J. Physiol. (1977), 265, *pp.* 615–636
With 8 *text-figures*
Printed in Great Britain

A PHYSIOLOGICAL AND BEHAVIOURAL STUDY IN CATS OF THE EFFECT OF EARLY VISUAL EXPERIENCE WITH CONTOURS OF A SINGLE ORIENTATION

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(*Received 29 April 1976*)

SUMMARY

1. Three kittens were reared in visual environments that consisted of stripes at one of three orientations – horizontal, right oblique, or left oblique. Two additional cats were reared as controls. One of these matured viewing right and left oblique stripes on alternate days. The other experienced a normal visual environment.

2. Following the completion of rearing, and after several weeks of normal visual experience, behavioural testing of the stripe-reared animals demonstrated a deficit in visual acuity for orientations which were not present in the early visual environment. No comparable deficit emerged for either of the control cats.

3. Following 1–3 years of further, normal, visual experience, each of the cats was shipped separately to California where single units were recorded from area 17 of the visual cortex and an effort made to guess the early visual history of each animal which was unknown to the experimenters. Cell samples from each experimental cat and the normal control cat allowed the physiologists to guess their early visual experience correctly. The control cat which matured viewing orthogonal sets of oblique stripes on alternate days demonstrated a bias for horizontal contours in his cell sample. In contrast to units recorded from normal cats, about 80% of

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which are binocular, only about 30% of the cells recorded from the stripe-reared animals could be influenced by both eyes.

INTRODUCTION

Wiesel & Hubel (1963, 1965) made the important observation that the pattern of binocular innervation of cortical neurones can be altered by preventing normal binocular vision during the early neonatal months. These original observations on the modifiability of the connexions of cortical neurones have now been extended to other aspects of their innervation such as those underlying preference for stimulus orientation (Blakemore & Cooper, 1970; Hirsch & Spinelli, 1970, 1971), binocular retinal disparity (Schlaer, 1971), movement (Olson & Pettigrew, 1974; Cynader, Berman & Hein, 1973, 1975), and configuration or size of stimulus (Van Sluyters & Blakemore, 1973; Pettigrew & Freeman, 1973).

The changes which have been reported in the orientation specificity of cortical neurones are striking (Blakemore & Cooper, 1970; Hirsch & Spinelli, 1970, 1971; Blakemore & Mitchell, 1973; Freeman & Pettigrew, 1973; Pettigrew, Olson & Hirsch, 1973) and probably apply to man (Mitchell, Freeman, Millodot & Haegerstrom, 1973; Mitchell & Wilkinson, 1974). For these reasons we thought the phenomenon might provide a suitable basis for a study of the elusive relationship between the perceptual abilities of an animal and the properties of single neurones. We examined this relationship by raising kittens in an early visual environment which contained contours of a single orientation only and then making a detailed study of the biases which had developed in both the behaviour of the whole animal and the responses of its cortical neurones. Data obtained from the behaviour and physiology of the same animal suggest a direct relationship between them.

Since the completion of this study, new experimental results have been reported (Stryker & Sherk, 1975) which cast doubt on the phenomenon of orientational plasticity as originally described by Blakemore & Cooper (1970). Accordingly, we shall discuss the present findings in relation to both the original observations and the more recent negative findings.

METHODS

Six male cats were used in this study. While each of the cats was known to the experimenters by a code name which bore no relation to the conditions of his rearing, we have substituted mnemonic names (LOBL, ROBL, etc.) at the time of writing in order to facilitate comparisons between individual cats and their individual rearing conditions (left oblique, right oblique, etc.). Two cats (NOR1, NOR2), reared in a normal visual environment, were used as controls. With the exception of HOR which began seeing stripes at the age of 20 days, each of the remaining animals spent the first 45 days of its life in total darkness. For an additional 65 days (i.e. until 110 days of age), it was exposed to a unique visual environment for an average of two hours per day. In between exposures the animals lived in darkness. While HOR was raised according to the procedure of Blakemore & Cooper (1970), moving freely and viewing horizontal black and white stripes, the other three cats experienced an environment which has not been previously described. Each cat was tightly wrapped in cheesecloth and packed with foam rubber into a closely fitting box with its head protruding

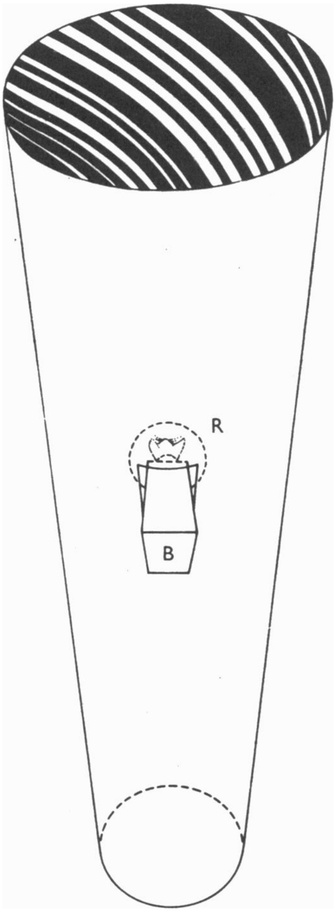

Fig. 1. A diagram of the apparatus in which the kittens received their early selected visual experience. The kittens were firmly wrapped in cheesecloth and placed in a box, B, that was partially slid through an opening cut into the side of a tall cylinder approximately 2 m high with an internal diameter of 45 cm. The kittens wore an opaque ruff, R, in order to prevent them from seeing their own bodies or the front of the box in which they were placed. The stripes on the inside wall were either oriented at 45 degrees or (as shown) 135 degrees.

through a hole in one end (Fig. 1). The box was partly slid through a window cut half way up the side of a cylinder, 1·8 m in height and 50 cm in diameter, so that the cat's head was just inside. Oblique black and white stripes of different widths appeared on the inside walls of the cylinder. LOBL saw stripes oriented at 135 degrees, ROBL saw stripes oriented at 45 degrees, and LROBL's visual environment alternated between 45 and 135 degrees on successive days (note: references to orientation refer to degrees in standard polar co-ordinates; see Fig. 2*A*). An opaque ruff (R) placed around the animal's head ensured that visual experience was restricted to stripes of one orientation. The inside walls of the cylinder (mean luminance 75 cd/m^2) were illuminated from above and from below through the two translucent perspex covers which formed the top and bottom of the cylinder. Although each cat was able to rotate its head, this was observed to occur only rarely and the extent to which it was possible for the head to be turned relative to the stripes was less than it is in those cases where the animal is fully free to move its body in the environment (Blakemore & Cooper, 1970).

