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OBSERVER SENSITIVITY.

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THE BINOCULAR INTERACTION OF SIZE AND ORIENTATION  
CHANNELS: EVOKED POTENTIALS AND  
OBSERVER SENSITIVITY

by

Vernon Leo Towle

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Approved by

  
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APPROVAL PAGE

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The interaction between spatial frequency and orientation feature processing was investigated in the human visual system. The psychophysical ( $d'$ ) and visual evoked potential (VEP) responses to test gratings flashed to one eye were investigated as a function of the nature of a continuously presented suppressing grating viewed either ipsiocularly or contraocularly. The test and suppressing gratings were varied both in bar width (9' vs. 36') and orientation (vertical vs. horizontal).

The specificity of the suppression of the monocular VEPs depended on the latency measured. Early latencies (100-125 msec) were suppressed only when the flashed and continuous gratings were the same orientation. Intermediate latencies (200-250 msec) were suppressed when the gratings were the same size or orientation. Late latencies (275-380 msec) were suppressed only when the two gratings were the same size and orientation. The reduction in observer sensitivity ( $d'$ ) paralleled the changes found in the late VEP measures. These effects were evident under both the intraocular and interocular suppressing conditions.

The results were interpreted as supporting both sequential and parallel feature processing in human visual cortex with orientation being encoded before spatial frequency.

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CHAPTER I  
INTRODUCTION

During the last few years researchers have made significant advances in determining how the human visual system extracts pattern information from the environment. Most theoretical formulations have postulated that this is accomplished by a hierarchy of parallel feature detectors which signals the presence of features in the visual image to higher mechanisms, which then synthesize this information into visual percepts (e.g., Neisser, 1966; Selfridge, 1959). Those detectors which respond to the same features can be thought of as comprising an information-processing channel. Appropriately, many visual neurophysiologists have attempted to define exactly which aspects of visual patterns serve as features and have sought to determine the characteristics of the alleged feature detectors and channels.

Evidence now indicates that these feature detectors may be single neurons, because cells in the cortices of infra-human mammals have been shown to respond selectively to certain patterns of stimulation. In order to effectively drive most cortical neurons, such stimulus characteristics as the location, speed, shape, size, and orientation of patterns have to be optimized. Cells at all levels of the hierarchy responsive to a given size or orientation in a

visual pattern can be thought of as comprising the channel through which that aspect of the stimulus is processed.

If the visual system is conceived of as being comprised of information channels, a number of questions arise as to how they might be organized. For example, is information about the size of a stimulus extracted before information about orientation? Are these two features processed serially or in parallel? How selective are channels tuned to various sizes or orientations? To what degree does the activity in a given size channel affect processing in another size or orientation channel?

Most experiments in this area have manipulated only one feature at a time to measure channel characteristics, and have demonstrated that two channels processing different values of the same type of feature interact only if the values are fairly close to each other. For example, the presence of a line of a given orientation might affect cells processing a line of a slightly different orientation but not one that was very different in orientation. Little research has been directed, however, to the question of how activity in a channel processing one feature varies as a function of activity in channels tuned to another feature--that is, the independence of various kinds of channels. Are the cells which are activated by narrow horizontal lines also activated by both wide horizontal lines and narrow vertical lines? The experiment to be described was designed

to answer some of these questions. By examining how patterns of various sizes and orientations interact with each other, using psychophysical and evoked potential techniques, it is possible to determine the degree to which size and orientation channels are independent, as well as the relative salience of these two visual features. The experiment was designed to determine whether size and orientation channels are organized in a serial or parallel manner and to what degree they act independently.

The review of the related single unit, psychophysical, and evoked potential literature is organized as follows: The selectivity of cortical visual neurons for pattern size and orientation will first be described. The anatomical organization of these cells in cortex as a function of their size and orientation preferences will then be described, along with the implications this has in terms of information channels. Psychophysical experiments which have examined the bandwidths of size and orientation channels and their interactions will then be described. Finally, evoked potential studies which have addressed the issue of neural information channels will be reviewed.

#### Single Unit Studies of Feature Selectivity

The systemic properties related to orientation and spatial frequency (size) are most likely a function of channel characteristics, which are ultimately determined by

the stimulus specificity of the cortical cells comprising the channels. The first experiments to be described therefore deal with the orientation and spatial frequency selectivity of single cortical neurons.

Orientation selectivity of single cortical cells.

Hubel and Wiesel (1959, 1962) first demonstrated that cells in the visual cortex of cats showed selectivity for the orientation of bar or edge stimuli that fell in their receptive fields. While they did not try to quantify this selectivity, they noted that as a bar was moved away from its optimal orientation its ability to stimulate the cell markedly decreased. They proposed a model (Hubel & Wiesel, 1962) in which a number of lateral geniculate nucleus (LGN) cells whose concentric center-surround receptive fields were in a row in the visual field might synapse on a single cortical cell, thus generating orientation selectivity in the cortical cell.

A more quantitative empirical analysis of orientation selectivity was performed by Campbell, Cleland, Cooper, and Enroth-Cugell (1968), who measured the angular selectivity of cortical cells in the cat using drifting square gratings. They found that their measure of responsiveness (the time required for the cell to generate 500 spikes) decreased linearly as the grating was moved progressively away from the cell's optimal orientation. The half-amplitude half-bandwidth of this orientation selectivity varied

considerably between cells, but most cells generated a value between  $14-26^\circ$ . They did not differentiate between simple and complex cells as Rose and Blakemore (1974) and Nelson, Kato, and Bishop (1977) subsequently did, who found the angular selectivity of complex cells to be less than that of simple cells. The latter authors found a weak and incomplete inhibition of the response to one eye when the orientation of the stimulus presented to the other eye was considerably discrepant. The significance of this finding will be more evident when the inter-ocular suppression observed in evoked potential studies is described.

Using computer-driven stimuli of various orientations, Schiller, Finlay, and Volman (1976a) have extensively examined the orientation tuning of simple (S-type) and complex (CX-type) cells in monkey cortex. Like Rose and Blakemore (1974) and Nelson, Kato, and Bishop (1977), they found that orientation tuning was greater for S-type cells than for CX-type cells. The orientation preference and selectivity of cells was similar for both eyes, regardless of the ocular dominance classification of the cell, implying to them that orientation selectivity is generated by "intracortical circuitry," rather than being due to the nature of the input from the LGN, as hypothesized by Hubel and Wiesel (1962). They suggested that these properties could be generated by the geometry of the apical dendritic tree of cortical cells. If the apical dendrite

bifurcated and spread horizontally in two directions in cortex, a stimulus whose orientation caused it to fall into these two inhibitory fields would not produce as large a response as one whose orientation caused it to fall between the two fields. The same mechanism would work (but at an orthogonal orientation) if the dendritic trees had an excitatory effect instead of an inhibitory effect on the cell.

Spatial frequency selectivity of single cortical cells.

While cortical cells are very broadly tuned to the width of single bars, they are much more narrowly tuned to gratings of different spatial frequencies. Campbell, Cooper, and Enroth-Cugell (1969) recorded the responses of single units in the LGN and visual cortex of the cat to moving sine- and square-wave gratings of different spatial frequencies. All cells showed an inverted U-shaped response function or contrast threshold function whose high spatial frequency side decreased exponentially. While their measure of central tuning (where the function dropped one log unit) for cortical cells ranged from .18 to 1.6 c/deg, they did not determine the average bandwidth of tuning for individual cells. They did conclude, however, that this arrangement would support a model based on spatial frequency channels.

Maffei and Fiorentini (1973) performed a similar analysis on ganglion, LGN, and cortical cells in the cat. The peak responsiveness of their 28 simple cells ranged from

.2 to 3 c/deg--values similar to those found by Campbell, Cooper, and Enroth-Cugell (1969). Additionally, cells were almost unresponsive to frequencies more than one octave away from their center frequency. Complex cells were more broadly tuned to lower spatial frequencies (.25 to .7 c/deg).

Interesting results were found by Schiller, Finlay, and Volman (1976b), who attempted to determine the mechanisms of spatial frequency specificity of monkey visual cortical cells with computer-presented bars and sine- and square-wave gratings. They found that while most cells showed spatial frequency selectivity to sine gratings, they showed little selectivity for the width of bars or square-wave gratings, probably due to the fact that sharp edges are extremely potent stimuli and override the spatial frequency aspects of the stimulus. According to them, spatial frequency analysis may only be functionally important in analyzing stimuli in the visual field which are out of focus.

In summary, empirical investigations of the properties of single units in the visual cortex of the cat and monkey have shown that cortical cells, especially simple ones, tend to be selective to the orientation and spatial frequency of patterns. This arrangement is commensurate with models of visual organization which postulate the existence of channels selective to specific orientations and/or spatial frequencies. The anatomical arrangement

of cells in visual cortex also supports such an interpretation, as the two studies described below will illustrate.

### Functional Organization of Cortical Cells

It turns out that cortical cells are not randomly spaced in relation to their orientation and spatial frequency tuning. Hubel and Wiesel (1974) have examined how cells of different orientations are functionally organized in monkey cortex. They found that cells that lay above or below each other in cortex tended to have the same orientation preference, but that this preference gradually shifted as their microelectrode was moved tangentially across cortex. They concluded that monkey cortex is organized into orientation "sheets" or "columns" approximately 25-50  $\mu$  thick, which shift 180° across approximately .5-1 mm of cortex (a "hypercolumn"), comparable to the width of ocular dominance columns. This type of organization would simplify cortical wiring and could easily mediate the inhibition between orientation channels which has been postulated on the basis of psychophysical data from humans.

In a more recent study, Maffei and Fiorentini (1977) have shown that cortical cells are also organized in terms of their spatial frequency preference. Using mapping techniques similar to those used by Hubel and Wiesel (1974), they found that penetrations perpendicular to the surface of cortex revealed cells tuned to a wide range of spatial frequencies and that a cell's center frequency was a function

of its depth in cortex. Cells in layers II and III were generally tuned to intermediate spatial frequencies, while those in layer IV were generally tuned to higher ones and those of layers V and VI were the lowest. Tangential penetrations across orientation columns, on the other hand, revealed cells having similar preferred spatial frequencies and acuities. This spatial arrangement of cells in visual cortex is shown in Figure 1. With this arrangement each orientation column can analyze a range of spatial frequencies and each spatial frequency layer can analyze a range of orientations. Each matrix of cells serves as a cortical unit which completely analyzes a given location of the visual field in terms of orientation and spatial frequency. This would be an efficient anatomical organization if information was processed in terms of orientation and spatial frequency channels; each would have its own anatomical location in cortex.

#### Psychophysical Studies of Channel Characteristics

Systemic data from psychophysical and evoked potential studies also support the channel hypothesis, as revealed in experiments which have ascertained the characteristics of individual channels. Two paradigms have been used in psychophysical studies to isolate channels of a given size or orientation: adaptation and masking paradigms. Both of these paradigms have involved intraocular and interocular processes, which have indicated that the effects seem to be cortically generated.

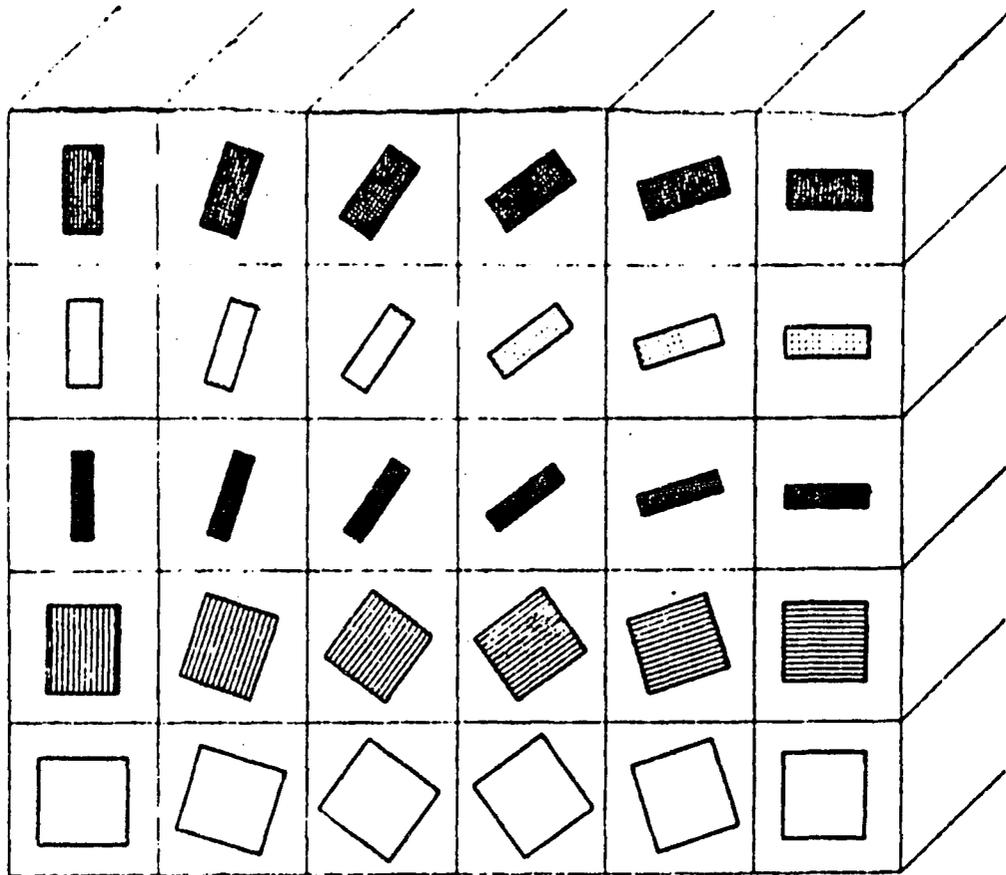


Figure 1. Sketch of a coronal section of the cat striate cortex describing the possible arrangement of receptive fields according to their preferred stimulus size and orientation. The rectangles in each row have the same width (to indicate a constant preferred stimulus period) and the rectangles in each column have parallel sides (to indicate a constant preferred stimulus orientation). (Photographed from Maffei & Fiorentini, 1977, their Figure 12.)

Orientation channels. The estimate of orientation channel bandwidth obtained by researchers seems to be a function of the paradigm which is employed. Kulikowski, Abadi, and King-Smith (1973) compared the results of three different psychophysical procedures and found that the narrowest half-amplitude half-bandwidth estimates were obtained with subthreshold summation techniques ( $3^\circ$ ); broader bandwidths were generated from adaptation procedures ( $7^\circ$ ); and still broader estimates were found with masking procedures ( $12^\circ$ ). They suggested that interchannel inhibition may account for the broad tuning generated by masking techniques, but that this inhibition is not activated by subthreshold procedures. They concluded that estimates from subthreshold summation techniques most closely approximate the actual bandwidth of the detectors.

