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THE VISUAL EVOKED POTENTIAL AS A FUNCTION OF CONTRAST OF A GRATING PATTERN

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SUMMARY

1. It was shown that the potentials evoked by using a grating pattern alternated in phase at 8 Hz is proportional to the logarithm of the supra-threshold contrast. Other functions were considered, but they did not describe the data so parsimoniously.

2. The same logarithmic function described the results when a grating was simply flashed on and off; therefore, the apparent movement accompanying the phase alternations is not necessary to evoke the potential.

3. The contrast at which the evoked potential reached the theoretically zero voltage (C_0) was compared with the psychophysical contrast threshold, determined by means of proportion-of-time seen measurements; the C_0 contrast corresponded to 50 % time seen.

4. The potential, corrected for the proportion-of-time seen, was found linearly related to contrast.

INTRODUCTION

If a grating stimulus changes in phase at a rate of 8 Hz the evoked potential recorded from the human scalp bears a simple relation to the contrast (Campbell & Maffei, 1970). This kind of a stimulus offers several advantages. First, bars of the grating pattern are modulated about some fixed luminance so that the complication of light and dark adaptation is avoided. The potential evoked by this stimulus must then be due to the change in local contrast of the grating bars for there is no change in the total light flux which enters the eye. Secondly, only sets of neurones sharing common properties such as orientation (Hubel & Wiesel, 1959, 1962, 1965, 1968 and Campbell, Cleland, Cooper & Enroth-Cugell, 1968) and spatial frequency selectivity (Campbell, Cooper & Enroth-Cugell,

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1969) are likely to be activated. Thirdly, it is easy to elicit the evoked potentials by interchanging light and dark bars; that is, switching the position of the grating periodically through 180° of phase shift. Since each interchange elicits the potential, there are two responses for one cycle of presentation. When the rate of presentations is 8 Hz the wave form of the potential becomes almost sinusoidal (having a frequency of 16 Hz) which makes the amplitude measurement much simpler over a wide range of contrast in comparison with ordinary evoked potentials consisting of several components. Finally, accurate fixation of the target is not required providing the grating pattern covers the central part of the field of vision.

For small and medium contrasts the results obtained by Campbell & Maffei (1970) were fitted by a regression line described by

$$V = K \log (C/C_0) \quad \text{for} \quad C/C_0 > 1 \tag{1}$$

where V = the voltage generated, C = contrast of the grating used to elicit the potential, C_0 = the contrast at which zero voltage is generated, and K = a proportionality constant. They also found that the psychophysical threshold was always close to the C_0 contrast. This was so under a variety of circumstances such as, different spatial frequencies, monocular versus binocular viewing (Campbell & Maffei, 1970) and the orientation of the grating (Maffei & Campbell, 1970). In these papers, the authors were using the logarithmic regression fit empirically, in order to estimate thresholds objectively. In this way, they were able to show electrophysiologically that there were mechanisms in the human visual cortex which were selectively sensitive to orientation and spatial frequency.

Since Matthews (1931) suggested that there was a linear relation between the frequency of firing in single stretch afferents, in the frog, and the logarithm of the load, there have been many attempts to apply this relation to psychophysical events and just as many denunciations and efforts to replace it with other functions, particularly with power laws. Rosner & Goff (1967) review this controversial arena and return to the starting point by showing that Matthews's data can be replotted satisfactorily on log–log coordinates and therefore be described by a power law.

Although we have no evidence that the magnitude of the evoked potential is in any simple way related to sensation, we felt that the onus was upon us to examine more carefully the original empirical relation advanced by Campbell & Maffei (1970).

METHODS

Stimulus

Vertical gratings, the luminance of which varies sinusoidally along the horizontal axis were generated on an oscilloscope. The grating could be turned on and off or varied through 180° in phase. The contrast of the grating was controlled by means of a logarithmic step-attenuator. Any variations, either in time or in contrast, did not change the space-average luminance which was equal to 50 cd/m².

The grating was presented on a circular screen subtending 2° diameter. The subject was J.J.K.

Recording of evoked potential

One electrode was placed 2·5 cm above the inion, the other was placed 2·5 cm lateral to it (right side). The ground electrode was placed on the forehead. Signals were differentially amplified. Low and high pass filters, with slopes of 12 db/octave and corner frequencies of 8 and 25 Hz attenuated signals outside this range in order to improve the signal-to-noise ratio.

