SEPARATION OF COMPONENTS OF THE PATTERN VER USING COMPLEX VISUAL TEXTURES

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SUMMARY

Modulation of a patterned stimulus elicits a visual evoked response (VER) that reflects the combined activity of many neural mechanisms. Underlying mechanisms with qualitatively different spatial features may have indistinguishable responses to the highly symmetric reversing checkerboard stimulus. However, additional information about the spatial organization of mechanisms contributing to the VER can be obtained by using stimuli with a more complex spatial structure. For example, stimuli based on alternation between pairs of stochastic black and white textures may be constructed in which luminance, contrast, and higher-order local structure can vary independently. To explain the dependence of the measured VER on the parameters of the stimulus, it is necessary to postulate two qualitatively different mechanisms. One mechanism appears to be sensitive only to contrast changes across individual edges. A second mechanism must rely on a more complex local process, in which edge-edge interactions are important, and must be of formal nonlinear order at least four.

INTRODUCTION

The VER is a readily-accessible signature of the electrophysiologic events underlying visual processing. It provides a research tool for the analysis of normal function of the visual pathways (5), (19) and a clinical tool for the detection of its pathology (2), (18). Although the VER is easy to record, a detailed physiological interpretation is difficult, because the VER represents the combined activity of many levels and parallel paths of neural processing. This paper will discuss a novel technique for isolating components of the VER that reflect complex spatial interactions.

It has been well-appreciated (7) that VERs elicited by patterned stimuli such as shifting checkerboards are more uniform in the normal population and have clearer changes in pathological states compared to flash VERs (1). This phenomenon likely reflects the fact that the flash VER has many components, some of which must be related to nonspecific arousal and others distorted by saturation effects (12). The pattern-shift VER, however, does not overdrive the retina with large luminance changes, but instead provides stimuli (spatial and temporal contrast changes) to which retinal and cortical neurons are tuned. Nevertheless, the checkerboard stimulus itself must drive multiple neural mechanisms at several stages of processing, and the pattern-shift VER therefore must contain many components (6), (14).

One approach to separating VER components relies on resolving sequential positive and negative waves in a transient response, or gross anatomical separation of the sources of these potentials (8) (9), (10). Although the qualitative conclusions may be valid, rigorous analysis of this kind is difficult because of the necessity to make assumptions about the geometry of the VER generators and the complex passive electrical properties of the head (17), (23). Individual variations in sulcal pattern and slight changes in electrode placement can significantly alter the relative sizes of the surface indicators of intracranial potentials; this may lead to significant differences in the conclusions drawn (13).

A related but distinct approach correlates direct microelectrode recording of brain activity with surface-recorded evoked potentials (3), (4). Animal studies using a vertical array of microelectrodes and current source density analysis (16), (23) have yielded insight into the laminar origin of components of the VER. However, the opportunity of direct application of this technique to man is limited.

Alternatively, one can use manipulation of the visual pattern as the primary tool for studying components of the VER. Spekreijse and coworkers (20) used dichoptic presentation of a checkboard stimulus to show that some contrast VER components are generated after binocular interaction, and therefore must be due to intracortical processing. Tyler and coworkers (21), (22) have used the complex spatiotemporal tuning of the VER to deduce evidence for parallel visual processing within small areas of cortex. Zemon and Ratliff (25) have isolated short-range lateral interactions using radially-symmetric patterns (see also this Workshop).

The present approach makes use of novel visual patterns to resolve two main components of the contrast VER. One component depends on complex spatial interactions (of formal order at least four); the second component appears to depend on local contrast changes across contours. The procedure will be described in intuitive terms initially;

then the comments necessary for rigor will be added.

VISUAL STIMULI

The standard checkerboard stimulus can be thought of as containing three kinds of local features: square regions, edges, and corners. In a contrast-reversal stimulus, all of these features are modulated in synchrony, and hence responses from mechanisms that they drive will be superimposed in time and will all generate even harmonics. However, by constructing variations on the checkerboard stimulus, responses driven by these features can be separated.

