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ELECTROPHYSIOLOGICAL EVIDENCE FOR THE EXISTENCE OF ORIENTATION AND SIZE DETECTORS IN THE HUMAN VISUAL SYSTEM

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SUMMARY

1. The evoked potential in response to a grating alternating in phase at 8 c/s was recorded as a function of contrast from the occiput of man.

2. It was found that a linear relation exists between the log. of contrast and the amplitude of the evoked potential.

3. Extrapolation to zero amplitude voltage of the regression line between the amplitude of the evoked potential and log. contrast predicts the psychophysical threshold. This law was found to hold over the wide range of spatial frequencies tested.

4. Below 3 c/deg the results are best fitted with two regression lines; one of these is generated from the foveal and the other from the parafoveal representation in the cortex.

5. The slope of the regression lines was found to be almost independent of either the spatial frequency or the area of the stimulus grating.

6. The slope of the regression lines could be markedly increased by using as a stimulus either two different spatial frequencies, or two different orientations, presented simultaneously.

7. Using the evoked potential the selectivity to orientation was found to be so high that a channel was not influenced by another orientation 15° away.

8. The channels selectively sensitive to spatial frequency were highly selective and were not influenced by another spatial frequency one octave removed in spatial frequency.

9. It is concluded that in man there exist neurones highly selective to both orientation and spatial frequency.

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INTRODUCTION

There have recently been a number of investigations into the mechanisms responsible for the transmission of spatial information in the visual system. The basic technique used in these studies has been to employ a stimulus consisting of a repetitive pattern, such as a grating, that is modulated in contrast while keeping the space-average luminance constant. In this manner it is possible to detect the functional properties of the mechanisms responsible for the transmission of spatial signals in isolation from complicating factors such as light and dark adaptation.

Using this common approach, the spatial properties and orientational properties of neurones in the visual system of the cat (Enroth-Cugell & Robson, 1966; Campbell, Cooper & Enroth-Cugell, 1969) and squirrel-monkey (Campbell, Cooper, Robson & Sachs, 1969) have been studied and compared with psychophysical observations made in man (Campbell & Kulikowski, 1966; Blakemore & Campbell, 1969). At least two difficulties arise in making such comparisons. Firstly, there is no guarantee that the visual mechanism of the cat and monkey are sufficiently similar to that of man, either qualitatively or quantitively, to justify such a comparison. Secondly, in these studies comparisons have been made between data obtained at threshold, in the psychophysical studies, and at supra-threshold levels of contrast in the neurophysiological experiments. These and other problems may arouse a distrust of the psychophysical approach in the minds of many neurophysiologists. Here we examine the justification for comparing and contrasting neurophysiological and psychophysical findings. In this paper we use as a linking technique the potential which can be recorded from the scalp of man in response to a visual stimulus.

The results will be presented in two parts. Part I deals with the characteristics of the evoked response and its relation to the psychophysical threshold. In Part II evidence is presented on the existence of neurones selectively sensitive to orientation and spatial frequency.

METHODS

Stimulus. Gratings, the luminance profiles of which varied sinusoidally, were generated on an oscilloscope as described by Campbell & Green (1965*a*). The phase of the grating was altered by 180° at a rate of 8 c/s without changing the space-average luminance. The contrast could be varied either in steps of 1 db (0·05 log. units), with a step attenuator, or smoothly by manually rotating a logarithmic potentiometer. The degree of attenuation of the contrast was monitored by a Lab '8' computer (Digital Inc.) which was also used to record the data and compute the statistics.

Recording of evoked potential. One electrode was placed on the inion and the other 2·5 cm temporally. Signals were differentially amplified with an earth electrode applied to the forehead. High and low pass filters with corner frequencies of 8 and 25 c/s (12 db per octave) were used in the amplifier. The output was applied to a computer of average transients (Enhancetron). Normally, if the average evoked potential is measured by accumulating the sum of a number of responses to a stimulus which is repeated at a slow rate, the resulting response has a complex waveform in which several components can be identified. Using our narrow band-pass filters and stimulating at a temporal frequency of 8 c/s these components have been reduced so that the final record looks like a sinusoidal wave. This procedure is arbitrary, in the sense that it was found to yield a simple measurable response (Fig. 1). It is important to note that the evoked potential obtained by this technique is generated by the movement of the grating and that the light flux entering the eye is constant. Gubisch (1967) and Cobb, Morton & Ettlinger (1967) have used a similar stimulus.

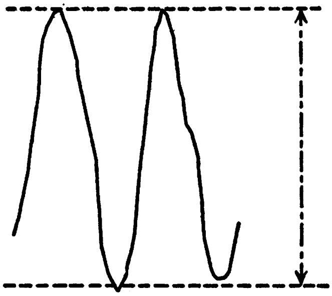

Fig. 1. A record of the averaged evoked potential obtained after 1000 averages obtained with a grating of 4 c/deg and a contrast of 1 log. unit above the psychophysical threshold. The duration of the record is 125 msec. The amplitude was gauged by eye as shown with the dotted lines.

