MB: $t = -3.27$, $t(.01, 12) = -2.68$). Measurement of latency to the positive peak resulted in sufficient heterogeneity of variance to preclude regression analysis for AH's data while for MB inspection reveals the absence of a systematic relationship making further analysis superflous.

Figure 9A-B shows VEP amplitude as a positive function of the vernier offset size. A logarithmic transform

Figure 7A. VEP's recorded to vernier offsets of varying size for subject AH. The first five epochs in the series are responses recorded to the vernier offset size shown. The sixth epoch is the response recorded to the entire stimulus line displacing the indicated distance. Order of stimulus presentation was haphazard. Stimulus duration and period were 100 msec and 1.5 sec respectively.

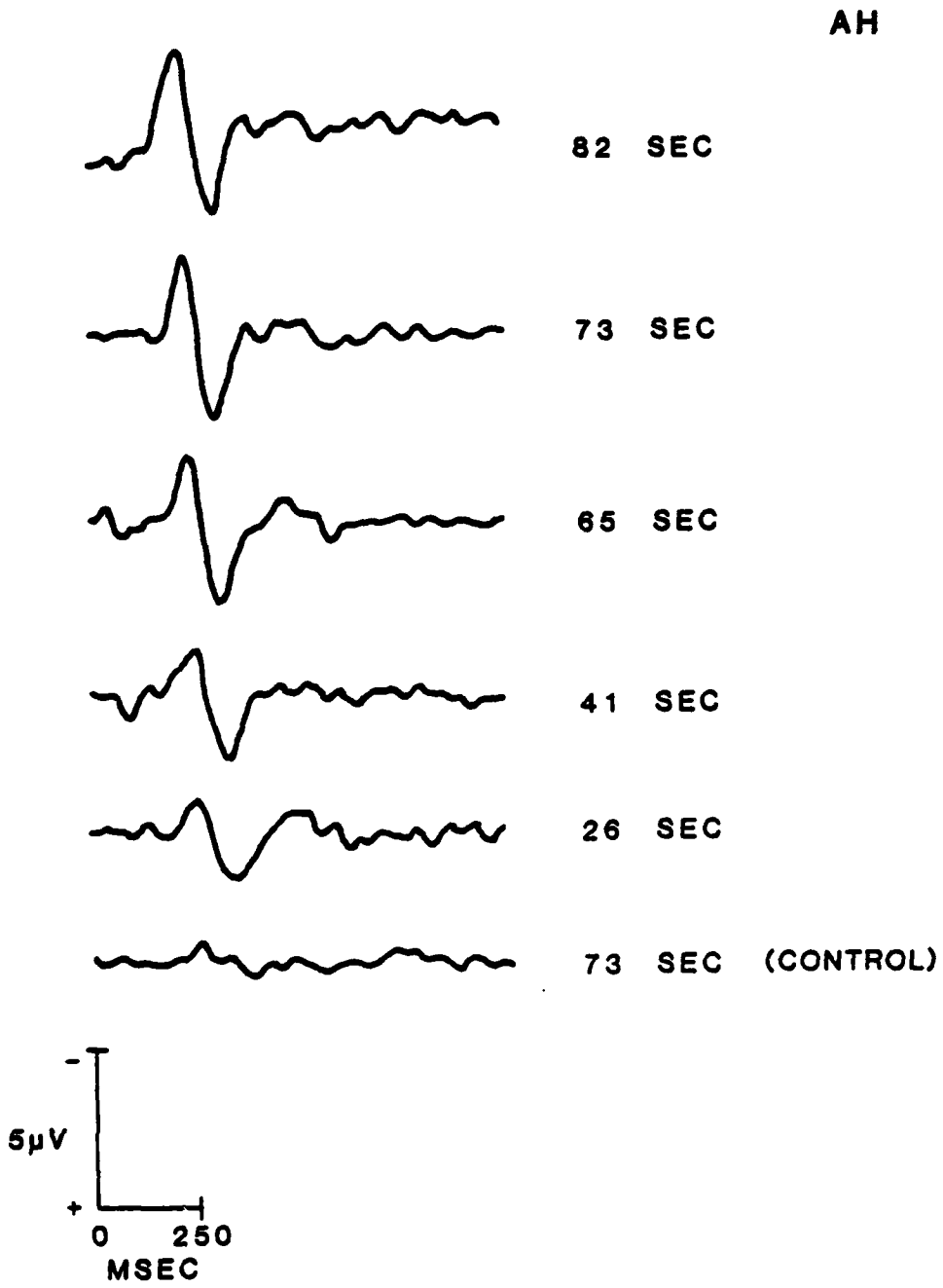

AH
82 SEC
73 SEC
65 SEC
41 SEC
26 SEC
73 SEC (CONTROL)
-
5μV
+
0
250
MSEC

Figure 7B. VEP's recorded to vernier offsets of varying size for subject MB. Refer to Figure 7A for details. Note the similarity in response waveform and latency to those of AH.

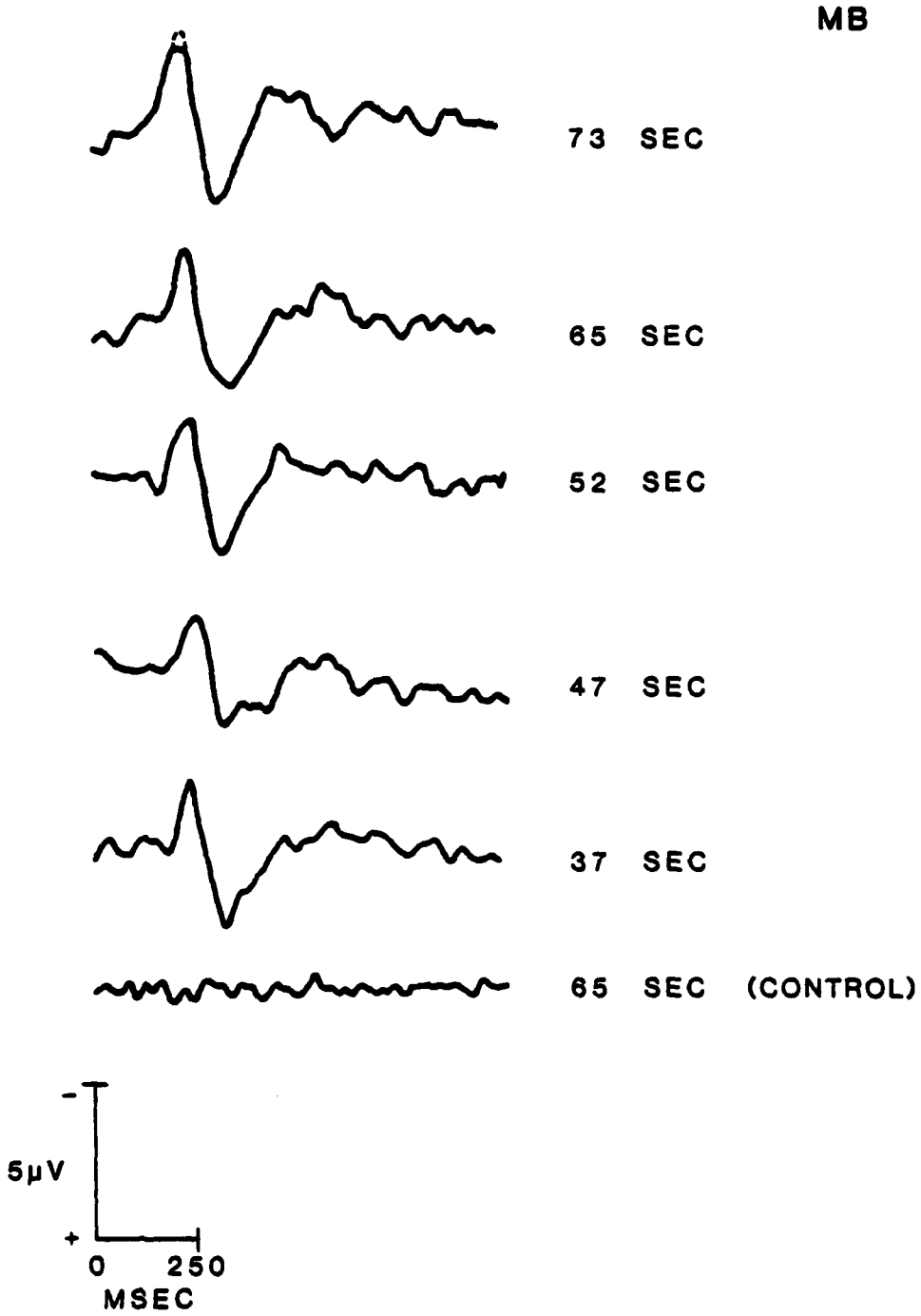

MB
73 SEC
65 SEC
52 SEC
47 SEC
37 SEC
65 SEC (CONTROL)
-
5μV
+
0
250
MSEC

Figure 7C. VEP's recorded to vernier offsets of varying size for subject RZ. Refer to Figure 7A for details. Note the presence of larger amplitude noise when compared to AH and MB data.

