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# Visual evoked potentials: Evidence for lateral interactions

(human brain/visual cortex/contrast reversal)

VANCE ZEMON AND FLOYD RATLIFF

Laboratory of Biophysics, The Rockefeller University, 1230 York Avenue, New York, New York 10021

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**ABSTRACT** Electrical potentials evoked in the human brain by visual stimulation can easily be recorded by using electrodes attached to the scalp. It is difficult, however, to relate these visual evoked potentials (VEPs) to specific neural processes: scalp electrodes, far removed from the brain, sum potentials from large areas of cortex. We improved identification and localization of lateral interactions by differentially modulating small neighboring parts of a "windmill-dartboard" stimulus pattern—a central disc surrounded by three contiguous annuli, all radially divided into light and dark segments. With temporal contrast reversal of all segments in the pattern, the major component of the VEP is at the second harmonic of the frequency of modulation—as expected. Temporal contrast reversal of the segments in the central disc and second annulus, with contrast of segments held constant in the first and third annuli, unexpectedly amplifies the VEP at the fundamental frequency of modulation and attenuates it at the second harmonic. Slight spatial separation of static and dynamic zones reduces both the amplification of the fundamental and the attenuation of the second harmonic. Thus, both phenomena appear to result from strong lateral interactions over relatively short distances. Nevertheless, different neural mechanisms must be involved; fundamental and second-harmonic components of the VEP are different functions of spatial separation and relative contrast of the segments in contiguous static and dynamic zones.

Visual evoked potentials (VEPs) recorded from the surface of the head are used widely in basic research on vision and as an aid in the diagnosis of ophthalmic and neurological disorders. Patterned stimuli that vary periodically in both space and time are commonly used to elicit the VEPs. Typical examples of such stimuli are gratings or checkerboards in which the contrast is reversed sinusoidally in time. The VEP elicited by these patterns consists of a major component at twice the frequency (the second harmonic) of the sinusoidal modulation. A significant component at the frequency of modulation (the fundamental frequency) is not present in these VEPs. Contrast reversal of these conventional patterns produces essentially identical percepts during each half of the modulation cycle (the only difference being a spatial phase shift of 180°). This type of stimulus, because of its symmetry about contrast reversal, necessarily permits only even-order nonlinear components (second harmonics, fourth harmonics, sixth harmonics, etc.) to appear in the response. Odd-order components (fundamentals, third harmonics, fifth harmonics, etc.), if elicited in the brain and conducted to the scalp, would not appear in the recorded response because the equal magnitude but out-of-phase contributions at these frequencies would cancel one another at the recording site.

We introduced an asymmetry into a radial stimulus pattern by surrounding concentric contrast-reversing zones of the pattern with contiguous static zones. During one cycle of contrast reversal, the percept changed from that of a windmill to a dartboard. This asymmetrical stimulus arrangement resulted in the generation of a large fundamental component and the attenuation of the prominent second-harmonic component normally generated by contrast reversal alone. The manner in which these two effects on the VEP vary with changes in stimulus parameters provides information concerning lateral interactions within the human visual system.

## MATERIALS AND METHODS

The basic windmill-dartboard pattern (1) is illustrated in Fig. 1*A Right*. All other patterns used (Fig. 1*A Left*, Figs. 2–4 *Insets*) were variations on this one. The results do not depend on the radial design, which was chosen to match the radial distribution of spatial resolving power around the fovea and thus improve the signal/noise ratio (2–6). The stimuli were generated on the screen (P31 phosphor) of a microcomputer-controlled oscilloscope (7). The display subtended a visual angle of 5° (viewed binocularly at 1 m). Mean luminance was 197 cd/m$^2$. Contrast of pattern segments was defined by the equation $(L_{max} - L_{min})/(L_{max} + L_{min})$, where $L$ is luminance. We used standard methods and procedures for recording and analyzing the VEP (1, 8, 9).