At low contrast levels the potential recorded from the scalp is very small (about 1 μV) and several thousand responses have to be averaged to obtain a reasonable signal-to-noise ratio. It is therefore important to avoid any time locked artifact, arising from the stimulus equipment, entering the recording system. To ensure that such artifacts were not occurring, we found it useful to record for some time with the subject seated in his usual position but not looking at the stimulus grating.

RESULTS

Part I

Evoked potential and psychophysics

A grating of fixed spatial frequency was inspected by the observer and the experimenter reduced the contrast in steps of 0·05 log. units until the psychophysical threshold was reached. The precision of this setting is about ± 0·05 log. units. In the Figures this threshold contrast is marked with an arrow.

The contrast of the gratings was then increased in uniform steps and the evoked potential was measured for each contrast level. Fig. 2 shows the results obtained at spatial frequencies of 3·5, 9 and 18 c/deg. The abscissa is the contrast of the stimulus grating and the ordinate represents the amplitude of the evoked potential in relative units. It can be seen that, within this range of spatial frequencies, there is a linear relationship between the log. of the stimulus contrast and the amplitude of the evoked potential. The straight lines were fitted by the least-squares method. The gradients are not significantly different from each other. The dotted section of each line is the extrapolation of these lines to the zero voltage point. It will be noted that the psychophysical threshold contrasts (arrows) agree well with the zero voltage extrapolation.

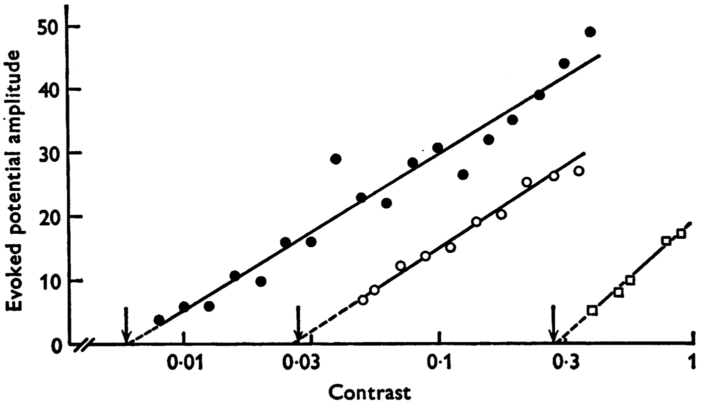

Fig. 2. The three sets of results were obtained at spatial frequencies of 3·5, 9 and 18 c/deg from left to right respectively. The arrows indicate the psychophysical threshold obtained at each frequency. The evoked potential amplitude is measured in relative units.

We have not attempted to investigate the behaviour of the evoked response closer than 0·1 log. units to the extrapolated zero voltage point. Although from the point of view of signal detection theory it would be interesting to know what does happen in this region it would take an inordinate amount of time to obtain the data. For example, in order to obtain a measurable response at 0·1 log. units above threshold, it was necessary to sum 5000 responses which, at 8 c/s, occupies some 10 min. To justify this linear extrapolation to within 0·01 log. units would theoretically require one hundred times this period, that is some 16 hr of summation.

Using a large field (5° × 4°) we found that at any spatial frequency less than 3·3 c/deg the results could not be described by one regression line. As an example, the results obtained with a frequency of 2·5 c/deg is shown by filled circles in Fig. 3. As can be seen, the results are well fitted with two regression lines. However, extrapolation to the zero voltage point of the shallower slope gives good agreement with the psychophysical threshold.

A possible explanation of this double slope is that at these low spatial frequencies the foveal contribution might be relatively small and the parafoveal contribution relatively large. This was tested by restricting the stimulus field to 2° diameter. The results are shown as open circles in Fig. 3. At low contrast levels the results can be fitted with a regression line which extrapolates to the psychophysical threshold, but at higher contrast levels the evoked potential reaches a constant amplitude. The slope of the regression line is shallow compared with that obtained at higher spatial frequencies such as in Fig. 2. Now we mask the central 2° of the field exposing only the parafoveal field. The subject fixated the centre of the field. The results are shown as squares in Fig. 3. These results can be well fitted with a single regression line. Its slope is not significantly different from the shallower slope obtained with the whole field (filled circles). This finding suggests that at low spatial frequencies the main part of the evoked response arises from the parafovea. The results obtained with the whole field cannot be accounted for by simple addition of the results obtained with the foveal and parafoveal regions.