Using a psychophysical masking paradigm, Campbell and Kulikowski (1966) examined the robustness of the tuning of human orientation channels. They found that the contrast threshold of a sinusoidal grating was a function of the orientation of a masking grating that they superimposed on top of it. The contrast threshold decreased exponentially as the angle between the gratings increased, regardless of the phase coherence, contrast of the masking grating, or focus. This paradigm does not produce the interocular rivalry seen at small angles when the gratings are presented to the two eyes separately (Campbell & Maffei, 1970).

Although the orientation bandwidth of the masking effect did not change as a function of the above variables, the magnitude of the effect did change--poor phase coherence reduced the effect more than the other manipulations. For similarly oriented gratings (at high contrasts), the change in threshold of the test grating was as much as 1.5 log units.

Campbell and Kulikowski (1966) also found that if the test grating was presented at an oblique orientation ( $45^\circ$ ), the half-amplitude half-bandwidth of the effect increased from  $12^\circ$  to  $15^\circ$ ; defocusing the vertical series indicated that this was not due to reduced acuity for oblique gratings. Interestingly, Rose and Blakemore (1974), who carefully measured the orientation tuning of cortical cells in the cat, found that simple cells were also significantly more broadly tuned if their orientation preferences were oblique rather than horizontal or vertical.

Abadi (1976) has used a dichoptic viewing situation to psychophysically determine the orientation and spatial frequency specificity of the human visual system using a masking paradigm. Subjects were required to increase the contrast of a sinusoidal grating presented to one eye until rivalry was generated with another grating presented to the other eye. He examined the way in which the rivalry threshold changed as a function of the orientation and spatial frequency of the two patterns. Orientation had its

half-amplitude half-bandwidth at around  $19^\circ$ . He interpreted the U-shaped curve as a function of the difference in orientation between the patterns presented to the two eyes as indicating inhibition between cells in nearby orientation columns.

Other psychophysical studies have generated data consistent with the concept of orientation channels using various psychophysical techniques. Some spatial after-effects and optical illusions can be explained in terms of adaptation of orientation channels (Coltheart, 1971; Sutherland, 1961). As will be seen below, many of the techniques used to study orientation channels have also been used to study size or spatial frequency channels.

Spatial frequency channels. Many studies have obtained results commensurate with the hypothesis of spatial frequency channels, but only a few will be described here. The discussion of whether these should be called size channels or spatial frequency channels will not be entered, since for the most part the implications are the same for both types of model. The terms will therefore be used interchangeably. Campbell and Robson (1968) examined the contrast sensitivity of different types of gratings over a wide range of spatial frequencies. They attempted to demonstrate that the visual system analyzes patterns in terms of Fourier analysis. They found that the visual system is maximally sensitive to spatial frequencies around

4 c/deg, and that the sensitivity to a grating is determined by whether or not its fundamental frequency is above threshold. For example, square waves (which are comprised of a sum of the odd harmonics of the fundamental spatial frequency) are not detected as square-wave gratings until the third harmonic is above threshold. They proposed a model of visual system functioning based on independent detectors, each tuned to a different spatial frequency, which are preceded by filters that are about an octave wide. These detectors must feed into synthesis mechanisms that are binocular in nature, because Maffei and Fiorentini (1972) presented sine-wave gratings of different spatial frequencies to the two eyes and the subjects perceived pattern configurations that would be predicted by Fourier analysis. For example, when they presented a sine grating to one eye and its third harmonic to the other eye, the subject's perception was that of a square grating, as Campbell and Robson (1968) found using a dioptic viewing paradigm.

Blakemore and Campbell (1969) performed similar experiments but used an adaptation paradigm. After adaptation to a given spatial frequency, the threshold was raised as much as five times. Although the procedure did not work for spatial frequencies below 1.3 c/deg, the half-amplitude half-bandwidth of this change in threshold was about one octave (slightly less above 14 c/deg).

An interesting study reported by Blakemore, Nachmias and Sutton (1970) reveals how closely spatial frequency detectors may be related to perception. They found that after adapting to a given spatial frequency, nearby spatial frequencies seemed to be shifted away from the adapting spatial frequency. However, no distortion was seen for the adapting frequency nor those greater than two octaves away. The effect was also found to be orientation specific and transferred interocularly. These results imply that our perception of a grating is based on the activity in an array of medium-tuned spatial frequency detectors. Adapting to a given spatial frequency causes a decrease in the output of nearby detectors. When presented with a grating which normally activates some of these detectors, the peak of the distribution of activity is shifted away from the adapted spatial frequency detectors, causing a similar shift in perception.

#### Orientation and spatial frequency interactions.

Relatively few studies have taken the next logical step and examined interactions between spatial frequency and orientation channels. Parker (1972) tested whether the tilt after-effect was spatial frequency specific. He found no difference in the magnitude of the effect when the adapting and test stimuli were one octave apart in spatial frequency, and noted that this does not fit the predictions that would be made from the orientation and spatial frequency

characteristics of single units--which would predict a decrement in the effect for different spatial frequencies. According to Parker, the effect could be mediated by a set of neurons that are selective to orientation but not spatial frequency. The failure to demonstrate spatial frequency specificity for the tilt aftereffect suggests that orientation might be processed before spatial frequency is processed, as suggested by Campbell and Maffei (1971). On the other hand, Georgeson (1973) has demonstrated spatial frequency specificity for a simultaneous tilt illusion which does not rely on adaptation. The mechanisms generating these two illusions are probably, therefore, quite different.

Parker's finding that grating size is not important in an orientation illusion and the noncomplementary finding reported by Blakemore, Nachmias, and Sutton (1970) and Abadi (1976) that orientation is important in size illusions suggests a serial information-processing model. These findings would be expected if orientation is processed before size. The predictions of various models of size and information processing will be discussed when the rationale for the proposed study is explained.

Before examining the evoked potential literature on this topic, it is interesting to speculate at what level in the visual system the adaptation described by these authors takes place. Maffei, Fiorentini, and Bisti (1973) have examined the neural correlates of the adaptation to

gratings in cats. They sampled 101 single units from visual cortex and recorded the effects of a one-minute adaptation period to a drifting grating of the optimal size and orientation for each cell. Simple cells showed a decreased firing rate for about 30 seconds after the adapting stimulus was terminated. Complex cells either adapted for only up to 15 seconds or did not adapt at all. They concluded that the adaptation which Blakemore and Campbell (1969) described was cortically generated because (1) geniculate fibers adapted for 2-3 seconds at most, and (2) the effect transferred interocularly. Adaptation to gratings is therefore probably mediated by simple cells.

#### Evoked Potential Studies of Channel Characteristics

A parallel literature using evoked potentials instead of psychophysical thresholds as the dependent measure to isolate the characteristics of individual channels has also evolved. For example, Campbell and Maffei (1970) demonstrated orientation channel specificity with evoked potentials using an adaptation procedure. They recorded VEPs to a low contrast reversing sine grating (12 c/deg) with a vertical orientation after adapting to high contrast gratings of various orientations for one minute. The adaptation caused virtually no decrease in VEP amplitude if the adapting grating was 15-20° or greater away from the vertical test grating. They performed the analogous

experiment adapting to a variety of spatial frequencies before testing and found the spatial frequency effect to be about an octave wide.

A variety of techniques can be used to demonstrate channel specificity using visual evoked potentials. For example, using pattern reversal evoked potentials, Campbell and Maffei (1970) measured the selectivity of spatial frequencies in the upper, middle, and lower thirds of a display. The regression coefficient of the evoked potential contrast-amplitude function was 2.6 times that of a single spatial frequency presented in the same visual area. They interpreted the increased amplitude as resulting from the algebraic summation of activity from three different spatial frequency channels. This interpretation assumes that a spatial frequency channel is not localized to a particular area of the visual field, since they are seen to summate even though the three patterns are presented to different areas of the visual field. This is at variance with the model proposed by Maffei and Fiorentini (1977) described earlier, in which each portion of cortex responds to a localized area in the visual field.

Mecacci and Spinelli (1976) also examined the effects of adaptation to a specific spatial frequency on the amplitude of evoked potentials generated by a sinusoidal grating reversing at 8 Hz. After adapting to a 4 c/deg grating for 15 minutes, the evoked potential size-amplitude

function (which peaked at 4 c/deg in the unadapted state) showed a dip about two octaves wide in the region of the adapting stimulus. They also examined the parameters of the time course of adaptation of the evoked potential and corresponding contrast threshold increment. They found that in order to demonstrate stable adaptation effects they had to adapt subjects for about 15 minutes. The succeeding adaptation effects lasted for about five minutes. The bandwidth of adaptation was the same whether they adapted for 15 minutes or 60 minutes. However, whereas the evoked potential showed some adaptation for about 10-20 minutes until it completely recovered, the contrast threshold remained elevated for as long as two hours. At the peak of the function, adaptation caused an 80-90% reduction in the amplitude of the VEP.

Interocular summation and suppression. Under normal circumstances information from the two eyes summates in visual cortex, resulting in higher acuity and contrast sensitivity under binocular as compared to monocular viewing conditions (Blake & Levinson, 1977; Campbell & Green, 1965). However, since information must be time-locked to the averaging process if it is to contribute to the averaged evoked potential, a continuously presented pattern will not add to the neural activity generated by an identical pattern flashed to the other eye. For example, Harter, Seiple, and Salmon (1973) found that the information from the two eyes

summated, creating larger evoked potentials when both eyes were simultaneously flashed with the same pattern, as compared to when both eyes viewed the patterns but only one eye was flashed. If only one eye is flashed and the other eye is allowed to view the same pattern (but is not flashed), the evoked potential is suppressed, compared to when the nonflashed eye views diffuse light (Harter, Towle, & Musso, 1976; Harter, Towle, Zakrzewski, & Moyer, 1977) or darkness (Harter, Conder, & Towle, submitted for publication). Since the information processed by the nonflashed eye is not time-locked to the averaging process, it does not directly contribute to the evoked potential. It indirectly reduces evoked potential amplitude, apparently by saturating binocular neurons that would normally respond to the flashed pattern viewed by the other eye. For example, Spekreijse, Van der Tweel, and Regan (1972) found that presenting a high contrast, constantly illuminated checkerboard to one eye suppressed the response to an appearing-disappearing checkerboard presented to the other eye. However, if the continuous checkerboard was presented as a stabilized retinal image and was no longer visible, the interocular suppression effect disappeared.

Binocular summation and suppression has been used to demonstrate channel specificity, as described below. Campbell and Maffei (1970) obtained pattern reversal evoked potentials from a vertical sinusoidal grating presented to

the left eye and a horizontal grating presented to the right eye. When each eye was stimulated individually, the two contrast-amplitude functions had identical slopes. However, when evoked potentials were recorded from both patterns reversing simultaneously, the resulting contrast-amplitude function had twice the slope, implying that the two gratings were each stimulating different cortical neurons, the responses of which were summing in the evoked potential. This technique is more in line with the model of cortex presented in Figure 1 than was their prior technique of dividing the visual field into thirds. They also attempted to demonstrate the selectivity of these orientation channels by slowly decreasing the difference in orientation between the gratings presented to the two eyes and observing the decrease in evoked potential amplitude as the gratings presented to the two eyes approached the same orientation. They found, unfortunately, that rivalry interfered at small differences in orientation, and were forced to demonstrate channel specificity using an adaptation paradigm.

In this situation, flashed patterns have a distinct advantage over constant luminance modes of stimulation: the brief nature of the flash does not allow enough time for rivalry to develop. Harter, Conder, and Towle (submitted for publication) were able to use a variation of this paradigm to demonstrate orientation channel specificity. By continuously presenting gratings of various orientations

to one eye they found that the evoked potential from a grating flashed to the other eye was gradually suppressed at 110 msec latency as the orientation of the two gratings became more similar (see Figure 2). They interpreted this as indicating that the binocular orientation channel common to the two eyes was saturated by the continuous grating, causing the evoked potential to the grating flashed to the other eye to be suppressed. The half-amplitude, half-bandwidth of the suppression was about  $22^\circ$ .

Harter, Towle, and Musso (1976) have used VEPs to demonstrate the existence of size-specific binocular channels in the visual system of humans using the same technique. They probed one size channel by flashing a checkerboard of a given size to one eye and then saturated different size channels by continuously presenting various sized checkerboards to the other eye. As the channel that was saturated became closer to the probe stimuli (12' or 35' checks) the amplitude of the VEP 160 msec after the flash was reduced (see Figure 3). The bandwidth of the suppression was on the order of an octave in this study.

Both the study dealing with orientation and the study dealing with size yielded results commensurate with a channel hypotheses. Notwithstanding, there were differences in how the two variables manifested themselves in the evoked potential. The peak effect for size was at a latency of 160 msec while the peak effect for orientation was at 110

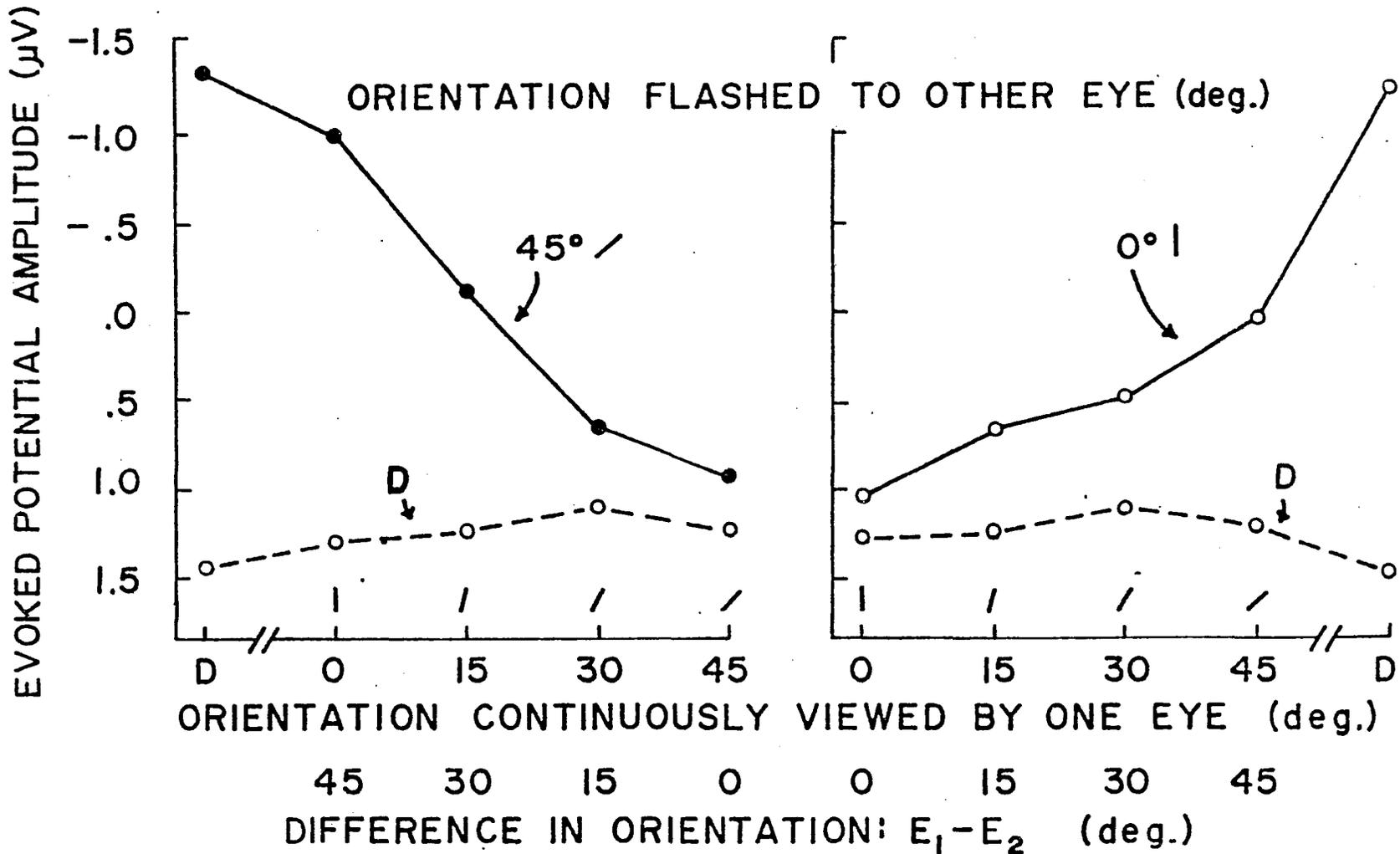


Figure 2. Effects of changing the continuous suppressing stimulus viewed by one eye from diffuse light (D) to lined grids of various orientations on VEPs to test stimuli (diffuse light, 0° and 45° lined grids) flashed to the other eye. VEP amplitude was measured at 110 msec after the flash. Data have been averaged across six subjects, three replications, and two eyes. (Photographed from Harter, Conder, & Towle, submitted for publication.)