The pattern changed back and forth from windmill to dartboard when the contrast within the first and third annuli was constant at 30% while the segments of the central disc and the second annulus were temporally modulated (contrast reversed), with their peak contrast also at 30%. The extreme phases of this varying pattern are shown in Fig. 1*A Right*. When contrast of all segments in static zones was set at 0% so that dynamic zones were surrounded by homogeneous fields of light (equal in space-average luminance to dynamic zones), a different pattern was produced, with extreme phases as shown in Fig. 1*A Left*.

The temporal signals used to modulate contrast were a square wave (frequency, 1.02 Hz; duration, 2.0 min) and a sine wave (frequency, 4.19 Hz; duration, 1.0 min). The abrupt contrast reversals produced by square-wave modulation elicited so-called transient VEPs containing several rapid deflections. Sine-wave modulation elicited so-called steady-state VEPs having a much smoother wave form. For comparison, we first demonstrated the basic phenomena with both sine-wave and square-wave modulation. For our detailed analysis, we used sine-wave modulation only.

## RESULTS

**Square-Wave Modulation.** Typical VEPs elicited by square-wave temporal modulation of these two stimulus patterns are shown in Fig. 1C. With static contrast at 0% (*Left*), transient VEPs are elicited at twice the frequency of square-wave modulation—once at each reversal of contrast. VEPs resulting from each direction of square-wave contrast reversal are essentially

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Abbreviation: VEP, visual evoked potential.