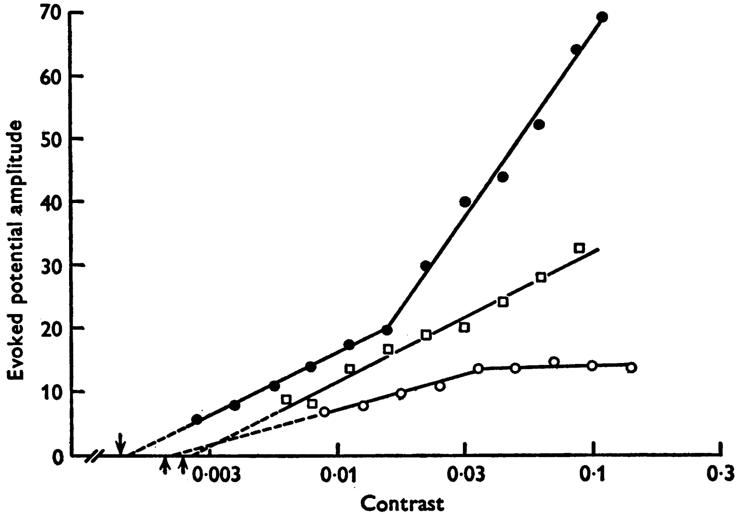

Fig. 3. These three results were obtained using a spatial frequency of 2·5 c/deg. For the filled circles (●) the screen dimension was 5° × 4°. For the open circles (○) the screen was restricted to 2° diameter. In the case of the squares (□) the central 2° diameter area of the screen was occluded.

In Fig. 4 we summarize the results obtained at many spatial frequencies. The closed circles are the contrast values obtained by extrapolating the evoked potential data to zero-voltage position. The open circles are the psychophysical thresholds. It will be noted that there is good agreement at all frequencies tested. It is well known that at frequencies less than 6 c/deg there is a decrease in contrast sensitivity. This has not been found here because the grating was being changed in phase at a rate of 8 c/s. Robson (1966) has shown that there is no low spatial frequency attenuation of the sensitivity function at this temporal frequency.

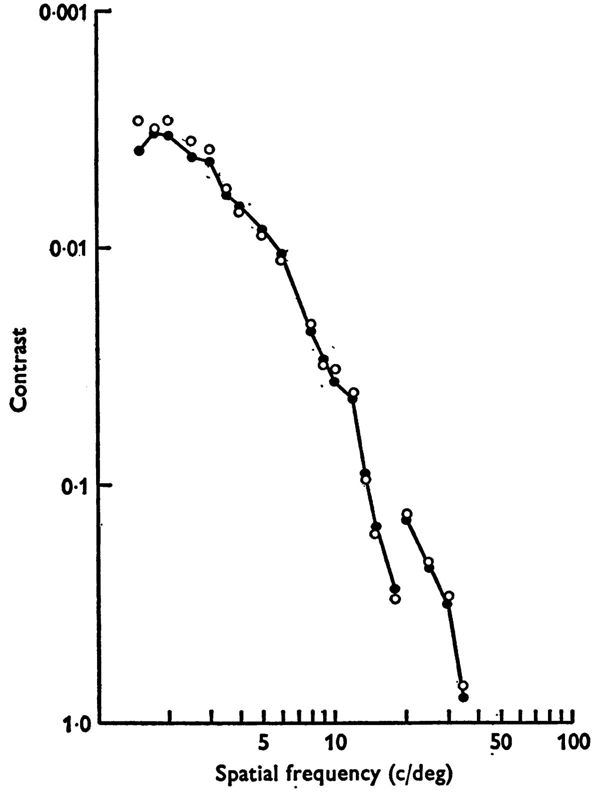

Fig. 4. The straight lines join the contrast value obtained by extrapolating to zero amplitude for a number of spatial frequencies. The open circles represent the psychophysical contrast threshold. The main curve to the left was obtained at a luminance of 9 cd/m^2 and the results to the right were obtained at a luminance of 21 cd/m^2.

This experiment was done with a large field (5° × 4°) using the full screen of the oscilloscope in order to avoid possible artifacts due to truncation of the grating. Under these conditions the space average luminance was only 9 cd/m^2. At this luminance the resolving power of the visual system is not maximal. We therefore repeated the observations with a smaller diameter field (1·6°) which had a higher luminance (21 cd/m^2). These are shown to the right of the main results in Fig. 4. Again there is good agreement between the evoked potential and psychophysical method even at the highest spatial frequencies.

The good agreement found so far between the psychophysical threshold and the evoked potential could be coincidental. For example, the gratings used to elicit the evoked potential have been orientated vertically and it could be that the particular position of the electrodes favours this agreement in the vertical meridian but not at other orientations. It is well known (Campbell, Kulikowski & Levinson 1966) that the visibility of gratings is less in the oblique meridians as compared with the vertical and horizontal meridian. We therefore tried the following experiment to see whether the changes in visibility were mirrored by changes in the evoked potential.