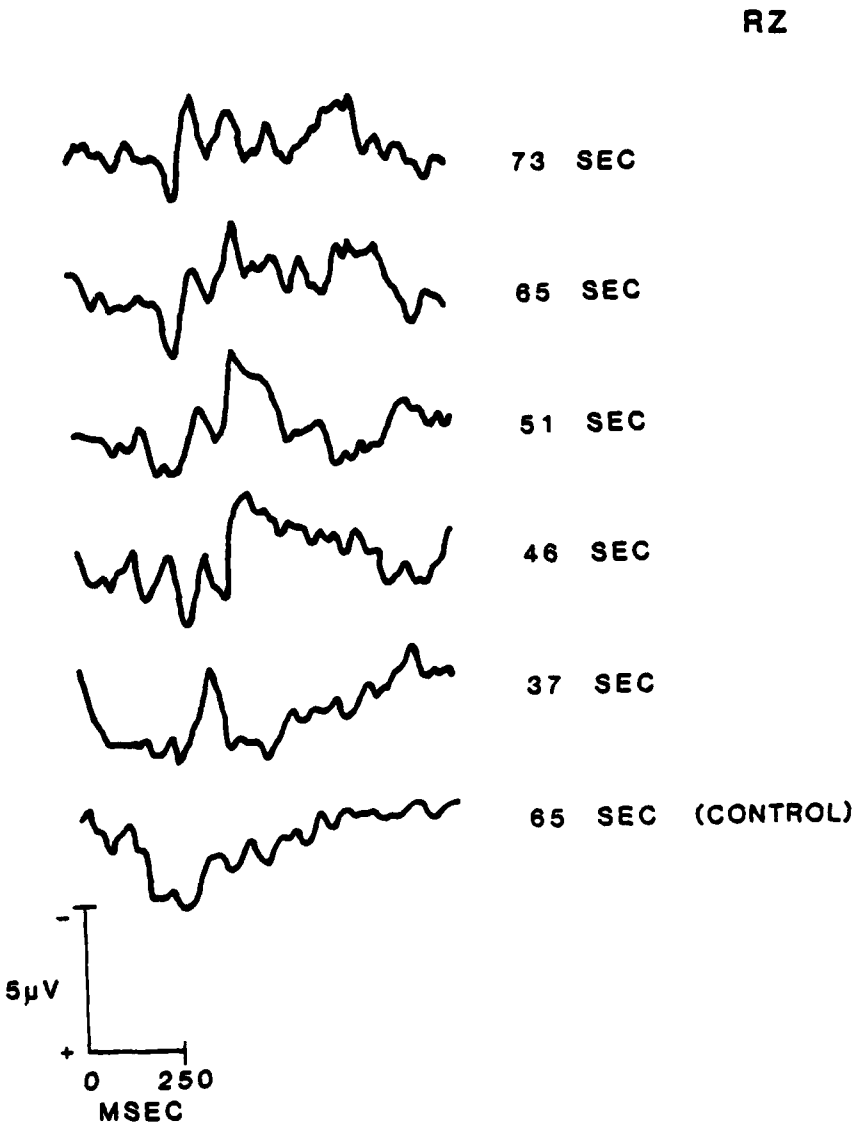

RZ
73 SEC
65 SEC
51 SEC
46 SEC
37 SEC
65 SEC (CONTROL)
-
5μV
+
0
250
MSEC

TABLE 1

VERNIER OFFSET SIZE AND VEP LATENCY

SUBJECT	OFFSET SIZE (SEC ARC)	MEAN LATENCY TO NEGATIVE PEAK (MSEC)	S (MSEC)	PEARSON r	MEAN LATENCY TO POSITIVE PEAK (MSEC)	S (MSEC)
AH	82	226.3	15.3	-.74	303.5	17.4
	73	227.0	12.8		304.2	13.9
	65	230.9	21.8		320.3	26.6
	41	251.5	18.7		328.7	19.8
	26	264.5	16.1		360.1	53.0
MB	73	210.3	5.8	-.66	287.5	20.7
	65	218.6	8.7		307.3	28.7
	51	227.8	8.7		305.8	14.8
	46	219.0	8.13		298.5	3.8
	37	229.3	6.12		290.0	18.8

Table 1. Mean peak latency as a function of offset size. All means were based on 3 measurements with the exception of the 46 second offset for MB which was based on 2. Listed Pearson product moment correlation coefficients are based on individual times, not means. For both subjects, the negative correlation was significant at $\alpha = .01$.

Figure 8A. Mean latency to negative peak vs offset size for subject AH. Latency values were derived from digitized data on the MINC system. Means are based on a sample of 3 points. Error bars represent $\pm$ 1 standard error.

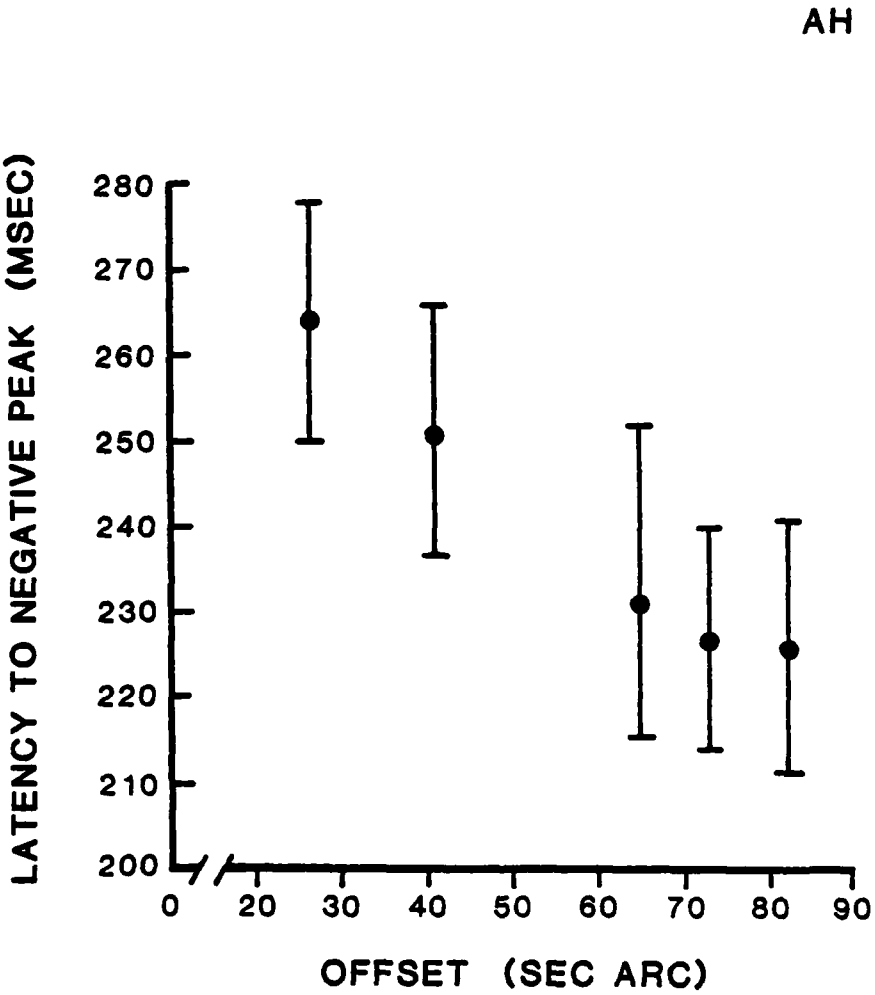

AH
LATENCY TO NEGATIVE PEAK (MSEC)
280
270
260
250
240
230
220
210
200
0
20
30
40
50
60
70
80
90
OFFSET (SEC ARC)

Figure 8B. Mean latency to negative peak vs offset size for subject MB. Details are the same as Figure 8A with the exception that the 46 second mean latency is based on 2 points.