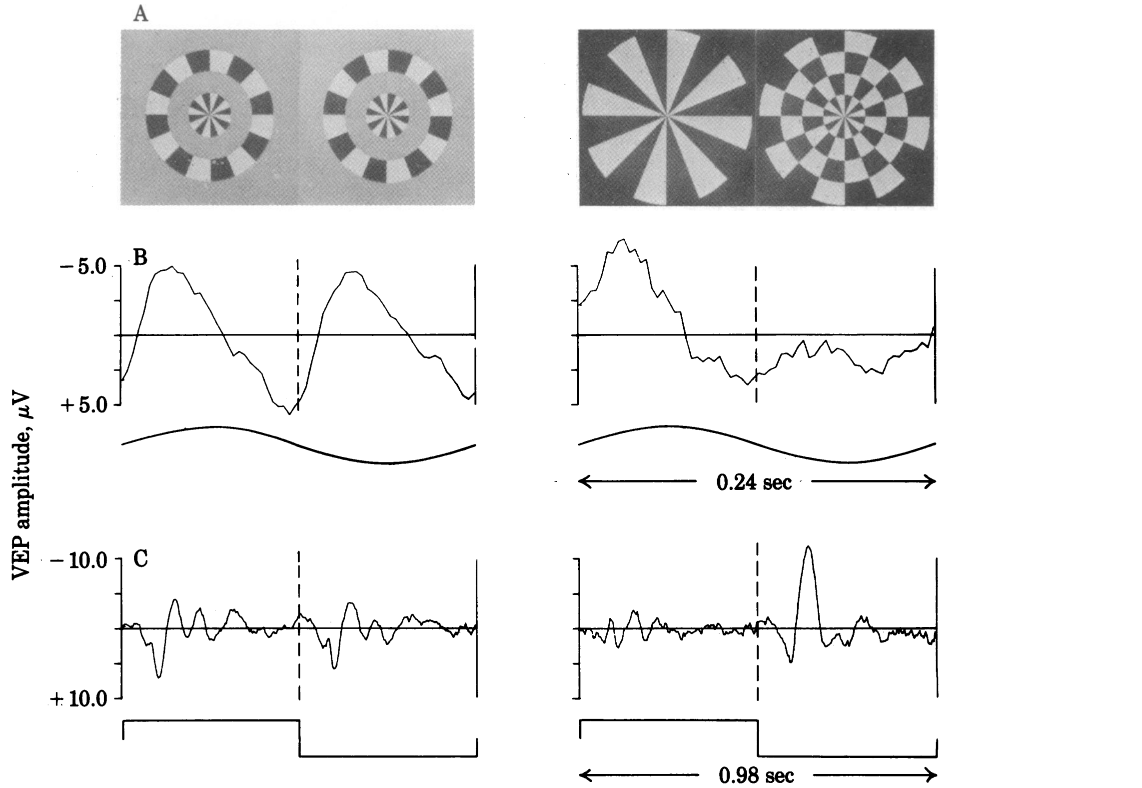


FIG. 1. (*A*) Windmill-dartboard patterns. (*B* and *C*) Amplitudes of VEPs elicited by sine-wave and square-wave contrast reversal, respectively, of dynamic segments of a dartboard when static segments are set at 0% (*Left*) and at 30% contrast (*Right*). Shown below each record is 1 cycle of the temporal signal used to reverse contrast.

identical. As expected, they are similar to those obtained from square-wave contrast reversal of conventional grating or checkerboard patterns (10). With contrast of static zones at 30% (*Right*), VEPs at succeeding reversals are very dissimilar. Unexpectedly, when the pattern switches to the windmill phase (first half-cycle) the negative wave of the VEP is greatly attenuated; when the pattern switches to the dartboard phase (second half-cycle) the negative wave is greatly amplified. [Application of bicuculline, a γ-aminobutyric acid blocker, to cat visual cortex produces a similar enhancement of negativity of the VEP elicited by conventional contrast reversal of grating stimuli (11).]

**Sine-Wave Modulation.** Typical VEPs elicited by sine-wave temporal modulation are shown in Fig. 1*B*. With static contrast at 0% (*Left*), the VEP elicited by sine-wave modulation shows frequency doubling. Potentials in each half of the cycle are essentially identical (as with comparable square-wave modulation). The saw-tooth wave-form indicates that there are also strong fourth-harmonic components. There is no significant component at the fundamental frequency of the sine wave. Presumably, out-of-phase potentials evoked by opposite luminance changes at the fundamental frequency average to zero when summed at the recording electrode. With contrast of static zones at 30% (*Right*), the second-harmonic component of the VEP is much attenuated and there is a strong fundamental component, negative during the first half-cycle (windmill phase), positive during the second half (dartboard phase). The question immediately arises: What is the dependence of these two components on the amount of contrast of the static pattern?

**Static Contrast.** We investigated this dependence by varying the static contrast over the range 0% to 95% in successive measurements while holding the peak dynamic (sine-wave-modulated) contrast at 30%. Results of one such experiment are shown in Fig. 2. (*Inset* is a pattern with static contrast one-half the peak dynamic contrast.) The amplitude of the fundamental component of the VEP is at the noise level when static contrast is 0%, increases with increasing static contrast to a maximum when static contrast is approximately equal to peak dynamic contrast, and then decreases with further increases in static contrast. If the peak dynamic contrast is set higher or lower, the maximum amplitude of the fundamental component shifts accordingly. Dependence of the fundamental component of the VEP on contrast of the static zones differs significantly from that of the second harmonic. The amplitude of the VEP at the second harmonic is greatest when static contrast is zero and decreases monotonically as static contrast increases. [Another example of attenuation of the second harmonic has been reported: the amplitude of the second harmonic generated by a contrast-reversing checkerboard is reduced by a trellis of black lines laid over the borders of the checks (12).]

**Spatial Phase.** We varied the contrast between the static zones and the dynamic zones in a different way by adjusting the spatial phase. Static contrast and peak dynamic contrast were both set at 30%. A measurement was made, as in the previous experiment, with all static and dynamic segments within each vane of the pattern in line. Then a measurement was made with the segments of the first and third (static) annuli rotated 5.625° with respect to the dynamic segments. This process was repeated with rotation increments of 5.625° until the segments were in line again. Fig. 3 shows the data obtained from one subject during one such session. (*Inset* is a pattern with the static segments shifted halfway across one vane of the pattern, a rotation of 11.25°.)

