J. Physiol (1987), **384**, *pp.* 293–309
With 8 text-figures
Printed in Great Britain

EFFECTS OF DARK-REARING ON THE DEVELOPMENT OF AREA 18 OF THE CAT'S VISUAL CORTEX

BY COLIN BLAKEMORE AND DAVID J. PRICE*
From the University Laboratory of Physiology, Parks Road, Oxford OX1 3PT

(*Received 4 June 1986*)

SUMMARY

1. We recorded extracellularly from 420 single units in area 18 in visually inexperienced kittens aged 7 days and dark-reared kittens aged between 3 and 12 weeks and from 60 single units in area 17 in dark-reared kittens aged 5 and 11 weeks.

2. Visual deprivation generally depressed the maturation of area 18, although some features were affected more than others and certain developmental improvements still occurred. The percentage of visually responsive units in area 18 increased from 40% in 7-day-old kittens to about 75% in dark-reared animals 10–12 weeks. At each age a proportion of cells was orientation biased (between 15 and 45%) and these neurones appeared to be arranged in a crude columnar fashion. However, dark-rearing, from birth, prevented the development of a significant proportion of orientation-selective cells in area 18; no more than 5% of neurones were orientation-selective at any age. We found no major bias in the over-all distribution of preferred orientations of cells in area 18 in dark-reared kittens.

3. Simple cells, which are found in area 18 even in very young, visually inexperienced kittens, persisted after dark-rearing, although most retained immature properties. Relatively few complex cells were found in area 18 in visually deprived animals.

4. The majority of neurones in area 18 of dark-reared kittens were binocularly driven, many equally well by either eye; evidence for regional variation in ocular dominance (indicative of a columnar pattern) was found in these deprived animals.

5. A laminar analysis in area 18 showed that percentages of non-oriented and orientation-biased cells changed little, if at all, in lower laminae (IV, V, and VI) but increased substantially in upper layers (above layer IV) in the absence of visual stimulation, over the first 12 post-natal weeks.

6. A comparison of the effects of dark-rearing on areas 17 and 18 indicates that the normal development of visual responsiveness and specific receptive field properties is suppressed in both areas during the first 12 post-natal weeks. It is possible that area 17 has a greater degree of orientation selectivity than area 18 in young visually deprived kittens and this may reflect a difference in the type of afferent inputs.

---

* To whom correspondence should be addressed.

INTRODUCTION

The normal post-natal development of the visual system of mammals results from an interaction between innate and environmental factors. Many studies have shown that the striate cortex of the cat fails to develop normally in the absence of visual experience of patterned images (Pettigrew, 1974; Blakemore & Van Sluyters, 1975; Imbert & Buisseret, 1975; Buisseret & Imbert, 1976; Cynader, Berman & Hein, 1976; Leventhal & Hirsch, 1977; Fregnac & Imbert, 1978; Bonds, 1979; Leventhal & Hirsch, 1980).

Relatively little is known about the effects of binocular deprivation on extrastriate visual cortical areas, although this is of interest since these regions lack an input from geniculate X cells and it has been suggested that visual deprivation affects the X- and Y-cell pathways differently (reviewed by Stone, 1983). Singer & Tretter (1976) studied the effects of visual deprivation by binocular eyelid suture on extrastriate cortex and concluded that areas 17 and 18 suffer to roughly the same extent. However, the extent to which binocular eyelid suture and dark-rearing (the two frequently employed methods of depriving animals of visual experience) have similar consequences is not established (Sherman & Spear, 1982). It is known that cells in area 17 in cats can be activated by visual stimulation through closed eyelids (Spear, Tong & Langsetmo, 1978) and this is even more likely to be the case for neurones in area 18, as Sclar & Freeman (1983) have suggested, since cells in area 18 respond best to relatively low spatial frequencies (Movshon, Thompson & Tolhurst, 1978). It is possible that binocular eyelid suture results in different degrees of residual visual activity in the various cortical areas, making comparisons of the long-term consequences of such deprivation difficult. Furthermore, differences in the effects of visual deprivation on striate and extrastriate visual areas may only be seen at young ages.

The aim of this study was to examine the effects of dark-rearing from birth on the maturation of area 18 in kittens during the first 3 months post-natally. Data were also obtained on the development of neurones in area 17 in these visually deprived animals, for comparison with results from previous deprivation studies and our own observations on the effects of dark-rearing on cells in area 18.

Preliminary reports of this work have been published previously (Price, 1985*a*, *b*).

METHODS

A total of seven tabby kittens, bred in an isolated colony, were used in these experiments. On the day of birth, litters were placed in a dark-room that was checked on several occasions with photographic paper to ensure that no light entered; before cages were cleaned each day, and when food and water were being introduced, the kittens were placed in a light-proof box. Five kittens were reared in this manner until the start of the experiment, and another two normal 7-day-old visually inexperienced kittens, whose eyelids had not opened naturally, were used; the eyelids of the two 7-day-old kittens were separated under ketamine hydrochloride anaesthesia (20 mg kg^{-1} intramuscularly). Area 18 was examined in the visually inexperienced 7-day-old kittens and in dark-reared kittens aged 3, 5, 10, 11 and 12 weeks (ages on the first day of experiment), while data from area 17 were obtained from two animals, aged 5 and 11 weeks.

Induction and maintenance of anaesthesia and paralysis, assessment of the animal's anaesthetic state, surgical procedures, optical preparation, electrophysiological recording methods, the strategy for sampling single units, receptive field classification and the technique of histological reconstruction were all identical to those described in the previous paper (Blakemore & Price, 1987).

RESULTS

In this study we made twelve penetrations through area 18 and studied 420 single units in visually inexperienced kittens aged between 7 days and 12 weeks; two penetrations were made through area 17 where sixty units were examined, nineteen in a 5-week-old and forty-one in an 11-week-old kitten.

The positions of areal borders were located in Nissl-stained (Garey, 1971) and cytochrome-oxidase-stained (Price, 1985*c*) sections, and cortical laminae were defined in cytochrome-oxidase-stained material following the scheme described in Blakemore & Price (1987). The term 'c.o. layer IV' is used to describe the full width of the dense cytochrome oxidase band that covers layer IV and extends into the lower part of the cytoarchitectonically defined layer III. The appearance of the visual cortex in sections stained with cresyl violet or reacted to reveal cytochrome oxidase activity with indistinguishable in dark-reared and normal kittens.

Area 18

Retinotopic organization. A retinotopic map of the contralateral visual hemifield has been described in area 18 in adult cats (Tusa, Rosenquist & Palmer, 1979) and in young kittens (Blakemore & Price, 1987), and such an organization is presumably also present in dark-reared kittens, since the eccentricity of receptive field centres in the visual field increased with distance from the area 17/18 border, in coronal planes that ran orthogonal to this boundary. Visual deprivation, for as long as 12 weeks, does not appear to disrupt the retinotopic organization of those neurones that are visually responsive, in at least the rostral part of area 18.