MB

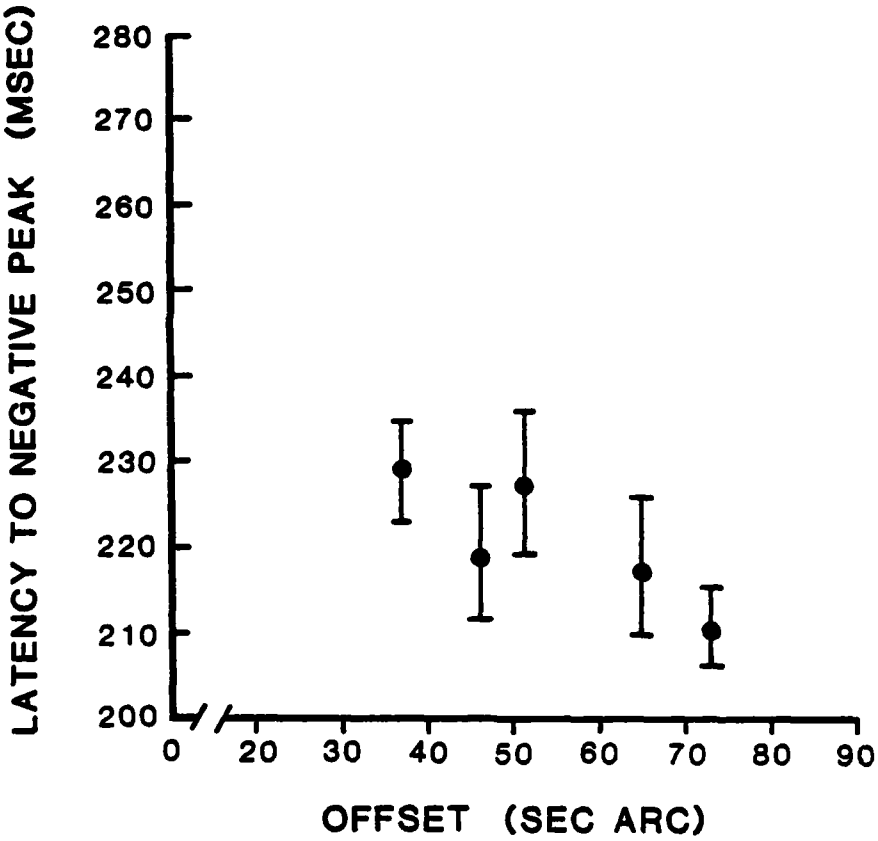

LATENCY TO NEGATIVE PEAK (MSEC)
280
270
260
250
240
230
220
210
200
0
20
30
40
50
60
70
80
90
OFFSET (SEC ARC)

Figure 9A. VEP amplitudes vs. log offset for subject AH. Different symbols represent separate experimental sessions. Regression lines were fit using least squares method based on 5 data points. Arrows indicate estimate of vernier acuity threshold.

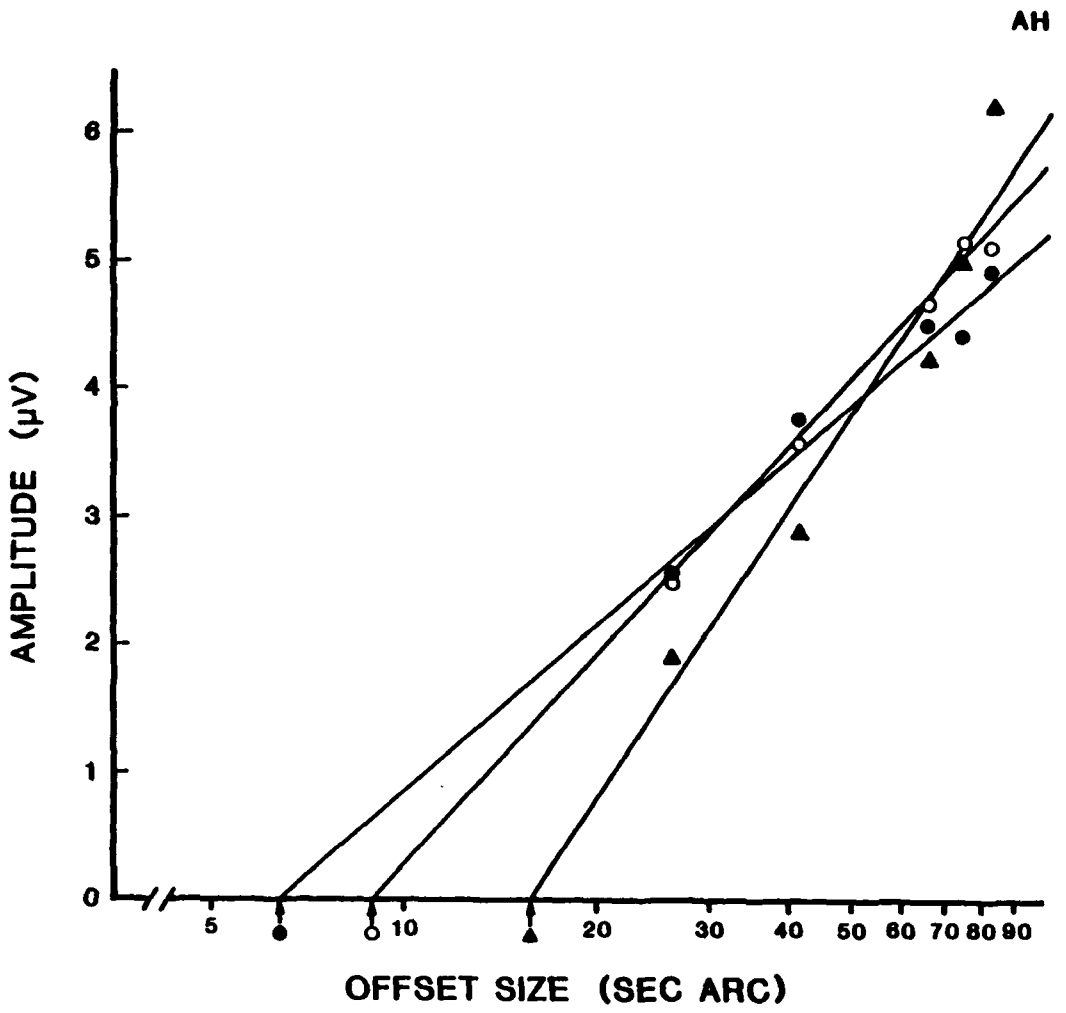
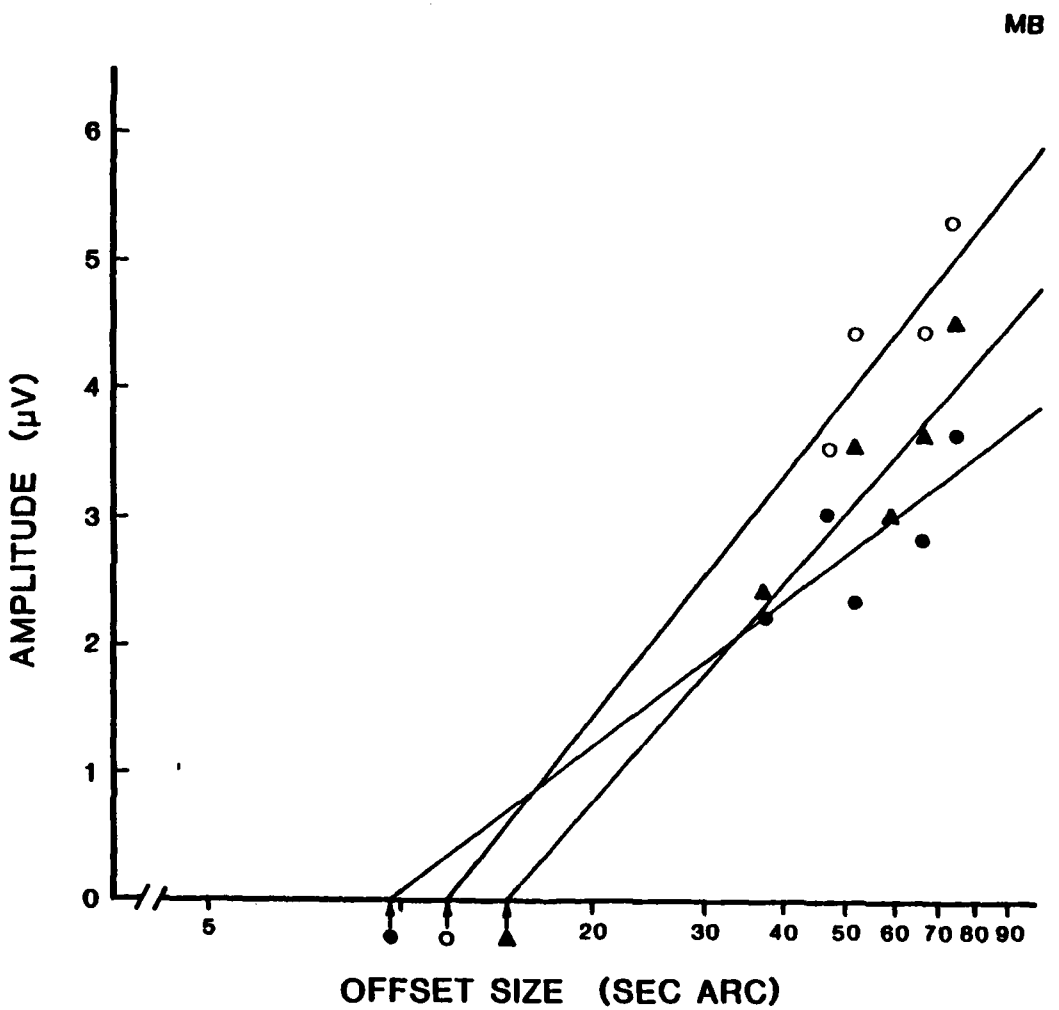

AH
AMPLITUDE (μV)
0
1
2
3
4
5
6
5
10
20
30
40
50
60
70
80
90
OFFSET SIZE (SEC ARC)

Figure 9B. VEP amplitudes vs. log offset for subject MB. Details are the same as in Figure 9A with the exception that the (▲) session is fit to 4 data points.


