

THE ANGULAR SELECTIVITY OF VISUAL CORTICAL CELLS TO MOVING GRATINGS

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SUMMARY

1. Grating patterns were used to obtain a quantitative description of cells in the visual cortex of the cat whose response amplitude depended critically upon the orientation of the moving grating.

2. In all such cells the impulse frequency was found to decrease linearly with angle on either side of an optimum angle (the preferred angle) until the response fell to zero or to a base frequency. The angular rate of change of response varied between cells and was expressed as the half-width at half amplitude (the angular selectivity).

3. The angular selectivity of thirty-five cells was determined and more than half (nineteen) of these fell within the range 14–26°.

4. Fourteen cells responded optimally only when the grating was moved in one direction. Twenty-one cells responded optimally to two directions of movement 180° apart, but the response in the two directions was not always equal.

5. No significant correlation was found between the response amplitude at the optimum angle and the angular selectivity.

6. The distribution of preferred angles did not show any difference between the oblique orientations and the vertical and horizontal orientations.

7. These results are compared with a previous psychophysical estimate of angular selectivity.

INTRODUCTION

In the past decade research on the cat and monkey has firmly established that information about images formed on the retina is transformed in very specific ways as the nervous signals pass up to the cortex. By recording

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from single cells in the visual cortex, Hubel & Wiesel (1959, 1962, 1968) have shown that many of the cells respond to lines or edges only when they are presented at a certain angle of orientation.

MacKay (1957), using the after-effects of viewing repetitive patterns, suggested the presence in man of channels sensitive to orientation. Moreover, Andrews (1965, 1967) and Sekuler (1965) concluded from psychophysical experiments that orientational organization might exist in the human. Campbell & Kulikowski (1966) chose to use psychophysically a visual stimulus which could subsequently be applied in neurophysiological experiments. In this manner it was hoped that it might be possible to compare more critically and quantitatively the neurophysiological findings with the psychophysical observations in the human. Neurophysiological observations on the cat are presented here.

METHODS

Preparation and recording. Experiments were conducted on the adult, anaesthetized cat for periods of up to 5 days. Atropine sulphate (200 μ g) was given before narcosis was initiated with diethyl ether and anaesthesia was maintained during the preparatory surgery with repeated doses of thiamylal sodium. Light anaesthesia was maintained with a nitrous oxide, oxygen mixture (75% N₂O, 25% O₂). The animal was respiration at 25 strokes/min and at such a tidal volume as to maintain the expired CO₂ within the range 2.5–3%. Eye movements were suppressed by a continuous intravenous infusion of gallamine triethiodide at a rate of 50 mg/kg.hr. This was reduced to 10–20 mg/kg.hr during the inactive stages of the experiment. Fluid balance was maintained with an intravenous infusion of 5% glucose solution. The rate of infusion was such as to offset the loss of urine, collected with a urethral cannula, and the loss due to lung vaporization, estimated from the condensate from the expired gases. Body temperature was maintained at 38° C. An additional 200 μ g of atropine sulphate was given daily as was 75,000 u. each of benzathine and procaine penicillin.

Both eyes were atropinized and phenylephrine hydrochloride was applied to retract the imitating membrane. Contact lenses, with artificial pupils of 4 mm diameter, were applied to each eye and were of such power (determined by retinoscopy) as to focus the stimulus on the retina.

The cat's head was fixed in a stereotaxic instrument and a rectangular piece of bone, together with the underlying dura, was removed from the top of the skull. All penetrations were between Horsley-Clarke co-ordinates F-2 to F+4 and RL 2 to RL 5. Tungsten electrodes with a tip diameter of approximately 0.5 μ (Hubel, 1957) were used. The electrodes were held in a manipulator with hydraulically controlled vertical motion. A cylinder of Perspex was fixed around the hole in the skull with dental impression compound and together with the base plate of the electrode-positioner formed a closed chamber above the exposed cortex. This chamber was filled with warm mineral oil through which the electrode entered the brain.