Cell types. In the two visually inexperienced kittens aged 7 days, the majority of units encountered (60 %) were visually unresponsive, 25 % were non-oriented, 15 % were orientation biased and none was orientation selective. Although orientation-selective cells were occasionally found in older kittens that had been reared in total darkness, no more than a few percent of the sample of neurones studied at any age were classified as truly orientation selective (Fig. 1). There appeared to be some increase in the proportion of visually responsive cells in area 18 with age, and the percentages of both orientation-biased and non-oriented neurones rose (Fig. 1). In dark-reared kittens aged 10, 11 and 12 weeks 2–4 % of cells were orientation selective, 30–45 % were orientation biased, 28–40 % were non-oriented and the remaining 22–28 % were visually unresponsive. It seems that some development of the properties of cells in area 18 occurs in the absence of visual stimulation, although normal maturation (Blakemore & Price, 1987) is clearly prevented, and in particular the wholesale development of orientation selectivity is suppressed.

Units with oriented receptive fields (that is, orientation-selective and orientation-biased cells) were classified as simple (or immature simple: see Blakemore & Price, 1987) or complex at each age in dark-reared kittens (Table 1). In all deprived animals the majority of cells classified in this manner were immature simple, even in kittens as old as 10–12 weeks, and very few complex cells were found. By contrast, most oriented cells in area 18 in normal animals aged 4 weeks or more were complex and none of the simple cells was classified as immature. These results show that both simple and complex cells can develop in area 18 (albeit usually with poor orientation tuning) in the absence of visual stimulation, but visual deprivation appears to prevent

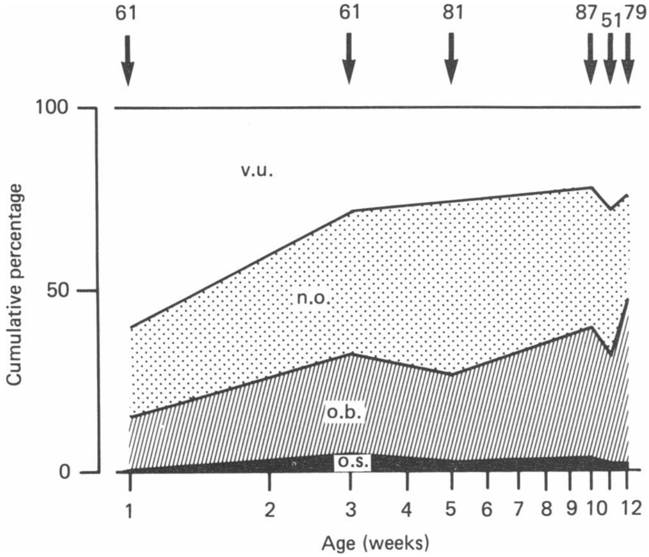

Fig. 1. This graph shows the cumulative percentages of orientation-selective (o.s.; filled area), orientation-biased (o.b.; hatched area), non-oriented (n.o.; stippled area) and visually unresponsive (v.u.; open area) units in area 18 of dark-reared kittens, plotted against age on a logarithmic scale. The numbers of neurones studied at each age are shown above the graph.

TABLE 1. Percentage of the *total* sample of cells that were classed as simple, immature simple or complex at various ages in dark-reared kittens and, for direct comparison, in normal kittens aged 4 weeks or more and adult cats. At all ages a number of cells with an orientation preference were poorly responsive, especially to stationary stimuli, and could not be classified. Data from animals aged 10–12 weeks were similar and are pooled. The total number of units (*n*) in each age group is indicated

<table>
<tr><th>Age (weeks)</th><th>Simple (%)</th><th>Immature simple (%)</th><th>Complex (%)</th><th>Unclassified oriented (%)</th><th><i>n</i></th></tr>
<tr><td colspan="6">Dark-reared animals</td></tr>
<tr><td>1</td><td>0</td><td>3</td><td></td><td></td><td></td></tr>
<tr><td></td><td colspan="2">3</td><td>0</td><td>12</td><td>61</td></tr>
<tr><td>3</td><td>2</td><td>12</td><td></td><td></td><td></td></tr>
<tr><td></td><td colspan="2">14</td><td>5</td><td>15</td><td>61</td></tr>
<tr><td>5</td><td>1</td><td>9</td><td></td><td></td><td></td></tr>
<tr><td></td><td colspan="2">10</td><td>2</td><td>15</td><td>81</td></tr>
<tr><td>10–12</td><td>2</td><td>16</td><td></td><td></td><td></td></tr>
<tr><td></td><td colspan="2">18</td><td>3</td><td>19</td><td>217</td></tr>
<tr><td colspan="6">Normal animals</td></tr>
<tr><td>4 or more</td><td>11</td><td>0</td><td></td><td></td><td></td></tr>
<tr><td></td><td colspan="2">11</td><td>48</td><td>31</td><td>629</td></tr>
</table>

the full maturation of the receptive fields characteristic of simple cells and the appearance of large numbers of complex cells. The proportion of cells with oriented receptive fields found in dark-reared kittens, at least up until 12 weeks of age, falls far short of the fraction seen in normal animals aged 4 weeks or more. There seemed to be no consistent difference between these dark-reared animals and normal cats and kittens (Blakemore & Price, 1987) in the proportion of cells with clear length preference or in the strength of such 'end-inhibition'.

Directionality. At all ages, from 7 days to 12 weeks, the majority of cells that were orientation selective and orientation biased in area 18 in visually inexperienced kittens were given directionality values of 0 or 1 (that is, they responded to movement of an oriented stimulus equally or almost equally in the two directions: Table 2). On the other hand, in normal kittens the percentage of neurones that responded to movement in only one direction or showed a strong preference for one direction (i.e. directionality 3 or 2) increased during the first 4 weeks post-natally to reach about 50 % in older kittens and adult cats. Visual deprivation appears, then, to prevent the normal development of selectivity for a particular direction of movement of an oriented stimulus for cells in area 18.