MB
AMPLITUDE (μV)
0
1
2
3
4
5
6
5
20
30
40
50
60
70
80
90
OFFSET SIZE (SEC ARC)

was applied to the size values (in units of seconds of arc) to linearize the function. Regression lines, fit using the least squares method, were linearly extrapolated to zero voltage to obtain a vernier acuity threshold estimate. Both sets of estimates clearly fall in the hyperacuity range. Table 2 lists the Pearson product moment correlation coefficients for each session. These coefficients were not tested for significance due to paucity of data points. (The number of data points for each session was limited to five because of subject fatigue.) Small samples, however, prompted the use of non-parametric methods. Table 3 shows the Spearman rank correlation coefficient for each subject's data set. Inspection reveals a strong and reliable correlation in the AH data and a moderately strong and reliable r_s for MB.

C. Experiment 2

Results of Experiment 2 show that interference lines have a suppressive effect on potentials evoked by a vernier offset. These effects are illustrated in Figures 10A-B and 11A-B. Very apparent is the general amplitude attenuation associated with interference line presence. For separations less than 4 minutes, amplitude is attenuated up to 50% for MB and 40% for AH. Reliability of this difference was tested using the nonparametric Sign Test. All replications, from both subjects, at a

TABLE 2

OFFSET SIZE AND VEP AMPLITUDE CORRELATIONS

SUBJECT	SESSION	r
AH	○	.99
	●	.98
	▲	.93
MB	○	.87
	●	.86
	▲	.89

Table 2. Pearson product moment correlations coefficients computed for each session by subject for Experiment 1. All values are based on n = 5 with the exception of the session for MB where n = 4. Values of r were not statistically tested.

TABLE 3

OFFSET SIZE AND VEP AMPLITUDE CORRELATION

(NON-PARAMETRIC)

SUBJECT	RUN	SPEARMAN r_s	
AH	○	1.0	
	●	1.0	
	▲	.95	r_s (5,.05) = .9
MB	○	.7	
	●	.7	
	▲	.7	

Table 3. Spearman rank correlation coefficients computed for each session by subject for Experiment 1.

Figure 10A. VEP amplitude vs. distance from stationary stimulus line to horizontal interference lines for subject AH. All responses were measured to an offset of 73 seconds with interference lines placed at indicated distances from the stationary stimulus line. Unconnected points at the right indicate the response amplitude to a 73 second offset alone, recorded during the same session. Different symbols represent separate experimental sessions.

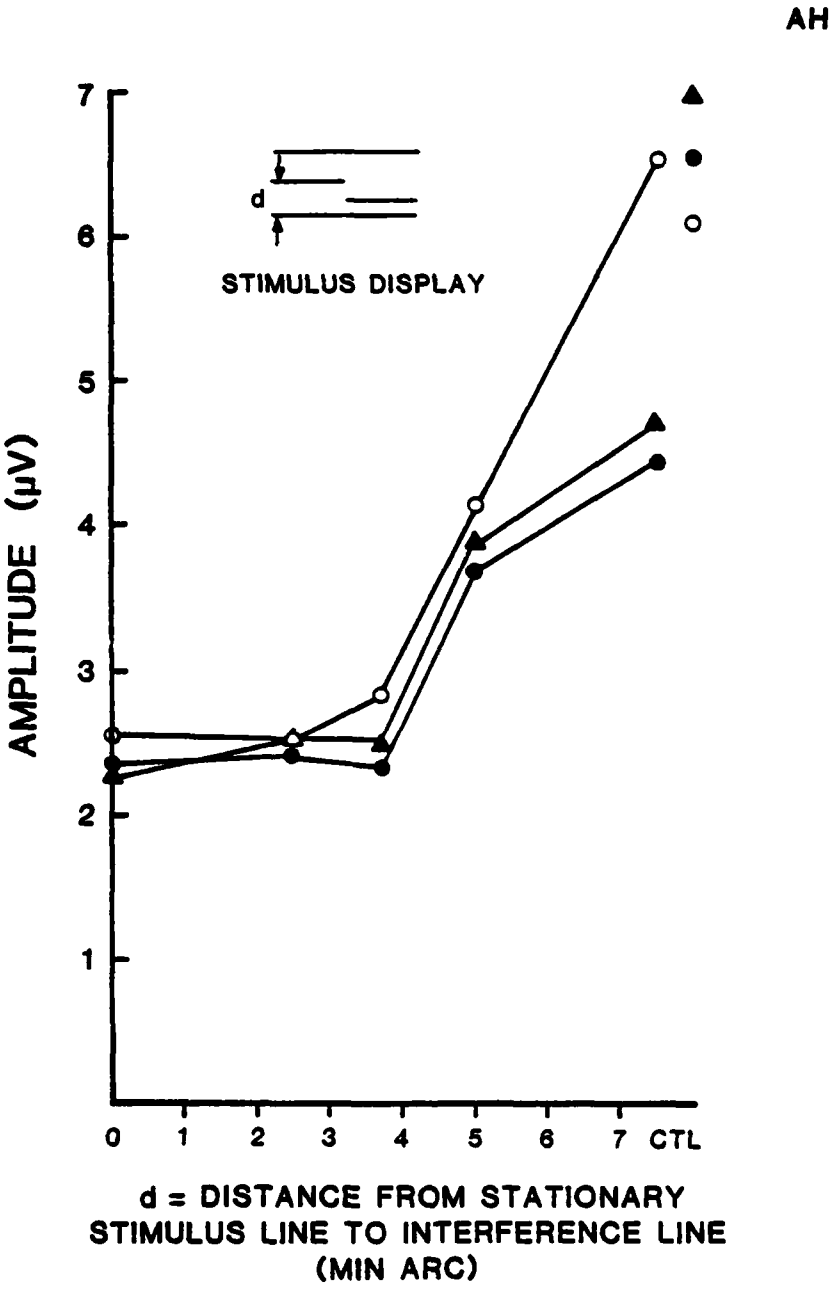

AH
AMPLITUDE (μV)
7
6
5
4
3
2
1
d
STIMULUS DISPLAY
0
1
2
3
4
5
6
7
CTL
d = DISTANCE FROM STATIONARY
STIMULUS LINE TO INTERFERENCE LINE
(MIN ARC)

Figure 10B. VEP amplitude vs. distance from stationary stimulus line to horizontal interference lines for subject MB. Refer to Figure 11A for details.

MB

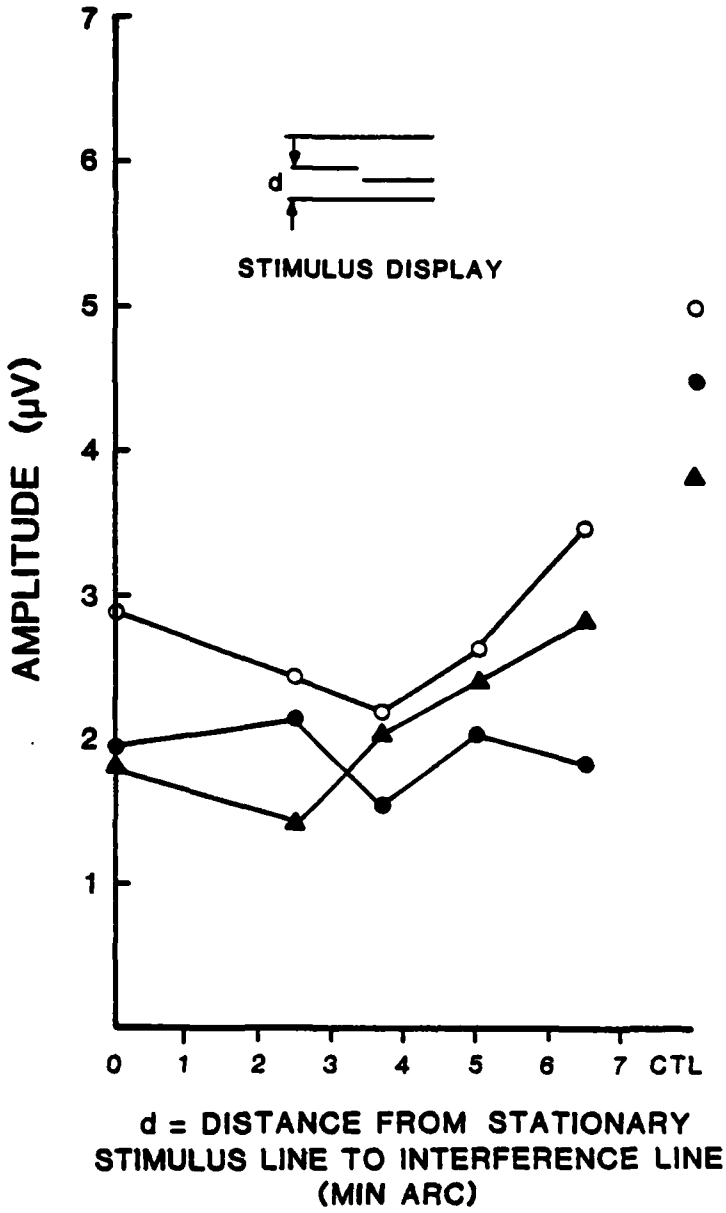

7
6
5
4
3
2
1
AMPLITUDE (μV)
d
STIMULUS DISPLAY
0
1
2
3
4
5
6
7
CTL
d = DISTANCE FROM STATIONARY
STIMULUS LINE TO INTERFERENCE LINE
(MIN ARC)

Figure 11A. VEP amplitude vs. distance from stationary stimulus line to vertical interference line for subject AH. All responses were measured to an offset of 73 seconds with interference lines placed at indicated distances from the stationary stimulus line. Unconnected points at the right indicate the response amplitude to a 73 second offset alone, recorded during the same session. Different symbols represent separate recording sessions.