Action potentials from single cortical units were amplified, displayed on an oscilloscope, monitored over a loudspeaker and recorded on magnetic tape together with the necessary stimulus signals. The mean frequency of the nerve discharge could be determined by counting the pulses with an electronic counter for periods of 10 sec or by measuring the time required for a fixed number of spikes (normally 500).

Stimulus. A square-wave grating pattern was provided by a cathode-ray tube display (Campbell & Green, 1965). The tube used, E.E.V. Type No. T980H with a P31 (blue-green)

phosphor, was contained in a magnetic screening shield and mounted so that it could readily be rotated about its gun axis. The image was reflected from a mirror immediately in front of the cat into its eye. The mirror could be rotated about its vertical and horizontal axes and the stimulus effectively positioned as desired in the visual field. A circular mask normally with an aperture of 10° was placed in front of the cathode-ray tube, but masks down to 1° were also available.

Square-wave grating patterns were produced on the otherwise uniformly illuminated screen. These patterns were made to drift across the screen at a constant velocity and the direction of motion (at right angles to the bars) could be varied through 360° by rotating the tube (Enroth-Cugell & Robson, 1966). The spatial frequency was measured as the number of cycles subtending an angle of 1° at the eye, and the drift frequency was measured as the number of cycles passing a given point each second. Contrast is defined as $(I_{\max} - I_{\min}) / (I_{\max} + I_{\min})$, where I is the stimulus luminance. Independent control was provided for contrast, spatial frequency, and drift frequency. The space averaged luminance of the grating pattern was 15 cd/m^2 . Alternatively, the oscilloscope screen could be evenly illuminated and switched between two luminances. In some cases the oscilloscope was covered with a white screen and a small spot of light (0.2°) projected into the screen. This spot could be moved as desired and flashed on and off.

RESULTS

Preliminary experiments. In order to stimulate units while advancing the electrode a disk (Fig. 1), subtending 75° , was rotated in either direction at 0.5 rev/sec. in front of the cat. The reason for using such a stimulus is to present moving bars of various orientations, thus increasing the probability of exciting cortical units, many of which are otherwise silent.

Once a unit had been found by listening to the response evoked by the rotating disk, each eye was covered in turn in order to determine the eye dominance. In the great majority of units one eye was more dominant than the other. There were a few units to which each eye contributed equally and a few were activated by one eye only. To avoid the complication of stereoscopic mechanisms (Barlow, Blakemore & Pettigrew, 1967), the eye which was found to have the least influence was covered.

Two different modes of response to the rotating disk (Fig. 1) could be quite clearly recognized. Some units gave a distinct burst of impulses as each and every bar of the disk crossed the receptive field; i.e. they responded for the whole of that part of the cycle during which the pattern was crossing the receptive field. However, other units only responded to those few bars that had the appropriate orientation; i.e. these units responded for only a brief portion of each revolution of the disk. Photographs of gratings were then moved about by hand in the visual field to locate the unit's receptive field. If the response was obtained from a position in the visual field that was within 20° of the visual axis the next stage of the experiment was embarked upon; i.e. stimulation with the spatial pattern displayed on the oscilloscope screen.

A continuously moving grating pattern was used, as this was found to be

a potent stimulus for these units and the adjustable mirror was used to centre this grating pattern on the receptive field. The centring was facilitated by using small circular masks, or by systematically obscuring the peripheral portions of the grating with a straight edge mask. Once the screen was optically aligned the next step was to see if the unit responded more vigorously to some orientation of the grating pattern than to others. This was almost invariably the case when the unit had responded only to a few bars of the rotating disk and these are the units whose behaviour is the primary topic of this paper. Those units which apparently responded

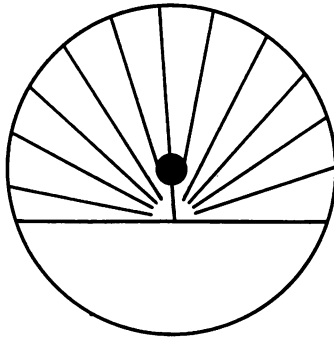


Fig. 1. The disk which was rotated to provide a stimulus while searching for cortical units. Centre of rotation in black spot. The width of each bar subtended 1° .

equally well to each and every bar on the disk had a response which seemed independent of the orientation of the oscilloscope pattern during this preliminary test (Fig. 2).