TABLE 2. Directionality of orientation-selective and orientation-biased cells in area 18 in visually inexperienced kittens at various ages and, for comparison, in normal kittens aged 4 weeks or more and adult cats. Percentages of cells with each directionality value and number of units (*n*) at each age are shown. Data from deprived animals aged 10–12 weeks were similar and are pooled

	Directionality value				
Age (weeks)	0 (%)	1 (%)	2 (%)	3 (%)	*n*
	Dark-reared animals				
1	50	50	0	0	6
3	74	13	13	0	15
5	89	6	5	0	19
10–12	74	16	9	1	77
	Normal animals				
4 or more	26	21	33	20	484

Responsiveness. As described above, many visually unresponsive units were found in area 18 in visually inexperienced kittens at all ages, and this contrasts with normal area 18 where hardly any neurones failed to respond to visual stimulation in kittens older than 4 weeks (Blakemore & Price, 1987). Even by 10–12 weeks in visually deprived kittens the majority of units (54 %) were given low responsiveness values of 0 or 1, although a relatively small proportion (18 %) did have the high responsiveness value of 3. On the other hand, in normal animals aged 4 weeks or more most cells (65 %) had responsiveness values of 2 or 3. In general, therefore, dark-rearing suppresses the visual responsiveness of area 18 but, nevertheless, a few briskly responsive cells are found, at least during the first 12 post-natal weeks, in deprived kittens.

Ocular dominance. In visually inexperienced kittens at all ages ocular dominance distributions (Fig. 2) were approximately symmetrical around group 4. Most cells in area 18 in normal kittens at all ages are binocularly activated (Blakemore & Price, 1987), and so it appears that dark-rearing, for as long as the first 12 weeks after birth, does not disrupt this property of neurones in area 18. Whereas there appeared to be a slight bias towards the contralateral eye in the ocular dominance distribution of cells in very young visually inexperienced 7-day-old kittens, there was an increase in the over-all influence of the ipsilateral eye with age in dark-reared animals (Fig. 2), as in normal kittens (Blakemore & Price, 1987).

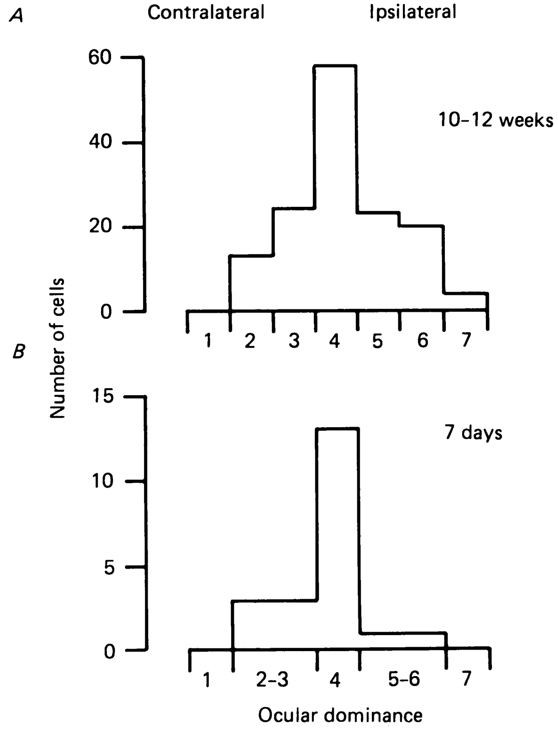

Fig. 2. Ocular dominance distributions of cells in area 18 are plotted for three dark-reared kittens aged 10–12 weeks (*A*) and two 7-day-old normal, but visually inexperienced kittens (*B*). In the 7-day-old kittens five groups were used, while in older animals cells were allocated to one of seven groups (see Blakemore & Price, 1987).

Preferred orientations. Data from visually inexperienced kittens of all ages were pooled, and the frequency distribution of preferred orientations amongst orientation-selective and orientation-biased cells in area 18 is shown in Fig. 3. These results were obtained from neurones with receptive field positions that were scattered over much of the left lower quadrant of the visual field (Fig. 3). All orientations are represented in the sample, and the biases to horizontal and vertical that we found in normal adult cats and kittens aged 4 weeks or more (Blakemore & Price, 1987) were not clearly seen; indeed, if anything, the distribution showed a small trough at horizontal (90 deg) and a slight peak at one oblique (135 deg), although these biases were not statistically significant (χ^2 test). When frequency distributions of preferred orientations were considered separately at each age in dark-reared kittens, a similar pattern emerged to that described for the pooled sample, indicating that in these visually deprived kittens no change occurred with age in the over-all distribution of orientation preference in the population of cells in the rostral part of area 18. It is possible that the characteristic bias towards horizontal orientations in the population

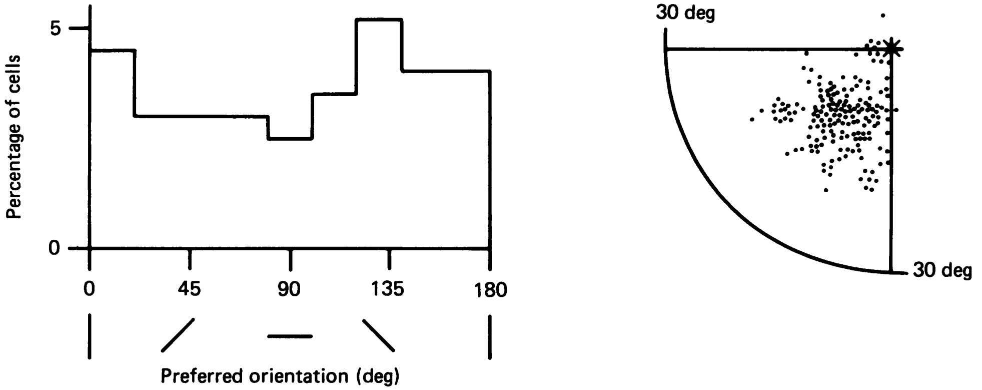

Fig. 3. Left panel: histogram showing the distribution of preferred orientations of cells (virtually all orientation biased) in area 18 of visually inexperienced and dark-reared kittens aged 7 days to 12 weeks. The number of cells preferring each orientation is expressed as a percentage of the total number of all cells in the sample. Right panel: the positions of the receptive field centres of the oriented units are shown (✱= projection of the area centralis). The cells studied in these animals were located rostral to the interaural coronal plane in area 18 and their receptive fields were mainly centred in the left lower quadrant of the visual field.

of neurones in rostral area 18 of normal mature cats (Blakemore & Price, 1987) does not develop in the absence of visual stimulation.

Laminar analysis. A laminar analysis was performed in these visually inexperienced kittens in a manner similar to that described for normal kittens by Blakemore & Price (1987). In cytochrome-oxidase-stained (c.o.) sections, superficial laminae (I, II and III) were distinguished from lower layers (layers VI, V and c.o. layer IV: see Blakemore & Price, 1987), and the percentages of orientation-selective, orientation-biased, non-oriented and visually unresponsive cells at each age were calculated separately for upper and lower laminae (Fig. 4). In this analysis data from kittens aged 10–12 weeks were pooled.

