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Modification of the Kitten's Visual Cortex by Exposure to Spatially Periodic Patterns

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Summary. Kittens were dark-reared except for exposure to three types of spatially periodic, vertically striped pattern:

1. single, widely spaced black bars;
2. wide areas of regular vertical grating separated by large blank patches;
3. a uniform, continuous grating with a spatial frequency of 0.5 c/deg.

In each case there was a bias towards vertical in the distribution of preferred orientations of cells recorded in the visual cortex. The contrast sensitivity of individual neurones for gratings of different spatial frequencies was analysed quantitatively. In kittens exposed to a uniform grating of 0.5 c/deg, many cells were maximally sensitive close to 0.5 c/deg, as they are in normal cats. The occipital potential evoked by vertical gratings higher in frequency than 0.3 c/deg was consistently greater in amplitude than that for horizontal, and a vertical grating of 0.5 c/deg produced the maximum activity. These results are compared with those of Maffei and Fiorentini (1974); the differences between our results and theirs may be attributable to the degree of variability in spatial frequency and orientation during rearing, and to the duration of exposure.

Key words: Visual cortex – Development – Kitten

The functional properties of neurones in the cat's visual cortex depend upon early visual experience. Restricting patterned visual input to one eye leaves most cortical cells excitable through that eye alone (e.g. Wiesel and Hubel, 1963; Hubel and Wiesel, 1970), while preventing normal congruent binocular visual stimulation in other ways creates, predominantly, two monocular populations of

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cortical cells and greatly reduces the proportion of binocular neurones (e.g. Hubel and Wiesel, 1965; Hirsch and Spinelli, 1970, 1971; Blakemore et al., 1975; Blakemore, 1976). Patterned visual experience of special kinds can also affect the feature-selectivity of cortical cells: orientation and direction preferences amongst the populations of neurones can be biased by restricting an animal's visual experience to limited ranges of these variables (e.g. Hirsch and Spinelli, 1970, 1971; Blakemore and Cooper, 1970; Cynader et al., 1975; Tretter et al., 1975; Stryker et al., 1976; Blasdel et al., 1977).

These experimental results all share a common feature: the population of neurones in the visual cortex becomes relatively less sensitive to stimuli that were not experienced early in life. A recent study (Maffei and Fiorentini, 1974; Fiorentini and Maffei, in preparation) is therefore of particular interest because it contradicts this general rule. Those authors reared kittens in a manner very similar to that used by Blakemore and Cooper (1970), restricting their visual experience to striped patterns of a single orientation but with bright and dark bars of equal width (square-wave gratings of constant spatial frequency): previous studies (except for those of Hirsch and Spinelli, 1970, 1971; Pettigrew and Garey, 1974; Tretter et al., 1975) had used striped patterns of irregular bar-width. Maffei and Fiorentini (1974) reported four effects produced by their rearing procedure:

1. There was no bias in the distribution of preferred orientations of cortical neurones.

2. There was a marked decrease in the amplitude of the cortical evoked potential for gratings of spatial frequency similar to that of the early visual experience.

3. The 'mass response' of cells in the lateral geniculate nucleus (LGN), recorded with a large microelectrode in the optic radiation, showed a relative reduction in strength for gratings of the experienced spatial frequency.

4. Some cells in the visual cortex and LGN, when tested with gratings of various spatial frequencies, had sensitivity troughs in their 'tuning curves' in the region of the experienced frequency.

Thus, in both LGN and visual cortex, the special rearing conditions, involving spatially-periodic stripes, resulted in a *decreased* sensitivity to the experienced pattern, while sensitivity to other patterns, unseen in early life, was apparently qualitatively normal. In view of the importance and unusual nature of these findings as an exception to those generally reported following restricted early experience, we have performed a similar experiment.

Methods

Rearing Conditions

Five kittens were reared in total darkness except for regular exposure in a controlled visual environment, using the general methods of Blakemore and Cooper (1970) as modified by Blakemore and Van Sluyters (1975). In particular, the animal was suspended in a transparent inner Perspex cylinder (diameter 28 cm) within the large tube (diameter 46 cm) on which the striped pattern was displayed. The range of straight-ahead viewing distances was about 9–27 cm, producing

approximately a ± 50% variation in spatial frequency, but if the kitten looked far up or down the cylinder it would be exposed to somewhat higher spatial frequencies. Exposure, lasting about 1 hour each day, was started at 3 weeks and continued until recording at 9–14 weeks of age. Each animal had about 50 hours of restricted experience. One control animal was reared normally in the colony and recorded at about 19 weeks of age.