Hubel (1960) recorded units from the visual cortex of the cat and considered that action potentials originated from fibres, as opposed to cell bodies, if they were generally initially positive from the time they were first seen and often purely positive. On the other hand, action potentials which were small and negative, or negative-positive when first seen but which often became much larger and positive-negative as the electrode advanced, he thought originated from cell bodies.

Our experiments, performed with Hubel's type of electrode, did not allow a conclusive distinction to be made between responses arising from incoming lateral geniculate fibres and cortical cell bodies. Nevertheless, the following evidence does suggest that the units which responded to the direction of movement were cortical cell bodies and those which responded equally well to all stimulus orientations were lateral geniculate fibres:

1. The great majority (sixty-one out of seventy-three) of the direction independent units had a positive action potential and only very few (seven out of seventy-three) exhibited a negative initial phase when first detected. The direction dependent units behaved quite differently, for a

rather small proportion (eleven out of fifty-eight) of the action potentials were purely positive and almost half (another twenty-seven of the fifty-eight) showed a negative initial phase.

2. The units could be tested by exposing them to the evenly illuminated screen and then suddenly changing the luminance of the screen. When twenty of the direction independent units were tested in this manner each

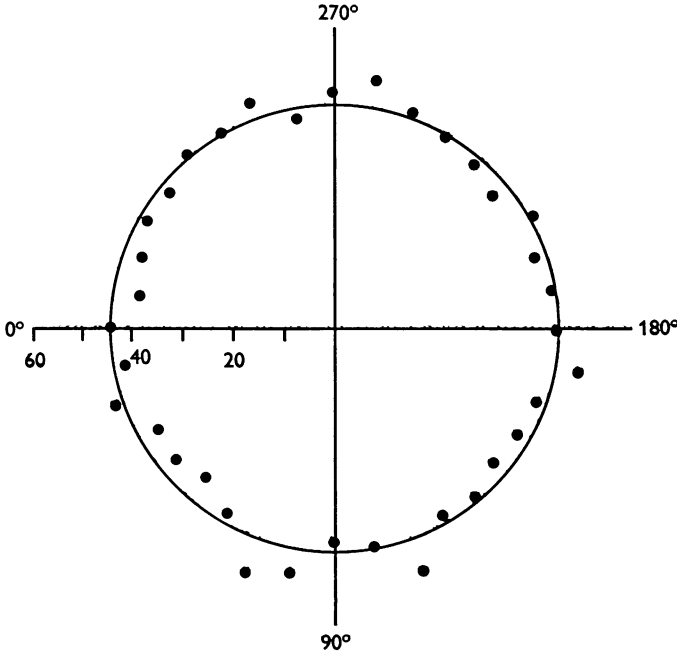


Fig. 2. Polar plot of the response amplitude of a unit which responds equally to all directions of movement of the stimulus grating. The circle is the mean response. Spatial frequency: 0.11 c/deg. Drift frequency: 6.5 c/s. Contrast: 0.5. 0° = a movement from right to left in the visual field; 90° = a downward movement.

and every one responded briskly, behaviour typical of geniculate neurones (Hubel & Wiesel, 1959). On the other hand, when twenty of the units whose response depended upon the stimulus orientation were similarly tested the majority (sixteen) failed to respond—a characteristic expected from cortical neurones.

Thus, although we do not have definitive evidence to exclude the existence of cortical cells which may respond equally to movement in any direction, the balance of evidence suggests that such responses are being recorded from the axons of the lateral geniculate terminating in the cortex. The responses which are dependent on the direction of motion certainly do appear to arise from cortical cells.

The alignment of the oscilloscope and the initial test for differences in

response magnitude with the angle of the pattern took 5–15 min from the time a unit had been first isolated. If by then the spike could still be clearly differentiated from other activity by means of pulse height, pulse shape and minimum spike interval the experiment proper started. This consisted of recording the response to a high-contrast (0.2–0.8) grating of constant drift frequency. Usually a drift frequency of 2–6 c/s and a spatial frequency of 0.1–0.5 c/deg were used as these conditions gave responses of maximum amplitude. The orientation of the bars was taken through a full 360°, usually in 10° steps. For each new step the response was allowed to settle down before pulse counting was started. As a measure of response magnitude we decided to take the time for a given number of impulses to occur. Usually a count of 500 was selected, as it is a useful compromise between precision and recording time.