In 7-day-old, visually inexperienced kittens almost all neurones (96 %) in the superficial laminae in area 18 were classified as visually unresponsive, and the only responsive cell found was non-oriented. On the other hand, the majority (64 %) of cells in deeper laminae in these kittens were visually responsive, 39 % being non-oriented and 25 % orientation biased.

The proportion of neurones in superficial laminae that were visually responsive increased with age in dark-reared kittens; initially there was an increase in the proportion of non-oriented cells, and later on orientation-biased neurones appeared and increased in number, but at no age were more than 8 % of cells orientation selective (Fig. 4*A*). Comparison of data from these dark-reared animals with results obtained in normal kittens (Fig. 7 of Blakemore & Price, 1987) shows that the development of visual responsiveness in the upper laminae in area 18 proceeds much more slowly in deprived animals and does not achieve normal levels during the 12 weeks post-natally, and that, while some cells eventually develop crude orientation preferences, very few become truly orientation selective.

In deeper layers there was virtually no change at all with age: there was a very slight increase in the proportion of cells that were visually responsive, and rises in

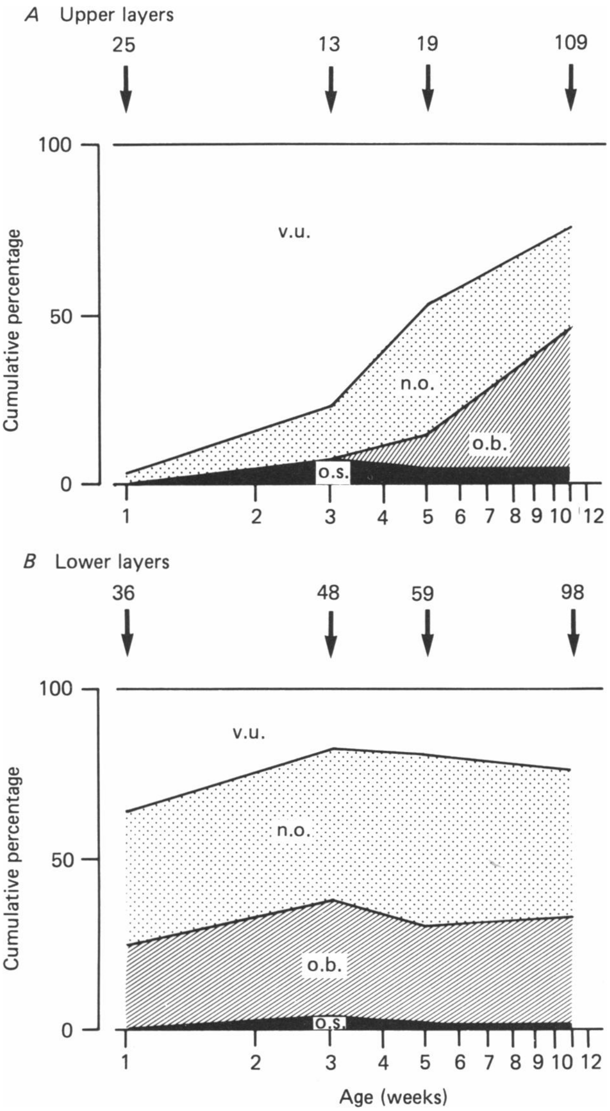

Fig. 4. Changes with age in the percentages of orientation-selective (o.s.), orientation-biased (o.b.), non-oriented (n.o.) and visually unresponsive (v.u.) cells are plotted as in Fig. 1. The units were recorded in laminae I, II and III (*A*) and c.o. layer IV, layers V and VI (*B*). Data from kittens aged 10, 11 and 12 weeks are pooled and are plotted at their average age. The numbers of units studied at the various ages are indicated above each graph.

the percentages of orientation-biased and non-oriented cells accounted for this small increase, since the proportion of cells that was orientation selective never rose above 4 % (Fig. 4*B*). The percentage of visually responsive units never reached levels found in normal kittens (Blakemore & Price, 1987) during the first 12 weeks post-natally; and, as in superficial laminae, dark-rearing prevented the appearance of significant numbers of orientation-selective cells.

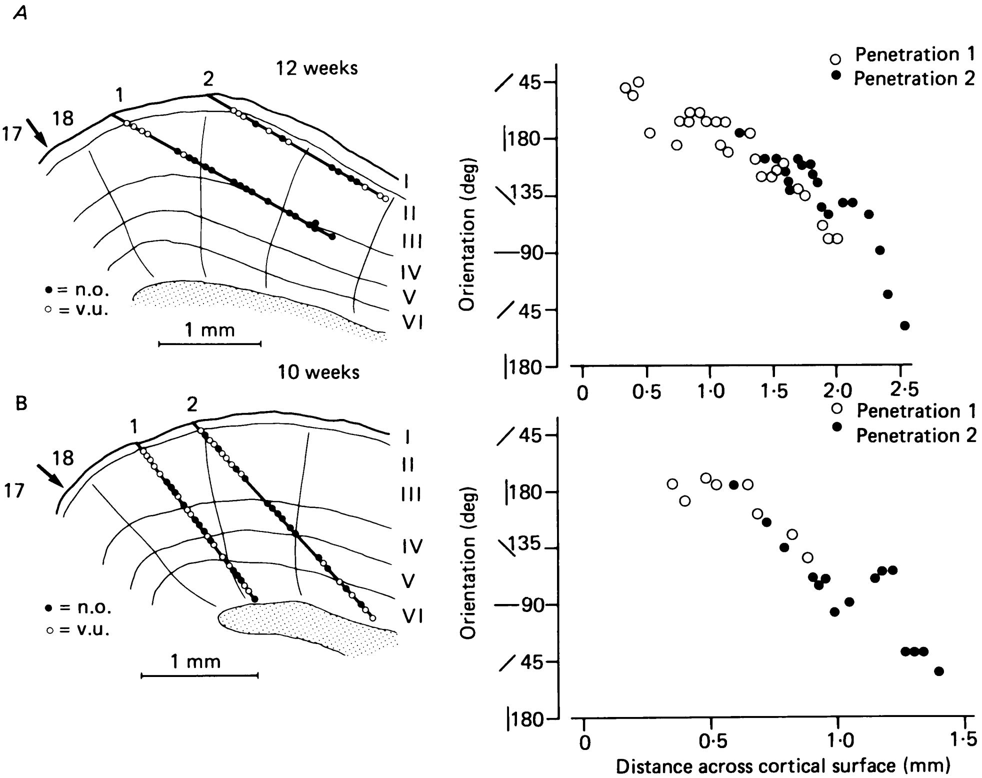

Fig. 5. Left panel: reconstructions of electrode penetrations angled laterally, passing through area 18 in a single coronal plane in dark-reared kittens aged 12 weeks (*A*) and 10 weeks (*B*). The area 17/18 border (arrow), cortical laminae, radial palisades of cell bodies visible in Nissl-stained sections, and the positions of non-oriented (n.o.) and visually unresponsive (v.u.) cells are indicated. Right panel: these graphs illustrate the shifts in preferred orientation along these penetrations. Each recording point has been projected up the palisade in which it is located to the cortical surface, and preferred orientation is plotted against the distance across the cortical surface to each projected location (zero is the point of entry of the most medial track). Progressions of orientation from the two, separate parallel tracks superimposed quite well for both animals, despite the diluting effect of large numbers of visually unresponsive and non-oriented units. In *A* the penetrations ran roughly parallel to the cortical surface for much of their length, and these tracks could be directly compared over a considerable distance along the cortical surface. Data in *B*, which involved all layers, indicate that the rudimentary orientation columns extend through much, if not all, of the cortical depth in area 18 of visually deprived kittens.