Electrophysiological Methods

Our general methods have been described elsewhere (Blakemore and van Sluyters, 1975). Animals were surgically prepared for electrophysiology under halothane (Fluothane) and barbiturate (Brietal) anaesthesia. Paralysis was achieved by continuous intravenous infusion of Gallamine triethiodide (Flaxedil: 10 mg/kg.hr) coupled with bilateral cervical sympathectomy; the animals were artificially hyperventilated with a mixture of about 75% N_2O/ 23% O_2/2% CO_2 and the exact percentage of inspired CO_2 was adjusted to bring end tidal CO_2 to about 4.5–5%.

Mydriasis and cycloplegia were produced by topical application of Homatropine sulphate and Phenylephrine HCl. The corneae were protected with clear contact lenses and 3 mm artificial pupils were placed directly in front of the eyes. Residual refractive errors were assessed by direct ophthalmoscopy and corrected with appropriate spectacle lenses.

Single Units: Recording and Visual Stimulation

The activity of single units was recorded with tungsten-in-glass microelectrodes (Levick, 1972) with an exposed tip length of 15–25 μm. Receptive fields were plotted using bars, slits, edges and spots of light back-projected on a tangent screen 57 or 114 cm from the cat's eyes. We took care to advance the electrode very slowly and searched for units by moving a visual 'noise figure' in front of the eyes; and we followed the procedures described by Blakemore and Van Sluyters (1975) to gain representative samples of neurones. The activity of nerve fibres from the lateral geniculate body was occasionally recorded in the cortex or the white matter of the optic radiation; these units were distinguished from cell-body recordings by their brief diphasic action potentials, concentric receptive field organization and monocular input. All the receptive fields were within 10 deg of the area centralis, and most were within 5 deg. 136 cortical cells were analysed qualitatively, together with 8 LGN neurones.

For quantitative experiments on 46 units, gratings of sinusoidal luminance profile were generated on the face of a display oscilloscope (Hewlett-Packard 1300A; P31 phosphor; mean luminance 6.8 cd/m^2) by the method of Campbell and Green (1965). The screen, which subtended 12 deg by 10 deg at an optical distance of 114 cm, faced upward and its image was reflected from a front-surfaced mirror at a 45° angle in front of the cat. By moving the oscilloscope and rotating it on a turntable, the grating could rapidly and accurately be positioned and orientated over the receptive field.

Occipital Evoked Potentials

In one animal we also used Ag/AgCl pellet electrodes to record the gross potentials evoked by grating patterns. Small holes were drilled in the skull at Horsley-Clarke coordinates P4 L2 above the right hemisphere and APO L2 on the left side, and the electrodes were inserted as tightly fitting plugs in contact with the dura. Evoked potentials were differentially amplified, filtered (bandpass 7–28 Hz) and fed to an averaging computer (Biomac 1000).

Histology

Electrolytic lesions were made at intervals along each microelectrode penetration, and the tracks were subsequently reconstructed histologically (Blakemore and Van Sluyters, 1975). All cortical penetrations lay within area 17.

Results

The Effects of Different Areas of Repetitive Stripes

Maffei and Fiorentini (1974) have argued that their results might be explained by the powerful suppressive effect that high-contrast gratings have on contrast sensitivity. Certainly exposure to a grating of a single spatial frequency temporarily depresses the occipital evoked potential and the contrast sensitivity of human observers (Blakemore and Campbell, 1969a, b; Campbell and Maffei, 1970) and reduces the evoked potential in cats and the responsiveness of some cortical cells (Campbell et al., 1973; Maffei et al., 1973). These effects are short-lived after adaptation for only a minute or two, but it is conceivable that exposure to identical stripes for 2 or 3 hours per day could have caused a profound and long-lasting suppression of activity in the visual cortex of Maffei and Fiorentini's kittens. (Indeed, Creutzfeldt and Heggelund (1975) have recently reported that regular prolonged exposure of *adult* cats to vertical stripes can even produce a reduction in the proportion of cortical cells responding to that orientation.)