Evoked potentials were measured for a grating of 7 c/deg placed either in the vertical, oblique or horizontal meridian. As expected the contrast threshold for the vertical and horizontal gratings are very similar while the threshold for the oblique position is 0·3 log. units less. Again the extrapolation of the evoked potential results to zero voltage agrees with the measured thresholds. The regression lines were found to be parallel. To elicit an evoked potential of a given amplitude it is necessary to increase the contrast in the oblique meridian by about 0·3 log. units (× 2) relative to the horizontal and vertical meridians (Maffei & Campbell, 1970).

Now we would like to investigate what factors affect the slope of the relation between the log. contrast of the stimulus grating and the amplitude of the evoked potential. In an earlier experiment it was noted that potentials arising from the foveal part of the visual field had a shallower slope than potentials arising from the peripheral field. To simplify the problem we investigated only the central region of the field.

Consider the linear relation found between the log. of the stimulus contrast and the amplitude of the evoked potential (Fig. 2). Imagine that we increased the gain of the amplifier used for recording the evoked potential by a factor of two. Clearly, the slope of this function would increase also by a factor of two, while the zero-voltage extrapolation point would remain at a constant position on the log. contrast axis. It follows that it might be expected that if we increased the area of the retina stimulated and thus changed the area of the visual cortex activated, a change in the amplitude of the signal reaching the electrodes should occur, and an increase in the slope should result.

The results of changing the diameter of a centrally fixated grating from 0·25 to 0·5 to 1·5° are shown in Fig. 5. As expected the increase in the size of the stimulated field has indeed increased the slope of the regression line. The diameter has increased by a factor of 6 and therefore the area has increased by a factor of 36; but the slope has increased by a factor of only 1·6. Thus the slope is remarkably insensitive to a change in the area of the retina stimulated. Daniel & Whitteridge (1961) have shown in the monkey that the area of cortex representing the foveal reigon is very much greater than that representing the peripheral retina. Our results might be explained by the rapidly diminishing contribution of the peripheral parts of the field activated by the larger stimuli. This possible explanation has been tested more critically by confining the stimulus to parts of the retina with similar cortical representation.

A vertical grating of 8 c/deg subtending a visual angle of 1·6° diameter was used as the stimulus. The subject always fixated the centre of this circular field. The relation between log. contrast and amplitude was obtained, as described previously, under three conditions. Firstly, the circular field was horizontally masked so that only the upper half was exposed. Secondly, the experiment was repeated with only the lower half exposed. As expected, comparison of the results showed no significant difference either in the slopes or in the extrapolated zero-voltage position (or in psychophysical threshold).

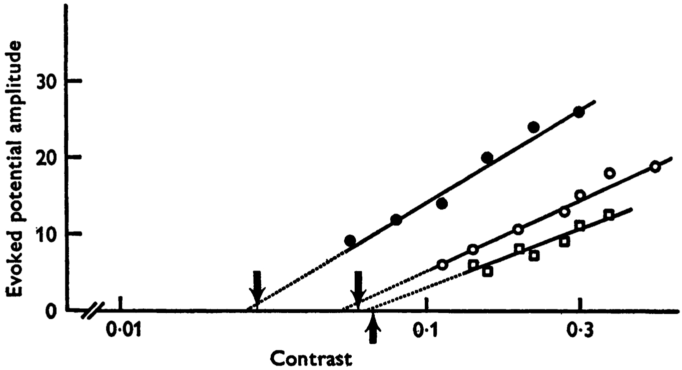

Fig. 5. Results obtained using three field sizes: filled circles (●) 1·5°, open circles (○) 0·5° and squares (□) 0·25°. Spatial frequency is 6 c/deg.

In the third experiment the complete field of 1·6° diameter was used as the stimulus. As can be seen from Fig. 6 the psychophysical threshold was reduced by 0·1 log. units, but the slope of the log. contrast versus amplitude relation for the whole field (●) was not significantly different from that obtained with a half field (○). The zero-voltage extrapolations agreed closely with the psychophysical thresholds.

We may thus conclude that doubling the area of the retina does not lead to any significant change of slope as we might have expected if the amplitude of the evoked potential was the result of the sum of the areas of cortex activated by the stimulus.

We now test the effect of doubling the input signal by comparing monocular with binocular vision. The results are shown in Fig. 7, where the circles represent the measurements obtained from left and right eyes viewing the stimulus independently and the squares give the results obtained when the stimulus was viewed binocularly. It can be seen from the position of the arrows that the psychophysical thresholds for monocular compared with binocular viewing differ by 0·15 log. units ($\sqrt{2}$). The regression slopes do not differ significantly from each other. Again the slope is not affected by doubling the input.

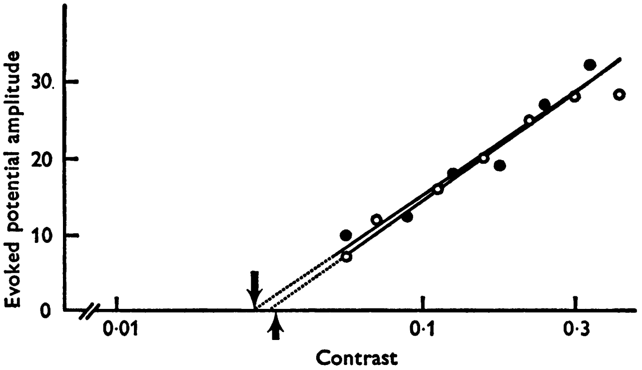

Fig. 6. The open circles (○) were obtained with only the upper half of the field exposed. For filled circles (●) the whole field (1·6° diameter) was exposed.