Following the period of selective visual exposure, cats were kept in the dark for 2 months. For the first few weeks after entering a normally lit environment they showed the sort of gross behavioural deficits described earlier (Muir & Mitchell, 1975), but after this time their behaviour began to appear increasingly normal to casual observation.

Behavioural testing

After the animals had been in the lighted environment for 3 months, their abilities to resolve gratings at different orientations were measured using standard operant procedures described in detail elsewhere (Berkeley, 1970; Muir & Mitchell, 1975). Briefly, cats were trained to discriminate between a square wave grating and a blank field of the same mean luminance in a simultaneous discrimination task with discrete trials. The stimuli were back-projected on to two screens and were separately viewed by the cat through two transparent, Perspex nose-keys located 32 cm from the screens. A cat was trained to press the nose-key through which the grating was visible; the side on which the grating appeared was randomly assigned on each trial. Following a correct response, the animal was fed 0·5 ml. beef baby food during which time shutters obscured the stimuli. After a 5 sec intertrial interval, the shutters were raised and a new trial began. If the cat pressed the nose-key through which the blank field was visible, it received no food and the length of the intertrial interval was increased to 10 sec. Two or more consecutive errors resulted in the intertrial interval being lengthened to 15 sec.

The grating had a contrast close to 1·0 and a space average luminance of 75 cd/m^2 as did the blank field. The cats received four daily sessions (eighty trials each) with gratings of only one orientation – vertical (90 degrees), horizontal (180 degrees), right oblique (45 degrees), or left oblique (135 degrees) – in each session. The order in which the different orientations appeared was changed from day to day.

Initially, the cats were trained on gratings with a low spatial frequency, 0·22 cycles/degree. But, as soon as an animal's performance reached 90 % correct on two consecutive days, the spatial frequency of the gratings was increased to 0·46 cycles/degree, and the procedure repeated with all four orientations. Thereafter, spatial frequency was increased when either the above criterion was reached, or after 4 consecutive days of performance at a level above 80 % correct on all four orientations. Eventually, with high spatial frequencies, neither of these criteria could be reached because the performance would always lie below 80 % correct. At this point the spatial frequency was increased every 6 days until the animal's performance approximated the level expected by chance. As with the animals of an earlier study (Muir & Mitchell, 1975), the daily performance scores for gratings of a given orientation and spatial frequency were remarkably similar.

Physiological recording

After periods of from 1 to 3 years of normal visual exposure, the cats were shipped separately from Halifax to California where (with the exception of NOR2) physiological recording was performed 'blind' since the physiologists did not know the early visual experience of any animal while it lived. Although they learned the conditions of rearing for a given animal soon after the completion of recording, they did not know the total range of rearing possibilities, nor the fact that control animals would be included. Attempts made by the physiologists to guess the early rearing conditions were therefore independent of one another.

Preparation for recording was by conventional techniques (e.g. Barlow, Blakemore & Pettigrew, 1967). Anaesthesia was induced and maintained during surgery with Halothane. Following the completion of surgical preparation (venous cannulation, tracheotomy, and craniotomy) Halothane was discontinued. Anaesthesia was maintained throughout the rest of the experiment by hyperventilating the animal with a mixture of 75 % N_2O, 22·5 % O_2 and 2·5 % CO_2. Paralysis was achieved with Flaxedil 5 mg/kg.hr + tubocurarine 0·5 mg/kg.hr given I.V. along with a dextrose solution. With the exceptions of LOBL and HOR, electrode tracks were placed down the post-lateral gyrus (AP-2 to AP-5) of the left hemisphere, inclined 20 degrees anterior from vertical, 1–1·5 mm from the mid line in order to sample from area 17. In the cases of LOBL and HOR, two additional penetrations were made in the right hemisphere. Penetrations were typically 5-6 mm long in order to sample across the radial boundaries of organization and thereby maximize the number of 'columns' of different orientation which were penetrated (Pettigrew *et al.* 1973). The number of penetrations varied between three and seven. Chloramphenicol was given I.V. on the second and third days of recording to reduce infection of wounds and recording site.

All units which could be clearly identified as single cells were studied. Most single cells exhibited completely normal properties. Occasionally with the normal cats, however, and more frequently with the stripe-reared ones, we encountered units whose responses were either the same to slits of all orientations or whose firing was so irregular and sluggish that it was impossible to determine reliable orientational parameters by hand. Since it was only rarely possible to demonstrate an orientational bias even by averaging the unit's response to a computer driven stimulus over many trials, such units were excluded from further analysis. Distances between successive 'normal' units varied between 20 and 200 μm with occasional 'silent areas' extending up to 500 μm. If a silent area was much larger than this, or if receptive field eccentricities increased beyond 10 degrees, the track was ended and a new one begun. For each cortical unit we determined the optimal parameters of stimulation including ocular dominance, stimulus location and shape (Hubel & Wiesel, 1962), velocity (Pettigrew, Nikara & Bishop, 1968), and orientation. The response to variation of the last parameter was examined very closely to determine both the 'preferred orientation' and the 'orientational selectivity'. These are operational definitions. Preferred orientation refers to the angle of a slit, which is oriented to give a maximal response. Orientation selectivity refers to the largest angle through which one can rotate a moving slit and still obtain a significant response. It should be pointed out that these estimations are iterative and a large number of trials are often required before one 'homes in' on the optimal stimulus.

Although our final analysis of cell samples relies entirely on orientation parameters which have been obtained by hand, the precision of a computer driven optical stimulator complemented and quantified the experimenters' insight whenever possible. Stimulus location, velocity, and configuration were optimized by hand and the values were fed into a computer along with a first estimate of the preferred orientation. The computer then took control and quantified the response of the unit at each of several different orientations. If a unit had low selectivity, tests were made