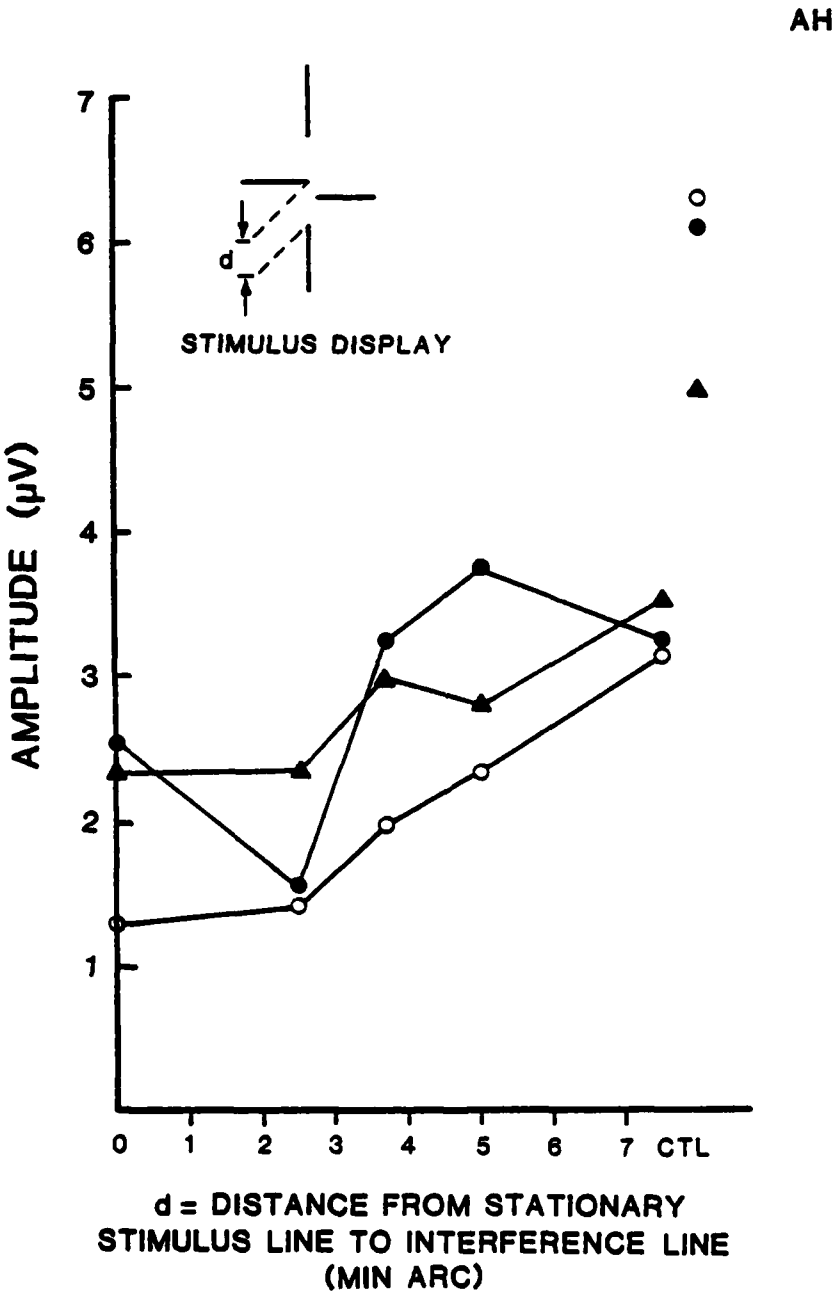
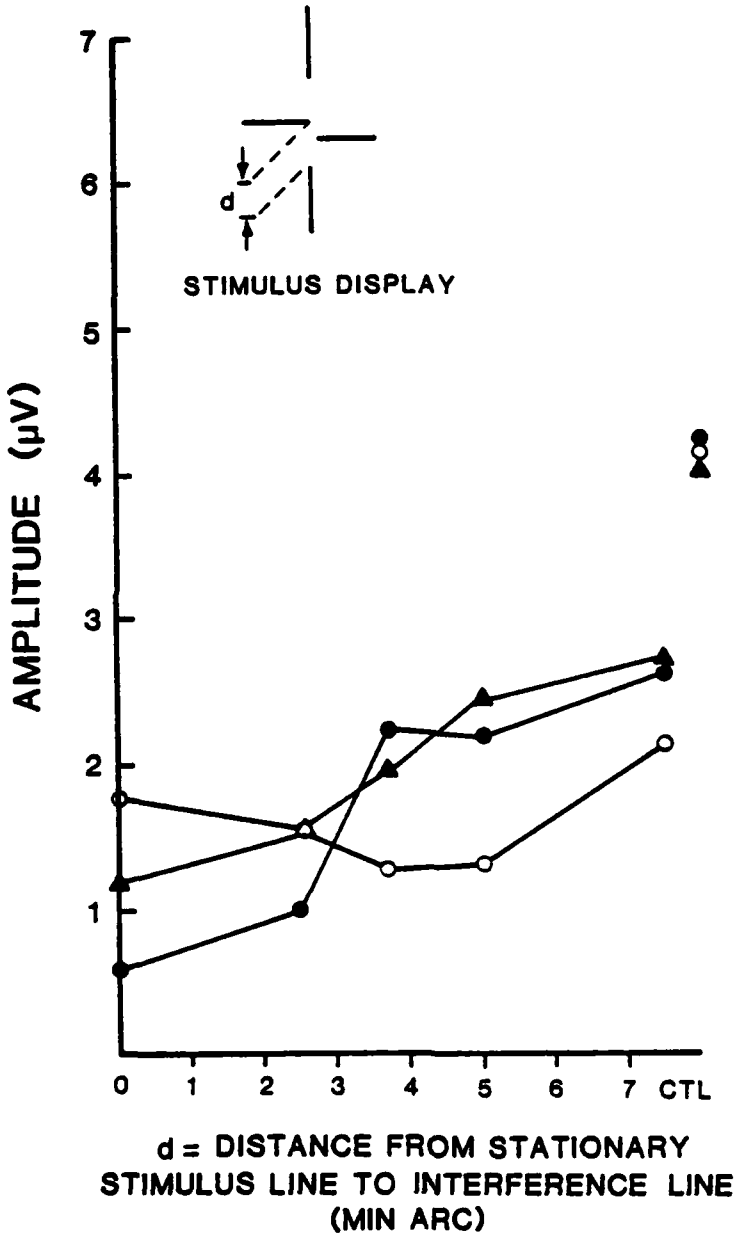

AH
STIMULUS DISPLAY
d
AMPLITUDE (μV)
7
6
5
4
3
2
1
0
1
2
3
4
5
6
7
CTL
d = DISTANCE FROM STATIONARY
STIMULUS LINE TO INTERFERENCE LINE
(MIN ARC)

Figure 11B. VEP amplitude vs. distance from stationary stimulus line to vertical interference line for subject MB. Refer to Figure 12A for details.

MB


7
6
5
4
3
2
1
AMPLITUDE (μV)
d
STIMULUS DISPLAY
0
1
2
3
4
5
6
7
CTL
d = DISTANCE FROM STATIONARY
STIMULUS LINE TO INTERFERENCE LINE
(MIN ARC)

single interference line distance were treated as one sample and compared to a second sample consisting of the amplitudes in response to the vernier offset alone. Results reveal the reliability of the suppression to exceed $\alpha = .05$ ($p = .016$) with the exception of the 7.5 minute horizontal condition ($p = .109$). Further inspection of the data reveals the amplitude differences to have a decreasing tendency associated with increasing interference line distance in both orientations. This trend is graphically evident in the plot of Figure 12A-B.

Qualitatively, the presence of the interference lines decreased signal to noise ratio during recording making identification of the response more difficult. This was especially true in the 0-4 minute distance range. A positive bias of these amplitude measurements is reasonably certain. Also in the 0 minute horizontal conditions, all three subjects reported difficulty seeing the offset and several records showed no identifiable response. Subjects reported no difficulty seeing offsets in other interference conditions even though evoked responses were attenuated.