After amplification and filtering the signals were added in a computer of average transients (Enhancetron) or on a PDP-8 and subsequently divided by the number of repetitions.

It is particularly important to avoid artifacts arising from time-locked signals. Before each recording session, a control run was conducted with all the apparatus functioning and the subject seated before the display, but not viewing the stimulus.

RESULTS

Is movement necessary to evoke a potential?

In order to elicit evoked potentials from the scalp, Campbell & Maffei (1970) alternated the positions of the bright and dark bars of the grating, that is alternated the phase of the grating by 180°. This alternation of phase at 8 Hz is perceived as an apparent movement (the phi phenomenon). Thus, the question arises as to whether it is the perceived movement as such which generates the evoked potential, rather than the point change in contrast. This may be answered by comparing the potentials evoked by this change in phase with the potential resulting from simply displaying a grating and alternating it with a blank screen of the same average luminance at 8 Hz.

It can be seen from the inset of Fig. 1 that the resulting evoked potentials are different. The upper one, evoked by changing phase, is almost sinusoidal in wave form and has twice the presentation frequency, that is 16 Hz. The lower record, evoked by presenting a grating which alternates with a blank screen, has a dominant frequency component at 8 Hz. Sometimes a small component is seen which might be due to the termination of the grating exposure. In the later presentation the phi phenomenon is not seen and the grating appears only to flicker, but no movement is perceived. Thus, it may be concluded that perceived movement is not necessary to evoke the potential and either mode of presentation can be used to determine the threshold.

As expected (Kulikowski, 1971) the contrast threshold for these stimuli is different by a factor of almost two, as it can be seen from Fig. 1 (arrows).

In both cases measurement of the amplitude of the evoked potential also shows this difference. Note that at a given contrast the amplitudes do *not* differ by this factor but there is a translation along the logarithmic contrast abscissa of 0·2 log units. It is clear that either method of presentation can be used.

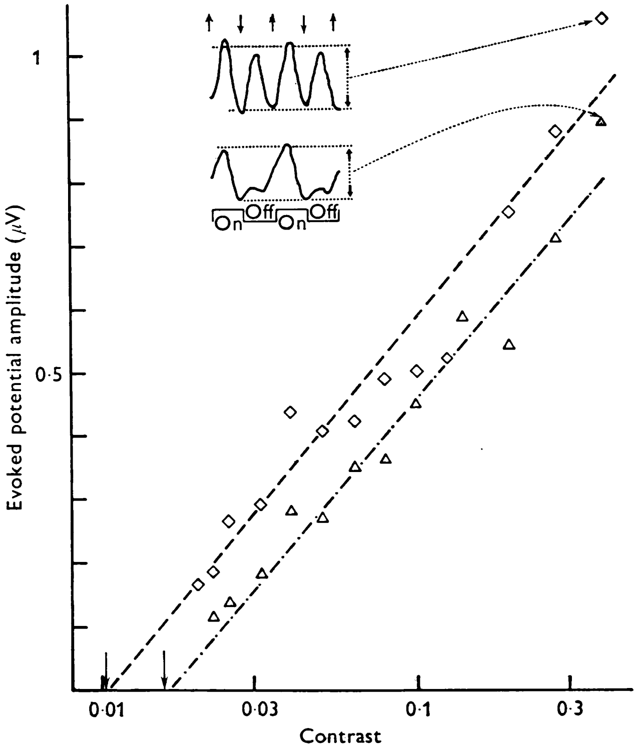

Fig. 1. Amplitude of the averaged potentials evoked either by alternating the phase of the 3·3 c/deg grating by 180° (◇) or by exchanging the grating with a blank screen (△) both at 8 Hz. The interrupted lines are regression lines. The arrows mark contrast thresholds. The inset shows the wave forms of potentials evoked by these two presentations.