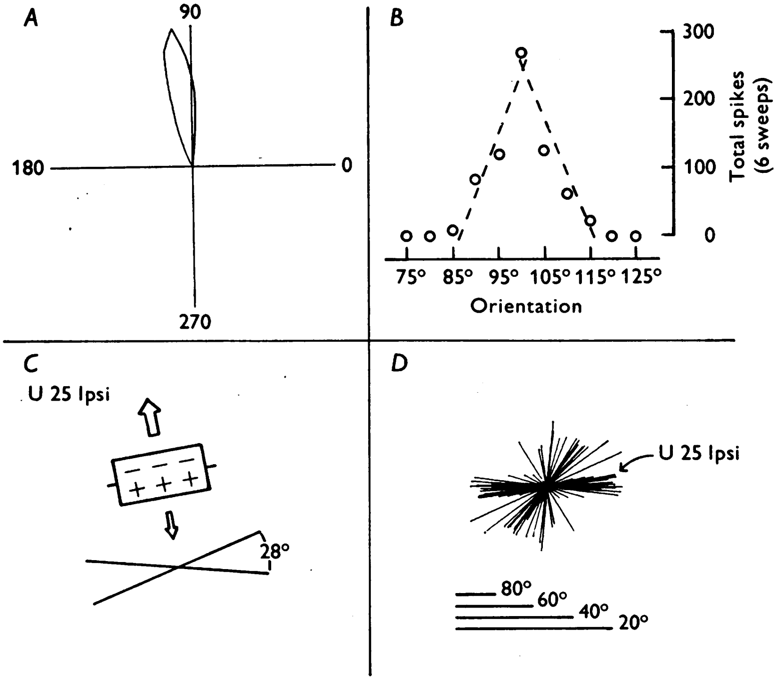

Fig. 2. Four different representations of the orientational preference and selectivity of one neurone (U 25i) recorded from HOR. The computer has tested the units response to a 0·5 × 4 degree slit (velocity = 2 deg/sec) at each of eleven equally spaced (5 degrees apart) orientations. *A*, a polar plot of the unit's response to different orientations which the computer has plotted on a storage oscilloscope (Tektronix 613). The distance between the origin and a point on the plot indicates the relative magnitude of the unit's response to a slit (whose orientation is at right angles) moving in that direction. *B*, the same data portrayed in the manner of Campbell *et al.* (1968). The intercepts of the linear regression lines on the abscissa indicate the orientational selectivity of this cell. Note the correspondence between computer determined orientation selectivity and the orientational limits which have been measured by hand (*C*). This correspondence is shown for a large sample of units in Fig. 3. *D*, one method for simultaneously presenting the orientational preferences and selectivities of many cells. In this diagram, the orientation of each line corresponds to the orientational preference of a particular cell. The length of the line is inversely proportional (see scale) to the cell's orientation selectivity. The arrow indicates the cell (U25i) illustrated in *A*, *B*, and *C*.

at each of twelve different orientations (i.e. every 30 degrees). If it was highly selective, the computer carefully tested the flanks of the recommended orientation, stepping the stimulus in 5 or 10 degree increments to each side until it failed to elicit a response. Computer driven sweeps were interleaved in pseudo-random order among the different orientations, over a period of 5–10 min, until 6 sweeps had been accumulated at each orientation. Simultaneous with each stimulus presentation, a post-stimulus time histogram was accumulated and displayed on a storage oscilloscope (Tektronix 611 or 613) and, following each run, the acquired data were automatically stored. At the completion of a run, data were viewed in a number of ways (see Fig. 2).

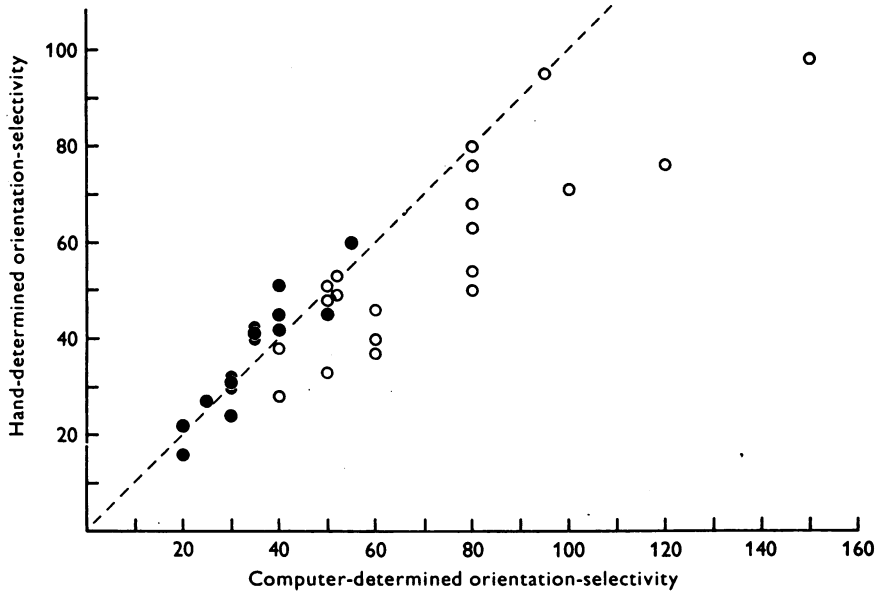

Fig. 3. An example of the agreement obtained between computer-determined orientational selectivity (Fig. 2*B*) and the hand-plotted value (Fig. 2*C*). Open circles refer to units recorded from LOBL. Filled circles indicate units recorded from HOR. LOBL and HOR are both stripe-reared animals.

Orientation selectively was calculated by fitting linear regression lines (Fig. 2*B*) to the sides of the orientation tuning curve and projecting them back to the abscissa or to the level of spontaneous activity when this was present (Campbell, Cleland, Cooper & Enroth-Cugell, 1968). Values obtained in this manner tended to agree very well with values which had been obtained by hand (Fig. 2*C*). The precision of this agreement is evident in Fig. 3 where we have plotted hand and computer-determined values for units from two cats (LOBL and HOR). The larger discrepancies between hand and computer-determined orientation limits for units which are broadly tuned is consistent with the large error introduced into the computer measurements by sampling responses over larger angular intervals with broadly tuned cells.

Because orientation selectivity varied so widely from cell to cell, we developed two ways of presenting the preferred orientations of large samples of cells. We found both of these presentations easier to interpret than the 'wheatsheaf diagrams' of Blakemore

& Cooper (1970) which give equal weight to all cells and whose visual effect is readily marred by the presence of small numbers of cells preferring orientations far from the mode. In the first of these alternative presentations, the computer represents a single cell's preferred orientation with a line whose length is inversely proportional to the unit's orientation selectivity (Fig. 6*B*). In this way undue emphasis is removed from weakly selective cells (responding over a wide range of orientations) in favour of more highly selective cells which do not respond to stimuli at angles greater than 10–20 degrees from their preferred orientations. The second mode of presentation also takes into account orientation selectivity. For this display (Fig. 6*C*), the computer calculates the proportion of cells which would be active at each of eighteen equally spaced orientations (i.e. every 10 degrees). Since our measures of preferred orientation and orientation selectivity define the range of orientations over which each unit is active, this presentation is readily obtained by integrating the ranges for all cells.