Main experiments. The results of the experiments described above were plotted in terms of impulse frequency versus direction of movement of the grating. Among those thirty-five cells which yielded complete data and whose response amplitude was highly dependent upon the angle, there was considerable variation in behaviour, as can be seen in Figs. 3–6. For comparison the corresponding data for a unit whose response amplitude did not vary with the direction of movement is shown in Fig. 2. In Fig. 3*A* the response of a unit is plotted linearly against the angle of motion of the grating. Two straight lines have been fitted to the data using the method of least squares. The point of inter-section of these two lines has been taken as the best estimate of the maximum response of the unit and its optimum angle (*preferred angle*). In this unit the estimated maximum response is 22 impulses/sec and the preferred angle is 22°. In order to facilitate the comparison of *angular selectivity* between units, the following procedure was adopted. The line *A–B* was drawn at half the maximum amplitude. Bisecting the angle determined by the length of this line gives the angular selectivity, which in this unit was equal to $\pm 19^\circ$. In Fig. 3*B* the same results are plotted in polar co-ordinates. The regression lines shown in Fig. 3*A* have been transferred to Fig. 3*B* and the preferred angle is also indicated. Note that the response has fallen to zero in this particular unit when the angle has reached 40° on either side of the preferred angle.

In twenty-four of the thirty-five units the count did not fall to zero whatever the direction of motion, but fell to a minimum (base) count. The mean level of this base count was computed and regression lines fitted to the rest of the data points by the method of least squares. Such a unit is illustrated in Fig. 4*A*. In calculating the angular selectivity of these units the half-amplitude level was taken as being midway between the mean base count and the estimated maximum response as indicated in the figure. The results are plotted in polar co-ordinates in Fig. 4*B*. There were fourteen

units of the type illustrated in Figs. 3 and 4 in that they only had one preferred angle. However, there were also units which had two preferred angles, i.e. their polar plot had two lobes. One of these units is illustrated in Fig. 5. This unit had a base count and it was treated in the same way as the unit in Fig. 4. The angular selectivities of the two lobes were $\pm 15^\circ$ and $\pm 17^\circ$ and the preferred angles were 222° and 47° respectively. It will be

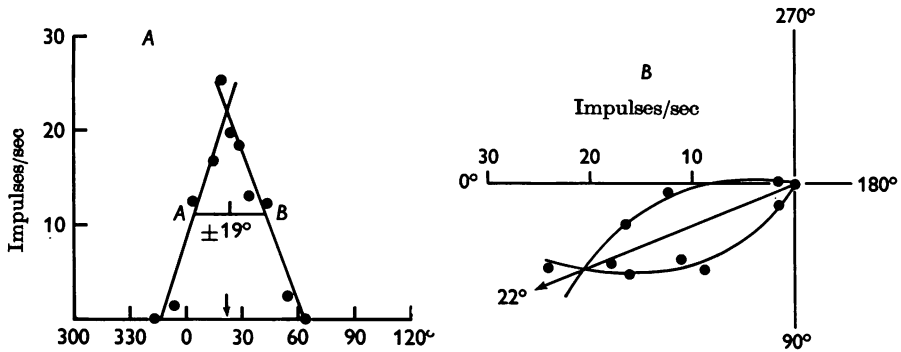


Fig. 3. *A.* Linear plot of response amplitude (mean spike frequency) versus the direction of movement (angle) of the stimulus grating. The two regression lines were obtained by the method of least squares and the significance levels for these two lines were 0.5 and 0.5%. (These levels are also given, in order left to right, for each regression line in Figs. 4, 5 and 6.) Their point of intersection is taken as the best estimate of the maximum response amplitude and the preferred angle (arrowed). The horizontal line is drawn at half the maximum response amplitude. Spatial frequency: 0.24 c/deg. Drift frequency: 3.8 c/s. Contrast: 0.7. *B.* Polar plot of results in *A.* The arrowed line indicates the preferred angle. 0° = a movement from right to left in the visual field; 90° = a downward movement.

