

THE HUMAN VISUAL EVOKED POTENTIAL: ANALYSIS OF COMPONENTS DUE TO ELEMENTARY AND COMPLEX ASPECTS OF FORM

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(Received 31 December 1984; in revised form 7 May 1985)

Abstract—The visual evoked potential (VEP) elicited by alternation between isodipole visual textures may be separated into an asymmetric and a symmetric part. The asymmetric part reflects processing of complex attributes of form. The spatial and temporal dependence of this response is used to evaluate models for the generation of this response. The symmetric part appears to reflect processing of local luminance and contrast changes. The relation of these components to the VEP elicited by contrast reversal, contrast modulation, and the windmill-dartboard stimulus is discussed.

Visual evoked potential Systems analysis Parallel visual processing Feature analysis Human

INTRODUCTION

The visual evoked potential (VEP) is the summed activity of a multiplicity of neuronal events, occurring at perhaps scores of sites (van Essen and Maunsell, 1983), consisting of both action potentials and graded potentials. The contribution of each kind of neuronal event depends on the geometry of the cellular elements involved, their synchrony in time, and the passive electrical properties of the brain (Creutzfeldt *et al.*, 1969; Jeffreys and Axford, 1972a,b; Nunez, 1981; Lehmann *et al.*, 1982; Nakayama, 1982). These factors combine to make a dissection of the VEP into its physiologically relevant components a stubborn problem.

One approach to this problem is to exploit the fact that neurons in different visual areas have qualitatively different receptive-field properties. For example, there is no binocular interaction prior to the cortex, and therefore cyclopean visual stimuli may be used to elicit evoked responses that derive purely from cortical processing (Bodis-Wollner *et al.*, 1981). In like manner, stimuli that elicit hyperacuity discriminations have been used as a means to isolate cortical responses (Levi *et al.*, 1983).

More generally, if two stimuli elicit identical bulk activity from a given population of neurons, any difference of the VEP elicited by the two stimuli must be due to processing elsewhere. Thus, the same approach may also be applied in the domain of pattern vision. Previously (Victor, 1985a; Victor and Zemon, 1984) we have described VEPs elicited by a family of visual texture pairs derived from isodipole textures (Julesz *et al.*, 1978). Based on the known properties of X cells and Y cells (Enroth-Cugell and Robson, 1966; Hochstein and Shapley, 1976; Victor

and Shapley, 1979; Kaplan and Shapley, 1982), it is probable that these patterns elicit virtually identical population responses from retinal ganglion cells and lateral geniculate neurons. However, the VEPs elicited by members of these texture pairs are quite asymmetric. This asymmetric response to alternation between members of such a texture pair isolates the contributions of mechanisms sensitive to complex aspects of the correlation structure of the firing pattern of lateral geniculate neurons. Presumably, this response is generated intracortically.

In this paper, we analyze the dependence of the VEP elicited by these isodipole stimuli on the contrast, dynamics and spatial scale of the isodipole patterns. These data are related to models of generation of the VEP, and to other methods of functional dissection of the VEP.

METHODS

Visual stimuli

The basic visual stimulus (Victor, 1985a) consists of alternation between two members of an isodipole texture pair (Julesz *et al.*, 1978). Both members of the pair, the "even" texture and the "odd" texture, consist of colorings of a black and white square lattice. The initial row and column of each texture is chosen according to a shift register sequence (Golomb, 1968). The interior of the textures is determined by a simple recursive rule. In the even texture, every 2×2 block of square cells contains an even number of black and white units. In the odd texture, every 2×2 block contains an odd number of black and white units. The resulting visual stimuli are shown in Fig. 1(A).

To use these textures as VEP stimuli, we exploit an important relation between even and odd textures built on the same initial row and column. Such even and odd textures may be interconverted by reversing the contrast (exchanging black for white and vice-versa) of the one-quarter of the squares at the intersection of an odd-numbered row and odd-numbered column. This interchange may be done abruptly, to elicit transient VEPs, or sinusoidally, to elicit steady-state VEPs. The remaining area, which constitutes three-quarters of the stimulus area, is not modulated in time.

Simple variations on this stimulus are useful for exploration of mechanisms that generate the VEP, and for comparison with the traditional checkerboard stimulus. The contrast of the modulated and unmodulated portions of the stimuli need not be identical. Figure 1(B) shows the appearance of the even and odd configurations of the stimulus when the contrast of the unmodulated portion is one-half of the contrast of the modulated portion. This modification preserves the isodipole nature of the texture pair.

It is also useful to set the contrast of the unmodulated portion of the stimulus to zero, so that the stimulus consists of a uniform gray interrupted at regular intervals by square islands of black and white [Fig. 1(C)]. In other experiments, the *unmodulated* portion of the stimulus is identical to that of the original texture, and the *modulated* cells consist of a checkerboard array in counterphase [Fig. 1(D)]. Here also, the contrast of the unmodulated portion of the stimulus may be reduced to zero [Fig. 1(E)]. In all of these cases, the two states of the stimuli are statistically indistinguishable from each other.

Evoked potential recording and analysis

Our methods for evoked potential recording were described in detail in another paper (Victor, 1985a). The visual stimuli were generated by specialized electronics driven by a PDP 11/23 computer (Milkman *et al.*, 1980), which produced a 256×256 -pixel raster at a frame rate of 270.3 Hz, with a mean luminance of 154 cd/m^2 .

Unless otherwise specified, experimental conditions consisted of a check size of 8.25 minutes (4×4 pixels), a contrast $[(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})]$, where L_{\max} is the maximum luminance and L_{\min} is the minimum luminance] of 0.3 for the unmodulated region, a modulation frequency of 4.19 Hz. The subject pool was identical to that of (Victor, 1985a), consisting of seven healthy adults with normal acuity (with correction, if necessary) and no neuro-ophthalmologic disease. Pilot studies with three subjects showed no qualitative differences between binocular and monocular viewing, except for a somewhat larger response in binocular conditions; binocular viewing was used in all data presented here.

The VEP was extracted by computer-averaging of the EEG recorded differentially at C_z and O_z , with P_z

as ground. In the potentials reproduced here, negativity at O_z is indicated by upward deflection. Band-pass filtering was performed by the preamplifiers (gain = 10000) at 0.03–100 Hz. Each experimental condition was run for a 1-min episode. An experimental session consisted of no more than 50 such episodes. At the conclusion of the session, runs from the beginning of the session were repeated as a check on stability.

Fourier components of the responses were obtained at the input frequency and its first six harmonics. For the fundamental, a phase of zero means no lead or lag relative to the input signal. For the second harmonic, a phase of zero indicates no phase shift relative to the second harmonic component that would be contained in the square of the input. For both fundamental and second harmonics, negative phases denote a phase lag of the output relative to the above-defined reference phases. The run-to-run variability of the Fourier components was on the order of $0.5 \mu\text{V}$ in the complex plane (for example, Table 2). In general, responses above $1.0 \mu\text{V}$ were judged to be significant. The run-to-run variability of the phases of such responses was on the order of 20 deg.