Latency to negative and positive peaks as a function of presence and separation of interference line was also examined. No relationships were apparent with negative peak latencies generally falling within one standard error of the mean latency for a 73 second offset pre-

Figure 12A. Mean amplitude vs. distance from stationary stimulus line to horizontal interference line. Filled symbols are responses from AH, open symbols are from MB. Unconnected points at right indicate mean response to offset alone. All points are based on 3 measurements. Error bars represent $\pm$ 1 standard error.

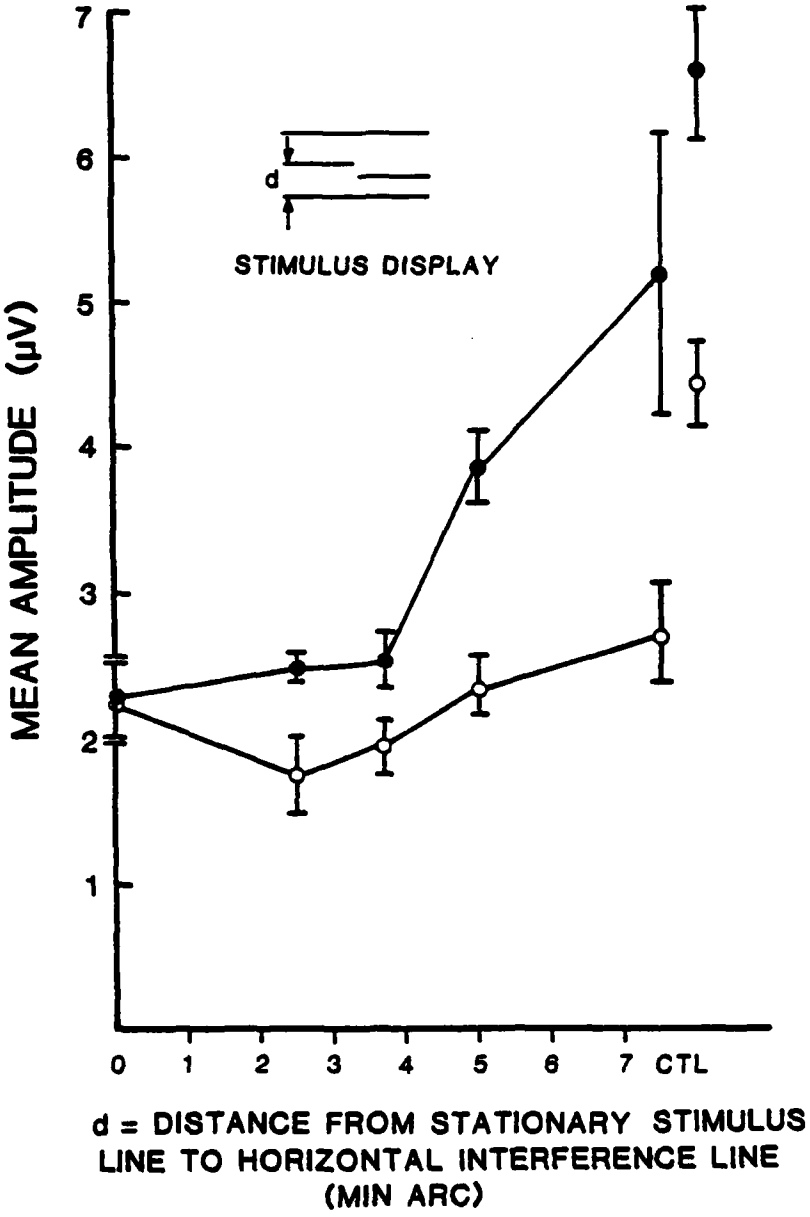
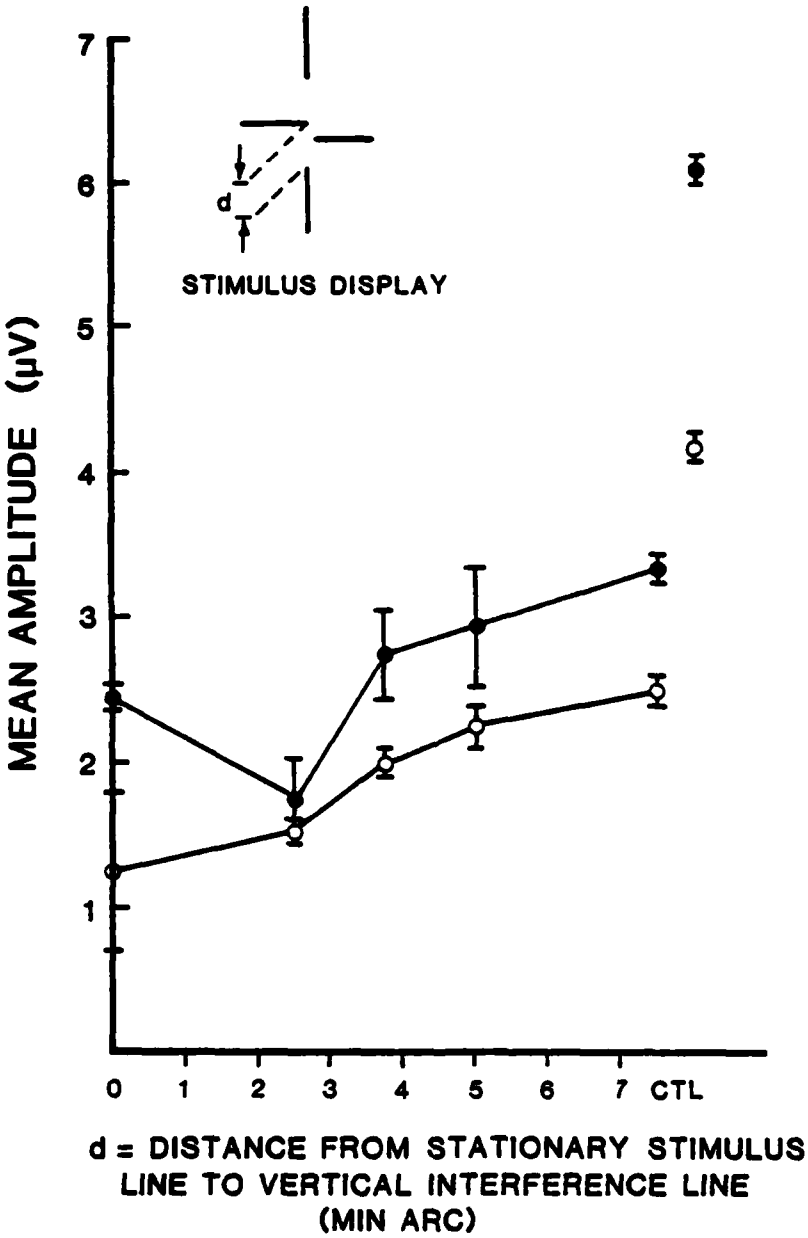

MEAN AMPLITUDE (μV)
7
6
5
4
3
2
1
d
STIMULUS DISPLAY
0
1
2
3
4
5
6
7
CTL
d = DISTANCE FROM STATIONARY STIMULUS LINE TO HORIZONTAL INTERFERENCE LINE (MIN ARC)

Figure 12B. Mean amplitude vs. distance from stationary stimulus line to vertical interference line. Refer to Figure 12A for details.


MEAN AMPLITUDE (μV)
7
6
5
4
3
2
1
d
STIMULUS DISPLAY
0
1
2
3
4
5
6
7
CTL
d = DISTANCE FROM STATIONARY STIMULUS LINE TO VERTICAL INTERFERENCE LINE (MIN ARC)

sented without interference lines.

Results for the other control conditions are illustrated in Figure 13. Inspection reveals perseveration of an evoked response across different configurations and vertical orientation and absence of a response to a line segment moving in a single hemifield. Although these records are somewhat noisy, waveform and latency are in close agreement with other vernier records.

D. Experiment 3

Vernier acuity thresholds obtained using psychophysics are presented and compared to electrophysiological estimates in Table 4. Each subject's mean psychophysical threshold is vased on three individual session measurements. Individual values for AH were 14.5, 13.3, 12.8 seconds (mean = 13.5); those for MB were 16.7, 13.2, 11.7 seconds (mean = 13.9) and those for RZ were 12.9, 12.3, 11.6 seconds (mean = 12.3). Thresholds obtained are clearly in the hyperacuity range but somewhat higher than figures generally reported in the literature.

DISCUSSION

The results of this study show that: a) the potentials evoked by a vernier offset stimulus vary systematically with the size of the offset and can be used in estimating subjective threshold of vernier acuity; b) the

Figure 13. VEP's recorded to control conditions: a) the offset was oriented horizontally; b) two offsets, separated by 9 minutes were presented with the center segment moving; c) two offsets, same as b, with the outer segments moving; d) single offset with both segments moving half the offset width; e) moving line segment presented to a single hemifield. Arrows indicate moving segment and direction of movement.