Such hypothetical adaptational effects would have been precluded in many of the previous experiments because the environment consisted of dark stripes of various widths whose spatial frequency components were therefore widely distributed. As the kitten's fixation moved from place to place, it would often have been faced successively by a high-contrast edge and then a blank area, permitting 'recovery' from any adaptational effect.

We attempted to test this general hypothesis by rearing kittens in three environments that included varying amounts of unrelieved vertical grating. The remainder of the time they were kept in total darkness.

1. Single Stripes. One kitten (K215) was exposed in an environment composed of single vertical black bars, 1 deg wide (at the average viewing distance of 18 cm, with the kitten in the middle of the inner transparent cylinder). The bars were separated by large white areas, 44 deg wide.
2. Interrupted Grating. Another kitten (K216) saw only a pattern consisting of wide strips of regular vertical grating of 0.5 c/deg (cycles per degree of visual angle). The width of each strip of grating was 29 deg and between each strip was a broad, blank white stripe, 61 deg across. Four such patches of stripes with blank intervals filled the entire 360° visual field.
3. Continuous Grating. Three animals (K217, 239 and 240) were exposed in a manner somewhat similar to that of Maffei and Fiorentini (1974) to a continuous regular vertical square-wave grating of 0.5 c/deg, with no blank strips at all. Cortical cells were recorded in two of these kittens, occipital evoked potentials and LGN cells in the third (K240). In each rearing condition the contrast of the patterns (difference between maximum and minimum intensities divided by twice their mean) was nearly 1.0.

We also recorded from the visual cortex of one 19 week old kitten (K226) that had been normally reared in the colony. All 18 cortical cells recorded in this animal were orientation selective. In the stripe-reared animals too, almost all cortical cells (109 out of 118) were clearly orientation selective (Hubel and

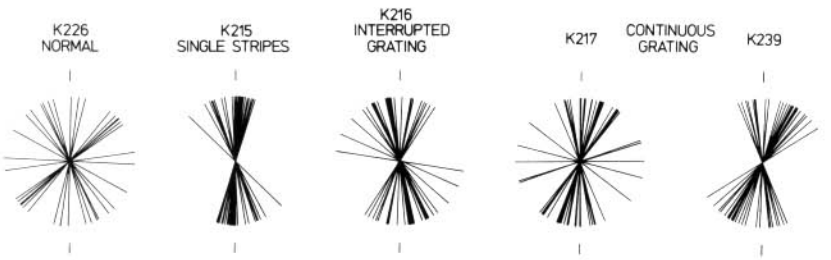

Fig. 1. In these polar diagrams each line represents the preferred orientation, in the dominant eye, for one cortical cell. Each diagram shows the total sample from a single animal. K226: a normal 19 week old kitten (18 cells). K215: exposed to widely-spaced vertical black stripes, 1 deg in width (28 cells). K216: exposed to a vertical grating of 0.5 c/deg, interrupted at 29 deg intervals by broad white vertical areas 61 deg wide (28 cells). K217 and K239: exposed to an uninterrupted vertical grating of 0.5 c/deg (27 and 24 cells)

Wiesel, 1962, 1965). The remainder were visually unresponsive (7 cells) or non-oriented (2 cells).

The Orientation Selectivity of Cortical Cells

We designed the three restricted environments to give increasingly concentrated exposure to stripes of 0.5 c/deg. In the first two cases, however, the energy at that frequency was diluted by the inclusion of large blank areas. If Maffei and Fiorentini's adaptational hypothesis is correct these three groups of animals should have shown decreasing modification of orientation selectivity in the cortex and decreasing sensitivity to patterns of 0.5 c/deg.

Our results, shown in Figure 1, do not support this hypothesis. While we found considerable variation in the bias of preferred orientations, there was no obvious relationship with the exact nature of the environment: the two animals exposed to the continuous grating gave practically the most impressive (K239) and least impressive (K217) bias from amongst the whole series. In all the experimental animals, even K217, the modification of the distribution of preferred orientations, compared with the normal animal, was statistically significant.