The function, $V = K \log (C/C_0)$

In order to test the reproducibility of the logarithmic relationship, we measured the evoked response to a grating on three separate occasions. Responses were obtained for twenty-eight different contrast levels, each 0·05 log units apart. Regression lines were computed using the least square method. On the first occasion $K = 0{\cdot}60\ \mu$V and $C_0 = 0{\cdot}01$; on the second run, next day, $K = 0{\cdot}64\ \mu$V and $C_0 = 0{\cdot}01$; on the third occasion, 7 days later, $K = 0{\cdot}66\ \mu$V and $C_0 = 0{\cdot}012$. We conclude that good reproducibility can be achieved by this method.

In Fig. 2 these results are pooled and the variation of individual points can be judged by the vertical lines which represent ± 1 S.E. ($n = 3$). Almost all of the means are within 1 S.E. of the regression line so that it may be concluded that the fitting of a straight regression line is justified. For all the data $K = 0{\cdot}62\,\mu V$ and $C_0 = 0{\cdot}0107$.

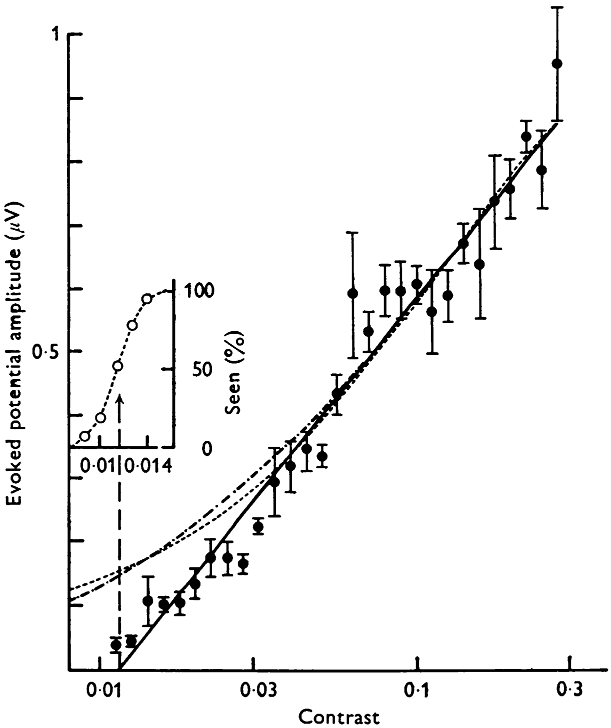

Fig. 2. Amplitude of the evoked potential as a function of the contrast of the 3·3 c/deg grating alternated at 8 Hz. The vertical bars represent $\pm$ S.E. ($n = 3$). The continuous line is the least-squares regression line fitting eqn. (1). The dash-dotted line fits eqn. (2) and the dashed line, eqn. (3). The inset shows the proportion-of-time during which a grating was seen at contrasts close to threshold (see Fig. 4*A*).

Probability considerations

It is well known that if a low intensity stimulus is presented a large number of times, it is sometimes detected and sometimes it is not. The proportion of times that it is detected gives a useful measure of its detectability. By repeating the observations for different intensity levels a frequency-of-seeing function may be established. Theoretically, a very weak stimulus if presented often enough will be detected on a very small number of occasions.

If the evoked potential is related to the psychophysical threshold then the function used in the previous section to describe the results appears to be unrealistic for it means that the amplitude of the evoked potential falls to zero at some finite contrast. Indeed, eqn. (1) even goes negative at lower contrasts. Possible alternative functions which asymptote to zero potential at low levels of contrast might be

$$V = K \log (C/C_0 + 1), \tag{2}$$

$$V = \tanh (KC)^n, \tag{3}$$

where n is an exponent.

Equation (3) has been found to fit much physiological data (Lipetz, 1971). Both these functions have been fitted to our data in Fig. 2 in such a way that their almost linear portions match the log fit of the data at medium and higher contrasts. It will be noticed that at lower contrasts neither of these two functions can fit the data (interrupted lines). However, the results at contrasts close to threshold appear to deviate also from the logarithmic function. We re-investigated the evoked potentials at contrasts close to threshold and we also measured the percentage of time during which presentations at a given contrast were seen.

The evoked potential at threshold

If the contrast of a grating, alternated in phase at a rate of 8 Hz, was set at very low levels of contrast the subject noticed that some of the time the grating was definitely seen and some of the time it disappeared. This waxing and waning of the appearance of the stimulus occurs slowly and irregularly with a periodicity of about 20 sec. We wondered whether it might be that the evoked potential was only generated when the grating was visible.