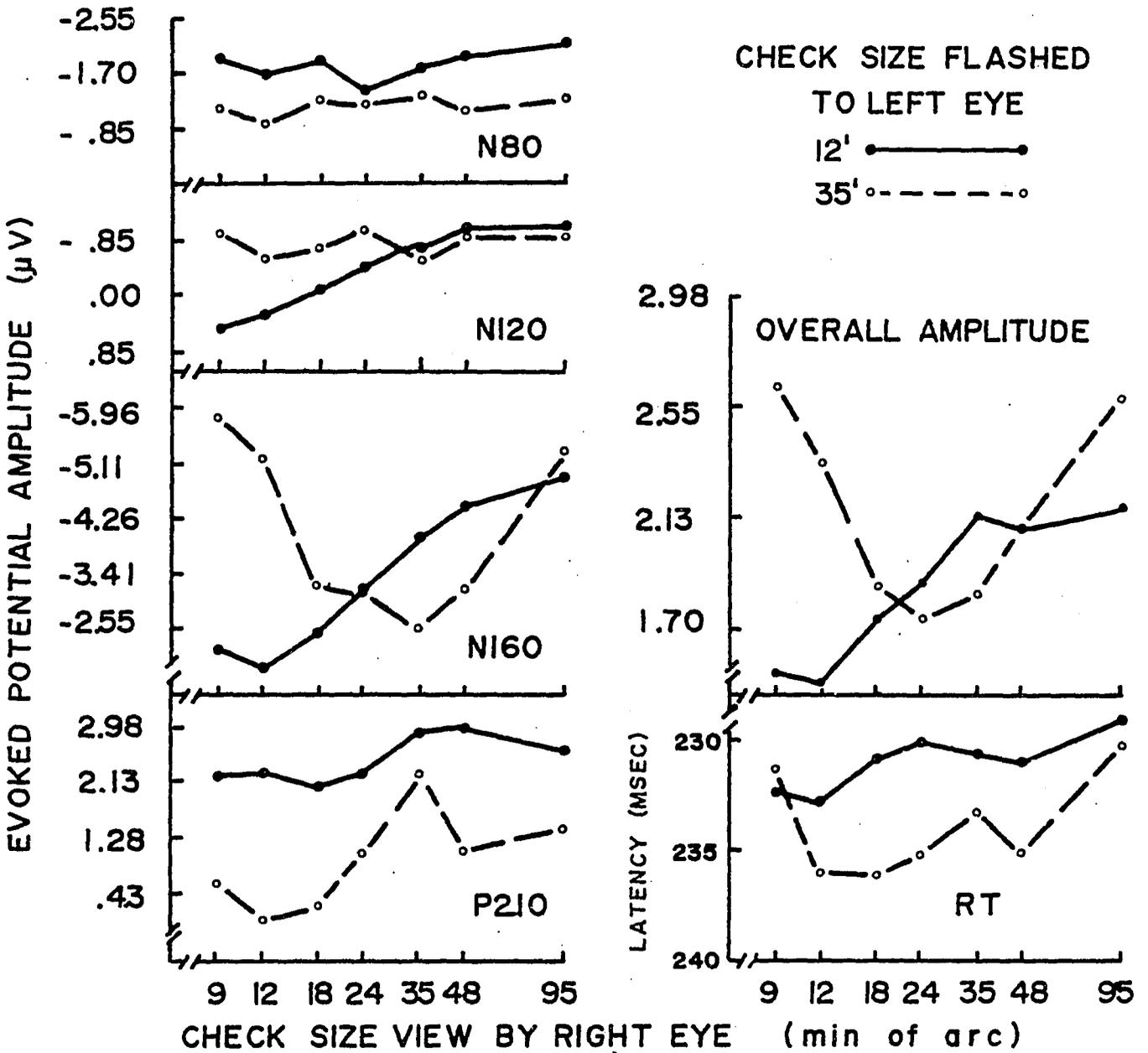


Figure 3. Changes in monocular VEP amplitude as a function of the check size flashed to the left eye, 12' (solid line) and 35' (dashed line), and the interocular effect due to the check size continuously viewed by the opposite (right) eye. N80, N120, N160, and P210 refer to the average polarity and latency at which the amplitude measures were taken. . . Each plotted point is a mean based on nine subjects and four replications. (Photographed from Harter, Towle, & Musso, 1976, their Figure 4.)

msec. Does this imply that orientation is processed before size in the visual system? Furthermore, the effects due to size were much greater than the effects due to orientation (cf. Figures 2 and 3). Does this mean that size is a more potent variable than orientation? It is difficult to interpret differences in the results of these two studies because they differed in a number of aspects. The orientation study used gratings, while the size study used checkerboards. There were also differences in luminance between the two studies. Is the fact that the size effect was stronger than the orientation effect perhaps due to the higher luminance of the suppressing checkerboards (35 mL) than the suppressing gratings (12 mL)? A subsequent study from this laboratory (Harter, Towle, Zakrzewski, & Moyer, 1977) demonstrated that interocular suppression was a function of both the luminance of the suppressing stimulus and the binocularity of the subject. The differences between the size and orientation effects in these two studies need to be examined under conditions in which both size and orientation are manipulated under identical stimulus conditions within the same subjects.

### Summary

In summary, the converging lines of evidence from single unit, evoked potential, and psychophysical experiments indicate that both the spatial frequency and orientation

of visual patterns are important features to which the visual system responds. Much effort has been devoted to determining how selectively the visual system responds to these variables at both the cellular and systemic levels.

Although channels selectively responding to size and orientation have been isolated in a number of experiments, the independence of these channels has not been clarified. Can the spatial frequency of a stimulus be changed without affecting processing taking place in cells tuned to a different orientation? Does the activity of different channels manifest itself in different components of the VEP? Are manipulations of spatial frequency more powerful than manipulations of orientation? It is to these questions that the following experiment is addressed.

## CHAPTER II

## METHOD

Subjects

Five males and one female (ages 14-50) volunteered to serve as subjects in the experiment. All six subjects had visual acuities correctable to 20/20 or better, stereoacuities better than twenty sec of arc as measured with a Bausch-Lomb Ortho-rater, and no detected astigmatism (except MRH, who had a slight amount in the vertical plane). Three of the six subjects had served in previous experiments in this laboratory, two of which (MRH and VLT) were aware of the experimental hypotheses under investigation.

Visual Stimulation

The visual patterns used in this experiment were black and white square-wave gratings photographically reproduced on transparency film (contrast = .9). Two sizes of gratings were presented at vertical and horizontal orientations, one with 9' bars (3.3 c/deg) and another with 36' bars (.83 c/deg). These sizes were chosen because they were four octaves apart in terms of their fundamental spatial frequencies and, therefore, activated different size channels. Likewise, the 90° difference in orientation was sufficient to activate different orientation channels.

Independent stimulation of each eye was obtained by means of a haploscope (see Figure 4). Monocular evoked potentials were obtained by flashing either 9' vertical or 36' horizontal square-wave gratings (7° dia. field) to the right eye. Flashed patterns were back-illuminated with a 10  $\mu$ sec light flash generated by a Grass Model PS-2 Photostimulator. Flashes occurred once every 750 msec and were 2 log units above psychophysical threshold (as measured with neutral density filters).

The flashed gratings were superimposed on continuously illuminated 8° x 10° stimuli viewed by both eyes. These continuous stimuli were either a 9' vertical (9V), 36' vertical (36V), 9' horizontal (9H), 36' horizontal (36H) grating, or a diffuse field. All stimuli were of equal space-average luminance ( $4 \pm 1$  mL).<sup>1</sup> There were two viewing conditions in this experiment: the intraocular suppression condition where both the flashed gratings and the continuously presented (non-flashed) gratings were viewed by the same (right) eye, while the left eye continuously viewed diffuse light; and the interocular suppression condition where

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<sup>1</sup>To compensate for the 50% reduction in light flux due to the beam splitter in the right half of the haploscope, either a checkerboard or 9' grating was placed behind the diffusing screen in the left eye. It was later discovered that the luminance transmittance of these two patterns was not exactly the same. When the grating was positioned behind the diffusing screen, the display was about 1 mL brighter than when the checkerboard was in position. The net effect was to make the continuous grating slightly brighter when it was being viewed by the left eye.

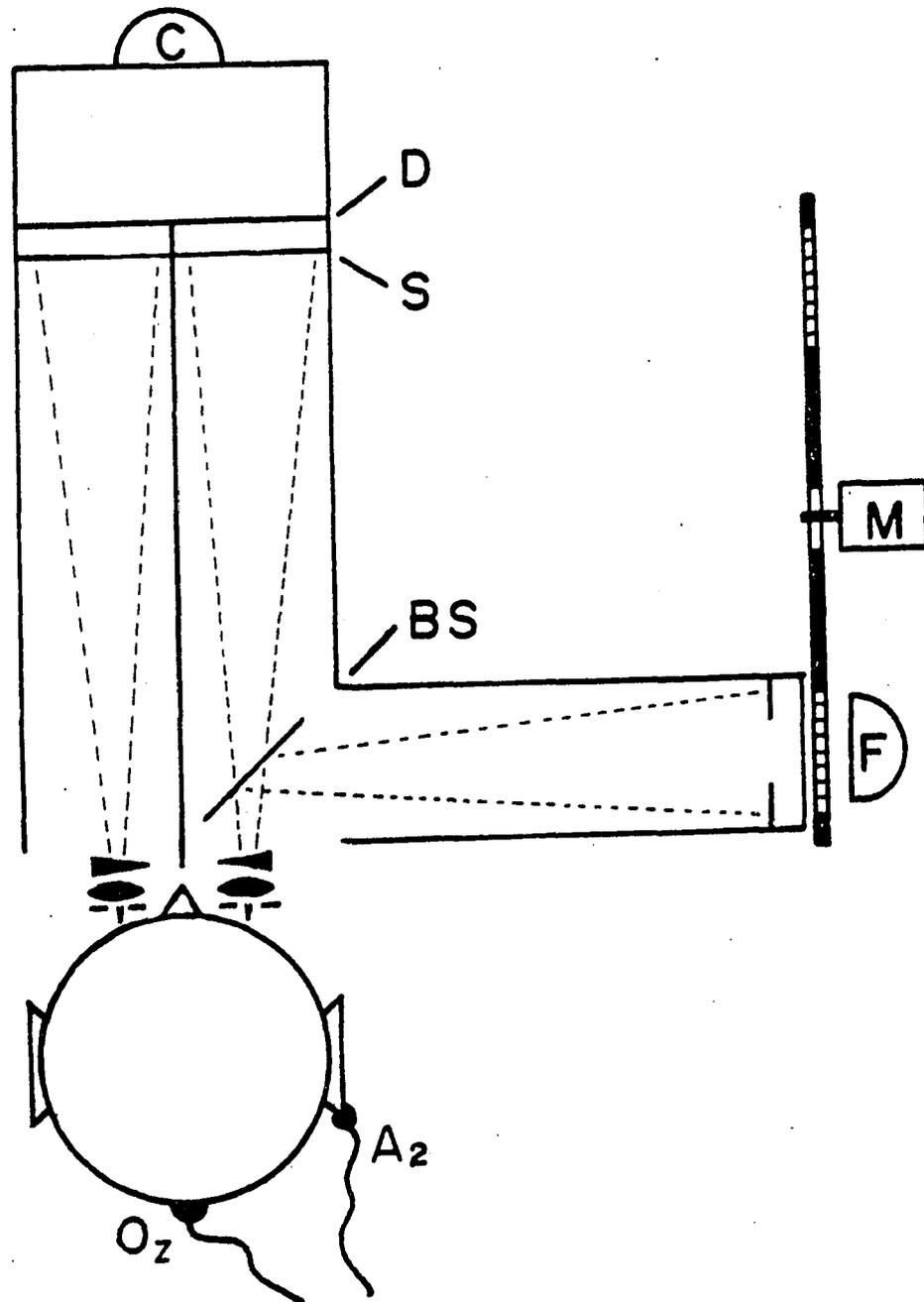


Figure 4. Experimental apparatus used to present stimuli. (Subjects dichoptically viewed suppressing stimuli (S), a grating for one eye and a diffuse field of equal luminance for the other, illuminated by a continuous incandescent light source (C) behind a diffusing screen (D). A beam splitter (BS) caused flashed stimuli (F) from the random access stimulator (M) to appear superimposed on continuous stimuli (S) viewed by the right eye. Subjects viewed the stimuli through +1 D spherical lenses, 8  $\Delta$  prisms, and 1 mm artificial pupils from a distance of 53 cm.)

the flashed and continuous gratings were viewed by the right and left eye respectively, while the right eye continuously viewed diffuse light. The ambient illumination of the subject cubicle was 1 mL. The subjects viewed the display through 1 mm artificial pupils, +1 D spherical lenses, and 8ΔD prisms (base out) from a distance of 53 cm.

### Procedure

The data collection for each subject was divided into two phases. In an initial two-hour session the subject became familiar with the laboratory situation, the laboratory recording procedures, and the reaction time (RT) task. In addition, the visual characteristics of the subject were ascertained and some preliminary control data were collected. VEPs were obtained to each of the two flashed gratings while the subject simultaneously viewed (1) an identical grating with the nonflashed eye (interocular suppression), (2) an identical grating with the flashed eye (intraocular suppression), and (3) diffuse light with both eyes (no suppression). Control conditions also were investigated to insure the relative phase of the flashed and nonflashed grating under the intraocular viewing condition would not account for the suppression effects.

