RESEARCH NOTE

CYCLOPEAN VISUAL EVOKED POTENTIALS: A NEW TEST OF BINOCULAR VISION

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Abstract—A new objective method is described to test binocular vision. Identical gratings are presented to each eye, but they are drifted in opposite directions. Uniocular stimulation does not produce a response, but binocular combination of the gratings results in robust visual evoked potentials. Data from cats are presented to illustrate the use of this technique.

Binocular vision  Visual evoked potentials  Cats

The assessment of binocular vision is difficult or impossible if a subject is unable to fuse images from each eye and respond to instructions. We have developed a technique which resolves this problem by use of a novel stimulus to elicit visual evoked potentials (VEPs). The key to this procedure is a decomposition of a visual stimulus into two components, one delivered to each eye. Each component by itself is an ineffective VEP stimulus and causes no response. However, when the segregated components are combined in the brain, a clear VEP response is obtained. This response is a cyclopean VEP, because it is elicited only when the two monocular components are combined (Julesz et al., 1980). Data from cats show that these cyclopean VEPs are robust, and that precise eye alignment is not required. Orientation of the stimuli, however, must be closely matched in the two eyes. This technique should provide new information on binocular function which cannot be obtained by other means.

A coordinated combination or fusion of images from the two eyes affords highly developed binocular vision to a wide variety of animals. Like other visual processes, this function develops to nearly full capacity in early postnatal months both in humans and other animals. If the developmental process is abnormal, serious detrimental consequences can occur resulting in visual disorders that are apparently permanent (see reviews by Mitchell and Timney, 1984; Frégnac and Imbert, 1984). It is therefore of critical importance to try to assess binocular function as early as possible, using an objective method. We have developed a new procedure which appears to provide this measurement in a clear and robust manner. In this report, we present data from cats to illustrate the features of the method and to explain its basis.

Consider the basis first. A standard stimulus used in vision research is a repeating pattern of light and dark bars (a grating) whose luminance varies sinusoidally across the bars. To elicit VEPs, temporal changes in the pattern are required. Clear VEP responses are generated by modulating the contrast of the pattern in time, sinusoidally. This pattern is stationary in space, but its phase is reversed in time to produce a standing wave, i.e. a counter-phased grating. We now note the following principle of wave theory. A counter-phased grating can be broken into two components, each a sine-wave of identical amplitude and frequency, moving in opposite directions at the same speed. The interesting feature of this decomposition is that each drifting grating component by itself, does not elicit any VEP response, while the original counter-phased grating is a very effective VEP stimulus. Since only the sum of the two components makes an effective stimulus, we wondered if it were possible to perform that summation at the level of binocular cells in the visual cortex by neurally combining the components presented to the separate eyes. The only way such a binocular combination can
generate a VEP is if a neural image of a counter-phased grating is synthesized from the activity caused by each drifting grating component. Such a scheme, by definition, requires a form of linear combination for the convergence of signals from the two eyes.

Our experimental results are consistent with this process. Figure 1 shows data from a cat that was prepared for physiological study using standard techniques (Sclar et al., 1986; Ohzawa and Freeman, 1986). Signals from recording electrodes were amplified, analyzed, and displayed, for the stimulus conditions depicted in the horizontal panel at the bottom. Results shown in the first two columns (A, A', B, B') are responses to a counter-phased grating presented to the left or right eye, respectively, while the other eye received no stimulus. Raw averaged VEP waveforms are shown in A and B, and corresponding amplitude spectra are illustrated in A' and B'. Waveforms are the result of averaging 200 sec of signals recorded from electrodes placed on the skull at Horsley–Clarke coordinates P4 and A20 along the midline. Note the clear response in A' and B' at 16 Hz which is twice the frequency of the stimulus. The response shown in C and C' is obtained by binocular stimulation using the same grating as in A and B. The binocular response is clearly larger than the monocular responses as found previously (Sclar et al., 1986). In the sequence illustrated in D, D', E, E', and F, F', the same stimulus set was used, i.e. left, right, and binocular stimulation, respectively. However, for these cases, the grating pattern is drifted instead of counter-phased. In marked contrast to the result in A, B and C, there is a complete lack of response in the VEP to drifting gratings. The condition of primary interest, i.e. gratings moving in opposite directions to each eye, is depicted by the last panel on the bottom. As shown in G and G', this stimulus pattern produces a clear response similar to those shown in A, B, and C. The magnitude of the

![Image: Figure 1. Cyclopean VEP responses from a cat are shown along with other measurements of monocular and binocular conditions. Each column represents a response to a stimulus condition depicted schematically at the bottom. The middle and top rows show raw averaged VEP waveforms and corresponding amplitude spectra, respectively. A, B, and C are responses to counter-phased gratings presented to the left, right, and both eyes, respectively. Similarly, responses to drifting gratings are presented in D, E, and F for the left, right, and both eyes, respectively. A cyclopean VEP, generated by gratings moving in opposite directions for the two eyes, is shown in G. For all conditions, the spatial and temporal frequencies were 0.3 c/deg and 8 Hz, respectively. Contrast was 50%. Orientation of the grating was horizontal for the right eye, but was tilted 9° from horizontal for the left eye (see text). Gratings were presented on a pair of Joyce Electronics displays with a mean luminance of 250 cd·m⁻² and a subtense of 22 × 22°. All conditions were randomly interleaved in a single run and presented in blocks of 10 sec for a total of 20 times.]


response is of the order of the monocular data shown in A and B. The response shown in G is clearly what would be expected if "opposite-drift" gratings are neurally combined to produce the effect of a counter-phased grating. Based on results of studies of single neurons, it is likely that the site of this neural combination is the visual cortex (Ohzawa and Freeman, 1986), but the current data do not permit precise localization.