This was tested by arranging a switch, operated by the subject, so that the evoked potential could be stored in one half of the Enhancetron's memory when the stimulus was visible and in the other half when it was not visible. The results of adopting this strategy are illustrated in Fig. 3. In spite of the fact that the subject could not operate the switch in perfect harmony with the waxing and waning of the pattern's appearance, the results clearly demonstrate that the evoked potential was much larger when the pattern was visible.

The feasibility of this experiment made it possible to examine more closely the evoked potentials which are generated by contrast levels close to threshold. For five contrast levels around threshold, evoked potentials were measured as in previous experiments. In the course of accumulating these averages, the subject operated a switch to indicate whether he was seeing, or not seeing, the stimulus. The proportion of time that the switch

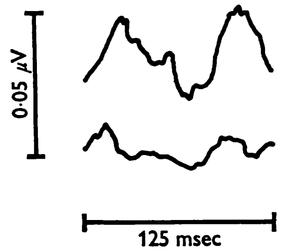

Fig. 3. The averaged potentials evoked by the grating alternated at 8 Hz when seen (upper record) and not seen (lower record). Contrast 0·01.

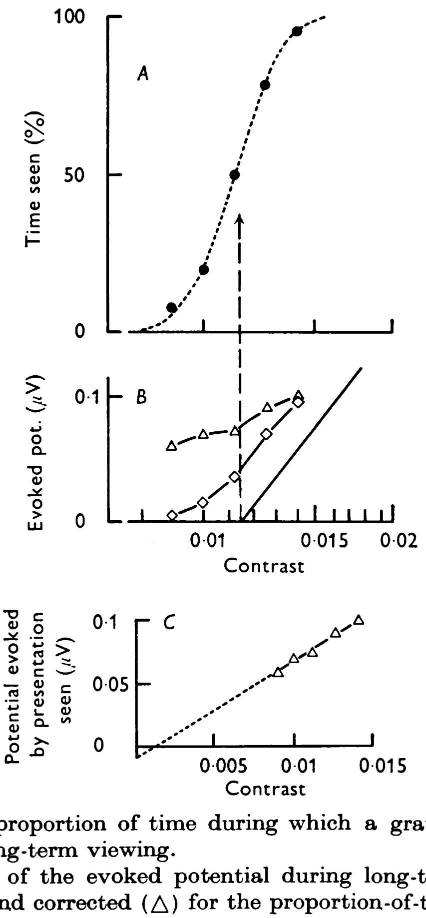

Fig. 4. *A*, the proportion of time during which a grating was seen in the course of long-term viewing.

B, amplitude of the evoked potential during long-term viewing not corrected (◇) and corrected (△) for the proportion-of-time seen.

C, amplitude of the evoked potential corrected for the proportion of time seen replotted from *B* on a linear scale of contrast.

was in each position was also measured, thus giving the proportion-of-time-seen.

For the five contrast levels used, the proportion-of-time-seen is plotted in Fig. 4*A*. This ogive has also been displayed in the inset of Fig. 2, and it will be noted that the C_0 value obtained in that experiment corresponds approximately to the 50 % proportion-of-time-seen obtained in this experiment. The squares in Fig. 4*B* represent the amplitudes of the evoked potentials obtained at each contrast level. The arrow represents the C_0 value obtained in Fig. 2. Note that in order to display these results we have magnified the contrast scale of Fig. 4 compared with Fig. 2.

DISCUSSION

Using single stimulus presentations, rather than those repetitive at 8 Hz, Campbell & Kulikowski (1971) were able to show that no significant evoked potential could be recorded when the subject reported that he could not see the grating stimulus in a frequency-of-seeing paradigm. If in the experiment described in Fig. 4, we assume that when the subject does not see the stimulus, zero voltage is generated, we can calculate the amplitude of the voltage generated by the 'yes' responses. Take the lowest contrast level measured, when the recorded voltage was 0·005 μV requiring 14,000 presentations to accumulate a reliable signal. At this level of contrast, the proportion-of-time-seen was 8 % so we multiply the recorded voltage by 100/8 to give us the corrected potential of 0·06 μV. This value is shown as a triangle in Fig. 4*B* at the lowest contrast level measured. Likewise, the other recorded voltages have been corrected.