noted that the peak responses of the two lobes are not equal. With our technique we were able to detect a second preferred angle in twenty-one units. The ratio of the estimated maximum responses at the two preferred angles we have called the *response ratio* of the unit. (This is equivalent to 'directional selectivity' or 'directional preference' as used by Hubel & Wiesel, 1968.) For this unit, dividing the response of the larger lobe by that of the smaller gives a response ratio of 2.2. For all units the response ratio ranged from 1.1 to 4.3 with a mean of 1.9; however one may consider those units in which we were unable to detect a second preferred angle to have a response ratio reaching towards infinity. In Fig. 6 a unit is illustrated which had a response ratio of 1.2 and a mean base count of zero.

Two hypotheses can be advanced to account for the cells which have two lobes; that is, cells which give a peak response at two directions. The cell could be fed either from two separate independent mechanisms, each of

which is activated at a given angle, or else it could be organized primarily as a single mechanism which responds to two angles. If organized in the latter manner it would be reasonable to find that the two lobes would be positioned exactly 180° apart and furthermore that the half-widths of the two lobes would have the same value. These predictions may be settled by

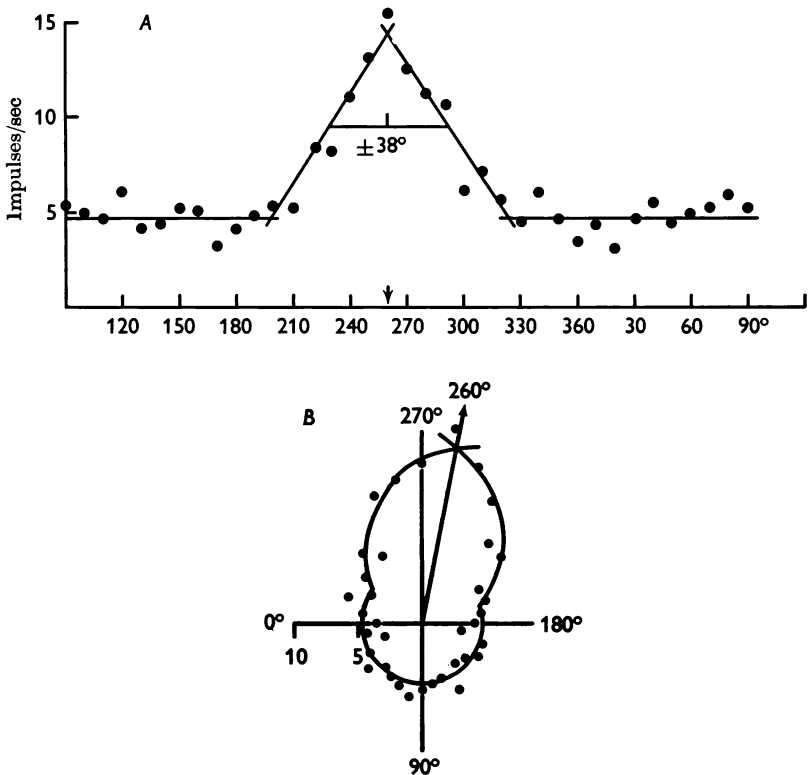


Fig. 4. *A, B.* As in Fig. 3 but showing results from a unit whose response on either side of the preferred angle fell to a non-zero base count. The horizontal lines on either side of the response peak were drawn through the mean of the base count and the line A-B is located midway between this mean and the maximum response. (Significance levels 0.5 and 0.5 %.) Spatial frequency: 0.08 c/deg. Drift frequency 2.2 c/s. Contrast: 0.17.

comparing the angular separation and half-widths of each pair of lobes in this population of units.

