J. Physiol. (1981), **316**, *pp.* 1–10
With 6 text-figures
Printed in Great Britain

THE DEVELOPMENT OF SPATIAL-FREQUENCY SELECTIVITY IN KITTEN STRIATE CORTEX

BY ANDREW M. DERRINGTON* AND ALBERT F. FUCHS†
From the Physiological Laboratory, University of Cambridge

(*Received 4 June 1980*)

SUMMARY

1. Single units were recorded in the striate cortex of kittens aged between 2 and 12 weeks. Contrast sensitivity measurements made using moving sinusoidal gratings were used to construct spatial-frequency tuning curves.

2. In young kittens cells had low sensitivities, responded only to low spatial frequencies and were unselective for spatial frequency. In addition 30% of the cells recorded in the youngest kittens were unresponsive to visual stimuli.

3. Sensitivity improved to near-adult values within 5–6 weeks.

4. Best spatial frequency improved more gradually, so that even in the oldest kittens best spatial frequencies were lower than adult values.

5. Selectivity for spatial frequency, considered both in terms of the numbers of selective cells and the narrowness of their tuning curves, improved rapidly, and reached adult values within the first 6 weeks.

6. These results are discussed in relation to other developmental studies.

INTRODUCTION

Since the first descriptions of the properties of cells in the striate cortex of the adult cat (Hubel & Wiesel, 1959, 1962) a great deal of experimental effort has been invested in attempts to outline the factors controlling their development. One property of cortical cells which has received rather little attention in developmental studies is their selectivity for the spatial configuration of their best stimulus (Hubel & Wiesel, 1962). This type of selectivity is most easily demonstrated by measuring spatial-frequency tuning curves using sinusoidal gratings. In the adult striate cortex of both cat (Cooper & Robson, 1968; Maffei & Fiorentini, 1973; Ikeda & Wright, 1975; Movshon, Thompson & Tolhurst, 1978*c*) and monkey (Schiller, Finlay & Volman, 1975) most cells show sharp spatial-frequency tuning which clearly distinguishes them from retinal ganglion cells and lateral geniculate nucleus (LGN) cells, which show rather broad tuning (Enroth-Cugell & Robson, 1966; Cooper & Robson, 1968; Maffei & Fiorentini, 1973).

* Beit Memorial Research Fellow. Present address: Laboratory of Experimental Psychology, University of Sussex, Falmer, Brighton BN1 9QG.

† Present address: Dept of Physiology and Biophysics, Regional Primate Research Center, University of Washington, Seattle, Washington 98195, U.S.A.

The aim of this paper is to trace the development of this characteristic spatial selectivity in the cortical cells of normally reared kittens. A preliminary report of some of the results has already appeared (Derrington, 1978).

METHODS

The development of spatial-frequency selectivity of cells in the striate cortex was followed by measuring contrast sensitivity to moving sinusoidal gratings of different spatial frequencies in twenty-one kittens aged between 2 and 12 weeks. The kittens were divided into groups according to age, as follows: 2 weeks (13–15 days, two cats, thirty cells), 3 weeks (20–22 days, three cats, forty-three cells), 4 weeks (26–29 days, four cats, seventy-four cells), 5–7 weeks (35–47 days, five cats, eighty-two cells) and 8–12 weeks (55–80 days, seven cats, seventy-nine cells).

Preparation for recording

The preparation and maintenance of kittens during acute recordings from the visual cortex were essentially as described by Blakemore & Van Sluyters (1975), with the few changes detailed below.

Anaesthesia. This was supplemented with small I.V. doses of Althesin or Nembutal when the nitrous oxide–oxygen mixture was insufficient to maintain a synchronized electroencephalogram pattern.

Optics. Contact lenses with 3 mm diameter circular artificial pupils were used. Refractive errors were assessed by ophthalmoscopic examination of the small blood vessels close to the area centralis. The position of the area centralis was estimated from the pattern of these vessels, and plotted on the tangent screen using an ophthalmoscope with a corner-cube prism to reverse the beam (Eldridge, 1979). In kittens of 4 weeks or older repeated plots of the area centralis were usually within 1° of one another. In young kittens the spread could be 5° or more. Estimates of receptive field eccentricity are likely to be in error by corresponding amounts.