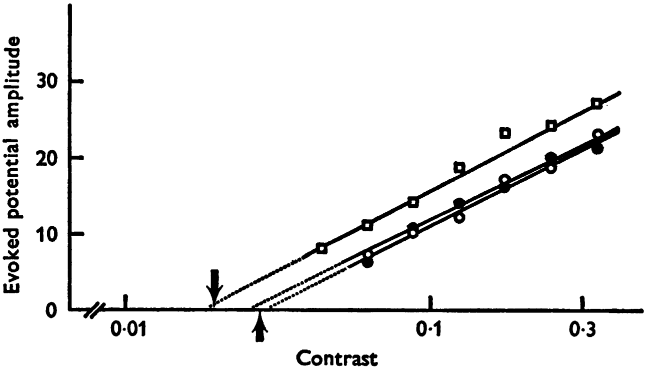

Fig. 7. The open circles (○) were obtained with the right eye exposed and the filled circles (●) obtained with the left eye exposed. The squares (□) were obtained with both eyes exposed. Spatial frequency used is 8 c/deg.

Part II

Channels selective to orientation and size

If the evoked potential or part of the evoked potential arises from neurones which have become specialized in abstracting the orientation and size of a moving retinal pattern, then it might be possible to use the evoked potential to measure the characteristics of these neurones.

Orientation selectivity. In Part I it has been shown that the slope of the regression line obtained by viewing the stimulus with one eye is the same as obtained when it is viewed with two eyes. We now test the effects of viewing two gratings simultaneously each with a different orientation—one orientation being presented to one eye and the other to the other.

This was done by placing a Dove prism before one of the eyes and rotating the prism to obtain the required orientation. The gratings were masked with a circular field (2° diameter) so that the subject could use this circular border to fuse the two images binocularly.

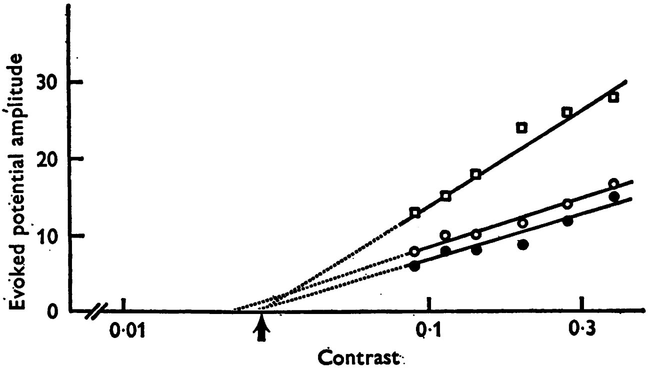

Fig. 8. Filled circles (●) were obtained by exposing the right eye to a vertical grating; open circles (○) for a horizontal grating exposed to left eye. Open squares (□) were obtained with binocular viewing of the two orientations. Arrow indicates the psychophysical threshold for both the horizontal and vertical grating.

The results are presented in Fig. 8. The filled circles are obtained with a vertical grating exposed to the left eye and the open circles were obtained with a horizontal grating exposed to the right eye. No significant difference was found between the slopes of the two regression lines obtained from each eye separately. The squares were obtained by exposing the two eyes together. In this case the slope of the regression line was a factor of 2·0 greater than for the monocular results.

This result could be accounted for by assuming that the activity in the two separate orientation channels had summed.

Further evidence for the existence of channels selectively sensitive to orientation was obtained by using an adaptation phenomenon described by Blakemore & Campbell (1969).

In this experiment the subject initially adapted to a high contrast grating of the same spatial frequency as the stimulus grating (12 c/deg) for a period of 1 min. He then viewed the stimulus grating which had a contrast 0·6 log. units above threshold for a period of 10–15 sec. During this period the experimenter switched on the computer of average transients and recorded the response. This procedure was repeated until a reasonably noise-free response was accumulated. Measurements were obtained with the test grating vertical and the high contrast adapting grating at a number of orientations on either side of the vertical.

The results are shown in Fig. 9. It is clear that when the stimulus and adapting grating were both vertical (0°) that the amplitude of the response obtained was less than that found at other orientations. As the angle between the adapting grating and the stimulus grating was increased the evoked potential gradually increased until the effect of the adapting grating was not significant beyond 15–20°.