The new stimuli are adapted from a texture pair initially introduced to study the psychophysics of pattern perception (11). The basic stimulus consists of alternation between an "even" and an "odd" configuration (see Figure 1). To construct the "even" configuration, choose the intensities of the squares in the first row and first column of a lattice from two levels equally-spaced above and below the mean ("light" and "dark"). Then, color the interior of the pattern so that every 2 x 2 block of squares contains an even number of light and dark squares. The "odd" configuration is constructed from the same first row and column, but every interior 2 x 2 block contains an odd number of light and dark squares. The two configurations are always of opposite luminance in the 1/4 of the squares that lie at the intersection of alternate rows and alternate columns; this will be called the "dynamic" region of the stimulus. The two configurations always have the same luminance in the remaining 3/4 of the squares; this will be called the "static" region.

Stimulus A consists of periodic interchange of these two configurations, by sinusoidal modulation of the luminance of the dynamic region about the mean. Thus, only 1/4 of the checks are modulated, and half of these are changing from light to dark while the other half are changing from dark to light. The other stimuli are simple modifications of Stimulus A. Stimulus B is formed by replacing the "static" region of stimulus A by unmodulated light at the mean luminance. Stimulus C has two varieties: C_+ is formed by replacing the static region of Stimulus A by unmodulated light at an intensity matching that of the light squares, and C_- is formed by replacing the static region by unmodulated light at the intensity of the dark squares.

Although the physical variations between these stimuli are minor (the modulated component is the same in all cases), the stimuli have important differences in their symmetries and statistical properties that enable an analysis of VER components. Figure 2 shows small patches of the stimuli that a hypothetical square region of the visual system might be exposed to.

Consider first a region that receives input from only one square of the stimulus. Three-quarters of such regions receive no modulated input. The other 1/4 are evenly-divided into patches which are light in the even phase and dark in the odd phase, or vice-versa. Consider a mechanism which sums light linearly over such a patch (including perhaps center-surround combination), whose output may be subjected to an arbitrary nonlinearity. Because of the above symmetries, such a mechanism can produce only even-harmonic responses to any of the stimuli A, B, or C, and the responses in all three cases must be identical.

Consider next a mechanism which receives input from both sides of an edge. Although only one-quarter of the squares of the stimulus are modulated, modulation occurs in squares adjacent to half of the edges. As shown in the second column of Figure 2, the possible inputs to this mechanism are again identical in the two configurations of any of the stimuli, so again, only even-harmonic responses can be generated. However, symmetry no longer requires that the even-harmonic response will be the same for all three stimuli.
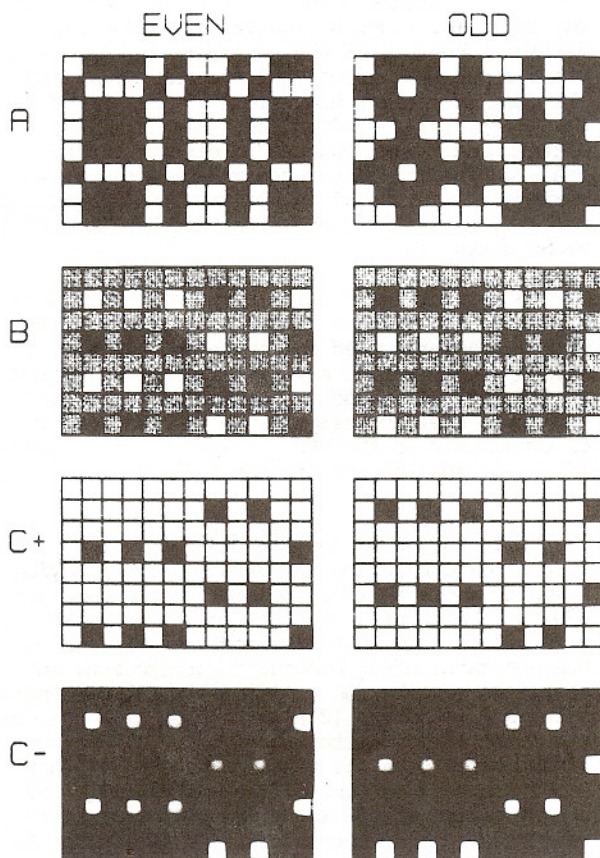