Recording

Two types of tungsten-in-glass micro-electrode were used to record single units. Electrolytically sharpened tungsten wires insulated with glass micropipettes (Levick, 1972) were used in early experiments. These were superseded by electrodes in which the tungsten was coated with molten glass by collapsing a capillary tube onto it under tension (Merrill & Ainsworth, 1972). These electrodes, while identical in their recording characteristics to the others, are much more robust and could usually be driven through the intact dura.

The electrode penetration was usually angled medially and anteriorly to pass down the medial bank of the marginal gyrus. Although this approach encountered cells with receptive fields at least 2° or 3° from the area centralis it obviated recording inadvertently from area 18. The penetration was stopped if (or when) cells with receptive fields more than 10° from the estimated position of the area centralis were encountered.

Receptive field plotting. Receptive fields were plotted using a bright line of variable length which was moved about by hand and projected onto a tangent screen 57 cm from the eye; dark bars, spots and edges were also used occasionally. The following data were gathered for each visually responsive unit.

1. The best orientation and the range of orientations to which the cell responded.
2. Preferred direction of movement.
3. The location and, if possible, the size and shape of the cell's 'minimum response field' (Barlow, Blakemore & Pettigrew, 1967).
4. The ocular dominance (Hubel & Wiesel, 1962).

Non-oriented cortical units were excluded unless they were distinguishable from LGN fibres by their binocularity, by the sluggishness of their responses, or by the shape and duration of their action potentials.

Spatial-frequency tuning. The receptive field plotted through the dominant eye was projected onto the face of an oscilloscope on which a moving grating was displayed in an area 25° by 30° which had a constant space-average luminance of 200 cd m^{-2}. The orientation, temporal frequency and direction of movement of the grating were optimized. Contrast sensitivity to gratings of different spatial frequencies was then measured by presenting gratings of different spatial frequencies in

random order, and adjusting the contrast of each until the cell just appeared to respond. Four estimates of threshold were made at each spatial frequency and a tuning curve relating contrast sensitivity (reciprocal of threshold) to spatial frequency was calculated by a smoothing and interpolation procedure (see Derrington & Fuchs, 1979, for details). The peak of each curve (the peak contrast sensitivity), the spatial frequency at which it occurred (the best spatial frequency), the highest spatial frequency at which the sensitivity exceeded 1·25 (the acuity), and the width of the curve 0·3 log units below the peak (band width at half-height) were measured by the computer. Fig. 1 illustrates the measurement of these parameters on a spatial-frequency tuning curve from a cell recorded in a 6-week-old cat.

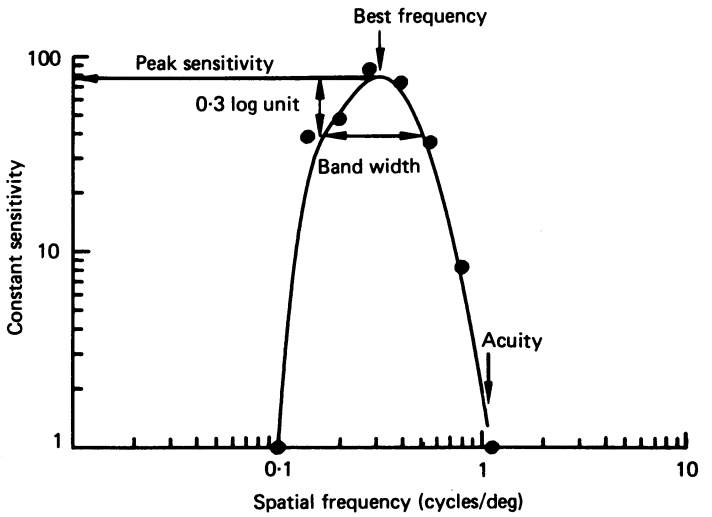

Fig. 1. Measurement of parameters describing a spatial-frequency tuning curve. The computer calculated the value of the interpolation function at intervals of 0·01 log units on the spatial-frequency axis, and measured the height (peak sensitivity), the width at half-height (band width) and the location of the peak (best frequency).