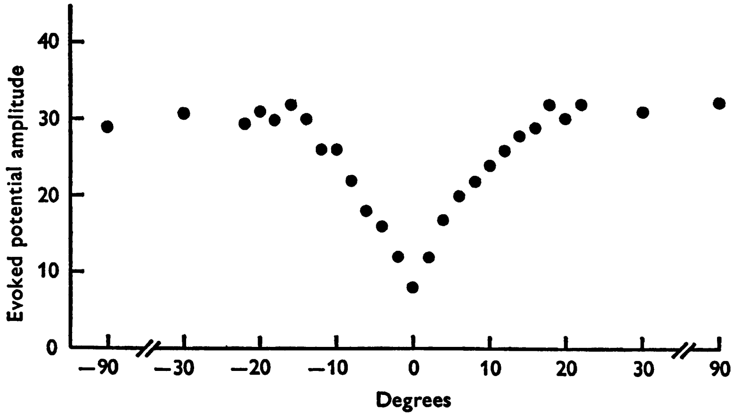

Fig. 9. The effect on the amplitude of the evoked potential of adapting to a high contrast grating at different orientations on either side of the vertical meridian (0°). Clockwise rotation displacement is positive and anticlockwise rotation is negative. Spatial frequency used is 12 c/deg.

The experiment was repeated with the adapting grating orientated obliquely at 45°. The results were similar to those obtained with the adapting grating vertical.

It may therefore be concluded that the selectivity of an orientational channel is such that it cannot be influenced by another orientation 15° away.

Spatial selectivity. To establish whether there are channels selectively sensitive to spatial frequency we use the same strategy as used to detect the orientational channels. In this instance we use a stimulus which consists of two spatial frequencies, one fixed and one variable. The expectation is that when the two frequencies are sufficiently far apart in frequency, two separate channels will be activated and thus the slope of the regression line will be greater.

A spatial frequency of 7 c/deg was generated on the screen of the oscilloscope and it was masked by an aperture subtending 2° diameter placed

20 cm in front of it. Between the oscilloscope screen and the mask is placed a lens of +4D which has been cut so that it covers the lower half of the circular field. When the lens is placed in contact with the screen the upper and lower part of the screen present the same spatial frequency. As the lens is moved towards the subject the spatial frequency appears to be decreased by an amount depending upon the distance between the screen and the lens. This optical arrangement has the advantage that the colour, luminance and the timing of the 8 c/sec phase change are common to both halves of the field. Only the spatial frequency is different.

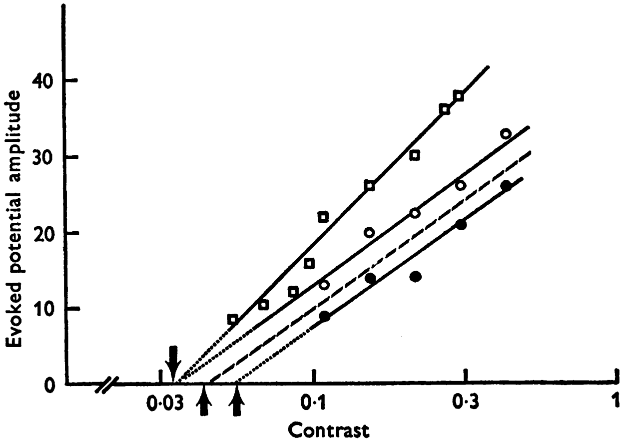

Fig. 10. The effect of stimulating with two different spatial frequencies separately, filled circles (●) 6 c/deg and open circles (○) 4 c/deg. Squares (□) show the results obtained with the two spatial frequencies exposed together. The dashed line is the regression line for the whole screen filled with a grating of 5 c/deg.

The results of the initial experiment are shown in Fig. 10. The open circles (○) were obtained with half of the screen filled with a spatial frequency of 4 c/deg and the filled circles (●) were obtained with the upper half of the screen filled with a frequency of 6 c/deg. As expected from the previous experiments, the regression lines are parallel and the 6 c/deg results are shifted to the right. Next, both spatial frequencies are presented together in their respective half fields. The results are shown as squares (□). The slope of the regression line for the double presentation has increased by a factor of 1·4. Now it could be argued that the increased slope obtained when both frequencies were used is due to the increase in the area of the stimulus even though we have shown in a previous experiment (Figs. 5, 6) that this is unlikely. To make doubly sure that the increase in slope is due to the presence of two different frequencies we did the following control. The whole field was filled with a grating intermediate in frequency between the two test frequencies (5 c/deg). The regression line for the control results is shown as a dashed line.

In the second experiment the frequency in the upper part of the field was held constant at 7 c/deg and the frequency in the lower part of the screen was varied. For each combination of frequency the slope was calculated. The slope of each regression line (M) was divided by the slope obtained for the 7 c/deg regression line (M_0). This ratio (M/M_0) is plotted in Fig. 11 against the ratio of the variable spatial frequency to 7 c/deg. This ratio of the spatial frequencies is expressed in octaves. It is clear that the maximum effect is reached by about one octave (3·5 c/deg); we may conclude that when the spatial frequencies are separated by an octave they are almost independent.