The fundamental component of the VEP depends strongly on spatial phase. The maximal amplitude of the VEP at the fundamental frequency occurs when the static and dynamic seg-

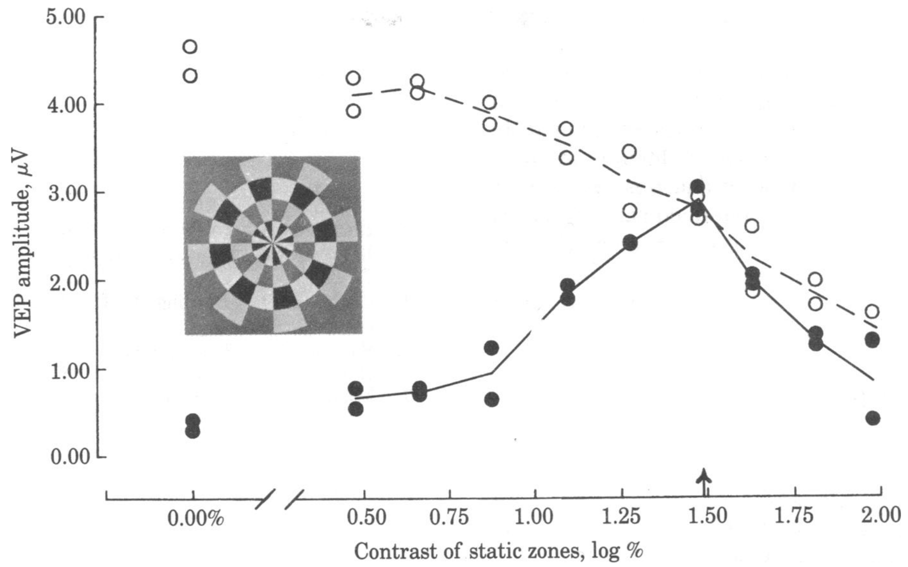


FIG. 2. Amplitude of the fundamental (●) and second-harmonic (○) components of the VEP as a function of the logarithm of the percent contrast of static segments of the stimulus pattern. At left, static contrast is set at 0%. Pairs of data points (here and in Figs. 3 and 4) are from an ascending and a descending series of measurements. Peak contrast of the dynamic (contrast-reversing) segments is 30% (arrow on abscissa). (*Inset*) Pattern with static contrast one-half peak dynamic contrast.

ments are in line. Under this condition, the contrasts across all borders from static to dynamic zones vary sinusoidally by the same magnitude and with the same sign. The minimal amplitude of the VEP at the fundamental occurs when the static and dynamic segments are farthest out of line. Under this condition, the contrasts across all borders between static and dynamic zones vary sinusoidally by the same magnitude but with opposite signs in adjacent halves of the misaligned segments. The second-harmonic component of the VEP is strongly attenuated at all spatial phases. (Compare with the control condition in which the static contrast was set at 0%.) Thus, the misalignment of static and dynamic segments markedly reduces the amplitude of the VEP at the fundamental frequency, but it decreases the attenuation of the second harmonic only slightly, if at all.

**Spatial Separation.** We tested the idea that contiguity of contrasting static and dynamic (sine-wave-modulated) segments is essential for amplification of the fundamental and attenuation of the second-harmonic component. We separated static and dynamic zones with a narrow uniform annulus of the same mean luminance as the patterned zones and of variable width. (See *Inset* in Fig. 4.) To localize the effect better, we used only the dynamic inner disc and a single static annulus (outer diameter, 4.67° of visual angle) containing segments of equal contrast to those in the disc (30%). The result of separating the static and dynamic zones is dramatic. The amplitude of the VEP at the fundamental frequency decreases noticeably with the smallest separation and plummets into the noise with a separation, in visual angle, of only a few minutes of arc—about 300 μm of cortex in the foveal projection area (13). The VEP at the second harmonic, however, follows the opposite course and increases significantly, but more gradually, as the separation of the static and dynamic zones increases.