Histological confirmation of recording sites

At the end of each penetration a number of lesions were made along the track by passing 5–15 μA (d.c. current, electrode negative) for 5–10 s through the electrode tip. In later experiments with more durable electrodes, lesions were made during the course of the penetration. Each recording experiment was terminated by deeply anaesthetizing the cat with an I.V. injection of Nembutal, and perfusing it through the left ventricle with Ringer solution followed by 10% formalin in saline. A block with a side parallel to the electrode tracks was cut from the brain and immersed in 30% sucrose/10% formalin for 24 h. It was then frozen and sectioned at 40 or 60 μm; sections from the region of each electrode track were mounted and stained with cresyl violet. In eighteen of the twenty-one cats histological reconstruction confirmed that recordings were from area 17. In the other three cats the location of the penetrations as assessed from the surface landmarks was also in area 17.

RESULTS

Comparison of tuning curves from young and old kittens

The salient differences between kitten and adult are illustrated in Fig. 2, which shows spatial-frequency tuning curves of all the cells from one of the youngest (2 weeks) and one of the oldest (8 weeks) cats. The cells from the older cat are much more sensitive and respond to higher spatial frequencies than those from the younger

one. Not only did the visually responsive cells in the younger cat show lower contrast sensitivities but six other cells (50 % of the total) were found which could not be driven by our visual stimuli; no visually unresponsive cells were found in the older cat or in most of the other older animals. The tuning curves of the cells recorded in the older cat also tended to be narrower. This comparison shows clearly that contrast

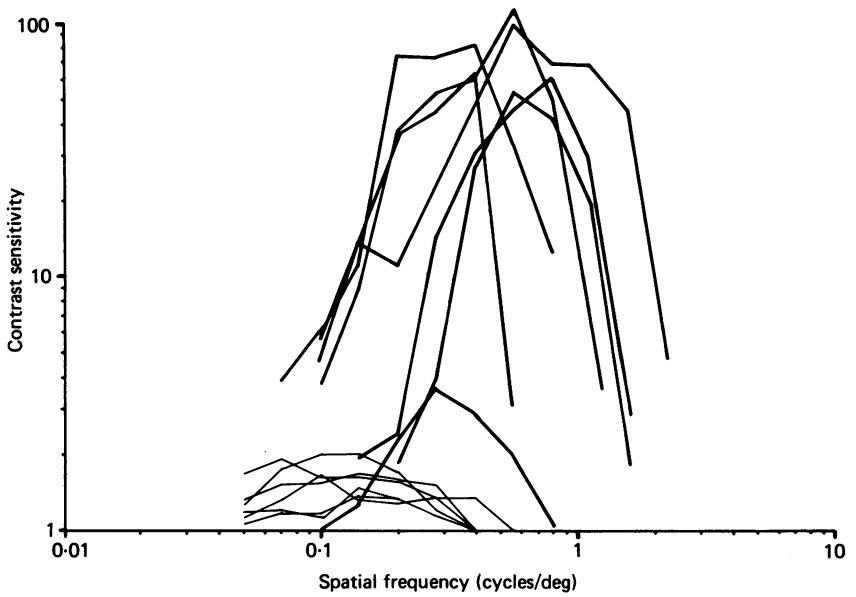

Fig. 2. Spatial-frequency tuning curves for cells from a 2-week-old (thin lines) and an 8-week-old (thick lines) cat. Each point is the reciprocal of the geometric mean of four estimates of the contrast at threshold. Direction and temporal frequency of movement and orientation were kept constant at their optimum values for each cell.

sensitivity, selectivity (i.e. narrowness of band width) and preferred spatial frequency all increase during development.