The second phase of data collection, the main part of the experiment, consisted of the subjects' receiving four one-hour replications (on separate days) of the 16 main

experimental conditions (four continuous gratings x two flashed gratings x two viewing conditions) in a completely counterbalanced Latin square design. The continuous gratings were changed after a block of 32 flashed gratings (taking about 45 seconds). After all four continuous gratings had been viewed in this manner, they were again viewed in the reverse order. A response to a total of 64 flashed gratings was obtained under each continuous grating condition. After a five-minute rest period the procedure was repeated for the other flashed grating and viewing condition. Subjects initiated the train of flashes at the beginning of each condition and could stop them if they needed to blink or rest their eyes.

### Psychophysical Task

Randomly interspersed among the 64 flashed gratings were 64 flashes of diffuse light of equal space-average luminance. The subject's task was to perform a finger-lift reaction time (RT) response to the patterned flashes but not to the diffuse flashes. If the subject didn't respond by 375 msec after the flash, feedback was given in the form of a "click" 25 msec later via a speaker in the ceiling of the subject cubicle. The detectability of the flashed grating, as a function of the intraocular and interocular suppression effects of the continuous grating, was calculated from the subject's "hits" and "false alarms" using signal detection theory. Evoked potentials were not obtained to the diffuse flashes.

### Visual Evoked Potentials

Recording procedures were identical to those of previous studies from this laboratory (Harter, Towle, & Musso, 1976; Harter, Towle, Zakrzewski, & Moyer, 1977). Evoked cortical potentials from the two gratings flashed to the right eye were recorded monopolarly by means of a 9 mm Grass gold-cup scalp electrode placed 2.5 cm above theinion on the midline ( $O_z$ ) referenced to the right earlobe ( $A_2$ ). Electroencephalograms were amplified with a Grass Model 7WC Polygraph with 1/2 amplitude high and low frequency filters set at 35 and 1 Hz respectively. BRS/LVE solid-state equipment was used to randomize the order of the diffuse flash and flashed grating and trigger a Fabritek 1062 signal-averaging computer. EEGs were monitored for movement and other artifacts on an oscilloscope. The subject was situated in an electrically shielded, partially soundproofed cubicle into which a sufficient level of white noise was piped to mask extraneous equipment noises.

### Statistical Analyses

The ANOVA program from the UCLA Biomedical statistical package (BMD-08V) was used to analyze the psychophysical and evoked potential data (Dixon, 1973). A fixed effect 2 x 2 x 4 x 4 repeated measures analysis of variance (flashed gratings x viewing conditions x continuous gratings x replications) with subjects used as a random error term

was chosen as most appropriate for the design used. When a significant effect was found which involved the continuous gratings, a Newman-Keuls multiple range test was used to determine which treatment means were significantly different (Weiner, 1965). The factor analysis program from this package (BMD-08M) was used to obtain the principal factors and factor scores.

## CHAPTER III

## RESULTS

Psychophysical Data

The detectability ( $d'$ ) of the 9V and 36H flashed gratings under each of the four intraocular and interocular suppression conditions was calculated using signal detection theory (Green & Swets, 1966) from the percentage of "hits" and "false alarms." The data were summed across the four replications of each condition before the  $d'$ s were calculated ( $n = 512$ ). The average observer sensitivity for the six subjects combined is shown in Figure 5, all subjects having shown the same general effect. Since the differences between the intraocular and interocular suppression conditions did not approach statistical significance, the data were averaged across these conditions. The 9V flashed grating was harder to detect than the 36H grating ( $F_F(1, 5) = 14.5, p < .025$ ). More importantly, the effects of the continuous suppressing grating reflected a pattern-specific interaction with the flashed gratings ( $F_{FC}(3, 15) = 69.2, p < .01$ ). Newman-Keuls multiple range tests applied separately to the 9V and 36H flashed gratings revealed that when the flashed and continuous (suppressing) gratings were identical in size and orientation, the detectability of the flashed gratings was significantly

lower than under the other suppression conditions (see Figure 5). The implications of this pattern of results in terms of information processing models will be discussed later (see Discussion).

### Visual Evoked Potentials

The X-Y plots of the data from the four replications of each experimental condition were traced onto graph paper in such a way that the average voltage of the first 50 msec of the waveform from each replication was superimposed. All amplitude measurements were made by hand relative to this baseline. The VEPs in Figure 6, which depicts all of the data from two of the six subjects, are representative of the VEP waveform of all subjects. The most consistent and recognizable deflection was a negative peak between 125-195 msec ( $\overline{N150}$ ) which was identifiable in each VEP waveform of all subjects. It was followed by a relatively long duration positive deflection which had either a single peak (MRH, Figure 7), or, more frequently, took the form of a "w-shaped" complex with two positive peaks (see Figure 6). These two positive peaks ranged in latency from 200-250 msec and 280-380 msec for  $\overline{P230}$  and  $\overline{P320}$  respectively. The amplitudes and latencies of these two peaks were measured using 50 msec windows. Since  $\overline{P320}$  was not easily identifiable under all conditions, its window was from 280-380 msec, the exact latency being defined by the

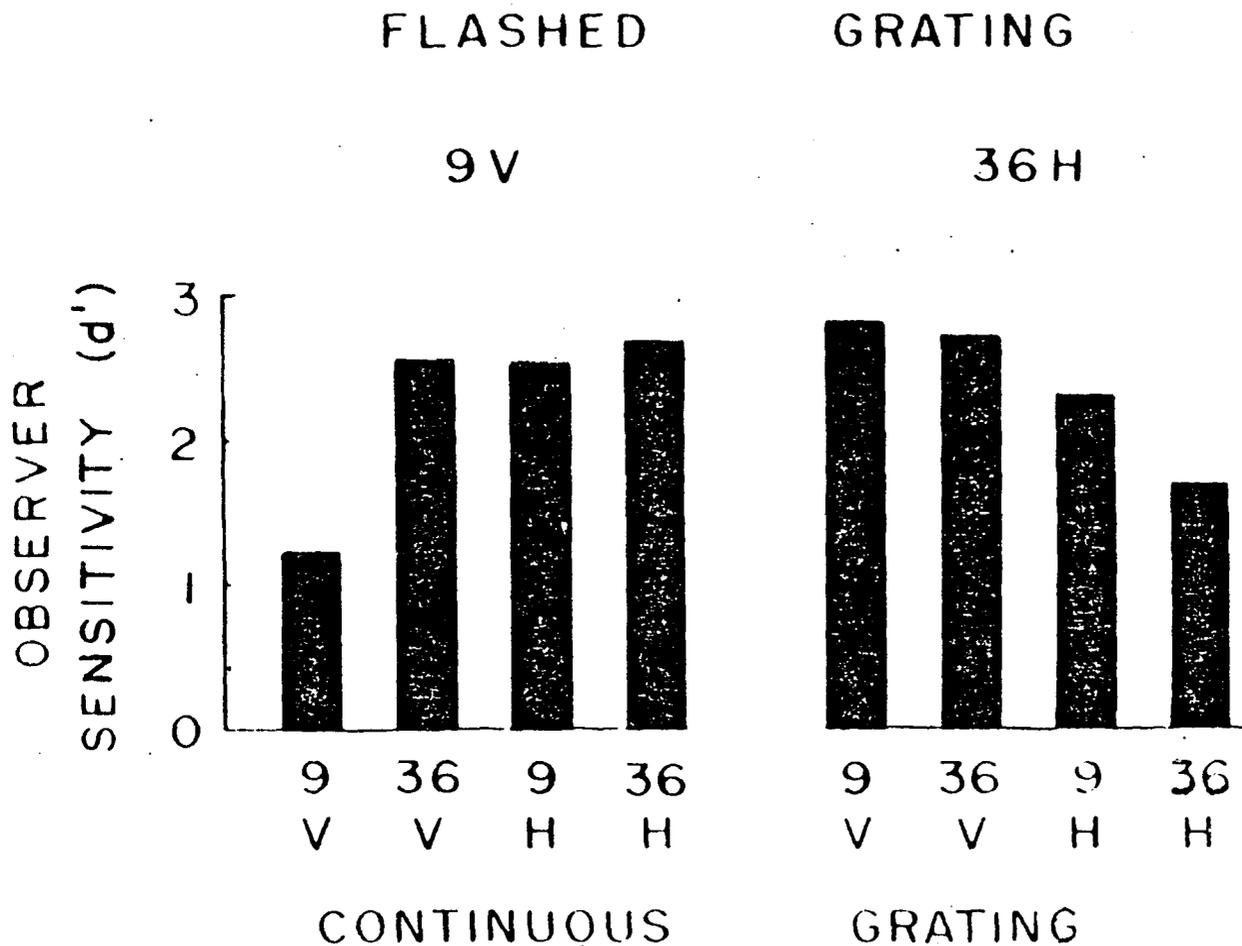


Figure 5. Average observer sensitivity ( $d'$ ) for detecting the flashed grating as a function of continuous gratings. (Nine & 36 refers to bar width of gratings in min of arc and V & H refers to vertical and horizontal grating orientation. Data have been averaged across intraocular and interocular viewing conditions, 4 replications, and 6 subjects ( $n = 3,072$ ).)

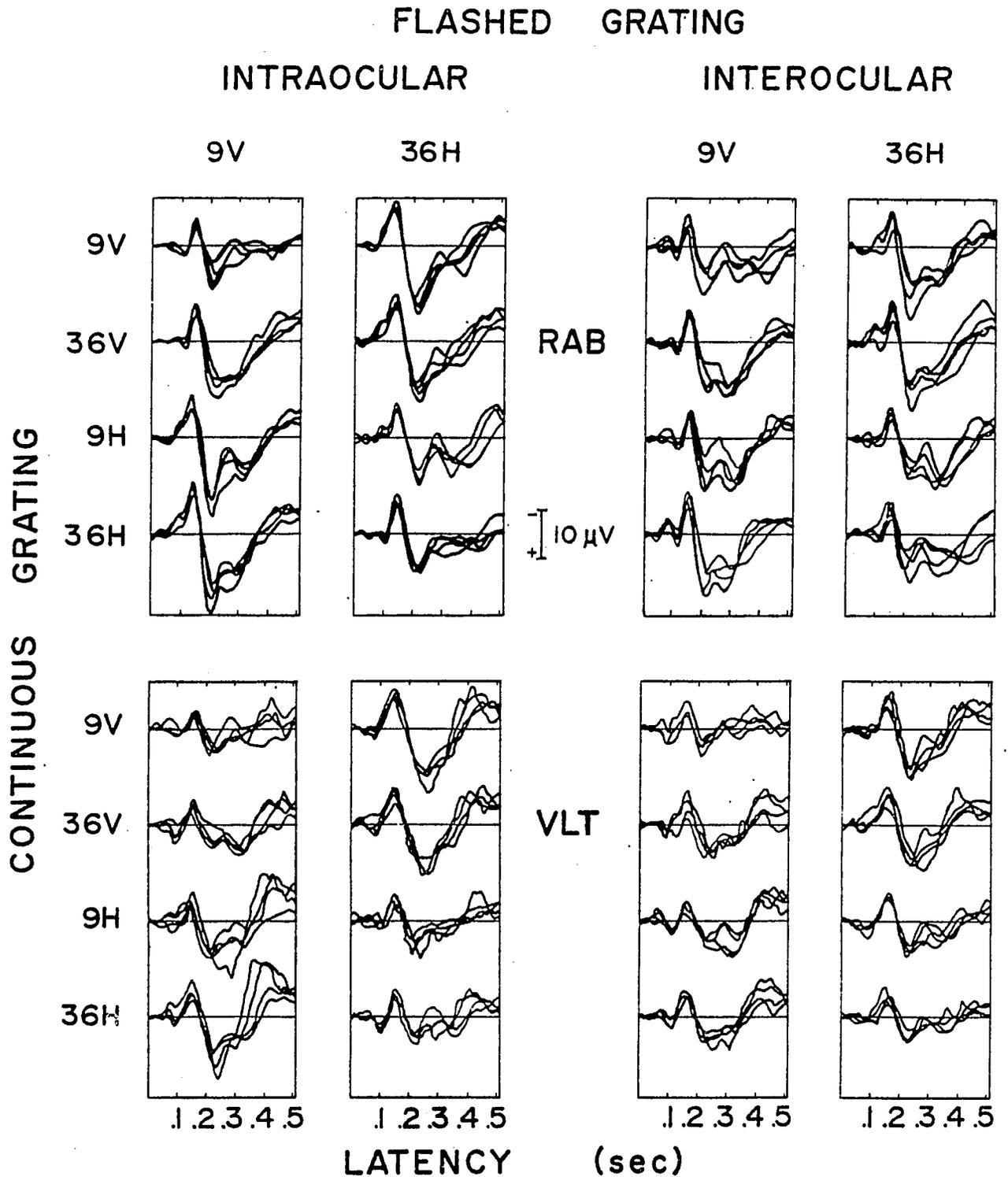


Figure 6. Average evoked potentials from two subjects (RAB & VLT) from flashed gratings as a function of continuous gratings and viewing conditions. ([See Figure 5 for explanation of grating abbreviations.] (n = 64))