Selectivity of Cortical and LGN Neurones for Spatial Frequency

For the first three experimental animals (K215, 216 and 217) the analysis of receptive fields was performed qualitatively, using hand-moved, projected stimuli. We examined spatial-frequency selectivity quantitatively for 24 cortical cells and 2 LGN fibres in one animal exposed to the uninterrupted grating (K239), for 3 LGN cells in another (K240), as well as for 17 cortical cells in the normal control kitten (K226).

For each cell the receptive fields were first plotted by hand, then the non-dominant eye was covered and the large display oscilloscope was set at the

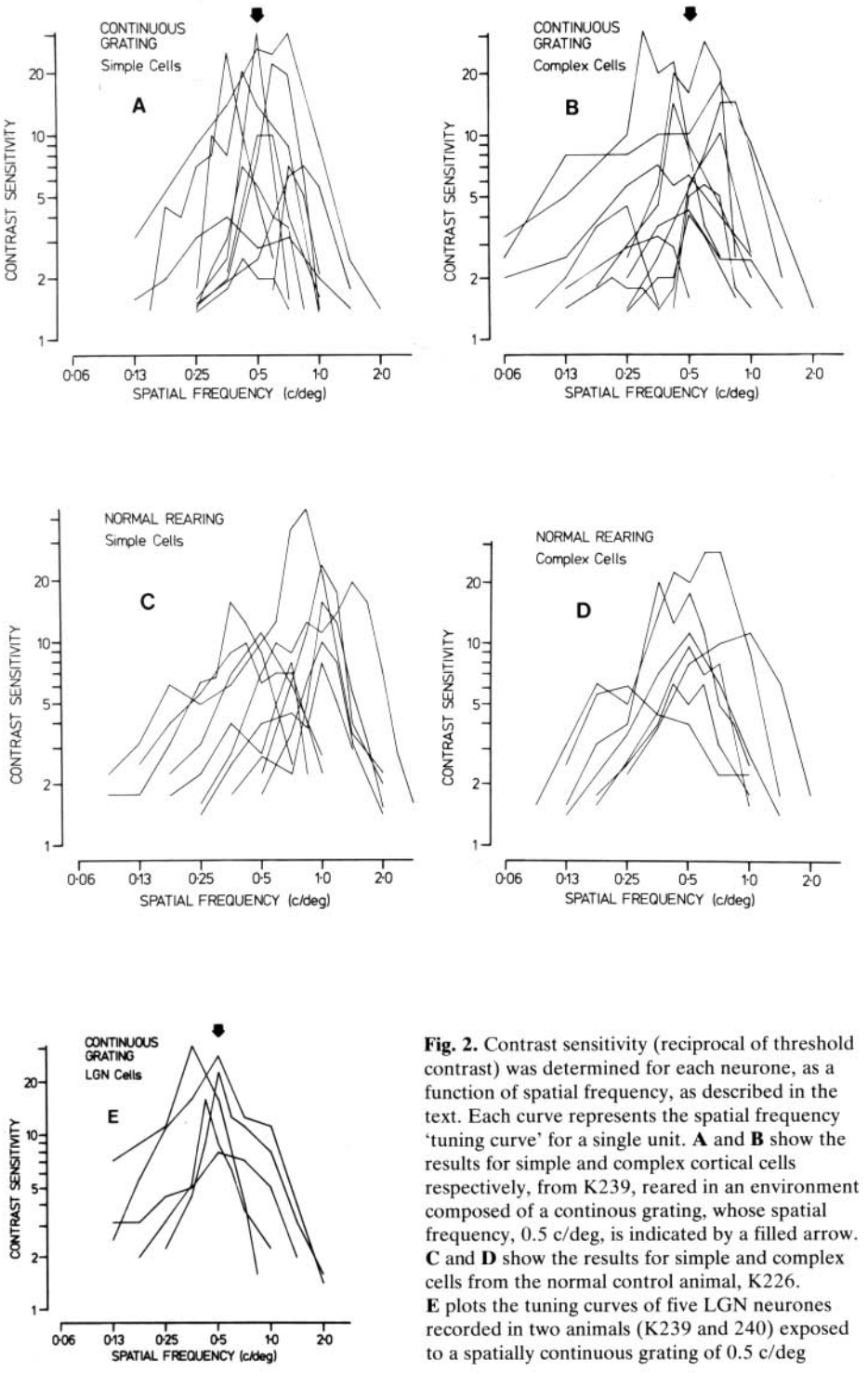

Fig. 2. Contrast sensitivity (reciprocal of threshold contrast) was determined for each neurone, as a function of spatial frequency, as described in the text. Each curve represents the spatial frequency 'tuning curve' for a single unit. **A** and **B** show the results for simple and complex cortical cells respectively, from K239, reared in an environment composed of a continous grating, whose spatial frequency, 0.5 c/deg, is indicated by a filled arrow. **C** and **D** show the results for simple and complex cells from the normal control animal, K226. **E** plots the tuning curves of five LGN neurones recorded in two animals (K239 and 240) exposed to a spatially continuous grating of 0.5 c/deg

optimal orientation for cortical cells, or at vertical for LGN units, and was centred over the receptive field of the dominant eye. A grating of variable contrast was generated on the screen and moved back and forth at a fixed angular velocity chosen to optimize the response of the neurone (usually 1–5 deg/sec), and with an amplitude of sweep large enough to move several cycles of the pattern across the receptive field whatever the spatial frequency, which was varied in an irregular sequence. At each spatial frequency, while the grating was moving, the contrast was adjusted in steps of 0.05 log units until a *threshold contrast* was found, at which the neurone produced a just reliable modulation of discharge or increase in mean firing (Enroth-Cugell and Robson, 1966). This is not a difficult judgement to make by ear and there was always excellent agreement between two experimenters listening to the action potentials at the same time.