Increases in contrast sensitivity with age

The improvement in contrast sensitivity with age is shown in Fig. 3, in which the mean log sensitivity of the cells studied in each cat is plotted against age. There is an erratic but unmistakable increase in sensitivity which lasts 35–40 days. When the entire age range is considered this increase is not very dramatic, and is only marginally significant ($r = 0{\cdot}51$, $t = 2{\cdot}56$, d.f. = 19, $P > 0{\cdot}05$). However, a much higher correlation is obtained if one considers only kittens younger than 30 ($r = 0{\cdot}87$, $t = 9{\cdot}47$, d.f. = $P < 0{\cdot}001$) or 50 days ($r = 0{\cdot}75$, $t = 5{\cdot}94$, d.f. = 12, $P < 0{\cdot}001$), supporting the impression given by Fig. 3 that the increase in sensitivity occurs mainly during the first 6 weeks or so. The mean peak sensitivity of sixty-nine cortical cells recorded in adult cats is shown by the arrow in fig. 3 (D. J. Tolhurst, personal communication). Although this is slightly higher than the mean values for kittens over 6 weeks old, such a difference could easily arise from our adoption of a more stringent criterion for a threshold response: our own measurements of sensitivity in

adult LGN X-cells (Derrington & Fuchs, 1979) are very close to the kitten cortical data.

Changes in best spatial frequency

There is a steady increase in best spatial frequency with age (Fig. 4), which appears to be more gradual than the change in sensitivity. The correlation between best spatial frequency and age is highly significant ($r = 0{\cdot}79$, $t = 5{\cdot}62$, d.f. $= 19$,

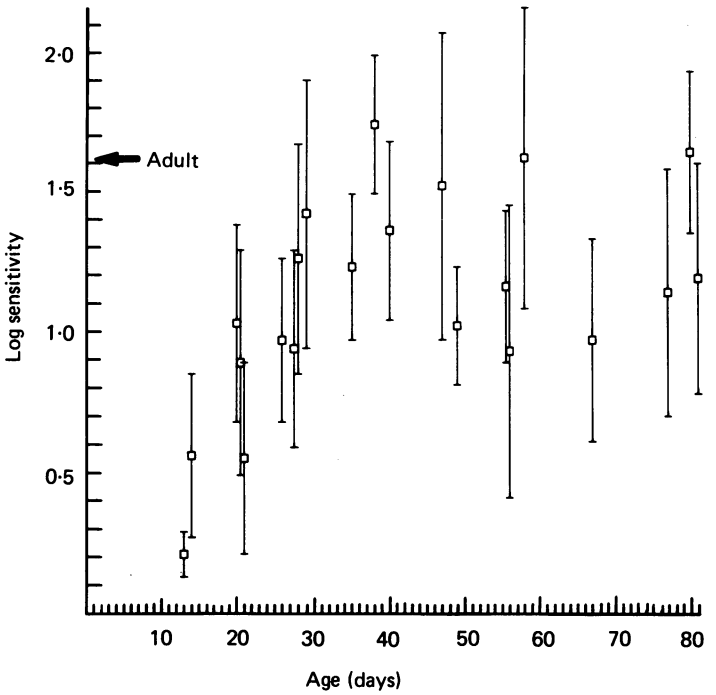

Fig. 3. Mean log sensitivity (±S.D.) of responsive cells for each cat plotted against age. The arrow indicates the mean sensitivity of a sample of adult cortical cells (D. J. Tolhurst, personal communication).

$P < 0{\cdot}001$). Furthermore, spatial frequency preferences may continue to increase beyond the range of ages we have studied: only one of the cats yielded a sample of cells with a mean best spatial frequency exceeding that of a sample of adult cortical cells recorded in very similar conditions (Movshon *et al.* 1978*c*), which is indicated by the arrow in Fig. 4. A continuing increase in best spatial frequency with age would be consistent with the time course of development of visual acuity in cats (Freeman & Marg, 1975; Mitchell, Giffin, Wilkinson, Anderson & Smith, 1976), which does not reach adult levels until about 6 months of age.