RESULTS

Transient responses

The most straightforward way of using the even and odd textures as visual stimuli is to abruptly reverse the luminance of one-quarter of the cells. The resulting textures [Fig. 1(A)] are perceptually quite distinct, despite the equality of their spatial frequency spectra and other properties.

Fig. 2(A) shows VEPs elicited by this stimulus at a modulation frequency of 1.02 Hz. The first half (490 msec) of the averaged response follows the transition from the odd configuration to the even configuration, and the second half (490 msec) follows the transition from the even configuration to the odd configuration. Both transient responses show an occiput-positive wave at a peak latency of approximately 100 msec. However, the latter portion of the response is different in the two halves of the stimulus cycle: the transient response to the even texture (first half of stimulus cycle) has a prominent negative wave following the 100-msec positivity; this feature is attenuated or absent in the response to the odd texture (second half of the stimulus cycle).

When the contrast of the unmodulated region is reduced to zero [resulting in the stimulus shown in Fig. 1(C)], the two configurations of the texture are now visually similar and statistically identical. The resulting VEP [Fig. 2(B)] again has an initial positive wave at 100 msec latency, but there is no apparent asymmetry in the response to the two configurations of the texture.

Part C of the figure shows the response to a conventional contrast-reversing checkerboard (not illustrated) of the same spatial structure and contrast.

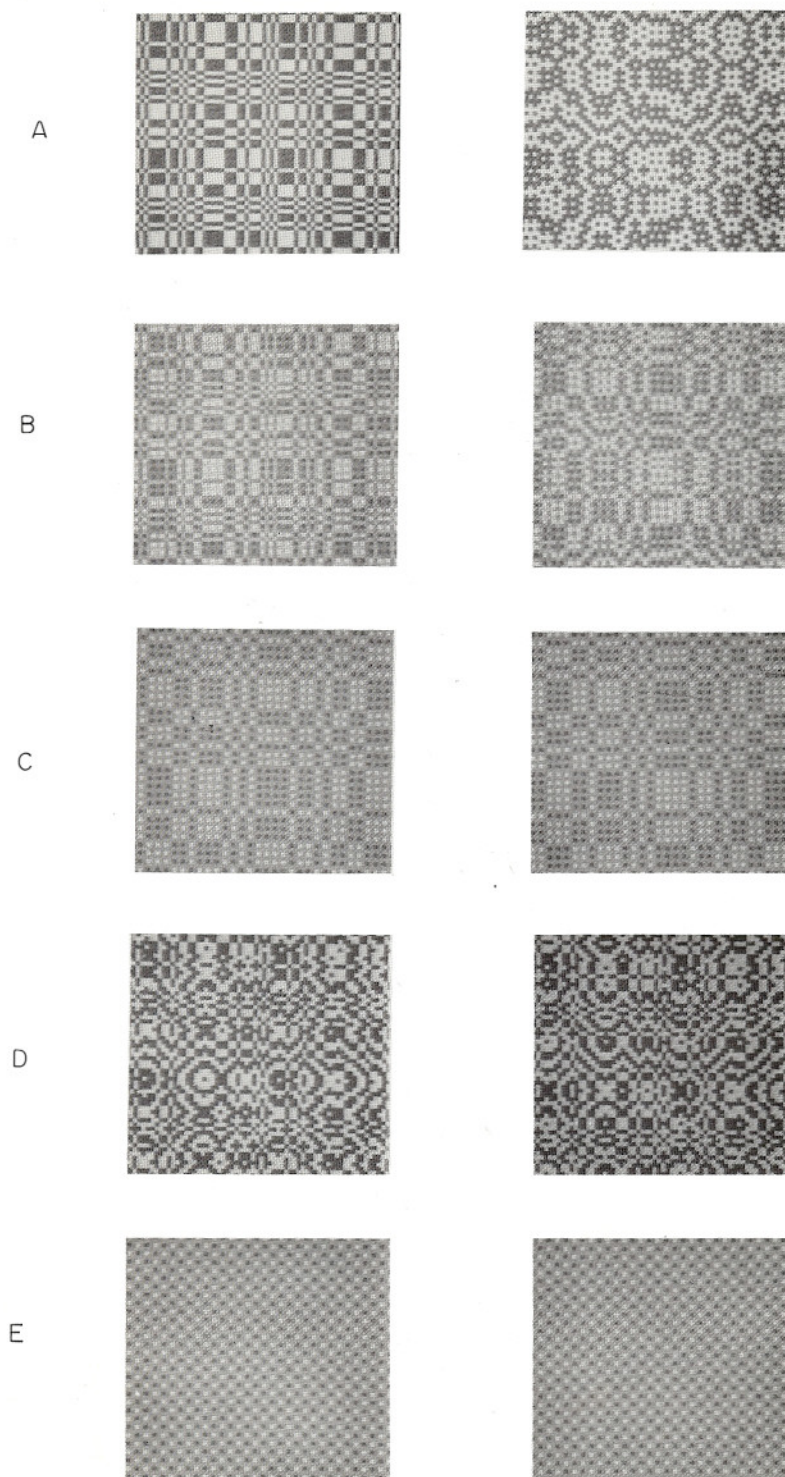


Fig. 1. Photographs of the "even" and "odd" configurations of some of the stimuli used. (A) The standard stimulus, with modulated and unmodulated portions at equal contrast. The even configuration is on the left; the odd configuration is on the right. (B) Unmodulated portion at half the contrast of the modulated portion. (C) Unmodulated portion at zero contrast, and intensity equal to the mean intensity of the bright and dark squares. (D) Unmodulated portion as in (A); modulated portion derived from a checkerboard instead of the recursion rule for the isodipole textures. (E) Unmodulated portion at zero contrast, and intensity equal to the mean intensity of the bright and dark squares; modulated portion as in (D). Note that in (C), (D), and (E), the two configurations are statistically indistinguishable.