RESULTS

Behavioural results

Fig. 4*A* shows, as a function of spatial frequency, the mean percentage of correct responses made by LOBL over the 2–6 days of testing at each spatial frequency and grating orientation. Where the performance is at a level exceeding 90 %, the data points are based on 180 trials; when the performance is at a level between 80 and 90 %, the data are based on 360 trials. For gratings of even higher spatial frequency, where the level of performance is below 80 % correct, the data are based on the results of 480 trials. With gratings of low spatial frequency (0·46 cycles/degree), cats were

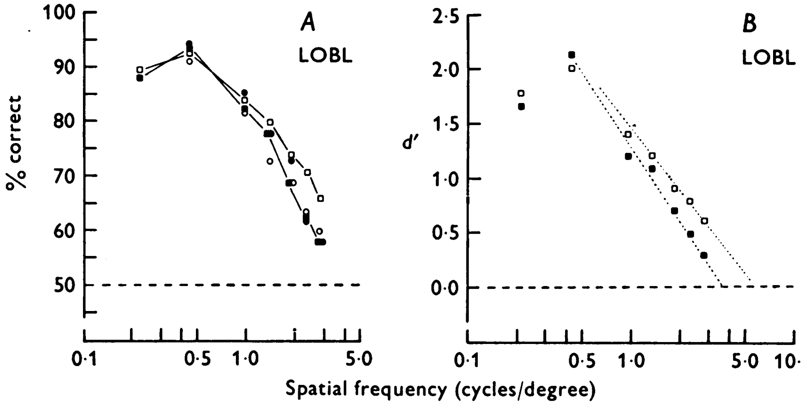

Fig. 4. *A*, the mean percentage of correct responses made by LOBL on a simultaneous discrimination between gratings of various orientations (filled circles, horizontal; open circles, vertical; filled squares, right oblique; open squares, left oblique) and a uniform field of the same average luminance. *B*, the same data for oblique gratings transformed into *d′* values for a two-alternative, forced choice procedure.

correct on more than 90 % of the presentations for all grating orientations. However, with gratings of higher spatial frequency, the proportion of correct responses decreased and clear differences became apparent among the results for different grating orientations. For spatial frequencies of 1 cycle/degree and higher, the performance was always best for gratings having the orientation of the stripes in the cat's early visual environment (135 degrees). Systematic differences of this sort have not been observed in normally reared animals (Muir & Mitchell, 1975).

In order to provide a more concise description of the deficit in the animal's performance for gratings of certain orientations, the percent correct scores were converted to d' values for a two-alternative, forced-choice procedure (Swets, 1964). This transformation permits the data for gratings with spatial frequencies of 0·46 cycles/degree or higher to be satisfactorily fitted by straight lines as can be seen from Fig. 4*B*. Only data for gratings oriented at 45 degrees and 135 degrees are shown, and lines of best fit (by eye) appear through the points for spatial frequencies of 0·46 cycles/degree and beyond. By extrapolating these lines to the abscissa, an estimate was made of the spatial frequency of the grating which would result in a chance level of performance ($d' = 0$). Although this is not the only interpretation that can be made (see Discussion), it may plausibly be argued that gratings with spatial frequencies higher than this cut-off spatial frequency are not perceived as they exert no influence on the animal's behaviour. Since the conditions of the experiment were not such as to optimize the animal's performance, these values may underestimate the animal's true visual acuity. More attention should therefore be given to orientational differences in these estimates than their absolute magnitudes.

The estimated cut-off spatial frequencies for LOBL, for gratings oriented at 45 degrees and 135 degrees, obtained by extrapolation of the lines of Fig. 4*B* to the abscissa, are 3·7 and 5·5 cycles/degree, respectively. This suggests that the early selective visual experience of this animal may have resulted in a reduction in the acuity for gratings oriented at 45 degrees of 33 %. From Fig. 4*A* it can also be seen that the performance of LOBL was worse for both vertical and horizontal gratings than it was for gratings oriented at 135 degrees and only marginally better than the performance achieved with 45 degrees. Estimates of the cut-off spatial frequency obtained in the manner shown in Fig. 4*B* were, however, slightly higher for horizontal (4·5 cycles/degree) than for vertical (4·0 cycles/degree) gratings.

Estimates of the cut-off spatial frequencies for each cat (except NOR2) appear in Table 1. Like those obtained from LOBL, the values obtained from ROBL and HOR clearly reflect their early visual environments, which were right oblique and horizontal, respectively. LROBL, whose early visual experience alternated between stripes oriented at 45 degrees and

TABLE 1. Summary of experimental results

Cat	Rearing. Orientation (degrees)	Behaviour. Cut-off spatial frequency at different orientations (angles in degrees) 0	45	90	135	Bias	Physiology. Percentage of responsive units at different orientations (angles in degrees) 0	45	90	135	Bias	Units
LOBL	135	4·5	3·7	4·0	5·5	1·49	44%	35%	44%	64%	1·83	92
LROBL	45 135	5·0	5·5	5·5	4·6	1·20*	39%	12%	34%	24%	1·15*	80
ROBL	45	—	5·5	—	3·3	1·67	20%	46%	26%	15%	3·06	46
NOR1	Normal	3·1	3·1	3·1	3·1	1*	49%	55%	69%	61%	1·41*	23
NOR2	Normal	—	—	—	—	—	44%	51%	56%	48%	1·27*	54
HOR	0	3·1	2·7	2·2	2·7	1·4	46%	25%	19%	11%	2·42	44

* For control animals (LROBL, NOR1, NOR2) biases are calculated as the ratio of the maximal value obtained (cut-off spatial frequency or percentage of responsive units) to the value obtained at the orthogonal orientation.

Behaviour: numbers show the cut-off spatial frequency obtained at each of four orientations – horizontal (0 degrees), right oblique (45 degrees), vertical (90 degrees), and left oblique (135 degrees). The bias was calculated by dividing the cut-off spatial frequency for the orientation of rearing by the cut-off spatial frequency for the orientation which was orthogonal to that of rearing. In order to calculate a bias for animals who were not reared with a single orientation, the orientation giving best performance was tentatively taken as the 'orientation of early experience.'