Relationship between cortical development and visual acuity

The increase in mean best spatial frequency with age is presumably related to the development of visual acuity which occurs in kittens during the first few months of

life (Freeman & Marg, 1975; Mitchell *et al.* 1976). However, rather than mean best spatial frequency, a more realistic neurophysiological predictor of the visual acuity would be given by the highest spatial frequency to which any cell responded with some criterion sensitivity. Fig. 5 shows how the acuity of each cat (defined as the highest spatial frequency at which any cell had a contrast sensitivity of 1·25 or more)

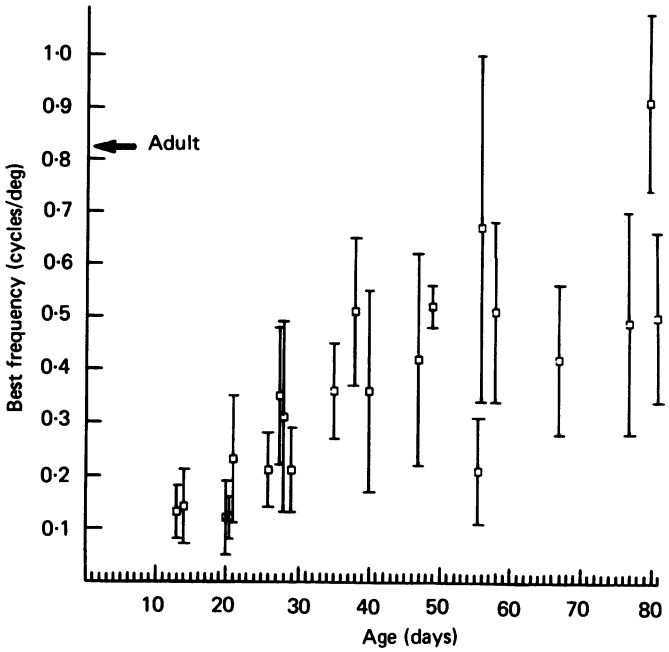

Fig. 4. Mean best spatial frequency (±S.D.) for each cat as a function of age. The arrow shows the mean best spatial frequency of a sample of cells from adult cats' striate cortex (Movshon *et al.* 1978*c*).

compares with behavioural estimates of acuity (Mitchell *et al.* 1976). The agreement is not very close: in young kittens neurophysiological acuity probably exceeds behavioural estimates, although it is hard to be sure. On the other hand the reverse is certainly the case after about 5 weeks of age. This latter discrepancy is almost certainly a consequence of the fact that our cells usually had receptive fields at least 2° or 3° from the area centralis, and so were presumably not the cells with the highest acuity.

Changes in selectivity for spatial frequency with age

We have measured the full width of the spatial-frequency tuning curve at half the peak height (band width at half-height) as an index of selectivity for spatial frequency. The distributions of band widths of cells in the different age groups are shown in Fig. 6. Cells that had peak contrast sensitivities of less than 2·5 were omitted because of the difficulty of measuring band width reliably. This difficulty occurs because the lowest measurable contrast sensitivity is, by definition, 1. Cells which

had unmeasurable band widths for this reason (about one third of those encountered in the youngest kittens) are plotted separately in Fig. 6. Cells which showed a decline in contrast sensitivity by less than a factor of 2 for the lowest spatial frequencies (usually 0·05 cycles/deg or less) also had an unmeasurable band width and are designated unselective cells (hatched columns, Fig. 6).