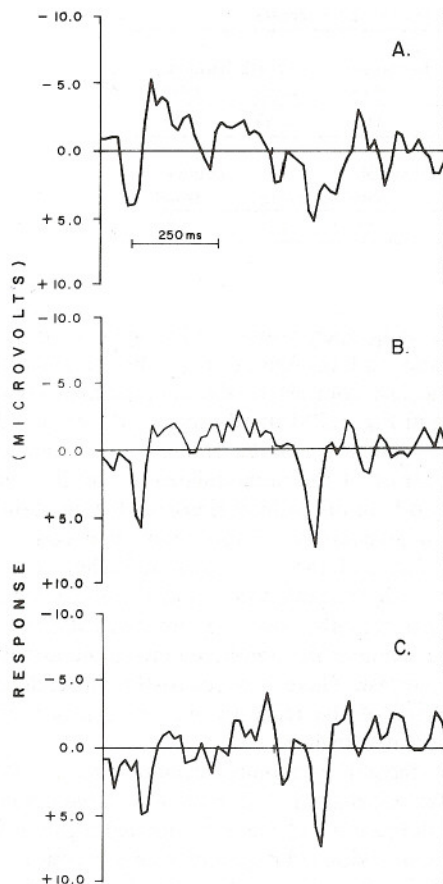


Fig. 2. (A) Transient responses to abrupt transitions between even and odd configurations of the basic texture stimulus, illustrated in Figure 1(A). (B) The response to the stimulus when the contrast of the unmodulated region is reduced to a contrast of zero [as in Fig. 1(C)]. (C) The response to a standard contrast-reversing checkerboard of the same contrast and spatial scale. Subject: Y.H.

As required by symmetry, the responses to both phases of contrast-reversal are identical. The major positive wave, with a latency of approximately 105 msec, is about the same size as that observed in response to the more complex stimuli of Parts A and

B. The amplitudes of the later components of the response to the checkerboard are diminished relative to the responses in Part A. These observations are particularly striking in view of the fact that only one-quarter as many cells are modulated in the even/odd stimulus, as compared with the checkerboard stimulus.

Steady-state responses

Although the transient responses shown in Fig. 2(A) have a reproducible asymmetry, it is clear that a more detailed analysis will require both a method of quantitation and an improved signal-to-noise ratio. For these (and other) reasons, we chose to study the VEP elicited by sinusoidal, rather than square-wave, variation of the luminance of the modulated cells (Regan, 1972, p. 234; Tyler *et al.*, 1978).

Fourier analysis of the response to these stimuli provides a convenient way to quantify the symmetric and asymmetric components of the response to texture interchange: second and higher even-order harmonics reflect components common to both textures, whereas fundamental and higher odd-order harmonics reflect response components that depend on differences between the textures. By choosing a range of temporal frequencies, the dynamics of the symmetric and asymmetric responses can be studied. In addition, the smooth modulation of the visual stimulus avoids transients that may potentially saturate an early stage of visual processing, and introduce additional but uninteresting nonlinearities.

Figure 3 shows responses to the even/odd stimuli using sinusoidal modulation. The asymmetric (fundamental) response occurs only when the unmodulated portion of the stimulus is present (Part A); it is absent when the unmodulated part of the stimulus is absent (Part B). This qualitative difference is more evident than in the transient responses of Fig. 2, obtained under otherwise identical conditions.

Fourier analysis of these responses is shown in Table 1. When the unmodulated region of the stimulus is patterned, the fundamental component exceeds the second harmonic in amplitude. The third-harmonic component, and higher odd harmonics (not

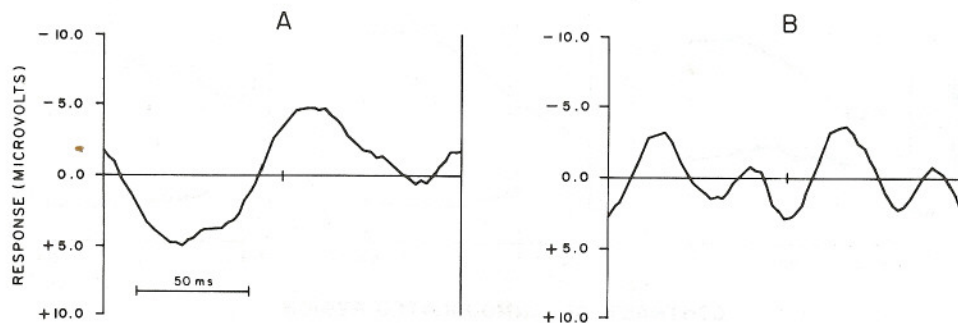


Fig. 3. Steady-state responses to the even/odd texture modulated at 4.19 Hz. (A) Modulated and unmodulated components of stimulus at a contrast of 0.3. (B) Modulated component at a contrast of 0.3; unmodulated component at a contrast of 0. Fourier components are presented in Table 1. Subject: Y.H.

Table 1. Fourier analysis of steady-state (sinusoidal) responses

Contrast of unmodulated region: 0.3							
Fundamental ampl.	phase	Second harmonic ampl.	phase	Third harmonic ampl.	phase	Fourth harmonic ampl.	phase
3.44	-157	2.21	61	0.41	115	0.60	59
Contrast of unmodulated region: 0.0							
Fundamental ampl.	phase	Second harmonic ampl.	phase	Third harmonic ampl.	phase	Fourth harmonic ampl.	phase
0.08	-128	1.66	60	0.22	81	1.99	-125

Amplitudes are in μV ; phases are in degrees.

shown) are small, as is typical in our data. Thus, the asymmetry of the response to the even/odd texture is contained in the fundamental. The fundamental and higher odd-harmonic components are small when the contrast of the unmodulated region is reduced to zero.

In general, the even-harmonic components are present both with and without pattern in the unmodulated region, but the amplitude and phase of these components depend on the pattern. For the subject whose data is illustrated in Table 1, the second-harmonic response is of similar amplitude with and without pattern in the unmodulated region, but its phase depends on whether the unmodulated region is patterned. The fourth-harmonic component is large when the unmodulated region is unpatterned.

Dependence on contrast

Figure 4 shows the amplitude and phase of the fundamental and second-harmonic responses parametric in the contrast of the unmodulated region for three subjects. Fundamental responses are shown using solid symbols; second harmonic responses are

shown using open symbols. [The appearance of the even and odd configuration of the stimulus at an intermediate contrast of the unmodulated region is shown in Fig. 1(B).] In all subjects, the amplitude of the fundamental response becomes appreciable when the contrast of the unmodulated region is approximately 0.1. In one subject (Part A), the amplitude of the fundamental has a maximum at a contrast of about 0.2, and then decreases at higher contrasts. (Recall that the peak contrast of the dynamic region is 0.3.) In the other two subjects tested (Parts B and C), the fundamental amplitude grows monotonically with contrast. There is no consistent dependence of the phase of the response on the contrast of the unmodulated region.

The second harmonic response has a different qualitative behavior. It is present at large amplitude when the contrast of the unmodulated region is zero. As the unmodulated region increases in contrast, the amplitude of the second harmonic decreases. In some subjects, the response passes through a minimum and increases again, but the phase has shifted by approximately half a cycle at the higher contrasts.