These five values are now replotted on a *linear* scale of contrast in Fig. 4*C*. The straight line is the least-squares regression fit. It will be noted that the regression line extrapolates to close to zero voltage at zero contrast. The fact that the extrapolation passes so close to this point, which must on any theory exist, makes us feel that this rather extensive extrapolation is probably justified, particularly as its acceptance is forced upon us by the difficulty of obtaining data at lower contrast levels in the face of the rapidly decreasing proportion-of-time-seen. If we accept the assumptions of zero voltage (or almost zero) when the stimulus is not seen, as well as the rather weak quantitative argument based on an extensive extrapolation, then we may conclude that the evoked potential voltage decreases linearly with contrast in the range where probability arguments have to be used.

Can we now understand the nature of 'threshold' in this domain of contrast? As we can trace the evoked potential down as low as the 8 % frequency-of-seeing level and as the extrapolation of these results passes close to the zero of both the contrast and voltage axes, we can eliminate the idea that there is some finite contrast, or voltage level, determining the threshold. We can also discount the possibility that the fluctuations in contrast detection, which gives rise to the ogive at threshold, is due to noise added to the signal before it is detected. If additive noise produced a voltage to which the subject responded there would be no reason for this voltage to be proportional to the stimulus contrast level, as was found in Fig. 4*C*.

Consider the possibility that multiplicative noise accounts for the moment to moment variation in threshold. By this we mean that the gain in the system transmitting the contrast is varying with time and that this variation in gain is independent of the contrast being transmitted. These fluctuations could arise in some peripheral part of the nervous system or even be due to some physical phenomenon, such as saccades during the period of presentation of the grating. The resulting 'noise' in the contrast domain would be reflected in the voltage generated. But, because we have to average many responses to get a reliable measure of this voltage, each data point will tend to indicate the average contrast getting through to the site of origin of the evoked potential. Thus, when a regression line is calculated from all of the data it would indicate the 50% probability contrast threshold – assuming, of course, that the log relation is indeed the correct relation to use, which should now be discussed.

Over the years there has raged great controversy as to whether supra-threshold estimates of the magnitude of sensation obey a power law or a logarithmic law. Data obtained from neurophysiological experiments have been cited to support one or other side in the belief that there must be some logical, mechanistic link between the behaviour of nervous tissue and sensation (see reviews by Werner, 1968 and Rosner & Goff, 1967). Although we find a close connexion between evoked potentials and threshold determination of contrast, we do not yet have any relevant information about the psychophysics of suprathreshold contrast. As this may be forthcoming, we feel that the onus is on us to show definitely whether a power function would describe our results.

The simple power function considered in many early studies was

$$S = KI^n, \tag{4}$$

where S is the sensation, I is the stimulus intensity and K and n are constants. Of course, we are not considering 'sensation' here but a voltage.

In differentiating between the functions (1) and (4) practical difficulties arise. First, if data is available only over a limited range of the variable, either law can be fitted. Secondly, a dramatic difference between the two functions really only occurs if measurements are made very close to threshold. To illustrate these points we reproduce again the data from Fig. 2 plotted as before on log contrast and linear voltage (right-hand scale and straight line of Fig. 5). These are replotted on a double log plot (log contrast and log voltage on left-hand scale). On this scale a simple power function, such as eqn. (4), would be represented as a straight line.