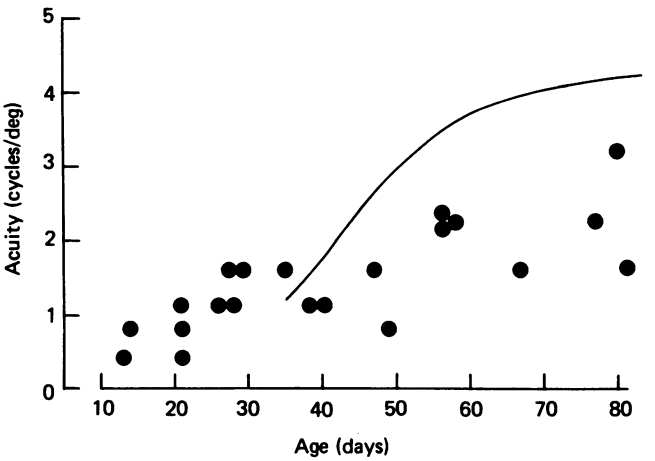

Fig. 5. Comparison of behavioural visual acuity and acuity of cortical cells as functions of age. Data points show the acuity of the best cell in each cat in this study (defined as the highest spatial frequency at which the sensitivity was greater than 1·25). The curve shows behavioural measurements of acuity (Mitchell *et al.* 1976).

The mean band width decreased between 2 and 3 weeks and showed only small changes thereafter. In cats older than 3 weeks the band width distributions are all clustered around the mean values found in adult cats under similar conditions (Movshon *et al.* 1978*c*), which are indicated by arrows in Fig. 6. The proportion of unselective cells decreased gradually from 33 % at 2 weeks to 4 % at 5–7 weeks; no unselective cells were found in the oldest age group. The lack of any marked change in band width after 3 weeks of age suggests that once a cortical cell moves out of the unselective category by reducing its relative sensitivity to low spatial frequencies there is little if any further narrowing of its tuning curve.

Visually unresponsive cells

In addition to the increase in sensitivity of the responsive cells (Fig. 3) there was a rapid decline in the numbers of visually unresponsive cells (filled columns, Fig. 6), from ten out of thirty at 2 weeks to only two out of forty-four at 3 weeks. No visually unresponsive cells were found in 4-week-old kittens, although one was found in an 8-week-old cat, suggesting that very small proportions of adult cortical cells may be visually unresponsive.

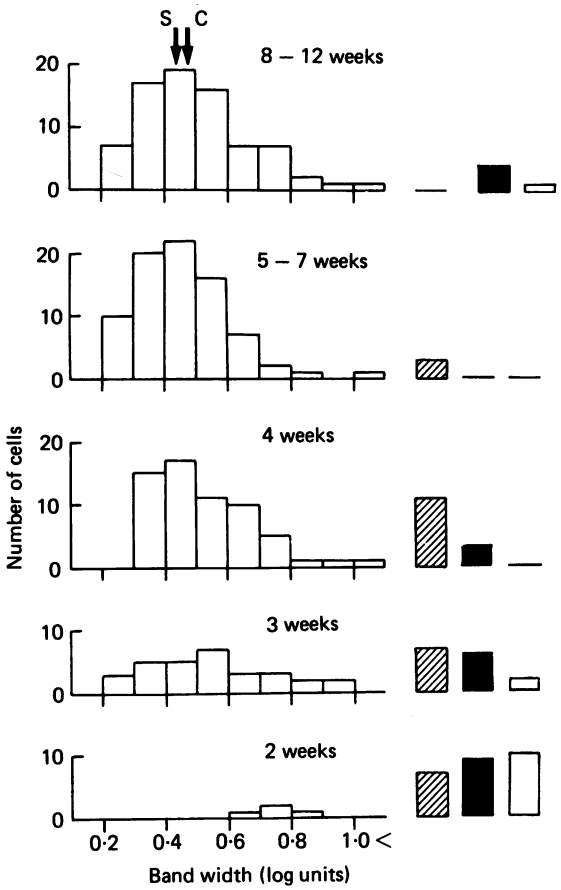

Fig. 6. Distribution of spatial-frequency tuning band widths of cells recorded in kittens in different age groups. Arrows above the top histogram show mean band widths of adult simple (S) and complex (C) cells (Movshon *et al.* 1978*c*). The columns to the right of each histogram show the numbers of unselective cells (hatched), of visually unresponsive cells (open) and of cells too insensitive to allow measurement of band width (filled), recorded at each age.