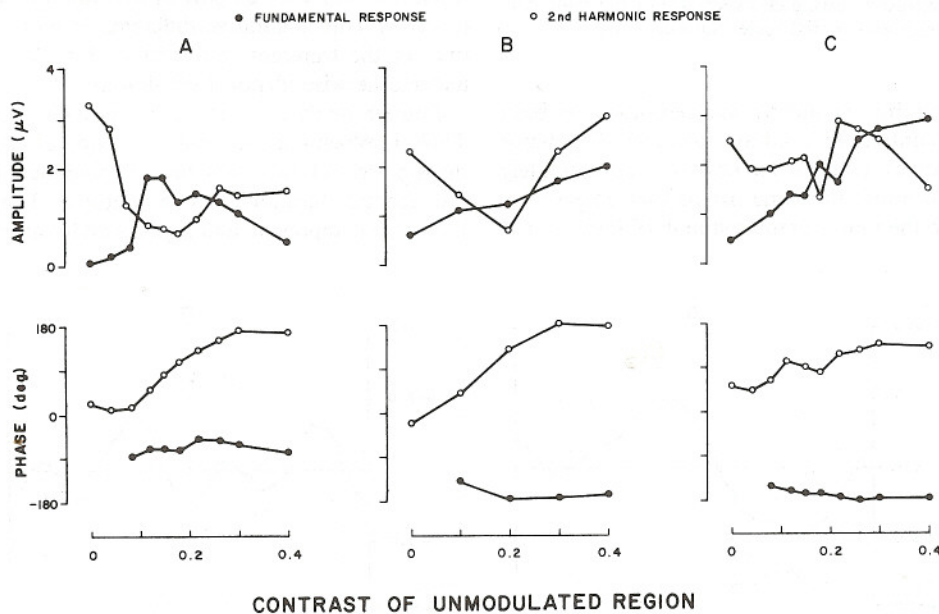


Fig. 4. Dependence of fundamental and second-harmonic responses on contrast of the unmodulated region. Phases are plotted only for responses that exceed $0.5 \mu\text{V}$. Subjects: J.V. (A), M.C. (B), and Y.H. (C).

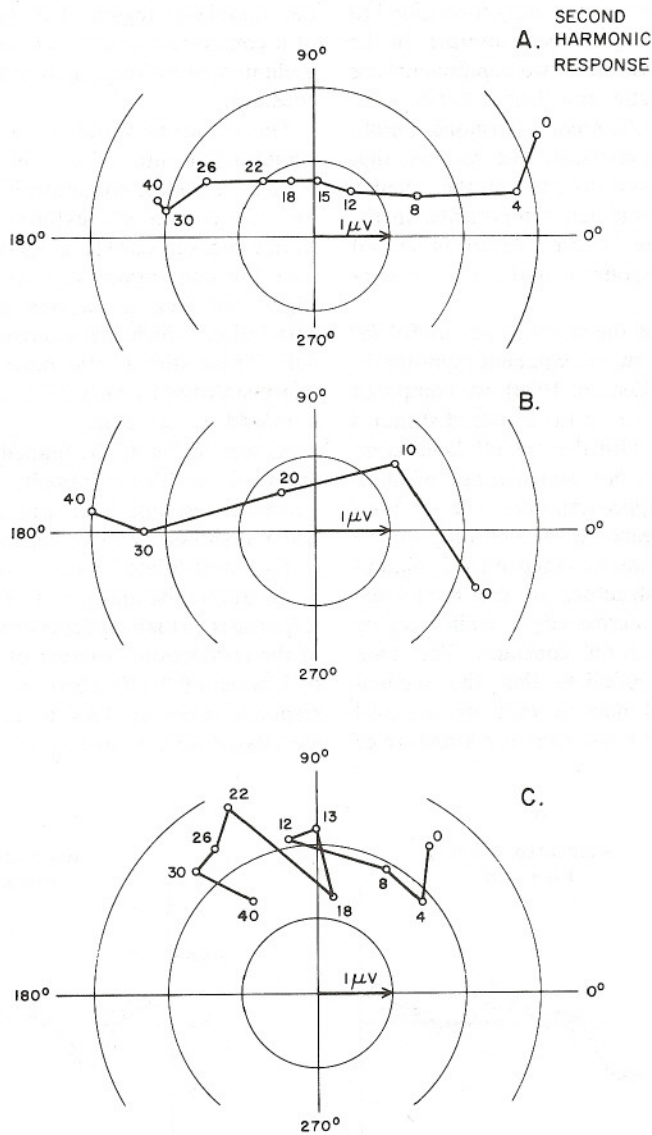


Fig. 5. Dependence of second-harmonic responses on contrast of the unmodulated region. The data of Fig. 4 have been replotted in polar form, with the number adjacent to each point indicating the contrast of the unmodulated region. Increasing phase (lead) is counterclockwise.

This complex behavior of the second-harmonic suggests that it may be the sum of two or more components. One way of testing this hypothesis is to plot the response amplitude and phase in polar form (Fig. 5). Plotted in this fashion, responses of component mechanisms that are additively combined (e.g. by passive volume conduction) will add vectorially. All subjects now show a consistent pattern. The effect of increasing the contrast of the unmodulated component of the pattern is to move the observed second-harmonic response in a straight line, in a direction nearly opposite to the response to the modulated portion alone (unmodulated portion at zero contrast).

Another hypothesis that one might entertain is that there is a single mechanism which drives the second

harmonic response, but its latency depends on the presence of the unmodulated component of the pattern. If this were the case, the plots of Fig. 5 would have resembled arcs at a constant distance from the origin. Thus, if there is just one mechanism which drives the second harmonic, both its latency and amplitude must depend on the presence of the unmodulated component; the two-component hypothesis is more parsimonious.

Thus, this analysis suggests that the second-harmonic response represents the sum of two components. One component is independent of the unmodulated region. This component may correspond to a mechanism sensitive only to local luminance. The second component has an amplitude which depends on the contrast of the unmodulated region, but has

a constant phase. This component may correspond to a mechanism sensitive only to local *contrast*. In the subjects of parts A and B, these two components are almost exactly antagonistic, and their net effect is to produce a minimum of the second harmonic amplitude at an intermediate contrast. The contrast that yields this minimum will depend on the relative strengths of the two postulated components. In the subject of part C, there is some deviation (about 30 deg) from pure antagonism, and no clear minimum is observed.

Some modifications of the stimulus are useful for further testing of this two-component hypothesis. Previously (Victor and Zemon, 1984), we compared second-harmonic responses to the standard stimulus [Fig. 1(A)], and stimuli with the unmodulated components at zero contrast but over a range of luminances. To a first approximation, the second-harmonic response appeared to depend only on the contrast across edges. Here, we independently manipulate the correlation structure of the modulated region and the contrast across edges, while keeping local luminance modulation constant. The two-component hypothesis predicts that the second-harmonic response will depend only on contrast across edges and not on the correlation structure of

the modulated region. The differential contribution of a component strictly sensitive to local luminance is eliminated by keeping local luminance modulation constant.