Figure 1: A diagram of the two configurations of the visual stimuli. Stippled squares are at the mean luminance, empty squares are at a higher luminance, and solid squares are at a lower luminance.

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Finally, consider a mechanism situated to receive input from the four corners about a lattice point. Each lattice point is adjacent to exactly one modulated square. The set of possible inputs that this mechanism is exposed to is different in the two configurations of Stimulus A: in the even configuration, only edges and 2 x 2 patches of checkerboards appear; in the odd configuration, only corners appear. Thus, a mechanism with input from all four squares about a point is able to produce asymmetric responses (odd harmonics) to the two configurations of Stimulus A. However, symmetry requires that only even-harmonic responses to Stimuli B and C can be produced.

NOTE

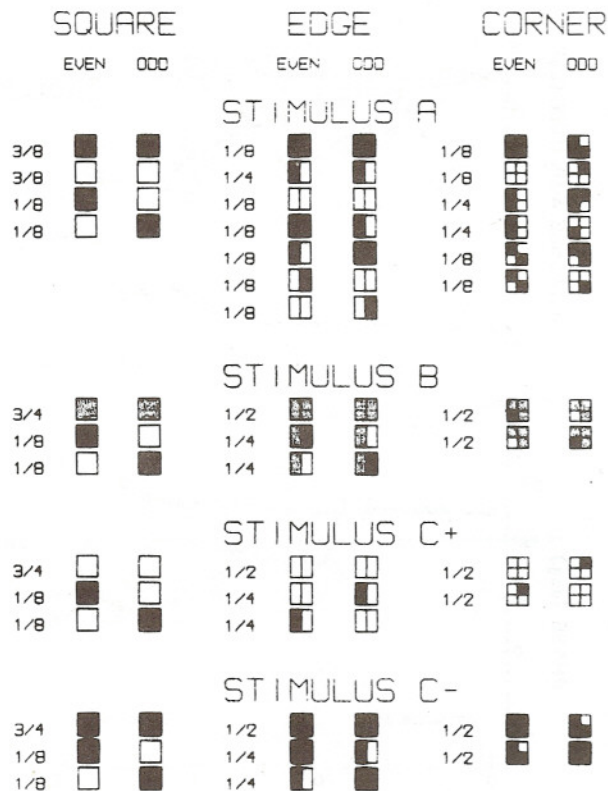Rigorously, these visual stimuli must be regarded as ensembles from which particular instances may be drawn. Care must be taken (e.g., through the use of shift register sequences, as is done in the present study) to ensure that the properties of the ensemble are typified by the example of the stimulus used. With this caveat, the two configurations of any of the stimuli have identical power spectra and third-order correlations. Even and odd configurations of Stimuli B and C are statistically indistinguishable. Thus, higher-order correlations of Stimuli B and C are also identical in the two configurations. However, fourth-order correlations of the two configurations of Stimulus A are different, as shown in Figure 1. Thus, any odd-harmonic response to Stimulus A reflects the contribution of nonlinear mechanism of order at least four. Mechanisms which sum light linearly from four or more checks and then perform a nonlinear transformation which contains fourth-order components (such as rectification) may in principle contribute, but calculations show that the contribution of this kind of mechanism is small. Thus, linear lateral interactions and nonlinear interactions of the kind seen in retinal Y cells (24) essentially contribute only to the even-harmonic responses.