The results are shown in Figure 2 as spatial frequency tuning characteristics, in which contrast sensitivity (reciprocal of contrast threshold) is plotted as a function of spatial frequency. The individual threshold values at different frequencies have been joined by lines, for each unit, to give an impression of each 'tuning curve'. Parts A and B illustrate curves for simple and complex cortical cells respectively from the kitten reared in the continuous grating environment; the solid arrow shows the experienced frequency (0.5 c/deg). Parts C and D show comparable results from the normal control animal. Part E shows the tuning curves for five LGN units from grating-reared kittens, three recorded as cells in the nucleus and two as optic radiation fibres beneath the visual cortex.

Inspection of these results shows that:

1. There was no tendency for tuning curves to be missing or depressed in sensitivity in the region of 0.5 c/deg, the frequency of stripes in the early environment.

2. The absolute contrast sensitivities of the most sensitive cells from the experimental and normal animals were quite similar.

3. Even for the LGN, the few units recorded had excellent sensitivity at 0.5 c/deg.

In Figure 3 the distributions of optimum spatial frequency (the peaks of the tuning characteristics) are plotted as histograms for the experimental and normal kittens, with simple, complex and LGN cells illustrated separately. It even appears from Figure 2 that the distribution of preferred spatial frequencies in the grating-reared kittens might have been more tightly clustered about 0.5 c/deg than it was for the normal control; but the significance of this observation is doubtful in view of the difficulty of obtaining data representative of the whole population from a small sample taken in a single experiment.

Occipital Evoked Potentials

In one grating-reared kitten (K240) we recorded the evoked potential from Ag/AgCl electrodes in contact with the dura above the visual cortex. The stimulus was a vertical or horizontal grating, generated on the display

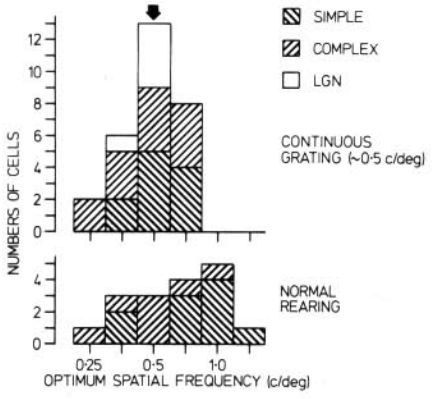

Fig. 3. Histograms showing the distribution of optimal spatial frequency (the peaks of the curves in Fig. 2) for: **A** simple and complex cortical cells, and lateral geniculate units, from animals exposed to a continous grating of 0.5 c/deg (marked with a filled arrow). **B** simple and complex cells from the normal control animal