DISCUSSION

Although there is a good deal of variability, contrast sensitivity, preferred spatial frequency and selectivity for spatial frequency clearly increase with age. By 6 weeks of age sensitivity and selectivity are comparable with adult levels. However, spatial frequency preferences probably continue increasing even beyond the age range we have studied. Some of these changes must result from changes in the way the cortex processes the signals it receives, whereas others almost certainly reflect changes lower in the visual pathway.

The observed increases in preferred spatial frequency and acuity are almost certainly a consequence of the increase in the range of spatial frequencies being transmitted through the LGN with age (Ikeda & Tremain, 1978). The possibility that

these improvements in spatial resolution in both cortex and LGN reflect nothing more than the improvement in quality of the kitten's visual optics has been excluded by measurements of image quality in the kitten's eye. Although the optical quality of the eye is much worse in young kittens than in adult cats (Bonds & Freeman, 1978; Derrington, 1979), the difference in transmission of spatial frequencies in the range of interest is only small: neither sensitivity nor resolution of cortical or geniculate cells is likely to be much affected by the optical quality of the eye, even in the youngest kittens.

It is likely that growth of the eye plays a small part in the improvement in resolution: the effect is simply that of increasing the magnification of the retinal image. The eye increases in length by a factor of 1·3 between birth and 8 weeks of age (Thorn, Gollender & Erickson, 1976). If we assume that the magnification of the retinal image is approximately proportional to the length of the eye then the preferred spatial frequencies of cortical cells would also be expected to increase by a factor of 1·3; this is only a fraction of the observed increase, which is about a factor of 4.

On the other hand, it seems likely that the improvement in spatial-frequency selectivity results almost entirely from changes within the cortex. First, cortical spatial-frequency selectivity is much greater than that shown in the LGN, and so must be generated by cortical mechanisms: a sample of LGN X-cells tested under identical conditions to our sample of kitten cortical cells showed less selectivity for spatial frequency (i.e. broader band widths and a smaller proportion of selective cells) than our sample of cortical cells from 3-week-old kittens (A. M. Derrington & A. F. Fuchs, unpublished observations). Secondly, spatial-frequency selectivity seems to begin developing in the cortex before it does in the LGN: at 5 weeks LGN cells show little evidence of spatial frequency selectivity and have poorly developed receptive field surrounds (Ikeda & Tremain, 1978), whereas the increase in cortical spatial frequency selectivity is well under way by 3 weeks, and is almost complete at 7 weeks.

Cortical spatial-frequency selectivity is generated by antagonistic flanks in receptive fields (Movshon *et al.* 1978*a*, *b*), which can be considered analogous to the surrounds of LGN cells. Paradoxically the intracortical inhibitory pathways generating this selectivity could also contribute to the improvement in sensitivity to gratings of the optimum spatial frequency: a similar increase in sensitivity generated by antagonistic surrounds has been proposed in retinal ganglion cells (Barlow & Levick, 1976). This would be consistent with the fact that sensitivity and selectivity changes both occur mainly in the first 6 weeks or so (Figs. 3 and 6), whereas the increase in spatial resolution (Figs. 4 and 5) is much slower. The improvements in sensitivity and selectivity coincide with the time of maximum sensitivity to the disruptive effects of monocular lid-suture (Hubel & Wiesel, 1970), and the time when cortical synapses are rapidly increasing in numbers (Cragg, 1972).

This research was supported by grants from the M.R.C. to H. B. Barlow and C. Blakemore, and by a grant from the Royal Society to H. B. Barlow. A. F. Fuchs was supported by a Macy Foundation Fellowship, A. M. Derrington by an M.R.C. studentship.

REFERENCES

BARLOW, H. B., BLAKEMORE, C. B. & PETTIGREW, J. D. (1967). The neural mechanism of binocular depth discrimination. *J. Physiol.* **193**, 327–342.

BARLOW, H. B. & LEVICK, W. R. (1976). Threshold setting by the surround of cat retinal ganglion cells. *J. Physiol.* **259**, 737–757.