Thus, odd-harmonic responses to Stimulus A should isolate complex lateral interactions that are likely to be cortical. The absence of odd harmonic responses to Stimuli B and C serve as a check mechanism on the statistical properties of the stimulus. Simpler mechanisms will be manifest as even-harmonic responses to all three stimuli; if the even-harmonic responses differ from stimulus to stimulus, then at least pairwise lateral interactions must be involved.

RESULTS

In these studies, the stimuli were displayed on a CRT with a mean luminance of 154 cd/m^2 and a maximum contrast of 0.3. The stimulus formed an 8.8 deg x 8.8 deg region at a distance of 57 cm. Typically, the stimuli were realized on a 64 x 64 lattice, so that each check was approximately 8 min x 8 min. The amplified potential $C_z - O_z$ was averaged for 1 min; in the figures shown, upward deflection indicates negativity at O_z. The stimulus was viewed binocularly. The computer-based controller that generates the patterns has been described previously (15).

An example of the response to Stimulus A with modulation at 6.3 Hz is shown in Figure 3. As is typically the case, both a fundamental and a second-harmonic component are visible, with smaller amounts of higher even harmonics. Stimulus B, under the same conditions, yields no odd harmonics. This control indicates that the odd-harmonic response to stimulus A truly represents lateral interactions between the static and dynamic regions, and not just deviations of the dynamic region from its statistical ideal. Furthermore, the amplitude and the phase of the second-harmonic response is very

Figure 2: Analysis of the structures that may occur in equal-sized square patches in each of the three stimulus types.

different in the two conditions. This implies that a lateral interaction also underlies the second-harmonic response, since responses derived from the luminance of the modulated squares alone would be identical in the two conditions.

The first- and second-harmonic responses have different dependences on the contrast of the static region. In Figure 4, the amplitude and the phase of these two components are plotted as a function of the contrast of the static region. (A static contrast of 0 is Stimulus B; a static contrast of 0.3 is Stimulus A; intermediate static contrasts produce intermediate stimuli.) The first-harmonic response has a threshold contrast of about 0.12 for the static region; its phase is constant provided that the response is reliably detectable.

As static ("background") contrast increases, the second harmonic amplitude steadily decreases, and its phase gradually advances. (For

second-harmonic responses, the phase convention is that a phase shift of zero means no delay relative to a square-law device.)

The dependence of the second harmonic on background contrast is further elucidated by plotting amplitude and phase simultaneously in polar form (Figure 5). As the contrast of the background increases, the response vector moves almost in a straight line, in a direction nearly opposite to the response with the background at zero contrast (Stimulus B). In some subjects, this results in a response amplitude that declines steadily as contrast increases (Figure 5A). In other subjects (e.g., Figure 5B), the size of the background-dependent contribution eventually exceeds the size of the background-dependent contribution. This results in second-harmonic responses that are large for Stimuli A and C, but of differing phases. In these subjects the second harmonic has a minimum amplitude for a stimulus with intermediate background contrast.
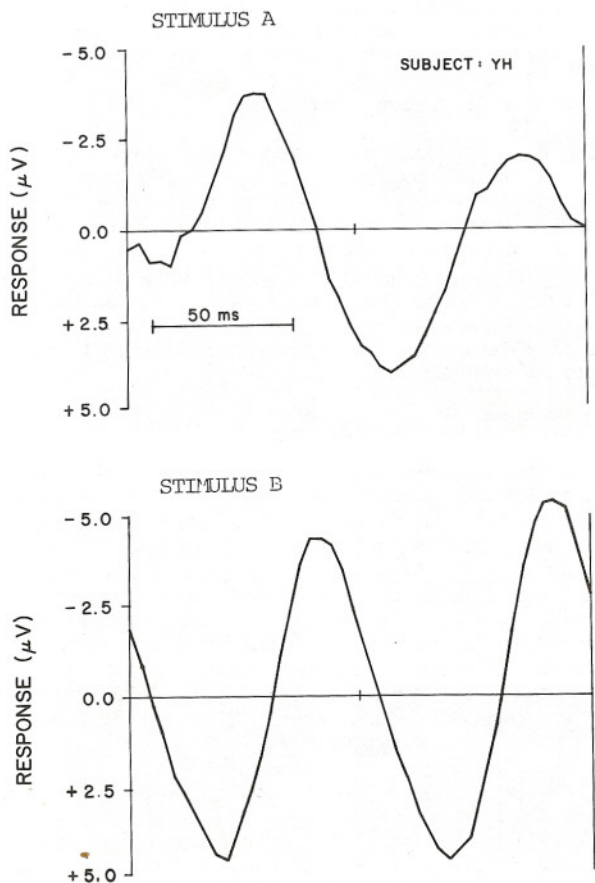