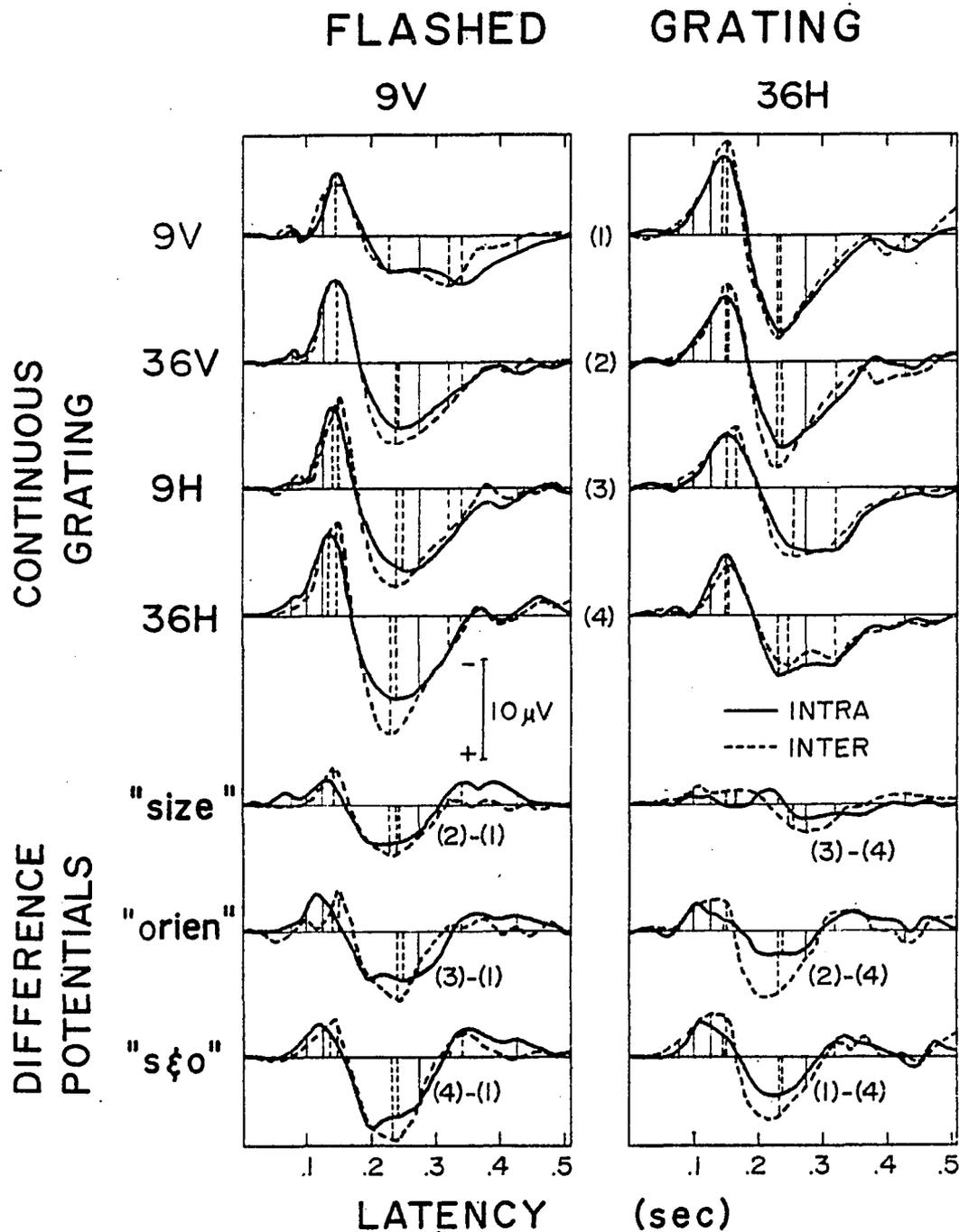


Figure 7. Average VEPs (upper tracings) for each condition and corresponding difference potentials (lower tracings) for subject MRH. (Solid vertical lines indicate latencies at which amplitude measures were taken (75, 100, 125, 275, 425 msec) and dotted vertical lines indicate peaks in raw waveforms (N150, P230, P320). Data have been averaged across four replications ( $n = 256$ ). See Figure 5 for explanation of grating abbreviations.)

greatest amplitude positive peak (negative-to-positive and positive-to-negative deflection) in all the VEPs for each subject.

Since evidence has been offered indicating that the peaks of raw VEP waveforms may not be the most appropriate VEP measure of information processing (Harter & Salmon, 1972; Donchin & Heffley, in press), additional measures were obtained based on the changes in VEP waveform due to the experimental manipulations. A second measurement technique was used in which changes in amplitude at fixed latencies were quantified. The specific latencies were chosen by subtracting the VEPs obtained from one continuous grating condition from those obtained in another condition (Harter & Salmon, 1972). The peaks of the resulting "difference potentials" indicated the points in time at which the VEP waveforms were most affected by changes in the continuous gratings (see Figure 7). Any deviations from a straight line in these difference potentials indicated the effect of changing the size, orientation, or size and orientation of the continuous gratings. These difference potentials reflect "functional components" in the VEP. On the basis of the latency of the peaks in the difference potentials for each subject, and latencies measured in previous experiments (Harter, Conder, & Towle, submitted for publication; Harter, Towle, & Musso, 1976; Harter, Towle, Zakrzewski, & Moyer, 1977), VEP amplitude was measured from

baseline at 75, 100, 125, 275, and 425 msec. Careful inspection of Figure 7 reveals that the points which differ most in amplitude between experimental conditions (peaks in the difference potentials) do not necessarily correspond to peaks in the raw waveforms.

### Principal Component Analysis

In order to determine whether the suppression of VEPs evident in Figures 5 and 6 was reflecting a single underlying process or a number of separate processes, a principal component (factor) analysis of the 11 VEP parameters was performed. This procedure groups variables into orthogonal components on the basis of their covariance. The components generated by this procedure represent independent sources of variation in the data and are one rationale for identifying the different neural processes which underlie the VEP.

The first step in this kind of analysis is to normalize all of the data and create a correlation matrix of the variables. The result of this first step is shown in Table 1, which gives the average amplitude and latency of the 11 measures, along with their standard deviations. The correlation matrix for the 11 parameters is shown in Table 2. A number of characteristics of VEPs in general are evident in this matrix. Points that were close to each other on the waveform and were of the same polarity tended

Table 1  
Means and Standard Deviations of 11 VEP Parameters

VEP Measure	Amplitude (uV)		Latency (msec)	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.
75 msec	.21	1.54	75*	0*
100 msec	-.20	2.20	100*	0*
125 msec	-2.79	2.58	125*	0*
$\overline{N150}$	-7.16	6.12	151	9.25
$\overline{P230}$	6.16	3.76	230	15.49
275 msec	4.24	3.47	275*	0*
$\overline{P320}$	5.10	2.74	320	22.49
425 msec	-1.39	3.78	425*	0*

\*by definition

Table 2  
Correlation Matrix for 11 VEP Parameters\*

		Amplitude							Latency			
		75	100	125	N150	P230	275	P320	425	N150	P230	P320
Amplitude	75	1.00										
	100	.37	1.00									
	125	.19	.69	1.00								
	N150		.44	.53	1.00							
	P230		-.41	-.41	-.35	1.00						
	275		-.29	-.34	-.42	.71	1.00					
	P320				-.39	.42	.71	1.00				
	425			.36	.25	.54	-.32	-.33	-.22	1.00		
Latency	N150			.24	.44		-.17			1.00		
	P230				-.14		.24		-.15	.14	1.00	
	P320			.28	.25	.64	-.54	-.62	-.50	.51		1.00

\*Correlations below .10 are not statistically significant and have been omitted for the sake of clarity.

to be correlated. The amplitudes of the measures at 100 and 125 msec and  $\overline{N150}$  were all positively correlated, as were  $\overline{P230}$ ,  $\overline{P320}$ , and the measure at 275 msec. Interestingly, the amplitude and latency of  $\overline{N150}$  and  $\overline{P230}$  were not significantly correlated, as has been observed previously (Bennett, Macdonald, Drance, & Uenoyama, 1971), but the amplitude and latency of  $\overline{P320}$  was correlated ( $r = -.50$ ). That the processes underlying the two early peaks in the VEP waveform are relatively fixed in time is implied by their small standard deviations relative to that of  $\overline{P320}$ . On the other hand, the processes signified by  $\overline{P320}$ , which has been associated with the time required to make a decision regarding the nature of the stimulus (Kutas, McCarthy, & Donchin, 1977) had a greater standard deviation. Fixed latency measures, therefore, appear more appropriate for the early components, while variable latency measures appear more appropriate for the later components of the evoked potential.

The "grand mean" waveform constructed from the means in Table 1 is shown in Figure 8 (top). The loadings of the eight amplitude measures on the two largest principal components of variation identified by a factor analysis are shown in Figure 8 (bottom). The three principal components (varimax rotation) were respectively associated with (1) the positive portion of the waveform between 200-400 msec, (2) the surface negative shift between 100-125 msec,

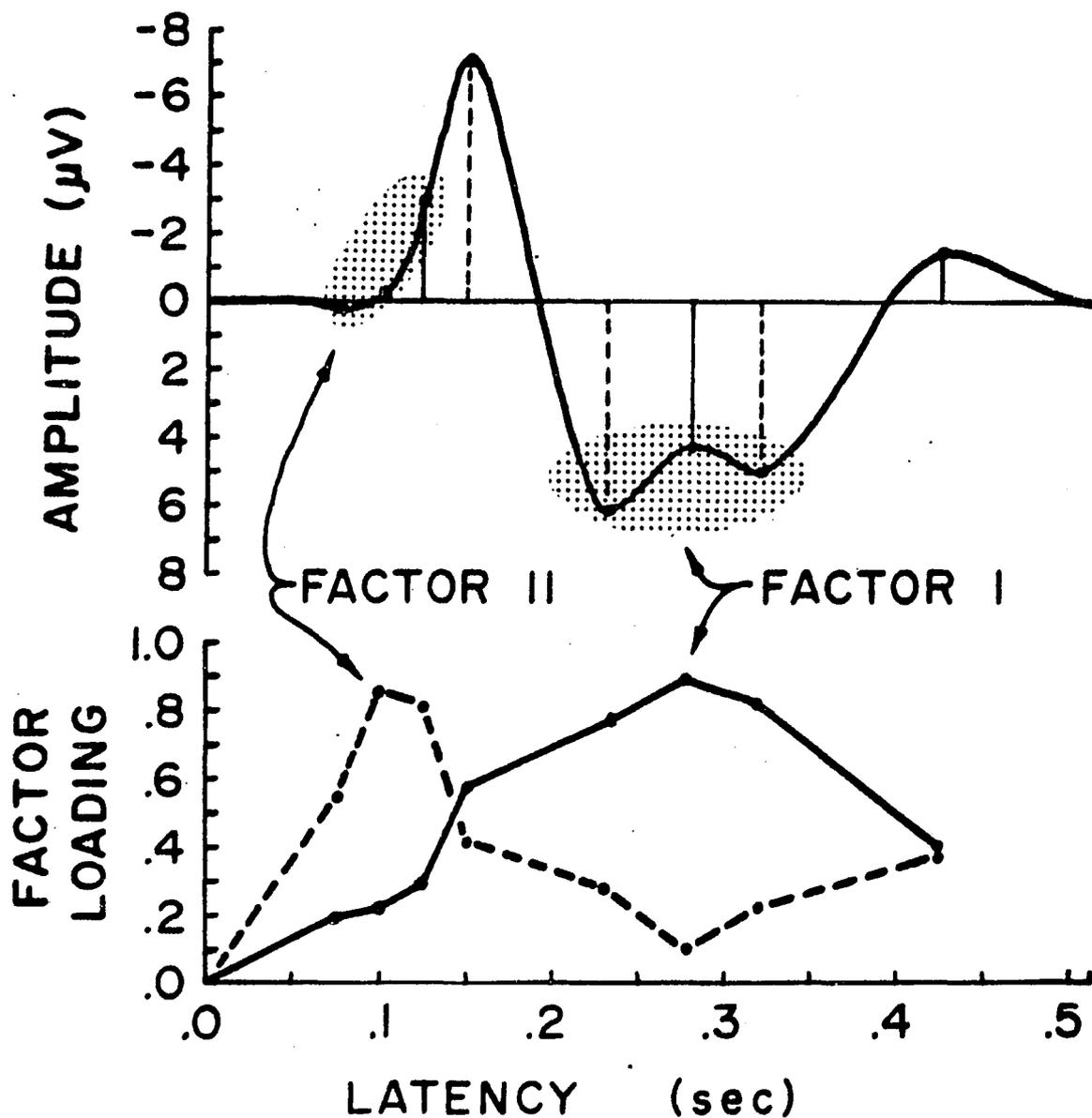


Figure 8. Principal component analysis. ((top) Grand mean waveform was constructed from the average amplitude and latency of the 11 VEP parameters in Table 1 ( $n = 24,576$ ). Shaded areas indicate regions of Factors I and II of principal component analysis. (bottom) Loading of each amplitude measure on Factor I (solid line) and Factor II (dashed line).)

and (3) the latency of the peaks at 150 and 230 msec. These three components are identified by the shaded areas in the grand mean waveform and accounted for 65% of the total variance of the 11 VEP parameters. As will be seen below, measures associated with the same component tended to be correlated and reacted in the same manner to the experimental manipulations. Measures associated with different principal components were poorly correlated and responded in different manners to the experimental manipulations.

The numerical loading of each VEP parameter on each of the three factors is given in Table 3. These loadings were used to compute a "factor score" for each of the 384 observations of each factor. When the factor scores for each condition were submitted to analysis of variance, the experimental manipulations which were associated with each factor were identified. Factor I, which accounted for 36% of the total variance of the 11 VEP parameters, and which loaded most heavily on the late positive portion of the waveform between 200-400 msec, showed a pattern-specific interaction ( $F_{FC}(3, 15) = 34.9, p < .01$ ) similar to that found for  $P\overline{230}$ ,  $P\overline{320}$ , and 275 msec (discussed below). A Newman-Keuls multiple range test revealed, as can be seen in Figure 9, that the condition in which the flashed and continuous patterns were identical in both size and orientation was different from the others.

Table 3  
 Loadings of the 11 VEP Parameters on the Three Factors  
 After Varimax Rotation

Parameter	Factor I	Factor II	Factor III
75 msec	.20	.54	.02
100 msec	-.22	.85	-.04
125 msec	-.30	.81	.11
275 msec	.88	-.10	.04
425 msec	-.40	.38	-.55
<u>N150</u> amp	-.58	.42	-.38
<u>P230</u> amp	.76	-.27	-.19
<u>P320</u> amp	.82	.22	.04
<u>N150</u> latency	-.13	.40	.65
<u>P230</u> latency	.05	.00	.62
<u>P320</u> latency	-.77	.15	-.28

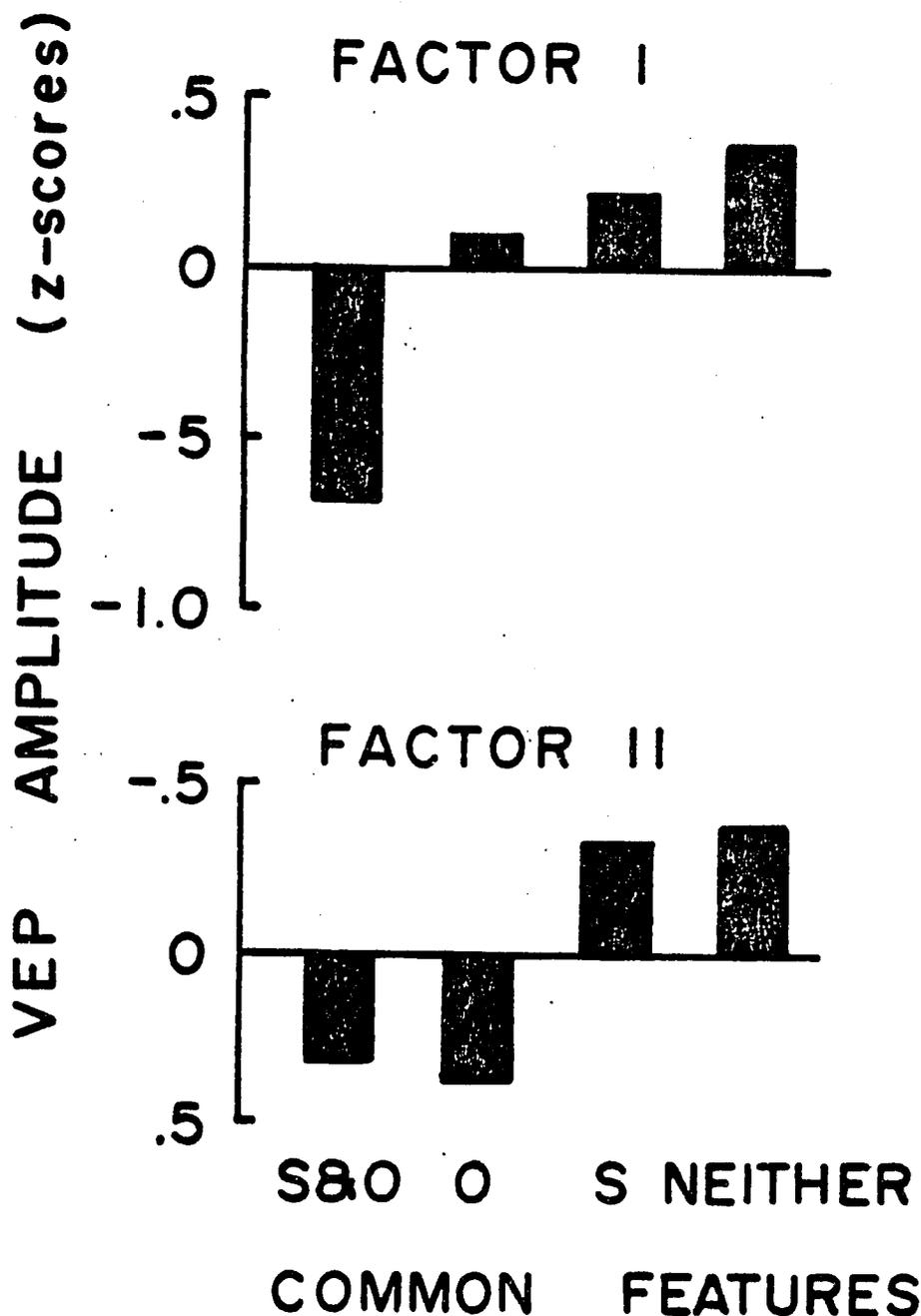


Figure 9. Factor scores. (Average factor scores for Factor I and II as a function of whether the flashed grating had features common to the continuous grating in terms of size (S) and orientation (O). Two different patterns of suppression are observed (see text). Data have been averaged across 2 flashed gratings, 2 viewing conditions, 6 subjects, and 4 replications ( $n = 6144$ ).)