Physiology: numbers show the percentage of neurones in the sample obtained which would be activated by each of the four orientations (0, 45, 90, and 135 degrees). These results are shown graphically in Fig. 7. The bias was calculated by dividing the percentage of units activated by the orientation of rearing by the percentage of units activated by the orientation orthogonal to that of rearing.

135 degrees, performed very similarly to gratings of all orientations. NOR1, who matured in a normally lit laboratory colony, also demonstrated no meridional bias in his visual acuity.

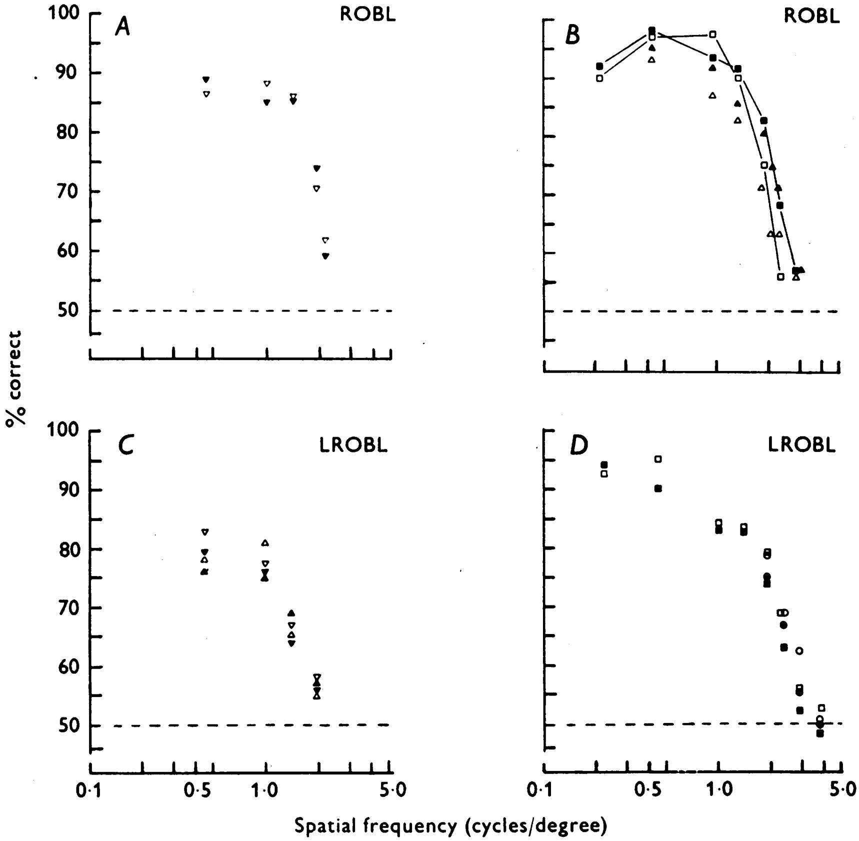

Fig. 5. The monocular and binocular grating discrimination performance of ROBL (*A* and *B*) who was reared in stripes oriented at 45 degrees, and LROBL (*C* and *D*) who was reared alternately in stripes at 45 degrees and 135 degrees. Performance with the left and right eye are depicted by upright and inverted triangles, respectively. Filled and open symbols refer to results obtained with gratings oriented at 45 degrees and 135 degrees, respectively. The results obtained under binocular viewing conditions (*B* and *D*) are depicted by squares and circles (filled circles, horizontal; open circles, vertical; filled squares, 45 degrees; open squares, 135 degrees).

All of the behavioural data from LOBL, NOR1, and HOR were obtained with the stimuli viewed binocularly. Since subsequent physiological recordings from these animals revealed a striking difference in the numbers of neurones influenced by the two eyes, the visual performances of LROBL and ROBL were tested monocularly as well as binocularly before the electrophysiological experiments. The results are shown in Fig. 5. Monocular testing with LROBL, which was performed several months after binocular testing, proved to be very difficult. For some unexplained reason, the animal's performance was poor even at low spatial frequencies. There was no evidence that one eye was poorer than the other. The performance of ROBL, on the other hand, was better with the left eye than with the right. In fact, the results obtained with the left eye alone were comparable to data obtained several months earlier using both eyes (Fig. 5*A*, *B*). When tested with the right eye alone, a consistent bias for the orientation of early exposure failed to emerge.

These behavioural experiments suggest that the early visual experience of LOBL, ROBL, and HOR may have resulted in small but nevertheless reliable differences in their abilities to resolve gratings at different orientations. Gratings having the orientation of the contours in the cats' early visual environment are resolved better than all others. On the other hand, two control animals (LROBL, whose early visual experience alternated between orthogonal sets of oblique stripes, and NOR1, who experienced a completely normal early visual environment) showed no such differences in their abilities to resolve gratings of different orientations. These results are thus concordant with earlier findings (Muir & Mitchell, 1973, 1975).

Physiological results

Recordings were obtained from 339 cortical units. Of these, eighty-seven either were not orientation selective or exhibited sufficiently 'pathological' properties (see Methods) for us to exclude them from our sample. We were left with 252 briskly responsive neurones for which we successfully determined many parameters including preferred orientation and orientation selectivity. As has been previously described for the monkey and cat (Hubel & Wiesel, 1974), the units preferred orientations tended to shift in an orderly fashion as the electrode advanced. This was true for both the stripe-reared and the normal animals. For one penetration in HOR, however, this was not the case. Thirteen units, sampled at approximately equal intervals over a distance of 3 mm, each possessed an orientation preference which was within 20 degrees of horizontal (the orientation of rearing). As pointed out by Hubel & Wiesel (1974), the probability of an electrode advancing parallel to an iso-orientation 'cortical slab' for a distance of 3 mm is small.

No serious attempt was made to guess an animal's early visual history until the completion of recording. For some animals (LOBL, ROBL) a bias became fairly evident following a casual examination of the receptive field plots. For others, one was not entirely confident of the 'correct' visual history even after three stages of data analysis. These stages consisted of the visual presentations previously described (Methods). Fig. 6 shows sixty-four units from LOBL displayed in the manner of Blakemore & Cooper (1970) as well as in the two variants of the polar plot which we have developed.