For each of the bi-lobed cells the preferred angle lying between 0° and 180° was subtracted from the angle lying between 180° and 360° . The mean angle of difference was found to be $178.9^\circ \pm \text{s.e. } 1.6^\circ$, which does not differ significantly from the expected value of 180° . Of course, a mean angle of difference between lobes of 180° would be expected whether the angle of

difference of all the cells is actually 180° or randomly distributed around 180° . However, if they are randomly distributed around 180° then the standard deviation of the angles of difference would be very large. As the s.d. is found to be small (7.2°) this supports the idea that the lobes may be arising from the same basic mechanism.

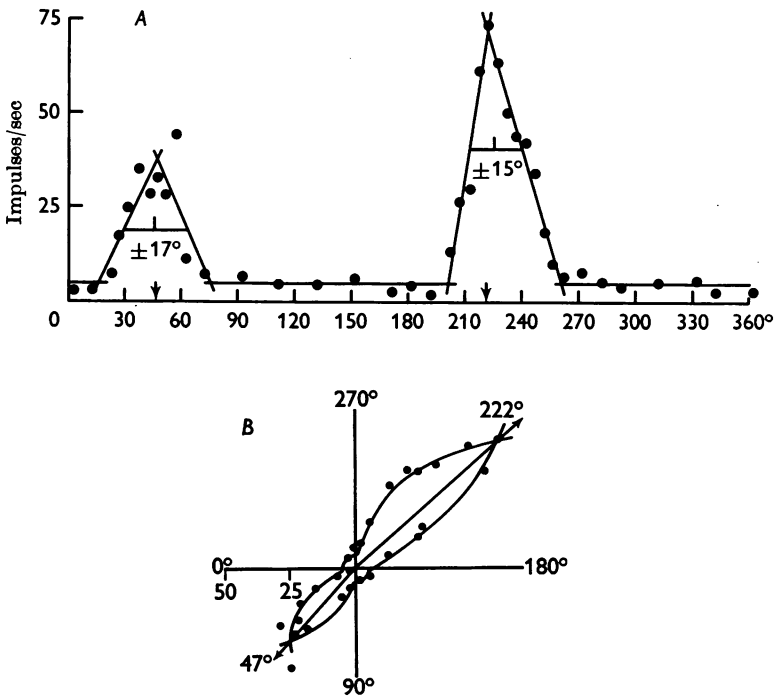


Fig. 5. *A.* Results from a unit which had two preferred angles. The responses for the two directions of movement were unequal. (Significance levels 2.5, > 10, 1.0, 0.5%.) Spatial frequency 0.22 c/deg. Drift frequency 5 c/s. Contrast: 0.8. *B.* In the polar plot some of the points contributing to the mean base count have been omitted for clarity.

Next, the half-widths of each pair of lobes were compared. The half-widths ranged from 14° to 52° . In spite of this wide range, the correlation coefficient between pairs of lobes is 0.80, which is not significantly different from unity ($n = 19$). This significantly high correlation again supports the contention that the two lobes have the same mechanism.

If the procedure of line fitting by the method of least squares is justifiable our results imply that impulse frequency decreases linearly with angle on either side of the optimum angle. At the point of intersection of the two regression lines the change of slopes is acute and it could be objected that this behaviour is rather unlikely in a biological system. Inspection of the

data supports the implication that impulse frequency decreases linearly with angle but, it should be realized that the minimum interval between points was normally 5° and this large interval could possibly obscure the fine details of the transition. For any one lobe the slopes of the two fitted lines were very similar. For fifty-two lobes the correlation coefficient was found to be 0.73.