Factor II, on the other hand loaded most heavily on the early amplitude measures (75, 100, 125 msec) and accounted for 16% of the total variance. The significant pattern-specific interaction exhibited by this factor ( $F_{FC}(3, 15) = 4.83, p < .025$ ) differed from that seen for Factor I, in that there was a significant difference when the flashed and continuous gratings shared the same orientation, compared to when they were of different orientations, regardless of size (see Figure 9). As will be seen later, the differences between the interactions for Factor I and II suggest different information processing models.

The third factor identified by the analysis accounted for only 11% of the total variance, only 2% more than the variance due to each measure by itself. The analysis of variance of the factor scores for this factor revealed that it was sensitive to whether the viewing condition was inter- or intraocular ( $F_V(1, 5) = 26.9, p < .01$ ). The latency of N150 and P230 loaded most heavily on this factor (see Table 3).

### Analysis of Pattern-Specific Interactions

Separate ANOVAs performed on each of the 11 VEP measures revealed a number of statistically significant effects due to the relationship between the flashed and continuous gratings, the viewing conditions, and replications (see Table 4). The interaction effects between the

Table 4

Summary of the Significance Levels of the Pattern-Specific Interactions  
of the 11 VEP Parameters (df = 3, 15)

VEP Measure	Interaction Effect							
	Viewing Condition x flashed x continuous		Flashed x continuous		Flashed x continuous (intraocular)		Flashed x continuous (interocular)	
	F	p <	F	p <	F	p <	F	p <
Amplitude								
75 msec	2.20	(ns)	< 1	(ns)	(na)	(na)	(na)	(na)
100 msec	2.65	.05	(na)	(na)	9.19	.01	3.55	.05
125 msec	9.04	.01	(na)	(na)	21.01	.01	1.69	(ns)
<u>N150</u>	3.94	.05	(na)	(na)	3.81	.05	3.02	(ns)
<u>P230</u>	2.48	(ns)	30.51	.01	(na)	(na)	(na)	(na)
275 msec	2.29	(ns)	27.80	.01	(na)	(na)	(na)	(na)
<u>P320</u>	4.58	.025	(na)	(na)	3.53	.05	3.22	(ns)
425 msec	1.10	(ns)	5.18	.025	(na)	(na)	(na)	(na)
Latency								
<u>N150</u>	3.67	.05	(na)	(na)	8.72	.01	1.97	(ns)
<u>P230</u>	1.65	(ns)	1.73	(ns)	(na)	(na)	(na)	(na)
<u>P320</u>	< 1	(ns)	15.02	.01	(na)	(na)	(na)	(na)

flashed and continuous gratings on measures of the VEP at different latencies after the flash will now be described.

Amplitude between 75-150 msec. The 75, 100, and 125 msec amplitude measures and the amplitude of  $\overline{NI50}$  all reacted in a similar manner to the pattern manipulations. These amplitude measures were sensitive to the relative orientation of the flashed and continuous gratings, but not to the relative size of the gratings. Newman-Keuls multiple range tests performed separately on VEPs to the two flashed gratings revealed that when the flashed and continuous gratings were of the same orientation the amplitude of these measures was less negative than when the flashed and continuous gratings were of different orientations (see Figure 10). The relative size of the two gratings had no statistically significant effect on VEP amplitude at these latencies. The effect of relative grating orientation on the VEP was stronger in the intraocular viewing conditions than in the interocular viewing conditions, as can be seen by comparing the changes in amplitude depicted in Figure 10 with their corresponding probability levels shown in Table 4. While none of the effects reached statistical significance for the 75 msec measure, the preceding factor analysis revealed that this measure responded to the experimental manipulations in a similar manner to these other measures. The pattern of suppression reflected by the 75,

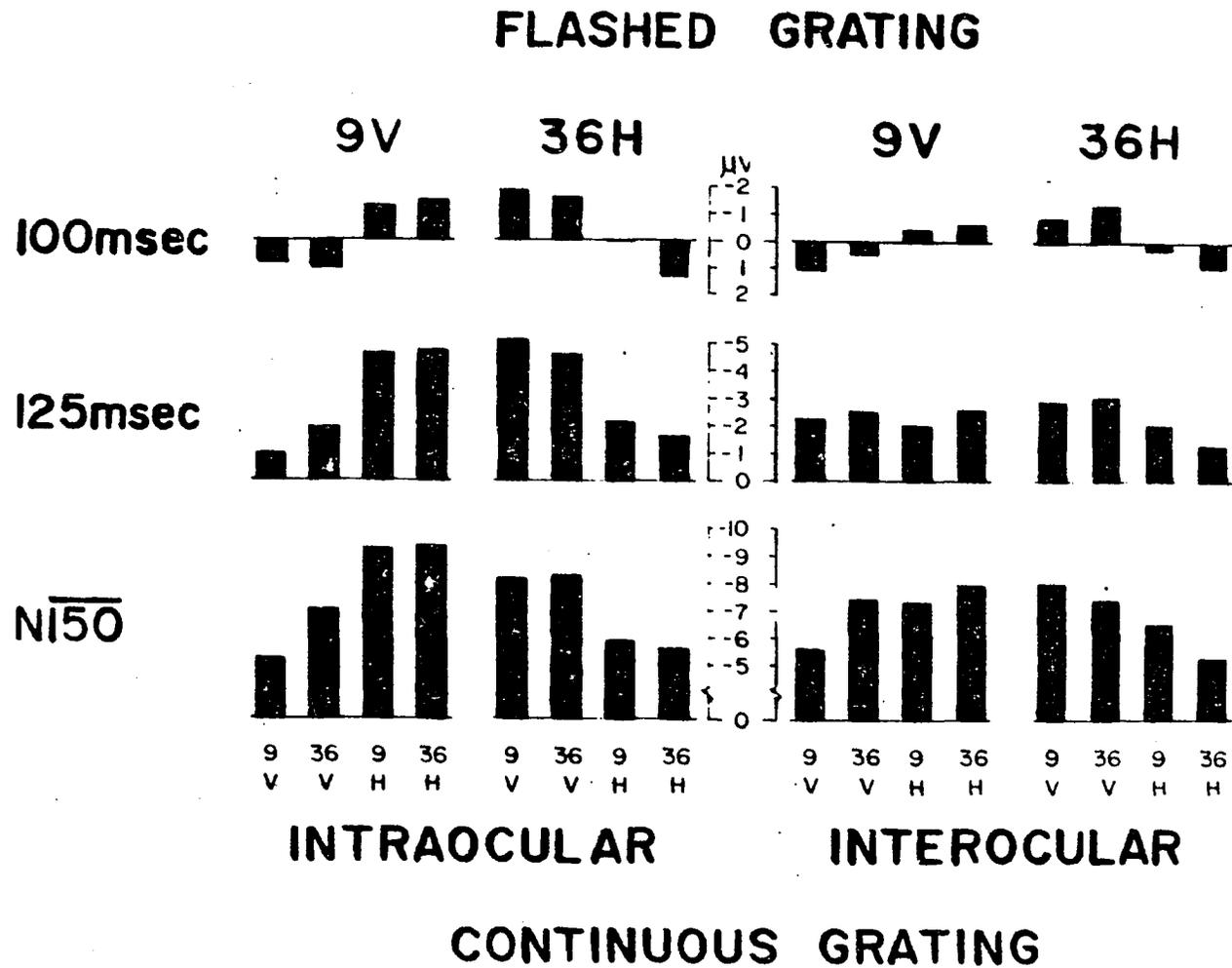


Figure 10. Early VEP measures. (Average VEP amplitude ( $\mu\text{V}$ ) at 100, 125 msec and N150 as a function of flashed grating, continuous grating, and viewing condition. Data have been averaged across 4 replications and 6 subjects ( $n = 1,536$ ). See Figure 5 for explanation of grating abbreviations.)

100, 125, and  $\overline{N150}$  measures is the same as that of Factor II of the principal component analysis (see Figure 9).

P230 amplitude. The large positive peak between 200-250 msec ( $\overline{P230}$ ) showed the largest changes in voltage as a result of changes in the continuous grating as well as reaching the highest level of statistical significance. These changes are seen as large deflections in the difference potentials at about this latency (see Figure 7). The pattern-specific interaction observed for this measure was different than that of the earlier measures in that changing the size, as well as the orientation, of the continuous grating had an effect on VEP amplitude (see Figure 11).  $\overline{P230}$  was smaller (less positive) when the flashed and continuous gratings were the same orientation or the same size. In further contrast to the earlier measures, there were no statistically significant differences in this interaction between the intraocular and interocular viewing conditions.

Amplitude between 275-380 msec. The pattern-specific interactions at 275 msec and for  $\overline{P320}$  were different from those found for the earlier measures. Compared to the other suppressing conditions, the amplitudes of these measures were significantly less positive only when both the size and orientation of the flashed and continuous gratings were the same. Changes in the amplitude of these two measures were most similar to changes in observer sensitivity (see Figure 11) and Factor I (see Figure 9). Separate analyses of the intraocular and interocular viewing conditions

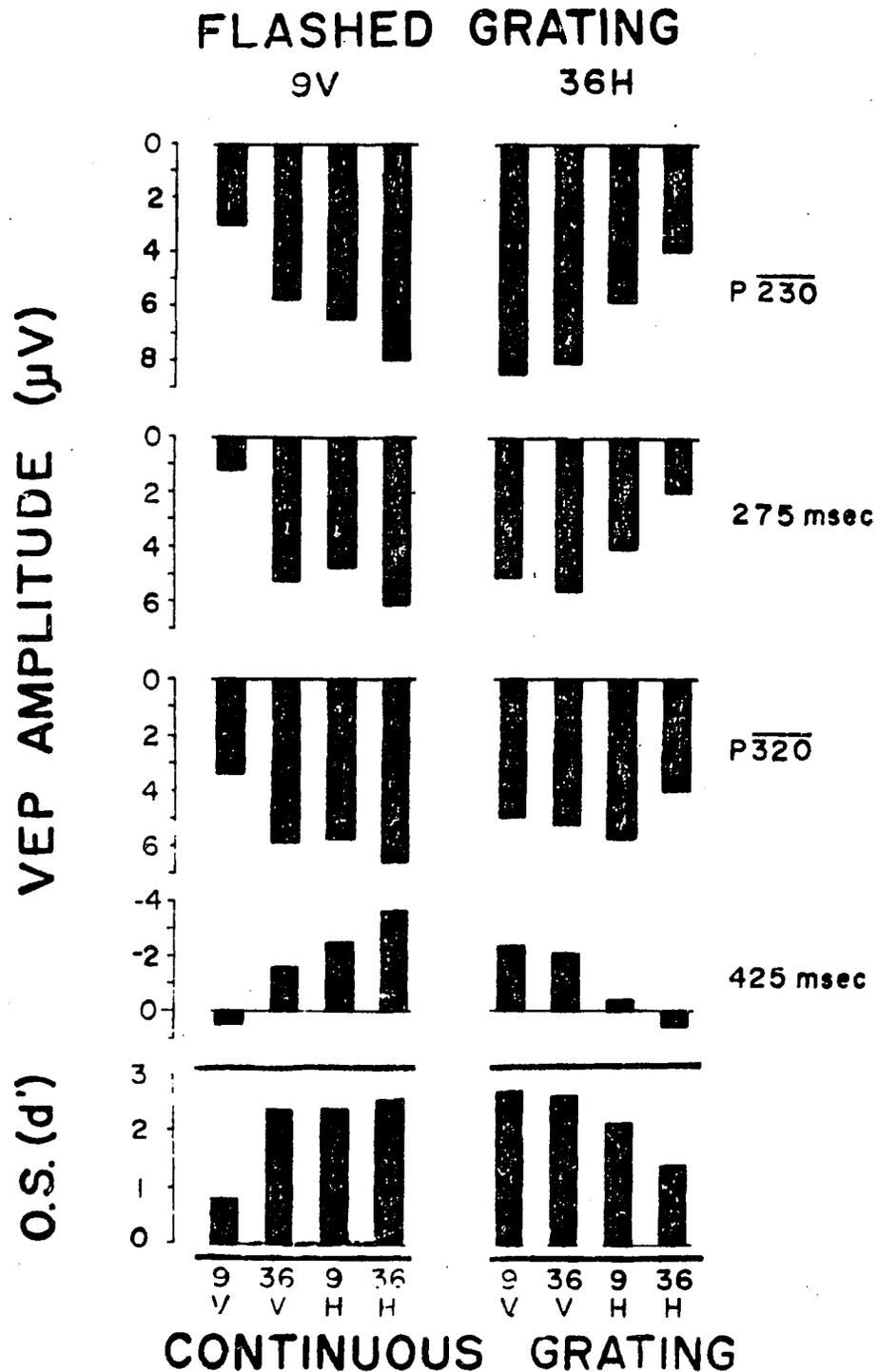


Figure 11. Late VEP measures and observer sensitivity. ((top four rows) Average amplitude ( $\mu\text{V}$ ) of evoked potential waveform at P230, 275 msec, P320, and 425 msec as a function of continuous gratings. (bottom) Average observer sensitivity ( $d'$ ) for detecting flashed gratings as a function of continuous gratings. Data have been averaged across 2 viewing conditions, 4 replications, and 6 subjects ( $n = 3,072$ ). See Figure 5 for explanation of grating abbreviations.)

for  $\overline{P320}$  reached statistical significance for the intraocular viewing condition only (see Table 4).