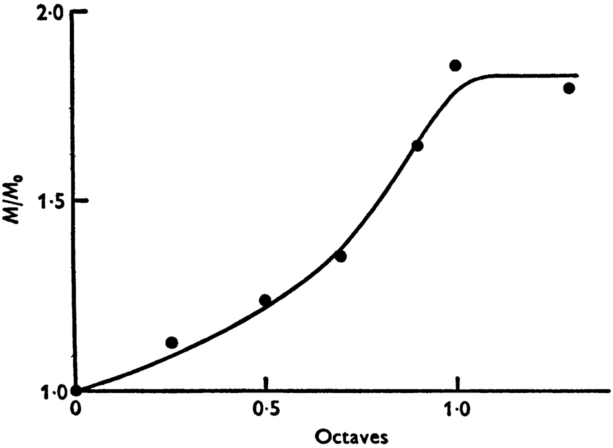

Fig. 11. The effect of increasing the spatial frequency ratio (in octaves) of two gratings presented simultaneously on the regression coefficient. The coefficients (M) have been normalized to the comparison frequency (M_0), which is at 7 c/deg.

For closer ratios there is a decreasing change in the slope of the regression lines. It may be inferred that as the two spatial frequencies become closer they interact until when the two frequencies are identical only one channel is activated. If it is true that the amplitude of the evoked potential does depend on the number of spatial frequency channels activated, then the steepness of the regression line should be further increased by increasing the number of frequencies. To test this prediction we used as a stimulus three spatial frequencies presented simultaneously (4, 8, 11 c/deg). The results are reported in Fig. 12. The open circles were obtained using a 4 c/deg grating which filled the whole screen (2° diameter). The regression coefficient for these results was found to be 0·7. In the next experiment the upper half of the field was filled with a grating of 4 c/deg and the lower half with a grating of 11 c/deg. The results are shown as squares. The regression coefficient was now 1·3.

In the final experiment three frequencies of 4, 8, 11 c/deg were placed on the upper middle and lower third of the screen. The results are shown as filled circles. Here the regression coefficient had increased to 2·6. The prediction is thus verified.

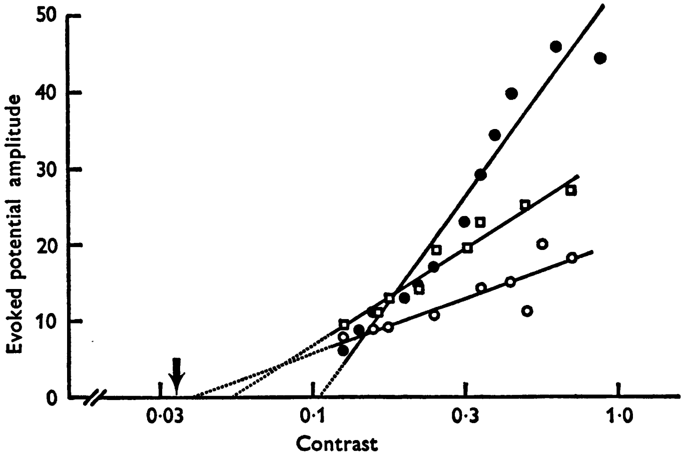

Fig. 12. The open circles (○) represent the results of stimulating with one frequency (4 c/deg) and the squares represent two frequencies at 4 and 11 c/deg (□). Finally the filled circles represent three frequencies of 4, 8 and 11 c/deg simultaneously (●). The arrow is the psychophysical threshold for the 4 c/deg grating alone.

DISCUSSION

In all the experiments there was no exception to the rule that the amplitude of the evoked potential was linearly related to the log. of contrast and that extrapolation to zero-voltage amplitude predicted the psychophysical threshold very closely. The threshold was measured simply by decreasing the contrast of the grating in steps of 0·05 log. units until the subject reported that the grating was never visible. This study leaves open the question of how the amplitude of the evoked potential very near threshold would behave and whether it would follow the frequency of seeing curve. To obtain this information very long averaging times would be required.

The linear relation between the amplitude of the evoked potential and the log. of the stimulus contrast over the range measured in these experiments can be interpreted as if the Fechner Law was operating in the domain of contrast.

Using an adaptation technique Blakemore & Campbell (1969) concluded that in the human central vision there were no channels sensitive to spatial frequency whose peak response was situated lower than 3 c/deg. Here we found that for spatial frequencies less than 3·3 c/deg the evoked potential characteristic had to be fitted by two regression lines instead of the single one found necessary for all the higher frequencies. It is established for these low frequencies that one slope is due to a contribution from the foveal region and the other from the parafovea. Thus it appears that in central vision spatial frequencies are processed from about 3 c/deg upwards. A separate system operates for lower spatial frequencies which involves the parafovea.