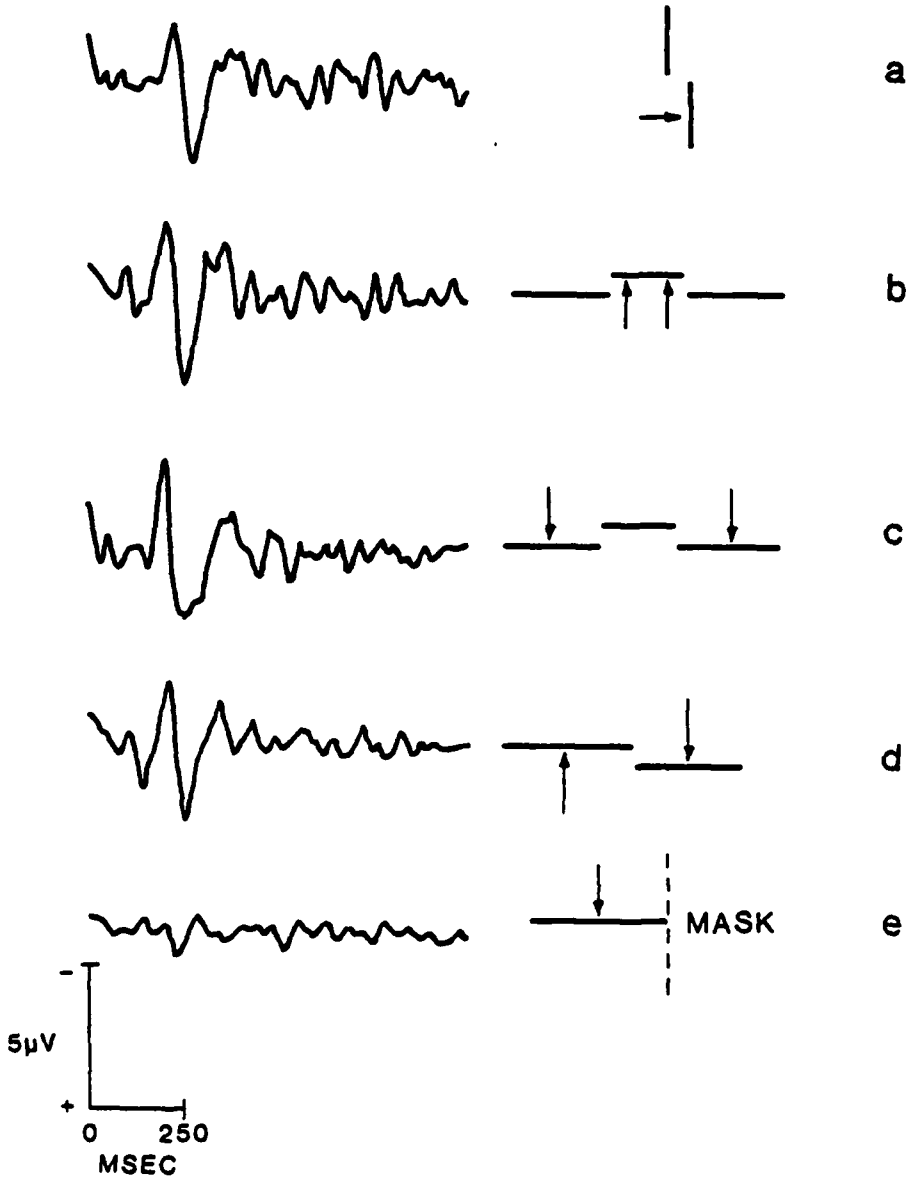

a
b
c
d
e
MASK
-
5μV
+
0
250
MSEC

TABLE 4

COMPARISON OF PSYCHOPHYSICAL THRESHOLD AND VEP ESTIMATE

SUBJECT	PSYCHOPHYSICAL THRESHOLD	VEP ESTIMATE	MEAN VEP ESTIMATE	S
AH	13.5	8.9 16.1 6.2	10.4	5.1
MB	13.9	9.1 14.4 13.2	12.2	2.8
RZ	12.3	N/A	N/A	N/A

TABLE 4. Psychophysical thresholds were derived with a single stimulus, forced choice paradigm using the method of constant stimuli. Each stimulus value was presented ten times. Threshold is defined as the offset size resulting in a 50% detection rate.

VEP's appear to be measures of a vernier information processing mechanism and c) the location of the mechanism appears to be outside visual cortex.

A. Threshold Estimation

The results of experiments 1 and 3 show that the systematic variation of VEP amplitude recorded in response to vernier offsets of different sizes can be used to estimate the subjective threshold of vernier acuity. Elaboration of this conclusion will focus on the relationship reliability, and the reliability and validity of the derived estimates of vernier threshold.

Although statistical evaluation techniques have revealed the reliability of the relationship ($p = .05$ for AH and .11 for MB), greater confidence can be derived from the replicability of the data across subjects, conditions and time. For both subjects, a similar positive correlation between offset size and VEP amplitude was found across experimental sessions which were separated by at least one day and, in two cases, several weeks. Waveform structure and derived latency at a single offset value did not vary significantly within subjects. Keeping in mind that the response in question is a signal buried in noise 10 to 100 times greater in amplitude (Regan, 1972), the assertion that these replications are chance occurrences becomes untenable.

Some individual estimate variability was seen and

was not unexpected as a result of the regression being fit to only five data points. The Levi et al. (1983 & 1983a) study, along with other work in which threshold estimates were derived by linear extrapolation (Campbell & Maffei, 1970; Campbell & Kukokowski, 1972; Sternheim & Cavonius, 1972), reduced this source of variance by pooling data points from several recording sessions into a single regression sample. Data was not originally pooled in this study due to the secondary experimental goal of assessing the efficiency of this technique in a clinical setting, e.g., very small samples. A post hoc combination of data, however, revealed Pearson product moment correlation coefficients of .92 for AH and .66 for MB, both with an alpha level exceeding .05 (AH: $t = 8.70$, $t(.05, 15) = 1.75$; MB: $t = 2.92$, $t(.05, 14) = 1.76$). Regression lines had respective slopes of 5.9 and 5.8, corresponding threshold estimates were 10.6 seconds and 14.2 seconds. Thus, these data appear to converge on the results of Levi et al. (1983 & 1983a) although they reported no values for individual session estimates.

A final aspect of reliability to be considered is the inability to record a consistent response for subject RZ. His records showed an occasional response at the appropriate latency but high amplitude noise masked its appearance in most cases (see Figures 6C and 7C). This

condition was probably due to some combination of cranial anatomy and scalp conductivity making him an unsuitable subject for VEP study.

Estimate validity is judged with respect to its relative and absolute accuracy. Relative estimate accuracy is judged by the criteria of the estimates being much less than the resolution acuity predicted by anatomical and optical properties of the eye (Westheimer, 1975) while absolute accuracy is judged by the difference between the VEP derived threshold estimates and subjectively determined thresholds. Although the standard for relative accuracy is met, judgements regarding absolute accuracy are not as straightforward. Strong practice effects, resulting in a 40% decrease in vernier threshold, have been reported by McKee and Westheimer (1977) when subjects reach approximately 2800 trials. In this study, subject MB had participated in previous experiments involving vernier acuity and reported his asymptotic threshold to be approximately 13 seconds which is in close agreement with his mean estimate of 12.2 seconds (see Table 4) and shows a maximum of 30% from any individual estimate. On the other hand, for subject AH this was the first experience with vernier offset detection and his mean psychophysical threshold of 13.7 seconds was based on considerably fewer trials than the number required for asymptotic performance. This value

differs from his mean estimate of 10.4 seconds by 30% and from the individual estimates by a maximum of 40% (see Table 4). It would be convenient to suggest that the subjective threshold would converge on the estimate with practice. McKee and Westheimer (1977), however, attribute the practice effect to increased sensitivity as opposed to criterion change. Assuming, for now, the VEP reflects the vernier acuity mechanism, a concomittant increase in amplitude would be expected with an increase in sensitivity. Design of this study does not lend itself to evaluation of this inference. Thus, the absolute precision to which the estimates predict the subjective threshold is not clear from these results and is subject to further experimental test.

B. VEP as a Measure of Vernier Processing

Experiments 1 and 2 show that the VEP's recorded in this study appear to reflect the neural processing of vernier information. Results indicating systematic variation of VEP characteristics with stimulus size, absence of a response under control conditions, and similar effects on both VEP's and subjective percepts by interference features support this conclusion.

When correlations between VEP characteristics and stimulus conditions can be shown to hold over a range of stimulus conditions, there can be greater confidence the correlation has physiological significance (Regan, 1972).

VEP's recorded in this study are highly similar to those reported by Levi et al. (1983 & 1983a) despite several differences in stimulus configuration, duration and presentation rate. In both studies, VEP latency and amplitude showed systematic variation with offset size. Variations of evoked potential amplitude with a change in a single stimulus feature has led other investigators to conclude the evoked potential reflected that feature's neural representation (Campbell & Maffei, 1970; Sperkeijse 1977). Similar logic applied to these results implies these VEP's are a measure of a vernier information processor.