Amplitude at 425 msec. The amplitude of the VEP at 425 msec showed a pattern-specific interaction that resembled the one observed for  $\overline{P230}$ , but was of the opposite polarity. It became progressively more positive as the flashed and continuous gratings were made the same orientation, size, and then size and orientation, respectively (see Figure 11).

Pattern-specific latency changes. The latency of  $\overline{N150}$  varied as a function of the relationship between the flashed and continuous gratings under the intraocular viewing condition ( $\underline{F}_{FC}(3, 15) = 8.72, p < .01$ ). It peaked significantly later when both the flashed and continuous patterns were 9' vertical gratings as compared to the other suppressing conditions (see Figure 12).  $\overline{P320}$  increased in latency under both viewing conditions when the continuous and flashed gratings were identical ( $\underline{F}_{FC}(3, 15) = 15.02, p < .01$ ).

#### Summary of Changes Over Time

The pattern-specific interactions resulting from changes in the suppressing gratings gradually increased and then decreased in strength as a function of the latency at which VEP amplitude was measured. The F ratios for the five successive fixed-latency measures of VEP amplitude gradually increased until 275 msec and then declined.



Furthermore, the relative contributions of size and orientation effects to the interactions varied differentially over time (see Figure 13). Overall, changing the orientation of the continuous gratings from different to the same as the flashed gratings had a greater suppression effect on VEP amplitude than did the comparable effect due to changing the size of the continuous gratings. Orientation suppression had its maximum effect between 100-125 msec, and then gradually decreased until 320 msec. Changes in the size of the continuous grating were beginning to affect VEP amplitude at 125 msec, but had their strongest effect at 230 msec. At 320 msec only changing both the size and orientation of the continuous grating to match the continuous grating affected VEP amplitude. At 425 msec changes in the size or orientation alone were again observed to influence VEP amplitude (see Figure 13).

#### Additional Findings

The analyses of each VEP parameter also revealed a number of effects that were not due to the relationship between the flashed and continuous gratings.  $\overline{NI50}$  showed a gradual monotonic decrease in latency of 5 msec across the four replications ( $\underline{F}_R(3, 15) = 5.06, p < .025$ ). The latency of  $\overline{NI50}$  also differed under the two viewing conditions. On the average,  $\overline{NI50}$  peaked 3 msec earlier under the intraocular viewing conditions than it did under the interocular viewing conditions ( $\underline{F}_V(1, 5) = 9.29, p < .05$ ).

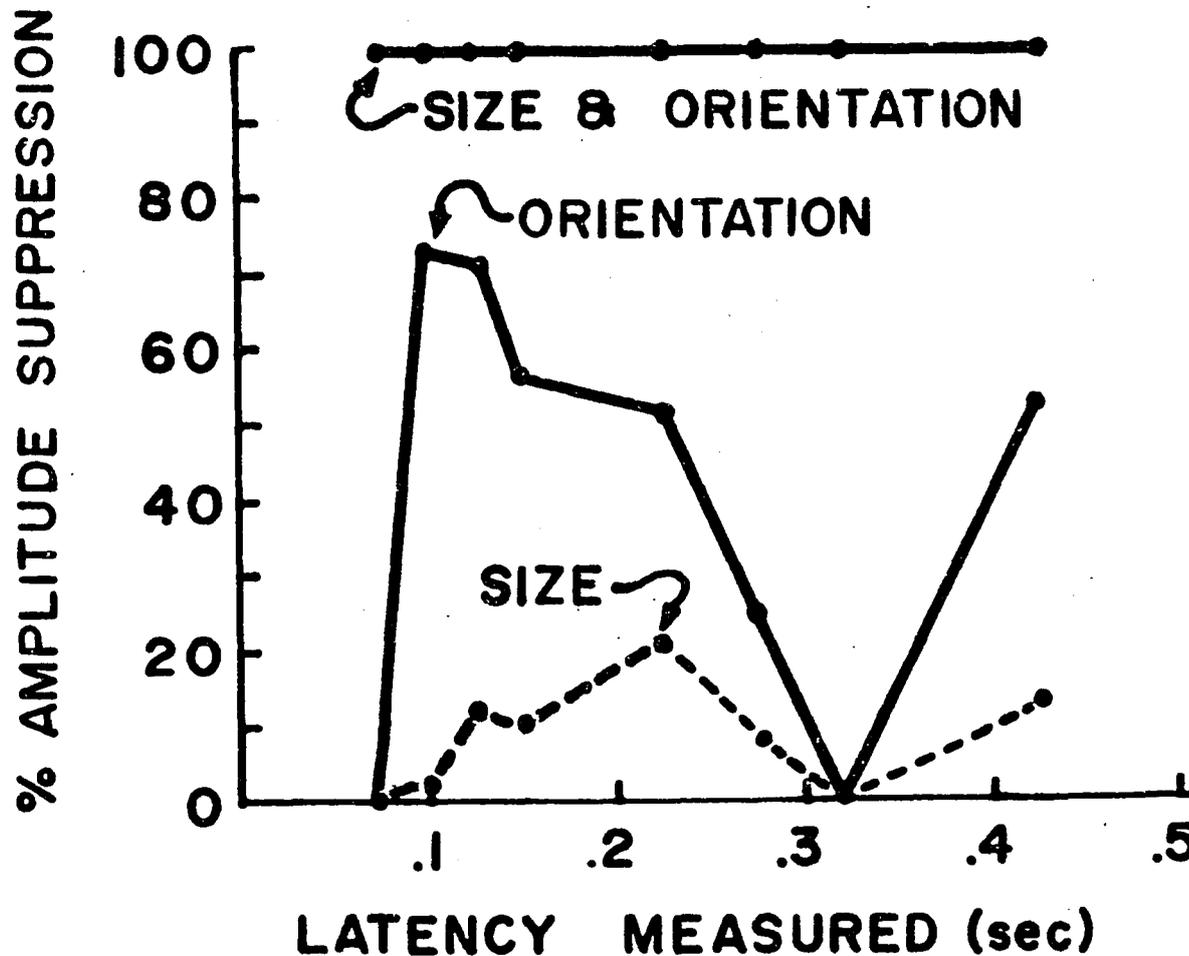


Figure 13. Suppression of VEP due to changes in orientation only (solid line) and size only (dashed line) of continuous gratings as a function of VEP latency. (These points are plotted relative to the suppression due to changes in both the size and orientation of the continuous gratings, which has been scaled to 100%. Each point represents the average across 2 flashed gratings, 6 subjects, and 4 replications (n = 3,072).)

The latency of  $\overline{P230}$  was also shorter in the intraocular viewing conditions, except when the subjects continuously viewed the 9V grating ( $\underline{F}_{VC}(3, 15) = 7.35, p < .01$ ). A similar interaction was found for the amplitude at 275 msec, which tended to be more positive in the interocular viewing conditions, except when the 9V grating was continuously being viewed ( $\underline{F}_{VC}(3, 15) = 7.10, p < .01$ ). There was also an interaction between the flashed grating, continuous grating, viewing condition, and replication at 100 msec ( $\underline{F}_{VFCR}(9, 45) = 2.15, p < .05$ ) and 125 msec ( $\underline{F}_{VFCR}(9, 45) = 4.92, p < .01$ ).

### Summary

In summary, the VEPs in this experiment seem to reflect at least three underlying processes, or components: The largest one (Factor I) was related to the late positive portion of the waveform (230-320 msec) and was sensitive to the condition in which the flashed and continuous gratings were identical. A second component (Factor II) was associated with the early negative portion of the waveform (75-125 msec) and was sensitive to the relative orientation of the gratings. A third component (Factor III) was primarily associated with the latency of the two major peaks in the waveform ( $\overline{N150}$  and  $\overline{P230}$ ) and was sensitive to the viewing condition.

## CHAPTER IV

## DISCUSSION

The data indicate that the monocular evoked potential elicited by flashing a grating to one eye is influenced by the nature of a grating that is being continuously viewed either by the same or opposite eye. In this experiment both the relative size and orientation of the flashed and continuous gratings influenced VEP amplitude. The suppression effects due to the relative size and orientation of the flashed and continuous gratings varied as a function of the latency of the evoked potential at which the effect was measured. These changes in the VEP will be discussed in terms of the possible organization of the neural channels that process size and orientation information in the human visual system.

VEP Suppression

The changes in VEPs observed in this experiment are interpreted as being due to the suppression of information processing in monocular and binocular information channels. When the flashed grating was identical to the continuous grating, the components which have previously been demonstrated to reflect pattern information processing exhibited amplitudes characteristic to those of VEPs elicited by

diffuse flashes. The amplitude at about 100 msec, for example, has been found to be negative in response to flashed patterns and positive in response to diffuse flashes (Harter & White, 1968, 1970; Reitveld, Tordior, Hagenouw, Lubbers, & Spoor, 1967; Towle & Harter, 1977). At about 200 msec the situation is reversed. More positive amplitudes indicate pattern processing and less positive or negative amplitudes at this latency indicate a reduction of pattern in the flash. When the flashed and continuous patterns were different in both size and orientation these two pattern components were not suppressed ( $\overline{N100}$  was negative and  $\overline{P200}$  was positive). When the flashed and continuous patterns were the same size and orientation, however, these two pattern components were suppressed (i.e.,  $\overline{N100}$  was pushed positive and  $\overline{P200}$  was pushed negative).

Further support for the interpretation of these changes in amplitude as indicating suppression of pattern processing is found in psychophysical data. In the present experiment, the detectability of the flashed gratings was poorest when they were identical to the continuous gratings in size and orientation. Also, the negative peak at 150 msec peaked later under these two conditions, a finding which is usually associated with less salient stimuli (Kulikowski, 1977).

Size and Orientation Channels and the VEP

The suppression observed here is interpreted in the same manner as in previous studies where the flashed and continuous gratings were assumed to be processed in either the same size channel (Harter, Towle, & Musso, 1976) or the same orientation channel (Harter, Conder, & Towle, submitted for publication). The reductions in observer sensitivity and the suppression of pattern components of the VEP imply that information processing in binocular information channels was being suppressed. When the visual system was processing the 9V continuous grating and the 9V grating was also flashed, the information from the two eyes was presumably processed by the same binocular neurons, and the response to the relatively weak flash was partially "occluded" or suppressed, because these neurons were already processing the continuous grating. On the other hand, if the two gratings differed in both size and orientation, as when the 36H grating was being continuously viewed and the 9V grating was flashed, the two gratings were processed in different size and orientation channels, and the neurons comprising the 9V channel were free to process the flashed grating. At every latency of the VEP measured (except 75 msec) there was suppression when identical gratings were being processed, relative to when the two gratings differed in both size and orientation. Different results were

obtained at various latencies, however, when the two gratings differed in size or orientation only.

The size-specific suppression obtained in this study was generally similar to that that has been obtained in a previous study by Harter, Towle, and Musso (1976). In that experiment, suppression was first evident between 120 and 160 msec, was greatest at about 160 msec, and then disappeared by 210 msec. In the present data size-specific suppression was first evident between 125-150 msec and was greatest at 230 msec. This 70 msec difference in the latency of the maximum effect might be due to the different stimuli used in the two experiments (checks vs. gratings) or to the fact that the flashed eye was in darkness during the inter-flash interval in the previous study. A more likely explanation is the difference in relative luminance of the flashed and continuous gratings in the two studies. The suppressing checkerboards were 35 mL and the flashed checkerboards were only 1.5 log units above threshold in the previous study, while the suppressing gratings were only 5 mL and the flashed gratings were 2 log units above threshold in this study. The relative luminance of the flashed and continuous patterns has been shown to influence interocular suppression of VEPs in a similar study by Harter, Towle, Zakrzewski, and Moyer (1977). They obtained size-specific suppression for the negative peak between 150-250 msec. Size-specific suppression was indicated

by a reduction in the amplitude of the negative peak in both that experiment and a previous experiment (Harter, Towle, & Musso, 1976). It was not evident until 230 msec in the present experiment, and was expressed by a reduction in the amplitude of a positive, rather than negative, peak in the raw waveforms.

In a study by Harter, Conder, and Towle (submitted for publication) orientation-specific suppression was found to be most prominent at 110 msec and, to a lesser degree, at 200 msec after the flash. This was partially replicated in the present experiment, where the maximum orientation-specific suppression (a positive shift) was found at 100-125 msec. However, the suppression at 230 msec in the present study was of the opposite polarity.

The reason for the differences in suppression for the later measures in the four experiments is probably the nature of the behavioral tasks that were required of the subjects. Harter, Conder, and Towle (submitted for publication) only required their subjects to count the flashes. Harter, Towle, and Musso (1976) and Harter, Towle, Zakrzewski, and Moyer (1977) required their subjects to respond to every flash with a finger-lift response. In the present experiment the subjects were required to make a psychophysical judgment concerning the nature of each flash and give a "go no-go" finger-lift response within 375 msec after the flash. Accordingly, the waveforms in

these experiments were quite different at later latencies. It seems that the effect of the task in the present study was to mask the effects of suppression at later latencies, as compared to the earlier studies.

The factor analysis of all 11 VEP parameters revealed that there were components associated with two kinds of pattern-specific interactions. One, associated with the early measures of VEP amplitude (Factor II), indicated that the relative orientation of the two gratings was the primary feature that determined suppression. If the patterns were processed in the same orientation channel, the VEP to the flashed grating was suppressed, regardless of the relative size of the two gratings. The other component, associated with the later measures of the VEP (Factor I), indicated suppression only when the two gratings were identical. These two types of pattern-specific suppression are predicted by different information-processing models, as discussed below.