**Intermodulation.** The effects of static contrast, spatial phase,

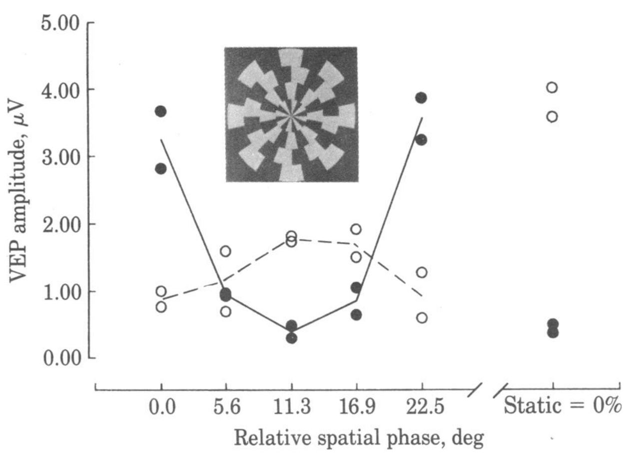


FIG. 3. Amplitude of the fundamental (●) and second-harmonic (○) components of the VEP as a function of relative spatial phase (in deg. of rotation) of the dynamic and static segments in contiguous zones of the stimulus pattern. At right, static contrast is set at 0%. (*Inset*) Pattern with static segments shifted halfway across one vane.

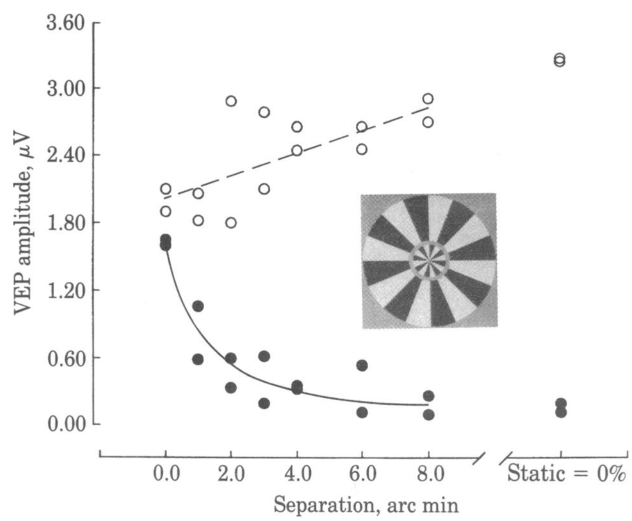


FIG. 4. Amplitude of the fundamental (●) and second-harmonic (○) components of the VEP as a function of separation of static and dynamic zones (in min of arc of visual angle) of the stimulus pattern. At right, static contrast is set at 0%. (*Inset*) Pattern with static and dynamic zones separated by a narrow uniform annulus having the same mean luminance as the patterned zones.

and spatial separation all point to variations in relative contrast of the static and dynamic segments in contiguous zones as the most significant feature of the stimulus. It should be possible, therefore, to produce equally effective variations in relative contrast by temporally modulating the contrast of segments in two contiguous zones simultaneously and at different frequencies. Preliminary experiments indicate that this reasoning is correct: strong VEPs are generated at intermodulation (sum and difference) frequencies that fall in the proper temporal range (9, 14). (The fundamental component observed in the experiments reported here is simply a special case of intermodulation that appears when one of the two frequencies is zero.)

## DISCUSSION

All of our experimental evidence is consistent with the hypothesis that highly localized lateral interactions, resulting from varying contrast at common borders of contiguous static and dynamic segments of the windmill-dartboard stimulus, amplify the fundamental component of the VEP. In addition, the presence of static contrast in the stimulus attenuates the second-harmonic component elicited by contrast reversal. The amplification of the fundamental and attenuation of the second harmonic have radically different characteristics; one is not simply the inverse of the other. These differences provide clues that may help further to identify and to localize the underlying neural mechanisms in the visual pathways.

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