Visual-evoked responses elicited by the onset and offset of sinusoidal gratings: latency, waveform, and topographic characteristics

D. M. Parker, E. A. Salzen, and J. R. Lishman

Transient evoked potentials (VERs) elicited by the onset and offset of sinusoidal gratings have been investigated. Results indicated that an increase in amplitude and a decrease in latency characteristics of the VER occur as monotonic functions of increasing contrast. The latencies were shorter for low than for medium spatial frequency gratings up to contrasts of 0.51. Previous reports of the latency of the VER increasing as a monotonic function of increasing spatial frequency are confirmed. Topographic studies of the scalp distribution of VERs indicated that the sites of maximal response were similar for low and medium spatial frequencies and that potentials elicited by stimulus offset had a similar distribution to the early onset response. These results indicate that the same cortical region may be responsible for generating these potentials despite their different latency and trigger features. Additional data are presented to illustrate the likely effects of differential recording on the waveform of the VER.

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In recent years a number of studies have investigated the properties of transient visual-evoked responses (VERs) elicited by sinusoidal gratings. These studies have found systematic variations in amplitude, waveform, and latency produced by changes in the contrast and spatial frequency of the stimuli. There are uncertainties in the interpretation of these VERs because information on their sites of origin is lacking. The shifts in peak latencies as spatial frequency is increased might simply reflect changes in components from separate cortical areas. Jones and Keck, using a differential recording technique, have claimed a pattern of latency changes and waveforms of the VERs that are quite unlike those of our own or of other comparable studies. It is unclear whether these differences are real or whether they are attributable to the differences in recording technique. Finally, it is possible that use of high-contrast gratings to elicit VERs may give a different pattern of results from those obtained with medium- and low-contrast stimuli because of saturation effects.

In the present study, we have obtained data on the site of origin of VERs elicited by sinusoidal gratings, the effects of contrast on amplitude and latency, the pattern of latency changes with increasing spatial frequency, and the likely effects on the VER of using differential recording techniques.
Methods

Visual stimulation. The stimuli were vertical sinusoidal gratings generated on a Tektronix Model 604 display oscilloscope according to the method of Campbell and Green. The gratings could be turned on and off without altering the mean luminance of the screen, which remained at 10.0 cd/m². The voltage applied to the z-axis of the oscilloscope could be attenuated to provide any required contrast between 0.0 and 0.51, at which value the spot intensity saturated. Contrast was defined as \( C = \frac{L_{\text{max}} - L_{\text{min}}}{2L_{\text{mean}}} \), where \( L \) is the luminance of any point on the screen. Luminance and contrast measurements were made with a photometer (Model 2020, Gamma Scientific, Inc.). The screen was masked to produce a circular or hemifield display area, and the surround was illuminated to produce the same mean luminance and color as the oscilloscope screen. The center of the field contained a small black spot to aid fixation when no grating was present on the screen. Viewing was binocular from a distance of 1.0 m.

Stimuli were presented at the rate of approximately 0.4 Hz, a random time delay of 0 to 200 msec being included to prevent electroencephalogram (EEG)-locking artifacts. The rise time of the stimuli was less than 2 msec. Except where noted, the stimulus duration was 200 msec, this being the minimum duration at which separate components to onset and offset of stimulation are apparent and do not interact occlusively. It is also the duration at which the apparent contrast of a single brief presentation matches the contrast of a continuously present grating.

Recording techniques. Conventional Ag-AgCl cup electrodes were secured to the subject’s scalp with collodion in the pattern desired for the par-
Fig. 2. Amplitude profiles of the early onset (●) and offset (○) waves at 1.0 (left, four subjects) and at 6.0 C deg⁻¹ (right, three subjects). The amplitude of the offset generated positive-going wave has been measured from the following negative peak for subjects V. M., I. M., and D. P. and from the preceding negative wave in subject R. N., who was run with a 300 msec stimulus duration (see extreme right of figure). These measurement baselines were selected to facilitate comparison between onset and offset waves (see text). Total sweep duration 500 msec. Stimulus was a centrally viewed 6° circular field. Contrast values: subject V. M., 0.5; subjects I. M. and D. P., 0.33; subject R. N., 0.21.

Subjects. The results presented in this report are based on data obtained from 12 subjects between 20 and 35 years of age. Subjects were either emmetropic or had corrected vision.

Peak identification and measurement. We identified PI as the first large positive peak and NI as the preceding negative peak. The off-response is the maximum positivity occurring after the end of the stimulus period. In the topographic study, the
positions of the peaks were fixed at the latencies of those at the OZ position (see Fig. 2, extreme right).

Results

**VER as a function of grating contrast.** Fig. 1 (top left) shows the amplitude of the N1-P1 wave of the VER at the OZ position as a function of contrast at two spatial frequencies for two subjects. It can be seen that as contrast increased there was a monotonic increase in the amplitude of this early wave elicited by stimulus onset. Below contrasts of 0.12, the gain of the VER appears to be lower than it is above this value. Accordingly, two linear functions, fitted by the method of least squares, are indicated by the dashed lines. The peak latency of the P1 as a function of contrast is indicated also in Fig. 1 (bottom left), where it can be seen that as contrast increased peak latency became progressively shorter. Because of the wider scatter of the latency data at low contrasts no attempt has been made to fit a curve to the results. Although these data have been plotted only for the early positive wave, inspection of the VER waveforms showed that there was a general trend for all peaks to fall in amplitude and increase in latency as contrast was reduced.