The negative correlation between offset size and latency is a more surprising feature of these results. In VEP's to pattern stimuli, latnecy change has been found to be associated with variation of luminance (MacKay & Jeffreys, 1973; Musselwhite & Jeffreys, 1982). In this study, luminance was constant within and across sessions in Experiment 1 linking the change in latency with the changing offset size. One possible explanation of this is in terms of mechanism efficiency. A larger offset may simply be processed more efficiently, within limits, than a smaller one. The absence of an effect of interference lines on VEP latency, however, tends to refute this explanation. An alternative is to consider the complex nature of a VEP waveform. The positive and

negative components of the large deflection may reflect different features of the underlying mechanism or there may be a third component of appropriate latency but smaller amplitude whose appearance is masked by the larger components. In either case, if one of these component's sensitivity is different with respect to the others, varying offset size will result in a shift of waveform peaks because of the averaging process used to generate the VEP display. Thus, the implicit time (latency of peak) as a measure of latency would appear to increase or decrease (M. Berkley, personal communication).

Several possible artifacts in the systematic variation data must be examined. First, the potentials could be a result of eye movements in response to a light stimulus changing positions in the visual field. The voluntary eye movement normally associated with a change in stimulus position is the saccade. Even microsaccades, however, do not normally exhibit amplitudes less than 1 minute of visual angle (Carpenter, 1977). Also, probability of saccade initiation decreases with shorter stimulus duration to an approximate value of .05 for a 100 msec stimulus duration. These facts, coupled with the absence of a response in the line movement alone conditions, confirms the unlikeliness of the potential being generated by eye movements. The same result also refutes

a second possible artifact which is the response to a light stimulus passing across the retina. Although examination of Figure 6 reveals a small evoked response at about 220 msec in some records, the amplitude and waveforms are sufficiently different from the vernier response to preclude these being generated by the same mechanism.

Two final objections to be considered are the possibilities that the response was an artifact of presenting movement in a single visual hemifield or a particular stimulus orientation. With the subject fixating on the point of offset, the moving stimulus segment is projected onto the temporal half of the left eye and the nasal half of the right eye. Therefore, movement was present in only one visual hemifield. Also, the offset typically had a vertical orientation. Absence of a response to line movement deliberately presented to a single hemifield and response perseveration in the configuration and orientation control conditions illustrated in Figure 7 should rule out the possibility of the response being either of the afore mentioned artifacts.

The similarity of results in Experiment 2 to those of Westheimer and Hauske (1975) also support the conclusion that these VEP's reflect vernier processing. The vernier stimulus used in this study was very similar to that employed in the above paper. Under conditions which

are associated with elevated subjective thresholds, VEP amplitude was attenuated. A reasonable extension of this result is to consider amplitude a measure of the mechanism responsible for this sensitivity.

Three limitations of this comparison should be noted. First, in the Westheimer and Hauske (1975) experiment, the stimulus consisted of both the vernier offset and interference features flashed to the subject. In this study, controls for flash artifact required the continuous presentation of line stimuli with a brief offset induced by displacing a single line segment. Comparison of results, however, seems justified on the grounds that the duration of simultaneous presence of vernier offset and interference feature is within the limits specified by Westheimer and Hauske (1975).

A second difference is that the distance to interference feature specified in this study is referenced to the stationary line segment of the stimulus while in the Westheimer and Hauske paper the distance was measured from center of offset (see Figure 2). Interference features remained stationary in this study to control for response to the coupled displacement of stimulus and interference feature. This had the result of an asymmetric stimulus configuration. This difference may have confounded the locus of maximum interference but does not alter the finding of interference line effect.

Third, there is a dissimilarity between the results of the present study and those of Westheimer and Hauske (1975) in the 0 minute interference condition. In the earlier study, threshold was unaffected when the interference line was superimposed on the offset. In the present study, the 0 minute condition differed in that the interference lines were superimposed on the stationary stimulus line and the VEP amplitude was attenuated. Exact reproduction of the Westheimer and Hauske stimulus configuration was precluded by the previously described requirement for control of flash artifact. As viewed by the subject, the VEP stimulus consisted of a single bright bar across the length of the viewing field with a segment, half the length and one third the brightness, displaced 73 seconds below it. This brightness difference could have reduced offset visibility because of the masking effect of retinal glare. This is a result of spreading of a feature's luminance distribution over the retina by the less than perfect optics of the eye (Campbell & Gubisch, 1966; Gubisch, 1967). This raises the issue of whether or not glare could account for interference effects at other distances. Westheimer and Hauske discount this possibility by reporting identical interference effects when offset and interference lines were presented dichoptically. Furthermore, Gubisch (1967) calculated the effective luminance of a narrow

bar's (one minute width) image on the retina at a point 2.5 minutes from its center to be approximately 10% of its peak. Thus, contrast masking of the offset from that distance and beyond should be minimal. To confirm that contrast reduction resulting from retinal glare was not a significant factor in reducing the VEP amplitudes in the non-zero conditions, responses were recorded to vernier offsets (no interference lines) with stimulus luminance values differing by 50%. If contrast of the offset was a primary determinant of the VEP amplitude, large differences would be seen in the records. No substantial differences in amplitude were found.

Finally, some supporting data regarding analogous interference effects on VEP's and subjective perception can be found in Levi et al. (1983b). They report that the amplitudes of VEP's recorded to a stimulus in which line segments were separated by 7.5 minutes were smaller than amplitudes recorded to abutting segments, resulting in higher thresholds. This result is in agreement with reported effects of line separation on subjective thresholds (Squillane & Bien, 1970; Sullivan et al., 1972, Westheimer & McKee, 1977a).

C. Cortical Locus of Vernier Processing

By virtue of their relatively long latency, the evoked potentials recorded in this study appear to originate outside of the visual cortex (Jeffreys, 1971 &

1977; Jeffreys & Axford, 1972; Halliday et al., 1977). Tentative experimental results in support of this conclusion were found in pilot work aimed toward assessing temporal interference effects on the vernier VEP. During those sessions, it was found that two distinct waveforms could be elicited by simultaneous presentation of a vernier stimulus and a flashed pair of vertical interference lines. Latency to the first peak of these VEP's had the expected values of 100 msec for the flash and 220 msec for the vernier offset. By presenting the two features asynchronously and appropriately adjusting the initiation of the recording sweep, the two waveforms could be superimposed during a single epoch. Measurement of the combined VEP amplitude revealed a close agreement with the sum of the component amplitudes. Such linear summation argues for independence of the component generators (Regan, 1972). Thus, the vernier information processing appears to occur outside of the visual cortex. Animal studies, however, suggest that while area 17 may not be the site of vernier processing per se, it is a necessary preprocessor in that cats with area 17 ablation cannot discriminate vernier targets although they show only mild deficits in other acuity measures (Berkley & Sprague, 1976).

This extra-striate localization of the vernier information processor is in direct conflict with the

vernier acuity models of both Barlow (1979) and Crick et al. (1981) who suggest that the processing of vernier information occurs in cortical area 17. Westheimer (1979 & 1981), on the other hand, hypothesizes the centroid detector which probably acts outside of the primary visual area. Latency of the electrophysiological measure of this mechanism reported here and by Levi et al. (1983 & 1983a) lend support to a more central neural locus. This agreement is tempered, however, by the inability of the centroid model to account for the reduced amplitude of the VEP measure in the interference line conditions. Barlow's reconstruction model and Crick et al.'s zero crossing detectors suffer the same deficit.

The demonstration of an electrophysiological correlate of vernier acuity has several possible applications to both basic and clinical research. While VEP methods are recognized to be potentially misleading in the absence of careful hypothesis formulation and appropriate experimental control, their potential contributions to the understanding of perceptual mechanisms is also widely recognized (MacKay & Jeffreys, 1973; Regan, 1981). This is especially true in the area of human sensory research where direct recordings at the cortical surface are not easily made. The results presented here and in Levi et al. (1983 & 1983a) lay groundwork for the design of

multiple electrode studies of vernier VEP's to further specify cortical location of the underlying mechanism along with interactive effects of changes in luminance, offset duration and other stimulus parameters. A better specification of how the determination of relative location of features is made should lead to a clearer picture of shape perception (Watt et al., 1983). On the boundary between clinical and basic research are the potential studies of developmental aspects of the vernier acuity mechanisms. The use of VEP's in developmental studies of other visual abilities is well documented (Regan, 1972 & 1981; MacKay & Jefferies, 1978; Atkinson et al., 1979). A limitation of this application, however, lies in the fact that some individuals may not be suitable for VEP methods. This fact also limits the clinical application of these methods for estimation of vernier threshold in nonverbal subjects. A negative result could be a false negative diagnosis in a subject who has vernier acuity but is unsuitable for the VEP method.

Despite limitations, the visual evoked potential to a vernier stimulus, as first found by Levi et al. (1983) and confirmed in this study should prove to be an important method for the further investigation of how the visual system processes information.

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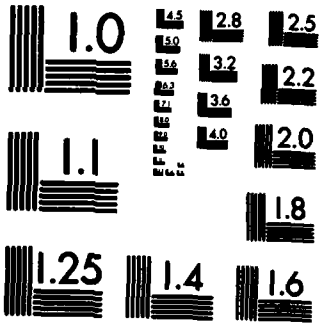

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