This requires a variation on the standard even/odd stimulus. The intensities of the cells of the modulated region are chosen not according to the recursion rule for the even and odd textures, but rather are derived from a checkerboard [Fig. 1(D) and (E)]. Such stimuli have the same appearance locally across individual edges, but lack the asymmetry of the high-order correlations which characterizes the even/odd texture pair. These stimuli also have the same local luminance statistics as each other, and as the unmodified even/odd texture pair.

As seen in Fig. 6, the fundamental response to this modified stimulus is absent. However, the second harmonic response is present in the modified stimulus, and shows the same dependence on the contrast of the unmodulated component. As shown in Table 2, the amplitude and phase of the second harmonic response is virtually independent of this manipulation of the correlation structure of the stimulus (varying by less than $0.2 \mu\text{V}$). However, the second harmonic response varies by $4 \mu\text{V}$ as the contrast of the unmodulated region (and therefore the contrast across

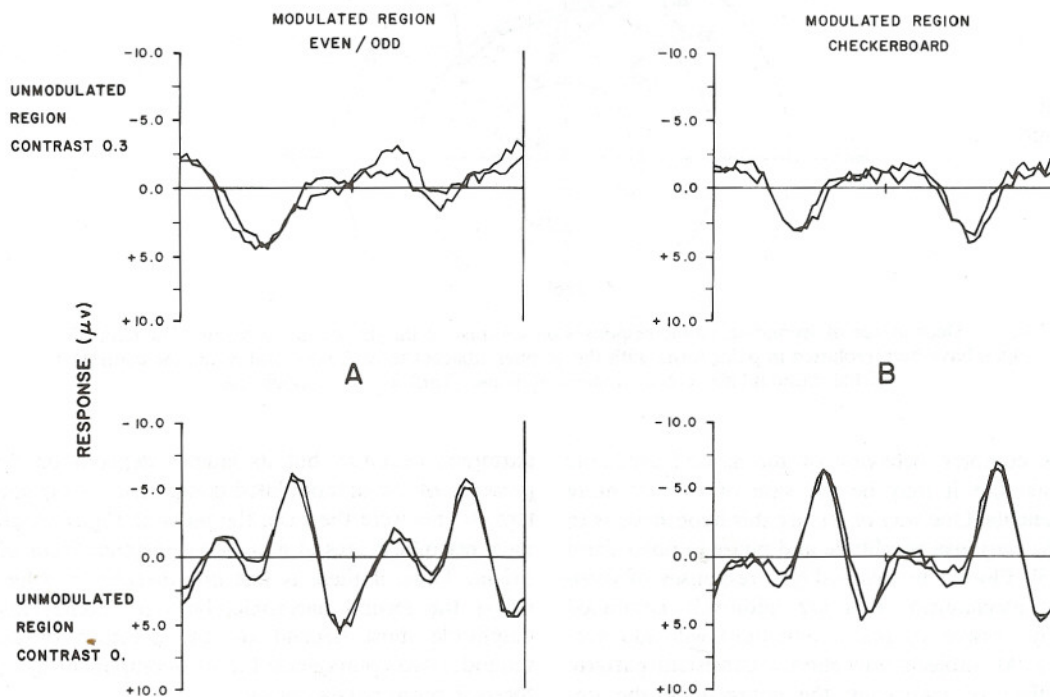


Fig. 6. Dependence of the response on contrast of the unmodulated portion of the stimulus and the correlation structure of the modulated and unmodulated regions. In the left half of the figure (A), the modulated cells are drawn from the even/odd texture with the unmodulated cells either at full contrast [Fig. 1(A)] or zero contrast [Fig. 1(C)]. In the right half of the figure (B), the modulated cells are drawn from a checkerboard, with the unmodulated cells either at full contrast [Fig. 1(D)] or zero contrast [Fig. 1(E)]. For each of the four conditions, two 1-min averages of the VEP are shown. A significant fundamental response is present only with the full even/odd stimulus. The second harmonic is independent of the correlation structure of the modulated region. Fourier components are presented in Table 2.

Subject: M.C.

Table 2. Fourier analysis of responses to stimuli with altered correlation structure, illustrated in Fig. 6

Contrast of unmodulated region: 0.3				
	Fundamental		Second harmonic	
	amplitude	phase	amplitude	phase
Modulated cells: even/odd				
trial 1:	1.29	156	2.02	93
trial 2:	1.96	179	1.75	74
average:	1.59	170	1.86	84
Modulated cells: checkerboard				
trial 1:	0.19	1	2.06	86
trial 2:	0.45	91	1.92	91
average:	0.24	68	1.99	88
Contrast of unmodulated region: 0.0				
	Fundamental		Second harmonic	
	amplitude	phase	amplitude	phase
Modulated cells: even/odd				
trial 1:	0.18	44	2.42	-108
trial 2:	0.16	-1	2.74	-99
average:	0.15	23	2.57	-103
Modulated cells: checkerboard				
trial 1:	0.41	-143	2.55	-117
trial 2:	0.24	-29	2.84	-123
average:	0.19	-107	2.69	-120

Amplitudes are in μV ; phases are in degrees.

individual edges) is changed from 0.0 to 0.3. Thus, contrast across edges, rather than complex spatial correlation structure, appears to govern the second-harmonic response.

Dependence on spatial scale and temporal frequency

We studied the size of the fundamental and second-harmonic response as a function of check size and

modulation frequency in five subjects. In view of the importance of the dependence of response on the contrast of the unmodulated region, responses were measured both for the full even/odd stimulus and with the contrast of the unmodulated region reduced to zero.

Figure 7 illustrates the response amplitudes and phases at a range of temporal frequencies, holding the check size fixed at the size that gives the greatest fundamental response (8.25 min). With the full even/odd stimulus [Fig. 7(A)], the fundamental response is tuned to a narrow range of temporal frequencies, centered around 4 Hz. The second harmonic response is more broadly-tuned, and persists to higher temporal frequencies.

When the contrast of the modulated region is reduced to zero [Fig. 7(B)], the fundamental response is markedly diminished if present at all. Raw amplitudes are all less than $0.5 \mu\text{V}$, and the phases (not shown) are random. The second harmonic response is large at low temporal frequencies, and its phase is shifted by about half a cycle with respect to the response to the full even/odd pattern.

The dependence of response phase on temporal frequency may be used to estimate a latency for the pathways that generate the responses to the even/odd stimulus [Fig. 7(A)]. In the range that the fundamental depends linearly on temporal frequency, phase shifts by a full cycle as the frequency increases by 5–6 Hz, which corresponds to a latency of about 160–200 msec. If the second harmonic were generated by a mechanism with a similar latency, its phase curve would have a slope which is twice that of the first harmonic.