Using evoked potentials recorded locally from the cortical surface, Daniel & Whitteridge (1961) and Cowey (1964) have shown in the monkey that the visual field is represented topologically on the visual cortex. They found that the central portions of the field have a much larger representation than the peripheral field. Using a small flashing light as a stimulus, Cowey (1964) found that there was little or no overlap from neighbouring parts of the visual field at the cortex. If the evoked potential, as recorded by us through the scalp, is the sum of the localized potentials one would expect that it would be very dependent on the area of visual field stimulated. This is not found even when symmetrical and therefore comparable regions are stimulated as we showed when the upper and lower parts of the foveal region were stimulated.

A possible explanation of this apparent paradox might be that the stimulus which we use preferentially activates neurones selectively sensitive to movement at a particular orientation. These might correspond to the complex and/or the hypercomplex cells described by Hubel and Wiesel in the cat and monkey. It is known that these cells can be activated by their particular 'trigger feature' over a large area of the visual field even though the stimulus occupies a small portion of it. If in the central visual field (about 2° diameter) many of such cells in the upper part of the fovea spread their receptive fields into the lower part, and vice versa, independence of the slope from the area stimulated might be accounted for.

Campbell & Green (1965*b*) have shown that at all spatial frequencies the contrast threshold for binocular vision is $\sqrt{2}$ lower than for monocular viewing. Here we confirm at one spatial frequency that the binocular threshold is lower by this ratio (arrows in Fig. 7). The new finding is that to obtain an evoked potential of any given amplitude with binocular stimulation it is necessary to decrease the contrast by $\sqrt{2}$ relative to the contrast needed to obtain that amplitude with monocular viewing.

Most of the cells selectively sensitive to orientation in the cat and monkey may be activated by either eye. This is not the case for geniculate neurones. It is therefore probable that the summation of the signals occurs at the neurones where binocular signals are first processed. The behaviour of the evoked potential for binocular vision suggests that the evoked potential is arising from or subsequent to, the cortical binocular cells.

The only way which we have found to increase the slope of the evoked potential was to stimulate with more than one spatial frequency or alternatively with more than one orientation. Such findings suggest that the magnitude of the evoked potential is related to the number of active orientational channels or active channels selectively sensitive to spatial frequency. However, within one of these channels the dimension of the stimulus affects only slightly the slope of the regression line. It would thus appear that within a channel the signal spreads to all the elements belonging to that channel.

In this paper we have offered further evidence for the existence in man of channels selectively sensitive to orientation and spatial frequency (Figs. 9 and 11). The selectivity for orientation is high, for by rotating the adapting grating by 15° its influence on the stimulus grating had decreased to zero (Fig. 9). This result is very similar to that established psychophysically by means of a masking technique (Campbell & Kulikowski, 1966). Unfortunately, we were unable to measure quantitatively the selectivity to orientation using the change of slope which occurs when two gratings of different orientation are present simultaneously (Fig. 8), for we found that marked binocular rivalry occurred when the angle between the two gratings was small. However, we were able to measure with this method the spatial frequency selectivity because it was technically easy to present two gratings of different frequency monocularly.

The experiment in which we demonstrated that the evoked potential is sensitive to the orientation of an adapting grating (Fig. 9) is firm evidence that part at least of the evoked potential arises from neurones which are highly sensitive to orientation. Such neurones have been described in the visual cortex of the cat (Hubel & Wiesel, 1962, 1965; Campbell *et al.* 1968) and the monkey (Hubel & Wiesel, 1965; Campbell, Cooper, Robson & Sachs, 1969). The adaptation did not completely abolish the evoked potential so that we cannot exclude the possibility that some of the components of the evoked potential arise from other structures.

The great majority of psychophysicists restrict their observations to threshold conditions and eschew suprathreshold observations at levels where we can actually detect a stimulus with natural ease. In this study we likewise have made no attempt to make psychophysical observations at suprathreshold levels of contrast, although we have measured evoked potentials well into the region of high visibility. If suprathreshold measurements of perceived contrast were made, and if these could be simply related to the amplitudes of the evoked potentials, it might be possible to obtain electrophysiological insight into the nature of sensation at more realistic levels of stimulation.

Campbell, Cooper, Robson & Sachs (1969) measured the selectivity to spatial frequency of the cortical cells and geniculate fibres of the cat and monkey. The response characteristics of these neurones were compared with channels selectively sensitive to spatial frequency in the human using a psychophysical adapting technique (Blakemore & Campbell, 1969). Our finding that the evoked potential is also selectively sensitive to spatial frequency strengthens the evidence that the organization of the visual system for the detection of size in the cat, monkey and man is very similar.

On indirect evidence, Campbell & Robson (1968) originally suggested that, in the human, there existed an array 'of functionally separate mechanisms in the visual system each responding maximally at some particular spatial frequency and hardly at all at spatial frequencies differing by a factor of two'. The electrophysiological evidence presented here confirms directly, without the use of psychophysics, the original suggestion.

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