**Latency changes with spatial frequency.** Seven subjects participated in this phase of the experiment, which used medium contrast (C = 0.21) gratings of 300 msec duration. The results for the OZ electrode are displayed in Fig. 1 (right), where the group average data show an increase in latency at spatial frequencies above 3 C deg^{-1}. Some indication of the subject variability is given in the figure by the values for the two most extreme subjects. All showed a minimum latency between 0.5 and 3.0 C deg^{-1}, with three subjects showing minimum at 0.5 C deg^{-1}, two at 1.0 C deg^{-1}, and one each at 2.0 and 3.0 C deg^{-1}, respectively. Only the data for the early positive wave have been plotted, but a similar change occurred in all peaks of the VER.

**Topographic features of VERs.** Recordings were made from a midline row of six electrodes running from inion to vertex. The results obtained with 1.0 and 6.0 C deg^{-1} gratings are displayed in Fig. 2. The values plotted were obtained by measuring the amplitude from the peak of the first positive deflection to stimulus onset to the peak of the preceding negative wave and, in the case of the offset response, from the peak of the first positive wave to the peak of the following negative wave, except in the case of subject R. N., where a 300 msec stimulus allowed use of an uncontaminated previous baseline. In both onset and offset responses it is apparent that the values have maxima in the occipital region. Furthermore there is a close correspondence in the amplitude profiles. Only one subject (D. P.) showed a slight relative shift in the peak location of the offset response and the profile is rather flat in this case. In the case of the 6.0 C deg^{-1} stimulus only one subject (R. N.) showed a clear offset response of sufficient amplitude to allow the production of an amplitude profile. It is perhaps worth emphasizing that the interest in these topographic studies is the location of the maximal response of the component measured. Whether a baseline-to-peak or a peak-to-peak measure is used does not affect the location of the maximum value. If absolute values were used (baseline to peak) this would have the effect of shifting the curves up or down the amplitude axis.

We examined the waveform of monopolar recordings obtained from electrodes placed in the midline and in lateral positions and compared these with the waveform of the potential difference between these sites (differential responses). The electrode sites and sample responses are displayed in Fig. 3, and it is clear that the difference potentials have waveforms that are dissimilar from those of the monopolar recordings. In particular it should be noted that the major positive deflection of the monopolar waveform (P1) coincides in latency with the major negative wave of the differential waveform (N1), whereas the N2 of the monopolar waveform (after the P1) coincides in latency with the major positive deflection of the differential waveform. A second noticeable feature of the differential waveforms is that their amplitude
Fig. 3. VERs recorded from a midline (OZ) and two lateral positions, O1 and O1 plus 10% of the distance from OZ to F polar point. The bottom two rows of responses are the potential differences between the OZ position and each of the two lateral positions. Note that these differential potentials do not reproduce the monopolar waveform recorded at any of the three electrode positions and may lead to erroneous comparisons between peaks; for example, in this case surface positive waves become negative waves in the differential records.

Discussion

The present results show that the amplitude of the early negative-positive deflection of the VER increases monotonically up to stimulus contrasts of 0.51 without evidence of saturation. Kulikowski and Leisman9 have also found a monotonic increase in the amplitude of this same component up to contrasts of 0.7. The progressive increase in the latency of VER components with decreasing stimulus contrasts found in the present study is also expected. It is probably an analogous effect to that of increasing latency with decreasing stimulus luminance previously reported by Vaughan et al.10 It does, however, emphasize the great care needed in specifying evoked potential components purely in terms of their latency.

The latency changes with spatial frequency previously reported by Parker and Salzen3-4 have been confirmed in the present study with stimulus contrasts lower than those previously used. It is clear from the results on the contrast gain of the VER that these latency changes were obtained with values far below those at which any contaminating effect of saturation may occur. Furthermore, Fig. 1 (bottom left) indicates that latency differences between a 1.0 and 6.0 C deg\(^{-1}\) grating were maintained throughout the contrast range tested. There was a tendency for subjects to show a minimum latency below 3 or 4
cy/deg as in the case of B. T.11 Our unpublished records for 22 subjects confirm this with three exceptions.

The topographic data show that the early negative-positive deflection of the VER to the onset and to the offset of stimulation is maximal in the occipital region close to the OZ position of the 10-20 system. Although the offset response is poor at high spatial frequencies (see Fig. 2), when a response was measurable, the scalp topography remained the same. The topographic data on the early onset response suggest that despite the different latency of this wave at 1 and 6 cy/deg, the response at both spatial frequencies is generated in the same cortical region. Although it is not possible to state with certainty that the early positive response is generated in striate cortex, our data are certainly compatible with such an interpretation.

Our data on the lateral topography of the VER show the difficulty of comparing records obtained by differential recording with those obtained by monopolar recording unless recordings from a number of sites are obtained. The difference potentials obtained in our study agree well with the differential recordings of Jones and Keck,6 even to the detail of a small positive-going potential appearing at the lowest spatial frequency. However, our data suggest that the peaks of the VERs in the Jones-Keck study may have been misidentified in comparison with those of Kulikowski and Leisman9 and Parker and Salzen,3,4 and in particular that the N1 of Jones-Keck results may correspond with what is usually called the P1 in monopolar recording. The suggestion made by Jones and Keck that the small amplitude (N0 – P0) early wave seen at low spatial frequencies reflects the activity of a transient system is difficult to evaluate given the difficulties raised by their chosen recording method. Although it is apparent in our records that at low spatial frequencies there is a positive potential difference between midline and laterally placed electrodes, there are no direct grounds for identifying this difference potential with the activity of a transient system.

REFERENCES