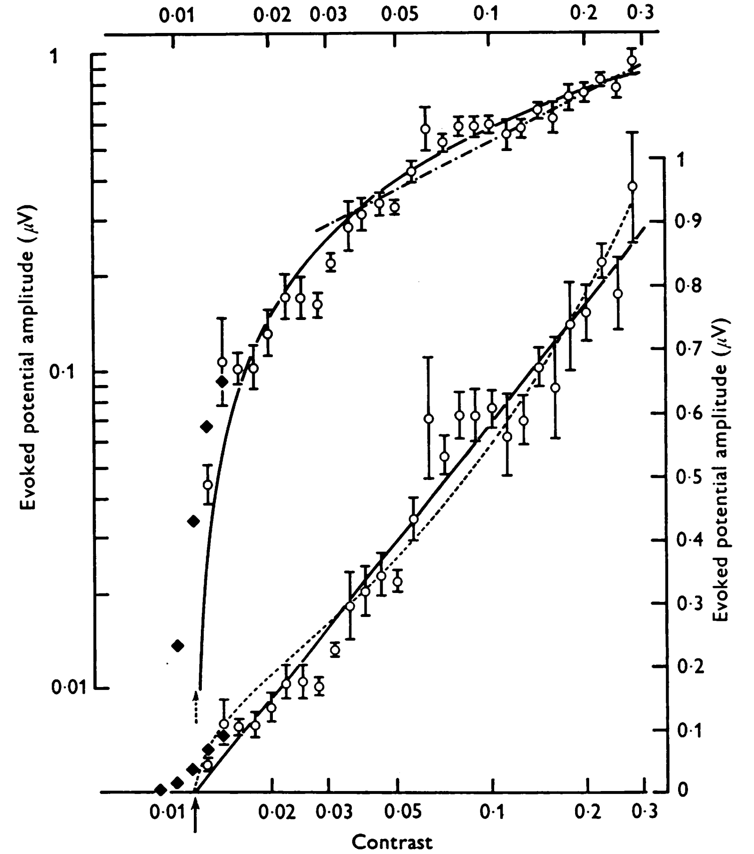

Fig. 5. Data from Fig. 2 (○) and from Fig. 4*B* (◇) plotted on a log–log scale (upper plot) and on a linear log scale (lower plot). The dash-dotted line shows an attempt to fit some of the data by eqn. (4). The dotted line fits eqn (5).

If we had only data for high contrast levels a straight line could indeed be drawn through the data, for example, as shown by a dash-dotted line in Fig. 5. When all the data are considered, a straight line fit is not appropriate, although even now much hinges on the precision of the lowest contrast points.

To make even more certain of our conclusion we have added the five low contrast results used in Fig. 4, and these are plotted as squares in Fig. 5.

It would thus seem that a simple power function cannot be fitted to our results.

In later studies of sensation magnitude, when data were collected close to threshold, it was noted that the simple power function (4) did not adequately describe the results. A modified power function was then introduced (Stevens, 1961). The embarrassing lack of fit at threshold of the simple power function (4) was overcome by subtracting the threshold as follows. In our case where the evoked potential is measured this leads to the equation

$$V = K(C-C_0)^n, \tag{5}$$

where V is voltage and K and n are constants. Here we shall consider contrast as the sensation modality under study, so that C is the contrast and C_0 is the contrast threshold. To see if our results fit this function we proceeded as follows.

We set C_0 equal to the 50% contrast at which proportion-of-time seen occurred (Fig. 3), which is almost identical to the value obtained by extrapolating the regression line used in the logarithmic fit. Using a computer, we then varied n and K in small increments and on each occasion calculated the mean square deviation of the data from the results expected from eqn (5). This was continued until the smallest mean square deviation was obtained. K then had the value $1{\cdot}727\ \mu V$ and n the value $0{\cdot}47$. The dotted curve in Fig. 5 represents the best fit statistically. Inspection by eye shows that there is little difference between the two formulations (1) and (5).

It is clear that there is only a small difference in practice between the logarithmic function (1) and the modified power function (5). In order to decide which is the better fit, we calculate the root mean square deviation of the data for each function. This was done not only for the three sets of results shown in Fig. 2 but also on six sets of results published by Campbell & Maffei (1970). In selecting the latter we only used experiments in which there were at least nine data points.

In almost every instance the root mean square deviation was less for the logarithmic function than for the modified power function in spite of the fact that the latter has more adjustable parameters (three). The ratio of the deviations were as follows: 1·12, 1·05, 1·00, 1·04, 1·36, 1·08, 1·16, 1·23 and 0·97. A value greater than 1 indicates that the logarithmic fit is better. The mean ratio is 1·11 with a S.E. of $\pm 0{\cdot}041$ ($n = 9$). This ratio differs significantly from unity ($P = 0{\cdot}02$). We may thus conclude that the logarithmic function (1) gives a more accurate and more parsimonious description of the results than the modified power function (5).

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