Figure 3: VER elicited by sinusoidal alternation between the two configurations of Stimulus A and Stimulus B.
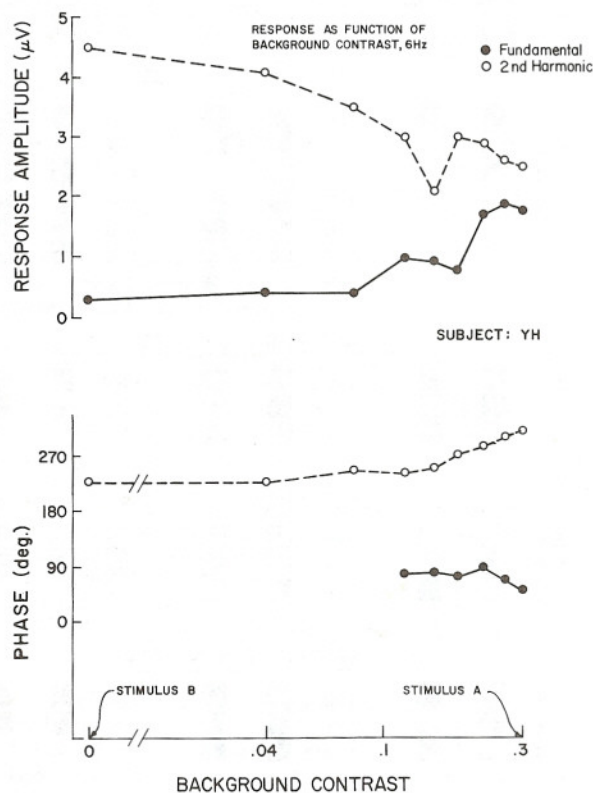
Figure 4: Dependence of the amplitude and phase of the first- and second-harmonic responses on the contrast of the static region. The abscissa scale is logarithmic.

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Thus, the second-harmonic response may be resolved into two parts: a component which is independent of the contrast of the static region, and a component at almost opposite phase which reflects an interaction of static and dynamic regions and increases in size as the contrast of the static region increases. The first component, which depends only on the dynamic region, may well be derived from a locally-generated luminance signal. The interaction component has dynamical properties which resemble the "second-harmonic suppression" component described by Zemon and Ratliff (25).

The C-type stimuli were used to analyze the lateral interactions which generate the second-harmonic responses. The contrast of the modulated region is again kept at 0.3, but the static region is either uniform (as in Stimuli B and C) or patterned (as in Stimulus A). A priori, the second-harmonic will have different behaviors in the C-type and the A-type stimuli, since the number of edges of each kind that are present will in general be different. However, the surprising result (Figure 6) is that these second-harmonic responses are nearly identical in the C and A stimuli, and differ substantially from the second-harmonic response to the B stimulus. This suggests that the lateral interactions which drive the second harmonic depend only on the size of the contrast step across contours (which is the same in A and C), and not on excursions from the mean (which is the same in A and B).