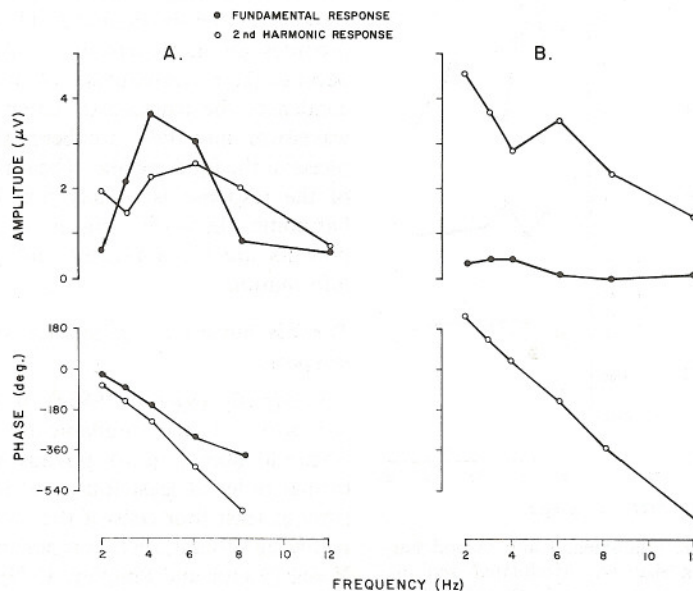


Fig. 7. Dependence of the fundamental and second harmonic response on modulation frequency. (A) Modulated and unmodulated regions at a contrast of 0.3. (B) Modulated region at a contrast of 0.3; unmodulated region at a contrast of 0. Phases are plotted only for responses that exceed $1.0 \mu\text{V}$. Check size is held constant at 8.25 min. Subject: Y.H.

Instead, the phase curve for the second harmonic is only slightly steeper. Second harmonic phase increases by a full cycle as input frequency increases by approximately 4 Hz. Thus, a full cycle of phase shift corresponds to an output frequency increase of 8 Hz. This corresponds to an approximate latency of 125 msec. These latency estimates may not correspond exactly to direct measurements of latencies in response to transient stimuli (Regan, 1972, p. 77). However, the difference between the fundamental and second-harmonic data suggests that the dynamics of the responsible mechanisms are distinct.

Figure 8(A) shows the dependence of the response on check size, with modulation frequency held constant at 4.19 Hz (near optimal for the fundamental response). Again, the fundamental response is sharply-tuned, with an optimal check size of about 8 min. Second harmonic responses increase monotonically as check size increases. There is no consistent phase dependence of either fundamental or second harmonic responses on check size.

With the unmodulated region reduced to a contrast of zero, the fundamental response is again negligible. But the second harmonic response shows a more complex dependence on check size, with two maxima: one at 3 min, and one at 12 min.

The data in Figs 7 and 8 are essentially slices parallel to the temporal and spatial axes of a complete spatiotemporal response function, akin to what has been measured for gratings (Tyler *et al.*, 1978).

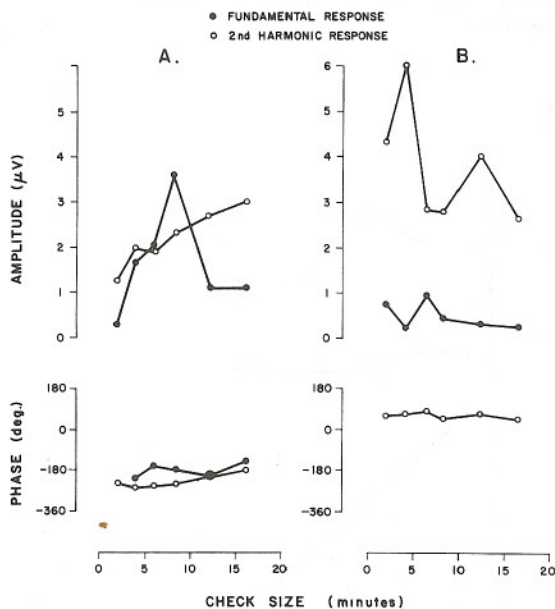


Fig. 8. Dependence of the fundamental and second harmonic response on check size. (A) Modulated and unmodulated regions at a contrast of 0.3. (B) Modulated region at a contrast of 0.3; unmodulated region at a contrast of 0. Phases are plotted only for responses that exceed $1.0 \mu\text{V}$. Modulation frequency is held constant at 4.19 Hz. Subject: Y.H.

The full amplitude surface of the measured function for this subject is shown in Fig. 9. This figure represents a smooth surface interpolated [by using a two-dimensional cubic spline (Ahlberg *et al.*, 1967)] through the measured amplitudes obtained at each indicated combination of temporal frequency and check size.

This response surface may be summarized as follows: the fundamental response is narrowly-tuned to a temporal frequency of approximately 5 Hz and a check size of approximately 8 min when the contrast of the unmodulated component is set to 0.3; it is absent at all temporal frequencies and spatial sizes when the unmodulated component of the texture is reduced to a contrast of zero. The second harmonic response to the full even/odd stimulus has a maximum at approximately 6 Hz, for check sizes of 10 min and larger. When the unmodulated component of the texture is replaced by zero contrast, a second peak is present at low temporal frequencies (4 Hz and possibly lower) and small check sizes. Naturally, the precision with which these peaks can be located is limited by the mesh on which the data were collected.

DISCUSSION

The dependence of the VEP on the contrast, scale, and dynamics of the texture stimulus provides clues to the nature of the underlying neural mechanisms that generate the response. The first step in our analysis of the data is the use of Fourier analysis, which subdivides the response into an asymmetric component (the odd harmonics) and a symmetric component (the even harmonics). In these studies, the only odd harmonic that reliably contains a significant response is the fundamental. Thus, Fourier analysis provides an improvement in signal-to-noise ratio, because (as a consequence of frequency binning) it condenses the asymmetric component of the VEP waveform into two numbers: the amplitude and phase of the fundamental. The symmetric component of the response is usually manifest in the second harmonic; however, higher even-harmonic components are often present and provide additional information.