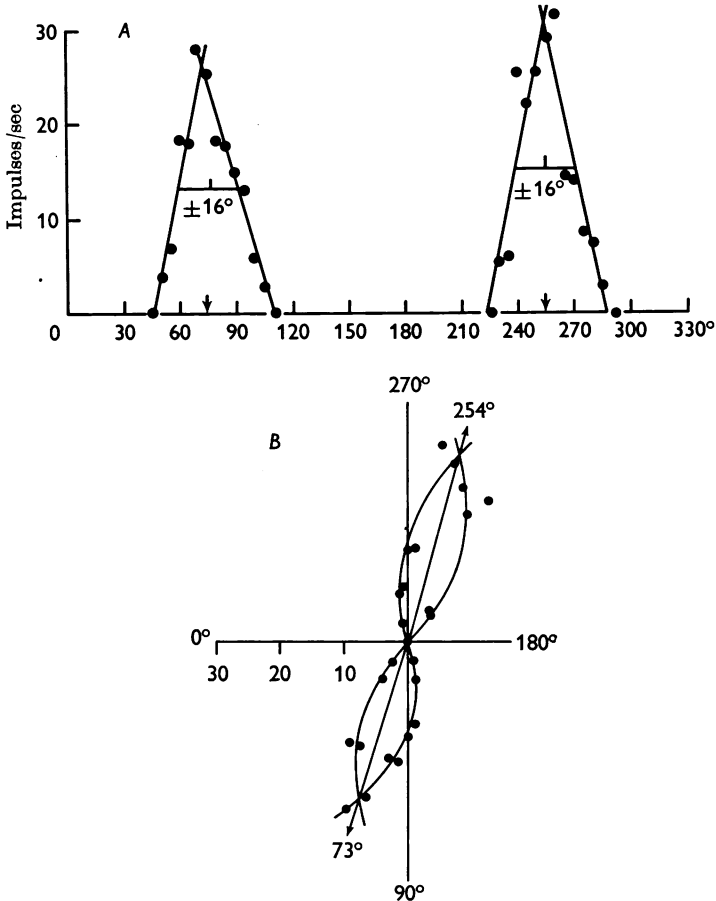


Fig. 6. *A, B.* A unit with two preferred angles and approximately equal maximum responses for each of them. (Significance levels 1.0, 0.5, 2.5 and 0.5%.) Spatial frequency: 0.22 c/deg. Drift frequency: 4 c/s. Contrast: 0.8.

There was no difference between the angular selectivities of the uni-lobed and the bi-lobed cells and both populations were therefore included in the histogram of Fig. 7. For those cells which showed two preferred angles it was found that there was a high correlation between the angular selectivity of the two lobes ($r = 0.80$, $n = 19$). Therefore only one, the

narrowest, has been presented for each cell. It should be noted that this high correlation was found even though there was a wide range of angular selectivities between different cells.

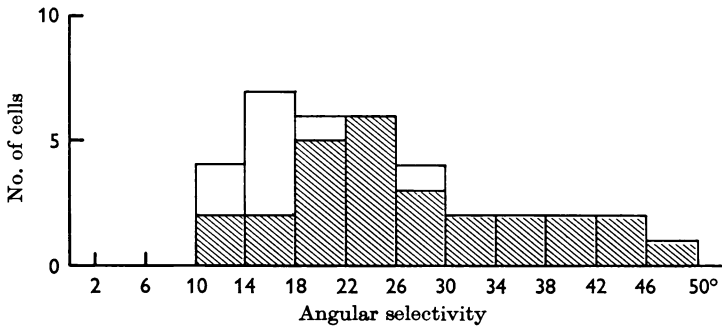


Fig. 7. Histogram showing the distribution of angular selectivity of thirty-five cells. Twenty-one of these were bi-lobed cells and the narrowest lobe was used for the histogram. The unhatched area indicates lobes for which one of the two regression lines had a significance level $> 5.0\%$, while the crosshatching shows that both lines had a significance level $< 5.0\%$.

The question can be asked: does the spatial frequency of the grating used to measure the orientational properties of the unit affect the angular selectivity? There are five cells for which data are available for determining the angular selectivity at a number of spatial frequencies, and from these it would appear that over the range of spatial frequencies used there is no consistent dependence of the angular selectivity on the spatial frequency of the grating. There is certainly not such a clearly defined effect as has been found by G. F. Cooper & J. G. Robson (unpublished observations) in a directionally selective cell of the squirrel retina, where five successive decreases in spatial frequency covering 1.5 log units steadily increased the half-width from 40° to 70° .