It appears that, during the first 12 post-natal weeks, the upper laminae can gradually develop a degree of visual responsiveness and even orientation preference in the absence of visual stimulation, while the lower layers (which are initially much more responsive than the upper layers and contain some cells with innate orientation preferences, even in 7-day-old kittens) paradoxically improve their visual responsiveness only very slightly. Neither upper nor lower layers seem able to develop significant levels of orientation selectivity in deprived animals.

As in normal kittens and adult cats (Blakemore & Price, 1987), the proportions of monocularly and binocularly driven cells were similar in each cortical layer at every age in area 18 in these dark-reared animals. There was no tendency in these samples for more cells to be monocularly driven in layer IV than in other laminae.

Orientation columns. Despite the fact that lack of visual experience clearly had a drastic effect on the maturation of stimulus specificity, area 18 retained the rudiments of a system of orientation columns, which is detectable in very young normal kittens (Blakemore & Price, 1987). In all these visually inexperienced kittens, aged between 7 days and 12 weeks, the electrode penetrations ran obliquely across the radially arranged palisades of cells in area 18, and where adjacent units displayed an orientation preference their optimum orientations tended to be quite similar. Despite the large number of visually unresponsive and non-oriented units in area 18 in these kittens, it was often possible to discern some degree of progressive shift of orientation preference along electrode tracks (Fig. 5). Often we made multiple parallel penetrations that ran obliquely through area 18 in one coronal plane, located rostrally in area 18 where the radial palisades of cells run vertically in the parasagittal plane. By studying data from multiple parallel oblique penetrations the preferred orientations of neurones at different depths within the same radial palisade of cells (or at least closely neighbouring palisades) could be compared. This was done by projecting each recording point to the cortical surface along the radial palisade in which the recording was made, so that progressive shifts in orientation along parallel electrode

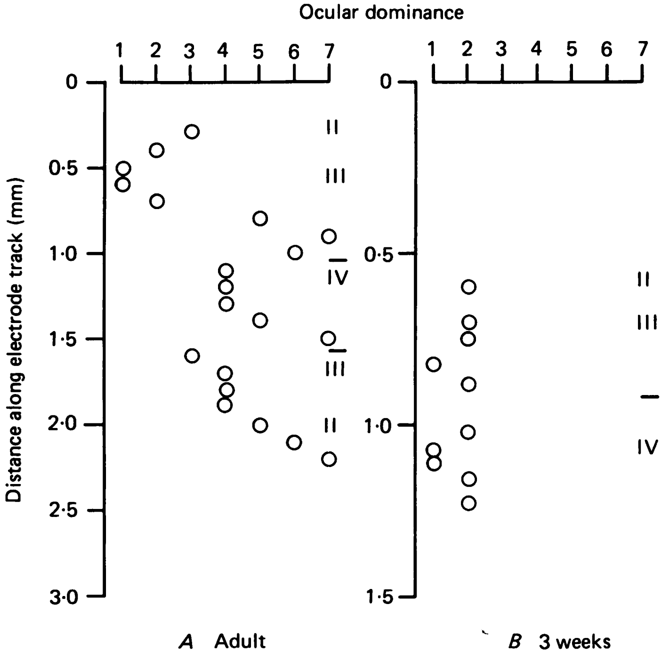

Fig. 6. Progressions of ocular dominance with depth along oblique electrode penetrations through area 18 are analysed for a 10-week-old dark-reared kitten (*A*) and a 3-week-old dark-reared kitten (*B*). In the 3-week-old deprived kitten (*B*) most cells in the superficial laminae were visually unresponsive. Cortical laminae are indicated to the right of each graph. We used seven ocular dominance groups in the 10-week-old kitten and five groups in the 3-week-old animal.

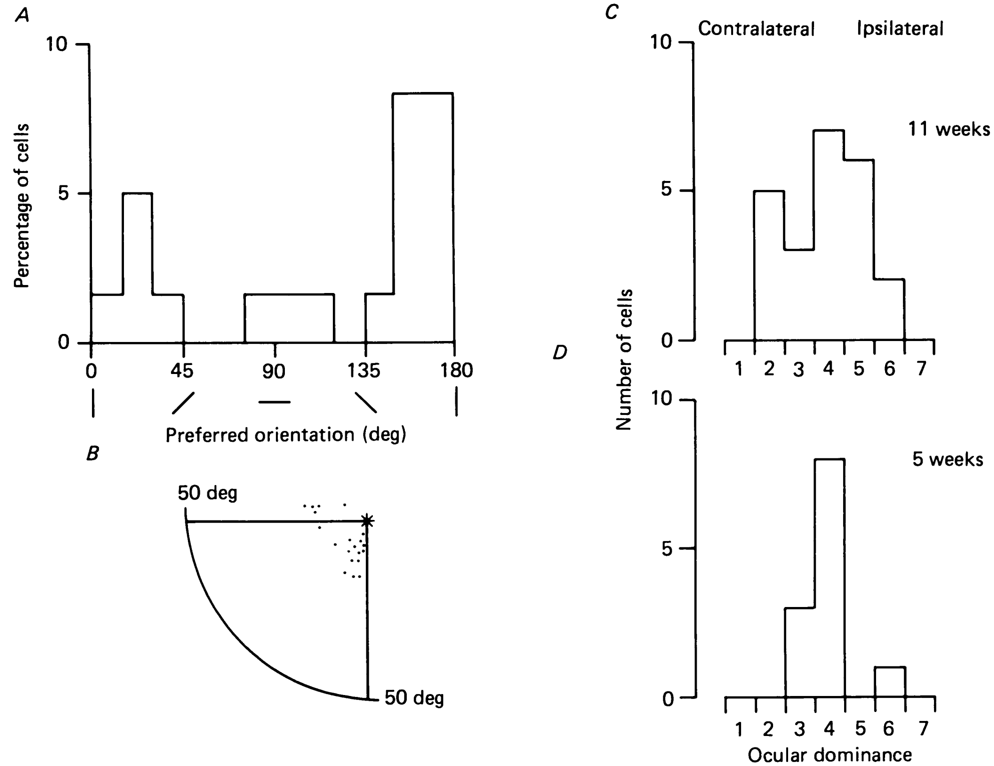

Fig. 7. *A*, distribution of preferred orientations in area 17 and 5- and 11-week-old dark-reared kittens. Numbers of cells are expressed as percentages of the total sample ($n = 60$). *B*, positions of receptive field centres of these orientation-selective and orientation-biased cells in area 17 in 5- and 11-week-old dark-reared kittens (✱= projection of area centralis). *C* and *D*, ocular dominance distributions of all responsive cells in area 17 in an 11-week-old (*C*) and a 5-week-old (*D*) dark-reared kitten.