BLAKEMORE, C. & VAN SLUYTERS, R. C. (1975). Innate and environmental factors in the development of the kitten's visual cortex. *J. Physiol.* **248**, 663–716.

BONDS, A. B. & FREEMAN, R. D. (1978). Development of optical quality in kitten eye. *Vision Res.* **18**, 391–398.

COOPER, G. F. & ROBSON, J. G. (1968). Successive transformations of information in the visual system. In *I.E.E.–N.P.L. Conference on Pattern Recognition, I.E.E. Conference Publication No. 43*, pp. 134–143. I.E.E.

CRAGG, B. G. (1972). Development of synapses in cat visual cortex. *Invest. Ophthal.* **11**, 391–398.

DERRINGTON, A. M. (1978). Development of selectivity in kitten striate cortex. *J. Physiol.* **276**, 46*P*–47*P*.

DERRINGTON, A. M. (1979). Direct measurements of image quality in the kitten's eye. *J. Physiol.* **295**, 16*P*–17*P*.

DERRINGTON, A. M. & FUCHS, A. F. (1979). Spatial and temporal properties of X and Y cells in the cat lateral geniculate nucleus. *J. Physiol.* **293**, 347–364.

ELDRIDGE, J. L. (1979). A reversible ophthalmoscope based on a corner-cube. *J. Physiol.* **295**, 1*P*–2*P*.

ENROTH-CUGELL, C. & ROBSON, J. G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *J. Physiol.* **187**, 517–552.

FREEMAN, D. N. & MARG, E. (1975). Visual acuity development coincides with the sensitive period in kittens. *Nature, Lond.* **254**, 614–615.

HUBEL, D. H. & WIESEL, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *J. Physiol.* **148**, 574–591.

HUBEL, D. H. & WIESEL, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* **160**, 106–154.

HUBEL, D. H. & WIESEL, T. N. (1970). The period of susceptibility to the physiological effects of unilateral eye closure in kittens. *J. Physiol.* **206**, 419–436.

IKEDA, H. & TREMAIN, K. E. (1978). Development of spatial resolving power of lateral geniculate neurones in kittens. *Expl Brain Res.* **31**, 193–206.

IKEDA, H. & WRIGHT, M. J. (1975). Spatial and temporal properties of 'sustained' and 'transient' neurones in area 17 of the cat's visual cortex. *Expl Brain Res.* **22**, 363–383.

LEVICK, W. R. (1972). Another tungsten microelectrode. *Med. biol. Engng* **10**, 510–515.

MAFFEI, L. & FIORENTINI, A. (1973). The visual cortex as a spatial frequency analyzer. *Vision Res.* **13**, 1255–1267.

MERRILL, E. G. & AINSWORTH, A. (1972). Glass-coated, platinum-plated tungsten microelectrodes. *Med. Biol. Engng* **10**, 662–672.

MITCHELL, D. E., GIFFIN, F., WILKINSON, F., ANDERSON, P. & SMITH, M. L. (1976). Visual resolution in young kittens. *Vision Res.* **16**, 363–366.

MOVSHON, J. A., THOMPSON, I. D. & TOLHURST, D. J. (1978*a*). Spatial summation in the receptive fields of simple cells in the cat's striate cortex. *J. Physiol.* **283**, 53–77.

MOVSHON, J. A., THOMPSON, I. D. & TOLHURST, D. J. (1978*b*). Receptive field organization in complex cells in the cat's striate cortex. *J. Physiol.* **283**, 79–99.

MOVSHON, J. A., THOMPSON, I. D. & TOLHURST, D. J. (1978*c*). Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. *J. Physiol.* **283**, 101–120.

SCHILLER, P. H., FINLAY, B. L. & VOLMAN, S. F. (1976). Quantitative studies of single units in monkey striate cortex. III. Spatial frequency. *J. Neurophysiol.* **39**, 1334–1351.

THORN, F., GOLLENDER, M. & ERICKSON, P. (1976). The development of the kitten's visual optics. *Vision Res.* **16**, 1145–1149.