The lack of dependence of angular selectivity on spatial frequency is further emphasized by the fact that fifty-two determinations of angular selectivity failed to show any correlation with the spatial frequency used. In this study we were primarily concerned with establishing the highest angular selectivity of these cortical cells so that a comparison could be drawn with the psychophysical data. Our experimental conditions were deliberately chosen so as to obtain the maximum response from the cells and this meant, of course, that we were operating within that portion of the spatial frequency range which yielded substantial responses. Thus, there is no evidence to suggest that there is a sufficiently large or consistent enough effect of spatial frequency on angular selectivity which could account for the discrepancy between these neurophysiological results and the psychophysical findings.

DISCUSSION

Emsley (1925) first noted that a visual acuity task was performed best if the target was aligned so as to lie in the vertical or horizontal orientation as compared with the oblique orientations and this finding has been confirmed for many types of target configuration (reviewed by Taylor, 1963). In our experiments the distribution of preferred angles did not show any difference between the oblique orientations and the horizontal and vertical orientations. Likewise Hubel & Wiesel (1962, 1965) did not find any special distribution in the cat. Moreover, in a recent investigation of such cells in the visual cortex of the monkey, Hubel & Wiesel (1968), who were on the look-out for just such a distribution, again failed to find it.

These experiments were designed to establish if the properties of cortical cells resemble the orientational selectivity found in the human. Campbell & Kulikowski (1966), using a simultaneous masking technique, found that if a high contrast grating was used to mask the detection of a low contrast test grating the degree of masking depended upon the angle between the gratings. If the test and masking gratings were aligned then the masking effect was maximal. But, if the gratings were at right angles to each other the influence of the masking grating on the contrast threshold of the test grating was slight or absent. The effect of the masking grating on the threshold for the test grating decreased exponentially with angle on either side of the aligned angle. The masking effect was reduced by a half when the masking grating was at an angle of 12–15° from the test grating.

In contradistinction, the results obtained in the cat do not show an exponential decrease in response on either side of the optimum orientation; indeed a finding common to all the cells examined was that the response rate decreased linearly with angle on either side of the optimum orientation. Furthermore, the angular selectivity in the cat cells was definitely lower and the half-width of most of the cells was found to be between 14° and 26° (Fig. 7). We have therefore failed to show that there is any simple quantitative link between the results obtained from the psychophysical experiments in man with the neurophysiological results obtained in the cat.

It remains to consider whether there is a fundamental difference between this orientational mechanism found in man and in the cat. It is significant to consider here the recent work of Hubel & Wiesel (1968), who found that the cortex of the monkey also contains cells which are sensitive to orientation, using the same techniques that they applied to the cat. They concluded that the orientationally sensitive cells in the monkey have a higher selectivity than in the cat, for they state: 'The rate of decline of this cell's responses as the stimulus orientation deviated from the optimum was fairly typical; while the decline varied to some extent from cell to cell, it

was generally steeper in the monkey than in the cat. Most field orientations could be specified to within 5° – 10° , as compared to 10° – 15° in the cat'. The typical cell to which Hubel & Wiesel (1968) are referring is shown in Fig. 2 of their paper, and there it can be seen that it only responds when the orientation of the bar is within $\pm 25^{\circ}$ of the optimum orientation. If the number of spikes which occur at each orientation is counted and plotted against the angle of orientation, then it shows that within this range the decline of the response is exponential and not linear. However, while this suggests that the performance of the monkey cortex bears a closer resemblance to that of the human than the cat does, too much significance should not be attached to this one set of data. Additional experiments should be undertaken in the monkey to measure more precisely the performance of cortical cells sensitive to orientation.

Burns (1968) considers that some optical illusions, such as the Muller-Lyer, provide support for the belief that 'cortical units are orientation-specific, being excited in proportion to the cosine of the angle between an appropriately placed, light-dark border in the visual field and the direction to which they are most sensitive.' Our results and those of Hubel & Wiesel (1968) demonstrate that a cosine function does not describe the behaviour of these orientation-specific cells.

The angular selectivity of the cat is clearly lower than the human, and since there appears to be a linear relationship between angle and response in the cat, and an exponential relationship between angle and sensitivity in the human, we conclude that there is a real difference between the orientationally selective mechanisms of cat and human, as revealed by these experiments.

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