penetrations could be superimposed on the basis of the column of cells to which the recorded units belonged (Fig. 5), as described by Blakemore & Price (1987). In dark-reared kittens a sufficient number of orientation-biased cells was found to show that progressive orientation shifts along parallel oblique penetrations superimpose well, even throughout the entire depth of the cortex (Fig. 5), indicating that a primitive system of radial orientation columns is present and can persist in the absence of visual stimulation.

Ocular dominance columns. In the oblique electrode penetrations made in all the kittens in this study, adjacent units were often placed in a similar ocular dominance group. In some penetrations there was little over-all shift in ocular dominance along electrode tracks, but in many cases progressive changes in ocular dominance were found (Fig. 6); ocular dominance shifts along electrode tracks were identified in young (3- and 5-week-old) dark-reared kittens as well as in older (10- to 12-week-old) deprived animals. These results are similar to those described in normal kittens (Blakemore & Price, 1987), and suggest that at least a local clustering according to ocular dominance is present in dark-reared kittens; it seems possible that ocular dominance columns exist in area 18 in these deprived animals.

Area 17

Electrode penetrations that ran through both upper and lower layers were made in area 17 in visually deprived kittens aged 5 and 11 weeks. In a 5-week-old dark-reared kitten, 16 % of cells recorded in area 17 were classified as orientation selective, 21 % were orientation biased, 53 % were non-oriented and 10 % were visually unresponsive ($n = 19$). At 11 weeks, only 5 % of cells were orientation selective, 25 % were orientation biased, 42 % were non-oriented and 28 % were visually unresponsive ($n = 41$). Dark-rearing clearly prevents the normal development of receptive field properties of cells in area 17, and it seems likely that there is actually a deterioration in visual responsiveness and orientation selectivity in area 17 in deprived kittens during the first 2–3 months after birth, as Blakemore & Van Sluyters (1975) have suggested.

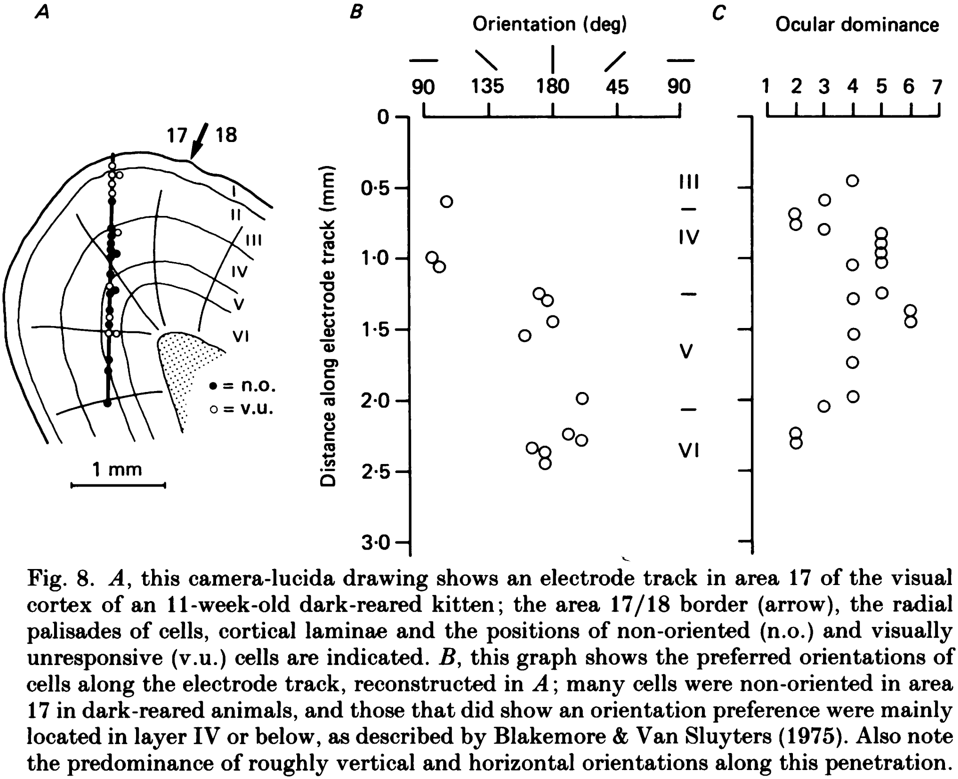

Fig. 8. *A*, this camera-lucida drawing shows an electrode track in area 17 of the visual cortex of an 11-week-old dark-reared kitten; the area 17/18 border (arrow), the radial palisades of cells, cortical laminae and the positions of non-oriented (n.o.) and visually unresponsive (v.u.) cells are indicated. *B*, this graph shows the preferred orientations of cells along the electrode track, reconstructed in *A*; many cells were non-oriented in area 17 in dark-reared animals, and those that did show an orientation preference were mainly located in layer IV or below, as described by Blakemore & Van Sluyters (1975). Also note the predominance of roughly vertical and horizontal orientations along this penetration. *C*, this graph plots the ocular dominance of all the visually responsive cells recorded along the electrode track shown in *A*. Cortical laminae, indicated on the right in *B*, apply to both graphs.

Fig. 7 shows the distribution of preferred orientations of units in area 17 in two dark-reared kittens, aged 5 and 11 weeks, and a bias towards horizontal and vertical is apparent. Similar biases in area 17 in visually deprived cats, towards horizontal and vertical, have been reported previously (Leventhal & Hirsch, 1977; Fregnac & Imbert, 1978).

Distributions of ocular dominance in area 17 are shown in Fig. 7 for a 5- and an

11-week-old kitten. In both cases group 4 contained a larger number of cells than any other, although many cells were strongly dominated by an input from one eye in the 11-week-old kitten (Fig. 7*C*).