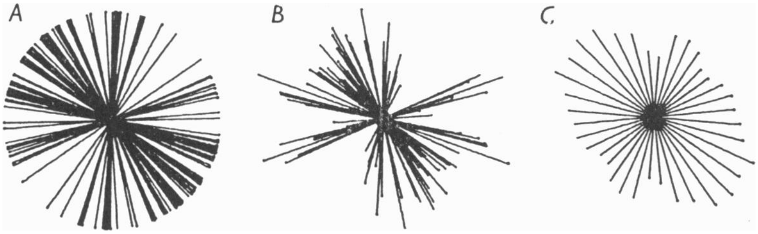

Fig. 6. Three different ways of presenting the cells sampled from one cat (LOBL). *A*, after Blakemore & Cooper (1970). Each unit is represented by a line. The units orientational preference corresponds to the angle of the line. *B*, similar to *A*, but orientational selectivity appears in the length of each line, tightly tuned units are represented by longer lines. *C*, the length of each line in this diagram corresponds to the percentage of the entire unit sample which would have responded to a stimulus at that orientation. The longest line in this particular diagram (for LOBL) corresponds to 64 %.

By referring to such polar diagrams, the physiologists correctly guessed the early visual environment for four of the five cats (LOBL, ROBL, NOR1, and HOR). The data base for these guesses is shown in Fig. 7 where a graphic representation of the behavioural data (Table 1) is also provided for comparison. While no cat had an absolute deficit of neurones with preferences at a particular orientation, there was a clear tendency for the orientation of rearing to coincide both with the preferences of the majority of neurones, and with the preferences of those neurones which were most sharply tuned for orientation. Thus, the polar plots for LOBL, ROBL, and HOR show biases for left oblique, right oblique, and horizontal, respectively. The units recorded from LROBL appeared non-random with a possible bias for horizontal. However, this animal matured viewing orthogonal orientations on alternate days (Methods) and it is therefore not clear what one should have concluded from the orientational trends in his cell sample. Even though NOR1 died early in the recording session, his sample of responsive cells (eighteen units) appeared striking in its radial symmetry (Fig. 7). After it was confirmed that he was a control normal cat, the physiologists set up an additional normal cat (NOR2) from their own colony in order to obtain a larger sample (fifty-four) of 'normal' units. As can be seen in Fig. 7, the polar histograms of units from NOR1 and NOR2 are similar and quite radially symmetric.

An unexpected feature in each of the four stripe-reared cats (LOBL,

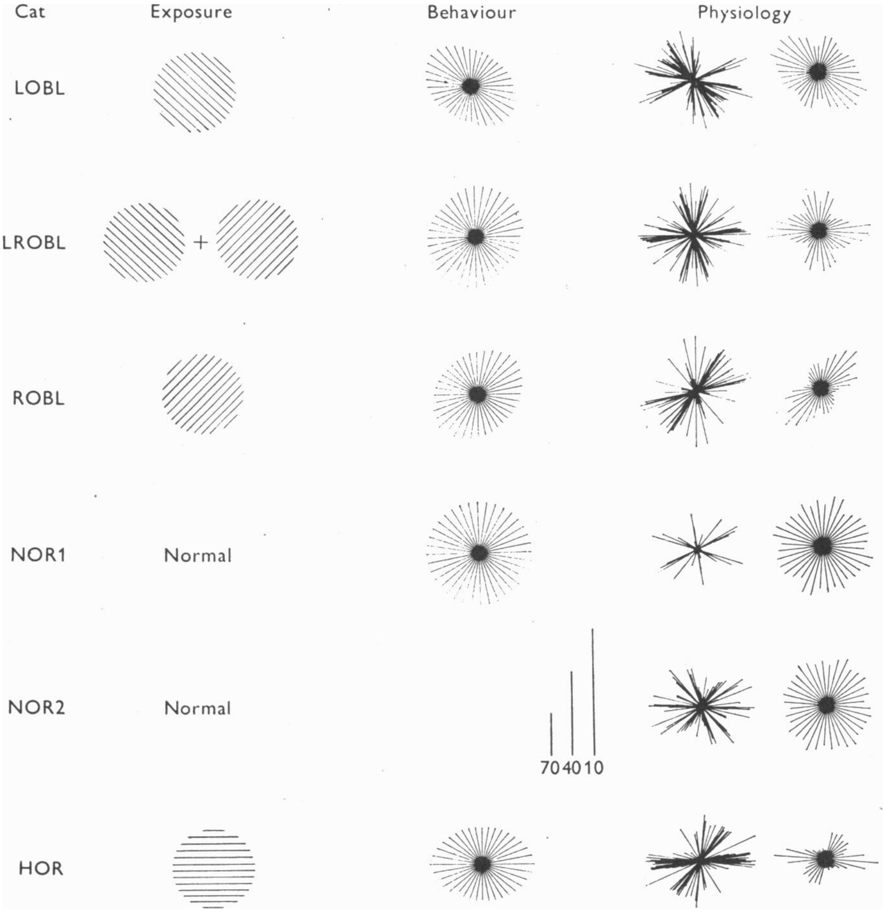

Fig. 7. Graphic representations of behavioural and physiological data for all cats. Gratings on the left indicate the orientation which an animal experienced during rearing. Data for the behavioural graphics are obtained from the cut-off spatial frequencies shown in Table 1. The length of each line indicates the animal's relative ability to perceive gratings oriented at that angle. Lines at orientations other than 0, 45, 90, and 135 degrees are added to facilitate comparison to the physiological diagrams. Their lengths were obtained by extrapolation. Physiological data appear for each cat in the styles of Fig. 6 *B* and *C*. Each line in the left-hand Figures (scale in degrees to the left of Figure for NOR2) represents a unit. The angle of the line corresponds to the unit's orientational preference while the length is inversely proportional to the width of tuning. The length of each line in the right-hand diagrams corresponds to the proportion of a cat's unit sample that would have been activated by a stimulus with that orientation. The absolute magnitudes of these proportions can be derived by consulting the physiological values in Table 1.

LROBL, ROBL, and HOR) was the paucity of binocular neurones. While the number of binocular cells averages over 80 % in a normal cat (Hubel & Wiesel, 1962), only 30 % of the cells recorded from the stripe-reared animals could be influenced by both eyes. Every one of these cells had a preferred orientation which lay within thirty degrees of the orientation of the early environment. In the case of LROBL, every binocular cell had a preferred orientation within 10 degrees of horizontal. In the case of monocular neurones the strength of orientation bias (Fig. 8) differed for units responding to the two eyes. While we recorded more units from LOBL which responded to the right eye, bias was more pronounced in units which responded to the left. Two penetrations in the right hemisphere of this animal gave a similar result. This effect also emerged in the orientational preferences of units recorded from ROBL. In this case, the stronger orientation bias for cells responding to the left eye (Fig. 8) correlates with the greater amount of bias which this animal demonstrated behaviourally when forced to use his left eye alone.