For the results presented above (Fig. 1), the ratio of the cyclopean VEP amplitude to the mean of the monocular responses was 11.6 \((2G'/(D'^2 + E'))\) at 16 Hz. These findings have been confirmed by data from two additional cats. In these cases, the ratios were 10.1 and 28.7. Additional experiments have been performed to address the following question. What is the matching requirement for the grating stimuli presented to the two eyes? This question is important because it can help substantiate that the neural recombination as shown above is in fact the basis of the response. Since neurons in the visual cortex are orientation selective, and for a given cell, preferred orientation is well matched between the two eyes (Skottun and Freeman, 1984), the orientation of both gratings must fall within the tuning width in order to stimulate the same cell. Thus, matching of the orientations is required if the VEP results from binocular combination in single cells. In addition, for a counter-phased grating to be generated, component gratings should be well-matched in orientation. As orientation of one grating varies with respect to the other, the trigonometric relation referred to above breaks down, and the perceived combination becomes a moving plaider pattern (Adelson and Movshon, 1982). Therefore, the geometry of the stimuli also requires the matching of orientations.

Effects of orientation mismatch are shown in Fig. 2. In A, results are given for the condition in which the grating presented to the right eye was oriented horizontally. We then systematically varied the orientation of the grating presented to the left eye in steps of 3° about the horizontal. To avoid possible problems with adaptation effects or changes over time, we interleaved all orientations presented in quasi-random order. The resulting curve of Fig. 2A is striking in that it demonstrates a fine matching requirement between the gratings presented to the two eyes. The response is reduced to half at 8.7° away from the peak (9.0 and 11.5° for the other cats). Note also that the peak of the curve is shifted by 9° away from 0°, as indicated by an arrow at the top. This almost certainly reflects the cyclotorsion of the eyes that is normally found in an anesthetized, paralyzed preparation (Blakemore et al., 1972). Results in Figs 2B and C are for tests similar to that shown in A. In these cases, however, the primary orientation is rotated by 20° and 90° in B and C, respectively.

There are two reasons to obtain data for these latter conditions. First, the curve in A shows that the peak of the tuning function is close to horizontal. However, this could be due to a
selectivity for horizontal rather than a matching requirement. Second, it is of interest to examine how the presence of horizontal disparity in stimuli may affect the cyclopean VEP. Note that our initial experiment was performed by use of horizontal gratings which contained minimal horizontal disparity. This was done intentionally because, unlike stereopsis, the basis for the VEP has no inherent requirement for the presence of horizontal disparity. Therefore, the interpretation of the result would be simpler if we could avoid activation of the stereoscopic mechanism as much as possible. The peak of the tuning function shown in Fig. 2B is clearly shifted by about 20° from that of the curve in A. This indicates that it is indeed the matching requirement that is demonstrated by these narrow tuning curves. The results with vertical gratings (Fig. 2C) do not show a substantial response, although there is a detectable peak at 95–100° compared with the noise level indicated as “NULL”. Since the generation of the neural image of a counter-phase grating from components, should be isotropic with respect to orientation, the reduced response with vertical gratings is unexpected. The reduction of the response was also found for the other animals. One possible explanation for the reduced responses with vertical gratings is related to the difference in the perception that “opposite-drift” gratings evoke at vertical and horizontal orientations. With vertical orientation, the stimuli evoke a sensation of motion-in-depth, rather than that of a flickering counter-phased grating (Tyler and Sutter, 1979). On the other hand, motion-in-depth is not perceived with horizontal gratings. Therefore, it is possible that the generation of a cyclopean VEP is dependent on the perception of flicker, which may readily be achieved only with stimulus orientations near horizontal. It is also possible that the reduced response for vertical gratings is due to other forms of interaction between a number of binocular mechanisms.

The cyclopean VEP demonstrates the existence of a linear mechanism of binocular combination in the visual cortex. Previous studies of individual neurons and psychophysical tests of humans have also found evidence for a linear binocular combination (Ohzawa and Freeman, 1986; Shadlen and Carney, 1986). The cyclopean VEP therefore provides a third line of evidence leading to the same conclusion. Taken together, the results presented above show clearly that binocular function can be tested using cyclopean VEPs. The exact relationship of this measure to other estimates of binocular vision, as determined physiologically or psychologically, remains to be examined. It is clear, however, that the cyclopean VEP can be used to determine if at least some binocular function is intact. Furthermore, this measurement does not depend on stereoscopic vision. As such, it represents a valuable potential tool for use with human subjects.

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REFERENCES