CONCLUSION

These experiments have separated, and begun to analyze, two kinds of lateral interactions which contribute to contrast-driven evoked responses. One interaction is a complex nonlinear mechanism which requires interaction of at least four parts of the stimulus, generating the odd-harmonic response unique to Stimulus A. The other interaction is a relatively simpler mechanism that depends only on contrast differences across edges. This mechanism generates a similar second-harmonic response in Stimuli A and C which is distinct from the second-harmonic generated in Stimulus B. It is hoped that this isolation of complex visual interactions will prove useful in studying normal function and pathophysiology of central visual processing.
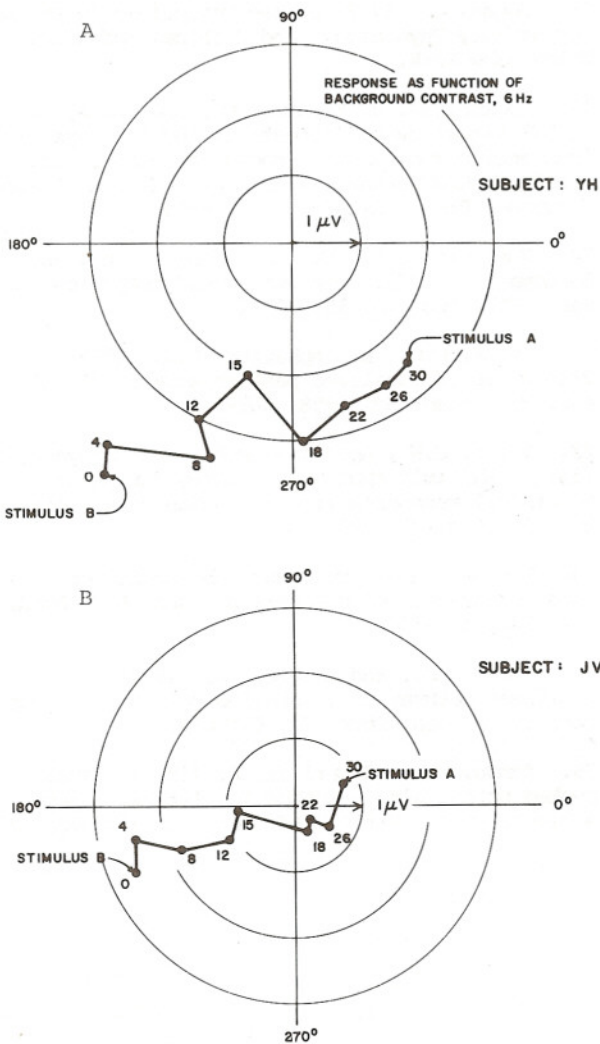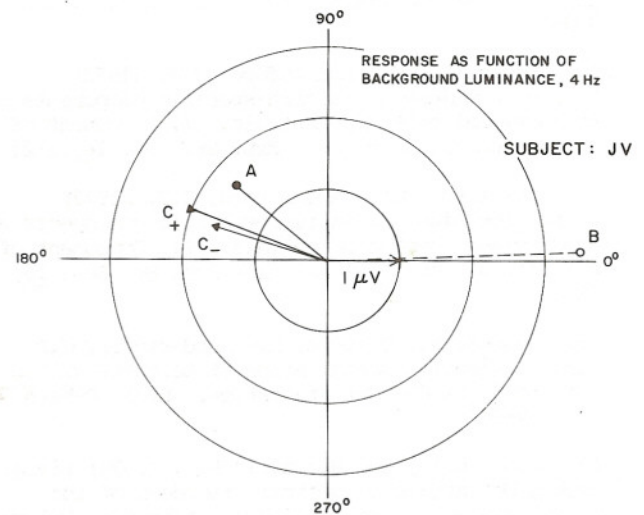

Figure 5: Polar plot of the second-harmonic response as a function of the contrast of the static region for the data of Figure 4 (part A) and a second subject (part B).

Figure 6: Second-harmonic responses to Stimuli A, B, and C.

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