DISCUSSION

These results confirm and extend a number of observations about the behavioural and physiological consequences of selective early visual exposure (Blakemore & Cooper, 1970; Muir & Mitchell, 1973, 1975). Early stripe-rearing leads to slight biases in both the behaviour of an animal and its cortical neurones that are well correlated with one another and long-lasting. For example, after as long as three years in a normal environment HOR had cortical physiology which indicated that he had matured in a visual environment of horizontal contours. We found that such indications were made particularly clear by the use of integrated polar plots.

There are, however, a number of disagreements with other studies. Our stripe-reared animals had reduced binocularity in contrast to the results of Blakemore & Van Sluyters (1974). These authors not only obtained normal binocularity after stripe-rearing, but claimed that exposure to stripes could prevent the loss of binocularity due to strabismus. We are at a loss to explain this difference since most aspects of rearing and recording were similar. The fact that three of our cats were restrained during conditioning does not appear to account for the difference, since HOR was not restrained and he too demonstrated a high percentage of monocular neurones. Another factor may be the longer period our kittens spent in the dark prior to stripe-rearing since dark-rearing can lead to strabismus (Kalil, 1975; Pettigrew, 1974), but again HOR began conditioning when he was 20 days old. We appear not to be alone in finding an increase in monocularity following stripe-rearing (M. Cynader, personal communication).

While there is a clear preponderance of neurones which prefer orientations close to that of early exposure, we did find a relatively large number of neurones which preferred orientations orthogonal to that of early exposure, as well as behavioural evidence for resolution of orthogonal gratings. This finding differs somewhat from the early results of Blakemore & Cooper (1970), who found a complete absence of neurones responding to

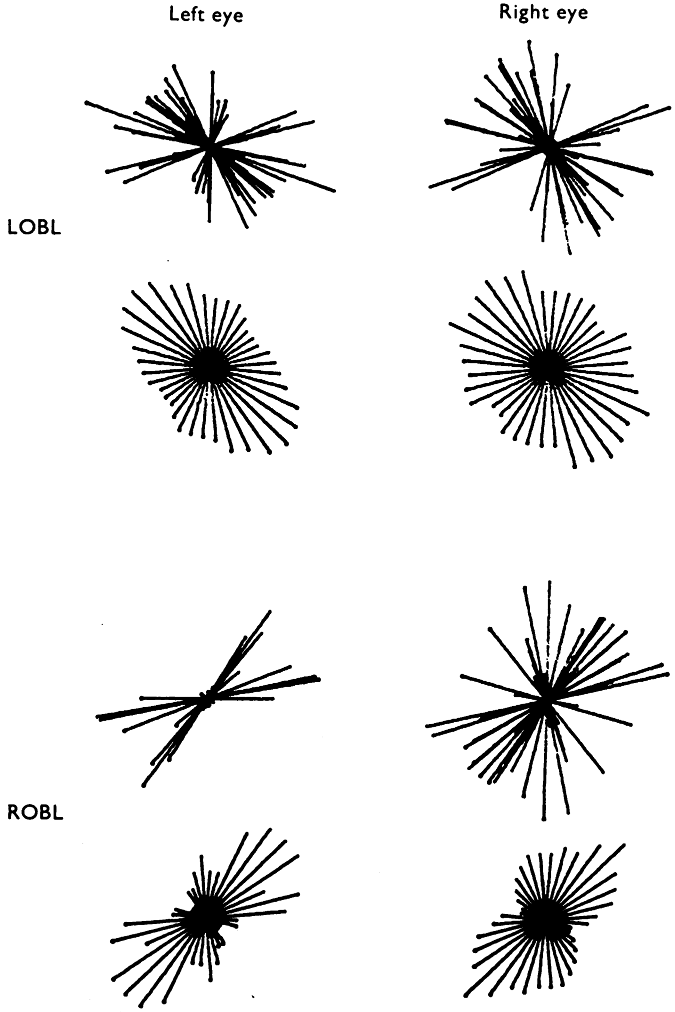

Fig. 8. Physiological data for LOBL and ROBL. Diagrams are similar to those appearing in Fig. 6. While more units were recorded which responded to the right eye of each animal, orientational bias is strongest in units responding to the left. This correlates with the greater perceptual bias which ROBL demonstrated (Fig. 5*A*, *B*) when forced to use his left eye.

the orthogonal orientation. It also differs from the recent observations of Stryker & Sherk (1975), who failed to find any bias whatsoever. Blakemore & Cooper's result that all recorded neurones reflect the orientation of early exposure appears puzzling inasmuch as animals with similar early visual experience demonstrate a definite, though diminished, acuity for the orthogonal orientation when tested behaviourally (Muir & Mitchell, 1975). This difference may be partly attributable to some degree of reversibility in the stripe-rearing effect. After all, stripe-reared kittens have an initial gross behavioural deficit which amounts to 'blindness' for contours orthogonal to the orientation of rearing. This gross deficit disappears after about 30 hr of normal visual experience (Muir & Mitchell, 1975), so it is conceivable that some aspects of cortical physiology might also change during this time. Units from Blakemore & Cooper's cats were generally obtained within the first 24 hr of recording when any orientational bias may have been more pronounced. Our cats, on the other hand, had been routinely tested with a wide variety of different orientations and had, in addition, lived 1–3 years in a normal visual environment before undergoing physiological examination. Some recovery of previously 'lost' neurones may have occurred during this time.

It is more difficult to explain why Stryker & Sherk (1975) have failed to replicate Blakemore & Cooper's result even partially. The strength of their finding resides in the three procedures they have used to ensure impartiality: (1) recordings were conducted 'blind'; (2) a computer was used to determine preferred orientation; and (3) one measurement was made at each of many equally spaced (100 μm) intervals along the electrode track. Since our study was also conducted 'blind', this in itself does not appear sufficient to generate a negative result. Neither does the use of a computer appear to be crucial. During the performance of a 'blind' experiment, the experimenter does not know the early visual history of an animal. Observer bias, on his part, should therefore apply to 'incorrect' orientations as well as 'correct' ones. With five rearing possibilities – horizontal, vertical, right oblique, left oblique, and normal – the chance of correctly guessing the early visual experience of very many cats (in this case four out of five) is small and any additional impartiality, attributable to the use of a computer, is hardly relevant.