#### Information-Processing Models

Channels processing size and orientation information may be organized in a variety of ways. Figure 14 shows four basic models: two involving only parallel processing and two with hierarchical schemes. Different patterns of suppression are predicted from these four models (right portion of Figure 14). In the interest of parsimony it will be assumed here that channels are completely selective to

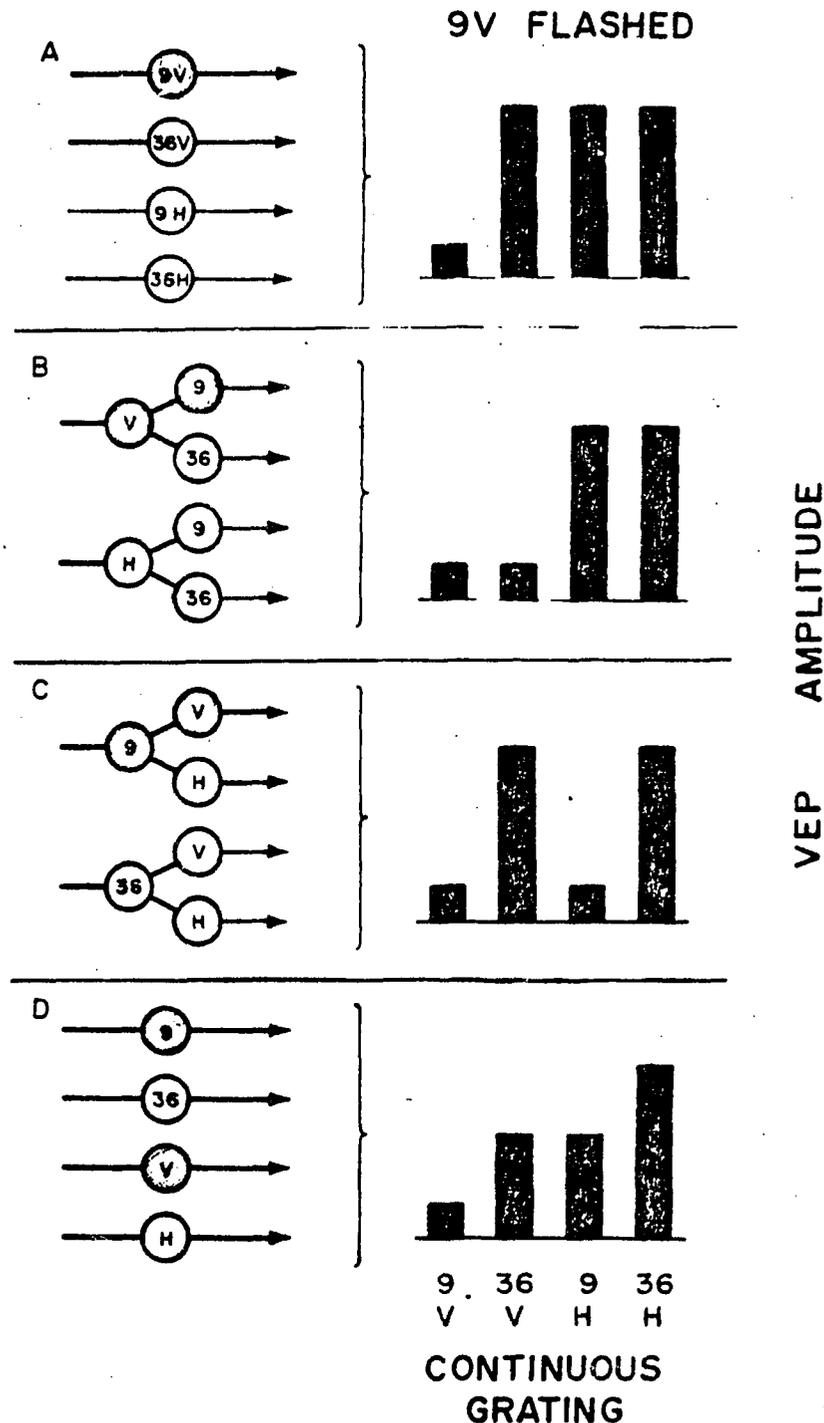


Figure 14. Four models of organization for size and orientation channels (left) and their corresponding predictions of VEP amplitude to a 9' vertical flashed grating (right). (Factor I most closely approximated model A predictions and Factor II most closely approximated model B predictions (cf. Figure 9).)

their feature and that the processing of a continuous grating by a channel completely occludes (100% suppression) processing of a flashed grating by that channel.

Model A in Figure 14 is a completely parallel processing model in which each channel is tuned to a specific size and orientation. Since the channels are completely independent, each channel would process a separate grating in this experiment. This model has many of the characteristics of the template models of pattern recognition described by Neisser (1966). In this scheme of information processing only an identical grating would suppress a flashed grating. This was the pattern of suppression that was observed for Factor I, which was associated with the late positive portion of the VEP (cf. Figure 9). As will be discussed in the next section, interpretations not based on neural channels also predict this pattern of suppression for the late positive portion of the VEP waveform.

Model B (Figure 14) is a hierarchical model in which first the orientation of the grating is encoded and then its size, as has been suggested by Campbell and Maffei (1971). Here, gratings of different sizes would initially be processed in the same channel. The response to a 9V grating, for example, would be suppressed by both a 9V and 36V grating. This pattern of suppression was exhibited by Factor II, which was associated with the early negative portion of the VEP waveform (cf. Figures 8 and 9).

In Model C size channels precede orientation channels. The opposite pattern of suppression would be predicted: continuous gratings of the same size as the flashed grating would be suppressed. This pattern of suppression was not observed in this experiment.

The model of information processing depicted in part D of Figure 14 is a parallel model, but in this case the channels are specific to a single feature, rather than to both features of the gratings. Each grating would be processed through two channels, one processing its size and another processing its orientation. A given orientation channel would process gratings of all sizes and a given size channel would process gratings of all orientations. In this model the response to a flashed grating would be partially suppressed by a continuous grating of the same size or orientation. The pattern of suppression exhibited by  $\overline{P230}$  resembled the pattern predicted by this model when the 9V grating was flashed.

Unfortunately, the strict application of Models B, D, and A to 75-150 msec,  $\overline{P230}$ , and 275-320 msec, respectively leads to some logical inconsistencies unless additional assumptions are made. For example, if size-specific suppression is absent during the first stage of processing--all gratings of the same orientation initially being suppressed--how do their VEPs recover at later stages of processing? Namely, how would the response to a

9V grating recover after it had been suppressed at an early latency by a 36V grating? This could only happen if additional parallel channels which do not contribute to the evoked potential carry the "suppressed" information. A more parsimonious interpretation of the pattern-specific interaction evidenced by the late positive portion of the waveform, and one that does not have to deal with temporary suppression of the evoked potential is that the late portion of the waveform is being influenced by the behavioral task, as described below.

#### P300 and Task Variables

The psychophysical data indicated that the flashed gratings were most difficult to discriminate from diffuse flashes when the flashed and continuous gratings were the same. Similarly, the late VEP measures, especially P320, were smaller in amplitude and peaked later in time in these conditions. This replicates many studies which have found that P300 latency increases with the difficulty of auditory (Adams & Benson, 1973; Ford, Roth, & Kopell, 1976; Ritter, Simpson, & Vaughn, 1972; Squires, Hillyard, & Lindsay, 1973) and visual (Squires, Donchin, Squires, & Grossberg, 1977) discriminations. The increased latency of P300 under these conditions most probably reflects the increased latency of the decision process (Kutas, McCarthy, & Donchin, 1977; Ritter, Simpson, & Vaughn, 1972).

Unfortunately, the latency of the reaction time, usually considered an indication of processing time, was not measured in this experiment. For the reaction time to have occurred before 375 msec, the response in the motor cortex may be assumed to have occurred 80-100 msec earlier (Ritter, Simpson, & Vaughan, 1972). The "decision" to respond, therefore, must have occurred before about 295 msec after the stimulus, at the approximate time of P $\overline{320}$  onset.

The decreased amplitude and increased latency of P $\overline{300}$  obtained under the conditions which were difficult to discriminate also may be due to the increased number of VEPs associated with misses and false alarms that were averaged into the waveform during these conditions. Evidence has been offered that misses and false alarms are associated with decreased amplitude and increased latency of P $\overline{300}$  (Hillyard, Squires, Bauer, & Lindsay, 1971; Parasuramen & Davies, 1975; Squires, Hillyard, & Lindsay, 1973; Squires, Squires, & Hillyard, 1975).

This considerable evidence that indicates P $\overline{300}$  is influenced by errors in decision (misses and false alarms) and the duration of processing time suggests the changes in amplitude and latency of P $\overline{320}$  in the present study may more appropriately be interpreted within the framework of task and cognitive demands than within the framework of sensory information channels.

### Locus of the Experimental Effects

Since pattern-specific suppression was observed in the interocular as well as the intraocular viewing conditions, it is reasonable to conclude that the locus of the suppression is cortical, rather than retinal (Blakemore & Campbell, 1969; Campbell & Maffei, 1971; Gilinsky & Doherty, 1969; Harter, Conder, & Towle, submitted for publication; Harter, Towle, & Musso, 1976; Harter, Towle, Zakrzewski, & Moyer, 1977; Maffei & Fiorentini, 1972; Ware & Mitchell, 1974). The binocular interaction observed in the LGN cells of the cat (Noda, Tamaki, & Iwama, 1972) is not orientation specific, and therefore could not have mediated the suppression observed here. This, along with the evidence that the components of the VEP between 75-160 msec are generated in striate cortex (Jeffreys & Axford, 1972a,b) leads to the conclusion that the suppression observed in this experiment is mediated by binocular size and orientation channels in visual cortex.

About 80% of the simple cells in cat visual cortex are binocular in the sense that they can be driven by either eye (Hubel & Wiesel, 1962). In contrast, only about 12% of the simple cells in monkey visual cortex are binocular (Schiller, Finlay, & Volman, 1976a), the proportion being unknown in humans. The interpretation of the present data does not depend on the existence of cells that are binocular in the Hubel and Wiesel sense (i.e., cells that can be driven

by either eye and therefore fall in ocular dominance categories 2-6). There are many cells which can only be driven by one eye--and are "monocular" in the Hubel and Wiesel sense--but whose response can be modified or inhibited by the nature of the stimulus presented to the opposite eye (Bishop, 1970; Nelson, Kato, & Bishop, 1977). This influence is presumed to be due to indirect, intracortical circuitry, rather than being due to a direct input from the opposite eye, as Hubel and Wiesel have theorized. It is therefore possible to have "monocular neurons" mediating the present suppression of the evoked potential.

There were systematic differences between the intraocular and interocular viewing conditions. The orientation-specific suppression was stronger when the flashed and continuous gratings were presented to the same eye, especially between 100-150 msec. Also,  $N_{150}$  peaked earlier under the intraocular conditions. This difference in latency was most likely related to whether or not the flashed eye was undergoing sustained perceptual suppression when the continuous grating was being viewed by the opposite eye (Spekreijse, van der Tweel, & Regan, 1972). Cobb, Ettlenger, and Morton (1968) also have reported that monocular VEPs were consistently smaller when perceptually suppressed, as compared to when unsuppressed, under conditions of rivalry. If the flashed eye may be assumed

to have been perceptually suppressed between flashes in the interocular viewing condition, the increased latency under the interocular viewing conditions may be the result of sustained inhibition generated by the continuous pattern presented to the opposite eye.

If, as is the case with other sensory qualities, such as color (DeValois, 1965), the nervous system encodes a parameter by making a comparison of the activity in different channels (Erickson, 1968), the finding that orientation-specific suppression precedes size-specific suppression in time may be the result of the functional organization of size and orientation channels in cortex. If the model proposed by Maffei and Fiorentini (1977) (see Figure 1) is interpreted in terms of channels, and the same organization exists in man, an interesting possibility arises. Since LGN afferents in the cat are known to synapse almost exclusively in layer IV neurons in striate cortex, visual information may initially arrive in many orientation channels but in only one size channel. Activity may then spread to the cells in other layers of cortex (and other size channels). Theoretically, this type of organization would enable comparisons between orientation channels before size channels.

#### VEP Measurement Techniques

Two kinds of amplitude measures were employed in the analysis: fixed-latency functional measures and

variable-latency peak amplitude measures. Many quantification techniques have been used to describe transient evoked potential data, including peak-to-peak (Buchsbaum, 1970), prestimulus baseline-to-waveform (Towle & Harter, 1977), average voltage-to-waveform (Donchin & Heffley, in press), area-under-the-curve (Squires, Hillyard, & Lindsay, 1973), and even the total excursion of the waveform (Dustman & Beck, 1969) measures. The proliferation of VEP measurement techniques (each with its own theoretical assumptions) is due, in part, to our lack of a basic understanding of the underlying generators which create VEP waveforms (Schlag, 1973) and the variable relationship observed between the excitability of single cells and simultaneously recorded field potentials (Elul, 1972; Fox & Norman, 1968). Most researchers believe that VEPs are "signs" of neural processing, but are not the actual "codes" used by the nervous system (Uttal, 1966). This viewpoint has been adopted here. The average waveform is thought to be the algebraic summation of many generators, following the principles of volume conduction theory (Brazier, 1949). The VEP waveform is therefore not viewed here as a unitary phenomenon, and measures which treat it as such are bound to confound or miss its more subtle changes. The use of multiple, independent measures, in conjunction with statistical, functional, and topographical methods for isolating the various components in VEP

waveforms, has resulted in considerable progress toward restricting the time course and locus of processes underlying pattern effects in VEPs.

### Unresolved Issues

One of the issues left unresolved by this experiment is the extent to which the early and late latencies of the evoked potential reflect stimulus or task manipulations. Clearly, the factor analysis of the data demonstrated two patterns of suppression which differentiated the early and late components of the VEP. If there had not been a psychophysical task in the present experiment, size and orientation suppression in the later measures would probably have been more similar to the suppression observed in the earlier studies (Harter, Conder, & Towle, submitted for publication; Harter, Towle, & Musso, 1976; Harter, Towle, Zakrzewski, & Moyer, 1977). Most likely, the pattern of suppression associated with Factor I would not have been so predominant if the subjects had passively observed the stimuli. The interactions between components related to stimulus and task manipulations (Harter & Previc, in preparation) could be better understood if a follow-up study were conducted comparing one group of subjects which made a difficult psychophysical judgment about the VEP eliciting stimuli with another group that did not. The use of electrodes over the vertex, and perhaps over motor cortex would enable a comparison with other studies more directly concerned with cognitive variables.

A second issue which merits further investigation is the differential effects of adaptation on VEP and psychophysical measures of pattern sensitivity reported by Mecacci and Spinelli (1976). They found that after a prolonged adaptation to a high contrast grating their steady-state VEPs recovered in amplitude after only a few minutes, but that the subject's contrast sensitivity thresholds remained elevated for a much longer period of time. They suggested that these two measures of systemic sensitivity were probably mediated by different neural processes.

There are also differences between simultaneous (masking) and successive (adaptation) induction techniques which are not yet understood. Adaptation to gratings has been shown to result in both contrast threshold increases and orientation aftereffects by Gilinski and Mayo (1971). Similarly, both threshold increases and spatial frequency aftereffects have been reported as a result of adaptation by Klein, Stromeyer, and Ganz (1974). The latter authors reported, however, that simultaneous induction caused spatial frequency aftereffects but did not cause corresponding increases in psychophysical thresholds. They concluded that these two phenomena were mediated by different neural mechanisms.

### Conclusion

Monocular visual evoked potential and psychophysical responses to flashed gratings were recorded as a function of their relative size and orientation, compared to continuous gratings viewed by either the flashed or nonflashed eye. The psychophysical responses indicated that identical gratings were more difficult to detect. The visual evoked potential, on the other hand, which has the advantage of reflecting the temporal sequence of neural events which lead up to the psychophysical response, indicated that first the orientation and then the size of the flashed gratings was encoded, and only after both features of the gratings had been identified by the nervous system was the psychophysical response initiated.

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