oscilloscope, which was centred on the visual axis of the right eye, with the left eye covered. The contrast of the grating was 0.36 and its phase was reversing at 14 Hz (interchanging the dark and light bars without variation in mean luminance). The responses were analysed on an averaging computer where each sweep included two phase reversals. 400 sweeps (800 phase-reversals) were taken for each condition. The spatial frequency range was covered in half-octave steps, in sequence, from 0.09 to 4.0 c/deg. At each spatial frequency the response was measured for vertical and horizontal gratings, one after the other. This strict sequence precluded any spurious differences between the two orientations due to gradual changes in the responsiveness of the preparation.

Sample records are shown in Figure 4A for five spatial frequencies. Each trace shows the averaged response to two phase reversals, so a comparison of the first and second half of each sweep gives an indication of the variability of the response under any one condition. It can be seen that for every spatial frequency except the lowest illustrated (0.13 c/deg) the potentials evoked by a vertical grating were larger in amplitude than those produced by a horizontal pattern. All the data are displayed graphically in Figure 4B, where each point shows the peak-to-trough amplitude of the evoked potential, averaged over the two cycles contained in each record. The dashed line (approximately 8 μV) was the largest amplitude of several control records taken under the same conditions but with no pattern present on the screen, and is thus a generous estimate of the noise level in the recordings. It is clear that at all frequencies above 0.13 c/deg the response to vertical gratings (filled circles) was larger than that to horizontal ones (unfilled circles). At very low frequencies there were so few cycles of the pattern present on the screen that their orientation was hardly discriminable. The screen almost appeared to be filled with flickering light.

For both vertical and horizontal gratings, the potential of maximum amplitude was evoked by a grating of 0.5 c/deg (marked with an open arrow), the experienced spatial frequency. Apart from the difference between vertical and horizontal gratings, these results are very similar to those reported by Berkley and Watkins (1973) and Campbell et al. (1973) for normal cats.

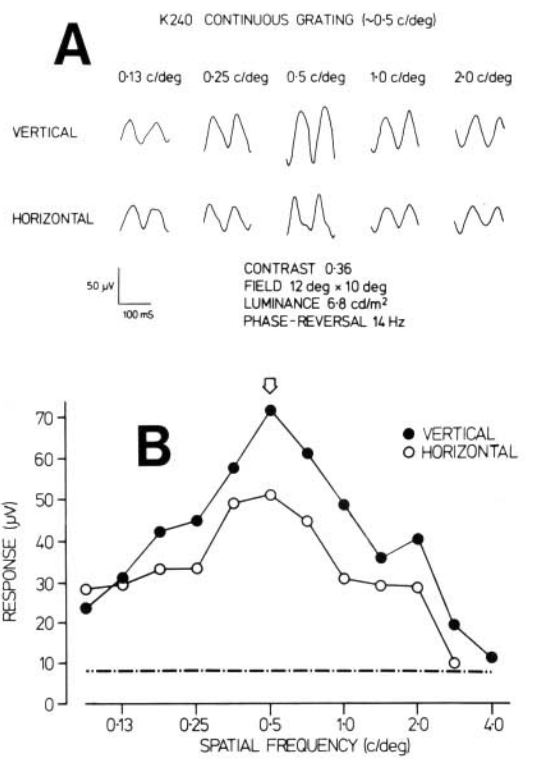

Fig. 4. A Sample records of evoked potentials produced by phase-alternation of a 0.36 contrast grating centred over the area centralis of the right eye of a kitten (K240) exposed during early life to an uninterrupted, vertical, 0.5 c/deg grating. Each trace is the average of 400 sweeps, where each sweep contains two phase-reversals. Comparison of the first and second half of each record therefore gives an indication of the variability of the signal. The upper records were produced by vertical gratings of the spatial frequencies indicated, while a horizontal grating was used for the lower records. The calibrations of amplitude and duration are shown below the records. **B** The peak-to-trough amplitude of the occipital evoked potential is plotted as a function of the spatial frequency of the alternating grating. Filled and open circles show the data for vertical and horizontal gratings respectively. The spatial frequency experienced is indicated by an unfilled arrow