Possible models for generation of the fundamental response

Previously (Victor, 1985a), it was shown that a generator of the fundamental response to the even/odd stimuli must possess nonlinearities with formal order at least four, and involve interactions from at least four cells of the texture. In principle a rectifying subunit, such as is postulated for the retinal Y cell (Victor and Shapley, 1979) and some cortical cells (Spitzer and Hochstein, 1984a,b) possesses such properties. This kind of model, however, would generate a fundamental response which is linked to the second harmonic response, and always much

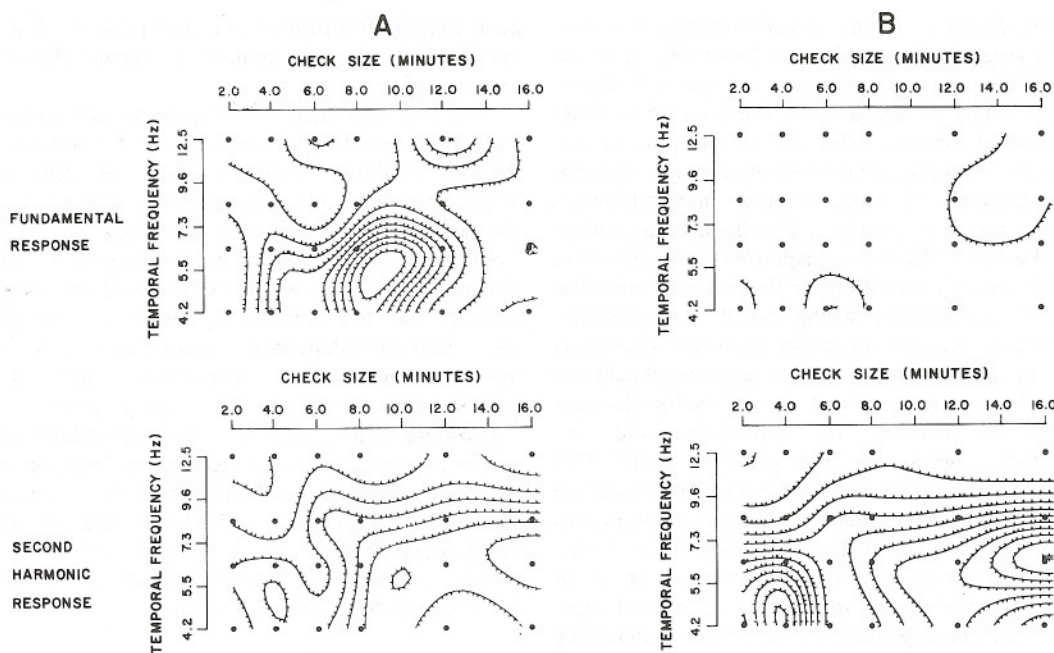


Fig. 9. Dependence of fundamental and second harmonic response amplitudes on the spatial and temporal parameters of the stimulus. Each contour line represents $0.5 \mu\text{V}$; the solid circles indicate the location of data points. A spline (Ahlberg *et al.*, 1967) is used for interpolation. (A) Modulated and unmodulated regions at a contrast of 0.3. (B) Modulated region at a contrast of 0.3; unmodulated region at a contrast of 0. Figures 7 and 8 are derived from this data set. Subject: Y.H.

smaller than the second harmonic. The very different spatial and temporal dependence of the fundamental and second harmonic components (Figs 7, 8, and 9) strongly argue that additional nonlinear mechanisms must be involved.

What other possible mechanisms might be invoked? Julesz and Bergen (1983) have hypothesized that the perceptual difference between even and odd configurations relies on the presence of large homogeneous areas (blob textures) in the even texture that are interrupted in the odd texture. This difference might in principle be detected by hypercomplex cells, or cells with similar receptive field properties. Certainly this feature, whatever the cellular basis for its detection, would provide for a robust distinction between the two textures. Its electrophysiological correlate would be expected to generate an asymmetric VEP to the present stimulus. But this hypothesis does not explain the observation that in some subjects, the peak fundamental response occurs when the unmodulated component has a contrast only half that of the modulated component [Fig. 4(A)]: in this stimulus configuration, neither even nor odd configurations contain any large homogeneous regions.

A mechanism that responds asymmetrically to the even/odd stimulus must embody a highly nonlinear interaction in space. In the frequency domain, this interaction may be viewed as a nonlinear interaction of spatial frequency components. In this context, the recent work of Movshon and coworkers (1984) in

extrastriate cortex may be relevant. Many single units in the middle temporal visual area (MT) respond in a directionally-selective fashion to moving patterns (crossed gratings). A subpopulation of MT units has the property that this "detection of movement" does not require that the pattern have any Fourier components moving in the preferred direction. However, the response properties of these units are well-modelled by a nonlinear interaction among the Fourier components of the stimulus. Determining whether this notion is more than analogy will require a more detailed understanding of the physiology of the extrastriate cortex and the VEP.

The second-harmonic component

The analysis of the second-harmonic component contrasts sharply with that of the fundamental. Because the second-harmonic component corresponds to VEP changes that are present at both even-to-odd and odd-to-even transitions, the many symmetry properties of the stimulus do not provide theoretical grounds to exclude the contributions of simply-constructed mechanisms. Instead, simple luminance and contrast mechanisms can contribute to this component of the VEP. Any even-order nonlinearity, even a local one, will suffice to prevent cancellation of signals averaged over the stimulus. Furthermore, any of the more complex mechanisms that might generate a fundamental response may, in general, generate a second-harmonic response as well.

Subcomponents of the second-harmonic response. These considerations raise the possibility that the second-harmonic response is a net result of several distinct kinds of mechanisms. Previous experiments (Victor and Zemon, 1984) showed that the second-harmonic response appeared to depend only on stimulus attributes no more complex than luminance changes across single edges. This hypothesis predicts that the second-harmonic response is independent of the high-order correlations of the even/odd stimulus.

Figure 6 provides a strong test of this prediction. In the first column, the usual even/odd stimulus is used. In the second column, the modulated cells are drawn from a checkerboard, so that the fourth-order correlations between the modulated and unmodulated regions are destroyed [Fig. 1(D)]. This eliminates the fundamental response, yet leaves the second-harmonic response unchanged. In both columns, when the contrast of the unmodulated portions is reduced to zero, the amplitudes and phases of the second-harmonic components are altered drastically. But the second-harmonic response elicited by the full even/odd stimulus, and the distinct second-harmonic response elicited by the stimulus with unmodulated contrast reduced to zero, are independent of the correlation structure of the modulated region (Table 2). Thus, the second-harmonic response depends only on simple local stimulus attributes: contrast and luminance.

Conversely, at least some spatial interaction is required to explain the qualitative behavior of the second-harmonic response; there is a dramatic difference in the amplitude and phase of the second-harmonic response depending on the contrast of the unmodulated region (Figs 3 and 4). When the contrast of the unmodulated region increases, the second-harmonic response moves approximately in a straight line in the complex plane (Fig. 5). This suggests that increasing the contrast of the unmodulated region results in addition of larger and larger contributions from a mechanism that depends on an interaction between the modulated and unmodulated regions. One possibility is that the interaction-dependent component is a "contrast" mechanism, and the interaction-independent component is a "luminance" mechanism. These two components are approximately 180 deg out of phase, although some subjects [Figs 4(C) and 5(C)] showed a clear deviation from pure antagonism.