The merits of the sampling technique of Stryker & Sherk (1975) are harder to dismiss. Since they sampled only one cell every 100 μm, their collection of preferred orientations is evenly distributed over the distance of the electrode track. Reports in the literature suggest that orientation 'columns' resemble ocular dominance 'columns' in their ability to expand and contract (Blakemore & Cooper, 1970; Pettigrew *et al.* 1973), and Stryker & Sherk's sampling method offers a clear-cut way of deciding whether or not this is true. The exact topographical arrangement of orientation 'columns' does not, however, always correlate well with the animal's visual capabilities. Wiesel & Hubel (1974) managed to resolve 'normal' orientational topography (i.e. progressive shifts in preferred orientation with increasing electrode distance) in the visual cortex of a monkey who had been binocularly deprived since birth, yet such an animal has disturbed visual performance. The only abnormality, noticed by Hubel & Wiesel, was a somewhat lower density of points from which they could obtain orientational data. Single unit recordings (using fine tipped microelectrodes) from binocularly deprived cats similarly show that visually responsive cells displaying normal selectivity, if present at all, are drastically reduced in number. Blakemore & Van Sluyters (1975) found that only 15% of the cells recorded from dark-reared animals demonstrated normal selectivity and Pettigrew (1974) found even fewer. Since binocularly deprived animals initially show very poor visual performance (Wiesel & Hubel, 1965; Kalil, 1975), visual behaviour appears to correlate best with the density of normal, responsive cells. If this density changes as one advances an electrode through successive orientation columns, our method of sampling would reflect this change, whereas single, equally spaced samples might not. In view of the more recent success of Stryker & Sherk (1975) at replicating the results of Hirsch & Spinelli (1970, 1971), however it seems possible that the reasons behind their earlier failure reside much less in the three techniques they have introduced to ensure impartiality than in the technique of rearing.

Returning to the behavioural measurements which were obtained from our cats (Figs. 4 and 5), one sees that the performance of each stripe-reared animal changed as gratings were presented at different orientations. In confirmation of earlier findings (Muir & Mitchell, 1975) there was no evidence of any permanent blindness to contours that were not present in the animal's early visual environment. Instead the animals simply performed somewhat poorer on a discrimination task between gratings of various spatial frequencies and a uniform field of the same mean luminance when the gratings were orthogonal to the stripes the animals saw as kittens. Estimates of the cut-off spatial frequencies for gratings of different orientations obtained from this data by extrapolating to the spatial frequency that first failed to exert control over the animal's behaviour (Table 1) revealed small but reliable deficits for gratings orthogonal to the stripes they saw during early rearing of between 29 (HOR) and 40% (ROBL). Although these estimates should only be equated with visual acuity with caution, since the absence of control over behaviour need not necessarily mean that the gratings cannot be perceived, the results nevertheless indicate quite clearly that at worst our selectively deprived animals suffer only a slight reduction in their acuity for gratings perpendicular to the contours in which they were reared. Furthermore, while the acuity may have been reduced for these orientations, it never rose above normal values at other orientations. This appears to reflect a trend in the results of deprivation experiments pointed out by Barlow (1975), viz. it is easy to produce noticeable deficits via one manipulation or another, but it is very difficult to demonstrate any improvement in visual acuity which can be attributed to selective early exposure.

Since our behavioural measure, of the highest spatial frequency that exerts control over behaviour, is so different from our physiological measures, it may be important to devote some discussion to the two sets of observations. Although we have not collected enough data which bear on the point, we think it likely that cells with the narrowest orientation selectivity also possess the sharpest frequency selectivity and may respond to the finest gratings.

While it might be argued that neurones need not respond exclusively to high spatial frequencies in order to detect them, cells which select high spatial frequencies (as well as very narrow bars and slits) certainly exist. Presumably their existence benefits the animal's perception. If there were mutual inhibition of adjacent cells (which preferred other spatial frequencies) there would be a greater signal to noise ratio for these cells during the discrimination of fine gratings, than for cells which respond to both high and low spatial frequencies.

The link between these parameters must be established by further experiments, but may be suggested by the following lines of reasoning.

On the basis of psychophysical experiments, Blakemore *et al.* (1970) have suggested that inhibitory interconnexions might increase the selectivity of individual cortical neurones for certain orientations by vetoing responses to non-optimally oriented stimuli. The fineness of tuning which can be achieved through inhibitory interaction probably increases with increasing similarity in stimulus requirements. Cells which differ only slightly in their preferred orientations can make more precise adjustments in each other's selectivity than cells which prefer orthogonal orientations. Similarly, cells whose receptive fields overlap might be expected to make one another more selective with respect to spatial frequency than cells whose receptive fields are separate. Since intracortical inhibition is limited to fairly short distances (Fiskin, Garey & Powell, 1973), the closer two cells reside, the more strongly they interact. Interaction is strongest between cells which respond to overlapping regions in visual space and which prefer similar stimuli (for example, orientational preference). Therefore, one can easily imagine that the tightness of tuning, both to orientation and to spatial frequency, might vary with the local density of responsive, orientationally selective cells.

While it appears unlikely that we can increase the density of cells in a column above normal values, it is possible that, by depriving an animal of contours at one orientation, we can reduce the density of responsive cells in the 'columns' which represent that orientation. Cells which might have developed a preference for the deprived orientation may either become unresponsive (thereby explaining orientational plasticity as a result of attrition) or they may adopt a preference for the orientation of early exposure (in which case we have plasticity as a function of columnar expansion). It is not at present possible to decide between these two possibilities.

The fact that our experimental animals had fewer units responding to the deprived orientation than to the non-deprived orientation is evident from Table 1 and from the integrated polar plots in Fig. 7. A tendency for units preferring orientations orthogonal to those of early exposure to be more broadly tuned for orientation is also apparent in the diagrams of Fig. 7. On the basis of the arguments just outlined, we suggest that the selectivity for spatial frequency (high spatial frequencies in particular) of individual cortical cells is also reduced at orientations not present in the early environment, and that this reduction accounts for the behavioural observations.

Initial support for the electrophysiological recording was from the National Eye Institute to Horace Barlow and work was completed with the help of a Spencer Foundation grant and U.S. Public Health Service grant MH 25852 to J.D.P. The behavioural work was supported by grants to D.E.M. from the Medical (MA-5027) and National (APA-7660) Research Councils of Canada. We wish to thank Frances Wilkinson for her assistance with some of the behavioural experiments, Carl Olson for assistance with some of the early recordings, Pete Goodeve for programming the Nova and Larry Crowder and Herb Adams for technical assistance. We thank Drs Horace Barlow and John Robson for helpful comments on the manuscript.

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