Discussion

In these experiments, exposure to repetitive stripes, whether in the form of an uninterrupted grating, a grating interrupted at intervals or single black bars, caused a noticeable bias in the distribution of preferred orientations amongst cortical cells (Fig. 1). Quantitative analysis of contrast thresholds showed no evidence of a depression in sensitivity at the experienced spatial frequency for LGN neurones or cortical cells (Fig. 2). Indeed, many units had optimum spatial frequencies close to the experienced frequency (Fig. 3). Measurement of occipital evoked potentials again showed a clear superiority in response for vertical gratings. Detailed interpretation of Figure 4 is hindered by the fact that the experienced frequency, 0.5 c/deg, is near the peak of the normal cat's contrast sensitivity function (Campbell et al., 1973; Blake et al., 1974; Bisti and Maffei, 1974), but there is certainly no evidence for a general depression of sensitivity at that frequency.

Our results on the orientation selectivity of cortical cells are similar to many of those that have previously been reported (e.g. Hirsch and Spinelli, 1970, 1971; Blakemore and Cooper, 1970; Pettigrew and Garey, 1974; Tretter et al., 1975; Blasdel et al., 1977), showing a bias, of variable magnitude, toward the orientation of the pattern experienced in early life, in the recorded population of cortical cells. This contrasts with Maffei and Fiorentini's (1974) finding of a lack

of bias after exposure to gratings. However, interpretation of this difference is complicated by another recent report (Stryker and Sherk, 1975) failing to show an abnormal distribution of cortical orientation selectivity following exposure of kittens to irregular striped patterns in cylinders. These same authors have, however, reported a kind of biasing effect (which they explain in terms of selective degenerative changes amongst cells unstimulated by the stripes) following rearing with striped patterns contained in goggles (Stryker and Sherk, 1975; Stryker et al., 1976). Neither we nor Maffei and Fiorentini (1974) used the special techniques of Stryker and Sherk (1975) to ensure even sampling across cortical columns, to measure orientation selectivity quantitatively and to keep the experimenters unaware of the visual experience received by each kitten; so our observations on this point should be interpreted with caution. While the bias of orientation selectivity even after exposure in a striped cylinder has recently been confirmed (Blasdel et al., 1977), the exact cause of this effect, whether due to simple 'functional validation' of certain cells or actual modification of the orientation preferences of individual neurones, remains to be elucidated.

In view of the more consistent effects seen by authors using goggles to control the animals' visual experience, we feel that the difference in results between laboratories may lie in the stringency with which exposure is restricted to the particular pattern in use during rearing (Blakemore, 1977). One requirement that the experimenter cannot with certainty guarantee is that the animal should not be so active that it exposes itself to inappropriate visual stimuli by rolling on its back, turing its head a great deal, or constantly staring up or down at the extremities of the cylindrical display. Some kittens *do* this, especially when they become strong and very mobile, after the age of about 8 weeks. We have found quite consistently that if exposure is continued into the third month the orientational modification is *less* reliable than if experience is limited to the first few weeks, and we suspect that such increased activity might be the explanation. Maffei and Fiorentini's kittens were given regular exposure until $2^1/_2$–3 months of age and this might explain the lack of orientational modification.

However, such an argument cannot explain a reduction in neuronal activity for the experienced spatial frequency. The only remaining difference which might account for this discrepancy in results lies in the total duration and regularity of the exposure. First, there is no doubt that the variation in spatial frequency during exposure was very much greater in our apparatus (with a fairly large range of viewing distance) than in Maffei and Fiorentini's (where the grating was displayed at a long distance from the animal or was actually fixed in goggles worn by the kitten). Their stimulus was, therefore, much more constant and uniform in frequency than ours. Second, our animals were exposed to a single spatial frequency for a total of about 50 hours, Pettigrew and Garey's (1974) for 20 hours, Tretter et al's (1975) for up to 12 hours. Maffei and Fiorentini's (1974) kittens had regular daily exposure for a total of more than 150 hours. While our experiments do not support their adaptational hypothesis, it may offer an explanation for the depressive changes that they found after such a long exposure.

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