When electrode penetrations were made through area 17 in these dark-reared kittens, adjacent cells that displayed an orientation preference often responded best to similar orientations (Fig. 8). Adjacent visually responsive units also often fell into similar ocular dominance groups (Fig. 8). These results suggest that, as in area 18, local clustering according to preferred orientation and ocular dominance develops and survives in area 17 despite dark-rearing. It seems possible that rudimentary orientation and ocular dominance columns are present in area 17 in these deprived animals, though we do not have sufficient data from multiple parallel tracks to be sure about the radial extent of these local clusters in area 17. The picture from single penetrations (like the one reconstructed in Fig. 8) was compatible with persistent clusters of orientation-selective cells, lying mainly in layer IV and below.

DISCUSSION

The development of area 18 in dark-reared kittens

In general, dark-rearing for up to 12 weeks from birth has devastating effects on area 18 of the visual cortex of kittens. However, it appears that some aspects of the post-natal development of area 18 are disturbed more than others by such deprivation, and that innate and environmental factors interact to varying degrees in determining the different features of the organization of area 18.

In the absence of visual experience, orientation selectivity hardly develops at all in area 18 during the first 12 weeks post-natally, and we think it unlikely that a larger proportion of cells would become orientation selective in older dark-reared animals. On the other hand, the general level of visual responsiveness does seem to improve quite passively in area 18 (especially in the superficial layers), even though the proportion of cells that are visually responsive is still not normal by 12 weeks in deprived kittens. Furthermore, visual experience does not appear necessary for the generation of significant numbers of neurones with at least some degree of orientation preference (that is, orientation-biased cells) in area 18, although dark-rearing seems to prevent the appearance of a bias towards horizontal and vertical amongst the population of oriented cells, as is seen in area 18 in normal animals 4 weeks of age or more (Blakemore & Price, 1987). Therefore, innate factors alone are sufficient to promote some muted aspects of maturation in area 18 during the first 3 months after birth. However, it seems likely that the longer-term stabilization of the properties of neurones does require visual stimulation: Singer & Tretter (1976) reported that only 44 % of neurones in area 18 in binocularly deprived *adult* cats were visually responsive, whereas we found 72–78 % of cells responded to visual stimuli in 10- to 12-week-old dark-reared kittens.

Our results indicate that hardly any complex cells develop in area 18 during the first 12 post-natal weeks in the absence of visual experience, but a larger proportion of simple cells (almost all with immature receptive field properties) was seen following deprivation. Blakemore & Van Sluyters (1975) have suggested that in area 17 innate mechanisms can generate orientation-selective simple cells, whereas the maturation of complex cells requires visual stimulation. This seems to be true for area 18 as well, despite the differences in afferent input to the two areas.

A laminar analysis in area 18 in deprived kittens revealed that although virtually all cells in the superficial cortical laminae (I, II and III) were unresponsive to visual stimulation in 7-day-old visually inexperienced kittens, the fraction of visually responsive units increased substantially over the 10–12 weeks post-natally and many cells developed a degree of orientation preference. On the other hand, although the percentage of visually responsive cells in deeper laminae (c.o. layer IV, layers V and VI) was initially relatively high at 7 days, it increased only slightly over the following 11 weeks. In neither superficial nor deep layers did the degree of visual responsiveness reach the levels seen in normal kittens of similar age (Blakemore & Price, 1987).

It is likely that these differences in the development of superficial and deep cortical laminae are related to the fact that the predominant inputs to the cortex from the thalamus terminate in lower rather than superficial layers in both kittens and adult cats (Garey & Powell, 1971; Anker & Cragg, 1974; LeVay & Gilbert, 1976; Kato, Kawaguchi, Yamamoto, Samejima & Miyata, 1983; Henderson & Blakemore, 1986). The input to area 18 from the lateral geniculate nucleus, which consists of axons of Y (and probably W) cells but not X cells (Stone, 1983), may confer visual responsiveness to the lower layers and may even bias some cells to stimuli of a particular orientation in visually inexperienced 7-day-old kittens. These geniculate Y (and W) cell inputs seem capable of innately providing a degree of visual responsiveness and orientation preference in the deeper layers of area 18, but visual stimulation is then needed for the further maturation of neurones in these laminae. On the other hand, it is clear that the responsiveness and receptive field properties of cells in the upper layers in area 18 (although initially retarded compared with the lower layers) can improve greatly even in the absence of visual stimulation. The afferent inputs to the upper layers that determine this innate ability presumably arise intracortically, either relayed from the lower layers to the upper, or via cortico-cortical association projections from area 17, which, as we have already suggested, might influence the development of superficial laminae in area 18 in normal kittens (Blakemore & Price, 1987).

It appears that innate factors play a dominant role in determining some major features of the organization of area 18, which remain relatively undisturbed by deprivation during the first 12 post-natal weeks. In deprived kittens of all ages the distributions of ocular dominance for cells in area 18 peaked at group 4, and similar distributions were found in area 18 in all normal kittens, including visually inexperienced animals in their first post-natal week. It has been suggested that those cells in area 17 that receive their main inputs from geniculate Y cells are usually innately binocularly driven (Blakemore & Van Sluyters, 1975; Fregnac & Imbert, 1978) and this certainly seems to be the case for area 18. Finally, it appears that visual experience is not required for the production of at least a rudimentary radial columnar organization in area 18, although, again, visual activity is needed for the perfection of the columnar system.

Comparison of the effects of dark-rearing on areas 17 and 18

Data obtained from cells in area 17 in deprived kittens in this study agree well with results of Blakemore & Van Sluyters (1975) and show that, as in area 18, the normal post-natal development of many features of the striate cortex is severely depressed by dark-rearing from birth. However, some differences between the consequences of deprivation for areas 17 and 18, at least during the first 3 post-natal months, were suggested by our results.

On the basis of results from this present study and from previous work (Blakemore & Van Sluyters, 1975; Bonds, 1979; Albus & Wolf, 1984) it appears that a population of innately determined, clearly orientation-selective cells exists in area 17 in very young normal but visually inexperienced kittens. Blakemore & Van Sluyters (1975) suggested that innate orientation selectivity in area 17 is largely determined by inputs from geniculate X cells. The proportion of such orientation-selective cells probably decreases during subsequent deprivation in dark-reared animals: Cynader *et al.* (1976) reported that in *adult* cats that had been binocularly deprived from birth, either by eyelid suture or dark-rearing, 32 % of units in area 17 were visually unresponsive and of the remaining cells 86 % exhibited neither orientation selectivity nor direction selectivity. Thus, Cynader *et al.* (1976) have shown that in adult dark-reared and binocularly sutured cats only a very small proportion (about 10 %) of cells in area 17 show any degree of orientation preference, a considerably smaller percentage than we found in area 17 in younger dark-reared kittens (30–40 %).