Can the two components be unified? Formally, the interaction-dependent component is a second-harmonic response to stimulation in one region that depends on the contrast (but not polarity) of stimulation in a second region. Thus, the interaction-dependent component must be an interaction of two second-order processes, one in each region. If a single nonlinearity is responsible for this phenomenon, it must therefore be of fourth (or higher) even order. Furthermore, responses to the even/odd stimulus with the contrast of the unmodulated region held to

zero contain fourth-harmonic components (Fig. 3 and Table 1); this also requires a fourth-order nonlinearity of some sort.

Such a nonlinearity will, in general, also respond with even-harmonic components when the contrast of the unmodulated region is kept at zero (an interaction-independent component). The phase of this interaction-independent response may differ from the phase of the interaction-dependent component, depending on the dynamics of the spatial pooling and the nonlinearity. Is it possible that the interaction-dependent component and the interaction-independent component are both manifestations of a single nonlinear process?

Our data do not suffice to make detailed inferences on the dynamics of such a mechanism. However, we can draw at least one qualitative conclusion about the shape of the nonlinearity. We know from the previous paragraph that the nonlinearity must not be purely quadratic. For ease of analysis, assume that the nonlinearity is represented by

$$y = x^2 + kx^4.$$

Consider a mechanism which consists of spatial summation over a 2×2 patch of the texture followed by the above nonlinearity. The response of such a mechanism to the full even/odd pattern and the even/odd pattern with the unmodulated region reduced to zero contrast may be calculated by averaging the response of the nonlinearity to the kinds of patches that appear in the two stimuli. If the size of the nonlinear response grows more rapidly than a square-law device (k positive), the response with an unmodulated pattern present will be larger than the response with the unmodulated pattern absent, and in the same phase. In this case, the interaction-dependent component would appear to be in phase with the interaction-independent component. On the other hand, if the size of the nonlinear response grows less rapidly than a square-law device (k negative), the response with an unmodulated pattern present will be smaller than the response with the unmodulated pattern absent, or in opposite phase. In this case, the interaction-dependent component would appear to be antagonistic to the interaction-independent component.

Rectifiers and fractional power-law nonlinearities cannot in general be expressed as polynomials, but their behavior to a sinusoidal input may be analyzed by approximation with a series of orthogonal polynomials (Victor and Knight, 1979). For nonlinearities such as rectifiers, the first terms in the orthogonal expansion correspond to a negative k . On the other hand, for highly cooperative nonlinearities (power law with power greater than two), k is positive. Thus, we conclude that if the interaction-independent second harmonic and the antagonistic interaction-dependent second harmonic are due to a single nonlinearity, then this nonlinearity is qualitatively

consistent with linear spatial summation followed by rectification.

Comparison with contrast-reversal, contrast-modulation, and windmill-dartboard experiments

Our analysis of responses to the even/odd stimulus may be summarized as follows: the fundamental component depends on complex local interactions which require more processing than mere summation and rectification; the second-harmonic component is consistent with a model of summation (perhaps with lateral interactions providing spatiotemporal coupling) followed by rectification, but probably includes additional components.

The contrast-reversing checkerboard stimulus, which is used for the majority of clinical and basic studies, has symmetry properties that preclude the generation of a fundamental response unless the check size is so large that a foveal luminance response is significant. Thus, responses due to local luminance, local contrast changes, and more complex types of visual processing are all superimposed in the even-order responses, making a detailed physiological dissection difficult.

For this reason, some investigators have broken the symmetry of the checkerboard in order to exploit the differing receptive-field properties of neurons at different levels of the nervous system as a physiological means for dissecting the VEP. One simple and successful such approach is the use of a contrast-modulated (or appearance/disappearance) stimulus, rather than a contrast-reversal stimulus (Spekreijse *et al.*, 1973).

The minimal models that account for the fundamental response to contrast modulation and the fundamental response to the even/odd stimulus differ strikingly. The rectifying subunit model will yield a fundamental response in response to appearance/disappearance stimuli (Spekreijse *et al.*, 1973, 1977). As discussed above, rectifying subunits may well be responsible for the even-harmonic responses to the even/odd stimulus. However, rectifying subunits are unlikely to be responsible for the fundamental component of the response to the even/odd stimulus (Victor, 1985a).

The dynamical characteristics of the fundamental response to the even/odd stimulus are distinct from that seen with contrast modulation: the even/odd fundamental response is more prominent at low temporal frequencies, while the contrast-modulation fundamental response persists to high temporal frequencies. The approximate latency in the generation of the fundamental response to the even/odd stimulus is 160 msec (Fig. 7). The latency estimated in a similar fashion for the fundamental response to contrast modulation is 100–110 msec (Victor, 1985b). This suggests that the fundamental response to even/odd stimulation is generated at a later stage of processing than the fundamental response to contrast modulation. On the other hand, whatever mechanisms

contribute to the fundamental response to even/odd patterns may also generate a portion of the fundamental response to contrast modulation, which overlaps with the contribution of the rectifying subunit.

Ratliff and Zemon (1982) used a pattern in which a windmill and dartboard interchanged. This stimulus also elicits a VEP that contains both fundamental and second-harmonic components. As in the present studies, the fundamental response and the character of the second-harmonic response depend critically on the presence of a patterned but unmodulated background. The present analysis of the second-harmonic response elicited by the even/odd stimuli applies equally well to the second-harmonic response elicited by windmill-dartboard stimuli, and it is probable that the same underlying mechanisms are involved.

The fundamental responses obtained with the two methods cannot be identified as closely. There are certain similarities: for example, the fundamental response peaks at spatial scales for which the second-harmonic component is small (Fig. 9), as has been reported for the windmill/dartboard responses (Zemon and Ratliff, 1982). However, because the autocorrelations (and spatial frequency spectra) of the windmill and dartboard configurations are different, a rectifying subunit *can* generate a robust fundamental response. Thus the windmill-dartboard fundamental may contain components which do not correspond to the fundamental response driven by the even/odd stimuli. Zemon and Ratliff (1982, 1984) considered it unlikely that the fundamental and second-harmonic response were generated by the same mechanism, because the fundamental response was selectively sensitive to small separations of regions of the stimulus, corresponding to the width of a cortical column. Whether this fundamental response is in fact due to a separate, more complex mechanism (such as the mechanism which generates the fundamental response to the even/odd stimulus) or alternatively is a result of lateral interactions generated by rectifying subunits remains an open question.

Acknowledgement—We thank Mary Conte, Dr Jim Gordon, Yvonne Holland, Norman Milkman, Michelangelo Rossetto, and Gary Schick for their excellent technical assistance. We thank Drs Floyd Ratliff and Robert Shapley for their many helpful suggestions. The time willingly spent by members of the Biophysics Laboratory as subjects is gratefully appreciated. This work was supported in part by grants EY188, EY2439, EY5466, and NS877 from the National Institutes of Health, The Harry Frank Guggenheim Foundation, and The Klingenstein Fund. J.V. is a Hartford Fellow and received additional support from The McKnight Foundation.

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