These results from area 17 contrast somewhat with those from area 18. We found no evidence of a significant proportion of truly orientation-selective cells in area 18 in visually inexperienced kittens at any age. As discussed above it seems likely that inputs from geniculate Y cells can confer a relatively imprecise orientation preference on cortical neurones, at least in area 18, in deprived kittens. It is possible that levels of orientation selectivity may eventually become very similar in areas 17 and 18 in adult cats deprived from birth (Singer & Tretter, 1976).

The proportion of neurones strongly dominated by one eye may be larger in area 17 than in area 18 in visually deprived animals: indeed, it has been suggested that cortical cells in area 17 specifically with X-cell inputs cannot develop their normal mature degree of binocularity in the absence of normal visual stimulation (Blakemore & Van Sluyters, 1975; Leventhal & Hirsch, 1977).

Dark-rearing does not prevent the appearance of the basic elements of the modular structure of the cortex – the orientation and ocular dominance columns – in either area 17 or area 18. Swindale (1981), using the anatomical technique of transneuronal autoradiography, found that the competitive segregation of right-eye and left-eye terminals to form ocular dominance bands in layer IV is grossly retarded by dark-rearing. It is intriguing, then, that it does not seem to interfere with the appearance of physiological ocular dominance clustering throughout the layers of the cortex.

D. J. P., currently a Beit Memorial Fellow, held a Training Fellowship from the Medical Research Council during much of this work. The research was supported by an M.R.C. Programme Grant

(G7900491) and, in part, by grants from the Science and Engineering Research Council and Wellcome Trust. We thank May and Baker Ltd. for the donation of gallamine triethiodide (Flaxedil), John Eldridge, Duncan Fleming, Lynden Guiver and John Mittell for technical assistance and Lesley Annetts for drawing the Figures.

REFERENCES

ALBUS, K. & WOLF, W. (1984). Early post-natal development of neuronal function in the kitten's visual cortex: a laminar analysis. *Journal of Physiology* **348**, 153–185.

ANKER, R. L. & CRAGG, B. C. (1974). Development of the extrinsic connections of the visual cortex in the cat. *Journal of Comparative Neurology* **154**, 29–42.

BLAKEMORE, C. & PRICE, D. J. (1987). The organization and post-natal development of area 18 of the cat's visual cortex. *Journal of Physiology* **384**, 263–292.

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

BONDS, A. B. (1979). Development of orientation tuning in the visual cortex of kittens. In *Developmental Neurobiology of Vision*, ed. FREEMAN, R. D., pp. 31–41. New York, London: Plenum Press.

BUISSERET, P. & IMBERT, M. (1976). Visual cortical cells: their developmental properties in normal and dark reared kittens. *Journal of Physiology* **255**, 511–525.

CYNADER, M., BERMAN, N. & HEIN, A. (1976). Recovery of function in cat visual cortex following deprivation. *Experimental Brain Research* **25**, 139–156.

FREGNAC, Y. & IMBERT, M. (1978). Early development of visual cortical cells in normal and dark-reared kittens: relationship between orientation selectivity and ocular dominance. *Journal of Physiology* **278**, 27–44.

GAREY, L. J. (1971). A light and electron microscopic study of the visual cortex of the cat and the monkey. *Proceedings of the Royal Society* B **179**, 21–40.

GAREY, L. J. & POWELL, T. P. S. (1971). An experimental study of the termination of the lateral geniculo-cortical pathway in the cat and monkey. *Proceedings of the Royal Society* B **179**, 41–63.

HENDERSON, Z. & BLAKEMORE, C. (1986). Organization of the visual pathways in the newborn kitten. *Neuroscience Research* **3**, 628–659.

IMBERT, M. & BUISSERET, P. (1975). Receptive field characteristics and plastic properties of visual cortical cells in kittens reared with or without visual experience. *Experimental Brain Research* **22**, 25–36.

KATO, N., KAWAGUCHI, S., YAMAMOTO, T., SAMEJIMA, A. & MIYATA, H. (1983). Postnatal development of the geniculocortical projection in the cat: electrophysiological and morphological studies. *Experimental Brain Research* **51**, 65–72.

LEVAY, S. & GILBERT, C. D. (1976). Laminar patterns of geniculocortical projection in the cat. *Brain Research* **113**, 1–19.

LEVENTHAL, A. G. & HIRSCH, H. V. B. (1977). Effects of early experience upon orientation sensitivity and binocularity of neurons in visual cortex of cats. *Proceedings of the National Academy of Sciences of the U.S.A.* **74**, 1272–1276.

LEVENTHAL, A. G. & HIRSCH, H. V. B. (1980). Receptive-field properties of different classes of neurons in visual cortex of normal and dark-reared cats. *Journal of Neurophysiology* **42**, 1111–1132.

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

PETTIGREW, J. D. (1974). The effect of visual experience on the development of stimulus specificity by kitten cortical neurones. *Journal of Physiology* **237**, 49–74.

PRICE, D. J. (1985*a*). The development of orientation-selectivity in area 18 of the visual cortex in normal and dark-reared kittens. *Journal of Physiology* **369**, 39*P*.

PRICE, D. J. (1985*b*). Effects of dark-rearing on the development of area 18 of the visual cortex of the cat. *Neuroscience Letters Supplement* **22**, S64.

PRICE, D. J. (1985*c*). Patterns of cytochrome oxidase activity in areas 17, 18 and 19 of the visual cortex of cats and kittens. *Experimental Brain Research*, **58**, 125–133.

Sclar, G. & Freeman, R. D. (1983). Regional variations in the effects of monocular deprivation on area 18 of the cat. *Experimental Brain Research* **51**, 388–396.

Sherman, S. M. & Spear, P. D. (1982). Organization of visual pathways in normal and visually deprived cats. *Physiological Reviews* **62**, 738–855.

Singer, W. & Tretter, F. (1976). Receptive-field properties and neuronal connectivity in striate and parastriate cortex of contour-deprived cats. *Journal of Neurophysiology* **39**, 613–630.

Spear, P. D., Tong, L. & Langsetmo, A. (1978). Striate cortex neurons of binocularly deprived kittens respond to visual stimuli through the closed eyelids. *Brain Research* **155**, 141–146.

Stone, J. (1983). *Parallel Processing in the Visual System.* New York: Plenum Press.

Swindale, N. V. (1981). Absence of ocular dominance patches in dark-reared cats. *Nature* **290**, 332–333.

Tusa, R. J., Rosenquist, A. C. & Palmer, L. A. (1979). Retinotopic organization of areas 18 and 19 in the cat. *Journal of Comparative Neurology* **185**, 657–678.